

Defining the limit to resistance in a drought-tolerant grassland: long-term severe drought significantly reduces the dominant species and increases ruderals

Sarah E. Evans^{1*}, Kerry M. Byrne¹, William K. Lauenroth² and Ingrid C. Burke^{3,4}

¹Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80521, USA; ²Department of Botany and Program in Ecology, University of Wyoming, Laramie, WY 82071, USA; ³Environment and Natural Resources Program, Department of Botany, University of Wyoming, Laramie, WY 82071, USA; and ⁴Department of Renewable Resources and Program in Ecology, University of Wyoming, Laramie, WY 82071, USA

Summary

1. Models predict that the duration and intensity of drought will increase under future climate regimes. Although semi-arid grasslands are adapted to moisture limitation, the sensitivity of semi-arid grassland vegetation to extreme and sustained dry periods that may occur in the future has not been tested.

2. In this study, we analysed vegetation cover data from an 11-year drought manipulation in the semi-arid shortgrass steppe in Colorado, USA. We examined changes in total vegetation cover, dominant plant (*Bouteloua gracilis*) cover and ruderal cover in plots receiving 25% and 50% of ambient precipitation during the growing season.

3. We found that 11 years of drought resulted in large reductions in total cover and cover of the dominant species, but significant differences did not emerge until the 4th and 7th year of drought. Drought severity significantly influenced the degree to which ruderal cover increased in the later period of the drought, but reductions in *B. gracilis* cover under drought were not significantly different under different drought severities. *Bouteloua gracilis* reduction did correspond strongly with increases in ruderal cover and species richness, suggesting that the dominant species plays a strong role in maintaining the structure of communities in the shortgrass steppe.

4. Synthesis. Our results suggest that the shortgrass steppe, and most notably the dominant species *B. gracilis*, can be significantly perturbed by long-term droughts that may be more common in future decades. By quantifying the resistance-limit of a drought-tolerant system, our results can inform theories of stability and management decisions for grassland systems under new climate regimes and provide a new temporal context for previous and future manipulation studies.

Key-words: *Bouteloua gracilis*, climate change, dominant species, drought, grassland, plant species composition, plant–climate interactions, precipitation manipulation, shortgrass steppe

Introduction

Human activities since the industrial revolution have contributed to regional and global changes in climate, including an increase in global temperature and changes in precipitation patterns (IPCC 2007). Global change will not affect the earth uniformly—temperature and precipitation alterations will vary across regions, and responses will depend on an ecosystem's sensitivity to climate parameters. Predicting the effects of climate change in grasslands is especially important, as they are the potential natural vegetation for over 40% of the earth's

land surface (White *et al.* 2000) and currently support many productive agricultural areas. The central grassland region of North America is an ideal ecosystem for studying the effects of climate change on grasslands. The region represents 12.5% of North America and 2% of the Earth's terrestrial surface (Lauenroth, Burke & Gutmann 1999). Both temperature and precipitation vary along the north–south and east–west gradients of the region, and this range of climates makes it comparable to similar grasslands world-wide. Climate models predict increased frequency and duration of summer droughts in the central grassland region by the end of the century (IPCC 2007; CCSP 2008). Because ecosystems in this region are most frequently water limited (Noy-Meir 1973; Sala *et al.* 1988), precipitation changes are expected to have dramatic effects on

*Correspondence author. E-mail: sarah.evans@colostate.edu

ecosystem dynamics including agricultural production (Baker *et al.* 1993; Weltzin *et al.*, 2003; Motha & Baier 2005).

There has been extensive research examining precipitation controls on vegetation in semi-arid areas. Many studies have been observational and therefore not ideally suited to investigate responses to future events outside an ecosystem's historical range of variability (Groffman *et al.* 2006; Smith, Knapp & Collins 2009). Weaver (1954) recorded changes in plant species composition during and after a multiple-year drought in the early 1930s in the central grassland region. Other studies have examined plant responses to interannual variability in precipitation (Lauenroth & Sala 1992; Silvertown *et al.* 1994; Briggs & Knapp 1995; Jobbagy & Sala 2000) and changes over spatial precipitation gradients across the region (Sala *et al.* 1988; Austin & Sala 2002; McCulley *et al.* 2005). With a more recent focus on specific climate changes, some studies have focused on the effect of short-term extreme events, such as temporary severe drought or anomalous temperatures. These 'pulse' disturbance events can have a large effect on ecosystem processes, but global climate models also predict sustained change, or 'press' disturbances (Smith, Knapp & Collins 2009). Rainfall addition or reduction treatments (Heitschmidt *et al.* 1999; Zavaleta *et al.* 2003; Yahdjian & Sala 2006; Grime *et al.* 2008) can provide such a press disturbance, but manipulations are often difficult to extend over long periods of time, and therefore, most 'long-term' drought manipulations last 1–4 years.

