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Response of Vegetation to Extreme Weather Events

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Response of Vegetation to Extreme Weather Events

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Introduction

On this thesis

The topic of this dissertation thesis is the response of plant communities to climate change, more specifically, the investigation of the impacts of extreme weather events. For this purpose, an experimental approach was applied and the responses of model plant communities (artificial grassland and heath communities in three different functional compositions) to manipulated weather events (drought, heavy rainfall, and soil freeze-thaw cycles) were analyzed.

The following introductory paragraphs condense (1) current knowledge on the physical background of climate change, followed by an overview on the (2) impacts of climate change on terrestrial ecosystems studied so far. Afterwards, I briefly discuss the (3) challenges and options for research on the ecological impacts of extreme weather events with a focus on experiments and the need to relate such experiments to diversity experiments. After (4) a summary of the set of manuscripts which form this cumulative thesis and a description how they relate to each other, I continue with (5) summarizing conclusions and research challenges arising from these manuscripts. The introduction ends with information on the publishing status of the appended manuscripts, including a description of my own contribution in this process. Furthermore, a table (Table 2) which lists my own presentations of this research at conferences and a table (Table 3) which displays the temporal development of the EVENT experiment and my contribution within this project is presented. The EVENT-Experiment provides the frame of this thesis.

Climate Change

Human activities (fossil fuel burning and, to a lower degree, land use change) are leading to an increase in radiative forcing, and therefore to global warming. The comprehensiveness of the current report of the Intergovernmental Panel on Climate Change (IPCC 2007a), which incorporates virtually all observational and modeling studies in this field, allows for considerable confidence in these findings and the notion that current atmospheric greenhouse gas concentrations are unprecedented in at least the last 650 000 years. The rapidness of warming will also reach levels unknown in geological history. Anthropogenic carbon dioxide emissions continue to increase, despite the growing public awareness that led to political

agendas like the Kyoto Protocol. The emissions growth rate since 2000 is greater than even the most fossil-fuel intensive of the Intergovernmental Panel on Climate Change emissions scenarios (A1 FI), increasing from 1.1% y^{-1} for 1990-1999 to more than 3% y^{-1} for 2000-2004 (Raupach *et al.* 2007).

Although regional projections are still a major challenge, larger scale geographic patterns of observed and projected warming show the greatest temperature increases at high northern latitudes and over land, with less warming over the southern oceans (IPCC 2007a). The warming trend throughout Europe is well established (+0.90°C for 1901 to 2005; IPCC 2007a). For the 1977 to 2000 period, trends are stronger in Central and North-Eastern Europe and in mountainous regions, while weaker trends are found in the Mediterranean region (Bohm *et al.* 2001). Temperatures are increasing more in winter than summer (Jones & Moberg 2003). An increase of daily temperature variability was observed during the period 1977 to 2000 due to an increase in warm extremes, rather than a decrease in cold extremes (Tank *et al.* 2002; Tank & Konnen 2003).

Observations of and modeling for precipitation is more complicated because of the small-scale processes involved. Nevertheless, precipitation is projected with high confidence to increase in the tropical precipitation maxima, decrease in the subtropics and increase at high latitudes (IPCC 2007a). The increase in annual precipitation is considered very likely to occur throughout northern Europe as a consequence of an intensification of the global hydrological cycle (IPCC 2007a). In general, increasingly higher proportions of the annual precipitation occur as rain than snow in these regions, both in observations and projections. Most Atmosphere-Ocean General Circulation Models furthermore project increased summer dryness and winter wetness in most parts of the northern middle and high latitudes, a trend which is also projected for Central Europe (Giorgi *et al.* 2004; Raisanen *et al.* 2004). Even though precipitation trends are spatially variable, mean winter precipitation has already increased in most of Atlantic and Northern Europe (Tank *et al.* 2002).

Extreme events

In its first assessment of climate change in 1990 and in its supplement in 1992, the Intergovernmental Panel on Climate Change (IPCC) did not consider whether extreme weather events had increased in frequency and/or intensity, because data were too sparse. In 1995 the IPCC, in its second assessment, did examine this question, but concluded that data and analyses of changes in extreme events were ‘not comprehensive’ and thus the question could not be answered with any confidence. Since then, climatological knowledge on extreme events has rapidly accumulated. **Manuscript 1** provides a summary on this topic. Here, only some general remarks and updates are provided.

Warming accelerates land surface drying and increases the potential incidence and severity of droughts, a development which has been observed in many places worldwide (IPCC 2007a). However, the Clausius-Clapeyron relation determines that the water-holding capacity of the atmosphere increases by about 7% for every 1°C rise in temperature. Observations confirm that atmospheric water vapor indeed increased by about 5% in the atmosphere over the oceans (Dai 2006). Because precipitation stems mainly from weather systems that feed on the water vapor stored in the atmosphere, this generally increases precipitation intensity and the risk of heavy rain.

These theoretical considerations are supported by numerous observations which indicate that the number of heavy precipitation events as well as the number of drought events have increased globally, even in places where total amounts of rainfall have decreased (IPCC 2007a). A general overview of changes, human contribution and future projections on a global scale is provided in Table 1. Despite these facts, the availability of observational data still restricts the types of extremes that can be analyzed. For other climate parameters besides temperature extremes, such as drought, heavy rain, hurricanes, mid latitude wind systems, tornadoes, and thunderstorms, concern remains about the quality, comprehensiveness, and comparability of data (Nicholls & Alexander 2007). For some of these extremes, the problem is furthermore definitional – the Palmer Drought Severity Index for example is widely used to examine extremity of drought events. Its appropriateness, however, is questioned because it strongly relies on temperature trends (Nicholls & Alexander 2007). In general, it holds true that the rarer the event, the more difficult it is to identify long-term changes because there are fewer cases available.

Table 1: Recent trends, assessment of human influence on the trend and projections for extreme weather events for which there is an observed late-20th century trend (modified according to IPCC 2007a, table TS.4.). Likelihood is given as *virtually certain*: >99%; *very likely*: >90%; *likely*: >66%; *more likely than not*: >50%

Phenomenon and direction of trend	Likelihood that trend occurred in late 20 th century (typically post 1960)	Likelihood of a human contribution to observed trend	Likelihood of future trends based on projections for 21 st century using SRES scenarios
Fewer cold days and nights ^a over most land area	<i>Very likely</i>	<i>Likely^b</i>	<i>Virtually certain^b</i>
More frequent hot days and nights ^c over most land areas	<i>Very likely</i>	<i>Likely (nights)^b</i>	<i>Virtually certain^b</i>
More frequent warm spells/ heat waves ^d over most land areas	<i>Likely</i>	<i>More likely than not^e</i>	<i>Very likely</i>
More frequent heavy precipitation events ^f (or increased proportion of total rainfall from heavy falls) over most areas	<i>Likely</i>	<i>More likely than not^e</i>	<i>Very likely</i>
Increased area affected by drought ^g	<i>Likely in many regions since 1970</i>	<i>More likely than not</i>	<i>Likely</i>

^a based on the 10th percentile of the daily distribution 1961-1990.

^b warming of the most extreme days and nights each year.

^c based on the 90th percentile of the daily distribution 1961-1990.

^d episode of several consecutive hot days (see ^c).

^e magnitude of anthropogenic contributions not assessed. Attribution for these phenomena based on expert judgment rather than formal attribution studies.

^f percentage of days with precipitation exceeding the 95th or 99th percentile of the daily distribution 1961-1990.

^g precipitation deficit.

A more specific look at Central Europe reveals that an increase in precipitation variability has been observed at the majority of German weather stations during the last century and that this is expected to be indicative of an enhancement of the probability of both heavy precipitation events and droughts (Trömel & Schönwiese 2005). Likewise, the heat wave that affected many parts of Europe during the summer 2003 with record-breaking temperatures unprecedented in historic times (Luterbacher *et al.* 2004) was very probably the result of decreasing recurrence intervals for extreme weather events in the course of climate change (Schar *et al.* 2004). An exacerbating factor for this temperature extreme was the lack of precipitation in many parts of Western and Central Europe, leading to much-reduced soil moisture, surface evaporation, and transpiration, and thus to a strong positive feedback effect (Beniston & Diaz 2004). A general increase in mean precipitation per wet day is also ob-

served in most parts of the continent, even in some areas which are becoming drier (Frich *et al.* 2002; Tank *et al.* 2002; Alexander *et al.* 2006). Such an increase in the intensity of precipitation events is projected to accelerate in the future (Christensen & Christensen 2003; Giorgi *et al.* 2004; Kjellstrom 2004). But on the other hand, the longest yearly dry spell could increase by as much as 50% in Central Europe (Good *et al.* 2006).

Even though good progress is being made in the understanding of the climate system, biotic feedbacks remain a key source of uncertainty. Carbon uptake by the oceans and the terrestrial biosphere currently removes about 50 to 60% of anthropogenic carbon dioxide emissions with equal sharing between both sinks over recent decades (IPCC 2007a). Future warming, however, is expected to reduce the capacity of the earth system (land and ocean) to absorb anthropogenic CO₂. The response of the biosphere is accordingly a major area of research.

Vegetation response to climate change

Terrestrial ecosystems are projected to act as a carbon sink until the middle of this century, and then to turn into a source (IPCC 2007a), mainly because the respirative carbon loss due to warming is projected to surpass increased carbon sequestration due to increased growing seasons and CO₂ fertilization effects (Schroter *et al.* 2005). Observations of global net primary productivity between 1982 and 1999 show an increase of 6%, concentrated in the tropics, which is strongly correlated to greater solar radiation with reduced cloud cover (Nemani *et al.* 2003). In current global models, scaled-up effects of increased CO₂ content on plant and ecosystem biomass accumulation (CO₂ -fertilization) are largely responsible for the projected continued enhancement of NPP (Leemans *et al.* 2002). Responses to elevated CO₂ in grasslands that range from no change to 40% increase in biomass gain per season, mainly reflect CO₂ -induced water savings stimulated by reduced stomatal conductance (Morgan *et al.* 2004; Gerten *et al.* 2005). Based on experimental data, estimates of instantaneous CO₂ -induced water savings due to reduced stomatal aperture range from 5 to 15% (Wullschleger & Norby 2001; Cech *et al.* 2003) for humid conditions, but shrink in dry conditions. Desert shrubs, for example, only show increased production due to elevated CO₂ during wet periods and not in dry periods (Nowak *et al.* 2004b), contrasting with earlier expectations (Morgan *et al.* 2004).

CO₂-induced water savings, therefore, rely on current moisture regimes. There are few factorial experiments with multiple changing factors, but they suggest interactions that are not predictable from single factor experiments – such as the diminishing effects of elevated CO₂ on California grassland responses to increased rainfall, nitrogen fertilization and warming (Shaw *et al.* 2002). Increases in temperature and rainfall are also reported to affect the potential benefits of rising CO₂ for C3 relative to C4 grasses (Winslow *et al.* 2003), and European C3 grassland showed minor responses to a 3°C rise in temperature, possibly due to concomitant drying impacts (Gielen *et al.* 2005).

For middle and high latitude ecosystems, increased productivity can be further expected from the lengthening of the growing season due to global warming. Phenological studies on extensive datasets concurrently document a progressively earlier spring by 2.3 to 5.2 days per decade in the last 30 years in response to recent climate warming, leading to an extension of the growing season by up to 2 weeks in the second half of the 20th century (Sparks & Menzel 2002; Walther *et al.* 2002; Menzel *et al.* 2003; Parmesan & Yohe 2003; Root *et al.* 2003; phenological shifts in relation to climate change and single events are further discussed in **Manuscript 5**). Vegetation indices obtained by satellites (Myneni *et al.* 1997; Zhou *et al.* 2001; Lucht *et al.* 2002) and analysis of the atmospheric CO₂ signal (Keeling *et al.* 1996) confirm these findings. However, there are important differences between growth forms, as annual plants respond more strongly than congeneric perennials, insect-pollinated more than wind-pollinated plants, and woody less than herbaceous plants (Fitter & Fitter 2002). This finding is a first hint at the importance of species and functional composition in response to climate change.

But ecosystems are dynamic systems and species composition must therefore also be expected to change with changing environmental conditions. Just as species in a natural community do not respond in synchrony to external pressures, ecological communities existing today are expected to become disaggregated (Root & Schneider 2002). Short term genetic adaptations seem possible not only for short-lived insects (Umina *et al.* 2005), but even for plants (Bone & Farres 2001). Ecosystems can be expected to tolerate some level of future climate change and, in some form or another, will continue to persist, as they have done repeatedly with palaeoclimatic changes (IPCC 2007b). But regarding the stability of resident community composition, climate change has been identified as one of the major contributing factors for the increasing invasibility of plant communities (Dukes & Mooney 1999; **Manuscript 6**). The most important issue is therefore whether ecosystem resilience (understood as the disturbance an ecosystem can tolerate before it shifts into a different state, e.g., Scheffer *et*

al. 2001; Cropp & Gabric 2002; Folke *et al.* 2004) will be sufficient to tolerate future anthropogenic climate change (Harrison & Prentice 2003). Due to initial resilience, ecosystems are likely to respond to increasing external forcing in a non-linear manner. Most initial ecosystem responses appear to dampen change, but amplify it if thresholds in magnitude or rate of change are surpassed (Aber *et al.* 2001). Transitions between states may be triggered, or the ecosystem may even ‘collapse’ i.e., show a rapid transition to a community with reduced species number, lower productivity, and/ or other impairments such as degrading soils (Scheffer *et al.* 2001; Rietkerk *et al.* 2004; Schroder *et al.* 2005).

At key points during the future of climate change, ecosystem services such as carbon sequestration may therefore cease, or even reverse. While such thresholds are impossible to identify without substantial uncertainties, they may lead to irreversible effects such as biodiversity loss or, at the very least, impacts with slow recovery (e.g., soil degradation). Natural and semi-natural ecosystems seem more vulnerable to climate change than intensively managed systems because it usually takes decades for them to become established and therefore they are expected to adapt more slowly to climatic changes (Hitz & Smith 2004). Warming by 1°C can coarsely be translated to a shift of the respective climate situation by 160 km poleward or 160 m in altitude (Thuiller 2007), modeling of migration abilities is proceeding (Best *et al.* 2007), and this is leading to concerns if species can follow the projected shifts (Jentsch & Beierkuhnlein 2003; Midgley *et al.* 2006).

Range shifts which lead to changes in local community compositions have first been observed in mobile animals. Butterflies, for example, appear to follow warming patterns quickly with poleward shifts of their range (Parmesan *et al.* 1999). In a global meta-analysis of 99 animal and plant species, such poleward shifts were confirmed and correlated to increases in temperature (Parmesan & Yohe 2003). These trends can even pose threats to human health, because vectors of critical diseases also shift their range, e.g., visceral leishmaniasis nowadays is present in the Mediterranean region and climate change may expand the range of the disease northwards (Molyneux 2003; Lindgren & Naucke 2006). Altitudinal shifts of plant species concomitant with increasing temperatures are also documented (e.g., Grabherr *et al.* 1994; Dobbertin *et al.* 2005; Walther *et al.* 2005a). This upward shift has not yet led to species extirpations, but other facets of diversity have been affected. In a work not related to this thesis, we have shown that homogenization of alpine mountain summits is increasing, a process that reduces diversity at the landscape level (Jurasinski & Kreyling 2007).

Based on the crude estimates of climatic conditions of current species ranges and the projected change in these conditions, climate envelope studies forecast dramatic range shifts and species extinctions within this century. A Europe-wide modeling of the future distribution of 1,350 plant species under various greenhouse-gas emission scenarios indicates that more than half of these species could become vulnerable, endangered, critically endangered or committed to extinction by 2080 if unable to disperse (Thuiller *et al.* 2005). Under the most severe climate scenario (A1), and assuming that species could adapt through dispersal, 22% of the species considered would become critically endangered, and 2% committed to extinction. Qualitatively similar results were obtained by other authors (Bakkenes *et al.* 2002; Thomas *et al.* 2004), and regional studies (Theurillat & Guisan 2002; Walther *et al.* 2005b) are consistent with Europe-wide projections.

Climate change is even considered to be the second major threat to biodiversity, behind land use change (Sala *et al.* 2000). Besides the inherent value of biodiversity itself, the link between biodiversity and ecosystem functioning (including the maintenance of ecosystem services) (Duraiappah *et al.* 2005; Hooper *et al.* 2005; Diaz *et al.* 2006; Worm *et al.* 2006) is important in this context. The IPCC (2007b) concludes that extinctions critical for ecosystem functioning, be they global or local, are virtually certain to reduce societal options for adaptation responses.

Significant biological changes including species extinctions have accompanied large climate perturbations in the past (Overpeck & Bartlein 2005). The recovery of biodiversity after such major extinction events in the geological past took several millions of years (Kirchner & Weil 2000). Hotspots of endemic biodiversity are therefore concentrated in regions that have experienced lower variability during the Pleistocene (from about 2 million years ago) (Jansson 2003). Range shifts have been a major species response during past climatic perturbations (Lovejoy & Hannah 2005), although genetic and physiological responses also occurred (Davis & Shaw 2001). Projected future climate change together with other human-induced pressures, however, are unprecedented compared with the past several hundred millennia (Petit *et al.* 1999; Augustin *et al.* 2004; Siegenthaler *et al.* 2005).

Climate change will be exacerbated by other human-induced pressures, especially land-use change, which by itself is causing a progressive decline in biodiversity (Lovejoy & Hannah 2005). Habitat fragmentation (Hill *et al.* 1999; Warren *et al.* 2001) or simply the absence of suitable areas for colonization, e.g., at higher elevations, also play important roles (Wilson *et al.* 2005), especially in species extinction (Williams *et al.* 2003; Pounds *et al.*

2006). However, this is likely to be a complex relationship, and reduced pressure from land-use change is also expected in some regions (Goklany 2005; Rounsevell *et al.* 2006). Even in Europe significant pressure remains from acidification, terrestrial nitrogen deposition, ozone, particulate matter and heavy metals pollution despite general reductions in the extent of air pollution over the last decades (WGE 2004). Nevertheless, Europe is considered a special case in which projected ecosystem vulnerability is mostly related to climate change, due to slow population increase and stable economic situation (Schroter *et al.* 2005). But biotic interactions further complicate this picture. In the Mediterranean region, for example, defoliation of *Pinus sylvestris* is associated with previous warm winters, implying that future climatic warming may affect this tree indirectly through insect damage rather than through direct warming effects (Hodar & Zamora 2004). The interactive coupling between ecosystems, the climate system, and the multiple interacting drivers of global change have been identified by the IPCC (2007b) as key uncertainty in the response of ecosystems to climate change. The IPCC report concludes that research is especially needed on “improved understanding of the role of disturbance regimes, i.e., frequency and intensity of episodic events (drought, fire, insect outbreaks, diseases, floods and wind-storms)”.

Easterling *et al.* (2000) and Meehl *et al.* (2000) even propose that the ecological effects of extreme weather events are stronger than the effects of changes in mean values, especially because extreme weather events possess the power of breaking inertia by eliminating biomass and organisms on a large scale (De Boeck *et al.* 2007). Despite this general acknowledgement of the ecological importance of extreme weather events (see also Agrawal *et al.* 2007), only a few studies on their effects are available compared to the number of studies on rising CO₂ content or increasing temperatures (**Manuscript 1**). The extinction of the butterfly *Euphydryas editha bayensis*, however, has been linked to increased climatic variability rather than to general trends in mean conditions (McLaughlin *et al.* 2002b, 2002a). Extreme weather events even have the power to reverse carbon sequestration. The extreme hot and dry summer of 2003, for example, turned temperate European ecosystems from a carbon sink into a strong carbon source, with unknown long-term effects (Ciais *et al.* 2005). On the other hand, single drought events can also increase carbon uptake of grasslands and thresholds were this process is reversed have to be expected, but are unknown (**Manuscript 3**). A literature review on and theoretical considerations of the ecological importance of extreme weather events are given in **Manuscript 1**. A very recent example highlights the importance of understanding ecological responses to extreme events for climate projections with Global Circulation Models. In these models, drought is expected to lead to dieback of the Amazon forest, a process that would

strongly influence global carbon balance, but a severe drought event showed in reality an increased greenness due to higher incoming radiation while water uptake from deep layers prevented water stress, at least for a single dry season (Saleska *et al.* 2007).

Challenges and options for research on the ecological impacts of extreme weather events

The extremity of weather events can be obtained from extreme value statistics of climate data series (**Manuscript 1**). A first problem that arises is the lack of suitable long-term data series in daily resolution (Easterling *et al.* 2000). More fundamental, however, is the notion that statistical extremity does not go along with ecological extremity and that adequate temporal resolutions need to be chosen in relation to the study object (**Manuscript 1**). Using one-year steps and coming up with a 100-year event might be adequate for tree individuals or mayfly populations, but totally uninteresting for mayfly individuals, being ephemeral insects living only a few days. Meaningful weather events need therefore to be defined relative to the life span of the affected organisms (White & Jentsch 2001, Jentsch 2006).

Even for a single factor, e.g., drought, one can think of many different scenarios in which way ecosystems might be affected. Studies on the available amount of water during a whole growing season are likely to result in different results than studies on consecutive days without rainfall, even though both scenarios can be viewed as extreme events and their statistical extremity can be obtained. A literature review on the importance of drought for plant root production showed, for example, that generally dry conditions differ strongly from shorter periods of complete water withdrawal (**Manuscript 4**). Furthermore, interest is not only in the magnitude of the single event but also in the frequency, as both are predicted to change. This multitude of study options differs strongly from research on CO₂ content or mean warming, and limits comparability between the few existing studies.

As for most other ecological questions, there are three research options in the study of ecological consequences of extreme weather events, observations, modeling, and experiments. Due to their very nature, extreme weather events are rare events which can hardly be studied by observational research. In particular, magnitudes projected for the future which are unprecedented up to now can not be covered by field observations. Furthermore, the lack of any control conditions to compare to prevents causal conclusions from observations. Long-term observations offer the option to compare extreme events, if encountered at all, to “normal” years or long-term conditions (Ciais *et al.* 2005). Such monitoring approaches are very valuable for understanding ongoing changes in ecosystems, but conclusions on the importance

of single events remain problematic due to the fact that any given year differs in many other climate factors. Comparisons to long-term conditions are also problematic. First, averaging climate parameters over several years leads to statistical homogenization in the necessary daily resolution which has no ecological meaning, and second, there is no way to attribute for changes in the studied system due to natural succession. Long-term observations together with theoretical considerations provide the ground to generate hypotheses, but only modeling and experimental approaches can test these hypotheses (Beierkuhnlein & Nesshoever 2006).

Two classes of models are currently being applied to project the impacts of climate change on species and ecosystems, i.e., correlative and mechanistic models. Correlative models (climate envelope models) use knowledge of the current spatial distribution of species to relate the probability of their occurrence to climatic and other factors (Pearson *et al.* 2004; Guisan & Thuiller 2005). These models are criticized for assumptions of equilibrium between species and current climate, an inability to account for species interactions, lack of a physiological mechanism, and an inability to account for population processes and migration (Pearson & Dawson 2003; Pearson 2006). A suggested improvement is the use of multiple models within an ensemble forecasting framework including probabilistic techniques (Araujo & New 2007). But insights from exotic species invasions show that climate envelope studies of the native range fail to predict the occurrence in new habitats, as both, species with small native ranges as well as species with large native ranges, become naturalized well outside their climate envelopes (Sax *et al.* 2007). Mechanistic models include the modeling of ecosystem structure and function. They are based on the current understanding of energy, biomass, carbon, nutrient and water relations, but present models are still restricted in their potential to cover interacting dynamics with and among species and disturbances (Betts & Shugart 2005; Sutherst *et al.* 2007). Furthermore, most of these models use either a very limited number of e.g. tree species in fine scale gap models, or broad plant functional types at larger spatial scales (Smith *et al.* 2001). But functional groups are hard to define and simple growth form based groups have serious drawbacks (Gitay & Noble 1997; Diaz & Cabido 2001; Dorrepaal 2007). Even if modeling is made at the species level, genetic differences (ecotypes) and adaptations may change projections considerably. The ultimate drawback of models is that they simply cannot be better than the knowledge that is entered into them (Beierkuhnlein & Nesshoever 2006). Even though considering different shapes in a given relationship and comparing their outcome is a means to use models in a meaningful way even in the absence of knowledge on the exact shape of a link (Hughes *et al.* 2007). Despite all these drawbacks, modeling remains the only option for projections into the future. But model results need to be

treated cautiously, and improvements depend on insights from empirical tests (Thuiller 2007). Controlled experiments are therefore a promising tool to improve model projections and allow for causal analysis (Beier 2004). Their shortcomings, however, need to be considered in order to prevent misunderstandings.

Experiments – advantages and drawbacks

The complexity and spatio-temporal heterogeneity of ecological objects requires simplifications, such as reductionism, or generalizations such as holism (Beierkuhnlein & Nesshoever 2006). In any case it is necessary to concentrate or filter, as it is clearly impossible to cope comprehensively with an entire ecosystem. In experiments, the simulation of future conditions is possible, but as we do not know how systems will behave under novel circumstances (e.g. at higher temperatures, with less species), experiments are always not only reductionistic but also actualistic (Beierkuhnlein & Nesshoever 2006). Noise from other processes, such as abiotic site conditions are controlled in the experimental approach, (“*ceteris paribus*”; Cartwright 1983). The quality of an experimental analysis, however, depends on whether the effective variables are really considered (Hurlbert 1984). In complex experiments, the key variables are often superimposed by other factors that have not been considered in the experimental design. Huston (1997) criticizes experimental approaches which ignore “hidden treatments” in species assemblages of diversity experiments. Another example from this class of problems is that site productivity and resource availability are known to control the performance of plant communities. If experiments were carried out on sites where nutrients or other resources were limiting factors, small differences in habitat carrying capacity may consequently alter the relationship between diversity and functioning (Huston & McBride 2002; Aarssen *et al.* 2003). Even a realistic manipulation of climate scenarios at stand levels, such as rain-out shelters to simulate drought, remains challenging (Fay *et al.* 2000).

Norby and Luo (2004) therefore state that experiments will always remain case studies even though experimental approaches are required for mechanistic explanations of ecological phenomena (Agrawal *et al.* 2007). Careful interpretation of experimental data is crucial to avoid over-interpretation of experimental results, especially concerning the temporal and spatial scales of experiments (Walther 2007). Ecological experiments have been criticized for their lack of relevance for real-world conditions (Belovsky *et al.* 2004) but the search for a compromise between simplification and complexity is challenging and requires expert knowl-

edge best described by Tukey (1962): “Far better an approximate answer to the right question which is often vague, than an exact answer to the wrong question which can always be made precise”. More formal, there exists a trade-off between internal validity (whether an effect is due to the manipulated factor) and external validity (whether a result can be generalized) of experiments without a single best answer and, in some cases, even contradicting results (Naeem 2001).

Especially for long-living systems, changing responses at different developmental stages can only be managed in experiments with compromises in other factors. A European boreal forest system, for example, showed significantly smaller CO₂ growth stimulation in mature trees under field conditions than expected from results for saplings (Rasmussen *et al.* 2002). But homogenous environmental conditions could only be assumed for the mature trees. The ultimate drawback of ecological experiments is therefore that the complexity of nature can not be established to allow for causal analysis, but that the complexity and diversity of ecosystems is expected to change the response to perturbations. Therefore, there is a need to design experiments with relevance to real-world conditions (Belovsky *et al.* 2004).

Experiments on vegetation response to climate change

One solution for higher practical and theoretical relevance is the use of large-scale (ecosystem level) manipulations in climate change experiments (Beier 2004). Prominent examples which led to key ecological insights are the Hubbard Brook Experiment (Likens *et al.* 1977), the Norwegian RAIN project (Wright *et al.* 1993), the European EXMAN and NITREX projects (Wright & Rasmussen 1998), the Gårdsjön roof project in Sweden (Hultberg & Skeffington 1998), the whole watershed manipulations in the US at the Bear Brook Watershed in Maine (Norton & Fernandez 1999) and in the Fernow Experimental Forest in West Virginia (Gilliam *et al.* 1996), or the Solling experiments in European spruce forests (Bredemeier *et al.* 1998). Despite the complexity and spatial as well as temporal variability of ecosystem processes, such field-scale manipulation experiments have become an important tool for generating knowledge about ecosystem processes and responses if process, species, community and ecosystem level studies are coupled (Beier 2004).

But besides the scale and complexity of the study objects, the majority of climate change experiments to date have focused on single climate factors. A large number of warming studies were carried out by various techniques in the 1990s (synthesized by Rustad *et al.* 2001) and a number of field scale CO₂ enrichment studies have been carried out by the FACE

technique (synthesized by Nowak *et al.* 2004a). The few examples of combinations of CO₂ and warming, however, led to divergent results which are not predictable based on the individual effects (Beier 2004). Results from the climate change experiment at Jasper Ridge, CA, USA, for example, have clearly demonstrated how complex ecosystem responses are. This annual grassland was exposed to combinations of elevated CO₂, increased temperature, increased precipitation, and nitrogen deposition. All treatments involving increased temperature, precipitation or N deposition and their combination, as well as CO₂ alone, tended to promote the above ground biomass production and net primary productivity (NPP) in the ecosystem. But all combinations of elevated CO₂ together with the other treatments reduced this increase (Shaw *et al.* 2002).

Therefore multifactor experiments are crucial both to generate the knowledge needed to build models, and even more importantly, to validate their results. But the complexity and unpredictability becomes even worse when one considers that important effects may be driven by changes in off-season processes, seasonality and extreme events – as illustrated by Loik *et al.* (2004) showing how warming affects the freezing tolerance for certain species, or **Manuscript 7** showing how freeze-thaw cycling in winter can influence grassland productivity.

A way to optimize experiments and improve the generality of results is to combine experiments and gradients by conducting the same ecosystem experiments at different or comparable ecosystems along climatic gradients. This strategy was used in the International Tundra Experiment (ITEX) and resulted in important ecological findings in response to warming (Arft *et al.* 1999). The European CLIMOR and VULCAN projects (Beier *et al.* 2004) showed how variable effects of droughts and warming are among sites under different climatic conditions (Emmett *et al.* 2004; Penuelas *et al.* 2004). Implications from these latter projects are further discussed in the concluding section of this introduction.

Only a few studies have addressed the impacts of extreme weather events experimentally (reviewed in **Manuscript 1**), despite the general consensus on their ecological significance (IPCC 2007b). An important difference between experiments on extreme events and experiments on long-term trends in mean conditions is the notion that the latter strongly depend on the long-term duration of manipulations, as it must be expected that community level changes are slow and probably do not occur within a few years (Walther 2007). Grassland community reordering, for example, takes about ten years to reach quasi-equilibrium with persistent changes in the precipitation regime (Heisler & Weltzin 2006). Experiments on extreme events, in contrast, are not intended to reach such a state, even though there should be

Even though experimental techniques are available which allow for statistically sound identification of diversity effects (Hurlbert 1984; Huston 1997; Allison 1999; Deutschman 2001; Loreau & Hector 2001; Naeem 2002; Schmid *et al.* 2002; Diaz *et al.* 2003), problems remain due to the fact that species numbers are only one part of diversity, functional group and trait diversity being other important components which need to be considered. Ecosystem functioning depends for example just as much on which species or functional traits are present as on how many species are present (Tilman *et al.* 2007). The importance of trophic complexity furthermore complicates this topic (Duffy *et al.* 2007), even though effects on the basal level (primary producers) have been shown to affect fundamental ecosystem processes most strongly (Knops *et al.* 1999). But already within one trophic level there is a multitude of possible functional trait classifications for which we do not know the relevance yet (for plants, e.g., root architecture, or secondary metabolite production). Even by concentrating on one aspect with replications of different species compositions it will be hard to build conclusive experiments at all, because other aspects will inevitably vary with changes in the species compositions (Hector & Bagchi 2007). Focusing on how the strength of interactions between species changes with abiotic context, however, has been identified by the US National Science Foundation as a key gap of knowledge in ecology (Agrawal *et al.* 2007), where it is furthermore stated that theory on species diversity and coexistence has outpaced experimental empirical validation.

Most importantly, one-way interactions (e.g., impacts of biodiversity on ecosystem functioning) will be influenced by reciprocal effects (e.g., ecosystem properties drive biodiversity), at least at some scales (Agrawal *et al.* 2007). A recent review of potential feedbacks between biodiversity and disturbance combined with theoretical modeling demonstrates the importance of such a reciprocal relationship (Hughes *et al.* 2007): Disturbance determines community diversity and diversity determines realized disturbance severity, with the outcome dependent on disturbance severity, initial diversity, competition, and recruitment after the disturbance. Both directions of this relationship have received much attention (the diversity-stability debate, see above; as well as e.g. the intermediate disturbance hypothesis, Connell 1978; Mackey & Currie 2000; Sousa 2001). In terrestrial grasslands, for example, severe drought reduced species richness because of the extirpation of drought-susceptible species (Tilman & Elhaddi 1992). Several of these species remained absent after two years of normal precipitation, suggesting that recruitment (or lack thereof) contributes to the effects of disturbance on diversity. Nevertheless, grassland species richness influenced realized disturbance,

with more diverse plots exhibiting greater drought resistance in terms of biomass production (Tilman & Downing 1994).

As Hughes *et al.* (2007) demonstrate with their model, the result of such an interaction between diversity and disturbance can be a stabilizing feedback, in which the counteracting forces of diversity reducing the magnitude of realized disturbance, and low disturbance leading to competitive exclusion might cause communities to converge at intermediate levels of diversity. In respect to climate change, the question is how the projected increase in frequency and magnitude of extreme events influences this feedback. The changes in competition and recruitment in particular need to be tested experimentally in real communities, as they are the driving factors in this model. Given that humans are at the same time directly decreasing diversity and increasing disturbance with land use and climate change, the existence of feedbacks suggests that these stressors could act synergistically: the result could be an acceleration of species loss beyond our expectations from the direct human modification of habitats (Hughes *et al.* 2007). Empirical understanding of this two way relationship between diversity and disturbance (here: extreme weather events) is therefore clearly needed to understand the development of ecosystems in the future.

Summary of the following manuscripts

Manuscript 1 provides the specific background for the whole study by reviewing knowledge on changes in frequency and magnitude of extreme weather events and by discussing their high importance for ecological processes. This manuscript furthermore contains a literature survey resulting in the finding that work on the impacts of extreme weather events is underrepresented compared to the number of experiments on plant-related climate impacts of changes in mean conditions. In the last section of this manuscript, research challenges are discussed and the specific experimental set-up of the EVENT-experiment is described. All following manuscripts took place in the EVENT-experiment.

Another important insight from the literature survey was that in almost all experiments conducted so far, aboveground biomass production was used as response parameter. Other parameters of high ecological significance are widely ignored. The following papers therefore report on different response parameters within the EVENT case study.

The sequence starts with **Manuscript 2**, a paper that also reports on the widely used parameters above-ground productivity and plant cover as affected by drought and heavy rainfall. Even though increased stress response and species-specific shifts were found in the model plant communities of different species compositions, above-ground productivity at the community level remained surprisingly stable in face of the applied drought and heavy rainfall events. An interesting divergence in die-back was found between the two vegetation types; the grassland communities showed decreased stress with increasing diversity, whereas the opposite was true for the heath communities.

The quantification of carbon fluxes in **Manuscript 3** led furthermore to the unexpected finding that overcompensation and shifts in carbon allocation from reproductive towards vegetative growth after an extreme drought event can result in increased carbon uptake by grassland communities. No significant effects were found in the heavy rainfall manipulation. For these carbon flux measurements, no data was recorded in the heath communities.

Manuscript 4 investigates below-ground processes, which are expected to have high ecological relevance in response to changes in the moisture regime caused by drought and heavy rainfall. Root growth, cellulose decomposition and enzymatic activity were, however, very stable in response to drought, but responded with increased activity to the heavy rainfall manipulation. We furthermore found an increase in below-ground plant biomass and activity of soil biota with increasing community diversity for both vegetation types. Grassland generally reacted stronger to changes in species composition, whereas heath was affected more

strongly by the weather manipulations (mainly rainfall). Regarding the unexpected stability during and after extreme weather events, the importance of a relative and local definition of extreme events is further discussed.

