

REVIEW AND SYNTHESIS

Precipitation manipulation experiments – challenges and recommendations for the future

Claus Beier,^{1*} Carl Beierkuhnlein,² Thomas Wohlgemuth,³ Josep Penuelas,⁴ Bridget Emmett,⁵ Christian Körner,⁶ Hans de Boeck,⁷ Jens Hesselbjerg Christensen,^{8,9} Sebastian Leuzinger¹⁰ Ivan A. Janssens⁷ and Karin Hansen¹¹

Abstract

Climatic changes, including altered precipitation regimes, will affect key ecosystem processes, such as plant productivity and biodiversity for many terrestrial ecosystems. Past and ongoing precipitation experiments have been conducted to quantify these potential changes. An analysis of these experiments indicates that they have provided important information on how water regulates ecosystem processes. However, they do not adequately represent global biomes nor forecasted precipitation scenarios and their potential contribution to advance our understanding of ecosystem responses to precipitation changes is therefore limited, as is their potential value for the development and testing of ecosystem models. This highlights the need for new precipitation experiments in biomes and ambient climatic conditions hitherto poorly studied applying relevant complex scenarios including changes in precipitation frequency and amplitude, seasonality, extremity and interactions with other global change drivers. A systematic and holistic approach to investigate how soil and plant community characteristics change with altered precipitation regimes and the consequent effects on ecosystem processes and functioning within these experiments will greatly increase their value to the climate change and ecosystem research communities. Experiments should specifically test how changes in precipitation leading to exceedance of biological thresholds affect ecosystem resilience and acclimation.

Keywords

Climate change, experimental design, manipulative experiments, precipitation change, precipitation patterns, precipitation scenarios.

Ecology Letters (2012) 15: 899–911

INTRODUCTION

Climate change involves simultaneous changes in the key drivers for plant growth and biogeochemical cycles, i.e. CO₂, temperature and water (IPCC 2007). With respect to the latter, future water regimes as projected by Global Circulation Models (GCM) are characterised by a general intensification of the global water cycle (e.g. Huntington 2006). This involves changes in annual amounts, timing, variability and extremity (intensity and frequency distribution) of the precipitation inputs and changes in the relative contribution of various types of precipitation, such as rain, snow, fog and hail (e.g. IPCC 2007; Seneviratne *et al.* 2010; Min *et al.* 2011). Records from weather stations already indicate a change in precipitation patterns, globally (e.g. IPCC 2007) as well as at the continental scale in Europe (Brazdil *et al.* 2010) and US (Gutowski *et al.* 2008) and projections for the future are generally in line with these trends and

suggest further enhancements in terms of extreme events (e.g. Christensen & Christensen 2007; IPCC 2012).

The changes in precipitation regimes, whether being chronic changes in precipitation amounts, increased intensification of variability or stronger extremity, will be more spatially heterogeneous and less predictable than for other major climate change drivers and will lead to altered precipitation inputs as well as more intense flooding and long-term droughts at local and regional scales. Such changes can contribute to the modification of soil water availability also influenced directly and indirectly by other major climate change related factors such as increased atmospheric CO₂ concentration and temperature (e.g. Daly & Porporato 2005). In turn, altered water availability will affect ecosystem processes and functioning and may exacerbate ecosystem disturbance (e.g. drought induced mortality or wildfires). The direction and magnitude of such changes in ecosystem functioning will depend on how much the

¹Department of Chemical and Biochemical Engineering, Technical University of Denmark, DK-2800, Lyngby, Denmark

²Department of Biogeography, University of Bayreuth, Universitaetsstr. 25, D-95440, Bayreuth, Germany

³Swiss Federal Institute for Forest Snow and Landscape Research WSL, Forest Dynamics, Zürcherstrasse 111, CH-8903, Birmensdorf, Switzerland

⁴Department Global Ecology, CREA-CSIC Barcelona, Edifici C, UAB o8193, Bellaterra, Spain

⁵Centre for Ecology and Hydrology, Environment Centre Wales, Deiniol Road, UK-LL57 2UW, Bangor, Wales, UK

⁶Institute of Botany, University of Basel, Schoenbeinstr. 6, CH-4056, Basel, Switzerland

⁷University of Antwerp, Plant and Vegetation Ecology, Universiteitsplein 1, BE-2610, Wilrijk, Belgium

⁸Danish Climate Centre, Danish Meteorological Institute, Lyngbyvej 100, DK-2100, Copenhagen Ø, Denmark

⁹Greenland Climate Research Centre, Nuuk, Greenland

¹⁰ETH Zurich Forest Ecology, Environmental Sciences, Universitätsstrasse 16, CH-8092, Basel, Switzerland

¹¹IVL Swedish Environmental Research Institute, P.O. Box 210 60, SE-100 31, Stockholm, Sweden

*Correspondence: E-mail: clbe@kt.dtu.dk.

change in precipitation deviates from the existing variability, the ability of the system to buffer the changes (e.g. determined by pool sizes, dominant plant species or diversity; Smith *et al.* 2009) and the ability of the plant and soil biota to acclimate or adapt to the new conditions.

Knowledge of the impacts of changing water regimes can be gained from observations of already realised impacts of ongoing changes in precipitation such as long-term observations in the UK suggesting an increase in hygrophilic plants, which reflects the rainfall signal in the same period (Dunnett *et al.* 1998). Responses across short natural moisture gradients or to recent water table changes also offer a source for information and increased understanding. However, information from both of these observations-based approaches is sparse and may be confounded by other covarying factors. Manipulative experiments involving precipitation changes provide a complimentary tool enabling replication, control for confounding factors and multiple scenarios to be studied simultaneously. During recent decades several experiments have been conducted in natural and semi-natural ecosystems exploiting this potential. Wu *et al.* (2011) analysed 34 of these precipitation experiments and found that, in addition to the expected positive correlation between precipitation amounts and productivity and C cycling across climates, ecosystems appeared more responsive to water addition than to water removal.

In addition to the experiments and data analyses, there are several conceptual frameworks which can help to support and structure our understanding of impacts of altered precipitation regimes leading to chronic resource alterations (e.g. the 'Hierarchical Response Framework', Smith *et al.* 2009) or to increased variation in resources, threshold exceedance and disturbance (e.g. Scheffer & Carpenter 2003; Briske *et al.* 2006; Knapp *et al.* 2008). However, the validity of syntheses and meta-analyses (e.g. Wu *et al.* 2011) and the provision of a coherent understanding on impacts of precipitation change in terrestrial ecosystems across the globe critically depend on the data provided. In particular, it matters how well observations or experiments are representative for global ecosystems, current climatic conditions and the forecasted precipitation changes as well as the comparability of measurements across experiments. The synthesis by Wu *et al.* (2011) is to our knowledge the only existing meta-analysis related to precipitation change experiments. It brings together responses in the relatively few carbon flux measurements generally available from these experiments and illustrates that we have a good understanding of the general role of water in controlling ecosystem processes. However, it also illustrates that available data and knowledge of global change driven precipitation effects on ecosystems are limited and less consistent relative to the effects of other climate change drivers (i.e. elevated CO₂ and warming). This may be due to the fact that changes in precipitation regimes are temporally and spatially more complex and uncertain compared with those in CO₂ and temperature, making scenarios more difficult to define and making the range of experimental conditions required more complex and less comparable. This has contributed to less consistent and integrated research efforts concerning precipitation effects on ecosystem functioning relative to other drivers. This further exacerbates a general lack of consistent experimental data for improvement and rigorous testing of models and validation of predictions, as was recently emphasised in studies aiming to predict responses of ecosystem functioning to various climate change-related precipitation scenarios (Gerten *et al.* 2008; Luo *et al.* 2008).

The aim of this study was to (1) provide a comprehensive analysis of the past and ongoing precipitation manipulation experiments in natural and semi-natural terrestrial ecosystems with respect to their coverage of global biomes and forecasted precipitation change, (2) identify key characteristics for design of future precipitation experiments and (3) identify future research needs with respect to precipitation experiments.

PRECIPITATION EXPERIMENTS – STATE OF THE ART

If we are to project the future changes in ecosystem functioning in response to precipitation change, observations and experiments related to changes in precipitation should cover the range of global ecosystems and current and future climate scenarios.

Geographic representation, site conditions and ecosystems

Responses of terrestrial ecosystems to changes in precipitation depend upon a number of currently prevailing site-specific factors such as climatic conditions and soil and ecosystem characteristics. As the sensitivity and vulnerability as well as resilience to the changes may not be easily interpolated between different systems, experiments need to embrace the variance in these site-specific factors and characteristics as well as their present and potential future combinations.