We analysed data from an 11-year experimental drought on the shortgrass steppe. This is one of the longest-running precipitation manipulations published to date. The semi-arid shortgrass steppe lies on the western edge of the central grassland region of North America. Precipitation is highly variable, and the dominant plant species have long been considered resistant to drought (Lauenroth 2008). The system is unique in that it is dominated by a single plant species, the C₄ perennial grass *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths. *Bouteloua gracilis* consistently makes up 80% or more of above-ground net primary production (ANPP) (Milchunas *et al.* 1989), so any process that reduces the predominance of *B. gracilis* will have a large effect on ecosystem structure and processes. The disturbance regime of the shortgrass steppe is dominated by frequent, small-scale events (Coffin & Lauenroth 1988), and few experimental manipulations have managed to drastically perturb this system, leaving the limits of its resistance and resilience unclear (Peters, Lauenroth & Burke 2008). Long-term, sustained droughts predicted for this region will provide a large-scale disturbance that may perturb the shortgrass steppe in novel ways.

The droughts of the 1930s and early 1950s were the most significant dry periods in the central grassland region in the last century, and the longest in the instrumental record, lasting 8 and 14 years (Seager *et al.* 2005; Stahle & Fye 2007). In contrast to these, tree-ring data suggests that several 'megadroughts' spanning multiple decades occurred during the past 1000 years in western North America (Cook & Seager 2010). Greenhouse gas forcing may result in the future occurrence of multi-decadal droughts similar to these 'megadroughts'. These longer droughts have no recent analogues (Woodhouse *et al.*

2010) and may 'press' the ecosystem in novel ways (Smith, Knapp & Collins 2009).

Our goal was to quantify the response of shortgrass steppe vegetation to two levels of experimental drought severity. Specifically, we asked: (i) How does total vegetation cover respond to 11 years of drought of two different severities? (ii) How does plant species composition change under two different drought severities? We were particularly interested in how the dominant species (*B. gracilis*) changed under drought and how these changes affected ruderal species cover and richness.

Materials and methods

STUDY SITE

The study site is located on the semi-arid shortgrass steppe at the Central Plains Experimental Range (CPER), 60 km north-east of Fort Collins, Colorado (40°49' N latitude, 104°46' W longitude). The CPER is administered by the USDA Agriculture Research Service and is also a National Science Foundation Long Term Ecological Research site (Lauenroth & Burke, 2008). Mean annual precipitation is 341 mm, and mean annual temperature is 8.2 °C. The site is dominated by typical upland vegetation, including the short-stature C₄ grasses blue grama (*B. gracilis*) and buffalograss (*Bouteloua dactyloides* (Nutt.) J.T. Columbus), and plains prickly-pear cactus (*Opuntia polyacantha* Haw.). Common dwarf shrubs include prairie sagewort (*Artemisia frigida* Willd.), spreading buckwheat (*Eriogonum effusum* Nutt), rubber rabbitbrush (*Chrysothamnus nauseosus* Pall. ex Pursh) and broom snakeweed (*Gutierrezia sarothrae* (Pursh) Britton & Rusby) (Lauenroth 2008) (Fig. S1 and Table S1 in Supporting Information). Patches of bare ground are prevalent.

EXPERIMENTAL DESIGN

In spring of 1998, two blocks were located within similar vegetation and soil types near the headquarters of the Shortgrass Steppe Long Term Ecological Research site (SGS-LTER) field site and divided into three 3-m² plots: a control plot that received ambient rainfall and two drought plots that received 50% and 25% of ambient rainfall. During the growing season (average dates 26 April–7 October), rain-out shelters automatically covered drought plots during rain events using a rain sensor. Each week, a proportion (25% or 50%) of the ambient rainfall for that week was manually re-added to the manipulated drought plots.

DATA COLLECTION

From 1999 to 2009, at peak biomass (dates ranged from 14 July to 18 August), the SGS-LTER Field Crew measured above-ground plant species composition and abundance non-destructively by visually estimating canopy cover and counting numbers of individuals in five 0.25-m² subplots.

DATA ANALYSIS

We conducted all data analysis in SAS (version 9.2, Cary, NC, USA) and created all graphs in R 2.10.0 (R Development Core Team 2007). We averaged all subplots to produce one cover value per plot, giving us two treatment replicates per year for all years except 2005, when data for one shelter was missing. To assess the effect of drought on

different vegetation groups, we divided total cover into *B. gracilis* cover, ruderal cover and other cover. We defined ruderals as species that are adapted to exploit stressful environmental conditions (Grime 2001). This includes short-lived, fast-growing native and non-native species often considered undesirable by range managers (ruderal and non-ruderal species list reported in Tables S1 and S2). We used the USDA NRCS Plants Database (2010) as our naming authority and for native and non-native status.

We performed a repeated-measures analysis in Proc Mixed (SAS v.9.2) on raw data for total cover, *B. gracilis* cover and ruderal cover. We included year (11 levels) and treatment (3 levels) as fixed effects and block (2) and the block by treatment interaction as random effects. We tested whether to include an additional autoregressive correlation between plots over time, but did not include this interaction in the final model because it resulted in higher or nearly equal Akaike Information Criterion constant (AIC_c) values compared with the model without it, for all three cover variables. If a significant ($P < 0.05$) treatment by year interaction occurred, we compared treatments separately within each year. We also compared average differences of grouped years within this model. Although significance at 0.1 or 0.05 level indicates high probability that we can reject the null hypothesis of no difference between treatments, confidence intervals provide a more fluid view of whether the lack of significance implies no difference (interval centred on 0). Therefore, we also examined the confidence intervals for differences to investigate whether non-significant differences supported the conclusion that treatment differences were near zero. In this case, the confidence interval would include zero and be relatively narrow, but also be centred on zero. To provide additional resolution and show which species made up the majority of the ruderal species grouping, we also calculated the most abundant ruderal species in each treatment, over all years.