Phenology, i.e. the timing of ecological events, has been identified as one of the most reactive parameters in observations on global climate change. **Manuscript 5** shows that extreme weather events can strongly shift flower phenology and flowering length when compared to the reported shifts related to warming. Changes within single species, however, occurred in different directions and could not be explained by current knowledge. Furthermore, community composition was found to affect flower phenology and to shift the response to the extreme weather events of single species.

Invasibility of a community is commonly viewed as another way of expressing its stability. Here, the invasibility was altered by the weather events with increased invasibility into the communities that experienced the heavy rainfall manipulation, and decreased invasibility due to the drought manipulation (**Manuscript 6**). Resource availability (e.g., water) is considered to be the main driver of this pattern in the absence of strong changes in above-ground biomass of the stands. Invasibility was furthermore altered by the composition of the stand, with decreased invasion into more diverse communities of both vegetation types. These results support expectations from current theories (fluctuating resource theory and niche concepts). The main finding, however, was that the effects of the changes in the physical environment and in the biotic resistance related to the species composition of the resident communities were independent from each other.

Manuscript 7 underlines the notion that short-term weather events have ecological implications over much longer time periods than their occurrences with insights from another climate parameter. Here, the number of soil freeze-thaw cycles increased above-ground productivity and the shoot to root ratio for at least the entirety of the following growing season in grassland plots.

Summarizing conclusions and emerging research challenges

Extremity of weather events

For the setting of the EVENT-experiment, (annually replicated) precipitation extremes of 100-year recurrence did not induce sudden, catastrophic shifts in the studied communities. In the context of a realistic manipulation strength such a non-significant result would be meaningful (Belovsky *et al.* 2004). The applied events, however, were capable of altering other important ecosystem properties and species interactions. The observed changes in community composition, invasibility, or phenology may furthermore become more important and may have implications for ecosystem functioning in the long run. Thus, extreme events may create legacies in the ecological memory which do not become apparent within short time or even in the absence of other events. An illustrative example of such a negative feedback mechanism emerged in September 1989, when the tropical storm Hugo led to biomass loss by almost 75 % of all trees in the Congaree Swamp National Monument, USA (Putz & Sharitz 1991). Trees with resprouted crowns were more likely to have been damaged due to poor branching patterns and stem rot. Thus, a preceding storm makes the next storm more likely to cause damage. The legacy of a given disturbance has therefore to be considered, not only the single event (White & Jentsch 2004). This implicates that monitoring after (simulated) extreme events should be continued over longer time (Walther 2007).

A step towards any generalizing conclusion on the importance of extreme weather events would be to make meta-analysis possible by identifying the relative local extremity of applied events in other ecological and climatological settings. The mixed effects of drought events in the VULCAN and CLIMEX studies (Beier *et al.* 2004; Emmett *et al.* 2004; Penuelas *et al.* 2004; also described above) could stem from the fact that the same length of drought was used in completely different environments. The Mediterranean sites of these projects face such a drought frequently, while it is rare in the humid settings of Great Britain. Adaptation can occur in face of commonly repeated events, but hardly in the face of rare events, no matter how extreme the event is. Winter in temperate systems is a good example of how species are able to adapt to unfavorable conditions if these occur repeatedly at expected return intervals. In regard to a general understanding of extreme weather events this implies that the relative local extremity of an event is better comparable across ecosystems than absolute magnitudes.

As mentioned above, projections of future extremes remain doubtful. On the other hand, thresholds and tipping points between stable states have to be considered (Scheffer & Carpenter 2003). The applied manipulation strengths in the EVENT experiment seemed not to surpass such thresholds. Identifying the position of such key points by creating parallel simulations of different manipulation strength is therefore worth doing. Up to now, such an approach has not yet been applied at the stand level. The comparison of such thresholds for different vegetation types or community compositions draws special interest.

Community composition

Taking the results of manuscripts 2, 4, 5, and 6 together, this work has shown that species interactions and community compositions are important drivers for the reactions of plant communities in the face of extreme weather events. In particular, the two studied vegetation types, grassland and heath, showed markedly different responses. With its realized species compositions, however, the EVENT-experiment is not suited to generate generalizations of diversity effects. As it seems certain that extreme weather events will occur more often in future and in unprecedented magnitudes, the step forward is to study their effects in a systematic diversity set-up which allows for a formal test of the insurance hypothesis (Yachi & Loreau 1999). The need for such approaches is already laid out above, and the findings within the EVENT-experiment hint furthermore at its importance and the necessity to consider biodiversity in all its aspects, from a genetic to the landscape level (Secretariat of the Convention on Biological Diversity 2005). For example, the proposed intensive production of biofuels (to mitigate climate change, IPCC 2007c) may require the conversion of relatively diverse semi-natural landscapes (or on a global scale of natural forest communities) to monocultures with limited genetic diversity. Based on the insurance hypothesis, such a scenario will increase the vulnerability of those landscapes across many scales against extreme events, or disturbance in general.

Vegetation related diversity experiments so far have concentrated almost exclusively on grasslands. Broadening this view is urgent, as the EVENT-setting suggests that the differences in the vegetation type (growth forms, longevity, species identity) are clearly more important for the response to extreme weather events than various diversity levels. Therefore, the other facets of diversity demand attention, such as functional types (Gitay & Noble 1997; Westoby & Leishman 1997) and trait diversity (Walker *et al.* 1999; Weiher *et al.* 1999). The

maintenance of interactions between trophic levels are especially uncertain in a more variable environment (Gastine *et al.* 2003).

Regarding the discrepancy in results of studies focusing on experimentally assembled communities and mature natural systems (Grace *et al.* 2007), it seems furthermore necessary to conduct removal experiments (Diaz *et al.* 2003) with statistically sound randomization and replication (Hurlbert 1984) combined with climate manipulations in natural systems.

Freeze-thaw cycles

Manuscript 7 deals with the ecological importance of soil freeze-thaw cycles (FTC) in plant communities. Especially in temperate ecosystems, this factor has not yet been studied in detail. Even local climatological datasets are missing from which trends and extremes in the number of freeze-thaw cycles could have been derived. Therefore, extremity of the applied manipulation cannot be calculated and the experimental set-up focused on maximizing the number of FTC. Other fundamental gaps in knowledge become evident when examining the results of this manuscript together with the currently available literature. Here, I discuss emerging research questions regarding (1) the mechanistic understanding of FTC, (2) the quantification of the ecological significance of FTC, and (3) methodological issues in analyzing the effects of the soil frost regime on long-term ecosystem processes.

(1) Freeze-thaw cycles contribute to nutrient dynamics, and micro-organisms are known to play an important role in the related processes. Knowledge on nutrient uptake capacity and competition between micro-organisms and plants in winter and early spring, however, is missing. Analyzing species specific effects and the role of plant functional traits seems to be particularly rewarding, including the question if plants (e.g. dwarf shrubs versus grasses, legumes versus non-legumes) are capable of storing nutrients during winter or early spring without an immediate increase in productivity. Mechanistically, the modifying role of different soil properties (such as soil type, organic matter content, or soil water status) and of winter soil temperature regime (such as number of freeze-thaw cycles, mean soil temperature, number of days with unfrozen soil, or absolute minimum soil temperature) remains a major challenge for assessing the impacts of FTC on physico-chemical soil processes, microbial activity, nutrient cycling, and plant nutrient uptake.

(2) The study of FTC seems to be further advanced in microbiology than in plant ecology (Grogan *et al.* 2004; Henry 2007). The role of plants and differences in vegetation types

in nutrient retention remains unaddressed in research, despite being crucial for understanding ecosystem processes and the protection of ecosystem services. An evaluation of how effectively different vegetation types can contribute to nutrient retention is missing. Additionally, studies on the effects of FTC on plant phenological rhythms are of high ecological importance. For example, the decoupling of plant-animal interactions such as rhythm of flower production and activity of insect pollinators (Memmott *et al.* 2007) could be a consequence of forward-shifted plant life cycles in spring after increased FTC in the previous winter. Furthermore, an analysis of the interacting effects of FTC with other climatic parameters on plant performance draws interest. For example, plant susceptibility to late air frost events or to spring drought could increase because of earlier tissue development and increased shoot-to-root ratio after frequent FTC in the previous winter.

Even though the direct response of microbial communities and their activity to FTC is fast and transient, plants shape microbial community structure and function at least in the rhizosphere (Milling *et al.* 2004; Sharma *et al.* 2005). FTC events therefore may also lead to indirect long term effects in bacterial and fungal populations, if vegetation is affected by FTC. The link between vegetation and microbial communities may furthermore be influenced by processes such as root exudates and mycorrhizal symbiosis. It is unclear if FTC have any effects on such processes.

(3) Several methodological issues arise when studying the importance of winter soil temperature effects on ecosystem functioning. A major challenge is the determination of appropriate time scales for studying FTC impacts on living organisms such as micro-organisms and plants. For example, the effects of FTC on plants are far out of proportion with the short duration of their cause, and this time lag may even be longer when interacting soil parameters are regarded.

In order to explicitly attribute effects of freeze-thaw cycling to microbial activity or plant performance, experiments with several controls are required, i.e. controlling the mean temperature, the number of unfrozen days, and the minimum and maximum temperature values. Here, the way of experimental heating is also a delicate issue (Henry 2007). Even though above-ground infra-red heaters might simulate conditions in a warmer world more realistically, they would probably affect above-ground plant biomass much stronger than the targeted below-ground processes when used to thaw frozen soil reasonably fast.

To sum it up, this work has shown that vegetation response to extreme weather events is already complex in a simplified experiment, as it depends on species interactions and species identities besides simple frequency and magnitude of the extreme events themselves. Future work in this field would benefit from applying several approaches: small-scale experiments to identify processes, large-scale experimental manipulations in natural settings to determine if these processes scale up, and research on non-linear processes that identifies thresholds in how systems respond. Furthermore, the importance of diversity, be it genetic diversity, species diversity or differences between vegetation types, need to be included in climate change experiments. With results from all these approaches, a better understanding of upcoming changes as well as an improvement in ecosystem modeling can be expected. But dealing with high uncertainty and preparing for surprises seems unavoidable with respect to future climate change.

List of Manuscripts and declaration of own contribution

“Writing” is understood as the actual formulation of sentences and paragraphs. Comments and inputs from discussions with the co-authors are covered under “concept and discussion”. Proof-reading and grammar editing was done either by professionals or by cooperating native speakers for each manuscript.

Manuscript 1:

Authors: Jentsch A, Kreyling J, Beierkuhnlein C

Title: A new generation of climate change experiments: events, not trends.

Status: published

Journal: Frontiers in Ecology and the Environment 5(7): 365-374

own contribution: first draft; literature study; writing: 50%; editing and figures: 75 %; concept and discussion: 25 %

Manuscript 2:

Authors: Kreyling J, Wenigmann M, Beierkuhnlein C, Jentsch A

Title: Effects of extreme weather events on plant productivity and tissue die-back are modified by community composition.

Status: accepted with minor revision

Journal: Ecosystems

own contribution: data collection: 50%; data analysis and figures: 90%, writing: 75%; concept and discussion: 50 %; corresponding author

Manuscript 3:

Authors: Mirzaei M, Kreyling J, Hussain MZ, Li Y, Tenhunen J, Beierkuhnlein C, Jentsch A

Title: Drought enhances carbon uptake in experimental grassland communities of two diversity levels.

Status: in press

Journal: Journal of Plant Nutrition and Soil Science

own contribution: data collection: 0%; data analysis and figures: 75% (all except applying the empirical model), writing: 90%; concept and discussion: 75 %; corresponding author

Manuscript 4:

Authors: Kreyling J, Beierkuhnlein C, Elmer M, Pritsch K, Radovski M, Schlöter M, Wöllecke J, Jentsch A

Title: Soil biotic processes remain surprisingly stable in face of 100-year extreme weather events in experimental grassland and heath.

Status: submitted 10/2007

Journal: Plant and Soil

own contribution: data collection: 50%; data analysis and figures: 75%, writing: 75%; concept and discussion: 50 %; literature study: 75%; corresponding author
remark: data collection, analysis, and interpretation of results on decomposition and soil enzymatic processes was done by the external cooperators)

Manuscript 5:

Authors: Jentsch A, Kreyling J, Böttcher-Treschkow J, Beierkuhnlein C

Title: Beyond gradual warming – extreme weather events alter flower phenology of European grassland and heath species.

Status: submitted 11/2007

Journal: Global Change Biology

own contribution: data collection: 25%; data analysis and figures: 100%, writing: 50%;
concept and discussion: 25 %

Manuscript 6:

Authors: Kreyling J, Beierkuhnlein C, Ellis L, Jentsch A

Title: Invasibility of grassland and heath communities exposed to extreme weather events
– additive effects of biotic resistance and fluctuating resources.

Status: submitted 11/ 2007

Journal: Oikos

own contribution: data collection: 75%; data analysis and figures: 100%, writing: 90%; concept and discussion: 75 %; corresponding author

Manuscript 7:

Authors: Kreyling J, Beierkuhnlein C, Jentsch A

Title: Recurrent soil freeze-thaw cycles enhance grassland productivity.

Status: in press

Journal: New Phytologist

own contribution: data collection: 75%; data analysis and figures: 90%, writing: 90%; concept and discussion: 75 %; corresponding author

remark: data collection, analysis, and interpretation of results on soil enzymatic processes was done by external cooperators)

Table 2: Own presentations of this research at conferences.

Date	Organization	Conference, location	Presentation title
16.10.2007	Bundesamt für Naturschutz	Biodiversität und Klimawandel – Vernetzung der Akteure in Deutschland, Insel Vilm	Extrem-Wetterereignisse und ihre Folgen - ein neues Experiment zur Auswirkung von Trockenheit, Starkregen und Frostwechseln auf Pflanzengemeinschaften und Ökosystemfunktionen
13.09.2007	Ecological Society of Germany, Austria and Switzerland (GfÖ)	37th Annual Meeting, Marburg	Extreme events pose new ecological challenges in the climate change debate
12.09.2007	Ecological Society of Germany, Austria and Switzerland (GfÖ)	37th Annual Meeting, Marburg	Recurrent soil freeze-thaw cycles promote plant community productivity
11.09.2007	Ecological Society of Germany, Austria and Switzerland (GfÖ)	37th Annual Meeting, Marburg	Extreme weather events (drought & heavy rainfall) modify flower phenology
08.08.2007	Ecological Society of America, (ESA)	92nd Annual Meeting, San Jose, USA	Vegetation types differ in their response to recurrent soil freeze-thaw cycles
21.05.2006	AK Biogeografie im Deutschen Geografentag	Jahrestagung, Bonn	Vegetationsdynamik nach simulierten Extremwetterereignissen
03.11.2005	Fachhochschule Zittau-Görlitz	Klimawandel und Erneuerbare Energien, Zittau	Vegetation und Klimaveränderungen – die Bedeutung von Extremereignissen

Table 3: The EVENT-experiment: Temporal progression and own contribution. The Experiment is funded by the UFZ-Helmholtz Centre for Environmental Research (Prof. Anke Jentsch) and the Chair of Biogeography, Bayreuth University (Prof. Beierkuhnlein).

Action	Time frame	Own contribution
Project idea (Anke Jentsch and Carl Beierkuhnlein)	2003	-
Proposal for DFG Collaborative Research Centre initiative (Carl Beierkuhnlein and Alex Weigelt)	2003	-
Further development of research questions and experimental design (Anke Jentsch and Carl Beierkuhnlein)	2004	Part of discussions, since 11-2004 organization of implementation and development of measuring protocols with a PhD-position at the UFZ
Installation of experimental site, pre-growing of plants and planting of experimental communities	12-2004 - 04-2005	Coordination and execution
Weather manipulations, data collection and site maintenance	06-2005 - 09-2007	Coordination and execution
Students preparing Master's and Bachelor's thesis and doing internships	04-2005 - 10-2007	Supervision and coordination
External co-operations	since 2004	Cooperation and coordination of data collection

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Manuscript 1:

A new generation of climate change experiments: events, not trends

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Abstract

Intensification of weather extremes is currently emerging as one of the most important facets of climate change. Research on extreme events (“event-focused” in contrast to “trend-focused”) has increased in recent years and, in 2004, accounted for one-fifth of the experimental climate change studies published. Numerous examples, ranging from microbiology and soil science to biogeography, demonstrate how extreme weather events can accelerate shifts in species composition and distribution, thereby facilitating changes in ecosystem functioning. However, assessing the importance of extreme events for ecological processes poses a major challenge because of the very nature of such events: their effects are out of proportion to their short duration. We propose that extreme events can be characterized by statistical extremity, timing, and abruptness relative to the life cycles of the organisms affected. To test system response to changing magnitude and frequency of weather events, controlled experiments are useful tools. These experiments provide essential insights for science and for societies that must develop coping strategies for such events. Here, we discuss future research needs for climate change experiments in ecology. For illustration, we describe an experimental plan showing how to meet the challenge posed by changes in the frequency or magnitude of extreme events.

In a nutshell

- Intensification of weather extremes is currently emerging as one of the most important facets of climate change
- Evidence suggests that the frequency and magnitude of extreme weather events is increasing in many regions in response to global climate change
- Extreme events can be distinguished from gradual trends by their statistical extremeness (magnitude) combined with their discreteness (duration) relative to the life span of the organisms in focus
- Experimental research on extreme weather events has increased recently and accounts for one-fifth of the experimental climate change studies published in 2004. Here, we lay out research needs and introduce an experimental plan to meet the challenges posed by extreme events

Ongoing climate change is considered to be a driving factor for ecosystems in the 21st century (IPCC 2001). Links between climate change and shifts in vegetation have been documented convincingly, mainly by modeling shifts in species distribution patterns and monitoring phenological rhythms (eg Walther *et al.* 2002; Root *et al.* 2003). Field and laboratory experiments have demonstrated the effects of changing climate parameters on vegetation (eg Harte and Shaw 1995; Beerling 1999). Although there is a high degree of uncertainty in the details of climate change, we propose separating the impacts of changes in mean climate values (what we term “trend effects”) from those produced by changes in the magnitude or frequency of extreme events (“event effects”). Event-focused research is difficult because the impacts of “extreme weather events” on ecosystems are out of proportion to their short duration. Thus, weather extremes, which are increasing in magnitude and frequency, have serious implications for ecosystems and societies (IPCC 2001; EEA 2004).

Here, we discuss (1) the ecological relevance of extreme events, (2) evidence of intensifying weather extremes in climate change, (3) definition issues with respect to discrete versus gradual processes, and (4) the current state of experimental climate change research. We conclude by discussing emerging research challenges and laying out an experimental plan to meet them.

Ecological importance of extreme weather events

To illustrate the ecological role of extreme weather events, let us consider catastrophic shifts in ecosystems (Scheffer and Carpenter 2003) due to extreme disturbance events that change system characteristics. For example, tropical hurricanes or temperate winter storms are capable of destroying entire forests (Figure 1). However, not all extreme events are so lethal (Turner *et al.* 1998) that they push a system beyond the threshold of dynamic equilibrium, resulting in a novel system trajectory (White and Jentsch 2001). Less severe disturbance events may change competitive interactions among plants and alter successional pathways by reducing the inertia of a system (Jentsch and Beierkuhnlein 2003; Figure 2).

Effects on the dynamics of biotic communities have often been associated with extreme weather events at ecological time scales (for reviews see Easterling *et al.* [2000b] and Parmesan *et al.* [2000]), and with climatic extremes at evolutionary time scales (Gutschick and BassiriRad 2003). Here, we discuss the ecological significance of extreme climatic parameters, using the following as illustrations: (1) minimum temperature, (2) heavy rainfall events, and (3) drought.

Minimum temperature

Minimum temperature tolerance determines the northern distribution boundaries of tree species; tropical trees suffer cold injuries even at temperatures above 0°C. Deciduous trees in temperate zones tolerate temperatures as low as -30°C, whereas boreal conifers may survive temperatures as low as -70°C or colder without serious damage (Woodward 1987; Larcher 2003). Minimum temperature is clearly one of the most important factors determining species distribution. Woodward (1987) found that minimum temperature effects or cold injuries can be sudden and often lethal. It is noteworthy that processes such as frost hardening in winter change tolerance limits dramatically, and that timing of extreme frost events can be more important than absolute temperature. A decrease in frequency and magnitude of extreme cold temperatures and a lengthening of the growing season are likely to be among the effects of global climate change. Evidence from historical records and model predictions demonstrate that the magnitude of temperature increases under global warming is greater in winter than in other seasons and greater at night than during the day.



Figure 1: Importance of extreme weather events. (a) Winter storm “Lothar” affected large forested areas in Central Europe in December 1999, as did winter storm “Kyrill” in January 2007. In Germany, Lothar blew down about 175 million m³ of timber, more than twice the amount of the annual silvicultural harvest (69 million m³) and nearly twice the annual increment (96 million m³). (b) Severe summer drought in central Europe in August 2003. In Germany, drought primarily affected deciduous trees, resulting in leaf senescence of large forest patches.

Heavy rainfall

In 1992, heavy rainfall events led to extraordinary biomass production by plants in a semi-arid, southwestern part of the US. This increase in forage availability facilitated population booms of deer mice (*Peromyscus maniculatus*). Overcrowding and forage shortage in the following year caused increased rodent activity in human buildings, and this in turn increased the contact between humans and mice, which carry hantavirus. Hantavirus cardiopulmonary syndrome is frequently lethal to humans, and a regional epidemic was observed in the area in 1993. The same chain of events was repeated between 1997 and 1999 (Hjelle and Glass 2000).

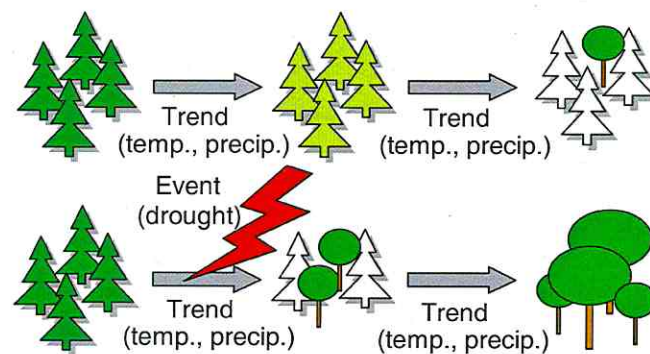


Figure 2: Extreme events can accelerate system changes by reducing inertia, which is represented in long-lived organisms, competitive balance, or clonal reproduction. Changes in mean values of climate parameters, such as temperature or precipitation, may lead to changing species composition of a given system. The introduction of extreme events can advance this process. Therefore, extreme events can bring systems into novel balance with novel climatic conditions.

Drought

One severe drought that affected northern New Mexico in the 1950s shifted the ecotone between ponderosa pine forest (*Pinus ponderosa*) and piñon–juniper woodland (*Pinus edulis* and *Juniperus monosperma*, respectively) extensively (> 2 km in < 5 yrs; Allen and Breshears 1998). The most striking feature of this example is that the ecotone has remained stable since then, even though climatic conditions returned to those prevalent before the drought.

The importance of extreme events is not yet acknowledged as widely as climatic mean attributes in biogeography and population ecology. Generally, mean values are easy to access, whereas climate data concerning weather extremes that are linked to ecosystems in proper spatial and temporal resolution are rare.

Weather extremes in climate change

The current scientific debate surrounding climate change (IPCC 2001) focuses on which climatic parameters are changing and how these will vary on regional spatial scales. With respect to shifts in intensity and frequency of extreme events, three types of evidence dominate scientific activity: observations, models, and theoretical considerations.

Observation of intensifying weather extremes based on time series seems to be the most straightforward approach to monitoring changes. However, several difficulties arise because extreme-value statistics in time series require historical datasets with reliable and precise measurements of extremes. Currently, weather stations are not evenly distributed across the globe, and only a few countries fulfill the conditions necessary to carry out extreme-value statistics for their biogeographical region (Easterling *et al.* 2000a). Standard routines to detect outliers may even eliminate very rare, real events, such as the 2003 heat wave in Central Europe, from climatological time series (Schar *et al.* 2004). Nevertheless, there are numerous studies observing changes in extremes: for instance, increased frequency of heavy precipitation events since 1920 in the US (Karl *et al.* 1995; Kunkel 2003), centennial increases in frequency of heavy precipitation events (10%–30%) in Switzerland (Schmidli and Frei 2005), and increases in duration of extremely wet conditions in winter (Schonwiese *et al.* 2003) and of unusually dry periods in summer (Beck *et al.* 2001) in Europe. The European heat wave of 2003 has convincingly been associated with anthropogenically forced global warming (Schar and Jendritzky 2004). Record-breaking temperature events are reported to be on the increase worldwide (Benestad 2004). With regard to hurricanes, there is considerable debate in the

climatological community as to whether climate change will lead to a change in intensity of these events (Emanuel 2005).

Predictive modeling is a powerful tool for identifying upcoming developments. Some 15 years ago, the General Circulation Model (GCM) approach predicted an increase in the variability of precipitation events (eg Mearns *et al.* 1990). Unfortunately, GCMs do not provide specific information about regional changes of extreme events, and modeling at ecologically meaningful spatial scales is just beginning. As regional climatic models are developed, changes in the frequency and intensity of extreme weather events are predicted for several parts of the world. They predict substantial regional differences, and even shifts in opposite directions and diverging developments in, for example, frequency of heavy precipitation events in North America (Easterling *et al.* 2000b; Milly *et al.* 2005), frequency and duration of heat waves and heavy rainfall events during summer in southern Europe, and frequency and duration of heat waves during winter in North Africa (Sanchez *et al.* 2004). Studies generally predict increasing frequency of heavy rainfall for Central Europe (Christensen and Christensen 2003), the UK, and Bangladesh (Palmer and Raisanen 2002), as well as increasing intensity (Raisanen and Joelsson 2001). Enhanced summer droughts are expected for southern Europe and central North America (Seneviratne *et al.* 2002). The variability of summer temperatures in Central Europe may in fact increase by more than 100% (Schar *et al.* 2004).

The theoretical line of evidence is independent of the problems associated with adequate datasets and meaningful spatial scales. Considering a given probability distribution of occurrence for any climatic parameter, changes in mean values as well as increased variance in amplitude will inevitably lead to more frequent and more intense extreme events at one tail of the distribution (Meehl *et al.* 2000; Figure 3). It should be noted that extremes at the minimum of a given parameter will virtually disappear when mean values increase, whereas historically unprecedented intensities arise at the maximum, so that biota will face novel events and habitat conditions. Statistically, evidence of changing mean values is easier to handle than evidence of intensifying extreme values. Many examples of shifting means are available (IPCC 2001). For the standard Gaussian distribution, an increase in the mean by one standard deviation makes an event with a former probability of occurrence of 1% 9.2 times more probable. A doubling of CO₂ is likely to produce changes of greater than one standard deviation in both precipitation and temperature. Intuitively, an increase in rainfall severity, for example, is probable. This is because a warmer atmosphere contains more latent energy (Kunkel 2003). For almost normally distributed parameters – such as temperature – changes in variance might

not be climatically relevant, although statistically sound. In contrast, for clearly non-normally distributed parameters – such as precipitation – changes in variance are predicted to increase significantly (IPCC 2001). Overall, evidence suggests that weather extremes are changing.

Terrestrial ecosystems across the globe are adapted to regional climate dynamics. Shifts in vegetation or ecosystems across large spatial and long temporal scales represent gradual changes in climate. In contrast, instead of only transiently affecting the dynamics of ecosystems at the local scale, we propose that discrete events of novel extreme magnitude and frequency can have long-term ecological significance and drive ecosystems beyond stability and resilience.

Accordingly, the debate about climate change has expanded from an analysis of trends to an interest in extreme events. Thus, we now aim to clarify the “event” character of climatic processes and to quantify their “extremeness”.

Event versus trend, extreme versus average

For decades, ecology has regarded mean values as powerful indicators of climatic site conditions. Short-term deviations were regarded as extraordinary and non-representative measurements. However, there is a smooth transition between discrete events and gradual trends of shifting means; any clear-cut distinction depends on the temporal resolution. Changes in annual precipitation are generally perceived as shifting means or trends, whereas changes in the duration of the longest drought period represent shifts in the intensity of extreme events.

For ecological investigations, we argue that a discrete event is distinguished from a continuous process by its abruptness, no matter whether the event is recurrent, expected, or normal (White and Jentsch 2001). Abruptness of an event is a function of magnitude over duration (Figure 4), which is best described relative to the life cycles of the organisms of interest or to the successional speed of the ecosystems in which they occur (Jentsch 2006). Using such relative currency to express abruptness allows comparison among organisms with different life spans. Using it to express frequency allows comparison among ecosystems of differing productivity.

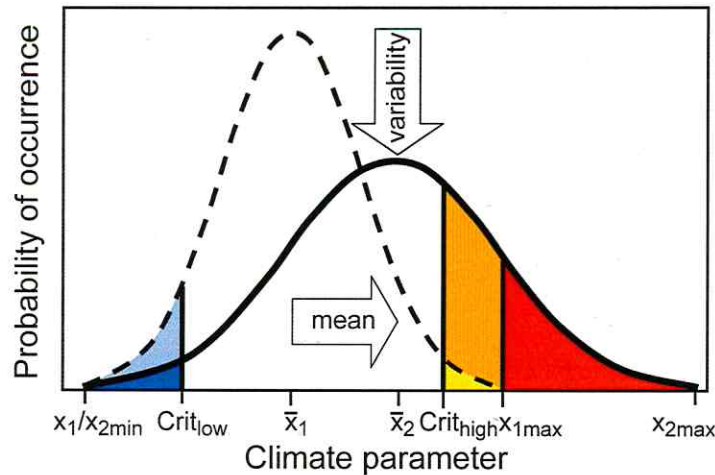


Figure 3: Expected changes in the probability of occurrence of extreme weather events under climate change for any given climate parameter (eg precipitation, temperature). From scenario A (dotted line; eg today) to scenario B (solid line; eg year 2050), mean value (\bar{x}_1 to \bar{x}_2) and overall variability (standard deviation or width of the curve) increase. The probability of situations exceeding critical thresholds (crit_{low} and $\text{crit}_{\text{high}}$) changes dramatically; for example, $\text{crit}_{\text{high}}$ shifts from including only the yellow area to including the whole orange and red area. Unprecedented extremes occur (red area) as novel maxima are reached ($x_{1\text{max}}$ to $x_{2\text{max}}$). On the other hand, current minima become less probable (light blue to dark blue). All alterations stress the increasing significance of extreme events with gradual shifts of climatic parameters. Note that the overall pattern will prevail, even if other probability distributions are appropriate. Adapted from Meehl et al. (2000).

The distinction between “event” and “trend” is therefore an issue of hierarchy. Event-based ecological research deals with several orders of magnitude in the life spans of response communities. The life cycles of individuals are nested within the dynamics of populations. Likewise, climatic events are nested within climatic trends, from annual to decadal or even millennial scales.

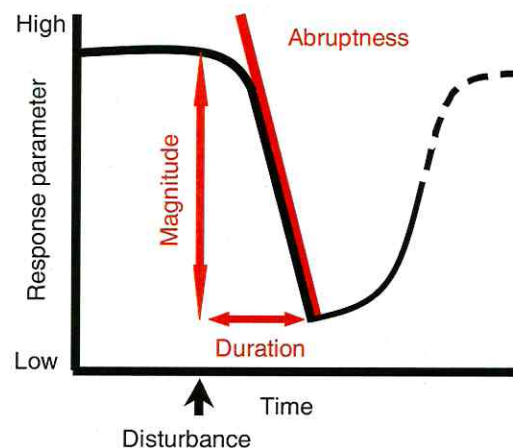


Figure 4. Test of a discrete event: abruptness. The abruptness of an event is a function of magnitude over duration. Note that magnitude of the disturbance event refers to its effect on the parameter studied, such as destruction of biomass. Duration of the disturbance event is to be perceived relative to the lifespan of the organisms studied (White and Jentsch 2001).

Extremeness of events can be determined by statistical extremity with respect to a historical reference period (eg extraordinary deviation from the median of probability distributions; Gumbel 1958; Reiss and Thomas 1997). Extremeness can be chosen in terms of a probable recurrence interval. The 100-year event – sometimes referred to as the 1% event, since there is a 1% chance of occurrence in any given year – is widely used in disciplines as disparate as hydrology and economics. However, an adequate time scale for analysis is especially crucial. Statistical extremes over longer time scales, not affecting single organisms or populations but possibly altering species evolution, may also be influential (Overpeck et al. 2003). We propose choosing the temporal resolution of the data in relation to the organisms studied.

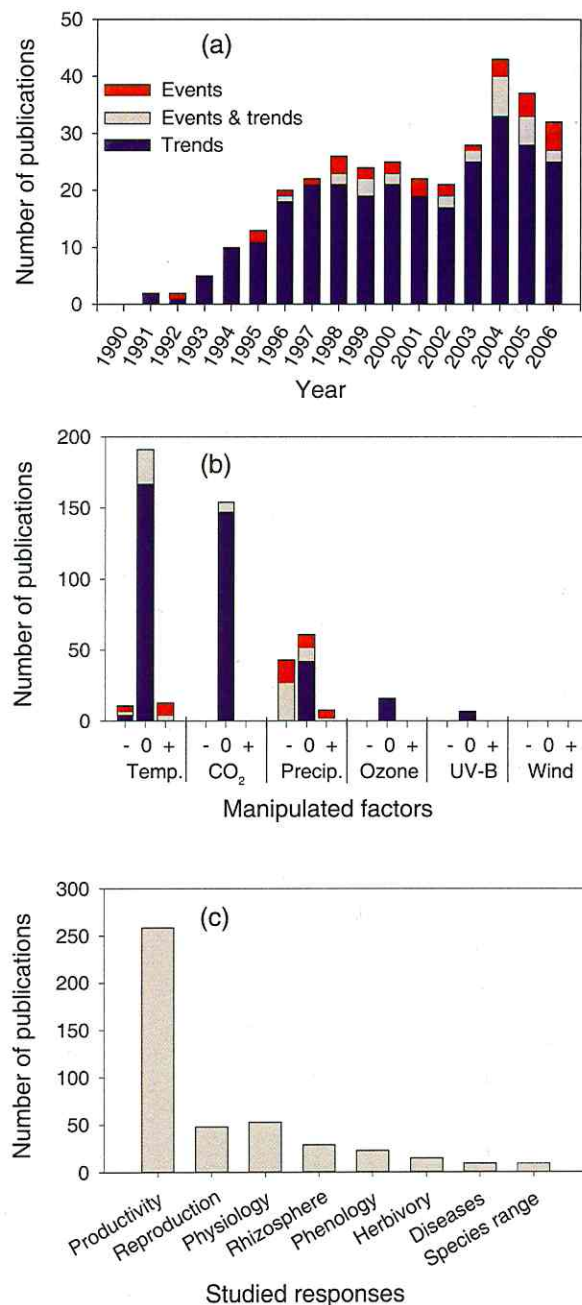


Figure 5. Trend and event research in climate change experiments. (a) Temporal development of the number of publications on trends versus events. (b) Manipulated climate factors, distinguished by mean value (0), low extreme value (-), and high extreme value (+) of the observed distribution tail (eg precipitation with drought and heavy rain). (c) Studied effects. Note that the term “growth” includes biomass gain, cover, and other measures of aboveground biomass production. “Rhizosphere” includes both root and mycorrhizal measures. All diagrams are based on analysis of 364 peer-reviewed papers. See text for information about literature search and distinction between trend and event.

In predicting extreme events in future climatic scenarios, we are faced with two different qualities of extremeness: (1) an increase in the probability of occurrence of a maximum or minimum of a given climatic parameter (frequency of event), such as a particular temperature, and (2) a novel crossing of the observed minimum or maximum of a climatic parameter (magnitude of event), such as length of drought period. In this context, the extremeness of an event is described independently of its effects on organisms. Taking together extreme value theory and discreteness of events, we are able to distinguish between shifts in mean trends and alterations in the occurrence, frequency, and magnitude of extreme events. However, further problems arise when we consider ecosystems with numerous communities and organisms displaying a diverse array of life spans, differences between appropriate time scales for individuals and populations, the rareness of adequate datasets, especially for tropical countries (Easterling *et al.* 2000b), and statistical extremes that change considerably over time (Luterbacher *et al.* 2004). Nevertheless, the use of rough estimates to study the ecological effects of extreme events experimentally is more promising than waiting for confirmed regional forecasts, which will soon become outdated.

