REGULAR ARTICLE

Ecosystem functions are resistant to extreme changes to rainfall regimes in a mesotrophic grassland

Ellen L. Fry · Pete Manning · Sally A. Power

Abstract

Aims Major changes to rainfall regimes are predicted for the future but the effect of such changes on terrestrial ecosystem function is largely unknown. We created a rainfall manipulation experiment to investigate the effects of extreme changes in rainfall regimes on ecosystem functioning in a grassland system.

Methods We applied two rainfall regimes; a prolonged drought treatment (30 % reduction over spring and summer) and drought/downpour treatment (long periods of no rainfall interspersed with downpours), with an ambient control. Both rainfall manipulations included increased winter rainfall. We measured plant community composition, CO_2 fluxes and soil nutrient availability.

Results Plant species richness and cover were lower in the drought/downpour treatment, and showed little recovery after the treatment ceased. Ecosystem processes were less affected, possibly due to winter rainfall additions buffering reduced summer rainfall, which saw relatively small soil moisture changes. However, soil extractable P and ecosystem respiration were significantly higher in rainfall change treatments than in the control.

Conclusions This grassland appears fairly resistant, in the short term, to even the more extreme rainfall changes that are predicted for the region, although prolonged study is needed to measure longer-term impacts. Differences in ecosystem responses between the two treatments emphasise the variety of ecosystem responses to changes in both the size and frequency of rainfall events. Given that model predictions are inconsistent there is therefore a need to assess ecosystem function under a range of potential climate change scenarios.

E. L. Fry · S. A. Power
Department of Life Sciences, Imperial College of Science, Technology and Medicine,
Silwood Park, Ascot SL5 7PY, UK

E. L. Fry (✉)
Faculty of Life Sciences, Michael Smith Building, University of Manchester,
Manchester M13 9PL, UK
e-mail: Ellen.Fry@manchester.ac.uk

P. Manning
Institute of Plant Sciences, University of Bern,
Altenbergrain 21, 3013 Bern, Switzerland

S. A. Power
Hawkesbury Institute for the Environment, University of Western Sydney,
Hawkesbury Campus, Locked Bag 1797, Penrith, NSW 2751, Australia

Introduction

Extreme weather events are increasing in frequency (Eade et al. 2012), and extreme changes to climate

regimes may also become commonplace in the future (Murphy et al. 2009). The effects of these changes on terrestrial ecosystems are potentially catastrophic, leading to urgent calls for research into their consequences (Easterling et al. 2000; Heisler-White et al. 2009; Beierkuhnlein et al. 2011; Smith 2011a). To date there are clear indications that temperate grasslands will show strong responses to climate change, which is of concern as they provide many valuable ecosystem services including forage production, carbon storage and opportunities for recreation. A major component of future climate change is altered rainfall. Given that rainfall patterns are important drivers of ecosystem function (Blankinship et al. 2011), research is needed to evaluate the consequences of predicted changes in rainfall patterns on key ecological processes and the plant communities that regulate these (Knapp et al. 2002; Smith 2011b; Fry et al. 2013).

Many drought simulation experiments have been undertaken in recent years, but for the most part these have considered a single change to rainfall patterns, usually a single rainfall exclusion event. Most have noted almost immediate effects of rainfall changes on many aspects of ecosystem function (Knapp et al. 2002; Xu et al. 2004; St Clair et al. 2009), but evidence suggests that the impacts of rainfall change vary depending upon the timing, duration and intensity of drought events (Knapp et al. 2002; Chimner and Welker 2005). Understanding this range of effects is important because rainfall change will vary between regions, and climate models are subject to many sources of uncertainty (IPCC 2013). Accordingly, field studies are beginning to incorporate the simulation of more complex and realistic rainfall models into their designs, although rainfall events and extreme changes to rainfall regimes in field experiments are still under-represented in the literature (Laporte et al. 2002; Smith 2011a; Beier et al. 2012). Some of the studies that have been conducted have simulated increasingly infrequent summer rainfall events in temperate areas, with occasional heavy downpours, in line with recent model projections (Fischlin et al. 2007; Murphy et al. 2009). Other empirical studies have also simulated 100-year extremes, where the system receives no rain at all for a prolonged period of time, before being treated with a substantial input (Jentsch et al. 2007; De Boeck et al. 2011; Bloor and Bardgett 2012). On the whole, experiments implementing more extreme events or regimes such as this show strong detrimental effects on ecosystem are functioning,

including significant reductions in productivity, nitrogen mineralisation and ecosystem respiration (Heisler-White et al. 2009; De Boeck et al. 2011; Bloor and Bardgett 2012). However, re-wetting following drought manipulation often leads to a pulse of microbial activity that exceeds the control treatment for a short time (Birch 1958; Borken and Matzner 2009), potentially resulting in no net difference to seasonally averaged fluxes or process rates (Bloor and Bardgett 2012). Heavy rainfall on previously very dry soil can also lead to greater runoff, soil erosion and the loss of nutrients from the system (Kehl et al. 2005). Soil nutrient levels are also likely to be altered by reduced rainfall and its effects on soil moisture patterns. Reduced soil water not only reduces mineralisation rates by suppressing microbial activity, but also reduces plant uptake by preventing nutrients in solution from being brought into proximity with root hairs (Borken and Matzner 2009). This could result in the accumulation of nutrients that are vulnerable to loss when drought is alleviated (Rice and Pancholy 1972).

Most climate models (such as HADCM3) predict that the northern hemisphere will not see consistent proportional changes to spring and autumn rainfall relative to current conditions (Murphy et al. 2009; IPCC 2013). However, even minor or infrequent changes in spring rainfall are likely to have a marked effect on grassland ecosystem functioning and could shift ecosystems from CO_2 sinks to sources (Kim et al. 1992). This may occur partly through the suppression of photosynthetic rates, and partly through the reduction of soil water, which transports root exudates and carbon in solution from the roots to the microbial community. This could prevent the microbial community from immobilizing and utilising carbon sources (Kim et al. 1992; Gorissen et al. 2004). Furthermore, given the phenological advance of spring over recent decades (2.5 days per decade) and associated lengthening of the growing season, it is likely that spring conditions will become increasingly significant drivers of ecosystem productivity and other key ecosystem functions (Menzel et al. 2006). Empirical studies show that drought extended over the entire growing season (spring through to autumn) is likely to have stronger effects upon primary productivity (Fay et al. 2003), seed germination (Stampfli and Zeiter 2008), seedling establishment (particularly grasses; Evans et al. 2011) and net ecosystem CO_2 exchange

rates (Kim et al. 1992) than drought occurring in summer alone. These studies show the seedling phase is the most vulnerable stage of a plant's life cycle, and indicate that drought induced seedling mortality can have legacy effects upon ecosystem productivity and community composition. Studies on the effect of drought in both spring and summer are few, but De Boeck et al. (2011) showed in a mesocosm study that spring drought did not significantly reduce photosynthesis, because the lack of a corresponding drop in soil moisture allowed plants to maintain adequate transpiration rates. Another mechanism of resistance to reduced rainfall is tissue die-back, which could improve plant-tissue water efficiency by reducing expendable surface area (Chaves et al. 2009). These studies suggest that grasslands may have some degree of resistance to seasonal climate changes (Wiegand et al. 2004).

