

Complexity in Climate Change Manipulation Experiments

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Climate change goes beyond gradual changes in mean conditions. It involves increased variability in climatic drivers and increased frequency and intensity of extreme events. Climate manipulation experiments are one major tool to explore the ecological impacts of climate change. Until now, precipitation experiments have dealt with temporal variability or extreme events, such as drought, resulting in a multitude of approaches and scenarios with limited comparability among studies. Temperature manipulations have mainly been focused only on warming, resulting in better comparability among studies. Congruent results of meta-analyses based on warming experiments, however, do not reflect a better general understanding of temperature effects, because the potential effects of more complex changes in temperature, including extreme events, are not yet covered well. Heat, frost, seasonality, and spatial variability in temperature are ecologically important. Embracing complexity in future climate change experiments in general is therefore crucial.

Keywords: climate change, experiments, warming, temporal variability, extreme events

Climate change will alter the fundamental conditions of future terrestrial ecosystems, with temperature and precipitation being the most affected (Solomon et al. 2007). Climate manipulation experiments are one important tool for understanding the response of ecosystems to such changes (e.g., Rustad 2008). Temperature and precipitation have different characteristics, which lead to different considerations regarding the design of experiments and the scenarios to be tested.

Precipitation is temporally and spatially variable, and future scenarios are relatively uncertain (Solomon et al. 2007). Recently, Beier and colleagues (2012) summed up the current state of the art in precipitation manipulation experiments and pointed out several crucial aspects to be considered in the future—for example, biased geographic coverage, artifacts related to rain-out shelter design, and the need for proper controls. One of their basic insights was that the available precipitation manipulations have been carried out in many different contexts, through many different designs, and they have been used to test very different (and often simplistic) precipitation scenarios. Therefore, these experiments are hardly comparable, which has led to a lack of formal meta-analyses. Beier and colleagues (2012) argued that this might be because changes in precipitation regimes are more complex and uncertain than those in temperature, which makes their scenarios more difficult to define and the required range of experimental conditions more complex and less comparable. Focusing on more

simple and uniform scenarios of change has been suggested as a strategy that would lead to better comparability (Knapp et al. 2012, Fraser et al. 2013) and has been the basis for meta-analyses (Wu et al. 2011).

Temperature is a continuous variable, and the climate-driven changes in temperature are less variable and more predictable than are those of precipitation. In experimentation, this apparent homogeneity in temperature relative to precipitation has led to the application of approaches almost entirely focused on average increases in temperature (figure 1). In consequence, the conducted warming experiments are more comparable, which facilitates comprehensive meta-analyses (e.g., Rustad et al. 2001, Lin et al. 2010, Dieleman et al. 2012). However, the focus on gradual and positive shifts of the mean temperature (figure 1; Jentsch et al. 2007) is accompanied by a lack of studies on extremes and temporal variability in these experiments. Consequently, complexity is not yet adequately reflected in temperature change experiments.

Locally and regionally, the global temperature increase will manifest through highly varied changes, including uneven warming and, in some places, even cooling and short- or long-term extreme temperature changes such as heat waves, increased freeze–thaw cycles, and winter warm spells (Solomon et al. 2007). Such changes may have large impacts on ecosystem processes and function. For instance, single heat waves can alter plant community compositions (White et al. 2000). Likewise, minimum temperature events during

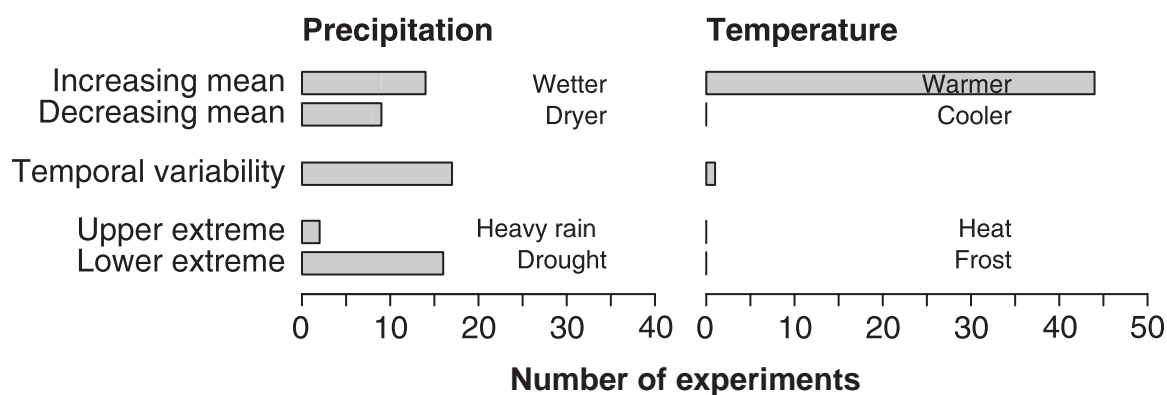


Figure 1. Complexity is embraced in precipitation experiments, whereas temperature experiments so far show a clear focus on rising mean temperatures (warming). Temporal variability includes increased or reduced variability in temperature or precipitation over time. The data include 45 temperature manipulation experiments and 43 precipitation experiments taken from the TERACC (Terrestrial Ecosystem Response to Atmospheric Climatic Change; www.umaine.edu/teracc) and INTERFACE (Integrated Network for Terrestrial Ecosystem Research on Feedbacks to the Atmosphere and Climate; www.bio.purdue.edu/INTERFACE) databases. Manipulations of more than one category were applied in several experiments; individual experiments could therefore be counted more than once.