Extreme events in experimental climate-change research

Experiments enable us to perform analyses of causation, whereas adequate controls are often missing in field observations of naturally occurring extreme weather events. In addition, experimental simulations are a useful tool to test the effects of forecasted extremes that have not yet occurred. Here, we focus on controlled field experiments in ecological climate change research.

We conducted a literature study, searching the ISI Web of Science for [“climate change” or “climatic change”] and “experiment*” and [“vegetation” or “plant*”]. In December 2006, this search yielded about 2300 published papers. From these, only original studies on the response of plants to experimentally manipulated climate parameters were selected, giving 364 studies. These were separated into research focusing on “events” and research focusing on shifts in mean “trends”. The results show that experimental climate change research has existed since the 1990s (Figure 5a). Within this field, event-focused research has increased and, in 2006, accounted for one fifth of the experimental climate change studies published. Generally, trend-based climate change research has focused primarily on elevated temperature and enhanced CO₂ (Figure 5b) and produced crucial knowledge about the effects on biomass production (Figure 5c), which is one of the most essential ecosystem processes.

However, only a few studies reported on other response parameters or compared both events and trends, thus allowing us to rate effects against each other.

One experiment comparing effects of events and trends manipulated rainfall timing (periodicity) and rainfall amount in a tall-grass prairie in Kansas (for experimental design, see Fay *et al.* [2000]). Redistribution of the total rainfall amount into fewer but more intense discrete events resulted in a reduction of aboveground net primary productivity (ANPP) and increased root to shoot ratios. Such responses are found to be highly species specific, leading to changes in competitive abilities. Increased variability in rainfall generated stronger reactions than a reduction of 30% in rainfall quantity without alteration of the timing of rainfall inputs (Fay *et al.* 2003). Interestingly, ANPP is not related to mean soil water content, but to temporal variability in soil water (Knapp *et al.* 2002).

Another field experiment carried out in four European countries (Beier *et al.* 2004) tests the effects of extreme drought events and increased night-time temperature as a trend in heath systems. Here, drought decreases aboveground biomass and flowering, whereas the effect of warming depends on overall soil moisture status, leading to enhanced productivity in more humid sites (ie UK, Netherlands) and to reduced productivity in drier sites (ie Spain; Penuelas *et al.* 2004).

Overall, event-based experiments have identified ecosystem responses capable of changing structure and composition of various communities (Table 1). Therefore, interferences of ecosystem functions and services are to be expected. Obviously, timing of events has crucial implications; periods of accelerated growth and reproduction are most susceptible (eg Koc 2001).

Table 1: Key findings of experiments manipulating weather events¹

Observed effect	Manipulation	Sources
Reduced aboveground productivity	Drought	Borghetti et al. 1998, Gordon et al. 1999, Sternberg et al. 1999, Grime et al. 2000, Koc 2001, Llorens et al. 2002, Filella et al. 2004, Gorissen et al. 2004, Llorens et al. 2004, Penuelas et al. 2004b, Kahmen et al. 2005, Le Roux et al. 2005, Erice et al. 2006
	Rain and Drought*	Fay et al. 2000, Fay et al. 2002, Knapp et al. 2002, Fay et al. 2003
	Frost	Weih and Karlsson 2002, Martin and Ogden 2005, Oksanen et al. 2005
	Heat	Marchand et al. 2005, Musil et al. 2005, Marchand et al. 2006
	Drought and Heat	Roden and Ball 1996, Ferris et al. 1998, Hamerlynck et al. 2000, Shah and Paulsen 2003, Xu and Zhou 2005
Reduced belowground productivity	Drought	Bassirad and Caldwell 1992, Beier et al. 1995, Asseng et al. 1998
	Rain	Martin and Ogden 2005
Altered species composition	Drought	Grime et al. 2000, Buckland et al. 2001, Koc 2001, Lloret et al. 2004, Schwinning et al. 2005
	Rain	Sternberg et al. 1999, Gillespie and Loik 2004
	Rain and Drought	Knapp et al. 2002, Bates et al. 2005, English et al. 2005
	Heat	White et al. 2000, 2001
Reduced reproductive success	Drought	Fox et al. 1999, Gordon et al. 1999, Lloret et al. 2004, Morecroft et al. 2004, Penuelas et al. 2004b, Llorens and Penuelas 2005, Lloret et al. 2005, Schwinning et al. 2005
	Rain	Germaine and McPherson 1998, de Luis et al. 2005
	Drought and Heat	Shah and Paulsen 2003
	Heat	Liu et al. 2006
Altered phenology	Drought	Llorens and Penuelas 2005
	Rain and Drought	Fay et al. 2000, Penuelas et al. 2004a

¹ Table 1 is based on 46 peer-reviewed publications. Bibliography is available in WebPanel 1

² Rain and Drought comprise manipulations of rainfall variability with intensified rainfall events as well as increased drought intensities

Research needs and experimental plan

Understanding the factors governing the response of biodiversity to extreme weather events will increase our ability to predict the future behavior of ecosystems. This is one of the next great challenges in the life and environmental sciences. So far, gradual climatic trends such as global warming and increasing levels of CO₂ have been studied in much more detail than have alterations in sudden events. Thus, there is a substantial lack of knowledge on how extreme weather events affect biodiversity and ecosystem functioning. Here, we discuss emerging research challenges. Aside from general frontiers in ecology, experimental research on extreme weather events needs to address five additional issues: (1) timing of events, (2) ecological memory, induced tolerance, and time lags in response, (3) hidden players (*sensu* Thompson *et al.* 2001), (4) quality of local climate data, including past records and future

model predictions, and (5) a historical control. After discussing these emerging issues, we lay out the experimental design of a new event-focused climate change experiment in Bayreuth, Germany, as an illustration of how we can meet some of the challenges.

Appropriate timing of manipulations is a sensitive experimental issue, which needs to take into account various underlying ecological rhythms: (1) interaction with different stages in the development of natural or artificial plant communities, including critical thresholds in ages of individuals and in the process of community assembly; (2) interactions with natural event regimes or with critical thresholds of gradual, sometimes hidden trends in environmental parameters; and (3) interactions with periodic pulses of productivity, such as yearly seasons or “bad and good years”. These long-term dynamics may produce resource reserves or buffers, which in turn modify the short-term performance of species in response to extreme events. Experiments have to either exclude or explicitly tackle some of this variation in order to test for particular effects. A simple experiment would profit from equally-aged artificial communities and a temporal design of manipulations specified by annual season.

The concept of “ecological memory” and the idea of “disturbance-induced community tolerance” point to the crucial role of history in climate change experiments. To date, there is no clear understanding of the speed or time lag with which biotic communities of different taxa can evolve or respond when subjected to sudden environmental change. Thus, an experimental design of extreme weather events would profit from manipulations that are recurrent and abrupt within the life spans of responding organisms. Data acquisition should be capable of capturing metapopulation dynamics in time.

Hidden players (*sensu* Thompson *et al.* 2001), such as microbes, fungi, and soil invertebrates, undoubtedly contribute to community performance in response to extreme weather events and to the complexity of system functioning at different scales. Thus, an experimental study would profit from interdisciplinary cooperation and from using aggregated information, such as the construct of functional groups across guilds, based on traits such as nitrogen fixation. This could also reveal the relative importance of redundancy versus complementarity for functional stability under new extremes.

For sound manipulation of extreme climatic events in the field, local climate data, including past weather records and future model predictions, are needed. Historical analyses can be carried out by means of extreme value theory; future climatic projections should be calculated according to one of the approved global change scenarios. A delicate problem may be imposed by natural extreme weather conditions during the course of the study. We therefore

suggest generating historical mean climatic conditions as an additional control to ambient conditions. This second control allows for conclusive results in case of extraordinary weather conditions during the years of experimental manipulation, such as the extreme European precipitation events in summer 2002, or the extreme drought in summer 2003.

This list of research needs is by no means comprehensive and could be supplemented by many other experiments such as, for example, the comparison of effects on artificially versus naturally grown communities, on species-rich versus species-poor communities, on different ecosystems or systems in different climatic zones (to date, very few studies have been conducted in the tropics), or on a range of other parameters.



Figure 6: Event-focused climate change experiment (EVENT) testing the effects of drought, heavy rain, and altered freeze–thaw cycles on biodiversity at Bayreuth University, Germany. Location is 49°55'19" N, 11°34'55" E; mean annual temperature = 7.8°C; mean annual precipitation = 709 mm. Soil consists of drained sandy loam, homogenized prior to planting in spring 2005. C/N ratio = 15.4–20.2; pH = 5.5.

We have recently initiated a new two-factorial field experiment in central Europe (EVENT), designed to test the effects of extreme weather events and plant diversity on performance of individual plant species in experimental communities (Figure 6 and 7). In the EVENT experiment, manipulations consist of recurrent 100-year extreme events, namely drought, heavy rain, and consecutive freeze–thaw cycles. We use rain-out shelters, portable irrigation systems, and buried heating wires. To avoid confounding effects of natural extreme events during the course of the experiment, we use two kinds of controls: ambient and historically-based. The first control represents ambient conditions, the second represents the mean weekly amount of precipitation over the past 30 years. The historical control is realized using

rain-out shelters, in which precipitation is artificially added. For each parameter, Gumbel I distributions were fitted to the annual extremes and 100-year recurrence events were calculated (Gumbel 1958). Additional manipulations of future climatic projections are based on data developed by the Max Planck Institute for Meteorology, according to a global change scenario (IPPC 2001).

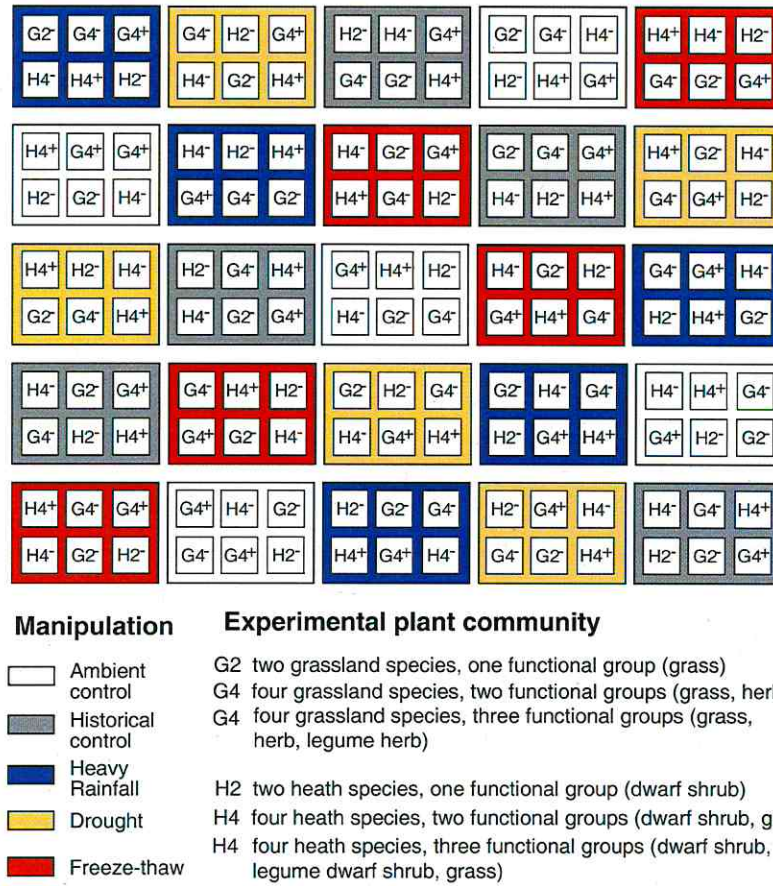


Figure 7: Design of the EVENT experiment. The manipulations consist of recurrent 100-year extreme events: (1) drought, (2) heavy rain, (3) consecutive freeze–thaw cycles, (4) ambient control, (5) historical control. The experimental plant communities represent different levels of functional and species diversity. $n = 5$ for each factorial combination, summing up to 150 plots of 2 m x 2 m.

The experimental plant communities ($n = 5$ for each factorial combination, summing up to 150 plots of 2 m x 2 m) consist of planted, equally-aged grassland and heath communities, representing different species richness levels (two or four species), different species compositions (six species combinations taken from a pool of 10 common species in each manipulation), different growth forms (perennial forbs, perennial grasses, or dwarf shrubs), and different abilities to fix atmospheric nitrogen (non-legume or legume). Species used are widespread in Central Europe and are of fundamental importance for agriculture and nature conservation (*Agrostis stolonifera*, *Arrhenatherum elatius*, *Calluna vulgaris*, *Deschampsia flexu-*

osa, *Genista tinctoria*, *Geranium pratense*, *Holcus lanatus*, *Lotus corniculatus*, *Plantago lanceolata*, and *Vaccinium myrtillus*). Current research activities stem from disciplines as disparate as community ecology, population biology, plant physiology, root ecology, invasion biology, soil fauna, microbiology, genomics, gas exchange analysis, hydrology, and micrometeorology.

Conclusions

We urgently need to advance research on extreme events and their consequences by collecting evidence on their effects from long-term observations and experimental studies in various ecosystems and on various time and magnitude scales. So far, the conceptual distinction between changing mean trends and modified event regimes has not been adequately acknowledged. The characteristics of a process can only be defined in relation to the organisms or systems being studied, and the extremeness only by statistics linked to the occurrences of the process itself. It is essential to take into account information on historical or projected extremes of simulated events (ie relative magnitude compared to mean conditions) though this is lacking in many event-based experiments. Otherwise, the predictive power of the results will be limited.

Event-based research on weather extremes will contribute substantially to the debate as to whether local weather extremes are relevant to the public and political community at large spatial scales and with long-term ecological impacts. Collaborative scientific efforts will contribute to our understanding of the role of biodiversity in the performance and resilience of vital ecosystem processes, goods, and services in the face of extreme climatic events.

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Manuscript 2:

Effects of extreme weather events on plant productivity and tissue die-back are modified by community composition

Ecosystems (accepted)

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Abstract

Extreme weather events are expected to increase in frequency and magnitude due to climate change. Their effects on vegetation are widely unknown. Here, experimental grassland and heath communities in Central Europe were exposed either to a simulated single drought or to a prolonged heavy rainfall event. The magnitude of manipulations imitated the local 100-year weather extreme according to extreme value statistics. Overall productivity of both plant communities remained stable in face of drought and heavy rainfall, despite significant effects on tissue die-back. Overall, grassland communities were more resistant against the extreme weather events than heath communities. Furthermore, effects of extreme weather events on community tissue die-back were modified by functional diversity, even though conclusiveness in this part is limited by the fact that only one species composition was available per diversity level within this case study. More diverse grassland communities exhibited less tissue die-back than less complex grassland communities. On the other side, more diverse heath communities were more vulnerable to extreme weather events compared to less complex heath communities. Furthermore, legumes did not effectively contribute to the buffering against extreme weather events in both vegetation types. Tissue die-back proved strong stress response in plant communities exposed to 100-year extreme weather events, even though one important ecosystem function, namely productivity, remained surprisingly stable in this experiment. Theories and concepts on biodiversity and ecosystem functioning (insurance hypothesis, redundancy hypothesis) may have to be adapted and modified when extreme weather conditions are considered.

Introduction

It is widely acknowledged that frequency and magnitude of extreme weather events will increase during ongoing global climate change (Easterling et al. 2000, Meehl et al. 2000, IPCC 2007). Changes in drought regime and heavy rainfall have already been reported for Europe according to climate data series (e.g. Beck et al. 2001, Schönwiese et al. 2003, Schmidli and Frei 2005), and are furthermore proposed from predictive modeling (e.g. Räsänen and Joelsson 2001, Christensen and Christensen 2003, Sanchez et al. 2004, Semmler and Jacob 2004). The effects of extreme weather events on vegetation and ecosystem functioning are likely much stronger than the effects of changes in mean values of temperature and precipitation (Easterling et al. 2000, Meehl et al. 2000). However, extreme weather events have not yet received much attention in vegetation related climate impact research (Jentsch et al. 2007). Furthermore, the few existing experimental studies on extreme weather events often lack details on magnitude or extremeness (Jentsch 2006) of applied manipulations relative to local mean conditions. Objectively choosing realistic extremeness and describing extremeness in relation to local conditions is crucial to allow for the identification of general mechanisms of ecosystem response to extreme weather events. Especially the insurance hypothesis (Yachi and Loreau 1999) and questions such as complementarity and redundancy (Naeem 1998) need to be re-addressed in this context.

We study the effects of drought and prolonged heavy rainfall in two vegetation types (grassland and heath) of different diversity levels. European grassland and heath communities are widespread, deliver economic value, provide many ecological services such as ground water recharge, and are important for nature conservation. As the species that contribute to these communities are widely distributed and common over large areas of Central Europe, the manipulations of weather extremes are likely to produce results that can be up-scaled to a large set of natural and semi-natural ecosystems.

Diversity and stability in face of extreme weather events

There is a long lasting debate whether the stability against environmental fluctuations is related to the diversity of communities (summary in Beierkuhnlein and Jentsch 2005). During the last decade, theories like the insurance hypothesis (Yachi and Loreau 1999) were generated. This theoretical concept 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 at the higher predictability of diverse communities and Naeem (1998) stresses that in face of sudden changes, high diversity increases the “reliabil-

ity” of communities. We test these ideas in connection with ongoing climate change. Accordingly, we propose that communities containing more species and growth forms are more stable in terms of aboveground productivity in face of extreme weather conditions.

Legume effect

In biodiversity experiments, facilitation of ecosystem functioning by legumes was found (Spehn et al. 2002, Beierkuhnlein and Nesshoever 2006). Mainly the presence of legumes resulted in a higher productivity of communities via increased nitrogen availability. In most temperate ecosystems, available soil nitrogen is a limiting factor for plant growth. An increased supply of nitrogen can promote the tolerance against other stressors (Larcher, 2003). Therefore we expect that communities containing legumes are more stable in productivity and stress response after experimentally applied extreme weather events than communities only including non-legumes.

Differences in vegetation types – grassland versus heath

In temperate grasslands, evidence suggests that drought events cause reduced biomass productivity (Sternberg et al. 1999, Grime et al. 2000, Kahmen et al. 2005), reduced reproductive success (Fox et al. 1999, Morecroft et al. 2004), and ultimately result in alterations of species composition (Grime et al. 2000, Buckland et al. 2001). Heavy rainfall events have received considerably less interest, even in well studied vegetation types such as temperate grasslands. It has been reported from a North American prairie, though, that heavy rainfall events, combined with elongated drought periods in between, are more effective in decreasing productivity and changing species composition than an overall decrease in precipitation by 30% (Fay et al. 2002, Knapp et al. 2002). However, compared with simulated extreme heat, one brief extreme rainfall resulted only in slight changes of species composition in New Zealand grassland communities (White et al. 2000).

European heath systems have also been found to show sensitive responses to extreme weather conditions. Heathland reacts to drought with decreased productivity (Gordon et al. 1999, Filella et al. 2004, Llorens et al. 2004, Penuelas et al. 2004), reduced reproductive success (Gordon et al. 1999, Lloret et al. 2004, Llorens and Penuelas 2005), and ultimately with changes in species composition (Lloret et al. 2005).

These findings suggest that both grassland and heath would respond similarly to extreme weather events. This is remarkable, because grassland and heath communities are composed of different species with very different functional traits such as e.g. mean life span or lignification of the predominant species. Differing from grasses, dwarf shrubs do not die back

completely over winter and can more effectively control transpiration rates. On the other hand, grasses are known to perform only weak stomata control.

Therefore, we suppose that grassland productivity is resilient in face of the applied weather manipulations, while heath productivity is resistant. Here, resilience shall be defined as the ability of a system to absorb a disturbance event and return to pre-disturbance characteristics after a short period of time, while resistance shall be defined as the ability of a system to remain almost unaffected (compare Grimm and Wissel 1997). This notion of grassland productivity being resilient and heath productivity being resistant thus implies higher vulnerability of grassland to extreme weather events in the short run.

Contrasting extreme weather events and community response

Drought and prolonged heavy rainfall are expected to affect plants via modified soil moisture. Water shortage leads to a decline in water potential and to water stress. In contrast, excess of water in soil pores creates oxygen deficits and produces a reducing milieu in the soil which is connected with effects on nutrient availability. The lack of oxygen can cause substantial short term fine root mortality, even though species reactions differ considerably (Crawford and Braendle 1996). Both mechanisms are capable of killing plants and of destroying whole systems if exceeding certain magnitudes. As both extreme events, drought and heavy rainfall, generate highly stressful conditions, we hypothesize that this may lead to comparable effects on plant communities and ecosystem functions.

Our objectives are to test (a) whether community composition, namely plant species richness and functional richness, is an important driver of system performance after extreme weather events, (b) whether legumes contribute to buffering the impact of extreme events on productivity and tissue die-back, (c) whether different vegetation types are affected comparably by extreme events, and (d) whether contrasting weather extremes cause similar effects on plant communities.

Materials and methods

Experimental Design

The field experiment (EVENT-experiment, Jentsch et al. 2007) was carried out in a three-factorial design manipulating (1) weather events (drought, heavy rainfall, control), and (2) vegetation type and (3) diversity level (Table 1). The design consisted of 90 plots, each two by two meters in size, with every factorial combination replicated five times. Experimental plant communities (vegetation type x diversity level) were blocked and randomly assigned within each weather manipulation. Original species composition was maintained by periodical weeding. Prior to the experiment an area of 50 m by 70 m was prepared with homogenized substrate (about 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 (measured in 1M KCl). Data acquisition was carried out in the central square meter of each plot only, in order to circumvent edge effects. The experiment is located in the Ecological-Botanical Garden of the University of Bayreuth, Germany (49°55'19"N, 11°34'55"E, 365 m asl). Mean annual temperature is 7.8°C; mean annual precipitation 709 mm (Data: German Weather Service). Usually, annual precipitation is distributed bi-modally with a major peak during June/ July and a second peak during December/ January.

Table 1: Experimental plant communities of two vegetation types (grassland, heath) were used in three functional diversity levels, resulting in six species combinations. Abbreviations: G: grassland, H: heath, 2/4: number of species, -: without legume, +: with legume.

Abbreviation	vegetation type	diversity level	Description	Species
G2 ⁻	grassland	1	two species, one functional group (grass)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i>
G4 ⁻	grassland	2	four species, two functional groups (grass, herb)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i> , <i>Plantago lanceolata</i> , <i>Geranium pratense</i>
G4 ⁺	grassland	3	four species, three functional groups (grass, herb, legume herb)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i> , <i>Plantago lanceolata</i> , <i>Lotus corniculatus</i>
H2 ⁻	heath	1	two species, one functional group (dwarf shrub)	<i>Calluna vulgaris</i> , <i>Vaccinium myrtillus</i>
H4 ⁻	heath	2	four species, two functional groups (dwarf shrub, grass)	<i>Calluna vulgaris</i> , <i>Vaccinium myrtillus</i> , <i>Agrostis stolonifera</i> , <i>Deschampsia flexuosa</i>
H4 ⁺	heath	3	four species, three functional groups (dwarf shrub, legume shrub, grass)	<i>Genista tinctoria</i> , <i>Vaccinium myrtillus</i> , <i>Agrostis stolonifera</i> , <i>Deschampsia flexuosa</i>

Factor 1: extreme weather events

The weather manipulations consisted of extreme drought, prolonged heavy rainfall and ambient conditions for control. Intensity of the treatments was based on the local 100-year extreme event in each category, i.e., we used a defined extremeness of weather events to measure ecological response, because we were interested if ecological response to the same weather event will differ between different plant communities. Vegetation periods (March to September) 1961-2000 were used as the reference period (data: German Weather Service). Gumbel I distributions were fitted to the annual extremes, and 100-year recurrence events were calculated (Gumbel 1958). Drought was defined as the number of consecutive days with less than 1 mm daily precipitation. Accordingly, a drought period of 32 days and a rainfall extreme of 170 mm over 14 days were applied in the experiment during peak growing season in June 2005 (drought manipulation: Days of the year 160-191; heavy rainfall manipulation: 178-191). Maximum values in the historical data set were 33 days without rain during June and July 1976 and 152 mm of precipitation during 14 days in June 1977.

Drought was simulated using rain-out shelters, constructed with a steel frame (Hochtunnel, E & R Stolte GmbH, Germany) and covered with transparent plastic sheet (material: 0.2mm polyethylene, SPR 5, Hermann Meyer KG, Germany), that permitted nearly 90 % penetration of photosynthetically active radiation. Near-surface air temperature was slightly (mean + 1.2°C), but not significantly (pairwise t-test with Bonferroni correction: $p = 0.12$), increased by the roofs during the weather manipulation period. Strong greenhouse effects were avoided by starting the roof at 80 cm height, allowing for near-surface air exchange.

Heavy rainfall was realized using portable irrigation systems. Drop size and rainfall intensity resembled natural heavy rainfall events through application by Veejet 80100 nozzles, commonly used in erosion research (Kehl et al. 2005). At 0.3 bar water pressure this system resulted in 2.8 mm water per minute. The whole amount of added water was divided into two applications per day to constantly ensure high soil water saturation. If natural precipitation occurred, then the amount of rain was subtracted from the respective dose. Lateral surface flow was avoided by the application of small plastic sheet pilings around treated plots.

Factor 2: Experimental plant communities

Overall, ten plant species were used to install artificial plant communities, which nevertheless represent naturally occurring species combinations in Germany. Species were chosen with respect to their belonging to one of the desired functional groups (grasses, herbs,

legumes, dwarf shrubs), to their life-span (perennials), to their overall importance in nearby and central European grassland and heath systems, and to the fact that they can naturally occur on similar substrate. 100 plant individuals per plot were planted in a systematic hexagonal grid with 20 cm distance between neighbors in early April (Day of the year 92) from pre grown individuals acclimated on site since February 2005. Communities were planted in three diversity levels for both vegetation types, resulting in six species combinations (Table 1). Please note that only one species composition was used per diversity level and vegetation type. However, 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).

Data acquisition - Response parameters

Aboveground Net Primary Productivity (ANPP) had to be quantified in different ways in the grassland and heath communities. For the grassland plots, aboveground harvests were conducted twice a year (one week after weather manipulations ended, Day of the year 200; and in September, Day of the year 255), resembling local agricultural routines. ANPP was calculated by subtracting the initial biomass at planting from the sum of biomass over both harvests. Initial biomass was obtained by destructive measurements of 10 representative individuals per species prior to planting. The resulting mean biomass was multiplied by the number of planted individuals per plot. For the heath plots, destructive sampling was not feasible due to the absence of such a disturbance in their natural environments and the chamaephytic life form of the key species. Instead, a set of non-destructive biometric measures were calibrated by multiple regression analysis against harvested individuals from outside the central plots, but inside the weather manipulations. For each species, a coefficient of correlation of $r^2 > 0.8$ was reached by a combination of two or three biometric measures.

Tissue die-back was quantified by cover measurements of standing-dead plant organs. A pin-point method was applied, recording the presence of plant organs in general and the

presence for each species separately at 100 vertically inserted steel needles. These values were treated as percent cover. The measurement was repeated four times over the course of the vegetation period.

Soil moisture was monitored over the growing period by weekly readings with a TDR tube access probe (Diviner 2000, Sentek) at 5, 12, 20, 28 cm soil depth in every plot. Near surface air temperature was logged continuously in 10 minutes intervals in the G4 communities of the drought and control treatments using thermistores (B57863-S302-F40, EPCOS).

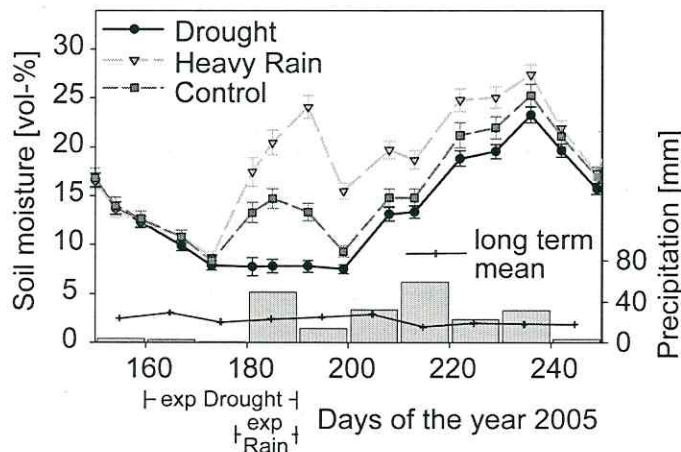


Figure 1: Soil moisture [% volume] at 12.5 cm depth varies significantly for the simulation of extreme weather events (left axis). Repeated measures ANOVA show differences (Greenhouse-Geisser) for the interaction with time between control and drought ($p = 0.000$, $F = 28.4$) as well as control and heavy rainfall ($p = 0.000$, $F = 39.1$). Soil moisture was measured by TDR tube access probe. As no differences for the experimental plant communities were detected, they were merged together. Mean values and standard errors are shown, $n = 3 \times 30$. Grey bars show natural precipitation sums for 10 day periods, measured on site by an automatic tipping bucket system (right axis), in comparison with the long term mean precipitation 1961-2000 (data: German Weather Service, Station Bayreuth). exp. drought = experimental drought manipulation, exp. rain = experimental heavy rainfall event.

Data analysis

It was tested for significant differences between groups by Analysis of Variance (ANOVA). Homogeneous groups of factor combinations (weather manipulation, vegetation type, and diversity level) were identified by Tukey HSD post hoc comparison. Repeated measure ANOVA's were used for measurements repeated over time (e.g. tissue die-back). Prior to statistical analysis, data were log or square root transformed, if conditions of normality were not met or to improve homogeneity of variances. Both characteristics were tested by examining pp-qq plots (Sachs 2004). All statistical analyses were performed using SPSS 12.0 for Windows.

Results

Effectiveness of weather manipulations on soil moisture availability

Soil moisture content displayed the effectiveness of applied weather manipulations (Figure 1). Dry conditions before the beginning of the drought manipulation (only 4 mm of precipitation in the 15 days before manipulation onset) had already led to a minimum in soil water content. During the drought treatment, soil water content remained at this minimum, thus differing from control. During rainfall treatment, it took nearly two weeks until soil moisture had reached its maximum.

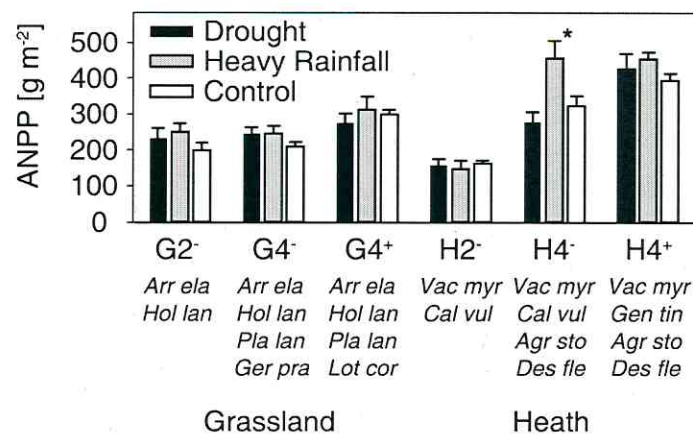


Figure 2: Effects of weather manipulations on community aboveground net primary productivity (ANPP) are small. Significant deviations from control within each experimental plant community are marked with an asterisk (ANOVA, Tukey's post hoc comparison, $p < 0.05$). Shown are mean values and standard errors over five replications of the biomass gain between Day of the year 92 (planting date) and 255. For the grassland communities, two destructive harvests were conducted (Day of the year 200 and 255). Regressions with non-destructive, biometric measurements, validated outside the plots, were used in the heath-plots. Abbreviations of the respective species names are provided below the graph.

General effects of weather extremes on ANPP and tissue die-back

Overall, simulated drought and prolonged heavy rainfall had no significant effect on community aboveground net primary productivity (ANPP), except in the heath community composed of grasses and dwarf shrubs (H4⁺, Figure 2). Here, heavy rainfall resulted in an increase in ANPP compared to control. The increase in biomass was due to the performance of one grass species, namely *Agrostis stolonifera* (Figure 3), which is known to profit from increased soil moisture. Two other species showed significant alterations in ANPP, *Vaccinium myrtillus* which decreased and *Geranium pratense* which increased ANPP after drought. An interesting, even though not significant finding is that all species in grassland communities

(G2⁻, G4⁻) increased in ANPP, whereas almost all species in heath communities (H2⁻, H4⁻) decreased in ANPP (Figure 3).

Community plant tissue die-back, recorded as cover percentage of dead fiber, is used here to express stress response. In the grassland communities, die-back rates were significantly higher after both drought and heavy rainfall as compared to control. In heath communities, die-back rates were only increased after drought (Figure 4, Table 2). After drought, five species showed significant negative stress response, four of them in heath communities (Figure 5).

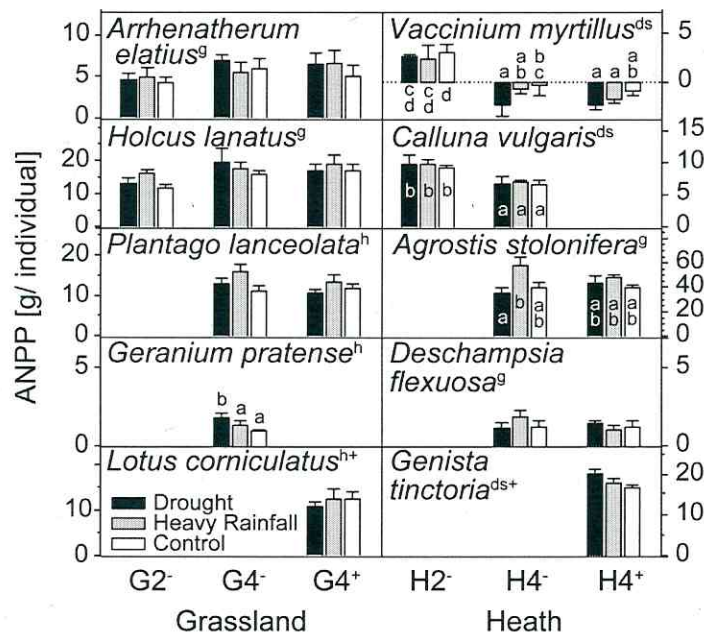


Figure 3: Mean species-specific aboveground net primary productivity (ANPP) per planted individual after planting date (Day of the year 92). Grassland plots (species on the left side) were harvested twice (Day of the year 200 and 255). ANPP of heath plots (species on the right side) was determined by correlations of non-destructive biometric measurements, validated against destructively harvested control plants outside the plots. Homogeneous groups according to Tukey HSD post-hoc comparison are indicated by letters (a, b, c, d) only if significant effects of weather manipulation and community composition occurred (ANOVA, $p < 0.05$). Mean values and standard errors of five replications are shown. ^g: grass, ^h: herb, ^{ds}: dwarf shrub; ⁺: legume. **G**: Grassland, **H**: Heath. **2**⁻: two species, one growth form; **4**⁻: four species, two growth forms, and **4**⁺: four species, two growth forms containing legumes.

Table 2: Mean tissue die-back due to simulated extreme weather events in the experimental plant communities over the growing season. Repeated measures ANOVA revealed a significant interaction between time, experimental plant community and manipulation (Greenhouse-Geisser: $p = 0.002$; $F = 8.2$). Significant treatment effects within one experimental plant community were evaluated in a pair-wise rmANOVA between one weather manipulation and control. Note that in the grassland communities aboveground biomass was harvested twice (Day of the year 200 and 255). **G:** Grassland, **H:** Heath. **2:** two species, one growth form; **4:** four species, two growth forms, and **4⁺:** four species, two growth forms containing legumes. Displayed are mean values over five replications.