To investigate the effect of extreme changes to rainfall regimes on temperate grasslands we experimentally implemented three different rainfall regimes using rainout shelters in a lowland grassland in south-east England. These rainfall regimes were based on A2 SRES climate change scenarios for southern England (Nakićenović and Swart 2000). Rainfall change treatments included: 1) a spring and summer reduction in rainfall (−30 % volume), (hereafter 'prolonged drought') and 2) a regime that combined prolonged periods of complete rainfall exclusion with heavy downpours, with no change in seasonal rainfall amount (hereafter 'drought/downpour'). Both treatments received additional (+ 15 %) winter rainfall, in line with consistent regional predictions and both were compared with a roofed ambient control (3). We then measured plant community composition and a suite of key ecosystem processes and properties linked to important ecosystem services of grasslands. We hypothesised that prolonged drought will reduce rates of photosynthesis and also impose stress during the crucial spring germination and establishment period, leading to lower plant species richness. We further hypothesised that the drought/downpour regime will cause substantial plant dieback, with cascading effects upon ecosystem function, including reductions in photosynthetic carbon uptake, but increases in ecosystem respiration associated with the decomposition of dying plant material following downpour events.

Methods

Study site

The study site is a mesotrophic grassland in south east England (Silwood Park, Berkshire, lat. 51.406371, long. −0.648648). It is located on loamy sand soil (92.98 % sand, 5.89 % silt, 1.13 % clay, average C:N 16.70), that is dominated by *Holcus mollis* (average 45 % cover), *Agrostis gigantea* (average 13 % cover) and *Cirsium arvense* (average 11 % cover) and contains *Arrhenatherum elatius*, *Rumex obtusifolius* and *Vicia tetrasperma* as frequent sub-dominants (average 6 % cover), (UK National Vegetation Classification MG6 type, Rodwell 1992). The climate is temperate with a 10-year average rainfall of 833 mm yr^{-1} and mean temperatures of 4.8 °C (January) and 17.2 °C (July). The site is relatively sheltered from wind by trees on three sides. In October 2007 the site was ploughed and all standing biomass removed. After this there was no grazing or cutting, thus making the site an undisturbed successional grassland. The site was rabbit-proof fenced, although there was some light deer browsing. The experiment was conducted on plots embedded within a larger and related experiment (the DIRECT experiment, Fry et al. 2013, 2014), which manipulated both rainfall and plant functional diversity and measured resulting changes in ecosystem function. The study described here represents data collected between March 2009 and September 2010.

The DIRECT experiment has a randomized blocked design where four blocks of plots are arranged east–west to accommodate a slight incline across the site. The western block was slightly elevated (top) and had considerably lower soil moisture compared with the eastern (bottom), 9.63 % volumetric soil moisture content compared with 13.83 %, averaged across the study; (0.096 cm^{3}cm^{-3} and 0.138 cm^{3}cm^{-3} respectively). The top was also more legume rich than the other three blocks (averaging 6.83 % cover compared with 1.15 %). The bottom block, being lower on the slope and wetter than the others, also had a higher pH (5.87 compared with 5.59 across the other blocks). All dominant species had increasing average percentage cover from the bottom to the top block, and the subdominants tended to display an approximately opposite pattern. There was no block level gradient of species richness.

Three plots in each block were used in the current study, one for each rainfall treatment ($n=12$). The plots

are 2.4 m×2.4 m, separated by 1 m wide walkways. Within the plots, we designated a 70 cm 'buffer zone' around the outside, leaving a 1 m×1 m 'experimental zone' in the centre, that would be less affected by rainfall drift or lateral soil water movement.

Rainfall change regimes

The two rainfall change treatments were designed to represent more extreme scenarios than that of the IPCC's 2007 model average for the region, which predicts a 30 % reduction in summer rainfall and a 15 % increase in winter rainfall (IPCC 2007). Rainfall treatments were achieved by building sloping rain shelters to intercept ambient rainfall, using transparent corrugated plastic (Fry et al. 2013).

Plots receiving rainfall manipulations had shelters equipped with guttering and water collection butts. The prolonged drought regime treatment was a 30 % reduction in rainfall volume from March 1st to August 31st, in both 2009 and 2010. This treatment extends IPCC (2007) projections for summertime reductions in rainfall volume in to the early part of the growing season. We also incorporated a projected change of rainfall *pattern*, where the average rainfall event is smaller but punctuated by occasional downpours, as predicted by the UKCP09 model (Murphy et al. 2009). This aspect followed the design of the main DIRECT experiment (Fry et al. 2013); when less than 20 mm of rain fell during 24 h, 50 % was reapplied and the rest discarded. When more than 20 mm fell, it was all reapplied. The 15 % increase in rainfall through the winter period was achieved by collecting rain (or snow) in plastic trays outside each plot between December 1st and February 28th and reapplying it daily. For actual seasonal rainfall volumes received, see Table 1. This regime is termed 'extreme' due to its lengthy nature and potential impact upon the germination period.

For the drought/downpour treatment, we aimed to alter the temporal pattern of rainfall inputs but not the seasonal volume, thus generating a more extreme version of the UKCP09 prediction. This regime took place through the summer period only (JJA). When less than 20 mm of rain fell, it was stored. When more than 20 mm fell, all of the stored rainfall was applied in a single large downpour event (Table 1). This regime is also described as 'extreme' because of the length of the dry periods. For actual realised monthly rainfall patterns of both rainfall change treatments see supplementary

material S1. Ambient plots also had shelters but with 2.5 cm diameter holes drilled through the plastic at approximately 5 cm intervals to allow through flow of rain. This was done to standardise microclimatic and light changes caused by the shelters, thus controlling for potentially confounding 'roof effects' (Vogel et al. 2013). Both the drought/downpour treatment and the ambient control were roofed from March 1st to May 31st. All shelters faced south-east into the prevailing wind.

Day-to-day rainfall volumes used in calculating treatment reapplications were measured using a WeatherLink Vantage Pro wireless weather station (Davis Instruments, USA). Soil moisture was measured weekly between August 2009 and September 2010, using a ThetaProbe Soil Moisture Meter HH2 with ML2x probe (Delta-T, Cambridge, UK); four measures in each plot were taken to a 10 cm depth and averaged. These averages were then used to generate a monthly mean for use as a covariate in statistical analysis (see below). A simple evaluation of the degree of drought stress imposed by the rainfall treatments was made by using soil particle size distributions to calculate soil hydraulic properties in four replicate locations adjacent to experimental plots, in each block. We used equations from Saxton et al. (1986) and Saxton and Rawls (2006) to calculate permanent wilt point (PWP, −1,500 kPa), field capacity (FC, −10 kPa) and saturation point (0 kPa). These three metrics offer an indication of water availability to plants in situ that is independent of plant species. We also measured soil water potential (SWP) for each of the three treatments using the equations of Saxton et al. (1986). Further, we calculated metrics of resistance using the formula of Chaer et al. (2009), who define resistance as the ability to withstand a perturbation or stress, to test whether soil moisture of the rainfall treatments was resistant relative to the ambient. The formula calculates the percentage of variable change relative to the ambient treatment.

