



Negative effects of climate change on upland grassland productivity and carbon fluxes are not attenuated by nitrogen status

Samuel Eze*, Sheila M. Palmer, Pippa J. Chapman

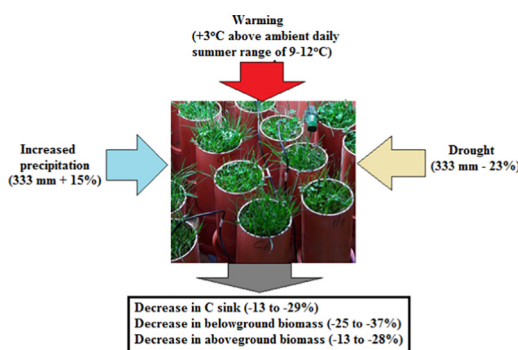
School of Geography, Faculty of Environment, University of Leeds, LS2 9JT Leeds, UK



HIGHLIGHTS

- Interactive effects of warming and drought on grasslands are not well understood
- Multifactorial manipulative experiment was used to study climate change impacts
- Short-term warming and drought reduced plant biomass productivity in UK grasslands
- Short-term warming and drought reduced net carbon uptake in UK upland grasslands
- Soil nitrogen level did not influence climate change impacts on UK grasslands

GRAPHICAL ABSTRACT



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ABSTRACT

Effects of climate change on managed grassland carbon (C) fluxes and biomass production are not well understood. In this study, we investigated the individual and interactive effects of experimental warming (+3 °C above ambient summer daily range of 9–12 °C), supplemental precipitation (333 mm +15%) and drought (333 mm –23%) on plant biomass, microbial biomass C (MBC), net ecosystem exchange (NEE) and dissolved organic C (DOC) flux in soil cores from two upland grasslands of different soil nitrogen (N) status (0.54% and 0.37%) in the UK. After one month of acclimation to ambient summer temperature and precipitation, five replicate cores of each treatment were subjected to three months of experimental warming, drought and supplemental precipitation, based on the projected regional summer climate by the end of the 21st Century, in a fully factorial design. NEE and DOC flux were measured throughout the experimental duration, alongside other environmental variables including soil temperature and moisture. Plant biomass and MBC were determined at the end of the experiment. Results showed that warming plus drought resulted in a significant decline in belowground plant biomass (–29 to –37%), aboveground plant biomass (–35 to –77%) and NEE (–13 to –29%), regardless of the N status of the soil. Supplemental precipitation could not reverse the negative effects of warming on the net ecosystem C uptake and plant biomass production. This was attributed to physiological stress imposed by warming which suggests that future summer climate will reduce the C sink capacity of the grasslands. Due to the low moisture retention observed in this study, and to verify our findings, it is recommended that future experiments aimed at measuring soil C dynamics under climate change should be carried out under field conditions. Longer term experiments are recommended to account for seasonal and annual variability, and adaptive changes in biota.

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* Corresponding author.

E-mail addresses: gyse@leeds.ac.uk (S. Eze), s.m.palmer@leeds.ac.uk (S.M. Palmer), p.j.chapman@leeds.ac.uk (P.J. Chapman).

1. Introduction

Ecosystem sequestration of atmospheric carbon (C) in terrestrial ecosystems is a function of the balance between C uptake by plants (gross primary productivity – GPP) and C loss via processes such as ecosystem respiration (ER) and leaching, and these processes are sensitive to climate, particularly precipitation and temperature (Albaladejo et al., 2013; Bellamy et al., 2005; Rees et al., 2005). The global climate is warming and precipitation patterns are also changing, with regional differences reported (IPCC, 2013; Jenkins et al., 2009). Rising temperature and changing precipitation is also expected throughout the 21st Century, with global mean surface temperature projected to increase by 0.3–0.7 °C by 2035 and 1.7–4.8 °C by 2100, relative to 1986–2005 baseline (IPCC, 2014).

Climate change is expected to exert significant effects on terrestrial ecosystem C pools and their fluxes including plant biomass (Hartmann and Niklaus, 2012), microbial biomass (Rui et al., 2011), net ecosystem exchange (NEE, the difference between GPP and ER; De Boeck et al., 2007), and the leaching of dissolved organic C (DOC) (Hagedorn and Joos, 2014), with possible feedbacks to climate change. A very useful method for investigating the response of these ecosystem processes to climate change is experimental manipulation of climate variables such as temperature and precipitation (Bloor et al., 2010). Climate manipulation experiments have been set up to explore the responses of plant productivity and ecosystem C fluxes to climate change in different ecosystems (e.g. Allison and Treseder, 2008; Baldwin et al., 2014; Beierkuhnlein et al., 2011). A synthesis of data from 85 of these experimental studies (Wu et al., 2011) in different ecosystems across the globe including forests, shrublands and grasslands shows that: 1) warming without manipulated precipitation enhanced both ecosystem photosynthesis and respiration with no effect on net C uptake, 2) increased precipitation without warming enhanced both ecosystem photosynthesis and respiration with an overall increase in net C uptake, and 3) decreased precipitation without warming suppressed both ecosystem photosynthesis and respiration with an overall decrease in net C uptake. Another recent synthesis of results of about 160 climate manipulation experiments in different ecosystems also revealed that warming increased both soil C input and loss with no significant effect on net C pool, whereas increased precipitation stimulated soil C input, and drought suppressed it (Ni et al., 2017). Thus, the balance of evidence indicates that altered precipitation patterns have greater control on net soil C store than warming.