Biogeographical representation

We analysed 95 terminated and running experiments (Table S1) conducted in natural and semi-natural ecosystems. A majority of the experiments were in grasslands (46%) and forests (30%) (Fig. 1a) and most of these (89%) were located at medium latitudes (30–60°) while only few studies were at latitudes < 30° (4%) and > 60° (7%). There was a clear under representation in the Southern hemisphere (4%), and in particular experiments representing Africa were missing. Climatically, most precipitation experiments (61%) were carried out in locations with mean annual temperatures (MAT) ranging from 5 ° to 15 °C (Fig. 1b) while precipitation experiments conducted at globally colder (MAT < 0 °C, 6%) and warmer conditions (MAT > 20 °C, 4%) were sparse. Also, experiments at sites with high rainfall inputs exceeding 1500 mm year⁻¹ were sparse (6%). Ironically, some of these high rainfall zones are projected to be most sensitive and to face the most significant changes (IPCC 2007).

Soil characteristics

Soils are the product of long-lasting vegetation successions influenced by climate, parent material, substrate and disturbance regimes and therefore vary in their physical (e.g. structure, texture, compactness, pore size and pore distribution) and biological (e.g. microbial and faunal biomass and community, rooting depth and root distribution) characteristics. These characteristics exhibit a strong influence on the response of ecosystem processes to altered precipitation regimes because they determine the water holding capacity and thus, water availability as well as the ability of the system to buffer water fluctuations. Interactions between soil characteristics and altered precipitation regimes and their effects on water availability at a given site can be explored by dynamic ecosystem models with a detailed soil hydrological component. This was recently done by Gu & Riley (2010) suggesting soil texture to

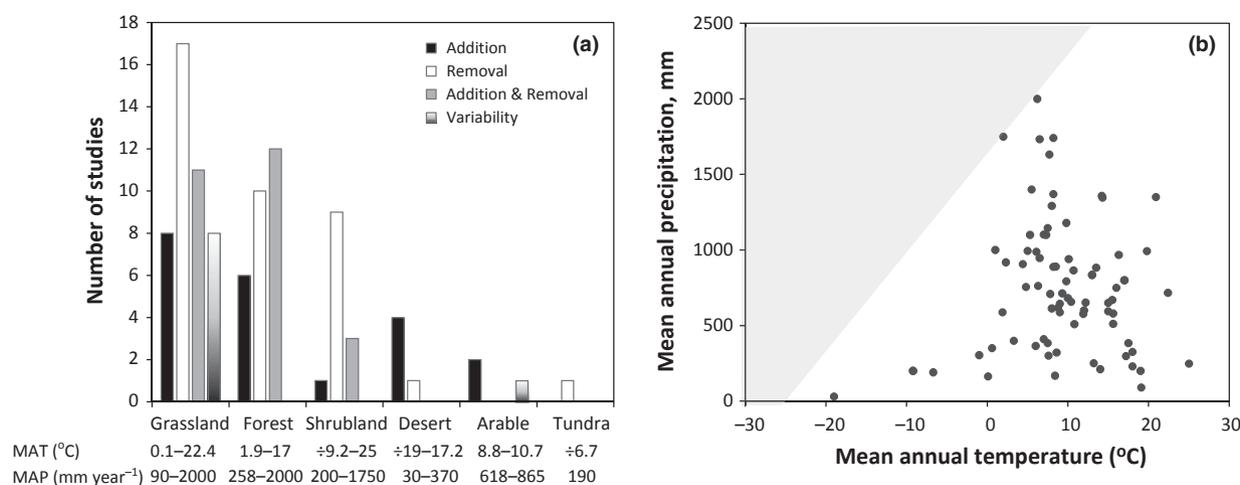


Figure 1 (a) Number of precipitation change experiments according to major ecosystem type (grassland, forest, shrubland, desert, arable and tundra) and manipulation type. For each ecosystem type the range of mean annual temperature (MAT, °C) and precipitation (MAP, mm year⁻¹) is indicated for the ecosystems included. (b) The distribution of all experiments along the climate space defined by MAT and MAP independent of type of manipulation and ecosystem [white area shows global climate space from global climate database (see Garbulsky *et al.* 2010)]. Data are from the ClimMani database (Table S1).

be a key feature controlling responses of nitrogen cycling to precipitation changes through the controls on soil moisture dynamics but this remains to be tested experimentally. Despite the well-known importance of soil characteristics in controlling and mediating the hydrological processes only few experiments have focussed on such complex interactions, which have resulted in a general lack of data to support and validate model predictions at the ecosystem level.

Plants, plant communities and species composition

Plant species are adapted to the moisture conditions at the given site using different functional and structural traits, such as plant size, plant architecture, allometry, tissue chemistry, rooting depth, ecophysiological characteristics and growth (Meinzer 2003). Among these, the resistance to transient changes in water availability, *i.e.* limitations by both water stress and water excess is crucial, as extreme events have been identified as the main mechanism which drives evolution and shapes communities (Gutschick & BassiriRad 2003). Ecosystems may be resilient to changes depending on the rate or strength of these changes (Smith *et al.* 2009), or plant species and communities may be able to acclimate or adapt to altered conditions (Jentsch *et al.* 2011). For example robust long-lived species may remain inert (*i.e.* resistant) to novel conditions for decades in their ecosystems because of the long generation times and consequent slow genetic changes and/or by preventing potentially better adapted species from invading (Eriksson 1996). On the other hand, impacts of changing water availability may be brought back into equilibrium faster (*i.e.* better resilience) in communities dominated by short-lived species due to shifts in dominance patterns and abundance (Jentsch *et al.* 2011). Grasslands, for example, generally deplete the soil water rapidly, leading to a fast suppression of evapotranspiration (Teuling *et al.* 2010) and eventually wilting of the above ground plant parts (Albert *et al.* 2011) whereas trees and shrubs are more resistant to drought. However, after severe drought stress, forests and shrublands will regain their former level of functioning relatively slowly (*e.g.* Granier *et al.* 2007), whereas grasslands are more resilient and regain their functioning much faster (*e.g.*

Albert *et al.* 2011) although succession trajectories may become more stochastic at the community level (Kreyling *et al.* 2011). Consequently, ecosystem responses to precipitation changes are not only controlled by instantaneous effects of changes in precipitation (*i.e.* resistance) but also by longtime or lag effects which themselves are influenced by factors, such as dominance, diversity, resources, trophic interactions and interactions with other drivers (*e.g.* Smith *et al.* 2009).

Within species, resilience of a plant population to weather extremes may be influenced by its genotypic diversity, but there is no empirical or experimental evidence yet for this. Also experimental testing of species-specific large-scale geographical patterns of phenotypic plasticity with respect to varied precipitation regimes is rare (Beierkuhnlein *et al.* 2011; Richter *et al.* 2012). Within the life cycle of individual plants adjustment effects may occur (*e.g.* Zavalloni *et al.* 2008; Walter *et al.* 2011) but studies of age-specific responses, demographical shifts and mortality of plant populations and communities are missing, especially for long-lived species, such as clonal plants, shrubs and trees. Finally, only few experiments have systematically tested how responses of ecosystems to increased variability and extremity in water availability depend on functional traits at the species and community level (but see Knapp *et al.* 2002; Smith 2011; Franks *et al.* 2007).

Tested precipitation scenarios

Assessment of the impacts of changes in key drivers affecting water availability requires experiments applying the drivers in relevant scenarios.

Extreme events and precipitation variability

The consistent finding among climate predictions of an increase in the variability of precipitation patterns with intensified extremity (IPCC 2007, 2012; Boberg *et al.* 2009) is not well covered by the treatments applied in precipitation experiments. Most studies on changes in precipitation regimes have focussed on increasing or decreasing amounts of precipitation through ‘addition’ (52%) or ‘removal’ (65%) experiments (including a combination) (Fig. 1a) leading to relatively abundant experimental field studies on the

effects of intensified and elongated droughts. These have demonstrated the potential of droughts to alter key processes in soils (Emmett *et al.* 2004) and plants (Peñuelas *et al.* 2007) with moist systems being particularly sensitive (Emmett *et al.* 2004; Sowerby *et al.* 2008) and repeated droughts having potential to fundamentally alter soil characteristics (e.g. Sowerby *et al.* 2010). Recently, experiments adding water to already moist systems, such as peatlands, flood plains and salt marshes have become increasingly relevant because of the role of these ecosystems as sources of greenhouse gases and DOC export (e.g. Knorr & Blodau 2009). Despite relatively many experiments testing 'extreme' precipitation events, these have generally been 'conservative' in the choice of changes and have applied realistic droughts in a statistical/historical sense (e.g. time span of 100 years; see 'dilemmas'). However, many ecosystems are likely to be exposed in the future to climatic conditions exceeding past and current variation (Christensen *et al.* 2007; Boberg *et al.* 2009; IPCC 2012). In this respect, our experimental support for understanding the ecological impacts of more extreme precipitation events (Smith 2011) including shifts in climate regimes is limited. Also experiments should be prioritised which test more extreme changes in precipitation in ecosystems composed of long-lived species such as forests: such systems may resist individual extremes better but at the same time may not be able to adapt to rapid shifts of climate regimes due to low species turnover (Thomas *et al.* 2004). If extreme impacts would result in declining performance of widespread ecosystems dominated by perennial plants and if their potential to compensate such events would be exceeded, global consequences for ecosystem fluxes and biodiversity would be severe.

