esa ECOSPHERE

Response of a mixed grass prairie to an extreme precipitation event

Amy L. Concilio,[1,†] Janet S. Prevéy,[2] Peter Omasta,[1] James O'Connor,[1] Jesse B. Nippert,[3] and Timothy R. Seastedt[1]

[1]*Institute of Arctic and Alpine Research and Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309 USA*
[2]*Swiss Federal Institute for Forest, Snow and Landscape Research, Flüelastrasse 11, 7260 Davos Dorf, Switzerland*
[3]*Division of Biology, Kansas State University, Manhattan, Kansas 66506 USA*

Citation: Concilio, A. L., J. S. Prevéy, P. Omasta, J. O'Connor, J. B. Nippert, and T. R. Seastedt. 2015. Response of a mixed grass prairie to an extreme precipitation event. Ecosphere 6(10):172. http://dx.doi.org/10.1890/ES15-00073.1

Abstract. Although much research has been conducted to measure vegetation response to directional shifts in climate change drivers, we know less about how plant communities will respond to extreme events. Here, we evaluate the response of a grassland community to an unprecedented 43 cm rainfall event that occurred in the Front Range of Colorado in September, 2013 using vegetation plots that had been monitored for response to simulated precipitation changes since 2011. This rain caused soils to stay at or above field capacity for multiple days, and much of the seed bank germinated following the early autumn event. Annual introduced grasses, especially cheatgrass (*Bromus tectorum*), and several introduced forbs demonstrated strong positive increases in cover the following growing season. Native cool season grasses and native forbs showed limited changes in absolute cover despite continued high soil water availability, while native warm season grasses increased in cover the following summer. Treatments that previously altered the amounts and seasonality of rainfall during the 2011–2013 interval showed legacy effects impacting cover responses of introduced species and warm-season native grasses. Resin bag estimates of inorganic nitrogen flux resulting from the event indicated twice as much nitrogen movement compared to any previous collections during the 2011–2013 interval. Nitrogen additions to a subset of plots made in spring of 2014 demonstrated that the relative cover of introduced species could be further increased with additional soil nitrogen. Collectively, these results support the contention that extreme precipitation events can favor species already benefiting from other environmental change drivers.

Key words: *Alyssum parviflorum*; *Bromus tectorum*; Colorado Front Range; *Erodium cicutarium*; introduced species; legacy effects; nitrogen; plant community change; precipitation seasonality; Rocky Mountains.

Received 5 February 2015; revised 16 March 2015; accepted 23 March 2015; **published** 6 October 2015. Corresponding Editor: D. P. C. Peters.

Copyright: © 2015 Concilio et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. http://creativecommons.org/licenses/by/3.0/

† **E-mail:** amyconcilio@colorado.edu

Introduction

Understanding the dynamics of plant communities in an era of rapid environmental change requires substantial knowledge of both environmental drivers and community interactions. Current management of plant communities requires a probabilistic rather than deterministic perspective, with future communities influenced by extrinsic and intrinsic factors in ways that can result in multiple outcomes (Denslow 2014). The presence of recently introduced plant species and changes in abiotic drivers such as climate, nitrogen deposition, and carbon dioxide fertil-

ization acting concurrently on communities makes both understanding and predicting changes difficult. For example, increased carbon dioxide fertilization, nitrogen deposition, and changes in the seasonality of precipitation are influencing plant competitive interactions of native and introduced species (e.g., Bowman et al. 2012, Prevéy and Seastedt 2014, Zelikova et al. 2014). These interactions become more confounded when consumer interactions are included (Beals et al. 2014). Natural and human-mediated disturbances are also influencing the composition of these communities. Native species are often assumed to be adapted to the historical range of disturbances such as fires and floods and therefore should persist or even benefit from these events (Hobbs and Huenneke 1992). However, when the intensity or frequency of the disturbance is outside the historical range experienced by the species or when the environmental conditions at the time of the disturbance are outside of historical ranges, then conditions created by the disturbance may benefit previously uncommon species or those that have only recently been introduced. The outcome can also be negative for all species present, with some species less impacted than others.