Tissue die-back		Day of the year				p (F) vs. control
[% cover]		166	195	234	252	
G2⁻	Drought	0.0	20.0	2.0	4.8	0.006 (10.7)
	Heavy Rain	0.0	16.0	5.0	3.2	0.046 (4.1)
	Control	0.0	5.4	1.4	2.2	
G4⁻	Drought	0.0	14.0	2.0	3.6	0.031 (3.9)
	Heavy Rain	0.0	11.8	5.8	2.8	0.044 (3.2)
	Control	0.0	6.4	0.0	1.8	
G4⁺	Drought	0.0	11.4	3.0	1.8	0.041 (3.9)
	Heavy Rain	0.0	9.2	4.6	1.0	0.179 (1.8)
	Control	0.0	4.2	4.2	0.6	
H2⁻	Drought	0.0	1.8	0.4	1.2	0.029 (3.8)
	Heavy Rain	0.0	0.6	0.8	0.2	0.386 (1.0)
	Control	0.0	0.0	0.6	0.0	
H4⁻	Drought	0.0	12.8	6.0	4.0	0.035 (5.8)
	Heavy Rain	0.0	3.8	0.6	1.2	0.800 (2.7)
	Control	0.0	5.2	1.6	1.6	
H4⁺	Drought	0.0	12.2	6.0	5.8	0.011 (7.4)
	Heavy Rain	0.0	5.6	0.8	0.6	0.170 (2.2)
	Control	0.0	4.6	1.6	2.8	

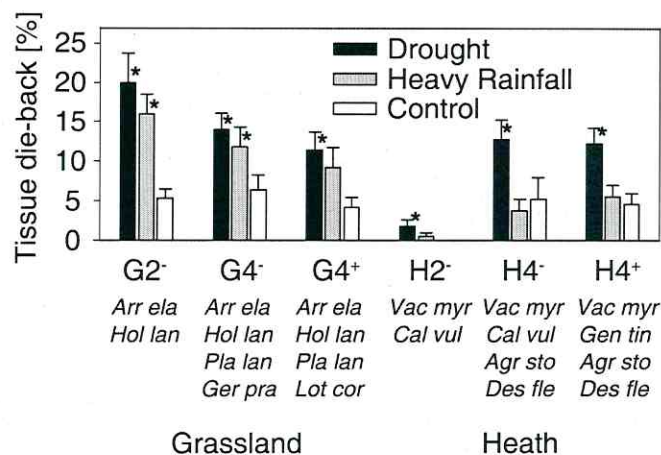


Figure 4: Tissue die-back due to simulated extreme weather events in the experimental plant communities one week after the extreme weather manipulations ended (Day of the year 195). Asterisks indicate significant differences between weather manipulation and control within each experimental plant community ($p < 0.05$, see Tab. 1). **G:** Grassland, **H:** Heath. **2:** two species, one growth form; **4:** four species, two growth forms, and **4⁺:** four species, two growth forms containing legumes. Displayed are mean values and standard errors over five replications.

Diversity and stability in face of extreme weather events

Based on our hypothesis, we expected community resistance in productivity to be a function of functional diversity, i.e. $2^- < 4^- < 4^+$ communities. In addition to the lack of any significant weather manipulation effect on community ANPP in the grassland plots, no significant differences were found between functional diversity levels within each weather manipulation, even though a trend towards increasing community productivity with increasing diversity seems to exist (Figure 2). Community productivity of heath communities followed the sequence $2^- < 4^- < 4^+$ with significant differences in community ANPP between all diversity levels in the drought manipulation. Also, less productivity for $H2^-$, but no significant difference between $H4^-$ and $H4^+$, was recorded after heavy rainfall. However, significant differences between all diversity levels were also found for control, and no significant interaction between extreme weather events and functional diversity levels was found.

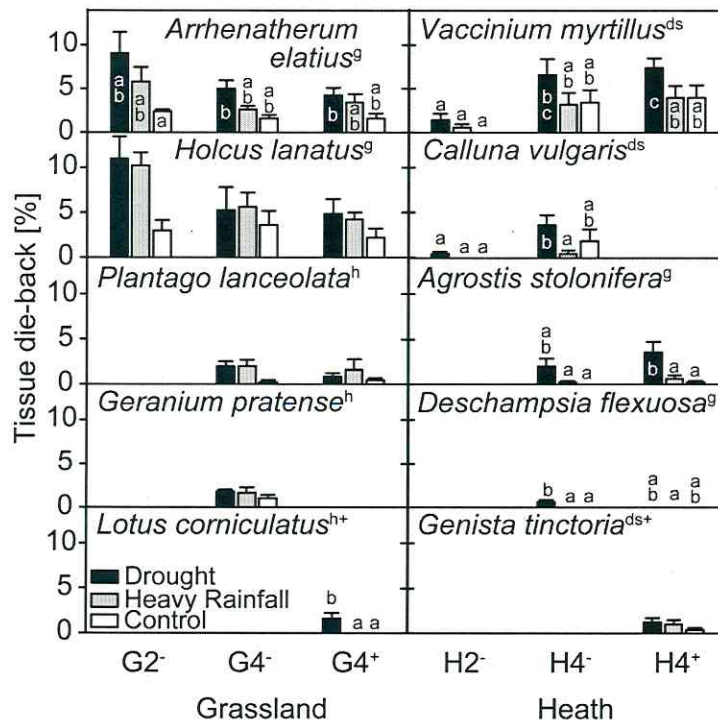


Figure 5: Species-specific tissue die-back one week after the extreme weather manipulations ended (Day of the year 195). Shown are mean values and standard errors measured by pinpoint method with 100 needles per plot. Homogeneous groups according to Tukey HSD post-hoc comparison are indicated by letters (a, b, c, d) only when significant effects of weather manipulation and community composition occurred (ANOVA, $p < 0.05$). Mean values and standard errors of five replications are shown. ^g: grass, ^h: herb, ^{ds}: dwarf shrub, ⁺: legume. **G**: Grassland, **H**: Heath. **2**⁻: two species, one growth form; **4**⁻: four species, two growth forms, and **4**⁺: four species, two growth forms containing legumes.

The missing insurance effect might also have been related to the additional species themselves in the more diverse communities (sampling effect). Therefore, it is important to look at the stress response of particular species in different communities. Significant effects on species ANPP were found only for two dwarf shrubs, namely *Vaccinium myrtillus* and *Calluna vulgaris* (Figure 3). Interestingly, performance of both species compared in different diversity levels was in contrast to the hypothesized sequence: they produced less biomass per planted individual in the more diverse communities. This phenomenon even increased with increasing diversity after drought compared to control.

The two vegetation types showed oppositely directed diversity effects compared to each other for community tissue die-back (Figure 4). Nearly no effect of weather extremes for heath communities composed of dwarf shrubs only (H2⁻) contrasted strongly with severe effects in communities composed of dwarf shrubs and grasses (H4⁻) after drought. Thus, the effect size increased with increasing diversity in heath communities after drought compared to control. Grassland communities showed the opposite response. The highest stress values occurred in communities composed of grasses only (G2⁻), whereas presence of herbs tended to attenuate the effect size.

Legume effect

Community ANPP showed no significant effect of extreme weather manipulation between communities with legumes (4⁺) and without legumes (4⁻). For the comparison between heavy rainfall and control, grassland community die-back rates were significantly increased without presence of a nitrogen-fixing species, and no longer significantly increased with a nitrogen-fixing species present. However, this effect seems to be small (Figure 4), and no other reaction supported the hypothesis of increased community stability due to legume presence.

Differences in vegetation types – grassland versus heath

Community ANPP was not affected by drought in any of the two vegetation types, and it increased after heavy rainfall in one heath community (Figure 2). Community tissue die-back rates revealed strong reactions of grassland communities to both extremes and of heath communities only to drought. By examining the significant species-specific die-back rates (Figure 5), however, grassland communities appeared to be slightly more tolerant with increased tissue die-back of only one species compared to increased tissue die-back of three species in the heath communities.

Contrasting extreme events and community response

Drought and heavy rainfall increased the amount of tissue die-back nearly equally in grassland plots (Figure 4). Differing from this, only drought caused similar reactions in the heath communities. Compared to each other, more significant species-specific effects are found after drought than after heavy rainfall in our experiment (5 versus 2).

Discussion

General effects of weather extremes on ANPP and tissue die-back

In our experiment, effects were moderate and communities appeared to be relatively stable in face of extreme weather events with a recurrence of 100 years. Remarkably, no species was driven to lethal reactions by the extreme weather manipulations. This supports the assumption that the chosen intensities can be tolerated by the species but may influence their performance at the community level. These changes might be driven by direct plant reactions to the applied weather manipulations or through indirect effects. E.g., effects of drought and water on plant growth can also be translated through changes in soil and microbial processes (Emmett et al. 2004). Such indirect effects are important to study in order to obtain a mechanistic understanding on the effects of extreme weather events.

Experimental weather manipulations resulted in an immediate severe reduction in productivity due to a single simulated drought in a study by Kahmen *et al.* (2005), but this can be explained by the more extreme manipulation (60 % longer rain-free period compared to this study in a comparable environment). This fact emphasizes the importance of reporting effects of extreme events relative to local mean conditions. Comparably small reactions are found in other experiments during the first year, too (Fay et al. 2000, Gorissen et al. 2004). In these experiments, effects became much more obvious after repeated weather manipulations. However, such an increase in recurrence describes another, undeniably important dimension of climate change, nevertheless leading away from the study of single events, which was the focus of our study. Our results imply that a single local 100-year extreme drought or prolonged heavy rainfall event can be tolerated by the studied vegetation types without adverse effects on productivity, despite high stress levels, which are indicated by significant tissue die-back. However, the significant reactions by single species might be capable of changing community compositions in the long term, probably leading to even more stable communities in the face of recurrent disturbance events of the same kind as the more tolerant species become more dominant.

Diversity and stability in face of extreme weather events

Looking at community tissue die-back (Figure 4), an insurance effect (McNaughton 1977, Yachi and Loreau 1999) through shift of performance between species or functional groups occurred in grassland communities. This increase in stability with increasing diversity, however, was even inverted in the heath communities. Although limited to one species composition per diversity level, it is interesting that the insurance hypothesis seems to be supported only in the grassland communities, where it was originally invented and subsequently tested. Negative effects on community parameters such as tissue die-back confuse some positive reactions of single species (e.g. *G. pratense* biomass increase after drought). As many as eight out of 19 significant species reactions were positive. This shows that single extreme events can already alter competitive pressure on particular species. Stability in terms of productivity of single species in face of disturbance events has been shown elsewhere to be influenced by community diversity (Greenlee and Callaway 1996, Callaway and Walker 1997, Kikvidze et al. 2006). The interplay between positive and negative interactions (facilitation versus competition) is expected to drive such changes in stability of species performances. Furthermore, the presence of changes in both directions at the species level together with no effects at the community level illustrates that stability at a higher level of organization may require overcoming stability at lower levels (Berkes et al. 2003). Shifts in different directions at the species level can therefore be viewed as integral part of the stability at the community level.

Legume effect

Facilitation by legumes, found in diversity experiments where biomass production is addressed as a key function (Spehn et al. 2002), could not be proven to have significant buffering effect against the applied weather events with respect to ANPP and tissue die-back in grassland and heath communities. However, species combinations integrating legumes produced the highest amounts of aboveground biomass in both vegetation types, irrespective of weather manipulations. Species-specific reactions indicated a higher susceptibility to extreme weather events if legumes were present, especially after drought. Negative effects of increased nitrogen availability on ecosystem functioning are also reported from other systems during periods of water stress. Nitrogen-fertilization makes vine plants more susceptible to drought due to decreased root to shoot ratio (Keller 2005). *Populus* species are also found to be more vulnerable to xylem cavitation due to water stress after high concentrations of nitrogen in the soil (Harvey and van den Driessche 1999).

Differences in vegetation types – grassland versus heath

The short literature review in the introduction suggested similar reactions to drought events for both vegetation types. Heavy rainfall has not yet been considered nearly as extensively as drought, rendering a literature comparison of both vegetation types with respect to this aspect impossible. We argued that the similarity between two such contrasting vegetation types might only be due to the fact that the experiments so far are not comparable in their manipulation magnitudes.

In our experiment, grassland and heath communities reacted differently to the weather manipulations. Overall, grassland remained surprisingly stable. More significant effects of weather manipulations were found in heath species, especially in the dwarf shrubs. These differences cannot be explained by the different treatments in terms of cutting twice only the grassland and not the heath communities. Even though this point complicates direct comparisons between the two vegetation types, our results indicate that vegetation types in their natural disturbance regimes differ in their reactions to extreme weather events.

The different reactions between both vegetation types can probably be explained by the contrasting life strategies of their dominant functional types. Nevertheless, it is surprising that dwarf-shrub communities with their rather conservative life strategies (longevity, lignification) are more strongly affected than grasses which are known to have a high turnover rate, exploit resources fast and die back when resource availability is limited until the conditions become favorable again. Competitive strength may be an explanation for the observed differences between grasses and dwarf shrubs. Strong competitors could be facilitated as their neighbor's mean competitive power decreases with increasing diversity. This would ultimately result in positive diversity effects only for strong competitors.

However, strong aboveground tissue die-back by the dwarf shrubs could also be interpreted as a hint of resource allocation to the root systems. This could indicate stress-induced adaptation and lead to higher stability against future recurrence of extreme events.

Contrasting extreme events and community response

As we used the same extremeness for both weather manipulations (statistical 100-year recurrence event), we find that our grassland and heath communities are more vulnerable to drought than to prolonged heavy rainfall events. However, this might partially be explained by the dry conditions before the onset of the drought manipulation (Figure 1). Under these conditions, excess of water did not immediately lead to soil saturation. Additionally, natural conditions during heavy rainfall manipulation were rather wet in relation to the long term

mean, resulting in less severe conditions in the heavy rainfall manipulation compared to control than expected beforehand. Ultimately, studies dealing with extreme weather events would benefit from a control simulating long-term mean conditions. Furthermore, upcoming changes in magnitude will probably not be parallel for both event regimes. Even if increasing temperatures will generally be accompanied with increased precipitation, the likelihood for strong drought effects may be higher at the landscape scale, and drought periods will occur with less spatial variability, whereas strong effects of prolonged heavy rainfall will be most likely restricted to places that do not allow for surface runoff.

Conclusions

One important ecosystem function, productivity, remained surprisingly stable in plant communities exposed to the chosen 100-year extreme weather events. The applied weather manipulations do not cover drought and heavy rainfall completely, other factors like the minimum amount of rainfall over longer time periods rather than the time without any precipitation, or the recurrence and timing of such events are worth studying as well. Nevertheless, tissue die-back proved strong stress response to the chosen weather manipulations. This response was modified by species composition or functional diversity, even though diversity levels used here are low. Interestingly, only grassland appeared to be stabilized against extreme weather events by increasing functional diversity, whereas heath communities were even more adversely affected in more diverse communities.

These findings pose new challenges to theories and concepts of biodiversity and ecosystem functioning. For extreme weather events, we show that the insurance hypothesis or buffering effects by legumes do not generally apply. Our case study shows that effects can be opposite to expectations. Especially, contrasting responses of different vegetation types need to be considered in more detail. Under this light, the diversity – stability debate attracts attention again. Mechanisms of coexistence and ecosystem functioning such as above-average effects of dominant species (sampling effect hypothesis), resource-use partitioning and complementarity gain current importance in the face of dramatically changing environments. In order to quantify upcoming changes in ecosystems under these circumstances, it is an urgent question, whether functional response types are adequate tools or whether species specific reactions have to be considered. In this context, the redundancy hypothesis needs to be revisited.

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Manuscript 3:

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

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Summary

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 carbon 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 CO₂ Exchange (NEE in $\mu\text{mol m}^{-2} \text{s}^{-1}$), as well as above-ground 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 CO₂ 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, above-ground 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 be-

tween reproductive and vegetative growth. The heavy rainfall manipulation resulted in no significant effects. Our data suggests that carbon 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.

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.

Grassland ecosystems comprise about one fifth of the earth's land surface and contain more than 10% of the global carbon stocks (*Eswaran et al.*, 1993). Carbon dioxide flux measurements have shown grasslands to be a net sink for atmospheric CO₂, and have also shown that rising CO₂ levels generally improve carbon sequestration in grassland ecosystems (see review by *Jones and Donnelly*, 2004). However, it is still unclear if global warming will turn grasslands into CO₂ 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 & Jackson* (2000) concluded from a gradient study that soil organic carbon decreases with increasing temperature and increases with higher rainfall. From satellite data it has been shown that reduced summer CO₂ 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 CO₂ growing-season 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 CO₂ 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 carbon uptake into a grassland system was, in contrast, reported from Ireland during a dry year; although even the dry year did not pose severe water stress to the plants (*Jaksic et al.*, 2006). Similarly, higher carbon 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 (*Chimner and Welker*, 2005). Contrary to these studies which indicate a net CO₂ 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 CO₂ 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 carbon fluxes and is further demonstrated by the finding that doubled precipitation can also increase soil CO₂ efflux in a tallgrass prairie (*Zhou et al.*, 2006). To sum up these findings, drought seems to limit CO₂ uptake in grassland ecosystems, but whether this ultimately results in carbon emission or sequestration is still unclear.

Global loss of plant species diversity is another factor capable of substantially altering ecosystem carbon fluxes and therefore could potentially modify the global carbon cycle (*Koch and Mooney*, 1996). There is experimental evidence that above-ground 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 CO₂ 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 carbon sequestration under climate change. In short, the presence of legumes tends to increase the carbon sink strength, at least under enhanced CO₂ conditions (*Soussana and Hartwig*, 1996; *Koerner*, 2003). The interaction of diversity with climate may therefore play an important role in carbon allocation to the soil, as it is found to increase in

functionally diverse communities under drought, as well as when CO₂ 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 carbon uptake and biomass production. We also expect (2) higher carbon 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 x 2 m in size. Original species composition was maintained by periodical weeding. Prior to the experiment an area of 50 m by 70 m was prepared with homogenized substrate (about 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)

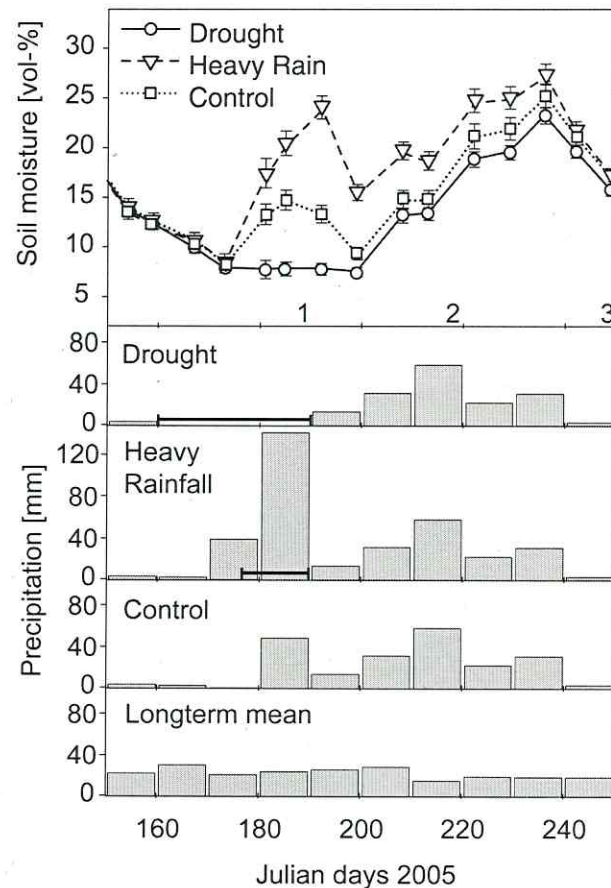
Manipulations consisted of extreme drought, heavy rainfall and control. The magnitude of manipulations was chosen according to the local 100-year extreme event in each category. Growing periods (March to September) 1961-2000 were used as a reference period (data: German Weather Service). For this time 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 days and a heavy rainfall event of 170 mm over 14 days were applied in the experiment during peak growing season in early summer 2005 (drought: June 9 - July 10; heavy rainfall: June 27 - July 10). The maximum values in the historical data set were 33 days without rain during June and July 1976 and 152 mm over 14 days in June 1977.

Drought was simulated using rain-out shelters, constructed with a steel frame and covered with transparent foil that permitted nearly 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 Figure 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 (Figure 1).

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 bio-mass harvests (1: June, 2: July, 3: September). Grey bars show precipitation sums over 10 day 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 horizontal bars.



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). 100 plant individuals per plot were planted in a systematic hexagonal grid with 20 cm distance between neighbors in early April (April 2) from pre grown 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 nitrogen 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*).

2.3 Data acquisition

Net Ecosystem Exchange (NEE) was measured using closed-dynamic ecosystem chambers, where NEE was calculated by CO₂ concentration changes over time measured with an infra-red gas analyzer (IRGA) connected by flexible inflow and outflow tubes to the chamber. CO₂ flux was measured over three campaigns in summer 2005 (June 6 - July 6, July 13 - August 5, August 30 - September 15). In each campaign measurements were taken for approximately 10 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 by 39 cm by 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 carbon sequestration due to their influence on many micro-climatological 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 carbon sequestration rates.

Following the flux measurement, above-ground 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 above-ground biomass.

2.4 Data processing

Light response curves depicting the Net Ecosystem Exchange 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 ($\mu\text{mol m}^{-2} \text{s}^{-1}$),

β is the maximum CO_2 uptake rate of the canopy ($\mu\text{mol m}^{-2} \text{s}^{-1}$),

Q is the photosynthetically active radiation (PAR, in $\mu\text{mol m}^{-2} \text{s}^{-1}$),

γ is an approximation of the average daytime ecosystem respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$)

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 (Table 1). An approximation of maximum canopy uptake capacity was calculated as:

$$\text{GPP}_{\text{max}} = \text{NEE}_{2000} - \text{R}_{\text{eco}}$$

Where:

NEE_{2000} is the Net Ecosystem Exchange at a high light intensity (here: $\text{PAR} = 2000 \mu\text{mol m}^{-2} \text{s}^{-1}$)

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 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 1000 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 examin-

ing 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: $p < 0.05$; Figure 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.

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 ($\mu\text{mol m}^{-2} \text{s}^{-1}$), β is the maximum CO_2 uptake rate of the canopy ($\mu\text{mol m}^{-2} \text{s}^{-1}$), γ is the average daytime ecosystem respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$).

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

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

Above-ground biomass production did not show significant reactions to the applied extreme weather manipulations (simplified mixed model: $p > 0.05$; Figure 4a). However, Leaf Area Index was 39 % higher in the drought manipulation as compared to the control over time (simplified mixed model: $p < 0.05$; Figure 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 significant after the end of the manipulation (Figure 4c). Averaged over all three time steps, the ratio between reproductive and vegetative biomass decreased by 57% in the drought manipulated plots.

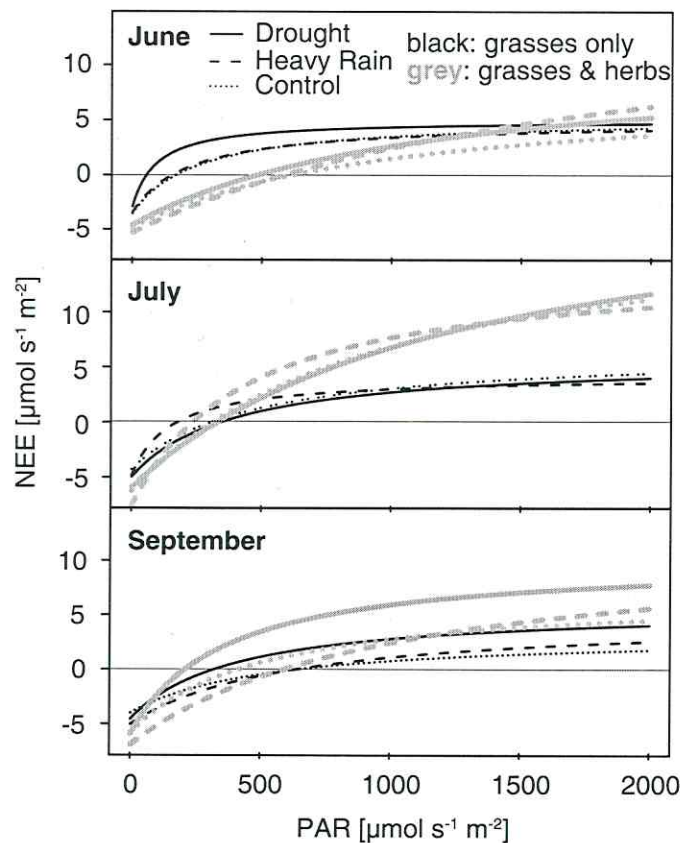


Figure 2: Light response curves of Net Ecosystem Exchange (NEE) in experimental grassland communities of two diversity levels during and after simulation of extreme weather events as a function of Photosynthetically Active Radiation (PAR). Weather manipulations took place in June. Significant effects were found for drought in parameter α and β , and for diversity level in parameter β and γ according to Mixed Models ($p < 0.05$).

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 CO₂ 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: $p < 0.05$; Figure 3). Above-ground biomass production and LAI were consistently higher in the more diverse community (for both parameters mixed models: $p < 0.05$; Figure 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.

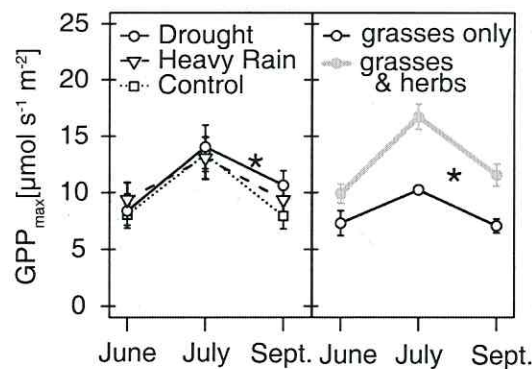


Figure 3: Maximum uptake capacity (GPP_{max}) over time in experimental grassland communities separated by weather manipulations (left) and species composition (right). Weather manipulations took place in June 2005. No significant interaction between weather manipulations and species composition was 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.

4 Discussion

4.1 Carbon fluxes and productivity as affected by extreme weather events

The drought event altered carbon fluxes in the grassland systems without significant change to above-ground biomass production. GPP_{max} and the uptake capacity were increased following the drought (increased values for α , β) without changes in respiration term (γ), thus indicating a net carbon uptake into the system. This increase in photosynthesis can be explained by a higher Leaf Area Index after drought compared to control. The increase in LAI is correlated with a shift in above-ground 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.* (in press) 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.

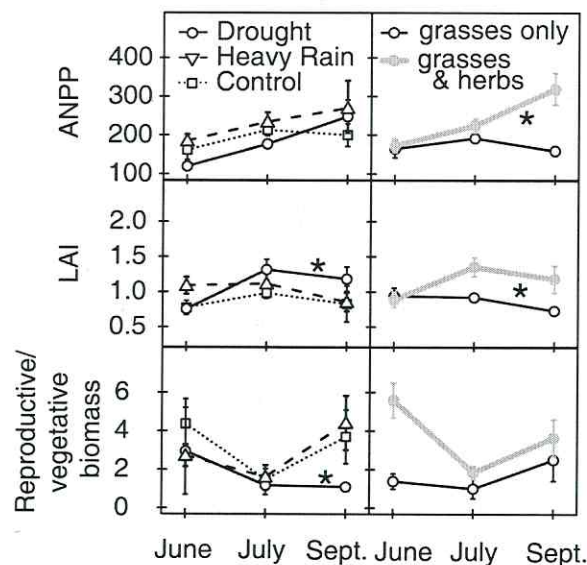


Figure 4: Above-ground stand development over time separated by weather manipulations (left) and species composition (right). a) Above-ground biomass; b) Leaf Area Index; and c) the ratio between reproductive and vegetative biomass. Weather manipulations took place in June. No significant interaction 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.

Above-ground productivity remained unchanged, and the observed changes in carbon flux therefore have to be interpreted as carbon allocation into below-ground 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 (unpublished data). However, plant roots contribute to soil carbon 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 carbon is stored. Even though carbon allocated to the root system might be more stably sequestered (*Jones and Donnelly, 2004*), the long-term duration of such effects, the consequences to soil carbon 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 lost carbon because respiration rates were higher than the increased uptake (*Miranda et al., 1997*). It is furthermore well known that mineralization peaks during rewetting after long, dry soil conditions (*Sponseller, 2007*). 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 carbon 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 (Figure 2 and 3), which is already two 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 above-ground 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 above-ground 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 interaction between several climate parameters, however, is an important point to be considered. Elevated atmospheric CO₂ concentrations, for example, 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 above-ground 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 (Figure 1). On the sandy substrate of the experimental site, the local 100-year rainfall extreme over two 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 carbon fluxes. Here, the more diverse community in terms of species richness, growth forms, and presence of legumes showed a higher potential for carbon uptake (β), but also an increase in respiration (γ). Net carbon 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 above-ground productivity for the more diverse community suggests that the net carbon uptake was transferred into above-ground biomass, which is an instable carbon 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 carbon 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 carbon fluxes in grasslands, even without altering above-ground biomass production. Based on our data, carbon 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 carbon sequestration need to be further evaluated. Community composition influenced carbon fluxes with increased carbon 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 carbon sequestration long after the weather events are over.

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Manuscript 4:

Soil biotic processes remain surprisingly stable after 100-year extreme weather events in experimental grassland and heath

Plant and Soil (in review)

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Abstract:

Climate change will increase the recurrence of extreme weather events such as drought and heavy rainfall. Evidence suggests that extreme weather events pose threats to ecosystem functioning, particularly to nutrient cycling and biomass production. These ecosystem functions depend strongly on below-ground biotic processes, including the activity and interactions amongst plants, soil fauna, and micro-organisms. Here, experimental grassland and heath communities of three phytodiversity levels were exposed either to a simulated single drought or to a heavy rainfall event. Both weather manipulations were repeated for two consecutive years in the EVENT-experiment. The magnitude of manipulations imitated the local 100-year extreme weather event. Below-ground plant biomass and root length, soil enzyme activities, and cellulose decomposition rate were measured. In contrast to expectations, extreme drought had no adverse effects on these below-ground processes independent from the plant community. However, heavy rainfall events increased below-ground plant biomass and stimulated soil enzyme activities as well as decomposition rates for both plant communities. The high resilience against the applied weather manipulations rendered it impossible to detect significant interactions between weather events and phytodiversity, despite the fact that phytodiversity itself appeared to be an important driver of below-ground biotic processes.

Introduction

The frequency and magnitude of extreme weather events will increase during ongoing global climate change (IPCC 2007). These events can have strong effects on above ground productivity as well as on below ground functionality of soil. Several empirical studies (e.g., Busch et al. 2006; Newman et al. 2006; Trillo and Fernandez 2005) have noted an increase in root biomass during dry conditions. Soil enzyme activities are also closely related to soil moisture content (Criquet et al. 2004; Sowerby et al. 2005) with optimal conditions for aerobic processes between the extremes of drought and water saturation. An example for this are heathland soils subjected to drought periods that showed increased, decreased or unchanged soil enzyme activities dependent on the site specific conditions (Sowerby et al. 2005).

Plant productivity and microbial as well as soil fauna activity are strongly linked (Gastine et al. 2003; Williamson and Wardle 2007), and these below-ground biotic processes are driving factors of important ecosystem functions such as nutrient cycling and, consequently, above-ground plant productivity. Soil enzyme activities are related to the microbial status (Aon and Colaneri 2001), but are also linked in the case of exoenzymes to soil physical and chemical properties (Sowerby et al. 2005). Changes in root biomass have been shown to alter abundance and activity of soil biota (Gastine et al. 2003; Salamon et al. 2004). Increased soil biological activity results in a higher decomposition rate and, thus, in more available nutrients for primary production (Geissen and Brümmer 1999; White et al. 2004). Changes in microbial activity and community structure may not only influence plants but also other soil biota like micro-arthropods and earthworms via food web connections (Hooper et al. 2000; Wardle and Lavelle 1997), which in turn act as drivers for plant growth. The other way round, plants, through root penetration, root exudation, and root uptake, may control soil abiotic parameters, such as soil nitrogen concentration, soil humidity or soil porosity, which can indirectly modify soil microbial and faunal activity and diversity (Paul and Clark 1989).

In respect to this complexity of interactions between trophic levels it is not surprising that there is an ongoing debate whether the diversity of communities is related to functional resilience in face of environmental fluctuations (summary in Beierkuhnlein and Jentsch 2005; and in White and Jentsch 2001). Here, resilience is the capacity of an ecological unit to absorb a disturbance event and to return to its previous reference state or reference dynamic without changing (Grimm and Wissel 1997). Related theories like the insurance hypothesis (Yachi and Loreau 1999) were tested mainly in single trophic levels, in particular in plant communities (Kahmen et al. 2005; Tilman et al. 2006). The insurance hypothesis states that communi-

ties which are more diverse in species or functional groups can be expected to be more resilient against environmental perturbations. McGrady-Steed et al. (1997) point at the higher predictability of diverse communities. Naeem (1998) stresses that in face of sudden changes, high diversity increases the “reliability” of communities. First evidence of the importance of phytodiversity for below-ground resilience in face of extreme weather events are reported from a semi-natural grassland in Germany (Kahmen et al. 2005). There, increased species richness significantly enhanced below-ground plant productivity when communities were exposed to a simulated drought event. However, there is still a lack of studies which may help to understand the functional resilience over different trophic levels.

In this contribution, we test four hypotheses related to soil biotic processes of grassland and heath exposed to extreme weather events. 1) Below-ground plant biomass will increase, and activity of soil biota will decrease due to drought conditions. 2) Below-ground plant biomass and activity of soil biota will decrease under heavy rainfall conditions. 3) Below-ground plant biomass and activity of soil biota will increase with higher phytodiversity. 4) Resilience of below-ground plant biomass and activity of soil biota in face of extreme weather events such as drought and heavy rainfall will increase with phytodiversity.

Materials and Methods

Experimental Design

This study is part of the EVENT experiment (Jentsch et al. 2007) testing the effects of extreme weather events on biodiversity and ecosystem functioning in central Europe. The experiment is located in the Ecological-Botanical Garden of the University of Bayreuth, Germany (49°55'19"N, 11°34'55"E, 365 m asl). Mean annual temperature is 7.8°C; mean annual precipitation 709 mm (Data: German Weather Service). Usually, annual precipitation is distributed bi-modally with a major peak during June/ July and a second peak during December/ January. The experiment was carried out with three fully crossed factors. The factors were (1) extreme weather events (drought, heavy rainfall, control), (2) vegetation type (grassland and heath), and (3) diversity level (two species of one functional group, four species of two functional groups, and four species of three functional groups; see Table 1 for details). The design consisted of 90 plots, each two by two meters in size, with every factorial combination replicated five times. Experimental plant communities (vegetation type x diversity level) were blocked and randomly assigned within each weather manipulation. Original species composition was maintained by periodical weeding. The soil of the experimental site consisted of homogenized substrate from a nearby sand quarry (about 80 cm in depth) underlain by drainage

facilities to avoid soil related singularities. The topsoil from this quarry was used to establish an upper horizon of 20 cm depth containing higher amounts of organic material (2 % total carbon against 0.2 % in the lower horizon). The soil is a 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. In order to circumvent edge effects, data acquisition was carried out in the central square meter of each plot only.

Factor 1: extreme weather events

The weather manipulations consisted of extreme drought, heavy rainfall and ambient conditions for control. Intensity of the treatments was based on the local 100-year extreme event in each category. Vegetation periods (March to September) 1961-2000 were used as the reference period (data: German Weather Service). Gumbel I distributions were fitted to the annual extremes, and 100-year recurrence events were calculated (Gumbel 1958). Drought was defined as the number of consecutive days with less than 1 mm daily precipitation. Accordingly, a drought period of 32 days (2005: June 09-July 10; 2006: May 24-June 24) and a rainfall extreme of 170 mm over 14 days (2005: June 27-July 10; 2006: June 10-June 23) were applied in the experiment during the peak growing season in June 2005 and 2006. Maximum values in the historical data set were 33 days without rain during June and July 1976 and 152 mm of precipitation during 14 days in June 1977.

Drought was simulated using rain-out shelters, constructed with a steel frame (Hochtunnel, E & R Stolte GmbH, Germany) and covered with transparent plastic sheet (material: 0.2mm polyethylene, SPR 5, Hermann Meyer KG, Germany) that permitted nearly 90 % penetration of photosynthetically active radiation. Near-surface air temperature was slightly (mean 2005: + 1.2°C; mean 2006: +1.4°C), but not significantly (pairwise t-test with Bonferroni correction: 2005: $p = 0.12$; 2006: $p = 0.26$), increased by the roofs during the weather manipulation period. Strong greenhouse effects were avoided by starting the roof at 80 cm height, allowing for near-surface air exchange.