Only relatively few studies have conducted experiments with changes in precipitation variability (c. 10%), and all of these have been in mesic grasslands (Fig. 1b). They have demonstrated how such changes can affect NPP (Fay *et al.* 2000) and in the long-term lead to species and community change (Knapp *et al.* 2002). Knowledge on effects of fluctuating rainfall patterns can also be obtained from studies in arid and semi-arid ecosystems with strong temporal fluctuation in water and nutrient resources, which may resemble future increased rainfall variability. These have shown how resource pulsing can determine key ecosystem processes such as carbon dynamics (Huxman *et al.* 2004), species competition and biogeochemistry (e.g. Chesson *et al.* 2004). Considering the consistent forecasts of increased variability in precipitation patterns and the potential impacts across all ecosystem types (Knapp *et al.* 2008) the lack of experimental studies on these changes is striking.

Seasonality

Seasonal precipitation patterns are also likely to shift in many regions. In northern Europe for example, this will generally result in more rain in winter and less rain in summer, whereas elsewhere, changes in the onset and termination of the monsoons may be affected (e.g. Christensen *et al.* 2007). This is sometimes referred to as the 'wet is getting wetter' and the 'dry is getting drier' (e.g. IPCC 2007). This altered seasonality may lead to changes in phenological patterns and potential biological asynchronies in timing (Peñuelas & Filella 2001), which in turn may drive local species extinction and changes in ecosystem functioning (e.g. Peñuelas *et al.* 2007). Most information on such phenological changes exists from long-term observations at regional and global scales (e.g. Singer & Parmesan 2010) whereas experimental studies are generally absent. Hence, it is difficult to infer responses for new climate states (Körner & Basler 2010).

Scenarios with interacting drivers

Future climatic changes involve simultaneous shifts in multiple drivers. In particular CO₂ and temperature exhibit strong interactions with ecosystem water conditions (see e.g. Morgan *et al.* 2004), because elevated CO₂ affects plant water use efficiency and temperature affects evaporation and transpiration rates both leading to changes in soil moisture. The combined effects of these changes are not necessarily additive (e.g. Beierkuhnlein *et al.* 2011; Larsen *et al.* 2011; Leuzinger *et al.* 2011) but few experiments have addressed such an interplay. Consequently, our knowledge about the effect of such climate driver interactions on ecosystems is generally limited and ecosystem models are poorly tested because of lack of experimental data. Such interactions may not only involve combinations of basic climatic drivers, as has been the case until now (e.g. Shaw *et al.* 2002; Mikkelsen *et al.* 2008) but also interactions of these drivers with precipitation timing, seasonality and climate extremes (De Boeck *et al.* 2011) and other environmental drivers such as atmospheric pollution and land management.

Long-term experiments

Responses of ecosystem processes to changes in precipitation patterns and extremity may not occur instantaneously but may exhibit delayed effects with potential non-linear response (Smith *et al.* 2009). Lagged effects have, for example, been shown as a change in plant fitness in one year in response to changes in water regimes in a previous year (Sherry *et al.* 2008). Memory effects and delayed drought responses have been observed in a grassland ecosystem where the effect of a late season drought on biomass production was reduced if the ecosystem was exposed to an early season drought (Walter *et al.* 2011). Similarly, a severe drought in a beech forest reduced tree growth in the following years (Granier *et al.* 2007). More long-term effects are likely to occur as a result of gradual changes in species composition, plant community structure and biodiversity in general (e.g. Smith *et al.* 2009; Kreyling *et al.* 2011). For example, in response to increased tree mortality after drought, forests became more drought-sensitive (Mueller *et al.* 2005), and ecosystem productivity in mesic grasslands was affected by changes in species composition in response to increased water variability (Knapp *et al.* 2002). Also, repeated drought events have been shown to have long-lasting effects on soil rewetting capabilities and soil respiration because of gradual changes in soil structure or soil microbial community (Sowerby *et al.* 2008). Such long-term perspectives of climate change can only be verified by long-term experiments, but only a few long-term experiments (> 10 years) exist.

DESIGN OF PRECIPITATION EXPERIMENTS

The design of precipitation experiments needs to consider a relevant precipitation scenario and ensure a realistic and relevant treatment in relation to the chosen scenario with minimal unwanted side effects and artefacts.

Selection of precipitation scenario

In a climate change perspective, it will often be tempting and politically most appropriate to conduct experiments related to established scenario-based projections e.g. by regional climate models derived from IPCC standards or the experimental scenario may be based on historical/statistical considerations of what is 'extreme' (e.g. Jentsch

et al. 2007; Pfister 2009; Smith 2011). Alternatively, the applied scenario may focus on potential biological responses, because a scenario that is climatically realistic and politically relevant but has no major effect on soil water availability is unlikely to elicit major biological changes (ecologically irrelevant). Therefore, the chosen scenario may consider not only the amount of precipitation but also factors potentially controlling exceedance of ecological thresholds for important and relevant processes, (e.g. Knapp *et al.* 2008) such as timing and duration of events, seasonality and long-lasting and extreme events (e.g. Katz & Brown 1992; Hegerl *et al.* 2011). This could for example follow the Extreme Climate Event framework defined by Smith (2011), which includes extremity from both a driver and a response point of view, but a definition of extreme conditions is not trivial.

Scenarios involving timing issues pose a particular challenge and uncertainty because precipitation forecasts are generally weak in spatial-temporal resolution and carry a substantial randomness and therefore, a specific 'correct' scenario may not be easy to identify. This is particularly true for scenarios involving increased extremity in precipitation patterns, because weather extremes can only be forecasted as probabilities with considerable uncertainty. The randomness in precipitation timing creates an additional complication as the applied scenario will interact with ambient climatic conditions. The seasonal performance of a given year will for example define whether a manipulation is drastic or not such as applying a drought in a naturally dry year. Also, the conditions at the start of an experiment, such as applying a drought on top of a naturally long dry period, can have long-lasting consequences and create a legacy of biotic structures that may constrain the interpretation of the results. It is advisable to fine tune the chosen scenario by pre-application of ecosystem models to predict the potential consequences for plant and ecosystem water availability.

As an alternative to scenario-based treatments it may be relevant to apply treatments to deliberately test the effects of various aspects related to altered precipitation patterns, timing issues and changes in water availability, such as severity of drought, length of water logging, repeated drying/rewetting cycles etc. This, together with the application of ecosystem models may increase our process understanding of precipitation timing, even if it is not following a specific forecasted scenario.

Dilemmas

Precipitation experiments often involve dilemmas (Table 1). For example, we typically refrain from applying a manipulation having detrimental effects on the ecosystem (e.g. mortality) meaning that certain extreme events may not be applied, even if these might be relevant for the long-term response of the specific ecosystem. This includes a refrain from applying or promoting ecosystem disturbances such as wild fires, flooding or herbivore attack, which may interact with the precipitation change and play significant roles for the long-term responses to climate change (see e.g. review by Borken & Matzner 2009). Such disturbances are typically unwanted in precipitation experiments or may be deliberately avoided, as they will interact strongly with the treatment applied and potentially impair the original experimental set-up.

The uncertainty and complexity in future precipitation scenarios pose another dilemma because experiments with several simultaneously interacting factors make it increasingly difficult to disentangle the cause of observed changes. A complete test of all relevant

factors in an experiment means that the number of treatments and study plots may increase tremendously with economic and practical consequences. Experimental designs are therefore most often faced with a choice of testing a limited selection of factors or combinations.

The relatively short time scale of experiments provides other dilemmas. First, the precipitation changes projected from climate models will generally be realised or developed over decades, but a precipitation experiment typically applies the full extent of the change in one step and typically in accordance with a traditional ANOVA design with only one level of precipitation change (see later about 'replication'). Second, the relative importance of inter- and intra-annual variability (Fay *et al.* 2011) and the occurrence of natural extremes (e.g. long-lasting drought within a 5-year experiment) are difficult to filter out in a shorter term experiment. Third, short-term experiments carry the trivial dilemma of having limited ability to inform about long-term consequences.

These dilemmas are often unavoidable and eventually result in well-justified choices for a given site. There is a need for new experiments which particularly address these 'dilemmas' such as threshold exceedance, plant mortality and disturbances to understand their roles for determining the long-term responses at the soil, plant population and ecosystem level.

Reference conditions

In precipitation experiments the effects of a treatment are typically assessed by comparison to a control or reference condition. This may sound trivial, but will nevertheless involve various considerations and a choice between at least two strategies:

Ambient control

Untreated or ambient control plots are often used for comparison with treatment responses. This may provide a challenge as the ambient precipitation conditions may exhibit strong inter- and intra-annual variability where conditions in the untreated ambient control in a given year may coincidentally be quite extreme and far from representing the true reference conditions at the site (see also 'Selection of precipitation scenarios' above). A treatment effect registered as the deviation from the untreated control may therefore not provide the relevant information. However, there is information in this background ambient variability that can be exploited and compared with experimental findings to identify inconsistencies.

