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Meeting report

Climate change experiments in temperate grasslands: synthesis and future directions

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The immediate need to understand the complex responses of grasslands to climate change, to ensure food supplies and to mitigate future climate change through carbon sequestration, necessitate a global, synthesized approach. Numerous manipulative experiments have altered temperature or precipitation, often in conjunction with other interacting factors such as grazing, to understand potential effects of climate change on the ecological integrity of temperate grasslands and understand the mechanisms of change. Although the different ways in which temperature and precipitation may change to effect grasslands were well represented, variability in methodology limited generalizations. Results from these experiments were also largely mixed and complex; thus, a broad understanding of temperate grassland responses to these factors remains elusive. A collaboration based on a set of globally dispersed, inexpensive experiments with consistent methodology would provide the data needed to better understand responses of temperate grassland to climate change.

Keywords: temperature; precipitation; productivity; community; plant ecology; vegetation science

1. INTRODUCTION

Temperate grasslands are important as major components of terrestrial land-cover and biodiversity, and for the ecosystem services they provide, including livestock forage and carbon sequestration. Not only is the extent of this ecosystem decreasing as it is converted for development and farmland, but also the remaining grasslands are increasingly under pressure from climate change and increased grazing with larger livestock herds. The immediate need to understand the responses of grasslands to these changes, to ensure food supplies and to mitigate future climate change through carbon sequestration, necessitate a global, synthesized approach.

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Over the last century, precipitation patterns have changed and average global temperatures have increased, as has the occurrence of extreme weather events; this climate change trend is expected to continue [1]. Grasslands are dynamic systems that are responsive to the dominant processes which control them: grazing, precipitation and fire. Thus, climate change, especially in conjunction with increased grazing pressure, might be expected to have long-term impacts on sustainability of these ecosystems. Already, observed responses of terrestrial ecosystems to climate change include changes to plant community structure [2] and productivity [3]. Experiments manipulating precipitation and temperature, and frequently incorporating grazing, have been conducted in temperate grasslands to explore responses and mechanisms of change. The next step remains to evaluate whether these experiments can be translated into a broad understanding of how temperate grasslands will respond to these pressures.

It was with the aim of discussing and synthesizing climate change experiments in temperate grasslands that the session 'Climate change experiments in temperate grasslands' was convened on 20 and 21 June 2011 in Lyon, France, during the 54th Annual Symposium of the International Association for Vegetation Science (IAVS). The session attracted many of the leading researchers in the field, with 19 oral presentations and poster contributions from 14 field experiments (see electronic supplementary material for complete list of contributions). Presenters came from six European and North American countries and discussed research from three continents. Owing to high participation, the session had to be moved to a larger lecture theatre than originally planned. Following the session, we recognized the call for a more casual and interactive forum for discussion, and held a well-attended additional workshop.

2. EXPERIMENTAL DESIGN

Although all research addressed temperate grassland responses to climate change, a variety of methodologies was used. Manipulations in either average temperature or precipitation, based on regional climate model projections, were applied in 10 of the 14 experiments described (table 1). Warming was achieved by a variety of methods: open-top chambers (OTCs), open-sided chambers (OSCs), overhead infrared heaters and heating cables, which all differ in their specific and unintended effects. Precipitation was decreased using either permanent or automatic rain-out shelters, and increased via manual water addition. These precipitation methods also were varied, limiting our ability to separate treatment effects from those of inconsistent methodology. For example, some of the rain-out shelter designs included controls with sham structures, while others did not.

Increased frequencies of heat waves, droughts and heavy precipitation events are associated with climate change; suitably, four experiments imposed extreme weather events (table 1). Only once was an extreme event (heat waves) investigated in combination with manipulation of average conditions (decreased precipitation). Although the different ways in which temperature and precipitation may change to affect grasslands were well represented, it was rare that more than two studies used similar methodology, limiting the generality of any finding.