Results

Compared with the long-term (40-year) average, the 11 years during which the drought manipulation was conducted were dry; 8 years were below the long-term average, including 2 years receiving less than half of average rainfall and only three receiving above average rainfall (Fig. 1). This year-to-

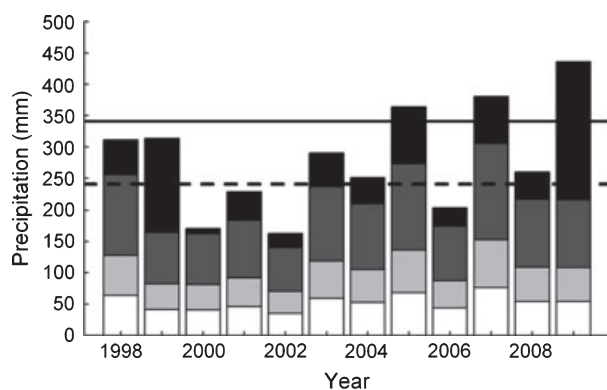


Fig. 1. Growing season precipitation in the 25% (white), 50% (light grey) and control (darker grey) treatments, and non-growing-season precipitation (black, the same for each treatment) during the 11-year drought experiment at the Central Plains Experimental Range. Each full bar shows annual precipitation for that year. Lines represent long-term average (1959–2009) annual precipitation (341 mm, solid line) and growing season precipitation (241 mm, dashed line).

year variation in precipitation (and percentage reductions) led to variability in vegetation cover, and annual precipitation was correlated with several cover variables (Table S3). As a result, in control plots receiving no drought treatment, there were differences in total canopy cover, in canopy cover of ruderals and *B. gracilis*, and in species richness from year-to-year during the 11-year experiment. To focus on species composition response to the drought treatments rather than these year-to-year fluctuations, we present *B. gracilis* and ruderal cover in 25% and 50% drought plots relative to cover in the control treatment in that year.

TOTAL CANOPY COVER

Total canopy cover in the 25% drought treatment was significantly lower than the control treatment beginning in the 5th year of the experiment (2002) and continued to be significantly lower for the majority of the remaining years (Fig. 2). Cover in the 50% drought treatment was significantly lower than cover in the control treatment for only 2 years of the experiment: 2003 and 2009. Confidence intervals did not centre on zero in non-significant years, but instead suggested that trends of reduced cover began in 2001 in 25% treatments and 2002 for 50% treatments. There was only a significant difference in cover between the 25% and 50% drought treatments in 2008. However, we could not interpret this as similar responses to drought as confidence intervals of differences in total cover in 25% and 50% treatments did not often centre on zero (Table S4).

COVER OF *B. GRACILIS*

Throughout the experiment, *B. gracilis* cover was consistently lower in the drought treatments than in the control treatment (Fig. 3). A statistically significant decrease in *B. gracilis* under a 25% drought reduction emerged in the 8th year of the drought manipulation (2005), and *B. gracilis* cover remained lower than control from 2005 to 2009. During this period, cover in the 25% treatment was on average 29% lower than in the control. This was significantly different from the 8% reduction in cover in 1999–2004 ($P < 0.01$ when years were grouped). There was never a significant difference between the 25% and 50% drought treatments, and trends in 25% and 50% differences from the control followed similar trajectories over time. Further, the confidence intervals for differences between 25% and 50% treatments were almost always centred on zero (Table S5).

COVER OF RUDERAL SPECIES

The response of ruderal species to drought was different between the two drought treatments early in the experiment (1999 and 2000); ruderal cover in the 25% treatment was less than the control in these years (Fig. 3). Thereafter, ruderal cover increased in both drought treatments over time, but more slowly in the 25% treatment. By 2005, ruderal cover in both drought treatments was significantly higher than it was in

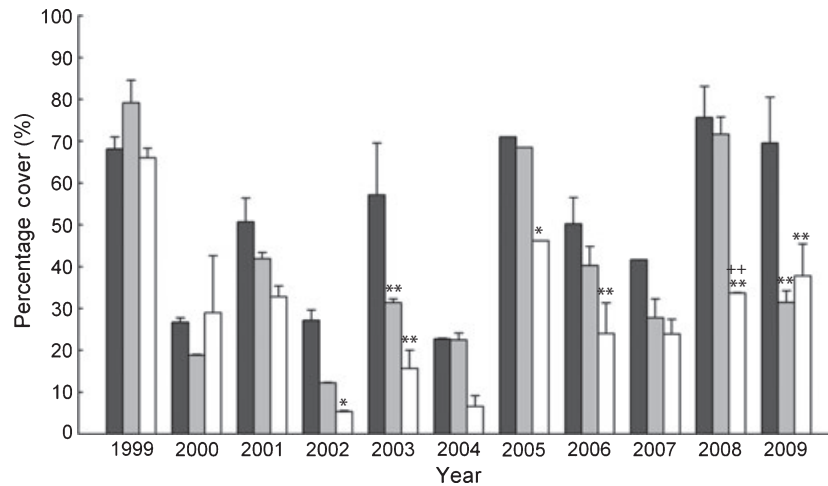


Fig. 2. Percentage total vegetation cover in the control (black bars), 50% (grey), and 25% (white) drought treatments. ** indicates treatment is significantly different from control at $P < 0.05$, * indicates significance at $P < 0.10$. ++ indicates 50% and 25% are significantly different in that year at $P < 0.05$. Error bars represent standard error of means ($N = 2$ except 2005 when $N = 1$). Significance was determined using homogenized variances used in repeated-measures analyses.