Long-term average control

Alternatively, a long-term reference may be established as a treatment exposed to the average long-term ambient climatic conditions (Jentsch *et al.* 2007; Richter *et al.* 2012). This approach minimises complications related to the above-mentioned inter-annual variability, but on the other hand it provides a technical challenge because it requires facilities to collect, store, chemically modify and add precipitation according to the long-term average scenario. Furthermore, climatic factors, such as temperature, radiation and wind affect the water balance making a long-term reference difficult to establish and maintain. In addition, it is scientifically challenging because a long-term average reference in a study conducted during many years eliminates the natural inter-annual variability and extremity, which may be a crucial driver for the system. In other words, a long-term average reference treatment should consider integrating

Table 1 Dilemmas (and examples) associated with the design of precipitation change experiments and the choice of treatment strength, applied scenario and the duration, space and replication of the experiment. The dilemmas should be considered carefully because a choice of, for example treatment, which may seem optimal from one point of view, may compromise the results from other points of view

Issue	Dilemma	Example
Treatment strength		
Threshold exceedance	Application of an experimental factor at a high amplitude may 'kill' plants or communities leading to fundamental change in ecosystem functioning	Severe drought or flooding exceeding the mortality threshold for certain plant species or microbes
Disturbance	Disturbances may be relevant and key drivers for the ecosystem development, but may interact with planned experimental factors	Increased frequency of herbivory or wild fires
Scenarios		
Complex scenario	Application of several factors simultaneously makes it difficult to disentangle the role of the different factors and difficult to parameterise these for model application.	Mix of changes in application and removal of water Mix of application frequency and amount
Multi factor application	Interactions among drivers may not be informed from testing factors in isolation. If applied as full factor combinations, the number of combinations increases rapidly leading to a high number of experimental plots	Climate change involves elevated CO ₂ , temperature and altered precipitation patterns. Application of all three factors at just one level for each require 8 different treatments. Testing more complex precipitation scenarios double the treatments for each complexity
Step change	Experimental testing of scenarios typically need to speed up the rate of change and therefore, often apply the 'full treatment' leading to a step change in drivers not being realistic or identical to the long-term scenario tested	Precipitation change may gradually develop over many years
Discrete vs. continuous driver	ANOVA designs typically apply discrete levels of drivers and require many replicates. This provides little information about the overall response surface across a range of precipitation values and provides little information for building and testing models	Precipitation is a continuous driver often applied at only one level of change
Duration, space and replication		
Time	Economic constraints prohibit sufficient extension of the experiment to provide the relevant information about long-term effects. Long-term experiment increases the risk for additional interacting factors to play a role, e.g. herbivory or single year extremes	Long-term changes in ecosystem functioning in response to extreme droughts or chronic changes in rainfall patterns or amounts
Space	Economic constraints restricts plot size and limit extent of sampling of these	Small plots limit test of species and genotype diversity (particular problem with trees)
Replication	Economic or practical constraints limit the number of replicates reducing the statistical power	Spatial heterogeneity requires high number of study plots per treatment

the variability and extremes that are characteristic for the current climate. It may furthermore be desirable to have an untreated ambient control, even though this will increase the number of study plots and therefore costs and practical efforts.

Size and spatial design

Experimental plot size

To reduce costs, the plot size is often kept as small as possible yet being representative for the ecosystem of concern. Small plots increases edge effects, which can be reduced by leaving areas at the edge of the treated plots unused for response measurements (e.g. Beier *et al.* 2004) or by trenching the study plots to avoid lateral water movement and root growth. Trenching, on the other hand, may cause disturbance and alter hydrological conditions near the trenching (Table 2). Small plots constrain the sampling strategy, because for example extensive soil sampling compromise the experiment (create a so called 'Swiss cheese' effect), especially if the experiment is designed to run for a long time. Tall vegetation such as mature trees pose a particular challenge for the treatment design as they require bigger plots and more extended, expensive and physically more exposed infrastructures. Special designs for precipitation experiments in mature forest ecosystems with roofs beneath the

canopies have been applied (e.g. Lamersdorf *et al.* 1998), but some experiments are inherently difficult or impossible to conduct in forest ecosystems. These spatial constraints are well known for other manipulative experiments such as CO₂ enrichment, but in view of the comparatively low costs of watering/water withholding treatments, it is advised to 'think big' and not to compromise with regard to plot size and replication.

Replication

Experimental designs typically follow an 'ANOVA approach' with many replicates to account for spatial variability. In ANOVA design, each treatment is applied at a given (one) level. However, as precipitation is a continuous driver, a 'regression approach' providing a response surface with information of responses at several levels of precipitation might be more relevant and worth considering. This might provide information of responses at a broader range of precipitation changes, which is relevant considering the uncertainty associated with most precipitation scenarios. Furthermore, a response surface will have advantages with respect to constructing models and will often be statistically more powerful (e.g. Cottingham *et al.* 2005). Furthermore, it is advisable to conduct pre-treatment measurements to strengthen the statistical analyses of the responses.

Table 2 Potential artefacts related to precipitation experiments and their causes, consequences and potential solutions. The artefacts may affect the water, nutrient and physical/climatic conditions and thereby interfere with the treatment responses and should be avoided or minimised by applying a proper design and methodological approach in the experiment

Artefact	Cause	Problem	Solution
General			
Lack of atmospheric feedback	Water manipulations alter actual evapotranspiration (ET)	Only actual ET but not potential ET is altered leading to unrealistic effects on the water balance	Simultaneous manipulation of temperature
Water related artefacts			
Uneven water distribution	Damaged or malfunctioning rain shelters, uneven sprinkling	Holes or cracks in rain shelters channel water into plots in isolated spots Malfunctioning rain shelters cover only part of the plots allowing uneven treatment	Check, maintain and test shelters Ensure well drained shelters (avoid water pooling)
Lateral water input	Lateral water flow	Spaced or overlapping sprinklers lead to uneven treatment Compacted soils, heavy rain events and slopes. Trampling and water channelling outside	Well tested sprinklers with even distribution Flat terrain, well drained soils, avoid plots
Alternative water supply	Deep or extensive rooted or clonal plants	Plants obtain water supply from water sources from below or outside treatment plots	Trenching (may also cause artefacts), avoid shallow ground water
Nutritional artefacts			
Altered chemistry/deposition	Water addition Permanent covers	Permanent covers remove dry deposition Artificial rain addition may have unnatural chemical composition Wrong chemical composition may have effects overriding or interacting with treatments	Avoid long-term permanent covers, use collected natural rain, replace removed chemicals/nutrients
Physical & micro climatic artefacts			
Shading	Permanent covers Major physical constructions	Covers and constructions reduce or change light conditions Impacts on ecophysiology	Light transparent covers, removable rain out shelters with short coverage time Automatic rain out shelters
Passive warming	Permanent covers	Covers may create passive warming	Automatic rain out shelters
Sheltering	Physical constructions Permanent covers	Constructions may affect wind speed. Impacts on ecophysiology	Avoid major obstructions, use removable rain out shelters
Trampling	No access facilities	Trampling will affect physical soil conditions channel water flow, cause lateral water flow and cause plant damage and plant death	Provide non-intrusive access facilities (board walks, cranes etc.)
Plant death	Trenching or trampling	Damage to plants or roots kill plants and change community structure, herbivore pressure, water flow etc.	Avoid trampling and fencing in sensitive systems
Lack of grazing	Fencing	Fencing may change the grazing pressure by leaving out bigger grazing animals	Avoid fencing or allow grazing for periods

Transfer/transplant experiments

Precipitation manipulations may be conducted by actively engaging precipitation gradients as a means to manipulate moisture. A way of doing this is by transferring or transplanting parts of the undisturbed ecosystem (e.g. mesocosms and lysimeters) from one area with certain precipitation conditions into another environment (Ineson *et al.* 1998). This approach has clear logistic advantages, as there is no need for an active manipulation infrastructure. However, the transplanting process may create large artefacts (e.g. damage to the soil profile or root system), that must be appropriately checked and controlled, and for practical reasons experimental units are usually relatively small which increases the risk for edge effects and makes transplant experiments impossible for ecosystems with big plants such as trees as well as for certain research questions (e.g. related to pests, pathogens and herbivores). Also, the applied treatment in a transplant experiment cannot be freely chosen but will follow the ambient conditions at the transplant site.