winter (Kreyling et al. 2012a) or spring (Gu et al. 2008) can create lethal stress, can alter the competitive balance within plant communities, and can affect biogeochemical cycles (Mulholland et al. 2009). The ecological and evolutionary importance of minimum temperature events in the context of climate change was summed up by Inouye (2000).

Until now, treatments were applied in most warming experiments only during the growing season (Rustad et al. 2001), whereas climate projections clearly indicate differences in warming trends between seasons, with strongest shifts expected for winter (Christensen et al. 2007). Warming during different seasons causes contrasting effects, with winter and spring warming more important than summer warming for plant phenology and productivity in cold, northern ecosystems (Aerts et al. 2006). An earlier onset of the growing season in response to global warming can furthermore increase the risk of frost damage (Inouye 2008, Augspurger 2013). Temperature variability over days or a few weeks is also ecologically relevant but not well investigated. Warming pulses of a few days over winter can lead to massive dieback in tundra vegetation (Bokhorst et al. 2009), and the effects of warming pulses may benefit some and be a detriment to other plant functional types in temperate zones (Kreyling et al. 2010). Changes in the frequency of freeze–thaw cycles can furthermore increase carbon loss from ecosystems and can affect microbial communities (Larsen et al. 2002).

The scientific community has applied different experimental approaches for precipitation and temperature manipulations: Precipitation experiments have been focused mostly on single events (in some cases, extreme events) and complexity, whereas temperature manipulations have been focused on shifts in mean conditions (figure 1). This is understandable, because precipitation is a discrete and

stochastic variable, whereas warming is a continuous variable. The availability of meta-analyses and their congruent results for temperature change (Rustad et al. 2001, Lin et al. 2010, Dieleman et al. 2012), however, should not be mistaken as a sign of a general understanding of temperature effects on terrestrial ecosystems, because these experiments cover only average warming and not the potential effects associated with extreme events and more complex changes in temperature. The examples presented above imply that temperature change also contains ecologically important challenges in regard to complexity (e.g., extremes, temporal variability).

For precipitation changes, Knapp and colleagues (2008) demonstrated that increased variability and extremity are likely to become crucial factors controlling ecological effects in terrestrial ecosystems at all moisture levels, especially because these changes will lead to increased frequency of threshold exceedance. Beier and colleagues (2012) further showed how these complexities need to be systematically addressed in future precipitation experiments. Similar arguments can be raised for temperature, and the examples given above clearly demonstrate that the complexity of temperature shifts is ecologically important. For temperature, there is therefore a clear need to embrace complexity in future, well-designed experiments.

In comparison with the study of chronic changes in mean conditions, several challenges arise for experimental designs focused on the complexity of climatic drivers (table 1). Projections of magnitudes and frequencies of occurrence of extreme events are generally uncertain, which complicates the choice of a single “correct” scenario to be experimentally tested. Here, gradient or regression-type experiments (Beier et al. 2012) appear useful to determine response surfaces rather than single responses and to identify the thresholds of

Table 1. Advantages and challenges for climate change manipulation experiments.

Factors	Focus	Advantages	Challenges
Single factor	Chronic shift of mean conditions	Sound projections from climate models available, few scenarios, easy to replicate across systems	To test generalization with multifactor and multisite experiments across biomes, to test gradients of different manipulation strengths
	Pulsed shifts in temporal variability and single (extreme) events	Extremes determine the exceedance of ecological thresholds and mortality	There are no sound projections from climate models available to test for thresholds (gradient or regression designs); sensitivity can be system specific, so generalization across sites might be elusive
Multifactor	Chronic shifts of mean conditions	More realistic than single-factor manipulations (multifactor experiments tend to level responses out among factors)	Selection of factor combinations (the number of combinations more than doubles for any new factor added)
	Chronic shifts of mean conditions combined with pulsed shifts in temporal variability and single (extreme) events	More realistic in relation to future scenarios	The unlimited number of scenarios (test system sensitivity to single factors first, use gradient or regression designs, couple with modeling, focus on process understanding)

sensitivities. These sensitivities, however, will differ among systems, just as limiting factors differ. Furthermore, the suite of possible scenarios for the different factors and their combinations are numerous, and identification of a “correct” scenario appears impossible. Therefore, such experiments should focus, rather, on process understanding first, before any step toward broader generalization is made. Seeking generalization by repeating manipulations across different systems (the multisite approach; Beier et al. 2004, Knapp et al. 2012, Fraser et al. 2013) is an important step forward in experimental climate impact assessments but is clearly limited by logistical constraints on the complexity of possible manipulations. We suggest that experiments on complexity should be initially focused on single factors at various strengths, intensities, or frequencies, should be carried out at single or a few sites, and should ideally be closely coupled with process-based modeling from the start in order to generate hypotheses, guide the choice of scenarios and the responses to be measured, and generalize the results beyond the site- and scenario-specific conditions. The link between virtual experiments with unlimited choices of scenarios using such models (e.g., Gerten et al. 2008, Luo et al. 2008) and the direct verification by process-based experiments appears to be crucial.