the control and, although not always significant, remained higher than that in the control for 3 of the 4 remaining years. In contrast to the early years of the experiment, in the last 4 years 25% and 50% treatments were not significantly different from each other; mean differences were $< 3\%$ cover and confidence intervals of these differences centred on zero (Table S6).

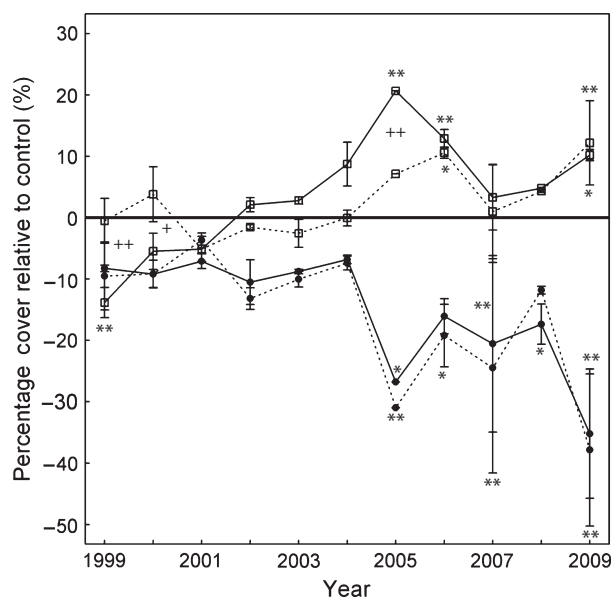


Fig. 3. Percentage cover of ruderal species (open squares) and *Bouteloua gracilis* (closed circles) in the 50% (solid lines) and 25% (dashed lines) drought treatments, relative to the control (bold solid line at 0). ** indicates treatment is significantly different from control at $P < 0.05$, * indicates significance at $P < 0.10$. ++ indicates 50% and 25% are significantly different in that year at $P < 0.05$ and + indicates significance at $P < 0.10$. Error bars represent standard error of means of differences ($N = 2$ except 2005 when $N = 1$). Significance was determined using homogenized variances used in repeated-measures analyses.

Over the course of the experiment in all treatments, *A. frigida*, a short-lived native dwarf shrub, was the ruderal species with the highest cover in control plots as well as under drought, although cover increased in drought plots (Table 1). The second and third most abundant ruderal species in the 25% drought were non-native annual forbs. Other important ruderal species in the control and 50% drought differed, but were native species.

SPECIES RICHNESS

The average number of species per plot in both drought treatments was lower than the control during the first part of the drought (though only statistically significant for 25% in 2002–2004) and higher than the control in the later part (Fig. 4). The number of species compared to the control began to increase in the 50% treatment in 2003, whereas this did not occur in the 25% treatment until 2007.

Discussion

Warming and changes in precipitation are predicted to result in more frequent severe droughts in the western United States (Cook *et al.* 2004), and average drought length may be longer than those recorded in the instrumental record (MacDonald 2010; Woodhouse *et al.* 2010). Such longer-term, extreme droughts will likely disturb grassland ecosystems in novel ways, and our results show two major effects in the shortgrass steppe. First, although vegetation in the shortgrass steppe may be resistant to severe short-term drought, it can be significantly perturbed by long-term drought. Second, resistance to drought and changes in community composition are largely determined by the dynamics of the dominant species, *B. gracilis*. This second result reinforces previous findings that *B. gracilis* plays an important role in maintaining ecosystem stability, and a reduction in *B. gracilis* will correspond to increases in ruderal species

Table 1. Cover of most abundant ruderal species in each treatment across all years

Treatment and species	Percentage cover		Native or Non-native
		Growth form	
Control			
<i>Artemisia frigida</i>	5.8	Dwarf shrub	Native
<i>Aristida purpurea</i>	3.4	Perennial grass	Native
<i>Pascopyrum smithii</i>	3.0	Perennial grass	Native
25% drought			
<i>Artemisia frigida</i>	7.0	Dwarf shrub	Native
<i>Bassia scoparia</i>	3.1	Annual forb	Non-native
<i>Salsola tragus</i>	2.6	Annual forb	Non-native
50% drought			
<i>Artemisia frigida</i>	8.0	Dwarf shrub	Native
<i>Chenopodium leptophyllum</i>	3.1	Annual forb	Native
<i>Elymus elymoides</i>	2.7	Perennial grass	Native