Extreme rainfall events are predicted to become more common under future climates, and in semi-arid or arid landscapes the consequences of this activity should often result in increased productivity (Knapp et al. 2008). Predicting the response of a plant community to a single event is more problematic and likely depends upon the nutrient status of the system at the time of the event, the phenological status of the species, and the composition and size of a seed bank present that might be able to exploit the event (Knapp et al. 2008, Wilcox et al. 2014). Diez et al. (2012) note that individual species may experience the disturbance as a resource pulse, either adding to a limiting resource or removing a resource limitation entirely. Conversely, those authors also note that the event can function as a stressor, by removing essential resources or simply inducing conditions leading to the mortality of the species. How an individual species may perceive an event is also influenced by how competitors or other biotic components of the community might attenuate or amplify the magnitude of the pulse or reduction in limiting resources.

Recent changes in the plant composition of the mixed grass prairies of North America have occurred due to the deliberate and accidental introduction of numerous non-native species. These ongoing changes are outcomes of complex interactions reflecting the differing competitive traits and niche dimensions of the introduced species (e.g., MacDougall et al. 2009), as modified by the specific abiotic and biotic factors already present in the system (Seastedt and Pyšek 2011). An important factor to recognize is that the abiotic environment of these systems is changing, and the integrated response functions of the biotic systems to these drivers are causing additional, ongoing change (Prevéy and Seastedt 2014). Understanding how disturbances and extreme events can influence the structure and function of these ecosystems therefore adds another level of complexity to these already dynamic plant communities. Indeed, extreme events may play important roles in shaping the trajectories of plant communities, though our research efforts to date have been much more focused on effects of changing means in climate than extremes (Jentsch et al. 2007, Thompson et al. 2013).

Many of the plant species that have successfully colonized North American mixed grass prairies in recent years are generalists with broad climatic tolerances (Dukes and Mooney 1999). Many are agricultural weeds that possess opportunistic growth strategies, combined with strong sensitivity to nutrient additions (e.g., Pyšek and Richardson 2007, Seastedt and Suding 2007, Blumenthal 2009). Accordingly, we might anticipate that these species would benefit from extreme events because of their abilities to exploit resource opportunities. In contrast, many of these species may have yet to experience an extreme event that might strongly and negatively affect their presence. The native plant species of North American grasslands have survived past extreme climatic conditions generated by a continental climate, and arguably should be adapted to at least persist if not exploit extreme conditions. Overall, however, disturbances tend to favor opportunistic species, and if introduced species dominate this group of plants, then we should expect them to benefit from such events.

Previously, Prevéy and Seastedt (2014) described the plant response of a grassland

composed of a mix of native and recently introduced species to manipulations in the seasonality and amounts of precipitation. This research site was impacted by an extreme precipitation event in September of 2013, providing a unique opportunity to measure impacts of an extreme event on this grassland community in the context of on-going directional change. In the spring and summer of 2014, we continued monitoring plants and soils in a number of the plots from the previous study to determine (1) which species and functional groups benefited most from the event, (2) how soil inorganic nitrogen was affected (using ion-exchange resin bags), and (3) whether plant community response to the event was affected by previous precipitation treatments (i.e., whether there were legacy effects that influenced response). Additionally, we set up a nitrogen (N) addition experiment to determine whether or not N limitation influenced observed vegetation responses. Our hypothesis was that early growing species (especially winter annuals) would benefit from the autumn precipitation, but that N limitation caused by excess leaching would mitigate the plant response. Based upon the Prevéy and Seastedt (2014) findings, we also expected the early-growing species to attenuate any response observed in the warm-season grasses.

Methods

Research was conducted on a Ponderosa savanna/grassland matrix at an elevation of 1798 m 15 km northwest of Boulder, Colorado, USA (40°07′ N, 105°18′ W). This meadow was part of a homestead established around 1880, and the area was grazed by cattle, some years extensively, until the autumn of 2006, when these animals were removed. The site continued to be grazed by a deer population and, occasionally, elk. The site receives an average precipitation of 475 mm per year, and has an average temperature of 10.5°C (WRCC 2014). The soils at the field site are colluvial, sandy loams (USDA 2001). Vegetation at this site is a mixture of warm- and cool-season, native grasses, with some native and nonnative forbs. The prairie was also impacted by a large population of the introduced annual grass, cheatgrass (*Bromus tectorum*), that we assume became abundant due to the heavy grazing history at the site.