Past climate manipulation experiments in different terrestrial ecosystems (see reviews by Liu et al., 2016; Ni et al., 2017; Wu et al., 2011) have usually explored the individual effects of warming, supplemental precipitation and drought on net C uptake. The interactive effects of changing temperature and precipitation on C cycling have rarely been examined and remain poorly understood (Lei et al., 2016), although global meta-analyses indicate that the interactive effects of warming and altered precipitation differ from their simple additive effects (Ni et al., 2017; Wu et al., 2011). This means that adding up the reported individual effects of manipulated climate variables will not give the true response of the ecosystem. The effects of experimental climate change on the terrestrial C cycle are also confounded by other site-specific characteristics and management practices such as vegetation type (Beierkuhnlein et al., 2011; Bloor and Bardgett, 2012; Miranda et al., 2009) and fertilizer application (Jonasson et al., 1999), especially nitrogen (N) fertilizers (Dukes et al., 2005). For example, Graham et al. (2014) found that the addition of 50 kg N/ha increased the positive effect of warming on soil C efflux by 12% in a New Zealand grassland. Thus, for an improved understanding of the response of managed ecosystems to climate change, there is need for multifactorial experiments where the interactive effects of management, warming, supplemental precipitation and drought will be investigated.

Grasslands store a significant amount (34%) of the global terrestrial C and provide important ecosystem services such as climate change

mitigation and forage for livestock production (White et al., 2000). In European grasslands, which are already net C sinks (Chang et al., 2015), the majority of the climate manipulation experiments (see Tables A1 and A2) have focused on the effects of climate change on aboveground biomass (AGB) and soil respiration (SR), and less attention has been given to other important C cycling processes such as NEE and DOC leaching. In published studies (Table A1) the main effects were: 1) warming alone stimulated both an increase and a decrease in AGB; 2) increased precipitation alone resulted in both an increase and a decrease in AGB; 3) drought alone decreased AGB and SR; and 4) both positive and negative interactive effects were observed when warming was combined with either increased precipitation or drought. The lack of definitive pattern of response to climate change in these studies may be partly due to pre-existing differences in grassland productivity. This is possible because less productive grasslands tend to be more resistant to climate perturbations (Grime et al., 2000). Fertilizer is widely used to improve grassland productivity (Yue et al., 2016), hence it is likely to be a major confounding factor in interpreting climate change effects. Whereas some grasslands are fertilised to increase vegetation biomass for livestock production, fertilizer application is discouraged in other grasslands due to environmental concerns such as protecting and enhancing biodiversity, or protecting water courses from pollution (Reed et al., 2009). The effects of climate change on fertilised and unfertilised grasslands need to be investigated. This will help inform future management decisions for targeted outcomes in the face of climate change.

The need to investigate climate change effects on managed grasslands is a particular concern for UK uplands. These areas mainly occur at 250–300 m above sea level and have witnessed changes in climate that are much greater than in the lowlands (House et al., 2010). For example, between 1961 and 2000, minimum temperatures increased more than maximum temperatures in the uplands, whereas there was no difference in the changes between minimum and maximum temperatures in the lowlands (Burt and Holden, 2010). Morecroft et al. (2009) also found that temperature trends between 1993 and 2007 differed between upland and lowland sites in the UK, with an average temperature increase of 1.2 °C in the uplands and 0.7 °C in the lowlands. The UK upland grasslands are considered sensitive environments and have important conservation values because they contain species of plants that are scarce in Europe, and are breeding grounds for nationally rare birds and amphibians (English Nature, 2001). These upland grasslands are predominantly managed for livestock production (Stevens et al., 2008) under both extensive management regimes with no fertilizer application, and more intensive management regimes with fertilizer application to improve forage productivity for silage and grazing.

Climate manipulation studies in the UK upland grasslands are few (e.g. Briones et al., 2009; Grime et al., 2008), and how grasslands under different management regimes might respond to warming and altered precipitation has not been considered. Briones et al. (2009) investigated the response of an unimproved acid grassland in Scotland to a 2-year soil warming (+3.5 °C) and found an increase in both ER and root biomass, and a decrease in AGB. Similarly, Grime et al. (2008) studied the response of an unfertilised grassland in Buxton (northern England) to 13 years of winter warming (+3.0 °C), supplemental summer precipitation (+26%) and summer drought (–77%). Warming, increased precipitation and drought both separately and in combination, had little effect on the ecosystem, however, there was a reduction in AGB under all the treatments (Grime et al., 2008). It remains to be known how fertilised upland grasslands respond to climate change. Specifically, there is a dearth of information on the effects of warming and altered precipitation on the net C uptake by plants and soil microbes as well as DOC flux.

The main aim of this study was to assess the individual and interactive effects of experimental warming, supplemental precipitation and drought on plant biomass, microbial biomass C (MBC), NEE, and DOC flux in two upland grassland fields of different soil N status in northern

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