Some experimental approaches have allowed for the study of extreme rainfall events (e.g., drought, heavy rainfall) and variability of precipitation (Fay et al. 2000, Beier et al. 2004, Jentsch et al. 2007), but challenges arise with regard to the simulation of temperature extremes and temperature variability in field experiments because of trade-offs among the demand for more intense heating, technical possibilities, and artifacts. Passive warming systems lack sufficient control to obtain high temperature increases for long periods of time (Bruhn et al. 2012), whereas greenhouses or chambers entail significant unwanted side effects on temperature, light, and wind (e.g., Rasmussen et al. 2002). Infrared heating treatments can simulate warm spells and heat waves, but they require large amounts of energy and, therefore, financial

resources and involve obvious constraints for application in large areas and with tall vegetation (De Boeck and Nijs 2011, De Boeck et al. 2012). Cooling is even more challenging in the field. In ecosystems with predictable winter snow cover, snow removal can be used to create cold extremes (e.g., Kreyling et al. 2012a). During other seasons and in systems without snow cover, portable devices for the simulation of air frost have been suggested (Thorpe et al. 1993). Alternatively, “realistic” experiments in the field may be combined with laboratory and chamber studies of specific processes in plants and mesocosms (e.g., Kreyling et al. 2012b) or with long-term monitoring in which naturally occurring extremes are analyzed (see, e.g., Ciais et al. 2005 as an example of the ecological consequences of an extreme heat wave). These alternatives clearly have drawbacks, because laboratory and chamber studies are associated with the above-mentioned artifacts and with a lack of ecosystem focus, and long-term monitoring data series will miss true controls or references and may not include the monitoring of relevant responses because of the unplanned nature of the extreme events.

Experiments on single extreme events and on long-term trends in mean conditions differ in the time scale needed for meaningful manipulations but not in that needed for meaningful quantification of the ecological responses. Grassland community shifts, for instance, take about 10 years to reach a new quasiequilibrium in response to alterations in the precipitation regime (Heisler and Weltzin 2006). Climate manipulations concerning mean conditions therefore need to be continued for several years to allow for sound investigations of their effects. Early responses may be transient and may lead to improper conclusions regarding long-term responses (Hollister et al. 2005). Similarly, experiments on single events should follow the effects over time to understand recovery, adaptation, and long-term consequences, which might differ from short-term effects (Kreyling et al. 2010). Although manipulations might be carried out just once over very short time periods, the effects of repeated

events over many years (e.g., Sowerby et al. 2008), as well as hysteresis and alternative stable states (Scheffer and Carpenter 2003) or ecological memory (Walter et al. 2013), are important aspects to be monitored in the long run.

Finally, climate factors work in combination. The few examples of combinations of average temperature, precipitation, and carbon dioxide (CO₂) change, however, led to divergent results that are not always predictable on the basis of the individual effects (Shaw et al. 2002, Larsen et al. 2011, Dieleman et al. 2012). Multifactor experiments are therefore crucial in order to test interactions among several simultaneous factors. In such experiments, the inclusion of temporal variability in drivers such as seasonality and extreme events will inevitably increase complexity considerably. In addition, nonclimatic drivers need to be taken into account, such as land-use change, biodiversity loss, soil structure change, nitrogen deposition or increased levels of atmospheric CO₂. Combining experiments and gradient studies by conducting the same experimental manipulations along environmental gradients can improve the external validity of controlled experiments (Arft et al. 1999, Peñuelas et al. 2007, Beier et al. 2008, 2012).

We advocate the incorporation of complexity into climate change experiments, especially with respect to temperature change. The almost exclusive focus on increases in mean temperature needs to be broadened to studies of seasonality, variability, and extreme events in order to allow for a sound understanding of the ecological implications of climate change. In addition to recently proposed multisite experiments across the globe focused on simple changes in mean climatic conditions (Fraser et al. 2013), we recommend testing the sensitivity of various systems to temperature and precipitation extremes and variability using gradient or regression approaches in single-factor experiments. Process-based modeling based on the results of these simple experiments will allow for virtual experiments on combined drivers in different settings for which the main findings need to be verified by more complex multifactor experiments.

Acknowledgments

We thank three anonymous reviewers for constructive critique on earlier versions of the manuscript. JK received financial support from the German Academic Exchange Service and CB from the Villum Kann Rasmussen Foundation's CLIMATE project, the European Union's INCREASE network (contract no. 227628), and the Analysis and Experimentation on Ecosystems project (contract no. 312690).

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