Perspectives in Plant Ecology, Evolution and Systematics 14 (2012) 193–204

Contents lists available at SciVerse ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.de/ppees

Research article

Stability of above-ground and below-ground processes to extreme drought in model grassland ecosystems: Interactions with plant species diversity and soil nitrogen availability

Juliette M.G. Bloor[a,*], Richard D. Bardgett[b]

[a] INRA, UR874-Grassland Ecosystem Research Unit, 234 Avenue du Brézet, F-63100 Clermont-Ferrand, France
[b] Soil and Ecosystem Ecology Laboratory, Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

ARTICLE INFO

Article history:
Received 12 July 2011
Received in revised form
29 November 2011
Accepted 2 December 2011

Keywords:
Climate change
CO_2 fluxes
Ecosystem services
Plant–soil interactions
Productivity
Soil fertility

ABSTRACT

Extreme drought events have the potential to cause dramatic changes in ecosystem structure and function, but the controls upon ecosystem stability to drought remain poorly understood. Here we used model systems of two commonly occurring, temperate grassland communities to investigate the short-term interactive effects of a simulated 100-year summer drought event, soil nitrogen (N) availability and plant species diversity (low/high) on key ecosystem processes related to carbon (C) and N cycling. Whole ecosystem CO_2 fluxes and leaching losses were recorded during drought and post-rewetting. Litter decomposition and C/N stocks in vegetation, soil and soil microbes were assessed 4 weeks after the end of drought. Experimental drought caused strong reductions in ecosystem respiration and net ecosystem CO_2 exchange, but ecosystem fluxes recovered rapidly following rewetting irrespective of N and species diversity. As expected, root C stocks and litter decomposition were adversely affected by drought across all N and plant diversity treatments. In contrast, drought increased soil water retention, organic nutrient leaching losses and soil fertility. Drought responses of above-ground vegetation C stocks varied depending on plant diversity, with greater stability of above-ground vegetation C to drought in the high versus low diversity treatment. This positive effect of high plant diversity on above-ground vegetation C stability coincided with a decrease in the stability of microbial biomass C. Unlike species diversity, soil N availability had limited effects on the stability of ecosystem processes to extreme drought. Overall, our findings indicate that extreme drought events promote post-drought soil nutrient retention and soil fertility, with cascading effects on ecosystem C fixation rates. Data on above-ground ecosystem processes underline the importance of species diversity for grassland function in a changing environment. Furthermore, our results suggest that plant–soil interactions play a key role for the short-term stability of above-ground vegetation C storage to extreme drought events.

Introduction

Mounting evidence suggests that ongoing climate change will result in an increase in the frequency of extreme weather events or climate anomalies such as unusually dry years (IPCC, 2007). Such extreme climatic events have the potential to cause dramatic changes in ecosystem structure and function via non-linear threshold dynamics, and are expected to be equally, if not more important than ecosystem responses to changes in mean temperature or precipitation (Easterling et al., 2000; Jentsch et al., 2007; Smith, 2011). However, impacts of extreme weather events (determined as a statistical extremity with respect to a historical reference period) have received far less attention compared with gradual climatic changes, and knowledge of how extreme weather affects ecosystem services is lacking (Jentsch et al., 2007; Smith, 2011).

Grassland responses to extreme drought events are of particular interest because precipitation regimes are known to be critical in determining grassland types, productivity and decomposition rates (Laurenroth and Sala, 1992; Knapp and Smith, 2001). In general, grasslands subjected to severe drought show a decrease in leaf-level photosynthesis, plant productivity, and an increase in carbon (C) allocation to roots, although the magnitude and duration of drought responses differ across studies (Kahmen et al., 2005; Kreyling et al., 2008; Gilgen and Buchmann, 2009; St. Clair et al., 2009; Jentsch et al., 2011). Drought also has feedback effects on the soil nitrogen (N) pool since the microbial processes that

* Corresponding author. Tel.: +33 473 62 44 25; fax: +33 473 62 44 57.
E-mail address: juliette.bloor@clermont.inra.fr (J.M.G. Bloor).

1433-8319/$ – see front matter © 2011 Elsevier GmbH. All rights reserved.
doi:10.1016/j.ppees.2011.12.001

regulate soil N availability are sensitive to short-term variations in soil moisture. For example, increased duration and intensity of drought are usually associated with decreasing N mineralisation and inorganic N fluxes (Borken and Matzner, 2009). This interdependence between precipitation and soil N availability is further strengthened because inorganic N is dissolved in soil solution, and water/rainfall affects its mobility and loss. Rewetting at the end of drought typically results in a short-term pulse of C and N mineralisation, and increased risks of nutrient leaching losses (Fierer and Schimel, 2002; Gordon et al., 2008). In contrast, longer-term effects of rewetting on microbial activity are more variable and may be driven by changes in microbial community composition (Schimel et al., 2007). Consequently the size and fluxes of the soil N pool are largely determined by precipitation events, and precipitation anomalies may have a large impact on C and N cycling at a variety of temporal scales (Verburg et al., 2009).