To obtain background information on soils and determine if soil nitrogen at our site was affected by introduced plant species, we sampled 10 sites in early spring of 2012 under relatively dense stands of the native grass, *Pascopyrum smithii,* or under 10 sites dominated by the introduced annual grass, *B. tectorum*. Each 10 cm deep soil sample was sieved to remove visible roots and coarse materials >2 mm^2. For each soil sample we measured total soil carbon (C), total soil nitrogen (N), C/N ratios, and inorganic N. To measure C/N ratios, subsamples were dried, ground, and analyzed for %C and %N with a Carlo Erba CHN analyzer. We measured inorganic nitrogen in September 2011, and April, June, and August 2012. To measure available inorganic nitrogen, wet soil subsamples were extracted with 2 M KCL. The amount of nitrite and nitrate (NO_2^- and NO_3^-, hereafter NO_3^-), and NH_4^+ in KCL extractions was measured on a Lachat QuickChem 8500 Flow injection analyzer.

Details on the original experimental design for precipitation changes to vegetation are provided in Prevéy (2014), with additional details and vegetation composition reported by Prevéy and Seastedt (2014). Water supplements and water removals were main experiments during this period. We chose to monitor 30 of these plots and compare plant composition results obtained during the 2011–2013 interval reported by Prevéy and Seastedt (2014) with similar data obtained in 2014 using point intercept methods described in the previous paper. These three treatments included 10 2×2 m^2 plots each of (1) control, (2) winter precipitation increased 50%, and (3) winter precipitation reduced 50%. At the time of the extreme event, 10 of the plots were covered with rain-out shelters that allowed only 50% of rainfall to enter the 4 m^2 areas. However, these plots did not use any gutters or trenching to prevent overland flow. The overland, surface, and subsurface flows associated with the estimated 430 mm of rainfall input erased any differences in soil moisture, as indicated by volumetric soil water sampling.

To estimate effects of precipitation manipulations on plant-available soil nitrogen, as well as the seasonal dynamics of soil inorganic nitrogen, we used ion-exchange resin bags. About 5 g of

resin (Amerlite MB-150 mixed bed resin) was placed into nylon bags similar to the procedure of Binkley and Matson (1983) and Lajtha (1988). Plastic hoops were used to provide all bags with a similar geometry. Bags were washed in a 0.5 M HCl solution, and then rinsed with deionized water. Two bags were buried just below a 5 cm depth in the center of each plot and remained in plots October 1–March 30, April 1–May 30, and June 1–September 30. After removal, resin bags were extracted in 40 mL of 2 M KCl. Inorganic nitrogen was analyzed colorimetrically on a on a Lachat QuickChem 8500 Flow injection analyzer.

To monitor soil moisture and temperature, we collected continuous data from 24 sensors (5TM, Decagon Devices, Pullman, Washington, USA) with 8 dataloggers (EM50G, Decagon Devices, Pullman, Washington, USA) placed throughout the study site beginning in summer 2012. Moisture (time domain reflectometry) and temperature probes were installed at 10 cm depths in the center of plots adjacent to the plots used in this study. Half of the probes were placed in the center of plots covered by rain-out shelters identical to those employed here during the non-growing season (October–March) and half were placed in plots receiving ambient levels of precipitation. Dataloggers were programmed to take measurements from sensors every 15 minutes. Data were routinely collected from January 2012 to October 2014. A weather station was installed at the site in 2012 to monitor precipitation (ECRN-100), wind speed and direction (Davis anemometer) photosynthetically active radiation (QSO-S PAR Photon Flux) and air temperature and humidity (EHT). All sensors were produced by Decagon Devices.