Gradients

To avoid some of the obvious scale dependent drawbacks of precipitation manipulation experiments, studies of ecosystem responses may be conducted along precipitation gradients. Such gradients may occur over small spatial distances (Scherrer *et al.* 2011) as well as

over large distances such as along latitudes or longitudes (e.g. Beier *et al.* 2004). Small spatial precipitation gradients have the advantage that most site conditions can be assumed relatively similar across the gradient (e.g. soil type, land use history and photoperiodicity). On the other hand, large-scale biogeographical gradients provide an option to search for generality in ecosystem responses beyond what is site dependent, e.g. studies along European East-West precipitation gradients have been conducted (e.g. Emmett *et al.* 2004). In short-distance gradient approaches, sites have to be carefully selected to ideally vary only in the key parameter(s) (e.g. precipitation amount, soil texture) and to be highly comparable in other aspects (e.g. slope, soil depth, water table, land use etc.). Potential autocorrelations and confounding effects need to be taken into account, because sites differ in many aspects as a consequence of their long-term difference in water supply (e.g. soil texture, microbial communities and soil chemistry) and the moisture effect must be disentangled from other correlated mechanisms. Also, experiments along gradients need to consider soil depth, as the same manipulative treatment would have different effects on shallow vs. deep soils as well as in stone free vs. stony soils. Gradient approaches are less suited to study multi-factor interactions and effects of increased extremity but can be combined with an experimental approach by conducting similar precipitation experiments at each site along the gradient (Beier *et al.* 2004).

Technological challenges artefacts

Any experiment will inevitably be associated with artefacts (Table 2). First, experiments affecting the water balance carry an unrealistic element within it according to the Bouchet complementarity relationship (Bouchet 1963). This is because in nature, potential and actual evapotranspiration are coupled, both in the present as well as in the future, whereas in a precipitation experiment, only the actual evapotranspiration is altered, commonly addressed as lack of atmospheric feedback (Table 2). Second, the physical design of an experiment will carry some unwanted side effects with it. Therefore, ecosystem experiments with precipitation treatments need to consider technological issues to be practically and economically feasible and to minimise unintended side effects and artefacts (Table 2 and see Weltzin *et al.* 2003).

Precipitation amounts, timing and rainfall type

The technical design of precipitation experiments first of all need to consider a 'correct' input of water to the plots. In precipitation addition experiments, collection, storage and sprinkling capacity need to satisfy the amounts, intensity, application rates and distribution patterns of precipitation defined by the scenario. In drought experiments on the other hand, automatic rain out shelters should respond rapidly to the onset of rain events to avoid significant amounts of water entering the plots due to system delays (e.g. Mikkelsen *et al.* 2008). Canopy interception needs to be considered by designing rain shelters or irrigation sprinklers to be placed above or below canopy (e.g. Dobbertin *et al.* 2010) and for example avoid permanent rain out shelters in areas where dew formation is considered to be important. Also, other alternative water sources such as lateral water flow and ground water upwelling should be avoided in order not to compromise the results. Manipulations of snow cover may be relatively easy in areas with permanent snow cover for extended periods, simply by accumulating snow behind snow fences (e.g. Seastedt & Vaccaro 2001) or adding/removing snow by shovelling (e.g. Wipf & Rixen 2010). However, in areas with fluctuating temperatures above and below freezing and consequent alternation between snow and rain, experiments may be difficult and especially automatic systems may be inoperable.

Evapotranspiration and vapour pressure deficit

In precipitation experiments the change in water input is not the only factor affecting the water conditions in the treatment plots. Also changes in the water loss from leaves is important. This depends on altered evaporative forcing and vapour pressure deficit (VPD), which may be affected by rainout shelters (e.g. Svejcar *et al.* 1999). Drought shelters, which are moved away when it does not rain, will still simulate the changes in the energy balance imposed by drought (canopy warming, greater leaf-air vapour gradients) and should be preferred. A technique to control humidity in the open air has recently been developed Kupper *et al.* (2011) and may reduce this artefact.

Precipitation chemistry

In precipitation experiments involving addition of water, associated changes in precipitation chemistry leading to fertilisation or nutrient depletion effects should be avoided, preferably using collected ambient rainwater. Alternatively irrigation water can be treated chemically

to be comparable to the ambient rainfall (e.g. de Visser *et al.* 1994). Unintended removal of wet and dry deposition should be avoided for example by employing automatic rain out shelters or by employing measures to compensate removal of nutrients although this may be difficult to do in a realistic way. Chemical contamination leached from structures supporting e.g. rain out shelters can act as biocides or provide unintended buffering capacity and should be avoided (e.g. coated surfaces).

Light, temperature and wind

Rain out shelters and the experimental structures inevitably create shade and change the spectral composition (Table 2), even when transparent materials are used. In addition, permanent shelters may cause passive warming. In short-statured vegetation, it is therefore advisable to engage retractable shelters which only cover the plots during the rain events (e.g. Grime *et al.* 2000; Beier *et al.* 2004; Richter *et al.* 2012). Automatic or permanent rain out shelters as well as other major infrastructures related to the experiment may obstruct the wind affecting both the temperature and wind stress inside the plots with potential impacts on plant physiology (e.g. Rasmussen *et al.* 2002).

Access and trampling

Access to the experimental plots for sampling should be considered and integrated in the experimental setup to minimise trampling and disturbance. This is because most ecosystems are sensitive to extensive walking in the plots and trampling may form paths in the plots and affect herbivores and pollinators and result in soil compaction, channelling of water and eventually local plant death (Table 2). This problem increases with the duration of the experiment.

Fencing and trenching

In many experiments fencing of the site may be needed to avoid damage to equipment and the experiment. However, fencing may lead to a change in grazing or disturbance pressure, which may interact with the treatments and the responses and thereby complicate data analyses (e.g. Larsen *et al.* 2011). If fencing cannot be avoided the natural disturbance effects need to be simulated, either statistically or practically (e.g. artificial or periodic grazing, measurements to quantify the grazing effect). Trenching to avoid lateral water or root movements between treatment plots and/or the outside may cut roots and cause plant death in the plots making this impossible or inadvisable at certain sites or systems.

Destructive sampling

Destructive sampling of vegetation and soil in experimental plots may affect ecosystem processes (e.g. change water movement, reduce photosynthesis and provoke infestation) and the responses measured (e.g. De Boeck *et al.* 2008). Therefore, sampling strategies must be carefully planned and destructive sampling potentially minimised or avoided, especially if experimental plots are small and/or the experiment is conducted over many years.

MEASUREMENTS, PROTOCOLS AND DATA

Treatment effects on key water-related drivers such as, water input, soil moisture content and soil temperature in the individual experimental plots need to be measured and documented. This may seem

self-evident but is, nevertheless, often done improperly or insufficiently. In addition, pre-treatment measurements from control and treatment plots are strongly advised and have great advantage for later data analyses. Quantification of the water balance and its components and analyses of experimental effects often require application of a hydrological model and therefore the respective measurements including soil physical characteristics and their change over time should be carried out to satisfy the model requirements. Involving a model in the early stage of the experiment can provide a useful guide to design the type and period of measurements (Rustad 2008).

Artefact control and documentation

Experimental artefacts have to be quantified to distinguish them from treatment responses (Table 2) and measurements must be planned to document and trace potential artefacts. Most importantly, unintended changes in the water balance need to be quantified (e.g. basic micro climatic conditions, water input and soil moisture) (Table 3). For example, the fraction of precipitation loss by interception is likely to change as a consequence of changes in

Table 3 In addition to the general set of response parameters measured as part of any given experiment, conducting additional measurements to improve the potential to compare and synthesise the results with other experiments will increase the value of the experiment significantly. These include measurements to document the strength of the treatments relative to the untreated reference condition, characteristic soil and plant features relevant for the hydrological cycle and, in the context of climate change, a set of carbon-related responses

Parameter	Example
Treatment documentation	
Treatment	Climatic drivers (continuous): Air temperature, precipitation, wind speed and radiation, timing of events Physical ecosystem responses (continuous): Soil moisture (relevant soil layers), soil temperature (relevant soil layers)
Artefacts	Light intensity (continuous – in plot) Wind speed (continuous – in plot)
System characteristics	
Soil characteristics determining the bucket size and drainage	Soil characteristics within rooting depth: texture, pF, pore size distribution, SOM characteristics (one off)
Plant characteristics determining the 'bucket size'	Rooting depth (seasonal)
Plant characteristics determining the water consumption	Plant community composition (seasonal/annual) Species specific water use, wilting point, drought recovery (one off) Root distribution and plant-microbial interactions (one off/annual)
Responses	
Ecosystem carbon characteristics	Plant biomass C pools (seasonal/annual) Soil C pools (annual) Plant litter production (annual) NEE (or proxy) and soil respiration (site & scenario relevant campaigns)
Biologically relevant information	Herbivore outbreak (event) Species specific growth/cover and wilting (seasonal and event)

both precipitation regimes as well as canopy structure. Secondly, unintended changes in other important drivers and responses must be quantified (e.g. light intensity, wind speed, soil and air temperature) (Table 3). For example, unintended changes in wind exposure may indirectly affect the hydrological balance through impacts on evapotranspiration.