Vegetation surveys

The vegetation in the plots was surveyed twice a year; June and September in 2009 and May and October in 2010, with an additional survey in July 2010 to capture the effects of a natural dry period that occurred in early summer. Surveys involved placing a 1 m² quadrat in the centre of the plots, and estimating percentage cover of each vascular plant species (nomenclature follows ITIS

Table 1 Target and actual rainfall volumes received by the three rainfall change treatments

Year	Season	Ambient		Prolonged drought		Drought/Downpour	
		% of rainfall applied	Actual vol received (mm)	% of rainfall applied	Actual vol received (mm)	% of rainfall applied	Actual vol received (mm)
2009	Spring (MAM)	100	87.1	70	43.6	100	87.1
	Summer (JJA)	100	166.3	70	115.9	100	166.3
	Autumn (SON)	100	221.1	100	221.1	100	221.1
	Winter (DJF)	100	382.3	115	439.6	115	439.6
2010	Spring	100	103.1	70	51.6	100	103.1
	Summer	100	136.3	70	103.2	100	136.3
	September	100	43.6	100	43.6	100	43.6

2013) and total vegetation cover. Cover estimates were then used to calculate percentage cover of grasses, forbs and legumes, as well as Shannon's diversity and equitability indices (Shannon and Weaver 1963). Vegetation was also grouped according to a bespoke classification arising from functional trait screening of species native to the study site (Fry et al. 2014). The groups arising from this are loosely described as perennials, caespitose grasses and annuals. The perennial group is characterised by high specific leaf area (SLA), low total biomass and high leaf N content (LNC). The caespitose grasses have high root and shoot biomass but low LNC, while the annuals possess low SLA, low biomass and high LNC.

CO$_2$ and water flux

Ecosystem CO$_2$ and water exchange were measured in February 2010 and then at monthly intervals between May and September 2010 using a Ciras-1 Infra-Red Gas Analyser (IRGA, PP Systems, Hitchin, UK) with a perspex chamber cuvette attached (299 cm^2 area, 8,959 cm^3 volume). The cuvette was placed over a pre-installed collar in the soil (5 cm deep, 5 cm above the soil, diameter 20 cm) to create a seal, and measurements of net ecosystem CO$_2$ exchange (NEE) and evapotranspiration (ET) were taken over two minute periods. This was carried out between 10 am and 3 pm in February, and 9 am and 5 pm between May and September, in sunny conditions. To provide a measure

of ecosystem respiration (R$_{eco}$) an opaque cover was placed over the cuvette after the initial measure, and a new measure was taken after a 60 s equilibration period (Kolari et al. 2006). Photosynthetic rate (A) was calculated as the difference between NEE and R$_{eco}$ (NEE values are generally negative during the day). Simultaneous measures of soil moisture, photosynthetically active radiation (PAR, Skye Instruments, Llandridod Wells, UK) and soil temperature (Hanna HI 98501, Bedfordshire, UK) were taken for use as covariates in statistical analysis (Wagner et al. 2009).

Soil extractable nutrients

Three soil cores (10 cm deep, 1 cm diameter) were taken in all plots in a random distribution from the central 1 m^2 and combined to form a composite sample. They were taken once a month throughout the summer (between May and September in 2009 and 2010) and also in December 2009. From these, ammonium (NH$_4$) and nitrate (NO$_3$) were extracted using 1 M potassium chloride (KCl) (20 g fresh soil: 75 ml KCl), and shaking at 150 rpm for one hour (Allen 1989). The samples were then analysed colourimetrically using a continuous flow analyser (Skalar, York, UK). Extractable P concentrations were determined by shaking 150 ml Truog's solution (0.01 M H$_2$ SO$_4$+0.3 % (NH$_4$)$_2$ SO$_4$) with 10 g fresh soil for one hour at 150 rpm, filtering and analysing in the same manner. Both analyses were run

with one analytical replicate and one treatment blank per 20 samples.

Statistical analysis

All analyses were performed in R2.14.2 (R Development Core Team 2009). Treatment differences in soil moisture were analysed using a one-way ANOVA for each month, with rainfall change as the explanatory variable and block as an error term. Vegetation and ecosystem function data were analysed using linear mixed effects models (LME) with month and rainfall change regime as interactive fixed effects, and a plot within block random effects structure. Non-normally distributed data were log-transformed, and percentage cover data were arcsine transformed. Species richness data were analysed using the lmer function with a Poisson distribution. These models assume constant variance over factor levels. This assumption was not always met so when variance differed by more than a factor of two between different months it was modelled by individual month, rather than as a full dataset, using the varIdent command in the nlme library of R. The significance of each term was evaluated using a likelihood ratio deletion test (Pinheiro and Bates 2000). For NEE, A and ET, mean PAR and soil temperature were included as covariates. For R_{eco}, only temperature was included. Where there were significant rainfall treatment effects on a given function, we then added soil moisture to test whether the treatment effect was occurring as a direct result of soil moisture change. Finally we tested these effects in individual months using lme.

Following this analysis we then assessed whether rainfall treatment effects were operating via changes to plant community biomass and composition or via changes to soil moisture. To do this the ecosystem function data were analysed again using the same model structure, but including either a soil moisture content or vegetation cover covariate if the rainfall change treatments had been found to significantly affect function. If the significant rainfall term became non-significant upon the inclusion of a cover term, it indicates that function changes were attributable to rainfall-driven changes in cover or soil moisture. In cases where vegetation covariates were used, the cover term covariate was the percentage cover of whichever of the three bespoke functional groups that had been significantly affected by rainfall change (Fry et al. 2014), and also, separately, with grass, forb and legume cover.

Results

Rainfall change and soil moisture

In 2009, rainfall followed a typical pattern for the region, with a dry, warm summer and autumn (Fig. 1). In 2009 253 mm of rain fell between 1st March and 31st August, with 166 mm of this between June and August. However, this was followed by an exceptionally wet winter period then a very dry period in early summer 2010. In 2010, 239 mm fell between March and August (10 year average 336 mm), of which 136 mm fell between June and August (10 year average 171 mm).

The soil moisture pattern followed that of rainfall (Fig. 1), with a slight time lag. Despite the differing regimes, soil moisture rarely differed significantly between the rainfall change treatments. The spring phase of the prolonged drought regime had little discernible effect on soil moisture, possibly because the differences in absolute rainfall volume were small. However, in July 2010 the soil moisture percentage in both rainfall change treatments had dropped below the calculated PWP (average PWP: 3.65 %, S2a,b), while the ambient remained above the FC level (average FC: 10.93 %, S2b,b). There were also clear treatment differences in SWP (S3). Wilt point (1500 kPa) was exceeded in the drought/downpour treatment over the majority of the summer 2010 period; the prolonged drought treatment generally exceeded the wilt point by a smaller amount, but for a longer period and earlier in the season. The ambient control never exceeded the wilt point. Chaer's resistance index showed that soil moisture was resistant to rainfall change treatments relative to ambient throughout the study, apart from during August 2010 when both rainfall treatments showed a marked lack of response to the applied treatments. However by September 2010 soil moisture in both treatments had returned to almost the same levels as the ambient (control) plots (S4).

Vegetation responses

Species richness was low in all treatments (2–13 spp m^{-2}) in all survey months (Fig. 2). Initial total cover and species richness did not significantly differ between blocks at the beginning of the experiment, although the block at the top of the incline had significantly higher legume abundance than other blocks, and this difference was maintained throughout the experiment