Table 1. Experiments presented at the session 'Climate change experiments in temperate grasslands' at the 2011 IAVS symposium, by lead author, location, treatments and response variables. Treatments are either described by methodology type or, in the case of precipitation, whether the resource was increased or decreased, as indicated by arrows. Double-headed arrows indicate precipitation was both increased and decreased. Dashed symbols (—) indicate the treatment or response variable was not included in the experiment. Above-ground and below-ground productivity is referred to as 'AG' and 'BG', respectively.

lead author	location	treatments				response variables			
		warming	precipitation	management	others	productivity	community	focal species	others
Fraser	British Columbia, Canada	OTCs	↑	clipping	productivity gradient	—	composition	—	community function
Cahill	Alberta, Canada	OTCs	↑	defoliation	—	AG/BG	composition, diversity	—	nutrient cycling, soil arthropods, etc.
Collins	Arid grasslands, USA	—	frequency	grazing	nitrogen addition	AG	—	function and physiology	—
Knapp	Central plains, USA	—	timing	—	arid and mesic sites	AG	—	—	—
Smith	Tallgrass prairie, USA	heat wave	↓	—	—	AG	—	physiology and biomass	—
Fridley	Calcareous grassland, England	cables	↑	—	—	—	composition	—	species introduction
Cleland	CA, USA	overhead heaters	↑	—	CO ₂ , nitrogen addition	—	composition	flower phenology	decomposition
Casper	Mongolian Steppe	OTCs and OSCs	↑	grazing	slope	—	—	—	flower phenology and production
Henry	Old field, Canada	overhead heaters	—	—	nitrogen addition, winter warming	AG	—	—	soil responses
Soussana	Montpellier, France	yes	↓	—	CO ₂ , mesic and alpine sites	AG	functional group	—	leaf traits
Jentsch	Central Europe	—	drought events	—	—	AG/BG	stability	—	physiological processes, nutrient cycling, phenology, etc.
Maalouf	Calcareous grassland, Europe	—	drought	mowing	—	AG	richness	transplant survival	litter decay
Mariotte	Alpine grassland, Europe	—	↓	—	subordinate species removal	AG	—	—	litter decomposition
Dutoit	Mediterranean steppe	—	↓	grazing	—	—	—	—	tree colonization

There is a potential for important interactions between temperature, precipitation and other treatments [4]. Six experiments included interactions between any temperature or precipitation treatment. A number of additional factors were also manipulated in conjunction with temperature or precipitation, especially those related to grazing. Grazing by animals was sometimes logistically precluded; in these cases, mowing, defoliation or clipping was used as a proxy for grazing. Other interacting factors included nitrogen, removal of subordinate species and CO₂ addition. Most of the treatments were applied for a relatively short (1–3 years) duration. A notable exception was the Buxton experiment reported by Jason Fridley (Syracuse University), which has been running for almost two decades.

In addition to variability in treatments applied, comparison among experiments is also complicated by the lack of consistency in response variables measured (table 1). Although the majority of the presentations discussed some aspect of above-ground productivity, less than half monitored plant community composition or species diversity. Despite the sensitivity of below-ground responses to climate change [5], and their importance in ecosystem responses [6], the experiments focused on above-ground responses. Within individual experiments, a breadth of response variables were monitored, including phenology, plant physiology, nutrient cycling, focal species, soil properties and micro-organisms. Although this provides insight into which grassland properties can be sensitive to climate change, because many of these response variables were included in only one or two experiments, conclusions can only be site-specific.

3. ANALYTICAL APPROACHES

Traditional GLM-type analyses were commonly used and are important in determining responses to treatments. However, researchers also used a diversity of analytical techniques to identify mechanisms of response. Instead of simply reporting how flowering phenology responded to treatments, Elsa Cleland (University of California-San Diego) differentiated changes between the contributions of interspecific plasticity and intra-specific abundances. Likewise, Pierre Mariotte (Ecole Polytechnique Fédérale de Lausanne) explored the involvement of subordinate versus dominant species in drought resistance. Both James Cahill (University of Alberta) and Anke Jentsch (University of Bayreuth) explored the contributions of multiple mechanisms to observed responses. Cahill accomplished this through a systems-level analysis, and Jentsch exhaustively surveyed plant physiological processes, linking them to ecosystem productivity.