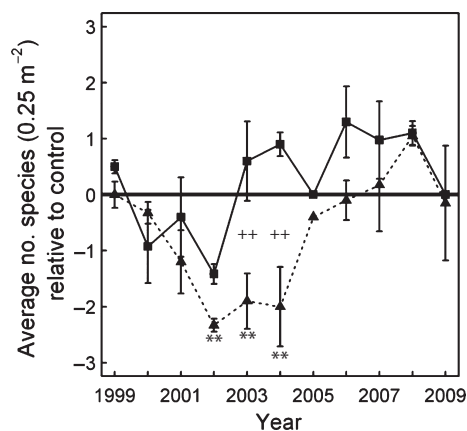


Fig. 4. Average number of species per 0.25-m² plot in 50% (square, solid line) and 25% (triangle, dashed line) drought treatments, relative to the control (bold solid line at 0). ** indicates treatment is significantly different from control at $P < 0.05$, * indicates significance at $P < 0.10$. ++ indicates 50% and 25% are significantly different in that year at $P < 0.05$ and + indicates significance at $P < 0.10$. Error bars represent standard error of means of differences ($N = 2$ except 2005 when $N = 1$). Significance was determined using homogenized variances from repeated-measures analyses.

under drought (Milchunas *et al.* 1990; Singh, Bourgeron & Lauenroth 1996). These changes in species composition under drought have major implications for ecosystem functions such as net primary production and carbon and nitrogen cycling (Vinton & Burke 1995), and recovery dynamics of semi-arid ecosystems under altered precipitation regimes.

Although there was a trend towards reduced total cover under drought in the first 4 years of the experiment (Table S4), a significant difference still did not emerge until the 4th year in the 25% plots and 5th year in the 50% plots (Fig. 2). Several 1- to 4-year studies in semi-arid ecosystems have reported small significant differences in ANPP, an ecosystem property that is closely related to vegetation cover, during drought periods (Heitschmidt *et al.* 1999; Jentsch, Kreyling & Beierkuhnlein 2007; Cipriotti *et al.* 2008). Under a very extreme drought

intensity (probability of 100-year recurrence) in an experimental grassland in Germany, Mirzaei *et al.* (2008) found no significant difference in ANPP after 1 year.

These studies, as well as our own results, reinforce the idea that grassland systems are resistant to water limitation, even if it is very severe, but they also show that 1- to 4-year manipulations are not long enough to reveal the limit of this resistance. The European precipitation manipulation outlined in Grime *et al.* (2000) lasted almost a decade, and, similarly, the authors did not find that vegetation cover in the drought plots diverged from the control for the first 4 years of the experiment (Morecroft *et al.* 2004). These findings provide a new temporal context for previous and future manipulation studies in grassland ecosystems that seek to determine the limit to drought resistance, and suggest that perhaps duration of drought is as, or perhaps more, important than severity in determining vegetation response to drought.

Previous research has found that *B. gracilis* is drought and grazing tolerant (Mueller & Weaver 1942; Hyder 1975; Milchunas, Sala & Lauenroth 1988). We found evidence to support this, as there was little reduction in *B. gracilis* for the first 6 years of our drought manipulation. The ability of *B. gracilis* to persist through disturbances has been shown to be imperative in preserving plant community structure in the shortgrass steppe (Hyder 1975), in maintaining larger-scale ecosystem processes (Hook, Burke & Lauenroth 1991) and in facilitating recovery. Survival of the dominant species under drought may have facilitated grassland recovery after the drought of the 1930s (Weaver & Mueller 1942). However, under large-scale disturbances that result in the death of multiple plants, the recovery of *B. gracilis* relies on seedling recruitment, which is limited under dry conditions (Lauenroth *et al.* 1994). In our study, *B. gracilis* was severely reduced in the 7th year of the drought (2005) and continued to be an average of 29% lower for the remainder of the study. This reduction corresponded with an increase in ruderals, as these species were likely able to successfully colonize the resulting bare ground, especially in the 50% plots where more moisture was available. Other studies have observed a decrease in perennial cover and increase in short-lived annuals and forbs in grasslands under drought in northern US grasslands (Clark *et al.* 2002) and ex-arable grasslands in England (Morecroft *et al.* 2004). This pattern supports previous assertions that *B. gracilis* plays an important role in maintaining community structure (Milchunas *et al.* 1990) and stability (Sasaki & Lauenroth 2011), and at a small scale, constrains species richness in the shortgrass steppe (Singh, Bourgeron & Lauenroth 1996).

Although length of drought was an important factor in whether vegetation cover decreased, severity was not. *Bouteloua gracilis* cover under the 25% drought treatment was not significantly different than the less severe drought treatment (50%) for any year of the study (Fig. 3, Table S4), and total cover displayed a similar trend (Fig. 2, Table S4). These findings have basic and applied ecological implications. First, considering the ecological and agricultural importance of the dominant species to the shortgrass steppe, it is important that a sustained 50% reduction in summer precipitation can

significantly reduce cover. Second, our results show that beyond a 50% rainfall reduction, *B. gracilis* was not additionally reduced by drought. This emphasizes the role of the dominant species in determining ecosystem response to disturbance. In a similar rainfall manipulation study in Argentina, Yahdjian & Sala (2006) found that ANPP was linearly related to the precipitation received by the experimental plot, perhaps because the dominant species at this site has a different sensitivity to drought than the dominant species in the shortgrass steppe.