Fig. 1 Volumetric soil moisture and applied rainfall over the course of the experiment. Asterisks represent differences in soil moisture between rainfall treatments compared using a one-way ANOVA ($^*p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$). Error bars on the soil moisture lines are omitted for clarity
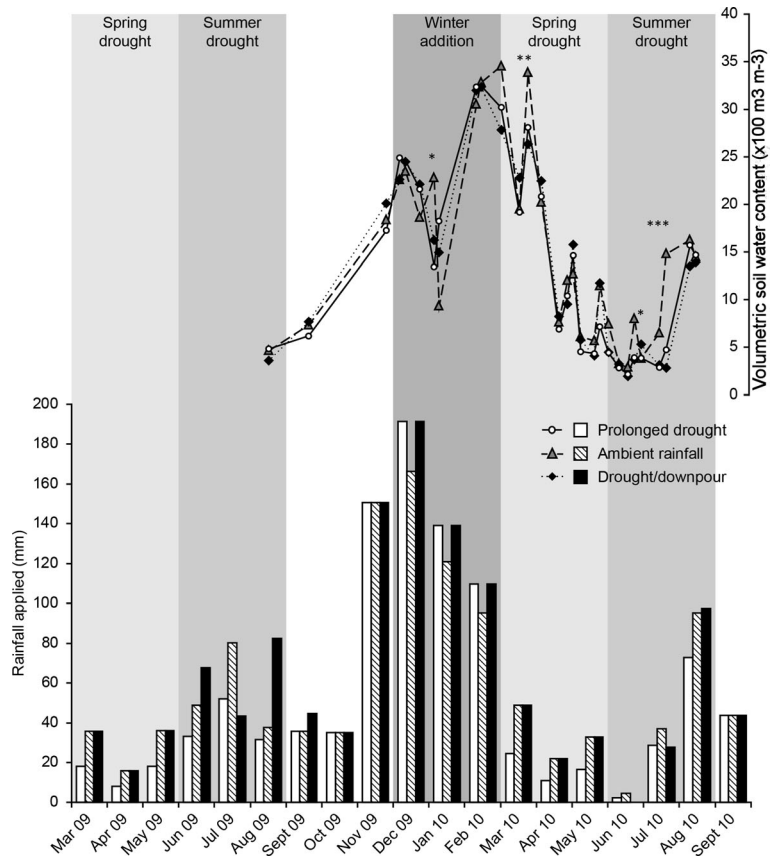
($F_{3,8}=12.38$, $p=0.002$). The highest species numbers were seen in May 2010, with an average of nine species per m^2 in all treatments. The very dry months that followed resulted in an average decrease of three species per m^2 by July 2010, coinciding with the highest SWP experienced during the experimental period, although the identity of these species losses were inconsistent between plots and there were no treatment level species extinctions over the duration of the study (S3). Species richness did not differ significantly between treatments on a month-by-month basis until September 2010 when, on average, four more species were recorded in the ambient and prolonged drought treatments than in the drought/downpour treatment (Fig. 2). This was reflected in a significant interaction between rainfall treatment and month ($F_{8,34}=3.07$, $p=0.010$).

Total vegetation cover was not significantly affected by rainfall treatment or by month (Table 2). Shannon's diversity (H) and equitability (E_H) indices were also unaffected by the rainfall treatments (main effects: H:
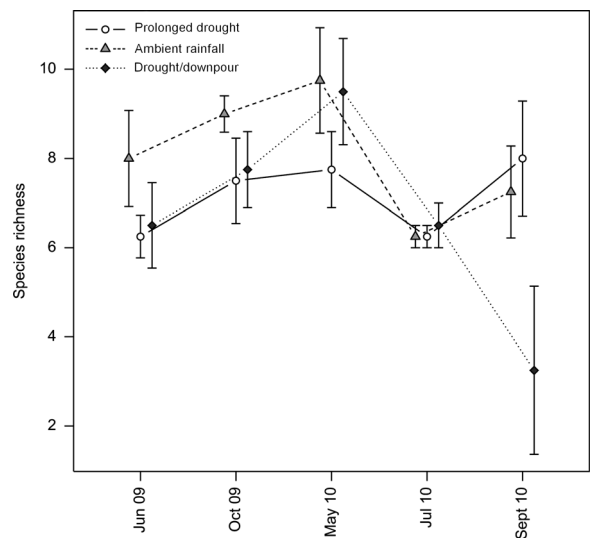
Fig. 2 Plant species richness in the different rainfall treatments through the experimental period (significant interaction between rainfall treatment and month $F_{8,34}=3.07$, $p=0.010$). Error bars depict ±1 SEM

Table 2 Linear mixed effects models of extreme rainfall change regimes affecting cover of grasses, forbs and legumes over months

		Percentage cover		Grass cover		Forb cover		Legume cover	
Treatment	d.f.	F	p	F	P	F	p	F	P
Intercept	1	264.76	<0.001	589.65	<0.001	75.20	<0.001	10.41	0.003
Month	4	1.98	0.119	2.04	0.111	1.14	0.356	3.62	0.015*
RC	2	0.88	0.423	0.29	0.750	3.11	0.058.	0.21	0.815
Month x RC	8	1.25	0.304	1.70	0.676	0.72	0.676	1.60	0.163
Residuals	34								

Effects are evaluated using likelihood ratio deletion F tests. Significant results at the $p<0.1$ level are asterisked

$F_{2,30}=0.66$, $p=0.525$ and E_H: $F_{2,30}=0.09$, $p=0.919$, rainfall treatment × month interactions: H: $F_{8,34}=1.21$, $p=0.370$, E_H: $F_{8,12}=0.93$, $p=0.526$, S5). Over the course of the experiment total live plant cover remained fairly low, at an average of 26.8 %. Grass cover did not change significantly over months or with treatment (Table 2). Forb cover responded significantly to both rainfall change treatments at the $p<0.1$ level of significance ($F_{2,34}=3.11$, $p=0.058$), showing an increase under the prolonged drought treatment at the beginning and end of the study (during the summer months), and a slight reduction in the drought/downpour treatment relative to the control after 2 years of rainfall manipulations (Fig. 3b). Legume cover was not significantly affected by the rainfall treatments, although there was a significant effect of month; in October 2009 legumes were most abundant (averaging 4.33 % cover), they then almost disappeared in May 2010, with the lowest cover of 1.08 %, before recovering slightly after the natural drought in the ambient treatment (Table 2, Fig. 3c).

Perennial species cover was affected by rainfall treatments; this was driven by generally higher perennial abundance in the prolonged drought treatment plots in early summer of both years, and an exceptionally low perennial abundance in the drought/downpour treatment in September 2010 (Table 3, Fig. 3d, $F_{2,34}=4.58$, $p=0.017$). Caespitose grass cover responded to both month and rainfall treatments at the $p<0.1$ level; coverage was the highest in May 2010 in both the drought/downpour and the ambient plots and subsequently declined during the natural summer drought period, with this group appearing to suffer a local extinction by the end of the study; in contrast, the prolonged drought treatment had very low cover but increased at the end of the study (Table 3, Fig. 3e, $F_{8,34}=1.93$, $p=0.087$). Annual plant

cover also only varied across the months (Table 3), with a peak in October 2009 followed by a steep decline. There was then a small increase in annuals at the end of summer 2010.

CO$_2$ and water flux

Net ecosystem CO_2 exchange (NEE) and photosynthetic rate (A) were not significantly affected by either month or rainfall change treatment (Table 4), although ecosystem respiration (R_{eco}) showed a significant interaction between month and rainfall regime (Fig. 4, $F_{10,43}=2.39$, $p=0.037$). Towards the end of the experiment the prolonged drought and drought/downpour treatments had higher R_{eco} than the ambient plots. This effect was especially pronounced in August 2010, coinciding with soil moisture falling below the wilt point in these treatments ($F_{2,6}=7.04$, $p=0.027$, S2b). We looked to see if compositional variables that had been significantly affected by rainfall change treatments were mediating the effect on R_{eco} (grasses in the GFL classification, Table 2, and perennial species from the bespoke classification, Table 3). However, the inclusion of these terms did not make the rainfall effect non-significant, thus suggesting that compositional shifts were not driving the response of R_{eco} to drought. Evapotranspiration (ET) was significantly affected by month, light levels and soil temperature only, with no effects of the rainfall treatments and no significant relationships with plant cover (Table 4).