Methods such as these provide insight into mechanisms that would be concealed with traditional methods. However, because there was little overlap in innovative analytical approaches, the opportunity to identify mechanisms at play in multiple experiments may have been missed.

4. UNDERSTANDING RESPONSES

Results from these experiments were largely mixed and complex; thus, a broad understanding of temperate grassland response to climate change remains elusive. In some

cases, grasslands were resistant to both temperature and precipitation. Generally, most grassland response variables were more sensitive to changes in precipitation than temperature, though exceptions to this abounded, especially when extreme heat waves, rather than smaller changes in average temperature, were imposed. There were also a number of experiments which manipulated only temperature or precipitation, limiting the robustness of this conclusion. Further complicating the results, a number of responses were dependent upon interactions between the treatments. This was true particularly for temperature and precipitation, as well as CO₂ in combination with other treatments, but not found for nitrogen. There were few interactions with the management treatments (grazing, clipping, etc.), though main effects were usually, though not always, substantial.

The direction of productivity change with both precipitation and warming was highly variable, switching between and within sites, and over the duration of the experiments. Lauchlan Fraser (Thompson Rivers University) found that effects of decreased water on plant biomass surprisingly switched in direction, based on the productivity gradient between experimental sites. Sites that were sensitive to one factor were not necessarily sensitive to another; James Cahill (University of Alberta) conducted a warming and precipitation reduction experiment across three sites in Canada, and found that warming decreased plant productivity in two sites, and reduced precipitation decreased plant productivity in a different combination of two sites. Scott Collins (University of New Mexico) and Alan Knapp (Colorado State University) provided insight into the complexity of precipitation responses by manipulating only size of rainfall events, rather than total precipitation, under different hydrological regimes.

5. FUTURE DIRECTIONS

From the many experiments that have been performed, it is clear that grasslands are responsive to climate change in general, though the magnitude and direction of response varies highly with both treatment and site. The research discussed represented a great variety of both methodological and analytical approaches, although perhaps at the expense of cohesiveness. Thus, we still remain largely unable to identify any site-specific conditions or mechanisms that may lead to predictable responses.

To identify general patterns and mechanisms of response, the workshop attendees identified the importance of a meta-experiment to determine temperate grassland responses to climate change. A meta-experiment approach will be pursued, rather than meta-analysis, as the current disparate methodology prohibits an informative meta-analysis. A standardized treatment methodology and sampling protocol with minimal financial cost will be developed, potentially modelled-off of the Nutrient Network [7], in which there is a small investment per investigator, but large scientific returns. The workshop attendees briefly discussed the treatments that would be used, probably precipitation removal and addition, and discussed costs, but identified the need to work on a synthesis paper and conduct a further workshop to determine details.

The workshop attendees also identified the need for increased research in overlooked geographical areas, and the critical need for funding opportunities for long-term research. Research was predominantly in North America or Europe, with the notable exception of Brenda Casper (University of Pennsylvania) in Mongolia. Although containing sizable temperate grasslands, Africa, Oceania and South America were missing from our session and have previously been identified as areas lacking research into the effects of climate change [4]. Similarly, though long-term studies have been identified as important for identifying and understanding responses [8], the majority of research presented was from short-term studies.

A collaboration based on a set of globally dispersed, inexpensive experiments with consistent methodology will provide the data needed to understand responses of temperate grassland to climate change. The high level of support and interest in future collaboration illustrates the importance of international meetings in fostering communication of similar, yet geographically dispersed, research. The session was a very successful first forum for discussion, and an impetus to develop experiments where this dialogue can be continued quantitatively.

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