If artefacts are unavoidable, separate study plots serving as 'artefact' or 'disturbance' controls may be required in addition to ambient/untreated controls (e.g. Peterjohn *et al.* 1995) to separate treatment effects from the artefacts. This may, for example, be the impact of experimental installations (e.g. roofs or fences) on temperature, light and water as well as the net effect of compensation measures such as an 'irrigation control'. Artefact controls do not necessarily run for years but may be conducted for a shorter duration of the experiment.

Response parameters, data and data-model interaction

Any precipitation experiment is based on specific scientific questions and hypotheses as well as political considerations relevant for the specific context that guides the experimental design and the response measurements conducted. Consequently, results from precipitation experiments will be inherently site and project specific but may nevertheless contribute to more general understanding if results are analysed and compared across a range of site conditions through traditional data syntheses (e.g. Beier *et al.* 2008), model integration and comparisons (e.g. Luo *et al.* 2008, 2011) or statistical meta-analyses (e.g. Rustad *et al.* 2001; Wu *et al.* 2011). It is therefore important that the response measurements are conducted according to general scientific standards and by generally accepted and documented methods. In addition, we suggest that some standard response parameters of broader scientific interest should be included for better comparability across experiments and application of ecosystem models (Table 3). We are aware that additional sensors and measurements pose additional costs to projects, and therefore an extensive list of soil, plant and water responses is clearly unrealistic. However, measurements providing basic hydrological characteristics of the system (e.g. soil texture, organic matter content, rooting depth and distribution, plant species and community characteristics) are essential for modelling and understanding the hydrological cycle of ecosystems and should always be provided. Furthermore, as most precipitation experiments are conducted in a climate change context, measurements to quantify the feedbacks between the ecosystem and the climate system, such as changes in pools and fluxes of carbon in the ecosystem would improve the value of any experiment in the context of others (Table 3). In addition, data analyses and syntheses are also constrained by a general lack of coherent and mutual or linked databases on ecosystem responses to experimental precipitation change.

Data mining may complement precipitation experiments to understand ongoing processes and responses to climate change. For example major data archives exist on plant traits, indicator and experience values (e.g. Ellenberg *et al.* 1991; Landolt *et al.* 2010; Kattge *et al.* 2011). These may provide important information by comparison across sites and climates and by validation against responses in experiments remembering potential limitations in the application of these values to, for example, certain specific regions or ecosystems.

SUMMARY AND RECOMMENDATIONS

Climate change involves complex changes in amounts, patterns and timing of precipitation as well as interactions with other global change factors such as temperature and elevated CO₂. The global change driven alterations in precipitation may have as strong or in many systems even stronger impacts on ecosystem functioning than other global change drivers such as warming and elevated CO₂ (e.g. Weltzin *et al.* 2003; Garbulska *et al.* 2010; Leuzinger & Körner 2010). Conceptual and theoretical frameworks exist for understanding and assessing impacts of precipitation change, but experimental data are needed to qualify and validate these and therefore, effect studies related to alterations in precipitation are increasingly needed. We herein analysed past experiments related to precipitation change and demonstrate clear limitations in the past and on-going experiments with respect to (1) the representation of the global conditions (climatic and ecosystem characteristics), (2) the applied precipitation scenarios (especially lack of focus on variability, extremity and interactions with other drivers) and (3) degree of species and genotype diversity included. Therefore, we are yet not able to provide a comprehensive set of experimental data to understand and predict how changes in precipitation regimes will affect terrestrial ecosystems. New precipitation experiments are needed to improve our understanding in this important area. On the basis of the analysis we recommend:

Site and manipulation characteristics

To better understand the ecological effects of climate driven changes in precipitation across the globe, experiments should embrace the width in biomes and water-related ecosystem characteristics and test relevant climate change-related scenarios.

We recommend:

- (1) Studies addressing changes in precipitation in understudied areas of the globe, especially moist and warm environments and cold and semi-cold environments.
- (2) Studies applying manipulations relevant for future climate change scenarios, particularly including altered rainfall frequency and intensity, altered seasonality and extreme events combined with site-specific hydrological modelling.
- (3) Studies determining the interaction between soil characteristics including water storage capacity and the effects of changing precipitation.
- (4) Studies that include plant community characteristics such as ecological traits and species and genotype diversity to detect functional ecosystem responses to changing precipitation regimes.
- (5) Studies that run for longer time periods (> 10 years) and address structural changes in the ecosystem (e.g. soil structure and plant- and microbial community).

Multi-factor and multi-control experiments

New experiments should be designed to ensure relevant control conditions for evaluation of experimental responses and should address the interactions between water and other key drivers related to climate and global change.

We recommend:

- (1) Studies that involve multi-factor experiments focussing on interactions of altered precipitation regimes with CO₂, temperature and nutrients.

- (2) Studies addressing impacts of altered precipitation and interactions with other complex changes such as disturbances.

- (3) Studies that employ multi controls to disentangle the treatment effects from the stochastic natural climate variability.

Functional responses and feedbacks

Ecosystem precipitation experiments should address factors controlling ecosystem responses and vulnerability to altered precipitation and extreme events and should improve integration and coordination across experiments

We recommend:

- (1) Studies focussing on factors and mechanisms controlling resilience/resistance and adaptation/acclimation to altered precipitation.
- (2) Studies investigating exceedance of biologically relevant thresholds including processes controlling mortality, differences in inter- and intra-species responses and dominance shifts in communities.
- (3) Studies employing multilevel treatments to investigate driver-response surfaces.
- (4) Studies including response measurements related to ecosystem functioning, ecosystem structure and biosphere-atmosphere feedbacks (e.g. ecophysiological performance, soil respiration, N-mineralisation, SOM turnover).

Data-model-design interactions

Data integration across experiments and application of ecosystem models as well as careful data mining of past results could lead to new insights. This requires development of reliable and improved common and coherent tools for data storage and retrieval.

We recommend:

- (1) Increased data integration and data mining of existing data across experiments using expertise based appropriate data stratification.
- (2) Studies that include close collaboration of ecologists and modellers in the phase of the project design as well as in its evaluation.

ACKNOWLEDGEMENTS

This study is based on a group discussion at a meeting in Basel October 2009, funded by the networking activity ClimMani (www.climmani.org) under the European Science Foundation (ESF). The authors want to thank the participants at the meeting for valuable ideas and inputs during the discussions. The study was further supported by the Danish V. Kann Rasmussen Foundation (www.vkrf.org/vkrf_home.php) through the Climate project. H.J. de Boeck is a post-doctoral fellow with FWO-Vlaanderen. S. Leuzingers participation was funded by the FP7 project ACQWA.

AUTHORSHIP

Claus Beier – Lead author, layout and draft of manuscript, ideas and considerations of experimental design, variability and thresholds and dilemmas, coordination. Carl Beierkuhnlein – Rapporteur from discussions, key inputs on drought-community designs and responses. Thomas Wohlgemuth – Discussion participant, inputs regarding climate change scenarios and plant physiological

responses. Josep Penuelas – Discussion participant, inputs regarding ecophysiological responses and observed drought effects. Bridget Emmett – Discussion participant, inputs regarding drought experiments, inputs on soil and soil structure responses and observed changes, data-model interactions. Christian Körner – Discussion participant, ecophysiological responses to changing water conditions. Hans de Boeck – Discussion participant, inputs on interactions or water with warming and experimental design considerations, artefacts. Jens Hesselbjerg Christensen – inputs regarding climate change scenarios and predictions. Sebastian Leuzinger – Discussion participant, inputs regarding experimental design, multifactor approaches and plant and ecosystem water use. Ivan Janssens – Discussion participant, inputs regarding climate change extreme events and soil carbon responses. Karin Hansen – Meeting organiser, inputs regarding forest ecosystems and water experiments.