In contrast to the trends for total cover and *B. gracilis* cover, ruderal cover dynamics differed in the 25% and 50% manipulations. Cover of ruderal species increased in the 50% drought more rapidly than in the more severe 25% drought, suggesting that the most severe drought was too dry for many ruderal species to colonize. Further, the species that most commonly made up the ruderal group were different in 25% and 50% treatments. *Artemisia frigida*, a native species, was the dominant ruderal in both drought plots and control (although cover and especially relative cover of this species did increase under drought). In contrast, the second and third most abundant species in the 25% plots were non-native annual forbs, while in the 50% plots, they were native species (Table 1). This suggests that a long-term extreme (25%) drought may correspond with an increase in non-native species in the shortgrass steppe, an ecosystem considered resistant to non-native species invasion (Milchunas *et al.* 1990; Milchunas, Lauenroth & Chapman 1992).

The number of species per 0.25 m² declined in the early stages of drought in our study (Fig. 4). This is similar to the decline in species richness that Weaver (1954) observed in the drought of the 1930s in the central grassland region. However, in the latter half of the study when *B. gracilis* cover was reduced and ruderal cover increased, the number of species increased. Although our study was long enough to observe general trends, we did not observe any significant differences in the number of species per plot in the first 4 years of drought. This is similar to our results for other parameters and provides additional evidence of the resistance of the shortgrass steppe to drought and further emphasizes the need for long-term studies. Other 2- to 4-year studies have found little or no change in species richness under drought manipulations (Knapp *et al.* 2002; Yahdjian & Sala 2006), but it is difficult to tell from these short-term studies how and when species richness might have responded.

Although we cannot extrapolate our specific findings beyond the shortgrass steppe, comparisons of our results with other studies indicate that it is difficult to generalize drought manipulation results across sites. Although reduced vegetation cover and a change in species composition is a common response, the time period over which they occur and whether there are different responses to multiple drought severities vary dramatically among sites. Our study, although long term, is poorly replicated. As rainout shelter designs improve (Yahdjian & Sala 2002), we encourage future studies to invest in greater replication and to consider multiple-site comparisons to refine our knowledge of the mechanisms and generalities of ecosystem drought response.

Our results support the idea that the response of dominant species can be an important, or perhaps the only needed, indicator for response of the entire community. A main finding in our study is that if a drought is long enough, it can significantly perturb the dominant species and that this perturbation correlates with other important changes in community structure. This suggests that the dominant species in the shortgrass steppe both maintains stability and constrains species richness, perhaps more than diversity *per se* (Singh, Bourgeron & Lauenroth 1996; Sasaki & Lauenroth 2011). In our effort to predict how ecosystem structure will respond to extreme climatic events, our results imply that coupling questions about the role of the dominant species with questions about the response of the dominant species to novel disturbances will be a useful approach (Smith & Knapp 2003), and will allow us to develop generalized responses to severe disturbances across ecosystems with a similar community structure.

Acknowledgements

This work was conducted at the Central Plains Experimental Range (CPER), which is administered by the USDA Agricultural Research Service (ARS) and is a Long Term Ecological Research site (SGS-LTER) funded by the National Science Foundation (NSF DEB 0823405 and NSF DEB 0217631). This work would not have been possible without the 1998–2010 SGS field crews and staff, the SGS-LTER Information Manager Nicole Kaplan and the initial design and setup of the rainout shelters by Kenneth Murphy. We acknowledge Dr. Phillip Chapman for statistical advising and three anonymous reviewers for helpful comments on the manuscript.

References

- Austin, A.T. & Sala, O.E. (2002) Carbon and nitrogen dynamics across a natural precipitation gradient in Patagonia, Argentina. *Journal of Vegetation Science*, **13**, 351–360.
- Baker, B.B., Hanson, J.D., Bourdon, R.M. & Eckert, J.B. (1993) The potential effects of climate change on ecosystem processes and cattle production on US rangelands. *Climatic Change*, **25**, 97–117.
- Briggs, J.M. & Knapp, A.K. (1995) Interannual variability in primary production in tallgrass prairie – climate, soil-moisture, topographic position, and fire as determinants of aboveground biomass. *American Journal of Botany*, **82**, 1024–1030.
- CCSP (2008) *The Effects of Climate Change on Agriculture, Land Resources, Water Resources, and Biodiversity. A Report by the US Climate Change Science Program and the Subcommittee on Global Change Research*. US Environmental Protection Agency, Washington, DC, USA.
- Cipriotti, P.A., Flombaum, P., Sala, O.E. & Aguiar, M.R. (2008) Does drought control emergence and survival of grass seedlings in semi-arid rangelands? An example with a Patagonian species *Journal of Arid Environments*, **72**, 162–174.
- Clark, J.S., Grimm, E.C., Donovan, J.J., Fritz, S.C., Engstrom, D.R. & Almenninger, J.E. (2002) Drought cycles and landscape responses to past aridity on prairies of the northern Great Plains, USA. *Ecology*, **83**, 595–601.
- Coffin, D.P. & Lauenroth, W.K. (1988) The effects of disturbance size and frequency on a shortgrass plant community. *Ecology*, **69**, 1609–1617.
- Cook, E.R. & Seager, R. (2010) Megadroughts in North America: placing IPCC projections of hydroclimatic change in a long-term paleoclimate context. *Journal of Quaternary Science*, **25**, 48–61.
- Cook, E.R., Woodhouse, C.A., Eakin, C.M., Meko, D.M. & Stahle, D.W. (2004) Long-term aridity changes in the western United States. *Science*, **306**, 1015–1018.
- Grime, J.P. (2001) *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. Wiley, New York.
- Grime, J.P., Brown, V.K., Thompson, K., Masters, G.J., Hillier, S.H., Clarke, I.P., Askew, A.P., Corker, D. & Kielty, J.P. (2000) The response of two contrasting limestone grasslands to simulated climate change. *Science*, **289**, 762–765.