Predicting grassland responses to drought events requires an understanding of the complex interplay between abiotic and biotic factors which determine ecosystem stability. For example, high soil N availability could increase ecosystem vulnerability to drought via: (i) greater plant water demand in high biomass systems which reduces soil moisture (Wang et al., 2007); (ii) root:shoot allocation patterns adapted to competition for light rather than below-ground resource acquisition (Tilman, 1990); (iii) short-lived plant organs and higher rates of nutrient turnover which lower plant resistance (MacGillivray et al., 1995). However, complementarity in water-use in diverse, multi-species communities may partly offset water stress during drought periods (De Boeck et al., 2006). Consequently, impacts of soil N availability on ecosystem stability could vary depending on plant community composition. Furthermore, it has long been suggested that communities which are more diverse in species or functional groups have greater stability against environmental perturbations (diversity-stability hypothesis, reviewed in Johnson et al., 1996; Hooper et al., 2005). In theory, redundancy of functionally similar species or compensation by better-adapted species may buffer ecosystem processes in diverse communities under changing conditions (Hooper et al., 2005). In practice, studies examining the relationship between species diversity and the stability of ecosystem processes to drought have yielded conflicting results (Pfisterer and Schmid, 2002; Van Peer et al., 2004; Kahmen et al., 2005; Wang et al., 2007; Kreyling et al., 2008). To date, interactions between soil N and plant species diversity on ecosystem stability to drought have yet to be tested.

Here we use an outdoor mesocosm experiment to examine short-term above-ground and below-ground grassland responses to a simulated 100-year extreme summer drought event. In order to better understand the consequences of extreme events in natural systems, we chose two temperate grassland communities that are widespread across Europe, but have contrasting levels of species richness, as a model system. The primary objective of this study was to determine the interactive effects of drought, soil N availability and plant community composition on key ecosystem processes related to C and N cycling (ecosystem CO_2 exchange rates, C/N soil leaching losses, litter decomposition rates, C/N storage in vegetation, soil and soil microbes). We focused on short-term drought responses to increase the detection of possible shifts in plant–soil interactions following drying-rewetting events (Hodge et al., 2000; Schimel et al., 2007). Specifically, we hypothesized that: (i) extreme drought has a negative impact on plant C storage and soil nutrient retention during rewetting; (ii) high soil N availability reduces ecosystem stability to drought, i.e. more negative drought effects in high N treatments versus low N treatments; (iii) plant communities with high plant diversity have greater stability to extreme drought, i.e. non-significant or less negative drought effects in high-diversity communities versus low-diversity communities; (iv) high plant species diversity mitigates effects of high soil N availability on ecosystem vulnerability to drought.

Materials and methods

Experimental design

The mesocosm experiment was conducted at the Lancaster University Field Station, UK (54°1′N, 2°46′W, 94 m a.s.l.), and comprised of three treatments in a fully factorial design: soil nutrient availability (low N, high N), plant species diversity (low, high), and rainfall (ambient, extreme drought event). Each of the eight treatment combinations was replicated five times, resulting in a total of 40 experimental mesocosms.

Mesocosms were established outdoors in September 2009; high density polypropylene pots (38 cm × 38 cm × 40 cm) with drainage holes were packed with a 8-cm layer of limestone chippings for improved drainage, followed by a 27-cm layer of topsoil (pH_{H2O} of 6.3, 0.25% N, 3.05% C) collected from a sandy loam pasture at the study site. Prior to pot-filling, the experimental soil was homogenized by mixing, and visible stones and roots were removed by hand. To generate the high N treatment, we added 27 g of dried, finely cut (1 mm) *Trifolium repens* shoots (4.5% N, 10.1 C:N) to the 0–5 cm soil layer of each mesocosm (equivalent to 1.22 g N per mesocosm or 84.5 kg N ha^{-1}). We used fresh organic material rather than inorganic fertilizer in the nutrient treatment as it provides a more realistic simulation of soil nutrient variability in natural ecosystems (Maestre and Reynolds, 2007). The organic material was thoroughly mixed with background soil (6.5 l) before filling the 0–5 cm layer. Added organic material resulted in an increase in soil C from 3.05 to 3.1% per mesocosm, and was considered to have little impact on the soil water- or nutrient-holding capacity over the course of the study. In the low N treatment, no organic material was added to the mesocosms.

Two experimental grassland communities with contrasting levels of plant species diversity were established in the mesocosms based on assemblages classified as *Anthoxanthum odoratum-Geranium sylvaticum* (MG3) and *Lolium perenne-Cynosurus cristatus* (MG6) by the UK National Vegetation Classification (Rodwell, 1998). Both community types comprised of common grassland species (including grasses, forbs and a legume species). The low diversity treatment (MG6 model) consisted of six species (*Cyanosurus christatus* L.; *Holcus lanatus* L.; *Lolium perenne* L.; *Cerastium fontanum* L.; *Trifolium repens* L.; *Festuca rubra* L.), whereas the high diversity treatment (MG3 model) consisted of 11 species (*C. christatus*; *H. lanatus*; *L. perenne*; *C. fontanum*; *T. repens*; *F. rubra*; *Agrostis capillaris* L.; *Anthoxanthum odoratum* L.; *Plantago lanceolata* L.; *Poa trivialis* L.; *Dactylis glomerata* L.). These levels of species richness are consistent with species numbers found in 40 cm × 40 cm quadrats in the field, i.e. quadrats equivalent to the size of the mesocosms in this study (J.M.G. Bloor, unpublished data). Experimental plants were grown from seed obtained from Emorsgate Seeds (Kings Lynn, UK) and germinated at room temperature in trays filled with compost (Scotts Levington M3 Professional Growing Medium). Newly established seedlings (<3 weeks old) were transplanted individually into plug trays filled with experimental soil and maintained in a glasshouse at Lancaster University. One week prior to planting in the mesocosms, plug trays with seedlings were put outside at the field site to acclimatize; at the time of planting (25th September 2009), all seedlings were 6–8 weeks old.

Thirty six seedlings were transplanted into each mesocosm; planting positions for each species were allocated at random, but the same planting grid pattern was maintained across mesocosms by using a wire grid secured to the top of the pots. Planting densities were consistent with species abundance patterns observed in