To measure effects of increased nitrogen availability on plant species at the research site, inorganic nitrogen fertilizer (10 g/m^2 N as calcium nitrate ($Ca(NO_3)_2$) was added in March of 2014 to half of each of 24 4 × 4 m plots used in a mowing study by Prevéy et al. (2014). These plots had not been managed in any form since 2012. The paired plot approach allowed us to control for previous treatment effects, if present. We measured plant community composition and aboveground primary productivity in the center of each +N (nitrogen added) and ambient N (N not added) subplot within the original 24 plots. Plant community composition was measured using the point-intercept method with a 60 × 60 cm^2 quadrat placed in the center of each of the 48 subplots in spring (June 11–12) and summer (September 1–2) of 2014. Absolute cover of each species was calculated by dividing the number of times that the species intercepted the quadrat by the total number of points in the quadrat. Relative cover was then calculated as the absolute cover of each species divided by the total cover of all species in each plot. All aboveground biomass within a 20 × 50 cm^2 quadrat was clipped in both spring (May 28–29) and summer (July 21–22) of 2014. We separated biomass into the following groups: *B. tectorum*, other introduced grasses, introduced forbs, native grasses, and native forbs. Samples were dried for 48 h at 60°C and weighed.

Statistical procedures

To compare soils from areas dominated by either cheatgrass or native grasses, we analyzed soil texture, % organic matter, total soil carbon (C), total soil N, C/N ratios with blocked ANOVAs. We analyzed ammonium (NH_4^+), nitrate (NO_3^-), and total nitrogen measured over the four dates with linear mixed-effects models. To analyze effects of the extreme event on vegetation, we used linear mixed-effects models to compare absolute cover of five functional groups (introduced grasses, introduced forbs, native cool-season grasses, native warm-season grasses, and native forbs) in monitoring plots in the three treatments (control, winter-wet, and winter-dry) between years from 2011 to 2014 (after the extreme event). We compared results from June and August surveys using separate models. Treatment and year were considered fixed factors, and plot was considered a random variable in these models. Cover values for introduced forbs, native forbs, and warm-season grasses were square-root transformed to better meet assumptions of normality.

Collection date and amount of cheatgrass cover were evaluated as factors affecting the amounts of inorganic N captured per gram of resin in soils. Prevéy and Seastedt (2014) had previously used most of the pre-event data and found that treatments did not significantly affect values. Here, we tested the effects of date of collection using a one-way ANOVA. We then averaged the inorganic N collected per gram of

Table 1. Comparison of carbon and nitrogen in soils under cheatgrass with those under native grasses (boldface values are significantly different at the $P < 0.05$ level).

Measurement	Beneath cheatgrass	Beneath native grass	P
Carbon, %	**3.74 ± 0.34**	**2.65 ± 0.15**	**0.0006**
Nitrogen, %	**0.32 ± 0.03**	**0.22 ± 0.01**	**0.0002**
C:N ratio	11.62 ± 0.21	11.85 ± 0.14	0.32
NH_4/g soil	7.09 ± 1.36	5.66 ± 0.96	0.14
NO_3/g soil	**9.52 ± 1.66**	**4.90 ± 1.38**	**0.001**
Total inorganic N	**16.61 ± 3.02**	**10.56 ± 2.33**	**0.0001**

Note: Values are means averaged over the growing season ± standard errors, and P values are from blocked ANOVA comparisons between the two soils.

resin per plot over the study interval and conducted an ANCOVA using treatment as the fixed effect and cheatgrass cover per plot measured in 2013 as the covariate.

Biomass and cover from the N-addition experiment were grouped by origin and life form (native forbs, introduced forbs, native grasses, introduced grasses) and compared by treatment (ambient N versus +N on split plots) using paired t tests. Since cheatgrass made up the overwhelming majority of introduced grass biomass and cover and was a focal species in this study, we also tested treatment effects on it alone. We tested the spring and summer sampling periods separately to isolate effects on cool season and warm season species. Variables were transformed to meet assumptions of normality with square-root and log transformations. We tested for homogeneity of variances using F tests, and for those variables with unequal variances we used a Welch correction. All statistical analyses were conducted in R (R Development Core Team 2012), and R scripts for analyses are included in the Supplement.