Soil extractable nutrients

Throughout the study extractable NH_4 and NO_3 were significantly affected by month but not by the rainfall change treatments (Table 5). For both N forms, seasonal changes occurred when the
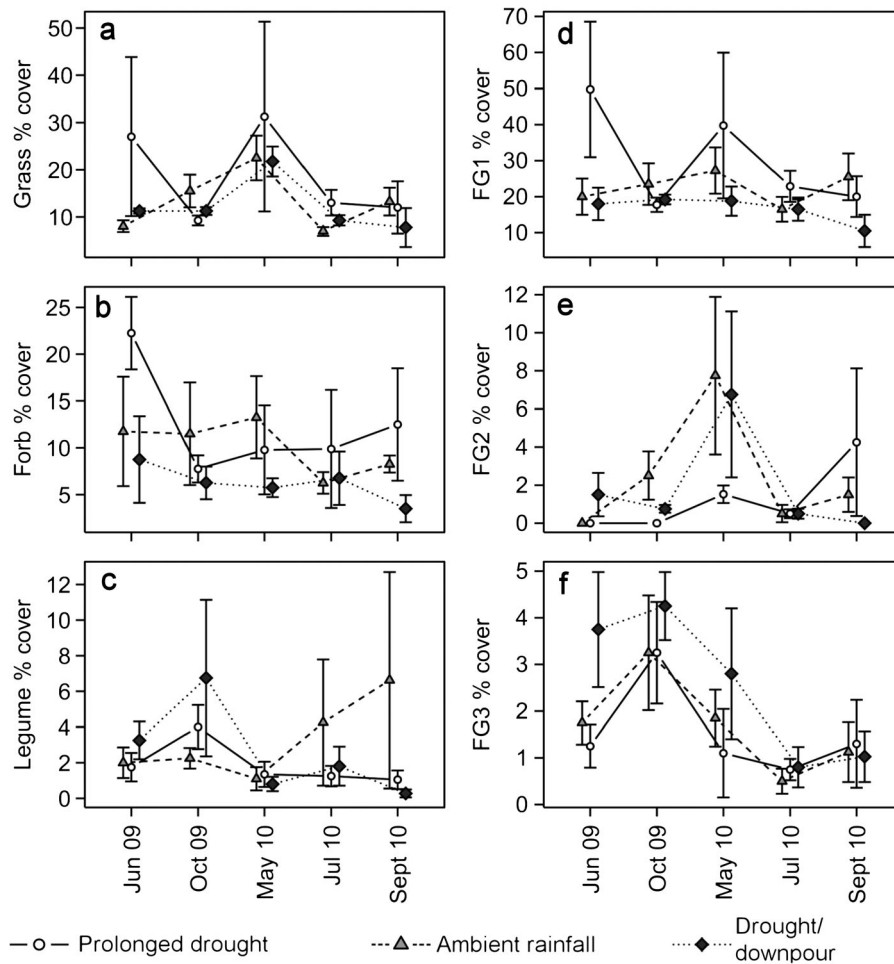
Fig. 3 Effects of rainfall treatment and month on vegetation parameters: **a** grass cover, **b** forb cover, **c** legume cover, **d** perennial cover (FG1), **e** caespitose grass cover (FG2), **f** annual cover (FG3). Error bars depict ±1 SEM

natural drought in June 2010 caused widespread plant dieback, and/or reduced plant uptake. Soil NO_3 was positively associated with soil moisture across the months studied, although not with the rainfall treatments ($F_{1,20}=9.86$, $p=0.005$).

Extractable P was significantly affected by the rainfall treatment ($F_{2,84}=5.39$, $p=0.046$) and by month ($F_{4,84}=11.93$, $p<0.001$) in an additive manner (Table 5, Fig. 5). Extractable P was significantly higher in both rainfall change treatments than in ambient plots,

Table 3 Linear mixed effects models of extreme rainfall change regimes affecting cover of plant functional groups over months

	d.f.	Perennial cover		Caespitose grass cover		Annual cover	
Treatment		F	p	F	p	F	P
Intercept	1	3,845.35	<0.001	65.06	<0.001	12.84	0.001
Month	4	0.83	0.330	5.50	0.002**	2.64	0.050·
RC	2	4.58	0.017*	2.13	0.134	0.83	0.443
Month x RC	8	0.77	0.63	1.93	0.087·	0.61	0.764
Residuals	34						

Effects are evaluated using likelihood ratio deletion F tests. Significant results at the $p<0.1$ level are asterisked

Table 4 Linear mixed effects models of extreme rainfall change regimes affecting CO_2 and water fluxes over months

|		R_{eco}		NEE		A		ET	
Treatment	d.f.	F	p	F	p	F	p	F	P
Intercept	1	16.43	<0.001	7.81	0.009	8.11	0.008	410.77	<0.001
Month	5	4.53	0.005**	1.33	0.279	1.57	0.205	32.97	<0.001**
RC	2	5.65	0.008**	1.58	0.222	1.59	0.219	0.57	0.569
Mean PAR	1	NA	NA	7.65	0.009**	8.03	0.008**	73.36	<0.001**
Soil temp	1	NA	NA	NA	NA	NA	NA	18.68	<0.001**
Month x RC	10	2.39	0.037*	0.35	0.937	0.35	0.937	0.73	0.719
Residuals	43								

R_{eco} denotes ecosystem respiration, NEE denotes net ecosystem CO_2 exchange, A denotes ecosystem-level photosynthetic rate, ET denotes evapotranspiration. Mean PAR is photosynthetically active radiation. Effects are evaluated using likelihood ratio deletion F tests. Significant results at the $p<0.1$ level are asterisked. NA occurs when the covariate is either not applicable, i.e. light levels for R_{eco}, or if it did not explain significant amounts of variation and was therefore removed from the analysis

particularly after the dry summer of 2010 when plants senesced early.

Discussion

Our study indicates that temperate grassland can be fairly resistant to changes in rainfall intensity and duration that are at the extreme end of future climate projections. Soil moisture was significantly reduced during the summer of 2010, but did not drop far below the wilt point for any prolonged amount of time. Therefore, the system can be perceived as largely resistant to changes in rainfall, because soil moisture change is the first response of a system to rainfall change and other ecosystem properties respond to this in turn (De Boeck et al. 2011). Throughout the summer period in 2010, the soil moisture averages 4.0 % in the rainfall treatments while the ambient was on average 7.4 %. The relatively dry soil in the ambient treatment could be why there were few significant effects on function under the two rainfall treatments. These did not affect ecosystem functioning in as significant a manner as might be expected, with available soil N being particularly insensitive to precipitation change. The main effects of the rainfall treatments were few and the prolonged drought treatment did not lead to significant changes in vegetation cover. In contrast, the drought/downpour treatment resulted in the mass dieback of perennial plants and there was little evidence of recovery one month after the rain shelters were removed, in September 2010. Despite these major vegetation changes there were surprisingly few associated

effects on ecosystem processes. While we could attribute this to small sample size, the F values for each time point did not exceed 2, a common statistical rule of thumb that means that the interpretation is unlikely to suffer from Type-II error (Murphy et al. 2009). An alternative explanation is that the ecosystem was largely resistant to the climate changes imposed upon it. We define resistance as "a measure of the amount of change which can be applied to a system before it is disrupted from its equilibrium" after Pimm (1984). In actuality, we measured the inverse of this, looking to measure the amount of change in response to a given stimulus.
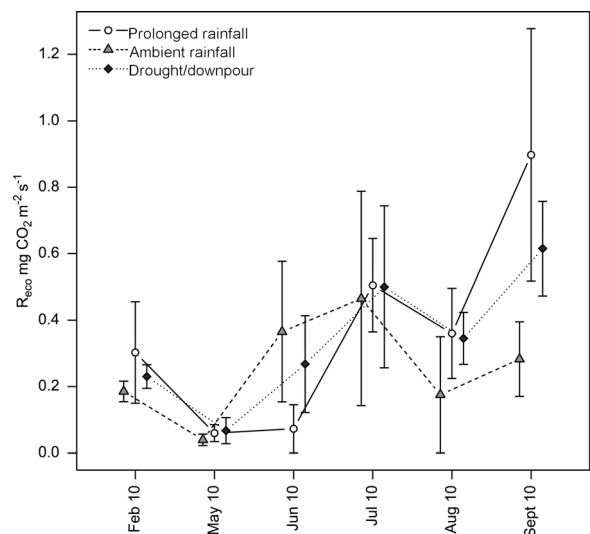
Fig. 4 Ecosystem respiration in relation to rainfall treatment and month ($F_{8,31}=2.39$, $p=0.037$). Error bars depict ±1 SEM