- Grime, J.P., Fridley, J.D., Askew, A.P., Thompson, K., Hodgson, J.G. & Bennett, C.R. (2008) Long-term resistance to simulated climate change in an infertile grassland. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 10028–10032.
- Groffman, P., Baron, J., Blett, T., Gold, A., Goodman, I., Gunderson, L. et al. (2006) Ecological thresholds: the key to successful environmental management or an important concept with no practical application? *Ecosystems*, **9**, 1–13.
- Heitschmidt, R.K., Haferkamp, M.R., Karl, M.G. & Hild, A.L. (1999) Drought and grazing: I. Effects on quantity of forage produced. *Journal of Range Management*, **52**, 440–446.
- Hook, P.B., Burke, I.C. & Lauenroth, W.K. (1991) Heterogeneity of soil and plant N and C associated with individual plants and openings in North-American shortgrass steppe. *Plant and Soil*, **138**, 247–256.
- Hyder, D.N. (1975) Ecological responses of native plants and guidelines for management of shortgrass range. *United States Department of Agriculture Technical Bulletin*, **1503**, 1–87.
- IPCC (2007) *Climate Change 2007: Synthesis Report*. Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge and New York.
- Jentsch, A., Kreyling, J. & Beierkuhnlein, C. (2007) A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment*, **5**, 365–374.
- Jobbagy, E.G. & Sala, O.E. (2000) Controls of grass and shrub aboveground production in the Patagonian steppe. *Ecological Applications*, **10**, 541–549.
- Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D., Harper, C.W., Danner, B.T., Lett, M.S. & McCarron, J.K. (2002) Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science*, **298**, 2202–2205.
- Lauenroth, W.K. (2008) Vegetation of the shortgrass steppe. *Ecology of the Shortgrass Steppe* (eds W.K. Lauenroth & I.C. Burke), pp. 70–83. Oxford University Press, New York.
- Lauenroth, W.K. & Burke, I.C. (2008) *Ecology of the Shortgrass Steppe: A Long-Term Perspective*. Oxford University Press, Oxford.
- Lauenroth, W.K. & Sala, O.E. (1992) Long-term forage production of North-American shortgrass steppe. *Ecological Applications*, **2**, 397–403.
- Lauenroth, W.K., Sala, O.E., Coffin, D.P. & Kirchner, T.B. (1994) Recruitment of *Bouteloua gracilis* in the shortgrass steppe: a simulation analysis of the role of soil water. *Ecological Applications*, **4**, 741–749.
- Lauenroth, W.K., Burke, I.C. & Gutmann, M.P. (1999) The Structure and function of ecosystems in the central North American grassland region. *Great Plains Research*, **9**, 223–259.
- MacDonald, G.M. (2010) Water, climate change, and sustainability in the southwest. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 21256–21262.
- McCulley, R.L., Burke, I.C., Nelson, J.A., Lauenroth, W.K., Knapp, A.K. & Kelly, E.F. (2005) Regional patterns in carbon cycling across the great plains of North America. *Ecosystems*, **8**, 106–121.
- Milchunas, D.G., Lauenroth, W.K. & Chapman, P.L. (1992) Plant competition, abiotic, and long-term and short-term effects of large herbivores on demography of opportunistic species in a semiarid grassland. *Oecologia*, **92**, 520–531.
- Milchunas, D.G., Sala, O.E. & Lauenroth, W.K. (1988) A Generalized-Model of the Effects of Grazing by Large Herbivores on Grassland Community Structure. *American Naturalist*, **132**, 87–106.
- Milchunas, D.G., Lauenroth, W.K., Chapman, P.L. & Kazempour, M.K. (1989) Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Plant Ecology*, **80**, 11–23.
- Milchunas, D.G., Lauenroth, W.K., Chapman, P.L. & Kazempour, M.K. (1990) Community attributes along a perturbation gradient in a shortgrass steppe. *Journal of Vegetation Science*, **1**, 375–384.
- Mirzaei, H., Kreyling, J., Hussain, M.Z., Li, Y.L., Tenhunen, J., Beierkuhnlein, C. & Jentsch, A. (2008) A single drought event of 100-year recurrence enhances subsequent carbon uptake and changes carbon allocation in experimental grassland communities. *Journal of Plant Nutrition and Soil Science*, **171**, 681–689.
- Morecroft, M.D., Masters, G.J., Brown, V.K., Clarke, I.P., Taylor, M.E. & Whitehouse, A.T. (2004) Changing precipitation patterns alter plant community dynamics and succession in an ex-arable grassland. *Functional Ecology*, **18**, 648–655.
- Motha, R.P. & Baier, W. (2005) Impacts of present and future climate change and climate variability on agriculture in the temperate regions: North America. *Climatic Change*, **70**, 137–164.
- Mueller, I.M. & Weaver, J.E. (1942) Relative drought resistance of seedlings of dominant prairie grasses. *Ecology*, **23**, 387–398.
- Noy-Meir, I. (1973) Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*, **4**, 25–51.