Heavy rainfall was realized using portable irrigation systems. Drop size and rainfall intensity resembled natural heavy rainfall events through application by Veejet 80100 nozzles, commonly used in erosion research (Kehl et al. 2005). At 0.3 bar water pressure this system resulted in 2.8 mm water per minute. The whole amount of added water was divided into two applications per day to constantly ensure high soil water saturation. If natural pre-

cipitation occurred, then the amount of rain was subtracted from the respective dose. Lateral surface flow was avoided by the application of small plastic sheet pilings around treated plots.

Table 1: In the EVENT experiment, plant communities of two vegetation types (grassland, heath) are installed in three functional diversity levels (A, B, C), resulting in six species combinations.

* G: grassland, H: heath, 2/4: number of species, -: without legume, +: with legume

Abbreviation [*]	vegetation type	diversity level	Description	Species
G2 ⁻	grassland	A	two species, one functional group (grass)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i>
G4 ⁻	grassland	B	four species, two functional groups (grass, herb)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i> , <i>Plantago lanceolata</i> , <i>Geranium pratense</i>
G4 ⁺	grassland	C	four species, three functional groups (grass, herb, legume herb)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i> , <i>Plantago lanceolata</i> , <i>Lotus corniculatus</i>
H2 ⁻	heath	A	two species, one functional group (dwarf shrub)	<i>Calluna vulgaris</i> , <i>Vaccinium myrtillus</i>
H4 ⁻	heath	B	four species, two functional groups (dwarf shrub, grass)	<i>Calluna vulgaris</i> , <i>Vaccinium myrtillus</i> , <i>Agrostis stolonifera</i> , <i>Deschampsia flexuosa</i>
H4 ⁺	heath	C	four species, three functional groups (dwarf shrub, legume shrub, grass)	<i>Genista tinctoria</i> , <i>Vaccinium myrtillus</i> , <i>Agrostis stolonifera</i> , <i>Deschampsia flexuosa</i>

Factor 2 and 3: Experimental plant communities

Overall, ten plant species were used to install artificial plant communities of two vegetation types (grassland and heath) in three diversity levels (Table 1). Species were chosen with respect to their belonging to one of the desired functional groups (grasses, herbs, legumes, dwarf shrubs), to their life-span (perennials), to their overall importance in nearby and central European grassland and heath systems, and to the fact that they can naturally occur on similar substrate. 100 individual plants per plot were planted from pre-grown, even-aged individuals in a systematic hexagonal grid with 20 cm distance between neighbours in April 2005. All grasses and herbs were grown from seeds in autumn 2004, the three dwarf shrub species were two years old when transferred to the experimental site. All species are perennial. One species composition was used per diversity level, replicated only in the other vegetation type. 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 (see detailed discussion in Beierkuhnlein and Nesshoever 2006).

Data acquisition – Response parameters

Below-ground plant biomass and root length

Root length was acquired by the minirhizotron-technique. One clear plastic tube (5 cm diameter) was installed at a 45-degree angle in each plot prior to planting. Tubes were installed to a depth of 45 cm. Portions of the tubes exposed at the surface were covered with adhesive aluminium foil and the ends were capped to prevent entry of water, light, and heat. Images of 4 cm² were collected at 5 cm, 15 cm, 25 cm, and 35 cm depth along each tube by a digital camera mounted on an endoscope (sampling dates 2005: June 28, July 21, August 18, September 7; 2006: March 21, May 15, June 25, August 28). Images were analysed for root length using the line intersection method (Tennant 1975) within a systematic grid (10 x 10, with a grid unit of 0.2 cm x 0.2 cm). In total, 2880 pictures were analysed.

Destructive root biomass sampling within the plots was conducted once directly after the manipulations ended in June 2006. Three soil cores of 39.6 mm inner diameter per plot were combined to one sample and subdivided by three depth layers (2.5 – 7.5 cm, 12.5 - 17.5 cm and 22.5 - 27.5 cm).

Total root biomass of single individuals of each species growing in plastic tubes (20 cm diameter and 20 cm length) inserted into the -ground within each weather manipulation outside the community plots was gained after the weather manipulations in July 2005 and 2006. Root biomass in both cases was determined after carefully washing of roots using a 2 mm sieve and drying for 48 hours at 75°C before weighing.

Soil enzyme activity

Soil enzyme activities are significantly related to decomposition and turnover processes in soils and are considered to reflect a relevant portion of microbial community functions (Waldrop and Firestone 2006). Therefore, we used soil enzyme activities to assess possible changes in soil functions due to extreme weather events and phytodiversity. Soil samples for determining soil enzyme activities were collected in June 2006 immediately after finishing the weather manipulations. 4 samples per plot (depth 0-5 cm) were combined, mixed and kept

at 4°C until further processing within 4 weeks after sampling. Soil suspensions (0.4 g fresh soil in 40 ml H₂O) were prepared from each sample. Enzyme activities were determined fluorimetrically on 96well micro-plates using methylumbelliferone (MU) coupled substrate analogues with the protocol described by Pritsch et al. (2005).

Three replicate assays of each sample were performed using the following substrates (corresponding enzymes), concentrations and incubation times: MU-phosphate (acid phosphatase,) 500 µM 20 min, MU-xyloside (β-xylosidase) 500 µM 1h, MU-cellobiohydrofurane (cellobiohydrolase) 400 µM 1h, MU-glucuronide (β-glucuronidase) 500 µM 1h, MU-N-acetyl- β-glucosaminide (chitinase) 500 µM 40 min, MU-β-glucoside (β-glucosidase) 500 µM 1h. Fluorescence detection was performed with an excitation at 365 nm and an emission wavelength of 450 nm. Sample values were compared to values from a standard curve derived from wells containing MU and soil suspension that was included in every measurement plate. Enzyme activities are expressed as MU-release per g soil dry weight per hour.

Cellulose decomposition

Biological activity of soil fauna and micro-organisms was determined indirectly from the decay of cellulose (Spehn et al. 2005) using minicontainer tubes. It is assumed that this method integrates all activities of soil organisms and abiotic factors (Eisenbeis et al. 1999). Especially in edaphically dry conditions, minicontainers have proven to be a valid tool to get an insight into decomposition processes (Dunger et al. 2001; Keplin and Hüttel 2001). 864 minicontainers were filled with 0.2 g of cellulose (poor in phosphorus, Schleicher & Schüll, Germany) each, closed with a 2 mm mesh, and put into container tubes, consisting of 12 minicontainers each. Two tubes per plot were buried horizontally 1 cm below soil surface at June 6, 2006 only in the grassland communities. After 94 days (September 8), one tube per plot was harvested, whereas the others were harvested after 186 days (December 9). After careful cleaning and drying, the decay of cellulose was determined by subtracting final ash free dry mass from initial dry mass (105°C).

Statistical Analysis

Linear models combined with analysis of variance (ANOVA) were applied to test for significant differences between groups at single points of time (e.g., for the analysis of the root biomass data from the root cores, soil enzyme activities, or decomposition). Homogene-

ous groups of factor combinations (weather manipulation, vegetation type, diversity level) were identified by Tukey HSD post hoc comparisons. Level of significance was set to $p < 0.05$. Prior to statistical analysis, data was log or square root transformed, if conditions of normality were not met, or to improve homogeneity of variances. Both characteristics were tested by examining the residuals versus fitted plots and the normal qq-plots of the Linear Models (Faraway 2005).

Linear Mixed Effects Models were employed to test for effects of weather manipulation, vegetation type, and diversity and their respective interactions on root length data while taking repeated measures into account (time used as random factor, Faraway 2006). When no significant interaction was found, the model was simplified by using only the weather manipulations as fixed effects and vegetation type, diversity level and time as random effects. Significance of differences ($p < 0.05$) was evaluated by Markov Chain Monte Carlo sampling of 1000 permutations (Bates and Campbell 2001). Prior to statistical analysis, data was log transformed, if conditions of normality were not met or 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. All statistical analyses were performed using R (R Development Core Team 2006).

Results

Soil moisture content measurements exhibited that the applied weather manipulations were effective (Figure 1). Dry conditions before the beginning of the drought manipulation in 2005 (only 4 mm of precipitation in the 15 days before manipulation onset) had already led to a minimum in soil water content. During the drought treatment, soil water content remained at this minimum, thus differing from the control, which received natural precipitation. During the heavy rainfall manipulation, it took nearly two weeks until soil moisture had reached its maximum, and soil moisture exceeded the field capacity of the soil only shortly. The year 2006 was characterized by wet conditions when the drought manipulation started, followed by relatively dry conditions afterwards, when the rainfall manipulation began. The difference between drought manipulation and control was therefore smaller in 2006 than in 2005, even though soil moisture values below the wilting point occurred more numerous in the drought manipulation.

Soil biotic processes and drought

The drought manipulation had no significant effect on root length over time at any soil depth (simplified Mixed Models, $p > 0.05$; Figure 2). Even the analysis of the two respective time steps right after the manipulations in the two years showed no significant drought effect (ANOVA, $p > 0.05$). Root biomass in June 2006 exhibited very similar patterns as root length (Figure 3), with no significant differences between drought manipulation and control (ANOVA, $p > 0.05$). None of the 10 plant species showed significant reactions in their respective root biomass to drought (Table 2).

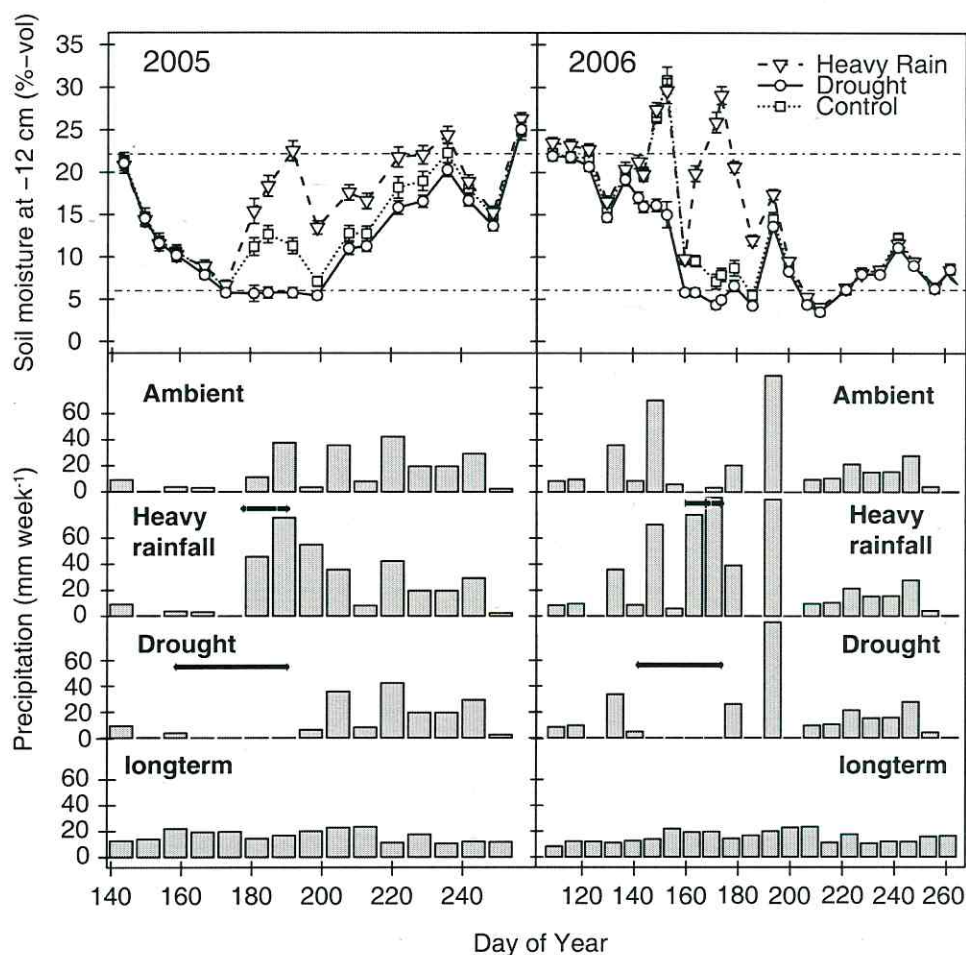


Figure 1: Soil moisture and precipitation in the EVENT experiment during manipulation and recovery after extreme drought and heavy rainfall events. Soil moisture (% volume) at 12.5 cm depth was measured by TDR tube access probe. As no difference in soil moisture as a function of experimental plant community was detected, all plant communities were merged together. Mean values and standard errors are given. Upper dot-dashed line indicates field capacity ($pF = 1.8$), lower dot-dashed line indicates permanent wilting point ($pF = 4.2$) of the soil substrate (AG Boden 1996). Grey bars show weekly precipitation for the weather manipulations in comparison with ambient conditions (control) and the long term mean precipitation 1961-2000 (data: German Weather Service, Station Bayreuth). Timing and duration of the weather manipulations is indicated by black vertical bars.

Soil enzyme activities (phosphatase, cellobiohydrolase, β -glucuronidase, chitinase, β -glucosidase, β -xylosidase) determined immediately after the weather manipulations had not changed due to the drought manipulation compared to the control (ANOVA, $p > 0.05$).

Decomposition of cellulose in the drought plots, however, was significantly higher than in the control plots three months after the treatment ($p < 0.05$, Figure 5). This effect was no longer visible after 6 months ($p > 0.05$).

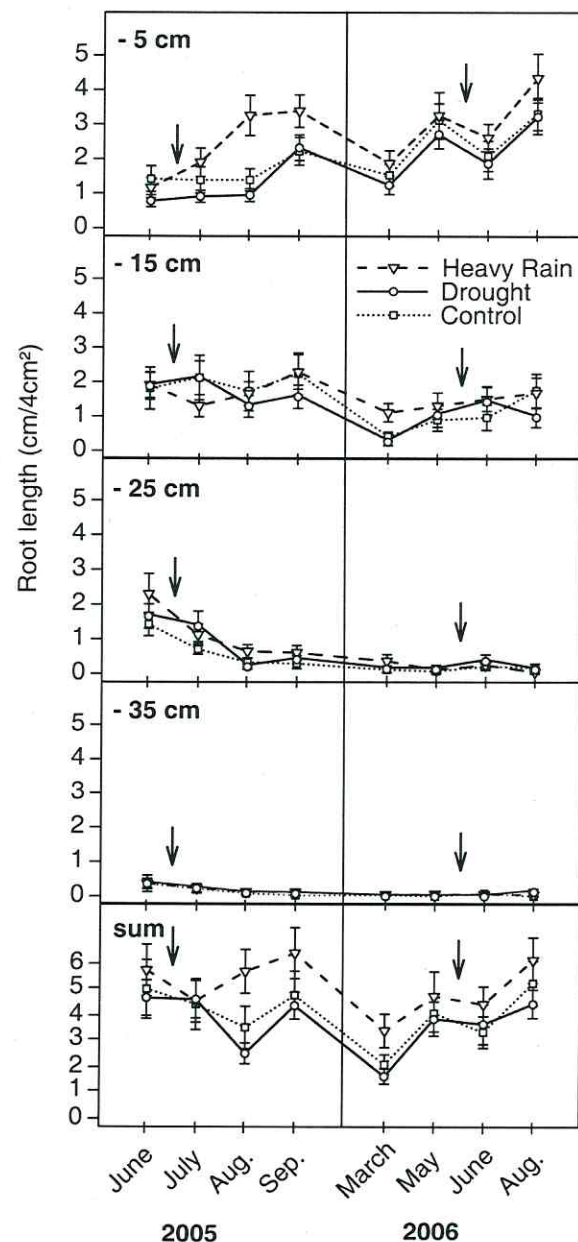


Figure 2: Plant root length at 5 cm, 15 cm, 25 cm, and 35 cm soil depth, averaged over all communities. Mean values and standard errors of root length measured by the minirhizotron technique are shown. The vertical arrow marks the timing of the weather manipulations. The simplified Mixed Model showed significant differences between heavy rainfall and control ($p < 0.05$) over time at 5 cm, 15 cm, 25 cm soil depth, as well as for the cumulative value. No effects were found at 35 cm depth, and no difference between drought and control was detected at any depth.

Soil biotic processes and heavy rainfall

The heavy rainfall manipulation significantly increased root length over time at 5 cm, 15 cm, and 25 cm depth, as well as for cumulative root length over all depth levels (simplified Mixed Models, $p < 0.05$; Figure 2). No effects were found for 35 cm depth, where almost no roots existed. The survey right after the end of the manipulations revealed a significant difference between root length after heavy rainfall manipulation and control in 2005 (ANOVA, TukeyHSD: $p = 0.0485$), but no significant effect in 2006. The increase in 2005 was probably driven by *Holcus lanatus*, as this was the only species with significant reactions in terms of root biomass (increase by nearly 400 %, Table 2). In 2006, no significant root length or root biomass reaction was found neither by the individual species in the pots, nor by the communities in the plots (ANOVA, $p > 0.05$, Table 2, Figure 3).

Phosphatase and chitinase enzyme activities measured directly after the weather manipulations were significantly increased in the heavy rainfall treatment compared to control in 2006 (Table 3a). The analysis was furthermore separated by vegetation types, because significant interactions between vegetation type and weather manipulation as well as between vegetation type and diversity level were found (Table 3a). While for grassland no significant effects were detected due to the manipulations (Table 3b), heath communities showed increased activity in the heavy rainfall treatment for most enzymes but with significant differences ($p < 0.05$) only for chitinase (Figure 4, Table 3c).

Additionally, decomposition of cellulose in the grassland communities in 2006 at the heavy rainfall plots was significantly higher both three months and six months after the weather manipulation ($p < 0.05$, Figure 5). This difference was found at all three grassland

Soil biotic processes and plant community diversity

Below-ground plant biomass and root length generally increased with increasing plant community diversity (Figure 3). Cumulative root length over time was significantly lower in the least diverse (diversity level A) than in the two more diverse communities (Mixed Model, $p < 0.05$, Figure 3a). The same was found for the single time steps after the manipulations in both years (ANOVA, TukeyHSD $p < 0.05$). In contrast, root biomass in 2006 was not significantly affected by plant community diversity (Figure 3b). Below-ground plant biomass and root length were consistently higher in heath than in grassland (Figure 3).

Table 2: Plant species-specific below-ground biomass production given as mean values (g per individual) of five replicates per species x weather manipulation. Plants were grown in bottomless pots next to the community plots within the weather manipulations and harvested destructively after the end of the weather manipulations in both years. Significance of TukeyHSD post hoc comparisons between each weather manipulation and control is shown if the respective ANOVA resulted in significant effects of weather manipulation ($p < 0.05$).

	2005					2006				
Plant species	Control	Drought	p	Rain	p	Control	Drought	p	Rain	p
<i>Calluna vulgaris</i>	20.3	27.5	n.s.	23.5	n.s.	11.9	8.4	n.s.	7.8	n.s.
<i>Vaccinium myrtillus</i>	9.6	8.2	n.s.	5.3	n.s.	7.1	6.6	n.s.	7.8	n.s.
<i>Deschampsia flexuosa</i>	1.9	3.8	n.s.	5.1	n.s.	24.2	26.6	n.s.	11.0	n.s.
<i>Agrostis stolonifera</i>	31.4	19.4	n.s.	48.7	n.s.	65.4	37.6	n.s.	42.2	n.s.
<i>Genista tinctoria</i>	15.1	10.3	n.s.	11.3	n.s.	27.7	25.4	n.s.	20.5	n.s.
<i>Arrhenatherum elatius</i>	8.9	5.8	n.s.	8.2	n.s.	9.2	8.1	n.s.	14.6	n.s.
<i>Holcus lanatus</i>	4.5	5.2	n.s.	16.9	0.0069	12.1	10.0	n.s.	14.8	n.s.
<i>Plantago lanceolata</i>	31.6	30.1	n.s.	27.1	n.s.	0.7	1.9	n.s.	1.7	n.s.
<i>Geranium pratense</i>	2.2	2.2	n.s.	2.0	n.s.	5.5	3.9	n.s.	4.0	n.s.
<i>Lotus corniculatus</i>	9.6	4.9	n.s.	6.0	n.s.	19.4	16.1	n.s.	16.3	n.s.

There was no overall significant influence of the plant community diversity on soil enzyme activities when both vegetation types were analysed together (Table 3a). In the grassland communities, however, phytodiversity had significant effects on phosphatase, cellobiohydrolase and β -glucuronidase activities (Figure 4a, Table 3b). Post Hoc analyses (Tukey HSD) revealed that these effects in soils of the grassland communities were related to the presence of the legume in the plant community with $p < 0.05$ for cellobiohydrolase and β -glucuronidase, and in tendency also for phosphatase ($p < 0.07$). No such trend was found for the heath communities, which reacted more strongly to the weather manipulations (Table 3c).

Decomposition of cellulose was also significantly higher at the grassland plots containing a legume ($p < 0.05$, Fig. 5), whereas no difference was found between the two other communities without legume. This effect was observed for both harvesting dates.

Phytodiversity and resilience of soil biotic processes in face of extreme weather events

Phytodiversity had no significant effect on the response of any measured parameter to the weather manipulations. This is not surprising, however, because no adverse effects of the weather manipulations was observed. Even where effects of weather manipulations were found, higher phytodiversity in the experimental communities had no effect on soil biotic response to the applied weather events (no significant interaction term in any of the Mixed Models or ANOVA's between phytodiversity and weather manipulation).

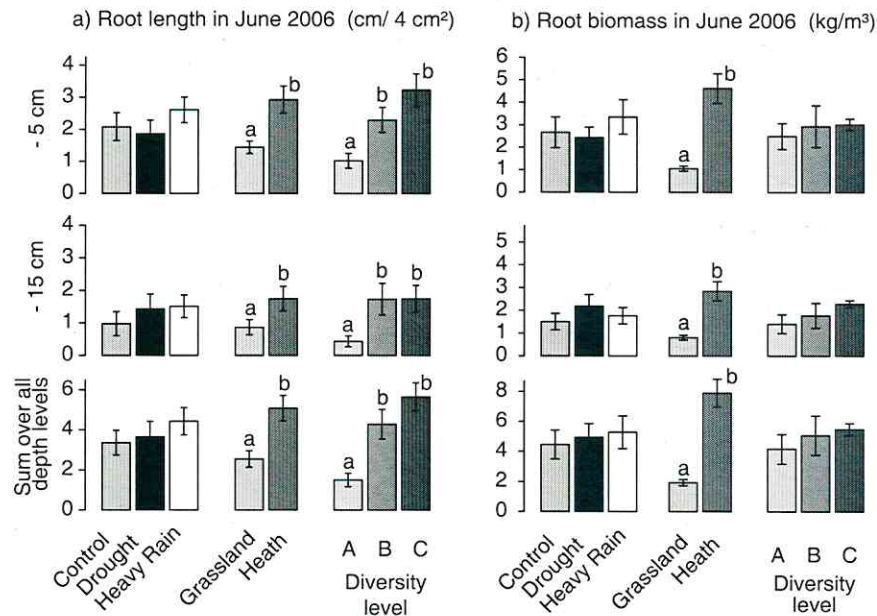


Figure 3: Plant root length (a) and plant root biomass (b) in June 2006 show similar effects. Displayed are mean values and standard errors, letters indicate homogeneous groups according to TukeyHSD post hoc comparisons ($p < 0.05$) for each factor separately and only if the factor was tested significant in the ANOVA. ANOVA for root length at -5 cm: weather manipulation $F = 1.5$, $p = 0.0858$, vegetation type $F = 8.2$, $p = 0.0056$, diversity level $F = 11.0$, $p < 0.0001$. ANOVA for root length at -15 cm: weather manipulation $F = 1.3$, $p = 0.2783$, vegetation type $F = 5.1$, $p = 0.0271$, diversity level: $F = 5.3$, $p < 0.0071$. ANOVA for cumulative root length over all depth levels: weather manipulation $F = 1.4$, $p = 0.2506$, vegetation type $F = 11.5$, $p = 0.0011$, diversity level: $F = 15.1$, $p < 0.0004$. ANOVA for root biomass at -5 cm: weather manipulation $F = 1.6$, $p = 0.1962$, vegetation type $F = 85.0$, $p < 0.00016$, diversity level: $F = 0.7$, $p = 0.5019$. ANOVA for root biomass at -15 cm: weather manipulation $F = 1.2$, $p = 0.3107$, vegetation type $F = 57.5$, $p < 0.0001$, diversity level $F = 1.2$, $p = 0.3154$. ANOVA for cumulative root biomass over all depth levels: weather manipulation $F = 0.8$, $p = 0.4716$, vegetation type $F = 110.9$, $p < 0.0001$, diversity level $F = 1.2$, $p = 0.3119$.

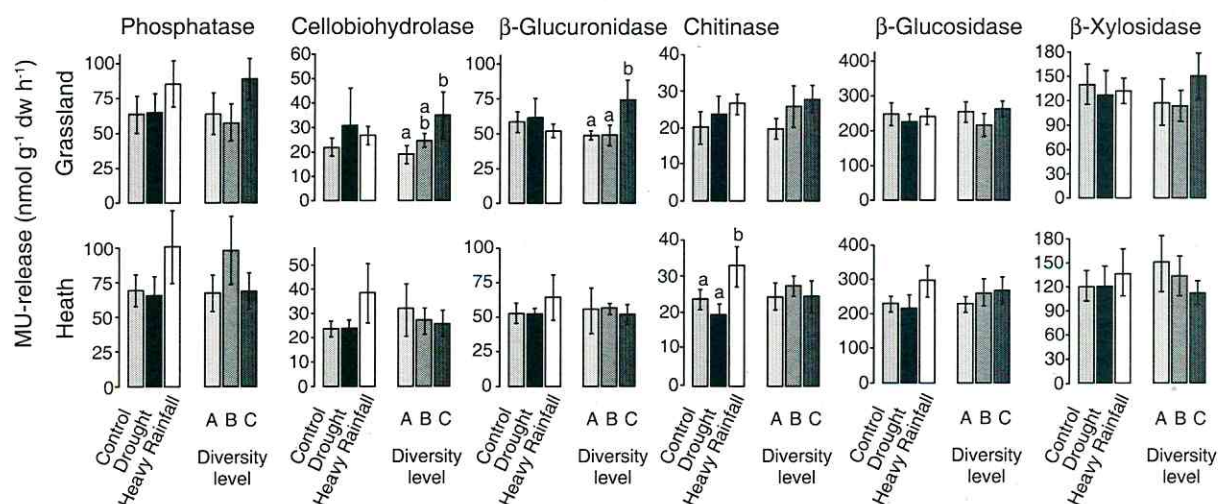


Figure 4: Enzyme activities in soil samples (0-5 cm depth) separated by vegetation types (upper panel: grassland; lower panel: heath). Displayed are mean values and standard errors, letters indicate homogeneous groups according to TukeyHSD post hoc comparisons ($p < 0.05$) for each factor separately and only if the factor was tested significant in the ANOVA (Table 3b and c). No significant interaction between weather manipulation and diversity level was found.

Discussion

Soil biotic processes and drought

Drought did not induce changes in below-ground plant parameters or soil enzyme activity. Decomposition was even transiently increased. These findings contradict our first hypothesis. Several empirical studies (e.g., Busch et al. 2006; Newman et al. 2006; Trillo and Fernandez 2005) have noted that root biomass increases during dry conditions, especially at lower soil depths, to enhance root absorption of minerals and water. Most of these studies, however, deal with decreased water supply over longer time periods and not with complete water withdrawal over defined periods of time. When constrained to the latter definition of drought, the findings become less clear (Table 4). Shorter drought events tend to have no effect on root biomass, whereas longer events generally decrease below-ground biomass. Unfortunately, none of the studies listed in Table 4 provides any information on extremeness (Jentsch 2006) of the manipulated weather events. For example, Kahmen et al. (2005) report enhanced below-ground biomass with increasing species diversity after 51 days of drought in semi-natural grasslands of an environment comparable to our study site. Transferred to our site, such a drought length would be an event with a recurrence of 10 000 years. Of course, local edaphic conditions differ between sites and are important drivers of ecological extremeness, but it is the statistical extremeness of weather events that changes with climate change. More drastic manipulations seem necessary for basic research on the role of phytodiversity in the (below-ground) response to extreme weather events. Our results indicate that the applied drought was not extreme enough to induce changes in below-ground biotic processes at our site. Nevertheless, species specific shifts under competition might still occur below-ground in the plant communities, as they have been found to do above-ground in the same experiment, even in the absence of changes in total above-ground productivity (Kreyling et al. in press). It might be speculated that soil biota are highly adapted to drought in this soil, because the low clay content reduces water holding capacity and even short periods of drought may lead to microsites with low water content. Plants might already have developed a root architecture that reflects these conditions. diversity levels ($G2^-$, $G4^-$, $G4^+$), but was less pronounced at the end of the experiment.

Soil enzyme activities were almost unchanged compared to the control directly after the drought manipulation in 2006, thereby indicating that the drought stress was not strong enough to affect soil microbes (Williamson and Wardle 2007). However, the stability of en

Table 3: a) F and p values (ANOVA) of soil enzyme activity data for three factors: (1) weather manipulations (heavy rain, drought, control), (2) vegetation type (grassland, heath), and (3) diversity level (see Table 1) and their interactions. Significant ($p < 0.05$) results are set bold, borderline significance ($0.05 \leq p < 0.10$) is marked in bold italics; abbreviations are as follows: weather manipulation (weather), vegetation type (veg), diversity level (div). Because of significant interactions with vegetation type, the analysis was further run separately for b) grassland and c) heath.

Enzyme	Phosphatase		Cellobio- hydrolase		β -Glu- curonidase		Chitinase		β -Glu- cosidase		β -Xylosidase	
F- and p-values	F	p	F	p	F	p	F	p	F	p	F	p
a)												
weather	4.06	0.0228	1.60	0.2106	0.09	0.9123	6.12	0.0040	2.56	0.0870	0.25	0.7812
vegetation type	1.15	0.2891	0.26	0.6128	0.00	0.9624	0.69	0.4088	0.05	0.8238	0.00	0.9658
diversity	1.51	0.2313	0.71	0.4954	1.23	0.3043	1.63	0.2054	0.82	0.4450	0.27	0.7673
weather * veg	0.26	0.7736	1.33	0.2731	0.92	0.4074	2.71	0.0756	1.90	0.1596	0.43	0.6549
weather * div	0.23	0.9203	0.44	0.7767	2.01	0.1127	0.72	0.5832	1.18	0.3313	0.33	0.8538
veg * div	3.81	0.0286	2.60	0.0838	2.30	0.1149	0.67	0.5145	1.23	0.3002	2.33	0.1066
weather * veg * div	1.78	0.1462	0.76	0.5578	1.86	0.1376	0.47	0.7568	0.59	0.6698	0.92	0.4577
b) Grassland												
weather	1.6	0.2239	0.9	0.4196	0.4	0.6997	1.0	0.3757	0.3	0.7479	0.2	0.8342
diversity	3.4	0.0484	5.1	0.0136	4.7	0.0217	1.8	0.1808	2.4	0.1131	1.4	0.2693
weather * div	1.5	0.2457	1.0	0.4003	1.6	0.2098	0.2	0.9323	0.8	0.5488	0.6	0.6713
c) Heath												
weather	2.5	0.1052	1.7	0.2024	0.6	0.5763	8.5	0.0014	3.1	0.0616	0.5	0.6092
diversity	2.3	0.1227	0.3	0.7546	0.1	0.9072	0.4	0.7060	0.4	0.6585	1.2	0.3120
weather * div	0.8	0.5644	0.4	0.7932	2.1	0.1255	1.1	0.3976	0.9	0.4601	0.7	0.6200

zyme activities might also be due to the fraction of abiotic enzymes (Sinsabaugh 1994) consisting of exoenzymes released into the surrounding soil by microorganisms before the drought period. Time series including samplings with longer periods from the end of the drought period could help to clarify this point especially with regard to increased decomposition rates in the drought plots. Decomposition was not reduced due to drought, as had been expected (Krivtsov et al. 2006; O'Neill et al. 2003). Moreover, the reduced soil moisture induced increasing decay rates, at least in the first three months following the end of the drought manipulation. This may be due to the promotion of microbial and faunal activity in the soil by the induced change of environmental conditions, as it has been shown that decomposition in arable soils is increased by recurrent drying-rewetting cycles compared to constant mean conditions (Mamilov and Dilly 2002).

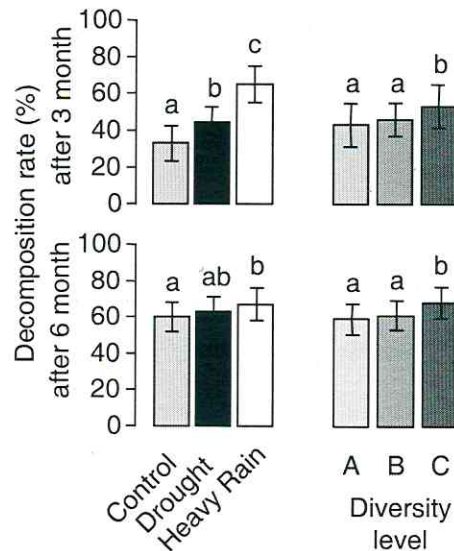


Figure 5: Decomposition rate of cellulose within the grassland communities determined 94 (upper panel) and 186 days (lower panel) after the manipulated weather events. Displayed are mean values and standard errors, letters indicate homogeneous groups according to TukeyHSD post hoc comparisons. ANOVA for weather manipulation $F = 92.4$, $p < 0.001$ (94 d); $F = 6.2$, $p = 0.002$ (186 d). ANOVA for diversity level $F = 7.0$, $p = 0.001$ (94 d); $F = 10.7$, $p < 0.001$ (186 d).

Soil biotic processes and heavy rainfall

The increase in below-ground biomass, soil enzyme activity, and decomposition rate in response to heavy rainfall is in contrast to our second hypothesis that below-ground plant biomass and activity of soil biota would decrease under heavy rainfall conditions. We expected death of fine roots and decrease in decomposition activity due to anoxic conditions (Baruch and Merida 1995). The results imply that the applied event did not lead to the expected soil saturation with anoxic conditions, probably because of the sandy substrate at the study site. Obviously, moisture conditions after additional rainfall were favourable leading to a significant increase of soil biotic activity. Hence, the biotic activity was enhanced by the higher soil moisture (Wardle 2002). From our study, we cannot determine a particular soil moisture saturation threshold, at which soil biotic activity may switch from being promoted to being constrained. Interestingly, the observed increase in below-ground biomass was not coupled to a change in above-ground biomass production (Kreyling et al. 2007).

Soil enzyme activities were stimulated by heavy rainfall in heath but not in grassland. The main difference in biological components of soil beneath ericaceous plants compared to grassland would be due to the ericoid mycorrhizal symbionts that are known for their high extracellular enzyme activity (Cairney and Burke 1998). Especially the significantly increased chitinase activity, an enzyme highly active in ericoid mycorrhizal fungi (Bougoure and Cair-

ney 2006), points towards fungi which may have been stimulated by enhanced root growth and favourable moisture conditions. The contribution of the ericoid mycobiont to soil enzyme activities could be tested directly on mycorrhizal roots as suggested by Courty et al. (2005).

Soil biotic processes and community diversity

In accordance with our third hypothesis, we found an increase in below-ground plant biomass and activity of soil biota with increasing community diversity for both vegetation types. The increased below-ground plant biomass and root length indicates an increased niche filling due to differences in spatial root architecture (Silvertown 2004). This finding also implies that more diverse communities will be able to take up more available water during times of water stress, as already demonstrated elsewhere (Kahmen et al. 2005).

In contrast to heath, grassland soil enzyme activities were not significantly altered by the weather manipulations but instead reacted to the composition of the plant community, i.e. the presence of a legume. In the grassland soil samples, the most stimulated enzymes were involved in microbial carbon cycling (cellobiohydrolase and β -glucuronidase) which hints to an increase in dead plant material (higher root turnover). Phosphatase was also stimulated indicating an increased demand of phosphate (Sinsabaugh 1994). This could be due to a better nitrogen supply provided by the legume, which would stimulate microbial and plant growth but simultaneously induce the need for phosphate. This reaction of phosphatase activity on increased N-supply has also been obtained in annual grasslands (Menge and Field 2007). The lack of a similar reaction in the heath community, however, cannot be explained accordingly.