Table 5 Linear mixed effects models of extreme rainfall change regimes upon extractable soil nutrients over months

|		NH_4		NO_3		PO_4	
Treatment	d.f.	F	p	F	p	F	P
Intercept	1	908.50	<0.001	95.20	<0.001	247.37	<0.001
Month	4	42.69	<0.001***	77.50	<0.001***	8.30	<0.001***
RC	2	1.23	0.357	0.65	0.556	6.68	0.004**
Soil moisture	1	NA	NA	NA	NA	0.48	0.497
Month x RC	8	1.34	0.262	1.04	0.432	1.18	0.357
Residuals	84						

Effects are evaluated using likelihood ratio deletion F tests. Significant results at the $p<0.1$ level are asterisked

The most likely cause of resistance to rainfall change is that soil moisture levels were not strongly affected by either reduced or intermittent rainfall inputs. This was surprising given the degree of perturbation; in the drought/downpour treatment there were periods of zero rainfall lasting for 44 and 38 days. Complete drought for over 30 days in a British summer has been described as a 1 in 100 year likelihood (Bloor and Bardgett 2012). As was shown in the study of De Boeck et al. (2011), this suggests that, despite very dry soils resulting in negative SWPs in July 2010, and soils reaching PWP in August 2010, the size and duration of treatment effects on soil moisture were not generally sufficient to alter ecosystem functioning. One potential explanation for the observed lack of response could be increased rainfall in the preceding winter. While there were no significant soil moisture increases arising from the winter rainfall additions in our study, the additional water could have been held in deeper soil layers. Ecosystem processes during dry summer periods could, therefore, have been maintained at normal levels due to recharge of soil moisture from lower soil layers, despite drought-induced plant dieback. Other studies have documented increased winter rainfall as insurance for summer drought by allowing water to reach deeper soil layers (Chimner and Welker 2005). This water remains in the soil profile throughout the spring and summer, and in the case of the prairielands in the USA where this was demonstrated, can lead to an increased summer R_{eco} and A where extra winter precipitation was received.

Where significant effects were seen, the two altered rainfall treatments had similar effects upon process rates to one another. There were higher R_{eco} rates and soil extractable P in the rainfall treatments at the end of the experiment relative to the ambient treatment. The long

lag time between rainfall changes and soil moisture responses, which also supports the hypothesis of recharge from deeper soil layers, may explain why effects were only seen at the end of the experiment and not throughout the growing season. It is likely that the rapid increase in ambient rainfall after June 2010, following the early drought, resulted in higher average soil moisture in all plots; this can be associated with a number of changes in the soil including microbial cell lysis due to sudden osmotic changes, comminution of soil aggregates and nutrient release through renewed decomposition, which would have released formerly inaccessible sources of nutrients. As this would have occurred in all treatments, it is likely that this contributed to the strong effects of month, and obscured treatment effects. It
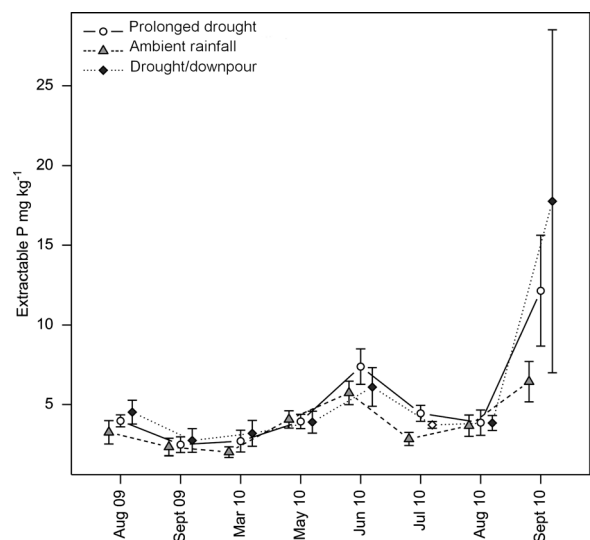
Fig. 5 Extractable phosphate concentrations in relation to rainfall treatment and month. Rainfall treatment: $F_{2,30}=6.68$, $p=0.004$. Error bars depict ±1 SEM

therefore appears, perhaps surprisingly, that temperate grasslands are more resistant to changes in rainfall pattern and drought duration than drier prairies, but that changes in plant community composition are dependent upon the precise nature of rainfall change scenario (Knapp et al. 2002). Function therefore appears to be more responsive to intra-annual variability in ambient precipitation, which is considerable and greater than even than extreme changes to overall rainfall regimes.

Vegetation responses

There were few consistent effects of the rainfall treatments on plant cover and species richness throughout the experiment. The plant community in the prolonged drought treatment was characterised by a highly variable abundance of perennials and a greater cover of non-legume forbs in the first spring and after the severe natural drought, in comparison to the ambient and drought/downpour treatments. This indicates that forbs may have established in gaps in the sward, contrary to our expectation that germination would be compromised by reduced rainfall. This may be because small pulses of water are either intercepted by the canopy or evaporate quickly from the soil surface, leaving deeper rooted plants at a disadvantage (Schwinning and Sala 2004; Borken and Matzner 2009). It is possible that continuing the experiment into future years could see increased abundance of autumn-germinating annuals as a result of competitive release from drought-sensitive grasses, a pattern demonstrated in a long term drought study in dry shrubland by (Lloret et al. 2009). Given the species-specific shifts in flowering dates and lengths observed by Jentsch et al. (2009) under extreme rainfall conditions, it is also likely that changing rainfall patterns could result in physiological adjustments that lead to earlier flowering and altered germination times rather than local extinctions. If strong seasonal shifts in dominance were to become the norm in this system they could lead to cascading effects on ecosystem function, and possibly delayed succession (Sternberg et al. 1999).

The drought/downpour regime was associated with a substantial loss of species richness and extensive plant dieback, which led to a high litter cover. The greater decline of grass cover compared to forbs through the growing season, and stronger dieback in September 2010 under this treatment, is consistent with the findings of Knapp et al. (2002), Morecroft et al. (2004) and Stampfli and Zeiter (2008), who all found that grass

seedlings are more susceptible to long dry periods than those of forbs. Evans et al. (2011) also showed that annual forbs displayed greater resilience than grasses in recovering from long-term drought stress. In our study, the cover of annuals in the drought/downpour after the dry period of summer 2010 was consistent with the average for the experiment, indicating either resistance to strong rainfall change, or continuous recruitment.

CO_2 fluxes

Effects of rainfall change on CO_2 and water fluxes in this study were small and inconsistent. Some studies attribute a similar lack of rainfall-induced responses to physiological acclimation or community reorganisation (Fridley et al. 2011; Lloret et al. 2012). In this study ecosystem level photosynthetic rate and net ecosystem CO_2 exchange were not explained by rainfall regime or functional group abundance, therefore indicating that these functions were resistant to changed rainfall patterns. This is likely to be attributed to changes in physiology, for example increases in water use efficiency.