REFERENCES

- Albert, K.R., Ro-Poulsen, H., Mikkelsen, T.N., Michelsen, A., Linden, L. & Beier, C. (2011). Effects of elevated CO₂, warming and drought episodes on plant carbon uptake in a temperate heath ecosystem are controlled by soil water status. *Plant Cell Environ.*, 4, 1207–1222.
- Beier, C., Emmett, B., Gundersen, P., Tietema, A., Penuelas, J., Estiarte, M. *et al.* (2004). Novel approaches to study climate change effects on terrestrial ecosystems in the field – drought and passive night time warming. *Ecosystems*, 7, 583–597.
- Beier, C., Emmett, B.A., Peñuelas, J., Schmidt, I.K., Tietema, A., Estiarte, M. *et al.* (2008). Carbon and nitrogen cycles in European ecosystems respond differently to global warming. *Sci. Total Environ.*, 407, 692–697.
- Beierkuhnlein, C., Jentsch, A., Thiel, D., Willner, E. & Kreyling, J. (2011). Ecotypes of European grass species respond specifically to warming and extreme drought. *J. Ecol.*, 99, 703–713.
- Boberg, F., Berg, P., Thejll, P., Gutowski, W.J. & Christensen, J.H. (2009). Improved confidence in climate change projections of precipitation evaluated using daily statistics from the PRUDENCE ensemble. *Clim. Dyn.*, 32, 1097–1106.
- Borken, W. & Matzner, E. (2009). Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. *Glob. Change Biol.*, 15, 808–824.
- Bouchet, R.J. (1963). Evapotranspiration réelle et potentielle, signification climatique. *Int. Assoc. Sci. Hydrol., Proc. Berkeley, Calif. Symp., Publ.*, 62, 134–142.
- Brazdil, R., Wheeler, D. & Pfister, C. (2010). European climate of the past 500 years based on documentary and instrumental data. *Clim. Change*, 101, 1–6.
- Briske, D.D., Fuhlendorf, F.D. & Smeins, F.E. (2006). A unified framework for assessment and application of ecological thresholds. *Rangeland Ecol. Manage.*, 59, 225–236.
- Chesson, P., Gebauer, R.L.E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K. *et al.* (2004). Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia*, 141, 236–253.
- Christensen, J.H. & Christensen, O.B. (2007). A summary of the PRUDENCE model projections of changes in European climate by the end of this century. *Clim. Change*, 81, 7–30.
- Christensen, J.H., Hewitson, B., Busiuc, A., Chen, A., Gao, X., Held, I. *et al.* (2007). Regional climate projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (ed. Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. and Miller, H.L.). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 847–940. Chapter 11.
- Cottingham, K.L., Lennon, J.T. & Brown, B.L. (2005). Knowing when to draw the line: designing more informative ecological experiments. *Front. Ecol. Environ.*, 3, 145–152.
- Daly, E. & Porporato, A. (2005). A review of soil moisture dynamics: from rainfall infiltration to ecosystem response. *Environ. Eng. Sci.*, 22, 9–24.
- De Boeck, H.J., Liberloo, M., Gielen, B., Nijs, I. & Ceulemans, R. (2008). The observer effect in plant science. *New Phytol.*, 177, 579–583.
- De Boeck, H.J., Dreesen, F.E., Janssens, I.A. & Nijs, I. (2011). Whole-system responses of experimental plant communities to climate extremes imposed in different seasons. *New Phytol.*, 189, 806–817.
- Dobbertin, M., Eilmann, B., Bleuler, P., Giuggiola, A., Pannatier, E.G., Landolt, W., Schleppei, P. & Rigling, A. (2010). Effect of irrigation on needle morphology, shoot and stem growth in a drought-exposed *Pinus sylvestris* forest. *Tree Physiol.*, 30, 346–360.
- Dunnett, N.P., Willis, A.J., Hunt, R. & Grime, J.P. (1998). A 38-year study of relations between weather and vegetation dynamics in road verges near Bibury, Gloucestershire. *J. Ecol.*, 86, 610–623.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. (1991). Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, XVIII, 248.
- Emmett, B.A., Beier, C., Estiarte, M., Tietema, A., Kristensen, H.L., Williams, D. *et al.* (2004). The response of soil processes to climate change: results from manipulation studies across an environmental gradient. *Ecosystems*, 7, 625–637.
- Eriksson, O. (1996). Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. *Oikos*, 77, 248–258.
- Fay, P.A., Carlisle, J.D., Knapp, A.K., Blair, J.M. & Collins, S.L. (2000). Altering rainfall timing and quantity in a mesic grassland ecosystem: design and performance of rainfall manipulation shelters. *Ecosystems*, 3, 308–319.
- Fay, P.A., Blair, J.M., Smith, M.D., Nippert, J.B., Carlisle, J.D. & Knapp, A.K. (2011). Relative effects of precipitation variability and warming on tallgrass prairie ecosystem function. *Biogeosciences*, 8, 3053–3068.
- Franks, S.J., Sim, S. & Weis, A.E. (2007). Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *PNAS*, 104, 1278–1282.
- Garbulsky, M.F., Penuelas, J., Papale, D., Ardö, J., Goulden, M.L., Kiely, G. *et al.* (2010). Patterns and controls of the variability of radiation use efficiency and primary productivity across terrestrial ecosystems. *Glob. Ecol. Biogeogr.*, 19, 253–267.
- Gerten, D., Luo, Y., le Maire, G., Parton, W.J., Keough, C., Weng, E. *et al.* (2008). Modelled effects of precipitation on ecosystem carbon and water dynamics in different climatic zones. *Glob. Change Biol.*, 14, 1–15.
- Granier, A., Reichstein, M., Bréda, N., Janssens, I.A., Falge, E., Ciais, P. *et al.* (2007). Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. *Agric. For. Meteorol.*, 143, 123–145.
- Grime, J.P., Brown, V.K., Thompson, K., Masters, G.J., Hillier, S.H., Clarke, I.P. *et al.* (2000). The response of two contrasting limestone grasslands to simulated climate change. *Science*, 289, 762–765.
- Gu, C. & Riley, W.J. (2010). Combined effects of short term rainfall patterns and soil texture on soil nitrogen cycling: A modeling analysis. *J. Contam. Hydrol.*, 112, 141–154.
- Gutowski, W.J., Hegerl, G.C., Holland, G.J., Knutson, T.R., Mearns, L.O., Stouffer, R.J. *et al.* (2008). Causes of observed changes in extremes and projections of future changes. In: *Weather and Climate Extremes in a Changing Climate: Regions of Focus: North America, Hawaii, Caribbean, and U.S. Pacific Islands* (ed. Karl, T.R., Meehl, G.A., Miller, C.D., Hassol, S.J., Waple, A.M. and Murray, W.L.). Synthesis and Assessment Product 3.3. U.S. Climate Change Science Program, Washington, DC, pp. 81–116.
- Gutschick, V.P. & BassiriRad, H. (2003). Extreme events as shaping physiology, ecology, and evolution of plants: toward a unified definition and evaluation of their consequences. *New Phytol.*, 160, 21–42.
- Hegerl, G., Hanlon, H. & Beierkuhnlein, C. (2011). Elusive extremes. *Nat. Geosci.*, 4, 142–143.
- Huntington, T.G. (2006). Evidence for intensification of the global water cycle: review and synthesis. *J. Hydrol.*, 319, 83–95.
- Huxman, T.E., Snyder, K.A., Tissue, D., Leffler, A.J., Ogle, K., Pockman, W.T. *et al.* (2004). Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia*, 141, 254–268.
- Ineson, P., Taylor, K., Harrison, A.F., Poskitt, J., Benham, D.G., Tipping, E. & Woof, C. (1998). Effects of climate change on nitrogen dynamics in upland soils. 1. A transplant approach. *Glob. Change Biol.*, 4, 143–152.
- IPCC (2007). Causes of observed changes in extremes and projections of future changes. In: *Climate Change 2007: The Physical Science Basis. Contribution of*

- Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. (ed. Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. and Miller, H.L.). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 996 pp.
- IPCC (2012): Summary for policymakers. In: *Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation* (eds Field, C.B., Barros, V., Stocker, T.F., Qin, D., Dokken, D.J., Ebi, K.L., Mastrandrea, M.D., Mach, K. J., Plattner, G.-K., Allen, S.K., Tignor, M. & Midgley, P.M.). A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK, and New York, NY, USA, pp. 1–19.
- Jentsch, A., Kreyling, J. & Beierkuhnlein, C. (2007). A new generation of climate change experiments: events, not trends. *Front. Ecol. Environ.*, 5, 365–374.
- Jentsch, A., Kreyling, J., Elmer, M., Gellesch, E., Glaser, B., Grant, K. et al. (2011). Climate extremes initiate ecosystem regulating functions while maintaining productivity. *J. Ecol.*, 99, 689–702.
- Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönsch, G. et al. (2011). TRY – a global database of plant traits. *Glob. Change Biol.*, 17, 2905–2935.
- Katz, W.R. & Brown, G. (1992). Extreme events in a changing climate: variability is more important than averages. *Clim. Change*, 21, 289–302.
- Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D. et al. (2002). Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science*, 298, 2202–2205.
- Knapp, A., Beier, C., Briske, D., Classen, A.T., Luo, Y., Reichstein, M. et al. (2008). Consequences of altered precipitation regimes for terrestrial ecosystems. *Bioscience*, 58, 1–11.
- Knorr, K.-H. & Blodau, C. (2009). Impact of experimental drought and rewetting on redox transformations and methanogenesis in mesocosms of a northern fen soil. *Soil Biol. Biochem.*, 41, 1187–1198.
- Körner, C. & Basler, D. (2010). Phenology under global warming. *Science*, 327, 1461–1462.
- Kreyling, J., Jentsch, A. & Beierkuhnlein, C. (2011). Stochastic trajectories of succession initiated by extreme climatic events. *Ecol. Lett.*, 14, 758–764.
- Kupper, P., Söber, J., Sellin, A., Löhmus, K., Tullus, A., Räm, O. et al. (2011). An experimental facility for free air humidity manipulation (FAHM) can alter water flux through deciduous tree canopy. *Environ. Exp. Bot.*, 72, 432–438.
- Lamersdorf, N.P., Beier, C., Blanck, K., Bredemeier, M., Cummins, T., Farrell, E.P. et al. (1998). Effect of drought experiments using roof installations on acidification/nitrification of soils. *For. Ecol. Manage.*, 101, 95–109.
- Landolt, E., Bäumler, B., Erhardt, A., Hegg, O., Klötzli, F., Lämmler, W., Nobis, M., Rudmann, K., Schweingruber, F.H., Theurillat, J.-P., Urmi, E., Vust, M. & Wohlgemuth, T. (2010). *Flora indicativa – Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen*. Verlag Haupt, Bern, 376 S.
- Larsen, K.S., Andresen, L.C., Beier, C., Jonasson, C., Albert, K.R., Ambus, P. et al. (2011). Reduced N cycling in response to drought, warming, and elevated CO₂ in a Danish heathland: Synthesizing results of the CLIMATE project after two years of treatments. *Glob. Change Biol.*, 17, 1884–1899.
- Leuzinger, S. & Körner, C. (2010). Rainfall distribution is the main driver of runoff under future CO₂-concentration in a temperate deciduous forest. *Glob. Change Biol.*, 16, 246–254.
- Leuzinger, S., Luo, Y., Beier, C., Dieleman, W., Vicca, S. & Körner, C. (2011). Do global change experiments overestimate impacts on terrestrial ecosystems? *Trends Ecol. Evol.*, 26, 236–241.
- Luo, Y., Gerten, D., Maire, G.L., Parton, W.J., Weng, E., Zhou, X. et al. (2008). Modelled interactive effects of precipitation, temperature and [CO₂] on ecosystem carbon and water dynamics in different climatic zones. *Glob. Change Biol.*, 14, 1986–1999.
- Luo, Y., Melillo, J., Niu, S., Beier, C., Clark, J., Classen, A. et al. (2011). Coordinated approaches to quantify long-term ecosystem dynamics in response to global change. *Glob. Change Biol.*, 17, 843–854.
- Meinzer, F.C. (2003). Functional convergence in plant response to the environment. *Oecologia*, 134, 1–11.
- Mikkelsen, T.N., Beier, C., Jonasson, S., Holmstrup, M., Schmidt, I.K., Ambus, P. et al. (2008). Experimental design of multifactor climate change experiments with elevated CO₂, warming and drought – the CLIMATE project. *Funct. Ecol.*, 22, 185–195.
- Min, S.K., Zhang, X.B., Zwiers, F.W. & Hegerl, G.C. (2011). Human contribution to more-intense precipitation extremes. *Nature*, 470, 376–379.
- Morgan, J.A., Pataki, D.E., Körner, C., Clark, H., Del Grosso, S.J., Grünzweig, J. M. et al. (2004). Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO₂. *Oecologia*, 140, 11–25.
- Mueller, R.C., Scudder, C.M., Porter, M.E., Trotter, R.T., Gehring, C.A. & Whitham, T.G. (2005). Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. *J. Ecol.*, 93, 1085–1093.
- Peñuelas, J. & Filella, I. (2001). Phenology: responses to a warming world. *Science*, 294, 793–795.
- Peñuelas, J., Prieto, P., Beier, C., Cesaraccio, C., De Angelis, P., de Dato, G. et al. (2007). Response of plant species richness and primary productivity in shrublands along a north-south gradient in Europe to seven years of experimental warming and drought. Reductions in primary productivity in the heat and drought year of 2003. *Glob. Change Biol.*, 13, 2563–2581.
- Peterjohn, W.T., Melillo, J.M., Steudler, P.A., Newkirk, K.M., Bowles, F.P. & Aber, J.D. (1995). Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. *Ecol. Appl.*, 4, 617–625.
- Pfister, C. (2009). The “Disaster Gap” of the 20th century and the loss of traditional disaster memory. *GALA – Ecol. Perspect. Sci. Soc.*, 18, 239–246.
- Rasmussen, L., Beier, C. & Bergstedt, A. (2002). Experimental manipulations of old pine forest ecosystems to predict the potential tree growth effects of increased CO₂ and temperature in a future climate. *For. Ecol. Manage.*, 158, 179–188.
- Richter, S., Kipfer, T., Wohlgemuth, T., Calderón Guerrero, C., Ghazoul, J. & Moser, B. (2012). Phenotypic plasticity facilitates resistance to climate change in a highly variable environment. *Oecologia*, 169, 269–279.
- Rustad, L. (2008). The response of terrestrial ecosystems to global climate change: towards an integrated approach. *Sci. Total Environ.*, 404, 222–235.
- Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E. et al. (2001). A meta-analysis of the response of soil respiration, net N mineralisation, and above-ground plant growth to experimental ecosystem warming. *Oecologia*, 126, 543–562.
- Scheffer, M. & Carpenter, S.R. (2003). Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecol. Evol.*, 18, 648–656.
- Scherer, D., Bader, M.K.F. & Körner, C. (2011). Drought sensitivity ranking of deciduous tree species based on thermal imaging of forest canopies. *Agric. For. Meteorol.*, 151, 163–1640.
- Seastedt, T.R. & Vaccaro, L. (2001). Plant species richness, productivity, and nitrogen and phosphorus limitations across a snowpack gradient in alpine tundra, Colorado, USA. *Arct. Antarct. Alp. Res.*, 33, 100–106.
- Seneviratne, S.I., Corti, T., Davin, E.L., Hirschi, M., Jaeger, E.B., Lehner, I. et al. (2010). Investigating soil moisture-climate interactions in a changing climate: a review. *Earth Sci. Rev.*, 99, 125–161.
- Shaw, M.R., Zavaleta, E.S., Chiariello, N.R., Cleland, E.E., Mooney, H.A. & Field, C.B. (2002). Grassland responses to global environmental changes suppressed by elevated CO₂. *Science*, 298, 1987–1990.
- Sherry, R.A., Weng, E.S., Arnone, J.A. III, Johnson, D., Schimel, D.S., Verburg, P.S. et al. (2008). Lagged effects of experimental warming and doubled precipitation on annual and seasonal aboveground biomass production in a tallgrass prairie. *Glob. Change Biol.*, 14, 2923–2936.
- Singer, M.C. & Parmesan, C. (2010). Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Philos. Trans. R. Soc. Lond.*, 365, 3161–3176.
- Smith, M.D. (2011). The ecological role of climate extremes: current understanding and future prospects. *J. Ecol.*, 99, 651–655.
- Smith, M.D., Knapp, A.K. & Collins, S.L. (2009). A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology*, 90, 3279–3289.
- Sowerby, A., Emmett, B.A., Tietema, A. & Beier, C. (2008). Contrasting effects of repeated summer drought on soil carbon efflux in hydric and mesic heathland soils. *Glob. Change Biol.*, 14, 2388–2404.
- Sowerby, A., Emmett, B.A., Williams, D., Beier, C. & Evans, C.D. (2010). The response of dissolved organic carbon (DOC) and ecosystem carbon balance to experimental drought in a temperate shrubland. *Eur. J. Soil Sci.*, 61, 697–709.

- Svejcar, T., Angell, R. & Miller, R. (1999). Fixed location rain shelters for studying precipitation effects on rangelands. *J. Arid Environ.*, 42, 187–193.
- Teuling, A.J., Seneviratne, S.I., Stöckli, R., Reichstein, M., Moors, E. & Ciais, P. (2010). Contrasting response of European forest and grassland energy exchange to heatwaves. *Nat. Geosci.*, 3, 722–727.
- Thomas, C.D., Cameron, A., Green, R.E. *et al.* (2004). Extinction risk from climate change. *Nature*, 427, 145–148.
- de Visser, P.H.B., Beier, C., Rasmussen, L., Kreutzer, K., Steinberg, N., Bredemeier, M. *et al.* (1994). Biological response of forest ecosystems to input changes of water, nutrients and atmospheric loads. *For. Ecol. Manage.*, 68, 15–29.
- Walter, J., Nagy, L., Hein, R., Rascher, U., Beierkuhnlein, C., Willner, E. *et al.* (2011). Do plants remember drought? Hints towards a drought-memory in grasses. *Environ. Exp. Bot.*, 71, 34–40.
- Weltzin, J.F. *et al.* (2003). Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience*, 53, 941–952.
- Wipf, S. & Rixen, C. (2010). A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. *Polar Res.*, 29, 95–109.
- Wu, Z., Dijkstra, P., Koch, G.W., Penuelas, J. & Hungate, B.A. (2011). Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Glob. Change Biol.*, 17, 927–942.
- Zavalloni, C., Gielen, B., Lemmens, C.M.H.M., De Boeck, H.J., Blasi, S., Van den Bergh, S. *et al.* (2008). Does a warmer climate with frequent mild water

shortages protect grassland communities against a prolonged drought?. *Plant Soil*, 308, 119–130.

SUPPORTING INFORMATION

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Editor, John Arnone

Manuscript received 24 November 2011

First decision made 7 January 2012

Second decision made 20 March 2012

Manuscript accepted 2 April 2012