Biomass and activity of soil micro-flora and -fauna are affected by the traits of the plant species present (Wardle 2002). The addition of a legume in our experiment resulted in an increase of cellulose decomposition, whereas the phytodiversity of the plant communities without a legume had no significant effect on the soil biotic activity. This is in correspondence with experimental results of Salamon et al. (2004), who attributed rising abundance and biomass of micro-flora and soil invertebrates to the presence of legumes.

Table 4: Literature survey on plant root response to drought events. Only experiments dealing with complete water withdrawal for a defined period of time were extracted from a search in the Web of Science [(belowground productivity or fine root or below-ground productivity) and (drought or rain or precipitation or water deficit)]. The list is ordered by increasing drought length, as generally no measure of extremity is provided.

Root response	Manipulation strength	Extremity	Ecosystem type/species	Geographical setting	Reference
increase	2 weeks	?	<i>Lupinus albus</i> crop	Mediterranean	Rodrigues et al. (1995)
no effect	2 weeks (replicated)	?	Softwood forest	central and eastern USA	Hallgren et al. (1991)
decrease	3 x 10 days	?	<i>Populus</i> tree saplings	greenhouse	Liu and Dickmann (1992)
no effect	5 weeks	100 year event	temperate grassland and heath shrubland	Bavaria, Germany	present study
no effect	7 weeks	?	<i>Quercus</i> trees	northern Greece	Fotelli et al. (2000)
increase	7 weeks	?	temperate grassland	Thuringen, Germany	Kahmen et al. (2005)
decrease	7 weeks	?	<i>Brassica oleracea</i> crop	Hannover, Germany	Kage et al. (2004)
no effect	8 weeks	?	<i>Quercus</i> trees	Lower Saxony, Germany	Gieger and Thomas (2002)
no effect	8 weeks	?	Heath shrublands	UK, Denmark, The Netherlands, Spain	Gorissen et al. (2004)
decrease	8 weeks	?	<i>Picea abies</i> forest	Klosterhede, Denmark	(Beier et al. 1995)
decrease	12 weeks	?	early successional forest	Central Europe	Aspelmeier and Leuschner (2006)
decrease	20 weeks	?	<i>Sorghum</i> crop	Sudan	Tsuji et al. (2005)
no effect	between 10 and 25 weeks	?	<i>Picea abies</i> forest	Solling, Germany	Bredemeier et al. (1998)
decrease	between 6 and 27 weeks	?	<i>Picea abies</i> forest	Solling, Germany	Blanck et al. (1995)
decrease	27 weeks (throughfall only)	?	<i>Cryptomeria japonica</i> forest	Kanto Plain, Japan	Konopka et al. (2007)

Phytodiversity and resilience of soil biotic processes in face of extreme weather events

The observed changes in soil biotic processes in face of extreme weather events were not affected by phytodiversity (species richness and composition of growth forms) in our study. However, the effects of extreme weather events were subtle or non-existent at all, thereby rendering the statistical detection of an interaction with phytodiversity unlikely to impossible. Although well designed to evaluate the impact of realistic extreme weather events on soil biotic processes, our experiment therefore fails to test buffering of soil biotic processes by phytodiversity. Even though evidence suggests that below-ground productivity is buffered

by increasing plant diversity during an extreme drought event (Kahmen et al. 2005), consequences of phytodiversity on other soil biotic processes are unclear (Gastine et al. 2003), in combination with extreme weather events even untested.

Conclusions

Overall, our findings indicate a high resilience of below-ground processes in model grassland and heath communities in face of drought and heavy rainfall events of 100 year recurrence. The relative strength of extreme events in relation to long-term local conditions needs to be taken into account in order to obtain realistic manipulation strengths when dealing with extreme weather events and their effects on ecosystem functioning. Contrary to current knowledge our results suggest ecosystems to be more stable against extreme weather events than previously thought, even though the influence of soil types on such effects demands further attention.

Phytodiversity seems capable of further stabilizing communities during drought events due to increased niche filling in the root system, despite no observed interaction between phytodiversity and weather events at the applied manipulation strengths. The differences in soil enzyme activity between the two vegetation types (grassland soils responsive to phytodiversity; heath soils responsive to weather events) point to the importance of plant functional composition for below-ground biotic processes and, thus, for ecosystem functions such as stability of productivity and nutrient cycling in a changing world.

Acknowledgements

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Manuscript 5:**Beyond gradual warming – extreme weather events alter flower phenology of European grassland and heath species.**

Global Change Biology (submitted 11/2007)

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Shifts in the phenology of plant and animal species or in the migratory arrival of birds are seen as “fingerprints” of global warming. However, even if such responses have been documented in large continent-wide datasets of the northern hemisphere, all studies up to date correlate the phenological pattern of various taxa with gradual climatic trends. Here we report a previously unobserved phenomenon: severe drought and heavy rain events caused phenological shifts in plants of the same magnitude as one decade of gradual warming. We present data from two vegetation periods in an experimental setting containing first evidence of shifted phenological response of 10 grassland and heath species to simulated 100-year extreme weather events in Central Europe. Averaged over all species, 32 days of drought significantly advanced the mid-flowering date by 4 days. The flowering length was significantly extended by 4 days. Heavy rainfall (170 mm over 14 days) had no significant effect on the mid flowering date. However, heavy rainfall reduced the flowering length by several days. Observed shifts were species-specific, e.g. drought advanced the mid flowering date for *Holcus lanatus* by 1.5 days and delayed the mid-flowering date for *Calluna vulgaris* by 5.7 days, heavy rain advanced mid-flowering date of *Lotus corniculatus* by 26.6 days and shortened the flowering length of the same species by 36.9 days. Interestingly, the phenological response of individual species was modified by community composition. For example, the mid-flowering date of *Calluna vulgaris* was delayed after drought by 9.3 days in communities composed of grasses and dwarf shrubs compared to communities composed of dwarf shrubs only. This indicates that responses to extreme events are context-specific. Additionally, the phenological response of experimental communities to extreme weather events can be modified by the functional diversity of a stand. Future studies on phenological response patterns related to climate change would profit from explicitly addressing the role of extreme weather events.

Introduction

Along with climate warming, an earlier onset of spring for mid-latitudes and higher latitudes and a significant extension of the growing season have been observed recently by numerous authors (Menzel & Fabian, 1999; Penuelas & Filella, 2001; Fitter & Fitter, 2002; Walther et al., 2002; Parmesan & Yohe, 2003). However, an important research frontier currently arising from the climate change debate is the expansion from an analysis of trends to an interest in extreme events (e.g. Easterling et al., 2000; Parmesan et al., 2000; Jentsch et al., 2007). Alterations in the magnitude and frequency of extreme weather events - such as heat waves, drought, heavy rainfall, or cold periods - have been experienced in the recent past, and their ecological importance is expected to increase in the near future in many parts of the world (IPCC, 2007). However, there is a substantial lack of knowledge on how extreme weather events affect biodiversity and ecosystem functioning.

Phenological shifts are regarded as a “fingerprint” (Walther et al., 2002) of global warming. Menzel et al. (2006) tested an extended data set from a systematic phenological network across 21 European countries, comprising more than 500 plant species that are differentiated by numerous life history traits, for phenological changes in response to gradual advances of spring and summer. Since 1960, the onset of spring has advanced in the northern hemisphere on average by 2.5 – 2.8 days per decade, or 4.6 days per 1 degree of temperature increase (Menzel et al., 2006; Memmott et al., 2007; Parmesan, 2007). Phenological response to such gradual change reveals a remarkable biogeographic differentiation; responsiveness of flower phenology to warming is more pronounced in warmer European countries than in colder ones. Additionally, early flowering species react more strongly to temperature increase than late flowering species (Dunne et al., 2003). There is indication that climate change can be accompanied by a multi-faceted divergence in flower phenology. Warming advances the flowering of early flowering species and delays the flowering of late flowering species in a tallgrass prairie in North America (Sherry et al., 2007). There, warming induces the expansion of reproductive periods of some species and the compression of others (Sherry et al., 2007). An emerging research challenge is to assess whether temperature-driven shifts in phenology put the maintenance of crucial plant-animal-interactions such as pollination at risk. Desynchronization of previously synchronized life cycles and a disruption of mutually beneficial interactions due to climate change appear possible (e.g., Harrison, 2000; Parmesan, 2007). Memmott et al. (2007) predict that between 17 % and 50% of all pollinator species will suffer a disruption of food supply, if plant phenology advances as much as 1-3 weeks.

ferroni correction: 2005: $p = 0.12$; 2006 $p = 0.26$) increased by the roofs during the weather manipulation period. Unwanted greenhouse effects were avoided by starting the roof from a height of 80 cm, allowing for near-surface air exchange. After the manipulation period, the roofs were removed.

Heavy rainfall was created using portable irrigation systems. Drop size and rainfall intensity resembled natural heavy rainfall events through application by Veejet 80100 nozzles, used in erosion research (Kehl et al., 2005). The calculated amount of added water was divided into two applications per day to ensure a constantly high soil water saturation. If natural precipitation occurred, this amount of rain was subtracted from the respective dose. A lateral surface flow was avoided by plastic sheet pilings around treated plots.

Experimental plant communities

Overall, grasslands and heath are spatially important ecosystems in Central Europe. Ten wide spread plant species were chosen from the regional flora. Species were selected with respect to their affiliation to defined functional groups (grasses, herbs, legumes, dwarf shrubs), to life-span (perennials), to overall importance in nearby and Central European grassland systems, and to the fact that they do naturally share substrate. 100 plant individuals per plot in defined quantitative composition were planted in a systematic hexagonal grid with 20 cm distance between individuals in early April (DOY 92) 2005 from pre grown individuals that have been acclimated on site since February 2005. These communities represent naturally occurring species combinations. Both, grassland and heath plots were established at two levels of species diversity (2 and 4 species) and three levels of functional diversity (1, 2, 3 functional groups), resulting in six species combinations or communities in total (Table 1).

Data acquisition and statistical analysis

For each species, weekly observations of the flowering status of four individuals per plot and species were carried out. As a surrogate, the mid-flowering date was calculated, i.e., the date of the 50 percentile of the flowering curve over time, and flowering length, i.e., the difference between the dates of the 25 percentile and of the 75 percentile of the flowering curve over time (see Figure 1 as an example). Individuals were counted as “flowering” when the anthers were visible in at least one flower. *Geranium pratense* had to be excluded from the analysis, because this species did not produce any flower in most plots.

Table 1: Experimental plant communities of two vegetation types (grassland, heath) were used at three functional diversity levels, resulting in six community compositions. Abbreviations: G: grassland, H: heath, 2/4: number of species, -: without legume, +: with legume.

Abbreviation	Vegetation type	Diversity level	Description	Species
G2 ⁻	grassland	A	two species, one functional group (grass)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i>
G4 ⁻	grassland	B	four species, two functional groups (grass, herb)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i> , <i>Plantago lanceolata</i> , <i>Geranium pratense</i>
G4 ⁺	grassland	C	four species, three functional groups (grass, herb, legume herb)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i> , <i>Plantago lanceolata</i> , <i>Lotus corniculatus</i>
H2 ⁻	heath	A	two species, one functional group (dwarf shrub)	<i>Calluna vulgaris</i> , <i>Vaccinium myrtillus</i>
H4 ⁻	heath	B	four species, two functional groups (dwarf shrub, grass)	<i>Calluna vulgaris</i> , <i>Vaccinium myrtillus</i> , <i>Agrostis stolonifera</i> , <i>Deschampsia flexuosa</i>
H4 ⁺	heath	C	four species, three functional groups (dwarf shrub, legume shrub, grass)	<i>Genista tinctoria</i> , <i>Vaccinium myrtillus</i> , <i>Agrostis stolonifera</i> , <i>Deschampsia flexuosa</i>

Phenological shifts of all species combined were analyzed using Linear Mixed Effects Models with weather manipulation as a fixed factor and species identity, community composition, and plot number as random factors (Faraway, 2006). The significance of differences between weather manipulation and control were evaluated using Markov Chain Monte Carlo sampling with the level of significance set to $p < 0.05$ in 1000 iterations (Bates & Campbell, 2001). Linear Mixed Effects Models were conducted with the function “lmer” (Bates & Sarkar, 2007). Since the Markov chain Monte Carlo sampling compares the measured difference to the 95 % confidence interval of the permutations, the output is whether or not the data are within this confidence interval. Therefore, instead of decimal values, p can only be reported as being above or below 0.05.

Linear models combined with analysis of variance (ANOVA) were applied to test for significant differences between factorial groups of weather manipulation and functional diversity level (Table 1) for each species separately. Prior to statistical analysis, data was log or square root transformed, if conditions of normality were not met, or to improve homogeneity of variances. Both characteristics were tested by examining the residuals versus fitted plots and the normal qq-plots of the Linear Models (Faraway, 2005). All statistical analyses were performed using R (R Development Core Team, 2006).

Divergence between early and late flowering species was studied by separating flowering periods before and after the 200th day of the year and examining mixed models of these two groups separately. Three species (*Genista tinctoria*, *Lotus corniculatus*, *Plantago lanceolata*) performed two distinct flowering periods, one before and one after the 200th day of the year, consequently, their first flowering period was placed in the early flowering group and the second into the late flowering group.

Results

Drought impact on mid flowering date and length of flowering period

Drought resulted in an advance of the mid-flowering date by four days in 2005, but in no significant reaction in 2006 on average over all species (Figure 2). At the species level, the length of the flowering period was rather uniformly modified, especially in 2006. Drought expanded the flowering period of all species (Table 2).

Further, drought resulted in a significant expansion of the flowering period by about four days compared to the control in both years on average over all species (Figure 2). At the species level, however, unidirectional shifts did not generally occur, especially in 2005 (Table 2). For example, drought significantly the mid-flowering date of *Holcus lanatus* and delayed the mid-flowering date of *Calluna vulgaris*. Even though few significant weather manipulation effects were found at the species level in 2006, phenological shifts appeared to be more homogenous than in 2005. The mid-flowering date of most species was advanced after a drought (7 out of 9 species) in 2006.

Table 2: Shifts in the mid flowering date and flowering length compared to the control. Average values over all functional diversity levels are shown for species which occurred in more than one community composition. Significant differences between weather manipulation and the control (p_{wm}) are in bold, for single species obtained by Analysis of Variance, for all species combined according to Markov Chain Monte Carlo sampling of Linear Mixed Effects Models. For all species occurring in more than one community composition, p_{dl} indicates significance of functional diversity according to ANOVA, and $p_{wm \times dl}$ indicates significance of interaction between weather manipulation and functional diversity according to ANOVA.

a) Mid flowering

Weather manipulation	Species	2005				2006			
		Shift (days)	P _{wm}	P _{dl}	P _{wm x dl}	Shift (days)	P _{wm}	P _{dl}	P _{wm x dl}
Heavy Rainfall	<i>A. elatius</i>	0.5	0.510	0.394	0.260	-1.0	0.223	0.918	0.692
	<i>H. lanatus</i>	-1.0	0.646	0.515	0.115	0.8	0.271	0.150	0.340
	<i>P. lanceolata</i>	-1.5	0.711	0.181	0.638	3.9	0.220	0.662	0.625
	<i>G. pratense</i>	x				#			
	<i>L. corniculatus</i>	-26.6	0.003			-4.1	0.114		
	<i>V. myrtillus</i>	-3.5	0.593	0.468	0.931	1.0	0.442	0.038	0.645
	<i>C. vulgaris</i>	1.6	0.240	0.584	0.321	0.1	0.944	0.153	0.184
	<i>G. tinctoria</i>	0.2	0.934			6.3	0.049		
	<i>A. stolonifera</i>	1.5	0.450	0.241	0.144	0.2	0.544	0.550	0.761
	<i>D. flexuosa</i>	x				0.1	0.834	0.723	0.010
	all species	-3.6	n.s.			0.81	n.s.		
Drought	<i>A. elatius</i>	0.5	0.979	0.040	0.398	-0.4	0.366	0.527	0.489
	<i>H. lanatus</i>	-1.5	0.344	0.070	0.145	-2.1	0.021	0.426	0.284
	<i>P. lanceolata</i>	0.6	0.960	0.057	0.010	-5.8	0.146	0.070	0.207
	<i>G. pratense</i>	x				#			
	<i>L. corniculatus</i>	-18.3	0.129			4.5	0.292		
	<i>V. myrtillus</i>	-3.4	0.568	0.555	0.770	-0.6	0.535	0.066	0.311
	<i>C. vulgaris</i>	5.7	0.002	0.005	0.012	-1.5	0.534	0.121	0.862
	<i>G. tinctoria</i>	-18.3	0.212			13.4	0.199		
	<i>A. stolonifera</i>	-0.5	0.749	0.819	0.560	-0.7	0.165	0.040	0.082
	<i>D. flexuosa</i>	-0.7	0.949	0.447	0.642	-0.4	0.297	0.098	0.061
	all species	-3.98	<0.05			0.71	n.s.		

b) Flowering length

Heavy Rainfall	<i>A. elatius</i>	0.1	0.897	n.s.	n.s.	-0.8	0.208	0.957	0.394
	<i>H. lanatus</i>	-0.8	0.782	n.s.	n.s.	-1.3	0.101	0.740	0.895
	<i>P. lanceolata</i>	-3.3	0.485	n.s.	n.s.	-6.5	0.800	0.246	0.609
	<i>G. pratense</i>	x				#			
	<i>L. corniculatus</i>	-36.9	0.001			-6.6	0.136		
	<i>V. myrtillus</i>	x				-0.5	0.768	0.954	1.000
	<i>C. vulgaris</i>	2.9	0.011	0.001	0.004	-3.7	0.009	0.048	0.936
	<i>G. tinctoria</i>	-4.7	0.757			-7.4	0.948		
	<i>A. stolonifera</i>	1.2	0.150	0.018	0.037	-1.0	0.111	0.077	0.848
	<i>D. flexuosa</i>	x				-0.5	0.369	0.536	0.112
	all species	-5.4	<0.05			-3.3	<0.05		
Drought	<i>A. elatius</i>	-0.2	0.979	0.041	0.394	0.2	0.571	0.502	0.747
	<i>H. lanatus</i>	-9.6	0.001	0.667	0.567	0.2	0.724	0.786	0.979
	<i>P. lanceolata</i>	3.6	0.893	0.477	0.049	13.3	0.089	0.341	0.511
	<i>G. pratense</i>	x				x			
	<i>L. corniculatus</i>	1.6	0.242			9.9	0.210		
	<i>V. myrtillus</i>	x				1.3	0.627	0.985	0.880
	<i>C. vulgaris</i>	9.6	0.434	0.785	0.124	1.6	0.495	0.183	0.684
	<i>G. tinctoria</i>	16.9	0.437			11.7	0.352		
	<i>A. stolonifera</i>	-2.1	0.503	0.018	0.210	1.3	0.294	0.128	0.936
	<i>D. flexuosa</i>	x		0.861	0.940	0.9	0.139	0.960	0.281
	all species	2.2	<0.05			4.38	<0.05		

Heavy rain impact on mid flowering date and length of flowering period

Heavy rainfall had no significant effect on the mid-flowering date in either year on average over all species. However, at the species level, the mid-flowering date of most species was delayed after heavy rainfall (7 out of nine species) in 2006.

Contrary to drought, heavy rainfall caused a significant compression of the flowering period by 5.4 days in 2005 and by 3.3 days in 2006 on average over all species. Compression of the flowering period occurred in 7 out of 9 species (Table 2).

Early versus late seasonal reproduction in plants

The advance and delay of the mid-flowering date (Figure 3) was not generally correlated with plant traits of early versus late reproduction (i.e. there was no significant shift in mixed models separated by early and late flowering species). Likewise, an extension and compression of the flowering period (Figure 3) was not correlated with plant traits of early versus late reproduction (i.e. there was no significant difference in mixed models separated by early and late flowering species).

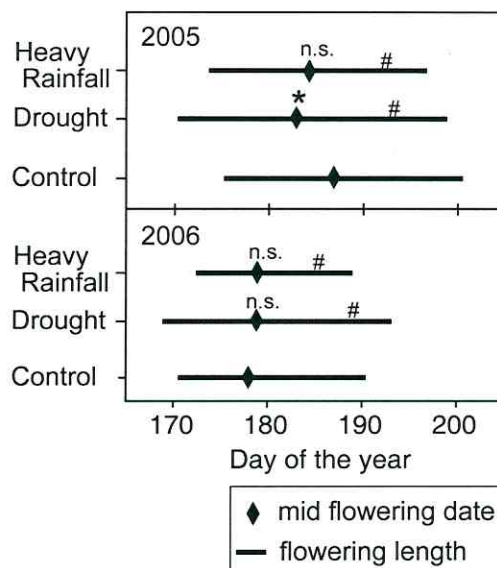


Figure 2: General effects of extreme weather events on the mid flowering date and flowering length of 10 common European species (Table 1). For each species, weekly observations of the flowering status of four individuals in five replications were used to obtain the mid-flowering date (date of the 50 percentile of the flowering curve over time) and flowering length (difference between the dates of the 25 percentile and of the 75 percentile of the flowering curve over time). Average values over all functional diversity levels were taken for each species which occurred in more than one community composition. Significant differences between weather manipulation and the control ($p < 0.05$) according to Markov Chain Monte Carlo sampling of Linear Mixed Effects Models are marked by “*” for the mid flowering date and “#” for the flowering length.

Interaction between extreme weather events and plant diversity

Remarkably, community composition significantly modified the phenological response of individual species (see Table 2). For example, a delay of the mid-flowering date of *Calluna vulgaris* by 9.3 days in communities composed of two grasses and two dwarf shrubs compared to communities composed of two dwarf shrubs only was found in the drought manipulation (Figure 1). No similar pattern was observed for the control, resulting in a significant interaction effect between the drought and the functional diversity level for *Calluna vulgaris*. All modifications of these shifts, however, were stronger with increasing diversity levels (Table 3).

Discussion*Effects of sudden drought on flower phenology*

The experimental data are in accordance with our hypothesis stating that extreme drought events advance flower onset (the mid-flowering date) and extend the flowering period of Central European plant species. Changes in the flowering period were highly significant and uniform over both years of observation (Figure 2). The magnitude of shift (around 4 days) observed in our data is remarkable when compared to findings from long-term observational datasets accounting for gradual warming over recent decades. Generally, global warming has advanced the first flowering date of plants by 4 days per degree C on average in the temperate zone (Memmott *et al.*, 2007). This phenological shift due to gradual warming is of the same magnitude as the phenological shift due to a single extreme drought event according to our data. In contrast, for Mediterranean plants, evidence suggests that dry conditions delay flowering phenophases (Penuelas *et al.*, 2004; Llorens & Penuelas, 2005), especially for drought sensitive species (Ogaya & Penuelas, 2003).

Studies focusing on climate warming that monitor many plant species over large areas and long time scales report comparable phenological shifts of 2 days per decade for Central Europe (Menzel & Fabian, 1999), 4.5 days per decade for the British Isles (Fitter & Fitter, 2002), 1.2-2.0 days per decade for North America (Walther *et al.*, 2002), and 1.4 - 2.3 days per decade for global datasets (Penuelas & Filella, 2001; Parmesan & Yohe, 2003). All these studies agree that the observed shifts are highly correlated with changes in mean temperature, especially in the months preceding the phenological event.

Probably, warming remains the most important driver of phenological shifts - observed as linear trends over the years - in the northern hemisphere (Root *et al.*, 2003; IPCC, 2007). It has been demonstrated that phenology is responsive to the temperature of the preceding months (Menzel *et al.*, 2006). However, our results suggest, that a single extreme drought event can have effects on flower phenology of similar or higher magnitude than gradual warming. We suppose that, taking the impact of extreme weather events on flower phenology into account, unexplained inter-annual variance observed so far in datasets solely based on gradual warming might be reduced. Zavaleta *et al.* (2003) come to a comparable conclusion in a study of grassland phenological response to elevated temperature, carbon dioxide, precipitation, and nitrogen deposition. They state that individual species were more sensitive to inter-annual variability and extreme events than to mean changes in environmental and resource conditions. Drought-induced modifications in the timing of flowering are known to affect the flower number and seed set (Saavedra *et al.*, 2003), which in turn affect reproductive fitness.

Effects of heavy rainfall on flower phenology

Our experimental data are partly in accordance with the hypothesis stating that heavy rainfall events compress the flowering period of plant species. However, our data suggest that heavy rainfall events do not influence the mid-flowering date. Generally, little is known about either the effects of heavy rainfall or of increased and reduced annual precipitation on flower phenology (Rathcke & Lacey, 1985; Ashton *et al.*, 1988). A compression of the flowering period by increased rainfall intensities combined with longer intervals of drought is reported from a tallgrass prairie in Kansas (Fay *et al.*, 2000). An advance of phenological development after additional water supply has been reported for woody species of higher latitudes (Wielgolaski, 2001). An increased amount of precipitation together with an increase in the length of the rainy season by 3 weeks in Spring had no consistent impact on phenology in an annual Californian grassland (Cleland *et al.*, 2006), and a double precipitation treatment without changes in the rainfall timing had no significant effect on flowering phenology in a perennial grassland in Oklahoma (Sherry *et al.*, 2007).

Divergence of flower phenology after extreme weather events

Our experimental data on 10 common European species including herbs, grasses and dwarf shrubs provide no evidence for a divergence in the advance and delay of the mid-flowering date or an extension and compression of the flowering period as a function of early versus late seasonal reproductive period. Analyses of large phenological datasets suggest that flower phenology responds most sensitively to mean monthly temperatures in the month of flower onset and the two preceding months (Menzel *et al.*, 2006). In our experiment 3 out of 10 species (*Genista tinctoria*, *Lotus corniculatus*, *Plantago lanceolata*) performed two distinct flowering periods during the course of a year, which were affected by the simulated extreme weather events (data not shown). Also, the impact of a single extreme weather event in Spring may vary by temporal distance to flower onset dates of various species.

Interaction between extreme weather events and functional diversity

The interaction between extreme weather events and community composition seems to play a crucial role in phenological shifts. The number of significant interactions for the seven species occurring in more than one community composition indicates that this phenomenon is no singular case, but rather a common feature (Table 2).

Facilitation by other growth forms is known to improve individual species performance (Bertness & Callaway, 1994; Bertness & Leonard, 1997). Increased disturbance and physical stress levels are thought to reduce the intensity and importance of competition and to increase the importance of facilitation (Holmgren *et al.*, 1997; Bertness, 1998; Brooker & Callaghan, 1998; Sthultz *et al.*, 2007). Callaway and Walker (1997) present examples of reduced importance of competition and increased facilitation in climatically extreme years compared to strong competition within low-stress years. The same kind of response is described for bunchgrass communities in the Rocky Mountains (Greenlee & Callaway, 1996). Kikvidze *et al.* (2006) recently showed that interactions between two dominant grassland species and their associated communities switched from competition during the early part of the growing season, when conditions were favorable, to facilitation during the late part of the growing season, when the site became more xeric. Species diversity on its own may enhance facilitation (Hacker & Gaines, 1997), and the presence of certain functional groups such as legumes is known to facilitate other species (Pugnaire & Luque, 2001; Spehn *et al.*, 2002; Beierkuhnlein & Nesshoever, 2006). Most of these studies used biomass production as a response parameter, however, facilitative neighbor effects are also reported for phenological events in harsh environments (Wipf *et al.*, 2006).

A significant interaction between an extreme weather event and functional diversity might be due to the fact that shifts in phenology are promoted as a consequence of resource partitioning due to higher functional diversity. For all significant interactions between species in a community setting (Table 2), no facilitative effect of higher functional diversity was found. All shifts were more pronounced in the more diverse communities (Table 3), with some species exhibiting shifts into different directions depending on the specific level of functional diversity. Thus, facilitation is not a direct function of functional diversity.

Conclusions

Phenological shifts are obviously driven by other factors besides temperature, moisture and photoperiodic conditions (e.g. Sawa *et al.*, 2007). We propose that field observations of altered phenological patterns related to climate change would profit from addressing the role of extreme weather events. Soil-drying might be a major environmental cue for phenological shifts. Especially with the emerging phenological network data sets which comprise data from many countries, it seems promising to broaden the debate on the effects of climate warming in ecosystems by including phenological responses to extreme weather events. Available climate data series with daily resolution should be screened for such events. On short-term time scales, extreme weather events might be even more powerful than gradual warming in disturbing the synchronization between organisms (e.g., Both *et al.*, 2006) and community organization, because their occurrence and return interval is much less predictable and the vigor of their effects may reach a decadal scale of warming. Understanding the ecosystem effects of extreme weather events is indispensable. Extreme events are forecasted to increase in magnitude and frequency along with ongoing climate warming, potentially having far-reaching consequences for ecology and evolution.

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Manuscript 6:

Invasibility of grassland and heath communities exposed to extreme weather events – additive effects of biotic resistance and fluctuating physical environment

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Abstract

Understanding the resistance of plant communities to invasion is urgent in times of changes in the physical environment due to climate change and changes in the resident communities due to biodiversity loss. Here, we test the interaction between repeated drought or heavy rainfall events and functional diversity of grassland and heath communities on invasibility, measured as the number of plant individuals invading from the matrix vegetation.

Invasibility of experimental plant communities was influenced by extreme weather events, although no change in above-ground productivity of the resident communities was observed. Drought decreased invasibility while heavy rainfall increased invasibility, a pattern that is consistent with the fluctuating resource hypothesis. Higher community diversity generally decreased invasibility, which can be explained by a combination of the fluctuating resource hypothesis and niche theory. The effects of the physical environment (extreme weather events) and biotic resistance (community composition) were additive, as they were independent from each other. Differences in the composition of invading species sets were found, and Indicator Species Analysis revealed several invading species with significant affinity to one particular extreme weather event or community composition. This finding supports niche theory and contradicts neutral species assembly.

Our data supports theories which predict decreased resistance of plant communities due to both increased climate variability and biodiversity loss. The effects of these two factors, however, appear to be independent from each other.

Introduction

Invasibility is an emergent property of ecological units such as plant communities and it is the outcome of three basic factors; (1) the physical environment, (2) the resident community, and (3) the traits of the invaders (Lonsdale 1999, Schoolmaster and Snyder 2007). For all three factors, a rich body of empirical data and theoretical considerations was generated within the last few years. Contradicting chains of reasoning nevertheless still prevail and general solutions integrating all aspects are not at hand (Fridley et al. 2007). Here, we consider the three basic factors of invasibility simultaneously within one experiment and compare the findings with current theories. Drought and heavy rainfall events of 100 year recurrence were applied to study the influence of changes in the physical environment, and two vegetation types (grassland and heath) differing in diversity allowed for simultaneous consideration of biotic resistance of the resident community. The patterns of invading species sets and the identity of successful invaders from the matrix vegetation are discussed in relation to plant functional traits.

Invasion theory applies equally well to both native and exotic invaders (Aarssen et al. 2003), and insights from community ecology are obviously relevant for invasion ecology and *vice versa* (Shea and Chesson 2002). Consequently, we call any species that enters a habitat in which it has not recently occurred an “invader”, whether or not it is a member of the regional flora.

The physical environment – drought and heavy rainfall

The fluctuating resource theory (Davis et al. 2000) states that fluctuations in resource availability is the key factor controlling invasibility. Unused resources can arise through a decrease in resource use in the resident community (e.g., due to disturbance) or through an increase in total resource abundance without immediate use by the residents (e.g., rainfall). To act as a facilitator for invasion, resource release should occur only intermittently and, to result in invasion at all, must coincide with availability of invading propagules (Davis and Pelsor 2001). Recently, this theory has been broadened by the environmental heterogeneity theory and has been shown to be in accordance with experiments and field observations (Melbourne et al. 2007).

Climate is one of the most important determinants of species distribution. Consequently, climate change is considered to be an important driver of community dynamics and invasibility. Climatic forcing, for example, has been identified as one of the major contribut-

ing factors for the increasing capability of exotic species to establish (Dukes and Mooney 1999). Especially extreme weather events can have strong implications for community composition (e.g., Buckland et al. 2001, White et al. 2001), as they create physical disturbance. Gap creation by disturbance is generally known to increase invasibility (see review in Hughes et al. 2007). However, consequences of extreme weather events such as drought and heavy rainfall for community resistance have hardly been addressed experimentally yet (Jentsch et al. 2007). Since weather extremes of unprecedented magnitudes and increased frequency are identified as one important aspect of current climate change (IPCC 2007), their consequences for invasibility of communities need to be considered.

The resident community – community composition and diversity

Biotic resistance, also termed the diversity resistance hypothesis, has long been hypothesized to act as a barrier against invasion (Elton 1958). Within this framework, resistance is thought to be due to a more competitive environment with increasing species richness. At fine spatial scales (the level at which all occurring plant individuals interact), more diverse communities generally decrease invasibility (see recent review in Fridley et al. 2007). Theoretically, this pattern can be explained by niche filling (Tilman 2004) or even by neutral processes (Hubbell 2001, Herben et al. 2004). It is, however, highly controversial which facet of diversity (species richness, functional group richness, key species with special importance of dominants) is responsible for this decreasing invasibility with increasing diversity (see review in Hooper et al. 2005).

In stochastic niche models, low invasibility is predicted to result from uniformly low levels of resources or open niches, not from diversity *per se* (Tilman 2004). This view supports the general theory of fluctuating resources as a trigger of invasion (see above). More diverse systems, however, generally fulfill the conditions of generating low levels of unused resources better than less diverse systems (see reviews and meta-analysis by Balvanera et al. 2006, Cardinale et al. 2006).

The absence of disturbance - or more generally of spatio-temporal heterogeneity - from many experimental studies on the relationship between diversity and invasibility has been criticized recently as being unrealistic and might even explain part of the invasion paradox (a negative relation between invasion and diversity at fine scales and the opposite pattern at large scales; Fridley et al. 2007). Spatial and temporal heterogeneity is even seen as a major driver of invasibility (Melbourne et al. 2007), and should therefore not be excluded in ex-

periments (Richardson and Pysek 2006). Consequently, we compare the interaction of biotic resistance and the role of plant diversity with disturbance or fluctuating resources caused by extreme weather events within the same experiment.

Based on the insurance hypothesis (Yachi and Loreau 1999), which states that more diverse systems are expected to be more resilient against perturbations, we expect that effects of extreme weather events and biotic resistance are non-additive. Viewed from the perspective of the fluctuating resource hypothesis, and given that a disturbance is a relatively discrete event in time that disrupts ecosystem structure and changes resource availability (White and Pickett 1985), the increased “predictability” (McGrady-Steed et al. 1997) or “reliability” (Naeem 1998) of more diverse communities would imply that less unused resources would occur even in times of strong environmental perturbations due to complementarity in disturbance response traits (White and Jentsch 2001). Since any situation in which residents do not keep resources at uniformly low levels is a potential colonization opportunity (Shea and Chesson 2002), the insurance hypothesis predicts less invasion opportunities in more diverse systems even in face of disturbance.

Consistent with this, e.g., Tilman *et al.* (2006) demonstrated a linear relationship between species diversity and the recovery of grassland after severe drought. But mixed results are also reported. A stabilizing effect of plant diversity during a manipulated extreme drought was found for below-ground biomass, but not for above-ground biomass in a semi-natural Central European grassland (Kahmen et al. 2005). Despite these studies, no experiment so far provides data for both controlled weather manipulations and controlled diversity levels. The reported results rely either on naturally occurring weather events without comparisons with controlled weather conditions, or on naturally occurring species diversity, which might also go along with differences in substrate and stand history. In aquatic microcosms, however, evidence suggests that community level resilience (Steiner et al. 2006) and stability (McGrady-Steed et al. 1997) increases with increasing diversity within and between trophic levels.