R_{eco} was only responsive to the rainfall treatments towards the end of the study. This is consistent with the findings of many others who have found that R_{eco} is relatively insensitive to rainfall change (Fierer et al. 2003; Maestre et al. 2010; Fry et al. 2013), though see Knapp et al. (2002). The most likely explanation for this resistance is the aforementioned lack of significant treatment effects upon soil moisture. Soil moisture recharge from deeper layers may have buffered soil moisture and, correspondingly, treatment effects on soil respiration during periods of low rain. However, these reserves may have been exhausted by the end of the summer 2010 season, resulting in the appearance of treatment effects after a time lag (most literature regarding soil water recharge concerns drylands and forests, but there is potential for the phenomenon to occur in temperate grasslands; Reynolds et al. 2004). Many ecosystem processes, including R_{eco}, are driven by the activity of microorganisms, which often become inactive in dry periods but can rapidly reactivate when a pulse of water is applied (Lee et al. 2004; St Clair et al. 2009). With the build-up of necromass that often occurs during periods of severe drought, subsequent rainfall pulses trigger a sudden increase in decomposition causing bursts of mineralisation (Sponseller 2007; Borken and Matzner 2009). This could explain the higher R_{eco} in rainfall-

manipulated plots, compared with ambient controls, in September when the rainfall treatments were finished.

Extractable nutrients

The lack of treatment effects on extractable N could also (like the gas flux measures) be linked to the relatively small effects on soil moisture content and the small magnitude of vegetation change. These changes were probably insufficient to make consistent and strong alterations to such a transient and variable pool. It is likely that the accumulation of N across all treatments resulted from the natural drought, which would have made uptake by roots difficult. This finding is consistent with those from the larger scale DIRECT experiment, where effects of a smaller rainfall shift on extractable nutrients were limited, despite accumulation of nutrients through the experimental period (Fry et al. 2013). We did not measure N leaching in this study, although it is possible that relatively small changes in soil moisture and plant uptake have led to slower soil N cycling, with the net result being a neutral effect of the rainfall treatments on N dynamics.

Extractable phosphate increased significantly in both rainfall treatments compared with ambient plots at the end of the study, indicating either greater release or less plant uptake. Increased availability may be attributable to greater rates of P mobilising enzyme activity and/or microbial lysis due to osmotic stress from drying and wetting. The latter could cause a pulse of nutrient release from microbial biomass, although tests of this phenomenon have proved inconclusive (Turner and Haygarth 2001; Butterly et al. 2009). A further cause could be soil disaggregation, which also arises from drying and wetting cycles, in a process known as 'slaking' (Bunemann et al. 2013).

Conclusions

Rainfall change effects in this experiment were smaller than expected and the system was largely resistant to extreme changes in rainfall regimes. However, this overall conclusion comes with a caveat attached. Near the beginning of the 2010 growing season there was a very strong natural drought, which, when combined with the rainfall treatments, may have overridden the resistance of the system and exhausted deep soil water reserves. In this period there were some treatment effects on

vegetation cover and functional group abundances, and on gas and water fluxes. Therefore, it can be postulated that temperate grasslands subject to prolonged summer rainfall stress recover slowly after the stress is alleviated. This may be due to a natural deceleration of biological activity and the possible decoupling of plant and microbial processes; in such cases there is potential for lasting damage to the system (Kreyling et al. 2008; Evans et al. 2011; Lloret et al. 2012). In the case of our study site, seed rain from outside the plots, seed bank regeneration and regrowth from belowground organs may buffer species loss and so such effects may be underestimated. At the end of the century, if climate change manifests as regular severe drought events, this could cause highly degraded semi-natural plant communities through seedling mortality, leaving mainly species that regenerate by clonal means and forbs with suitable seed dormancy strategies. This likelihood is consistent with long-term studies where recruitment of grass species was vastly reduced following drought, while short-lived forbs were less affected (Stampfli and Zeiter 2008).

While further study is needed for this experiment to test for effects of rainfall change on the long-term successional dynamics of the plant community, our results show that the effects of rainfall change differ subtly depending on the type of change experienced. It is therefore important to explore a range of different potential scenarios within field experiments to gain a more comprehensive picture of the possible effects that future climate changes will have. This is particularly important given the persistence of uncertainty in climate model predictions (IPCC 2013).

References

Allen SE (1989) Chemical analysis of ecological materials. Blackwell Scientific Publications, Oxford

Beier C, Beierkuhnlein C, Wohlgemuth T, Penuelas J, Emmett B, Körner C et al (2012) Precipitation manipulation experiments – challenges and recommendations for the future. Ecol Lett 15:899–911

Beierkuhnlein C, Thiel D, Jentsch A, Willner E, Kreyling J (2011) Ecotypes of European grass species respond differently to warming and extreme drought. J Ecol 99:703–713

Birch HF (1958) The effect of soil drying on humus decomposition and nitrogen availability. Plant Soil 10:9–31

Blankinship J, Niklaus P, Hungate B (2011) A meta-analysis of responses of soil biota to global change. Oecologia 165:553–565

Bloor JMG, Bardgett RD (2012) Stability of above-ground and below-ground processes to extreme drought in model grassland ecosystems: interactions with plant species diversity and soil nitrogen availability. Persp Plant Ecol Evol Syst 14:193–204

Borken W, Matzner E (2009) Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. Glob Chang Biol 15:808–824

Bunemann EK, Keller B, Hoop D, Jud K, Boivin P, Frossard E (2013) Increased availability of phosphorus after drying and rewetting of a grassland soil: processes and plant use. Plant Soil 370:511–526

Butterly CR, Bunemann EK, McNeill AM, Baldock JA, Marschner P (2009) Carbon pulses but not phosphorus pulses are related to decreases in microbial biomass during repeated drying and rewetting of soils. Soil Biol Biochem 41:1406–1416

Chaer G, Fernandes M, Myrold D, Bottomley P (2009) Comparative resistance and resilience of soil microbial communities and enzyme activities in adjacent native forest and agricultural soils. Microb Ecol 58:414–424

Chaves MM, Flexas J, Pinheiro C (2009) Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. Ann Bot 103:551–560

Chimner RA, Welker JM (2005) Ecosystem respiration responses to experimental manipulations of winter and summer precipitation in a Mixed grass Prairie, WY, USA. Biogeochemistry 73:257–270

De Boeck HJ, Dreesen FE, Janssens IA, Nijs I (2011) Whole-system responses of experimental plant communities to climate extremes imposed in different seasons. New Phytol 189:806–817

Eade R, Hamilton E, Smith DM, Graham RJ, Scaife AA (2012) Forecasting the number of extreme daily events out to a decade ahead. J Geophys Res 117:D21110

Easterling DR, Meehl J, Parmesan C, Chagnon S, Karl TR, Mearns LO (2000) Climate extremes: observations, modelling, and impacts. Science 289:268–274

Evans SE, Byrne KM, Lauenroth WK, Burke IC (2011) Defining the limit to resistance in a drought-tolerant grassland: long-term severe drought significantly reduces the dominant species and increases ruderals. J Ecol 99:1500–1507

Fay PA, Carlisle JD, Knapp AK, Blair JM, Collins SL (2003) Productivity responses to altered rainfall patterns in a C4-dominated grassland. Oecologia 137:245–251

Fierer N, Schimel JP, Holden PA (2003) Influence of drying–rewetting frequency on soil bacterial community structure. Microb Ecol 45:63–71