- Peters, D.P.C., Lauenroth, W.K. & Burke, I.C. (2008) The role of disturbance in shortgrass steppe community and ecosystem dynamics. *Ecology of the Shortgrass Steppe* (eds W.K. Lauenroth & I.C. Burke), pp. 84–118. Oxford University Press, New York.
- R Development Core Team (2007) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Sala, O.E., Parton, W.J., Joyce, L.A. & Lauenroth, W.K. (1988) Primary production of the central grassland region of the United-States. *Ecology*, **69**, 40–45.
- Sasaki, T. & Lauenroth, W.K. (2011) Dominant species, rather than diversity, regulates temporal stability of plant communities. *Oecologia*, **166**, 761–768.
- Seager, R., Kushnir, Y., Herweijer, C., Naik, N. & Velez, J. (2005) Modeling of tropical forcing of persistent droughts and pluvials over western North America. *Journal of Climate*, **18**, 4068–4091.
- Silvertown, J., Dodd, M.E., McConway, K., Potts, J. & Crawley, M. (1994) Rainfall, biomass variation, and community composition in the park grass experiment. *Ecology*, **75**, 2430–2437.
- Singh, J.S., Bourgeron, P. & Lauenroth, W.K. (1996) Plant species richness and species-area relations in a shortgrass steppe in Colorado. *Journal of Vegetation Science*, **7**, 645–650.
- Smith, M.D. & Knapp, A.K. (2003) Dominant species maintain ecosystem function with non-random species loss. *Ecology Letters*, **6**, 509–517.
- Smith, M.D., Knapp, A.K. & Collins, S.L. (2009) A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology*, **90**, 3279–3289.
- Stahle, D. & Fye, F. (2007) Tree-ring reconstructed megadroughts over North America since A.D. 1300. *Climate Change*, **83**, 133–149.
- USDA, NRCS (2010) *The PLANTS Database* (<http://plants.usda.gov>). National Plant Data Center, Baton Rouge, LA.
- Vinton, M.A. & Burke, I.C. (1995) Interactions between individual plant species and soil nutrient status in shortgrass steppe. *Ecology*, **76**, 1116–1133.
- Weaver, J.E. (1954) *North American Prairie*. Johnsen Publishing Company, Lincoln, Nebraska.
- Weaver, J.E. & Mueller, I.M. (1942) Role of seedlings in recovery of Midwestern ranges from drought. *Ecology*, **23**, 275–294.
- Weltzin, J.F., Loik, M.E., Schwinning, S., Williams, D.G., Fay, P.A., Haddad, B.M. et al. (2003) Assessing the response of terrestrial ecosystems to potential changes in precipitation. *BioScience*, **53**, 941–952.
- White, R.P., Murray, S., Rohweder, M., Prince, S.D. & Thompson, K.M.J. (2000) *Grassland Ecosystems*. World Resources Institute, Washington, DC.
- Woodhouse, C.A., Meko, D.M., MacDonald, G.M., Stahle, D.W. & Cooke, E.R. (2010) A 1,200-year perspective of 21st century drought in southwestern North America. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 21283–21288.
- Yahdjian, L. & Sala, O.E. (2002) A rainout shelter design for intercepting different amounts of rainfall. *Oecologia*, **133**, 95–101.
- Yahdjian, L. & Sala, O.E. (2006) Vegetation structure constrains primary production response to water availability in the Patagonian steppe. *Ecology*, **87**, 952–962.
- Zavaleta, E.S., Shaw, M.R., Chiariello, N.R., Thomas, B.D., Cleland, E.E., Field, C.B. & Mooney, H.A. (2003) Grassland responses to three years of elevated temperature, CO₂, precipitation, and N deposition. *Ecological Monographs*, **73**, 585–604.

Received 1 December 2010; accepted 8 June 2011

Handling Editor: Fernando Maestre

Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1. List of plant species considered ruderal in our analysis, species growth form and native status.

Table S2. List of other plant species (not considered ruderal) included in our analysis and species growth form. All species are native to the shortgrass steppe.

Table S3. Correlations between annual precipitation and cover response variables in the Control treatment.

Table S4. Total cover difference estimates, significance, and confidence intervals ($\alpha = 0.05$) from repeated-measures analysis among treatments within years.

Table S5. *Bouteloua gracilis* difference estimates, significance, and confidence intervals ($\alpha = 0.05$) from repeated-measures analysis among treatments within years.

Table S6. Ruderal cover difference estimates, significance, and confidence intervals ($\alpha = 0.05$) from repeated-measures analysis among treatments within years.

Figure S1. Typical shortgrass vegetation at the Central Plains Experimental Range, CO, USA, including the dominant grass *Bouteloua gracilis*, *Opuntia polyacantha* cactus, and dwarf-shrub *Artemisia frigida*. Photo credit: Sallie Sprague.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.