The traits of the invaders

Neutral or random assembly have been demonstrated to effectively predict observed processes in community invasibility (Herben et al. 2004). The validity of the neutral theory (Hubbell 2001) in this context, however, is questioned by the notion that resident species inhibit the establishment and growth of species similar to them more strongly than they inhibit

species with less similar functional traits (Fargione et al. 2003, Strauss et al. 2006, Mwangi et al. 2007), thereby supporting Darwin's naturalization hypothesis (Darwin 1859), which assumes intense competition between congeners, leading to easier invasion by non-allied genera. Modern analogues to this hypothesis are stochastic niche models (Tilman 2004). The above cited empirical studies evaluated the invasion success of species in relation to their functional and/ or phylogenetic similarity to resident species. We apply another approach to the same question by asking if the invaders themselves are randomly invading communities of different composition and environmental constraints or if significant differences in their affinity can be found.

With regard to the three basic factors which determine invasibility (the physical environment, the resident community, and the traits of the invaders), we test the following hypotheses. (1) Extreme weather events act as physical disturbance in the resident stand, with drought limiting water availability and heavy rainfall limiting soil oxygen availability, thereby leading to increased invasibility due to higher resource availability caused by reduced competition after the events according to the fluctuating resource hypothesis. (2) Increased diversity in terms of species richness and functional composition reduces invasibility according to expectations from the biotic resistance hypothesis. (3) Furthermore, increased diversity buffers effects of extreme weather events on invasibility according to the insurance hypothesis, with diversity and disturbance being non-additive in their effects on community invasibility. (4) Community assembly is not neutral, but depends on the identity of invaders.

Methods

Experimental Design

The EVENT-experiment (Jentsch et al. 2007) is located in the Ecological Botanical Garden of the University of Bayreuth, Germany (49°55'19"N, 11°34'55"E, 365m asl). Mean annual temperature is 7.8°C. Mean annual precipitation reaches 709 mm. Precipitation is distributed bi-modally with a major peak in June/July and second peak in December/January (data: German Weather Service). The experiment was carried out with three fully crossed factors. The factors were (1) extreme weather events (drought, heavy rain, and control), (2) community diversity (two species of one functional group, four species of two functional groups, and four species of three functional groups), and (3) two different vegetation types (grassland and heath). The setup consisted of 5 replicates of each factorial combination, with a total of 90 2 x 2 m plots. The factors are applied in a randomized block design with the

vegetation types and diversity levels blocked and randomly assigned within each weather manipulation (Jentsch et al. 2007). The soil of the experimental site consisted of homogenized substrate from a nearby sand quarry (about 80 cm in depth) underlain by drainage facilities to avoid soil related singularities. The topsoil from this quarry was used to build an upper horizon of 20 cm depth containing higher amounts of organic material (2 % total carbon against 0.2 % in the lower horizon). The texture of the soil body was loamy sand (82 % sand, 13 % silt, 5 % clay) with pH = 4.5 in the upper and pH = 6.2 in the lower soil layer (measured in 1M KCl).

The physical environment – drought and heavy rainfall

The weather manipulations consisted of extreme drought, heavy rainfall and ambient conditions for control. Intensity of the treatments was based on the local 100-year extreme event in each category. Vegetation periods (March to September) 1961-2000 were used as the reference period (data: German Weather Service). Gumbel I distributions were fitted to the annual extremes, and 100-year recurrence events were calculated. Drought was defined as the number of consecutive days with less than 1 mm daily precipitation. Accordingly, a drought period of 32 days and a rainfall extreme of 170 mm over 14 days were applied in the experiment during peak growing season in June 2005 and 2006. Maximum values in the local climate data set were 33 days without rain during June and July 1976 and 152 mm of precipitation during 14 days in June 1977.

Drought was simulated using rain-out shelters that permitted nearly 90 % penetration of photosynthetically active radiation. Near-surface air temperature was slightly (mean 2005: + 1.2°C; mean 2006 +1.4°C), but not significantly (pairwise t-test with Bonferroni correction: 2005: $p = 0.12$; 2006 $p = 0.26$) increased by the roofs during the weather manipulation period. Strong greenhouse effects were avoided by starting the roof at 80 cm height, allowing for near-surface air exchange.

Heavy rainfall was realized using portable irrigation systems. The whole amount of added water was divided into two applications per day to constantly ensure high soil water saturation. If natural precipitation occurred, then the amount of rain was subtracted from the respective dose. Lateral surface flow was avoided by the application of small plastic sheet pilings around treated plots.

The resident community – community composition and diversity

Overall, ten plant species were used to install experimental plant communities of various diversity levels, which represent naturally occurring species combinations in Germany (Table 1). Two richness levels (two and four species) and three functional diversity levels (2⁻: one growth form, 4⁻: two growth forms, and 4⁺: two growth forms with a legume being present) were created. Species were chosen with respect to their belonging to one of the desired functional groups (grasses, herbs, legumes, dwarf shrubs), to their life-span (perennials), to their overall importance in nearby and central European grassland systems, and to the fact that they can naturally occur on similar substrate. We use only very abundant species on comparable soil substrate. 100 individual plants per plot were planted from pre-grown, even-aged individuals in a systematic hexagonal grid with 20 cm distance between neighbors in April 2005. All grasses and herbs were grown from seeds in autumn 2004, the three dwarf shrub species were two years old when transferred to the experimental site.

The traits of the invaders - Response parameters

Invasibility of the experimental communities was recorded 3 times per year: before and after the weather manipulations in early summer, and in fall. Invading plant individuals were collected from the inner square meter of each plot, and subsequently separated by species. Removal took place only after the first true leaves (after the cotyledons) emerged. At this point in development, we expected that number of individuals give a measure of established invaders rather than chance germinations. All grasses were grouped together into one aggregate due to difficulties in determining the species of small grass seedlings. For each plot, the number of individuals per species was determined. The ten target species of the experiment were removed from the subsequent analysis, their offspring was removed only from those plots where they were not designed to be in the target species mix.

Data analysis

Linear models accounting for the split plot design with the six community compositions being blocked within the weather manipulations were combined with analysis of variance (ANOVA) to test for significant differences between groups. Homogeneous groups were identified by Tukey HSD post hoc comparisons. Level of significance was set to $p < 0.05$. Prior to statistical analysis, data was log or square root transformed if conditions of normality

were not met, or to improve homogeneity of variances. Both characteristics were tested by examining the residuals versus fitted plots and the normal qq-plots of the Linear Models (Faraway 2005).

In order to test for differences in invading species sets between factorial groups, we conducted Multi Response Permutation Procedures (MRPP). In the case of significant differences, pair-wise comparisons with Bonferroni corrections of the significance level were performed between all levels of the factor. MRPP is a non-parametric procedure for testing the hypothesis of no difference between two or more *a priori* groups. Test statistics describe the separation between the groups. Sørensen Index was used as the dissimilarity measure due to its robustness with vegetation data (Faith et al. 1987). MRPP was applied according to the method described by McCune and Grace (2002) using the function *mrpp* of package *vegan* for the R statistics system (R Development Core Team 2006). An unconstrained ordination was applied to illustrate the similarity between invading species compositions of each plot. We used Non-metrical Multidimensional Scaling (NMDS) according to the procedure recommended by Minchin (1987) using the function *metaMDS* of package *vegan* for the R statistics system (R Development Core Team 2005).

In order to examine the affinity of particular species to different weather manipulations or community compositions, we conducted an Indicator Species Analysis (Dufrene and Legendre 1997) on abundance data with the function *duleg* of package *labdsv* for the R statistics system (R Development Core Team 2006).

Table 1: Communities of two vegetation types (grassland, heath) are used in three functional diversity levels, resulting in six species combinations (Abbreviations: G: grassland, H: heath, 2/4: number of species, -: without legume, *: with legume).

Abbreviation	vegetation type	diversity level	Description	Species
G2 ⁻	grassland	2 ⁻	two species, one functional group (grass)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i>
G4 ⁻	grassland	4 ⁻	four species, two functional groups (grass, herb)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i> , <i>Plantago lanceolata</i> , <i>Geranium pratense</i>
G4 ⁺	grassland	4 ⁺	four species, three functional groups (grass, herb, legume herb)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i> , <i>Plantago lanceolata</i> , <i>Lotus corniculatus</i>
H2 ⁻	heath	2 ⁻	two species, one functional group (dwarf shrub)	<i>Calluna vulgaris</i> , <i>Vaccinium myrtillus</i>
H4 ⁻	heath	4 ⁻	four species, two functional groups (dwarf shrub, grass)	<i>Calluna vulgaris</i> , <i>Vaccinium myrtillus</i> , <i>Agrostis stolonifera</i> , <i>Deschampsia flexuosa</i>
H4 ⁺	heath	4 ⁺	four species, three functional groups (dwarf shrub, legume shrub, grass)	<i>Genista tinctoria</i> , <i>Vaccinium myrtillus</i> , <i>Agrostis stolonifera</i> , <i>Deschampsia flexuosa</i>

The number of invading plant individuals declined in our experiment in the second year, although no strong difference in the overall weather patterns was apparent. A limited soil seed bank in the sandy substrate of this experiment seemed to be the likely reason for this decline, as species typical for the former environment of the topsoil occurred only in the first year of this experiment. Consequently, the effects in 2005 seemed to be driven by founder effects and can not convincingly be related to the experimental treatments, a fact that is not surprising because ecological systems are known to show inertia and diversity effects in experiments also become apparent only from the second year on if founded from seeds (Pacala and Tilman 2002). Therefore, we focus on the year 2006 in the following presentations of results and in the discussion.

Results

Overall, 10631 individuals of 66 species or aggregates were found in 2006. The majority of the invading species also occurred in the vicinity of the experimental site and comprise common grassland and some ruderal species (data not shown).

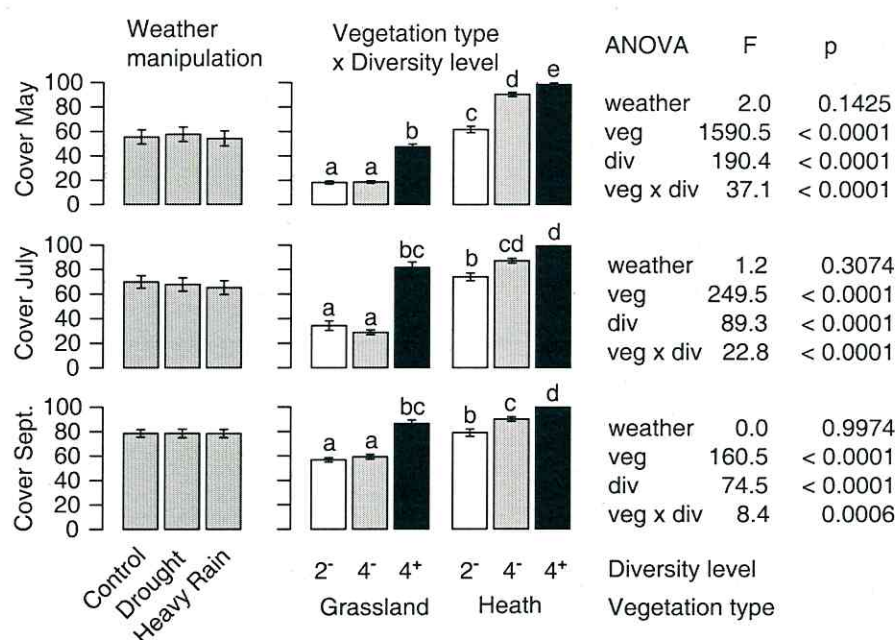


Figure 1: Above-ground plant cover of experimental communities in May, July and September 2006. Weather manipulations took place between the first and second measurement. Shown are mean values and standard errors of pinpoint measurements with 100 vertically inserted steel needles per m². Letters display homogenous groups of weather manipulations and of the interaction between vegetation type and diversity level according to TukeyHSD post hoc comparisons. No significant interaction with weather manipulation was found at any time, other ANOVA results are provided next to barplots.

The physical environment – drought and heavy rainfall

Even though the applied weather manipulations led to strong changes in soil moisture, we did not observe the expected creation of gaps in the resident stands. In fact, total resident cover as well as biomass remained surprisingly stable in face of repeated weather events of 100 year recurrence (Figure 1).

The drought manipulation, nevertheless, decreased invasibility for the whole year by 33 %, whereas the heavy rainfall manipulation nearly doubled invasibility (Figure 2a). This effect was not yet visible in spring 2006 before the second weather manipulation, significant directly after the second manipulation in summer 2006, and most pronounced in autumn (Figure 2b-d).

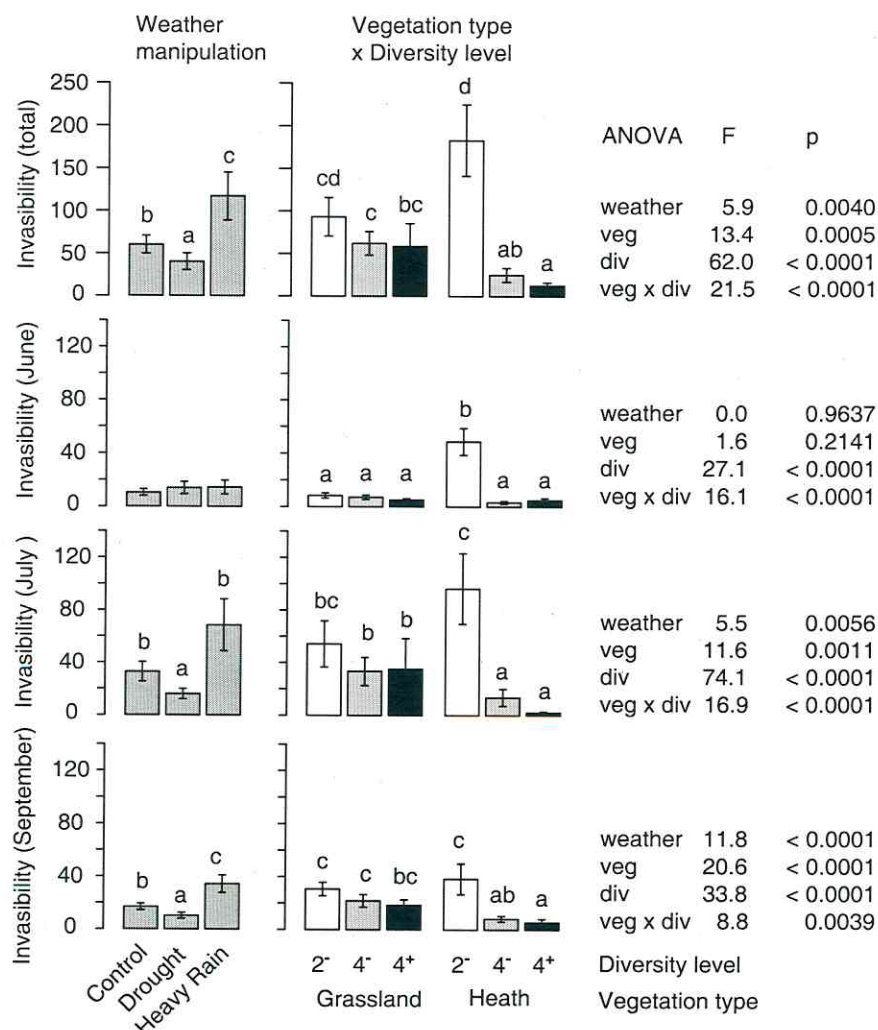


Figure 2: Total invasibility and temporal development in invasibility of experimental plant communities in 2006. Weather manipulations took place between the first and second measurement. Shown are mean numbers and standard errors of invading individuals per m². Letters display homogenous groups of weather manipulations and of the interaction between vegetation type and diversity level according to Tukey-HSD post hoc comparisons. No significant interaction with weather manipulation was found at any time, other ANOVA results are provided next to barplots.

The resident community – community composition and diversity

Invasibility was enhanced with decreasing community diversity (ANOVA: $F = 62.0$, $p < 0.0001$, Figure 2a). The differences between diversity levels, however, were only significant between the least diverse level (2^-) and the two other levels (4^- and 4^+ ; TukeyHSD post hoc comparison).

Higher invasibility was generally found for the heath communities compared to the grassland communities. The two vegetation types also exhibited a difference in their diversity effect (interaction between vegetation type and diversity level: $F = 21.9$, $p < 0.0001$; Figure 2a). This interaction effect between vegetation type and diversity level was due to the extremely high invasibility of the least diverse heath community. However, both vegetation types showed the same general decline of invasibility with increasing diversity, with only the slope of this decline differing.

Interaction between the physical environment and the resident community

The decreased invasibility due to increasing diversity and the changes in invasibility due to the extreme weather manipulations were additive, as no significant interaction between these two factors were found (Figure 2). This means that changes in the physical environment had the same effects irrespective of vegetation type or diversity level. And, *vice versa*, biotic resistance to invasion remained constant even under fluctuating conditions in the physical environment.

The traits of the invaders

Significant differences in the composition of the invading species sets within the three factors (extreme weather event, diversity level, vegetation type) were found by the Multi Response Permutation Procedure, but these differences were small and no clear grouping occurred in the ordination (Figure 3). In particular, the differences in species composition within weather manipulations and within vegetation types were subtle, although significant. Higher compositional differences in the invading species sets were found between diversity levels of the resident communities, where total difference in the invading species sets was already 12 %. In the pair-wise comparisons of diversity levels, the lowest level differed significantly from both other levels. The interaction between vegetation type and diversity level accounted for 18 % differences in the invading species compositions, with the lowest diverse and the

highest diverse heath community being most strongly distinguished from each other and from the other communities.

Several invading species showed significant affinities to one weather manipulation (Table 2). In general, species with high affinity to the heavy rainfall treatment are known to also occur naturally in moist conditions, whereas the species with significant affinity to the drought manipulation commonly occur in drier habitats (see Ellenberg Indicator Values in Table 2). There were also species with significant affinity to one or more of the experimental plant communities (Table 3). The general pattern of decreased invasibility into the more diverse communities is displayed by the fact that grouping by diversity level also resulted in significant indicator values, but all these species showed highest relative abundances in the least diverse communities.

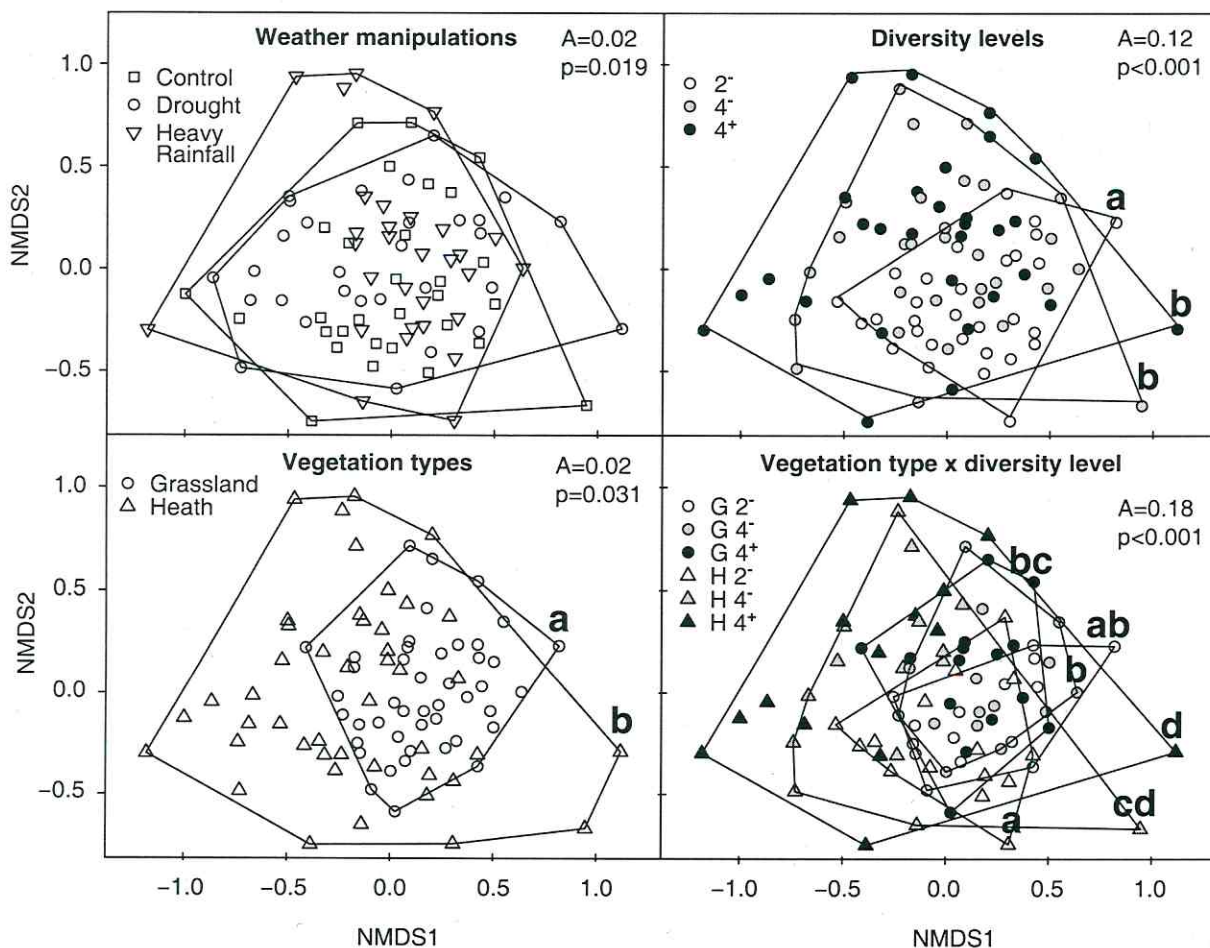


Figure 3: Ordination of species sets invading into the experimental plant communities. Shown is the output of a Non-metrical Multi-Dimensional Scaling ordination (NMDS) of invading species compositions after 20 random starts of a two-dimensional solution (final stress = 26.78, rmse = 0.0783, max residual = 0.36). Outlines of the positions of the three factors (weather manipulation, diversity level, vegetation type) and the interaction between vegetation type and diversity level (abbreviations see table 1) in ordination space (shortest distance) are shown in the four panels. Within-group homogeneity (A) and significance of differences between groups (p) are based on a Multi Response Permutation procedure (MRPP). Letters next to the outlines indicate homogenous groups within the factor according to pair-wise MRPP comparisons with Bonferroni corrections between all factor levels.

Discussion

We start the discussion with a closer look at the mechanisms which may have caused the different reactions of invasibility in response to the applied drought and heavy rainfall events. After these considerations of the role of the physical environment, we turn towards the role of biotic resistance or the resident species composition on determining invasibility. We continue by discussing the interaction between both the physical environment and biotic resistance, or more explicitly, the missing interaction between these two drivers of invasibility. Finally, the invading species traits and the differences in invading species sets are used to support niche theory against neutral theories.

The physical environment – drought and heavy rainfall

Application of weather events with 100 years recurrence did not alter resident above-ground cover, i.e. they did not provide changes in the invasibility by creating physical disturbance of the biomass or by creating bare ground in the first (Kreyling et al. in press) or second year of the weather manipulations in our experiment (Figure 1). We find no significant correlation between invasibility and above-ground productivity or cover of the resident stand (see Figure 4 with above-ground cover as an example).

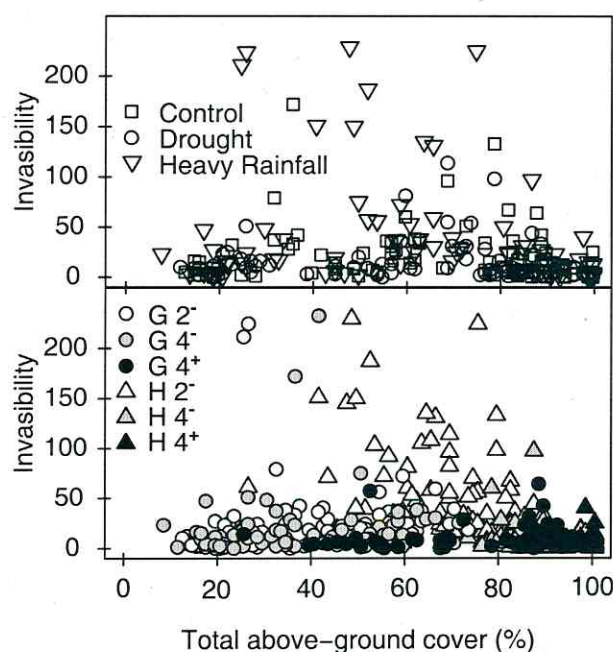


Figure 4: Invasibility (individuals m^{-2}) was not related to total aboveground cover of experimental plant communities ($r^2 = 0.04$ for a linear regression). Upper part: separated by weather manipulation, lower part: separated by the interaction between vegetation type and diversity level (abbreviations see table 1).

But despite the missing effects of extreme weather events on above-ground resident productivity, the applied events changed invasibility. The observed effects support expectations from the fluctuating resource hypothesis (Davis et al. 2000) or the environmental heterogeneity hypothesis (Melbourne et al. 2007) with increased invasibility during and after times of enhanced resource availability (heavy rainfall), and decreased invasibility during and after times of strong competition and resource limitation (drought). Fluctuating resources therefore challenge the competitive interaction between resident and invading species. The first experimental set-up to test the fluctuating resources hypothesis, in fact, applied weather manipulations remarkably similar to ours in an old field at Cedar Creek, USA (Davis and Pelsor 2001).

Water is known to be the limiting resource for plant performance in semi-arid ecosystems, with increased soil moisture availability generally enhancing invasibility (e.g., Thomsen and D'Antonio 2007). A review (Dukes and Mooney 1999) has shown that in dry regions, increase of water supply (whether by natural rainfall or by experimental additions) generally increases the invasibility, whereas imposed drought conditions decrease invasibility of the same communities (Davis et al. 1998).

It is somewhat surprising that water availability was able to act as the main determining factor in the temperate environment of our experiment. The sandy substrate may play an important role here, leading to fast water percolation. Furthermore, indirect effects such as decreased mineralization may add to our findings (Davis and Pelsor 2001).

Besides the effects of the manipulations themselves, the temporal development of invasibility is remarkable (Figure 2 b-d). Interestingly, the extreme weather effects were most significant in autumn, two months after the weather manipulations in June and after one removal of all initial invaders. Such a legacy of the effect is also described in another field experiment where fluctuations in water availability as short as a few weeks had a large impact on plant invasion success (survival and percentage cover) for up to one year following the fluctuations (Davis and Pelsor 2001). There, it was concluded that the primary reason for the legacy effect of wet or dry spells is their pronounced impact on the survival of the germinating seedlings. Even though we find a similar pattern, we cannot explain it by the proposed mechanism, because invaders present during the phase of precipitation manipulations were removed after the manipulations ended in July. A significant treatment effect, nevertheless, was still found in September. Thus, competitive balance of the resident community is affected longer than the short duration of the weather manipulation itself. Overall, our findings on in-

visibility related to changes in the physical environment can convincingly be explained by the fluctuating resource hypothesis.

The resident community – community composition and diversity

The fluctuating resource hypothesis, however, does not necessarily imply a relationship between resident species diversity and its susceptibility to invasion (Davis et al. 2000). Like many other (experimental) studies (see review in Fridley et al. 2007), we observe a decrease in invasibility with increasing diversity level. Although not a true diversity experiment due to the fact that diversity levels were not repeated with different species sets, the consistency between two functionally different vegetation types in our experiment implies some generality of this pattern. Such a negative relationship between resident diversity and invasibility can be brought into accordance with the fluctuating resource hypothesis when viewed together with ideas in stochastic niche concepts or niche opportunities. These concepts predict higher niche filling in functionally more diverse communities, leading generally to low levels of unused resources (Shea and Chesson 2002, Tilman 2004). Accordingly, total biomass of introduced species is often positively correlated with levels of available (unconsumed) resources, such as nitrate, initial bare ground, or light transmittance (Fargione et al. 2003).

Within the ongoing debate about which facet of diversity is responsible for the overall biotic resistance effect (see review by Richardson and Pysek 2006), competitive dominance has been proposed to be of high importance (Wardle 2001). Heath communities are naturally restricted to nutrient-poor habitats in Central Europe, and their plasticity in reacting to changing conditions may be limited due to their perennial, woody growth form. Under conditions of increased nutrient supply, grasses commonly out-compete dwarf-shrubs (Wessel et al. 2004). Thus, the particular growth form and life strategy may hint at a competitive disadvantage of the dwarf shrubs and could – rather than richness - help to explain the high levels of invasibility into the lowest diverse heath community, which is composed of only two dwarf shrubs.

The highly artificial community set-up of even-aged and evenly distributed plant individuals could have had an effect on invasibility itself besides being different from natural communities, but recent findings suggest that evenness of resident communities has no effect on invasibility in grasslands (Mattingly et al. 2007). Our findings generally support the biotic resistance hypothesis, which can be explained by niche theory.

Interaction between the physical environment and the resident community

The effects of fluctuating resources (due to the weather manipulations) and biotic resistance (due to community composition) were independent in our experiment, which means that the enhancement of biotic resistance due to higher diversity is not altered by fluctuating environmental conditions. No additional buffering in the more diverse communities *sensu* the insurance hypothesis (Yachi and Loreau 1999) was apparent. Resource fluctuations and differences in biotic resistance had about the same effect on invasibility (Figure 2), but we assume that their net balance will strongly, and maybe not even linearly, depend on differences in community composition (not only species richness) and magnitude of disturbance.

The observed pattern of biotic resistance in a fluctuating physical environment in our experiment can be explained by linking niche concepts and the fluctuating resource hypothesis. Theoretical models, however, provide no general support for the fluctuating resource hypothesis. Whether environmental fluctuations increase or decrease invasibility depends further on the interaction in timing of fluctuations and response by residents and invaders (Schoolmaster and Snyder 2007). This is in accordance to Shea and Chesson (2002), who state that invaders must nevertheless have an advantage over residents in some places or times via different life-history traits. This contradicts neutral assembly theories (Hubbell 2001, Herben et al. 2004), and we follow these ideas by having a closer look at community assembly processes and specific traits of the invaders.

The traits of the invaders

Subtle, but significant differences between the invading species sets were found, with stronger differences between the experimental plant communities than between the applied weather manipulations. The Indicator Species Analysis revealed several species with significantly higher affinity to one of the weather manipulations or resident community compositions. Species identity of the invading species therefore mattered for their invasive success. This clearly contradicts expectations from neutral species assembly (Hubbell 2001, Herben et al. 2004). Even short term resource fluctuations can therefore determine not only invasibility in general, but also invading species identity and, presumably, future community development.

Our findings indicate that short term changes in water availability already differentiate between the invading species. Species show successful establishment under conditions that, although only during the short manipulation events, resemble the conditions of their natural environments (Table 2). The conditions at time of seedling establishment are therefore of high

importance for the species composition of a given environment. This pattern can be explained in relation to niche theory; species with niche requirements poorly represented in relation to niche width at a given time may establish with relatively little resistance (Tilman 2004). From this study, however, we are not able to tell if these species, once they are established, would also survive in the long run, because they were removed after establishment. The removal of invaders causes inevitably minor soil disturbance, plots with higher numbers of invading individuals therefore also received a slightly increased density of soil disturbance. This potentially confounding factor is not further considered here.

Interestingly, all species with significant affinity to one of the grassland communities have a pappus (Table 3). Canopy roughness of grassland seems to favor this dispersal mode. In the heath communities, however, seeds with pappuses were often trapped in the more complex canopy of the stands, preventing them from reaching the ground (personnel observation). Therefore, in heath, small sized wind dispersed species without winged organs are facilitated. Furthermore, ant dispersal seems to be especially successful in the heath systems. Again, this contradicts expectations from neutral species assembly (Hubbell 2001, Herben et al. 2004) and points at the importance of individual species traits for successful invasion (Funk and Vitousek 2007). The observed differences in invasion success warn furthermore that general conclusions about invasibility of communities should not be drawn from studies on single invading species (Emery 2007).

Table 2: Invading species with significant indicator values for weather manipulations according to an Indicator Species analysis of all species which were found with more than 10 individuals in 2006. Shown are relative abundance values in each group and the significance p. Highest relative abundance values between groups are set off bold. Ellenberg indicator values of ecological behaviour for moisture run from 1 - extreme dryness - to 9 - often water saturated - (Ellenberg et al. 2001). If identification was not successful to the species level, values are given in parenthesis as range between the possible species.

	Control	Heavy Rainfall	Drought	p	Ellenberg moisture
<i>Juncus bufonius</i>	0,23	0,73	0,03	0,011	7
<i>Epilobium spec</i>	0,24	0,67	0,09	0,017	(5-7)
<i>Juncus spec</i>	0,28	0,64	0,09	0,025	(7-9)
<i>Taraxacum officinale</i>	0,26	0,62	0,12	0,001	5
<i>Carex c.f. ovalis</i>	0,26	0,57	0,17	0,025	7
<i>Trifolium repens</i>	0,26	0,48	0,27	0,011	5
<i>Sonchus spec</i>	0,00	0,40	0,60	0,020	(4-5)
<i>Rumex acetosella</i>	0,17	0,31	0,52	0,027	3

Table 3: Invading species with significant indicator values for community compositions (vegetation type x diversity level) according to an Indicator Species analysis of all species which were found with more than 10 individuals in 2006. Shown are relative abundance values in each group and the significance $p_{vt \cdot dl}$. Highest relative abundance values between groups are set off bold. p_{vt} indicates significance between vegetation types and p_{dl} between diversity levels.

vegetation type	dispersal agent	Grassland			Heath			$p_{vt \cdot dl}$	p_{vt}	p_{dl}
		A	B	C	A	B	C			
<i>Conyza canadensis</i>	wind (pappus)	0,62	0,26	0,09	0,01	0,01	0,00	0,009	0,001	0,159
<i>Gnaphalium uliginosum</i>	wind (pappus)	0,44	0,25	0,25	0,06	0,00	0,00	0,011	0,001	0,108
<i>Taraxacum officinale</i>	wind (pappus)	0,36	0,14	0,16	0,25	0,08	0,02	0,013	0,005	0,002
<i>Sonchus spec</i>	wind (pappus)	0,30	0,50	0,00	0,20	0,00	0,00	0,004	0,099	0,189
<i>Trifolium repens</i>	wind/ vegetat.	0,12	0,31	0,26	0,07	0,13	0,11	0,025	0,002	0,010
Lamiaceae spec	ants	0,00	0,00	0,00	1,00	0,00	0,00	0,017	0,221	0,114
<i>Cerastium glomeratum</i>	wind/ water	0,08	0,00	0,00	0,92	0,00	0,00	0,002	0,023	0,004
<i>Spergula arvensis</i>	wind	0,05	0,10	0,03	0,81	0,00	0,01	0,001	0,224	0,001
<i>Rumex acetosella</i>	unspecialized	0,18	0,08	0,11	0,58	0,03	0,02	0,002	0,666	0,001
Poaceaea aggregate	wind	0,25	0,10	0,09	0,51	0,04	0,02	0,001	0,988	0,001
<i>Viola arvensis</i>	ants	0,08	0,17	0,00	0,42	0,00	0,33	0,027	0,026	0,465

One important interaction not considered in our study is propagule pressure or the availability of propagules at favorable times for invasion (Ejrnæs et al. 2006, Thomsen and D'Antonio 2007). Propagule pressure appears to be especially important for invasibility because at least natural temperate grassland communities are recruitment limited (Tilman 1997), and ecosystems in general rarely show evidence of being saturated with species (Sax et al. 2007).

Conclusions

Increasing variability in precipitation and presumably also in other climate parameters are one important aspect of climate change (IPCC 2007). This development in the physical environment will have strong effects on plant community invasibility and therefore community development. In accordance to the fluctuating resource hypothesis, this implies that the predicted increase in variability of precipitation due to climate change may decrease resistance against invasion, or more general, that stochastic factors strongly influence invasibility.

On the other hand, our data support the notion that biotic resistance of community diversity is additive to such effects and can be explained by the interplay between the fluctuating resource hypothesis and niche opportunities. This fact highlights the need to protect diversity as an important tool to mitigate unwanted changes in ecosystems.

Understanding the role of environmental variation in the assembly and maintenance of communities is vital to our ability to predict community development - and thereby maintain ecosystem services. Linking fields such as invasion biology, community ecology and global change research seems necessary to improve our understanding of plant community development in a changing world.