Fischlin A, Midgley GF, Price JT, Leemans R, Gopal B, Turley C et al (2007) Ecosystems, their properties, goods and services. In: Parry ML, Canziani OF, Palutikof JP, Linden PJ, Hanson CE (eds) Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, pp. 211–272

Fridley JD, Grime JP, Askew AP, Moser B, Stevens CJ (2011) Soil heterogeneity buffers community response to climate change in species-rich grassland. Glob Chang Biol 17:2002–2011

Fry EL, Manning P, Allen DGP, Hurst A, Everwand G, Rimmler M et al (2013) Plant functional group composition modifies the effects of precipitation change on grassland ecosystem function. PLoS One 8:e57027

Fry EL, Power SA, Manning P (2014) Trait-based classification and manipulation of plant functional groups for biodiversity–ecosystem function experiments. J Veg Sci 25:248–261

Gorissen A, Tietma A, Joosten NN, Estiarte M, Penuelas J, Sowerby A et al (2004) Climate change affects carbon allocation to the soil in shrublands Ecosystems 7:650–661

Heisler-White JL, Blair JM, Kelly EF, Harmoney K, Knapp AK (2009) Contingent productivity responses to more extreme rainfall regimes across a grassland biome. Glob Chang Biol 15:2894–2904

IPCC (2007) Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, 2007. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) IPCC Fourth Assessment Report: Climate Change 2007

IPCC (2013) Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. In: Stocker T, Dahe Q, Plattner G-K (ed) Climate Change 2013: The Physical Science Basis

ITIS (2013) Integrated Taxonomic Information System online database. Available at: www.itis.gov

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, Boettcher-Treschkow J, Beierkuhnlein C (2009) Beyond gradual warming: extreme weather events alter flower phenology of European grassland and heath species. Glob Chang Biol 15:837–849

Kehl M, Everding C, Botschek J, Skowronek A (2005) Erosion processes and erodibility of cultivated soils in North Rhine-Westphalia under artificial rain–I. Site characteristics and results of laboratory experiments. J Plant Nutr Soil Sci 168:34–44

Kim JB, Verma SJ, Clement RJ (1992) Carbon dioxide budget in a temperate grassland ecosystem. J Geophys Res 97(D5):6057–6063

Knapp AK, Fay PA, Blair JM, Collins SL, Smith MD, Carlisle JD et al (2002) Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. Science 298:2202–2205

Kolari P, Pumpanen J, Kulmala L, Ilvesniemi H, Nikinmaa E, Gronholm T, Hari P (2006) Forest floor vegetation plays an important role in photosynthetic production of boreal forests. For Ecol Manag 221:241–248

Kreyling J, Beierkuhnlein C, Elmer M, Pritsch K, Radovski M, Schloter M et al (2008) Soil biotic processes remain remarkably stable after 100-year extreme weather events in experimental grassland and heath. Plant Soil 308:175–188

Laporte M, Duchesne LC, Wetzel S (2002) Effect of rainfall patterns on soil surface CO2 efflux, soil moisture, soil temperature and plant growth in a grassland ecosystem of

northern Ontario, Canada: implications for climate change. BMC Ecol 2:1–10

Lee X, Wu H-J, Sigler J, Oishi C, Siccama T (2004) Rapid and transient response of soil respiration to rain. Glob Chang Biol 10:1017–1026

Lloret F, Peñuelas J, Prieto P, Llorens L, Estiarte M (2009) Plant community changes induced by experimental climate change: seedling and adult species composition. Perspect Plant Ecol Evol Syst 11:53–63

Lloret F, Escudero A, Iriondo JM, Martínez-Vilalta J, Valladares F (2012) Extreme climatic events and vegetation: the role of stabilizing processes. Glob Chang Biol 18:797–805

Maestre FT, Bowker MA, Escolar C, Puche MD, Soliveres S, Maltez-Mouro S et al (2010) Do biotic interactions modulate ecosystem functioning along stress gradients? Insights from semi-arid plant and biological soil crust communities. Phil Trans B Biol Sci 365:2057–2070

Menzel A, Sparks TH, Estrella N, Koch E, Aasa A, Ahas R et al (2006) European phenological response to climate change matches the warming pattern. Glob Chang Biol 12:1969–1976

Morecroft MD, Masters GJ, Brown VK, Clarke IP, Taylor ME, Whitehouse AT (2004) Changing precipitation patterns alter plant community dynamics and succession in an ex-arable grassland. Funct Ecol 18:648–655

Murphy J, Sexton D, Jenkins G, Boorman P, Booth B, Brown K et al (2009) UK climate projections science report: climate change projections. Met Office Hadley Centre, Exeter

Nakićenović N, Swart R (eds) (2000) Emissions scenarios: a special report of working group III of the intergovernmental panel on climate change. Cambridge University Press, Cambridge

Pimm SL (1984) The complexity and stability of ecosystems. Nature 307:321

Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Springer, New York

R Development Core Team (2009) R: A Language and Environment for Statistical Computing. Vienna, Austria

Reynolds JF, Kemp PR, Ogle K, Fernández RJ (2004) Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. Oecologia 141:194–210

Rice C, Pancholy S (1972) Inhibition of nitrification by climax ecosystems. Am J Bot 59:1033–1040

Rodwell JS (Ed) (1992) British Plant Communities. Volume 3. Grassland and montane communities. Cambridge University Press

Saxton KE, Rawls WJ (2006) Soil water characteristic estimates by texture and organic matter for hydrologic solutions. Soil Sci Soc Am J 70:1569–1578

Saxton KE, Rawls WJ, Romberger JS, Papendick RI (1986) Estimating generalised soil-water characteristics from temperature. Soil Sci Soc Am J 50:1031–1036

Schwinning S, Sala OE (2004) Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141:211–220

Shannon CE, Weaver W (1963) The mathematical theory of communication. University Illinois Press, USA

Smith MD (2011a) An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. J Ecol 99:656–663

Smith MD (2011b) The ecological role of climate extremes: current understanding and future prospects. J Ecol 99:651–655

Sponseller RA (2007) Precipitation pulses and soil CO_2 flux in a Sonoran Desert ecosystem. Glob Chang Biol 13:426–436

St Clair SB, Sudderth EA, Fischer ML, Torn MS, Stuart SA, Salve R et al (2009) Soil drying and nitrogen availability modulate carbon and water exchange over a range of annual precipitation totals and grassland vegetation types. Glob Chang Biol 15:3018–3030

Stampfli A, Zeiter M (2008) Mechanisms of structural change derived from patterns of seedling emergence and mortality in a semi-natural meadow. J Veg Sci 19:563–574

Sternberg M, Brown VK, Masters GJ, Clarke IP (1999) Plant community dynamics in a calcareous grassland under climate change manipulations. Plant Ecol 143:29–37

Turner BL, Haygarth PM (2001) Biogeochemistry: phosphorus solubilization in rewetted soils. Nature 411:258

Vogel A, Fester T, Eisenhauer N, Scherer-Lorenzen M, Schmid B, Weisser WW, Weigelt A (2013) Separating drought effects from roof artifacts on ecosystem processes in a grassland drought experiment. PLoS One 8:e70997

Wagner S, Madsen P, Ammer C (2009) Evaluation of different approaches for modelling individual tree seedling height growth. Trees Struct Funct 23:701–715

Wiegand T, Snyman HA, Kellner K, Paruelo JM (2004) Do grasslands have a memory: modelling phytomass production of a semiarid South African grassland. Ecosystems 7:243–258

Xu LK, Baldocchi DD, Tang JW (2004) How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature. Global Biogeochem Cy 18:GB4002