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Manuscript 7:

Recurrent soil freeze-thaw cycles enhance grassland productivity

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Summary

- Ongoing global warming will increase the frequency of soil freeze-thaw cycles (FTC) in cool-temperate and other high-latitude regions. The spatial relevance of seasonally frozen ground amounts to about 55 % of the total land area of the Northern Hemisphere. Evidence suggests that freeze-thaw cycles (FTC) contribute to nutrient dynamics. Knowledge of their effects on plant communities is scarce, although plants may be the decisive factor in controlling ecosystem functions such as nutrient retention.
- Here, we analyse the effects of five additional FTC in winter for the above- and below-ground productivity of experimental grassland communities and soil enzymatic activity over the following growing season.
- FTC increased the above-ground productivity but reduced root length over the whole subsequent growing season. In summer, no changes in soil enzymatic activities representing the carbon, nitrogen and phosphorus cycle were observed in the FTC manipulated plots, except for an increased cellobiohydrolase activity.
- Changes in productivity resulting in an increased shoot-to-root ratio and shifts in timing are capable of altering ecosystem stability and ecosystem services, such as productivity and nutrient retention.

Introduction

Ongoing global warming (IPCC, 2007) will increase the frequency of soil freeze-thaw cycles (FTC) in cool-temperate and other high-latitude regions previously subject to prolonged winter soil frost periods. The maximum extent of seasonally frozen ground is about 55 million km² or 55 % of the total land area of the Northern Hemisphere (Zhang *et al.*, 2003). Although in some areas temperature increase will lead to an overall disappearance of soil freezing, in many regions a reduced snow cover in winter, and the consequentially decreased insulation of the soils against freezing, may increase FTC in frequency (Groffman *et al.*, 2001). Observations and future projections show that reduced amounts of snow increase the number of freeze-thaw events especially at temperate sites even though annual soil freezing days generally decline with increasing mean winter air temperature (Henry, in press).

FTC are a major factor contributing to the release of nutrients due to a physical disruption of soil aggregates and humic material (Christensen & Christensen, 1991; Herrmann & Witter, 2002; Grogan *et al.*, 2004). Additionally, a burst of nutrients is released from the biomass components that do not survive FTC (Schimel & Klein, 1996). Consequently, microbial activity increases sharply after thawing, leads together with the high water content of the soils to anaerobic microsites, and promotes processes such as denitrification (Sharma *et al.*, 2006). Transient N₂O effluxes are therefore another well known effect of FTC (Muller *et al.*, 2002; Ludwig *et al.*, 2006; Morkved *et al.*, 2006). However, the described effects cause only short term changes in the activity patterns of soil microbiota because 1 – 2 weeks after thawing, FTC treated soils can no longer be distinguished in the activity patterns from control soils that were not subjected to freezing and thawing (Sharma *et al.*, 2006). The concentrations of dissolved organic carbon and nitrogen, which are higher compared to control soils right after thawing, reach the base level 20 days later (Sharma *et al.*, 2006). The described scenario is typical for one FTC, but the consequences of consecutive FTC for the biotic and abiotic fraction of the soil are quite unclear (Henry, 2007). It can be speculated however that repeated FTC influence seasonal patterns of microbial activity and biogeochemical processes stronger than a single freeze-thaw event, even though evidence suggests that the response in microbial activity is weaker with every new FTC (Schimel & Klein, 1996). Long-term changes in plant community structure or plant phenology may have an indirect effect on bacteria, fungi and archaea, since rhizosphere effects through plants are among the factors most strongly influencing microbial presence (Wallenstein *et al.*, 2007; Yergeau *et al.*, 2007). Any external factor influencing plants may therefore indirectly affect microbes and vice versa.

Plants are known to be susceptible to air freeze-thaw events (Kennedy, 1993; Gorsuch & Oberbauer, 2002). Nevertheless, winter is no longer viewed as a dormant season, as it has been shown that vascular plants are performing photosynthesis under snow cover (Starr & Oberbauer, 2003), and even during periods with air and soil temperatures below zero (Steenberg-Larsen *et al.*, 2007). In the latter study, winter photosynthesis contributed to almost 20 % of annual photosynthesis in a subarctic heath ecosystem. Increased frequency of FTC had no effect on the activity of the plants during winter, but resulted in increased carbon uptake in early summer. The study of Steenberg-Larsen *et al.* (2007) is the only study apart from ours that evaluated the role of soil FTC in the performance of the plant-soil system over the following growing season. Ecosystems might react differently, however, to FTC depending on the type of management, the geographical region, the soil type, and the plant community. The potential of plants to acquire nutrients from the enhanced soil solution pool after FTC appears to be especially important in this respect. Uptake capacity early in the growing season may differ substantially between plant functional types such as grasses and dwarf shrubs, legumes and non-legumes. Alpine and arctic (Bilbrough *et al.*, 2000; Grogan *et al.*, 2004), as well as temperate (Andresen & Michelsen, 2005) species are known to even acquire nitrogen in winter. Alternately, root tissue mortality due to FTC by frost heaving and physical damage (Robitaille *et al.*, 1995; Tierney *et al.*, 2001) may result in increased labile carbon inputs to soil, thereby enhancing microbial activity. Studies focusing on plant performance are therefore necessary to fully evaluate freeze-thaw effects on ecosystem nutrient cycles (Grogan *et al.*, 2004; Henry, 2007).

Here, we studied whether increased soil FTC causes alterations in ecosystem functioning over a whole growing season in a temperate grassland. In particular, we tested the effects of additional FTC on above- and below-ground plant productivity and soil enzymatic activity over the subsequent growing season in experimental grassland communities. We hypothesized that (1) soil freeze-thaw cycles (FTC) in winter increase plant community productivity over the ensuing vegetation period. We additionally assumed that even though plant communities may show long-term reactions, microbial response and regeneration to freeze-thaw cycles is fast; therefore (2) soil enzymatic activities of bacteria, fungi and archaea in summer are no longer influenced by FTC from the previous winter after one year of altered winter conditions.

Materials and Methods

Experimental Design and Site description

Our research is part of the EVENT-experiment (Jentsch *et al.*, 2007) analyzing the effects of extreme weather events such as drought, heavy rain and recurrent soil-freeze-thaw cycles on biodiversity and ecosystem functioning. The experimental site is located in the Ecological-Botanical Garden of the University of Bayreuth, Germany (49°55'19"N, 11°34'55"E, 365 m asl). Mean annual air temperature is 7.8°C; mean annual precipitation 709 mm (Data: German Weather Service, 1961–2000). With average January air temperatures of minus 1°C, the site is located at the transition between oceanic and continental climate (Lueers & Foken, 2004). Winter soil frost heavily depends on site conditions. Early snow-pack or energy fluxes from ascending ground water can prevent soil frost completely. Well-drained, open sites that are subject to snow drift may freeze for several weeks.

The soil of the experimental site consisted of homogenized substrate from a nearby sand quarry (about 80 cm in depth) underlain by drainage facilities to avoid heterogeneity in soil conditions. The topsoil from this quarry was used to build an upper horizon of 20 cm depth containing higher amounts of organic material (2 % total carbon against 0.2 % in the lower horizon). The texture of the soil body was loamy sand (82 % sand, 13 % silt, 5 % clay) with pH = 4.5 in the upper and pH = 6.2 in the lower soil layer (measured in 1M KCl).

The experiment was carried out in a two-factorial design manipulating (1) freeze-thaw cycles, and (2) plant community composition (three grassland communities differing in their diversity; Table 1). The plant communities were blocked and randomly assigned within freeze-thaw manipulations and controls, with every factorial combination replicated five times (for the full experimental setup see Jentsch *et al.*, 2007). Each of the 30 plots was two by two meters in size. 100 individual plants per plot were planted from pre-grown individuals in a systematic hexagonal grid with 20 cm distance between neighbours in April 2005. All grasses and herbs were grown from seeds in autumn 2004. Original species composition was maintained by periodical weeding. All species have life spans of several years.

Freeze-Thaw Manipulation

Soil temperature was manipulated using buried heating wires (deviflex DTIP, DEVI, Vejle, Denmark) at a soil depth of 7 cm and 20 cm apart, achieving 100 W/m². Installation was finished in the year prior to planting of the experimental communities. Heating was started as soon as soil temperature permanently stayed below 0°C for at least 48 hours (meas-

ured at -4 cm, recorded every 10 minutes in each plot). Heating was stopped when soil temperatures permanently reached positive values for another 48 hours, a period that allows for considerable recovery of soil microbial activity (Sharma *et al.*, 2006). One freeze-thaw cycle is considered to be completed when the 0°C level is crossed twice, remaining at least 48 hours in each of the three states. Exceptionally low air temperatures made it necessary to additionally cover the plots from above with transparent plastic sheets, thereby reducing the heat loss from the plots. These covers did not result in significant differences in soil moisture at the beginning of the growing period (data not shown). During the course of the experiment, a longer-lasting natural snow cover was neither present on control nor on manipulated plots. The control plots stayed completely untreated. The evenness of heating was fairly good with a mean standard deviation of 0.7°C measured at random locations within the plots at 4 cm soil depth during the heating periods. Buried heating wires were used instead of above-ground infrared heaters because we were particularly interested in the importance of below-ground effects on plant performance. Additionally, above-ground heaters are less effective in creating fast soil frost thawing. It has been shown elsewhere that plants remain photosynthetically active during periods of mild soil and air frost irrespective of freeze thaw manipulations (Steenberg-Larsen *et al.*, 2007). Our plant communities, however, sustained almost no green biomass during the winter.

In addition to the 30 plots described so far, another 5 plots containing only the least diverse plant community received the complete heating wire installations. These plots were used as an artefact control without heating.

Table 1: Grassland communities were used in three functional diversity levels.

diversity level	Description	Species
A	two species, one functional group (grass)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i>
B	four species, two functional groups (grass, herb)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i> , <i>Plantago lanceolata</i> , <i>Geranium pratense</i>
C	four species, three functional groups (grass, herb, legume herb)	<i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i> , <i>Plantago lanceolata</i> , <i>Lotus corniculatus</i>

Response parameters

Plant data was collected prior to FTC manipulations during the growing period in 2005 and after FTC manipulations during the growing period in 2006. Data acquisition was carried out in the central square metre of each plot in order to circumvent edge effects.

Above-ground Net Primary Productivity (ANPP) was quantified by complete above-ground harvests of all standing biomass twice a year (July 4, 2006; September 11, 2006), resembling local agricultural routines. Harvested biomass from the central 1 m² of each plot was dried to constant weight at 75°C and weighed.

Vegetation cover was quantified by a pinpoint method, counting the touches of plant organs at 100 vertically inserted steel needles per square metre. These values were treated as per cent cover (sampling dates: September 9, 2005; May 5, 2006; July 2, 2006; September 5, 2006).

Root length was acquired by the minirhizotron-technique. One clear plastic tube (5 cm diameter) was installed at a 45-degree angle in each plot prior to planting. Tubes were installed to a depth of 45 cm. Portions of the tubes exposed at the surface were covered with adhesive aluminium foil and the ends were capped to prevent entry of water, light, and heat. Images of 4 cm² were collected at 5 cm, 15 cm, 25 cm, and 35 cm depth along each tube by a digital camera mounted on an endoscope (sampling dates: September 7, 2005; March 21, 2006; May 15, 2006; July 2, 2006; September 2, 2006). Images were analysed for root length using the line intersection method (Tennant, 1975) within a systematic grid (10 x 10, with a grid unit of 0.2 cm x 0.2 cm).

Shoot-to-root ratio was evaluated using the ratio between above-ground cover and below-ground root length at 5 cm soil depth. Both parameters were a priori standardized to the same mean and standard deviation.

Soil enzyme activities, representing turn-over processes related to the carbon, nitrogen and phosphorus cycle were determined in June 2006 from 4 pooled samples (depth 0-5 cm) per plot using methylumbelliferone (MU) coupled substrate analogues as described by Pritsch *et al.* (2005). In brief, the increase of fluorescence due to the release of methylumbelliferone from diverse substrates was compared to a standard curve (Pritsch *et al.*, 2005). In the present experiment, the following substrates (corresponding enzymes), concentrations and incubation times were used: MU-phosphate (acid phosphatase) 500 µM 20 min, MU-xyloside (β-xylosidase) 500 µM 1h, MU-cellobiohydrofurane (cellobiohydrolase) 400 µM 1h, MU-

glucuronide (β -glucuronidase) 500 μ M 1h, MU-N-acetyl- β -glucosaminide (chitinase) 500 μ M 40 min, MU- β -glucoside (β -glucosidase) 500 μ M 1h.

Data analysis

Repeated measure analysis was conducted with linear mixed effects models (Faraway, 2006). First, the interaction of treatment and diversity level with time as random factor was evaluated. As no significant interactions were found, the model was simplified by using only treatment as fixed effect, and diversity level and time as random effects. Significance of differences ($p < 0.05$) was evaluated by Markov Chain Monte Carlo sampling of 1000 permutations (Bates & Campbell, 2001). Since the Markov chain Monte Carlo sampling compares the measured difference to the 95 % confidence interval of the permutations, the output is whether or not the data are within this confidence interval. Therefore, instead of decimal values, p can only be reported as above or below 0.05.

Linear models combined with analysis of variance (ANOVA) were applied to test for significant differences between groups at single points of time. Homogeneous groups of factor combinations (manipulation, vegetation type) were identified by Tukey HSD post hoc comparisons. Level of significance was set to $p < 0.05$. Prior to statistical analysis, data was log or square root transformed, if conditions of normality were not met, or to improve homogeneity of variances. Both characteristics were tested by examining the residuals versus fitted plots and the normal qq-plots of the Linear Models (Faraway, 2005). All statistical analyses were performed using R (R Development Core Team, 2006).

In separate models, including only the least diverse communities, possible artefacts of the heating facilities were tested. No significant differences between the artefact control and the ambient control were detected for any response parameter at any point of time (ANOVA, data not shown). Therefore, freeze-thaw manipulation was compared only to ambient control in the subsequent analysis.

Because our analysis was not focused on the different functional diversity levels (Table 1), this factor was treated as a covariate. Even though functional diversity at the applied low levels had significant effects on above-ground and below-ground productivity (communities containing legumes produced more), no significant interaction with the freeze-thaw manipulation was detected at any parameter. This finding implies that community reaction to increased FTC did not change with increasing diversity. Therefore, it was justified to continue using diversity as a random effect throughout the following analysis.

Results

The winter of 2005/ 06 was characterized by very cold conditions at the experimental site with mean air temperatures from December to March nearly 2°C lower than in the 30-year average. This resulted in 62 days of average daily soil temperature below 0°C. This period was separated into three natural freeze-thaw cycles (FTC), one of them achieving 41 days of continuous soil frost (no soil temperature record above 0°C in any 10 minutes measuring interval). The minimum of daily average soil temperature was -4.3°C, the absolute minimum temperature measured in the soil was -8.8°C for one hour, both in control and freeze-thaw manipulated plots. Freeze-thaw manipulation resulted in five FTC in addition to three natural FTC (Fig. 1).

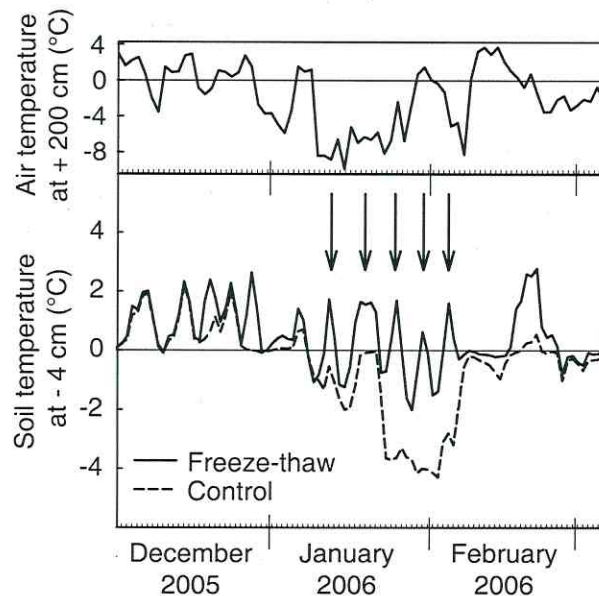


Figure 1: Average daily air (at + 200 cm) and soil temperature (at -4 cm) during winter 2005/ 2006 for manipulated and control plots. Vertical arrows mark the five additional freeze-thaw cycles. Mean values over all plant communities are given, $n = 30$. The difference between manipulation and control at the end of February is due to an unsuccessful freeze-thaw manipulation during which the control plots thawed as well.

Above-ground productivity

Cumulative plant ANPP differed between freeze-thaw manipulation and control over the growing season 2006 (mixed model: $p < 0.05$; Fig. 2). ANPP in June was 10 % higher in plant communities exposed to the freeze-thaw manipulation ($F = 4.7$, $p = 0.0394$). The difference remained constant over the whole growing season, since total ANPP in September was again 10 % higher in plant communities exposed to the freeze-thaw manipulation as compared to control ($F = 5.1$, $p = 0.0338$).

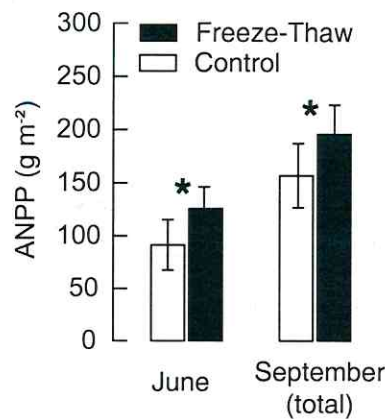


Figure 2: Above-ground Net Primary Productivity (ANPP) over the growing season following the freeze-thaw manipulations in the preceding winter (mean values and standard errors) from control (open bar) and freeze-thaw plots (black bar). ANPP from September 2005 until July 2006 and ANPP from September 2005 until September 2006. An asterisk marks significant treatment effects (ANOVA: $p < 0.05$).

Total vegetation cover was increased over the growing period due to the freeze-thaw manipulation in comparison to control (mixed model: $p < 0.05$; Fig. 3b). No differences in vegetation cover existed between freeze-thaw manipulation and control prior to the manipulation in September 2005 ($F = 0.2$, $p = 0.7018$). Higher vegetation cover following the additional FTC compared to control was most pronounced in May with an increase by 50 % ($F = 60.5$, $p < 0.0001$), weaker in July with an increase by 11 % ($F = 6.0$, $p = 0.0222$), and no longer significant in September 2006 ($F = 3.1$, $p = 0.0890$).

Below-ground productivity

Root length at 5 cm soil depth differed between plant communities exposed to freeze-thaw manipulation and control over time (mixed model: $p < 0.05$). Contrary to the above-ground developments, root length at 5 cm depth was reduced by the additional FTC (Figure 3a). In March, this reduction was especially strong in the manipulated communities as compared to control (0.1 versus 1.4 cm/ 4cm², $F = 15.7$, $p = 0.0006$). This difference was no longer significant in May (1.5 versus 2.4 cm/ 4cm², $F = 1.6$, $p = 0.1288$) and remained insignificant over summer (July: 1.0 versus 1.4 cm/ 4cm², $F = 0.2$, $p = 0.5710$). However, significantly reduced root length due to the freeze-thaw manipulation reappeared in September with lower values by about 60 % compared to control (1.5 versus 3.4 cm/ 4cm², $F = 6.9$, $p = 0.0144$). Contrary to 5 cm soil depth, more roots occurred at 15 cm soil depth over time after freeze-thaw manipulation as compared to control (mixed model: $p < 0.05$). This effect was not significant in March (0.6 versus 0.5 cm/ 4cm², $F = 1.2$, $p = 0.3195$), strongest in May (1.0 versus 0.4 cm/ 4cm², $F = 3.4$, $p = 0.0486$), and levelled off during summer without significant

differences in July (1.0 versus 0.8 cm/ 4cm²) and September (1.3 versus 1.3 cm/ 4cm²). Root length at and below -25 cm was negligible. Cumulative root length over all depth levels was dominated by the effects at -5 cm, where the majority of roots occurred. The analysis over all time steps detected lower total root length after freeze-thaw manipulation as compared to control (mixed model: $p < 0.05$). For the single time steps, significant differences were only found in September, when total root length decreased by 32 % as compared to control (ANOVA: $F = 4.5$, $p = 0.0454$).

Shoot-to-root ratio

The ratio between above-ground plant cover and below-ground root length at 5 cm soil depth exhibited significant changes over time with an increased shoot-to-root ratio after FTC manipulation in comparison to control (mixed model: $p < 0.05$, Fig. 3). This manipulation effect was significant in May with an increase by 25 % (ANOVA: $F = 19.9$, $p = 0.0008$) and in September by 12 % ($F = 4.2$, $p = 0.0498$). An increase by 8 % in July was not significant ($F = 1.9$, $p = 0.1789$).

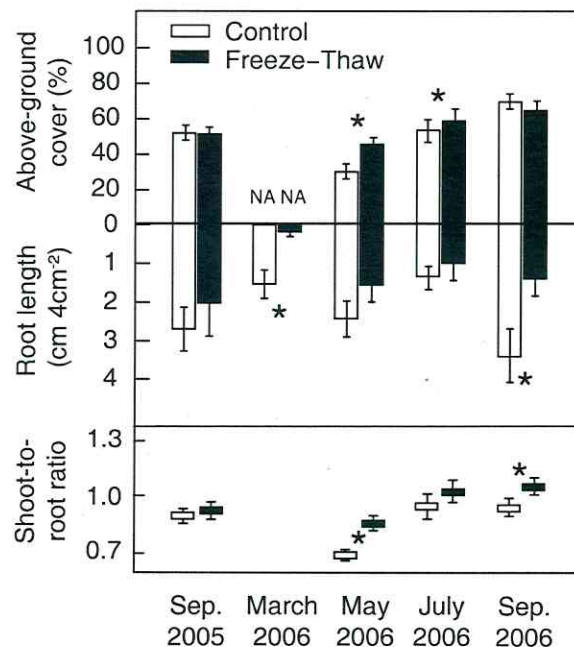


Figure 3: Total vegetation cover, root length, and shoot-to-root ratio from control (open bar) and freeze-thaw plots (black bar). Given are mean values and standard errors of pinpoint cover measurements with 100 steel needles, minirhizotron measurements at 5 cm soil depth, and the ratio between total above-ground cover and root length at -5 cm with both parameters apriori standardized to the same mean value and standard deviation. For all three parameters, significant differences between freeze-thaw manipulation and control were found over time (mixed models: $p < 0.05$). An asterisk marks significant treatment effects at the corresponding sampling dates (ANOVA: $p < 0.05$).

Soil enzymatic activity

No significant effects of the freeze-thaw manipulation were found for soil enzymatic activities contributing the carbon, nitrogen and phosphorus cycle in June, namely phosphatase, xylosidase, cellobiohydrolase, glucuronidase, chitinase, β -glucosidase. Only cellobiohydrolase activity was doubled due to the freeze-thaw manipulation compared to control ($F = 5.2$, $p = 0.0351$).

Discussion

The enhanced plant community productivity after additional FTC supports our first hypothesis: productivity of plant communities over the growing season is influenced by the freeze-thaw regime of the previous winter. However, we lack knowledge about the mechanisms driving this reaction. Enhanced plant productivity after multiple FTC can be explained by numerous factors such as an increase in nutrient supply in early spring (see introduction). The difference in ANPP could also result from damage to the control plants from deep frost versus the protection of the plants in the freeze-thaw manipulated plots due to artificial warming. Air and soil temperature minima, however, occurred on days without warming treatment, and were therefore similar for plants exposed to freeze-thaw manipulation and control. Coursolle *et al.* (2002) suggests that root freezing damage can cause reductions in seedling growth. The root systems of frost-hard temperate species, though, are not damaged by freezing itself during mild frost events, such as in our experiment. The damage is instead caused by mechanical stress due to frost heaving (Tierney *et al.*, 2001). Personnel observations confirm that frost heaving took place in the experiment: marking sticks inserted about 5 cm into the soil were removed from the ground during each FTC. An increase in FTC should therefore increase root damages more than single frost events, explaining the significant reduction in root length of the freeze-thaw manipulated plots in early spring.

Alterations in nutrient supply consequently appear to be the most obvious mechanism contributing to the enhanced plant productivity after FTC. However, our data indicate no difference in soil enzymatic activity in summer between plots subjected to repeated FTC and control. We conclude that in contrast to microbial activities in winter or spring, which are highly influenced by the FTC (see introduction), the regeneration of functional microbial patterns is fast and no effects can be found three months after the final thawing. This is also in accordance with recent findings (Sharma *et al.*, 2006), where a complete regeneration of the microflora was observed 9 days after a thawing event. Although the changes in amount and timing

of above-ground biomass production were obvious in response to FTC, this had only little influence on the measured enzymatic activities. Apparently, plant exudation and rhizodeposition, which are the main parameters driving microbial activity besides temperature and water supply, were not changed significantly due to FTC, at least at the times of sampling. This indicates a decoupling of plant productivity and microbial activity. The observed higher cellobiohydrolase activity in summer indicated that more plant residues (dead roots) were present in summer after additional winter FTC. However, other enzymes involved in degradation of plant cell wall components such as xylosidase, glucuronidase, and β -glucosidase did not differ between FTC manipulation and control, suggesting that the availability of the corresponding substrates was similar in both treatments. Easily available nitrogen and phosphorus forms that are liberated immediately after thawing (Freppaz *et al.*, 2007) have most likely been taken up by plants and microbes in spring and initiated the increase in above-ground plant biomass directly and indirectly due to release of nutrients during summer by the microbes, thus reducing the risk of losing these elements due to leaching or preferential flow into deeper soil layers. Detailed studies on the time course of soil enzymatic activity patterns may give interesting insights into the microbial C, N, and P-cycles after freeze-thaw events.

Tracer experiments after the final thaw confirm the very fast uptake of nutrients by herbaceous plants (Grogan *et al.*, 2004), even during winter (Andresen & Michelsen, 2005). In regions of temperate climate conditions grasses generally die back in winter and rebuild completely in spring, a feature that could be accompanied by fast nutrient uptake and resource allocation. The additional FTC in grassland caused an above-ground enhancement and a below-ground reduction in productivity that might initially be caused by root damage from frost heaving (Tierney *et al.*, 2001) combined with an increased nutrient supply (Herrmann & Witter, 2002; Grogan *et al.*, 2004). Accordingly, the marked reduction in root length only took place at a depth of 5 cm. The early increase in root length at -15 cm may indicate the beginning of nutrient leaching. Neither root damage nor an increase in above-ground biomass can however explain the difference in root development in late summer, when the FTC-manipulated stands showed almost no increase in root length between July and September, whereas root length in the control stands strongly increased. Theoretically, carbon allocation to the root system would counteract depletion in nutrient supply (Hermans *et al.*, 2006). A possible explanation of our findings is that plants had already completed their regeneration after additional FTC by mid summer.

Our findings imply that grassland reaction to increased FTC did not change with community diversity. It must be taken into account, however, that the realized differences in diversity and complexity of the stands in this study were low in comparison to natural communities. Especially other functional types, such as mosses or evergreen dwarf shrubs might respond differently to FTC due to their different strategies in over-wintering (Grogan *et al.*, 2004). Another important point to consider in relation to our results is the sandy substrate. It offers a fast formation of a typical soil structure, and therefore it can be assumed that despite the short running time of the experiment, the soil showed already typical responses. However, the results may not be transferable to other soil types, especially more structured soils with higher clay contents draw attention in this respect.

A major challenge for studying FTC impacts on living organisms such as micro-organisms and plants is the determination of appropriate time scales. For example, the effects of FTC on plants were far out of proportion to their short duration of occurrence. Entire plant communities with their interacting units may take even longer, and microbial-driven processes react much faster. In order to explicitly attribute effects of freeze-thaw cycling to microbial activity or plant performance, experiments with high temporal resolution and several controls are required, as e.g. the mean temperature, the number of unfrozen days, or the minimum and maximum temperature values are altered together with the manipulation of freeze-thaw events.

Taken our results together we find that short-term changes in winter temperature are important ecosystem drivers even outside arctic and alpine systems, and that more research is needed to understand their contribution to important ecosystem services. Changes in productivity resulting in increased shoot-to-root ratio and shifts in timing of biomass production may also interact with other climatic events such as drought or late frost events in altering ecosystem resilience, as well as ecosystem services such as productivity and nutrient retention.

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Summary

Besides trends in mean temperature and precipitation, ongoing climate change is expected to affect the occurrence of discrete extreme events such as summer drought or heavy rainfall. This thesis investigates the effects of extreme weather events on vegetation. The reactions of two different vegetation types (grassland and heath) were studied, and furthermore, the role of community composition in the response to extreme weather events was considered. Because of their unpredictability, knowledge on the ecological importance of extreme weather events is scarce and cannot be obtained from field observations or model simulations. Therefore, a controlled experiment was constructed at the University of Bayreuth in cooperation with the UFZ – Helmholtz Centre for Environmental Research. In this experiment, grassland and heath communities were planted and their response to simulated extreme precipitation events of 100 year recurrence was measured.

The results show that even though drought and heavy rainfall affected the productivity of single species, the overall biomass production of the stands remained almost constant. But die-back rates demonstrated increased stress caused by the weather manipulations. This reaction was buffered by increasing diversity in the grassland stands, but the opposite was true for the heath communities. Below-ground biotic processes (root biomass, cellulose decomposition, enzyme activity) were stimulated by heavy rainfall and remained surprisingly constant in face of the drought manipulation. Despite this stability in above- and below-ground productivity to the applied drought, this manipulation caused increased carbon uptake and altered carbon allocation in the stands. Furthermore, resistance against invasion by plant species from the matrix vegetation was strongly affected by the weather manipulations. This effect, however, was independent from a higher resistance of more diverse communities. Flowering length of the grasses, herbs, and dwarf shrubs was increased by four days in face of the drought manipulation and decreased by four days in face of the heavy rainfall manipulation.

In addition, it was shown for the first time in the EVENT-experiment that the freeze-thaw regime in winter does not only change short-term nutrient availability at final thaw in spring, but also influences plant growth sustainably. Superimposed soil freeze-thaw cycles in winter caused an increase in above-ground productivity by 10 % over the following growing period. Simultaneously, shoot to root ratio increased, which might have implications for susceptibility against other weather events such as drought or late frost.

This work has shown that extreme weather events have clear implications on different ecosystem properties, far out of proportion of their short duration of occurrence, even if the events do not reach magnitudes which lead to sudden damage to above-ground biomass. Plant interactions furthermore influence the effects of extreme weather events. The functional composition of communities seems particularly important, given that the two vegetation types grassland and heath differed in many of their responses.

Feedbacks within ecosystems and between ecosystems and the atmosphere have far reaching implications for society because they influence the course of climate change and also the provision of many other ecosystem services such as biomass production or ground water purification. Considerable uncertainty in forecasts for any of these services remains if extreme events are not considered. But this work has shown that vegetation response to such events is already complex in a simplified experiment, as it depends on species interactions besides simple frequency and magnitude of the extreme events themselves. Even though future work in this field will provide further insights and understanding, dealing with high uncertainty and preparing for surprises seems unavoidable with respect to future climate change.

Zusammenfassung

Die derzeit erwarteten globalen Veränderungen des Klimas werden sich neben Trends in Temperatur und Niederschlag vor allem im Auftreten zeitlich begrenzter, außergewöhnlicher Ereignisse wie Sommerdürren und Starkregen bemerkbar machen. Die vorliegende Arbeit beschäftigt sich mit den Effekten solcher Ereignisse auf Pflanzenbestände. Zusätzlich wurde untersucht, ob sich verschiedene Vegetationstypen (Grünland und Zwergstrauchheide) in ihren Reaktionen auf diese Wetterereignisse unterscheiden und welche Rolle die Diversität der Bestände bei diesen Reaktionen spielt. Wegen ihrer schweren Vorhersagbarkeit und dem daraus resultierenden Mangel an Wissen über ihre ökologischen Auswirkungen können die Folgen von Extremwetterereignissen weder in Freilandbeobachtungen noch in Modellsimulationen befriedigend untersucht werden. Deshalb wurde an der Universität Bayreuth in Kooperation mit dem UFZ-Helmholtzzentrum für Umweltforschung, ein Freilandexperiment mit Grünland- und Heidesystemen angelegt und deren Reaktion auf simulierte Extremereignisse im Niederschlag von 100-jähriger Wiederkehrzeit gemessen.

Die Ergebnisse belegen, dass sowohl Dürre- als auch Starkregenereignisse zwar die oberirdische Produktivität einzelner Arten verändern, sie beeinflussten die Gesamtbiomasseproduktion von Pflanzengemeinschaften aber kaum. Allerdings zeigten Absterberaten deutlich erhöhten Stress durch die manipulierten Wetterereignisse an. In den Grünlandsystemen wurde diese Reaktion durch erhöhte Diversität des Pflanzenbestandes abgeschwächt, in den Zwergstrauchheiden wurde allerdings genau das Gegenteil gefunden. Unterirdische biotische Prozesse (Wurzelbiomasse, Zelluloseabbau und Enzymaktivität) wurden durch Starkregen angeregt, während sie sich überraschend stabil gegenüber der Dürre zeigten. Trotz dieser ober- und unterirdischen Stabilität in der Biomasse führte die Dürrebehandlung zu einer erhöhten Kohlenstoffaufnahme in das System und zu veränderter Kohlenstoffallokation in der Vegetation. Auch die Stabilität gegenüber der Einwanderung von Pflanzen aus der Umgebung zeigte deutliche Veränderungen durch die Extremwetterereignisse. Dieser Effekt war unabhängig von einer erhöhten Stabilität diverserer Pflanzenbestände. Darüber hinaus wurde der Blühzeitraum von Gräsern, Kräutern und Zwergsträuchern durch Dürreereignisse um vier Tage verlängert, jedoch durch Starkregenereignisse um 4 Tage verkürzt.

Außerdem konnte im EVENT-Experiment erstmals gezeigt werden, dass das Frostwechselregime des vorhergegangenen Winters für temperate Grünlandbestände nicht nur kurzfristige Veränderungen im Nährstoffangebot zur Schneeschmelze bewirkt, sondern dass es auch das Pflanzenwachstum nachhaltig beeinflusst. Zusätzliche Boden-Frostwechselzyklen

im Winter führten zu einer Erhöhung der Produktivität um 10 % in der folgenden Vegetationsperiode. Gleichzeitig stieg allerdings das Verhältnis oberirdischer zu unterirdischer Biomasse deutlich an, was die Anfälligkeit der Bestände gegenüber anderen Wetterereignissen, wie z.B. Dürre oder Spätfrost, verstärken könnte.

Extreme Wetterereignisse haben also deutliche Auswirkungen auf verschiedene Ökosystemparameter weit über die kurze Dauer ihres Auftretens hinaus, auch wenn sie nicht in einer Stärke auftreten, die zu sofortigen Schäden in der oberirdischen Biomasse führt. Darüber hinaus beeinflussen pflanzliche Interaktionen die Wirkung von extremen Wetterereignissen. Die funktionelle Zusammensetzung von Pflanzenbeständen scheint von besonderer Bedeutung, denn die beiden Vegetationstypen Grünland und Zwergstrauchheide unterschieden sich in vielen ihrer Reaktionen deutlich voneinander.

Rückkopplungen innerhalb von Ökosystemen und zwischen Ökosystemen und der Atmosphäre haben weitreichende Folgen für die Gesellschaft weil sie den Verlauf des Klimawandels und auch die Sicherstellung vieler weiterer ökosystemarer Serviceleistungen, wie beispielsweise Biomasseproduktion oder Grundwasserreinhaltung, beeinflussen. Erhebliche Unsicherheiten in der Vorhersage der Entwicklung solcher Serviceleistungen besteht darin, dass Extremereignisse nicht berücksichtigt werden. Die vorliegende Arbeit hat allerdings gezeigt, dass die Reaktionen von Pflanzenbeständen auf solche Ereignisse bereits in einem vereinfachten Experiment äußerst kompliziert sind, da sie außer von der Stärke und der Auftretensfrequenz der Ereignisse selbst auch von pflanzlichen Interaktionen abhängen. Die Forschung auf diesem Gebiet wird in Zukunft weitergehende Erkenntnisse schaffen, trotzdem sind beim Umgang mit dem Klimawandel große Unsicherheiten und das Vorbereitetsein auf unvorhergesehene Entwicklungen unvermeidlich.

Hiermit erkläre ich,
dass ich die vorliegende Dissertationsschrift selbständig verfasst und keine anderen als die
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(gez. Jürgen Kreyling)