Results

Soils beneath areas dominated by cheatgrass and native grasses

Soils collected from under *P. smithii* and *B. tectorum* did not differ significantly in texture, % organic matter, C:N ratios, or different amounts of NH_4^+. However, both NO_3^- and total inorganic N were greater in soils beneath *B. tectorum* (Table 1). Soils taken beneath *B. tectorum* also had higher %C and %N, organic C and N, and higher soil microbial biomass C and N than soils beneath the native grass, *P. smithii*.

Resin bag collections of inorganic N prior to the extreme event were previously reported in Prevéy and Seastedt (2014). Here, those results have been averaged by collection date, and the last collection date included the extreme rainfall event (Fig. 1). The amount of inorganic N captured during the period that included the extreme event was double that of any other collection period ($P < 0.0001$ for either total inorganic N captured or N captured per day). An analysis of covariance of plot means found that daily inorganic N capture by resin was not affected by treatment ($P = 0.15$), but that a spring 2013 estimate of cheatgrass cover in the plots was positively related to average N capture ($P = 0.01$; results not shown). However, values relating cheatgrass cover to amounts of inorganic N captured during just the extreme event interval were not significant.

Description of the extreme event and soil response

Total rainfall in September 2013 amounted to 460 mm for the Boulder, Colorado area (NOAA 2014), most of which fell during a six day interval from the 10th through the 15th of September. At the prairie site, soil water measurements show that soil moisture began to increase on the 10th of September and continued to be elevated until the 16th (Fig. 2). These results suggest that soils were at or above field capacity for about five days. During that time both soil and air temperatures remained high. Soils averaged 19.7° ± 3.5°C during the rainfall interval. All of our rain gauges except those beneath the rainout shelters either malfunctioned or overflowed. The two gauges in the rainout shelters indicated 215 mm of precipitation. If the shelters were performing as documented by Prevéy (2014), then this amount represented half of the event, and 430 mm of rain occurred over this interval. This estimate is consistent with measurements from nearby rain

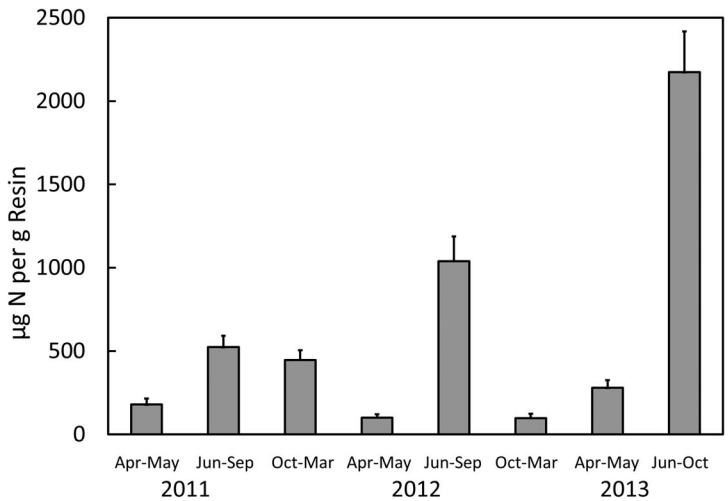

Fig. 1. Inorganic N (±SEM) collected by resin bags ($n = \sim 50$ per interval). The last collection in 2013 included the extreme precipitation event.

gauges (NOAA 2014). Probes continued to monitor soil moisture during the 2014 growing season and show that soils were usually well above permanent wilting values (~0.05 cc/cc) throughout that period (Appendix: Fig. A1).

Vegetation response

The five groups of plants reported here (introduced grass, introduced forb, native cool season grass, native warm season grass, and native forb) showed variable responses to the extreme event (Fig. 3). Based upon absolute cover measurements in June 2014, native cool season grasses and native forbs were unresponsive to the rainfall event (both $P > 0.41$), while native warm season grasses increased in cover in 2014 ($t = 3.53$, $P = 0.0006$). Introduced grasses (dominated by *B. tectorum*) and forbs had the highest

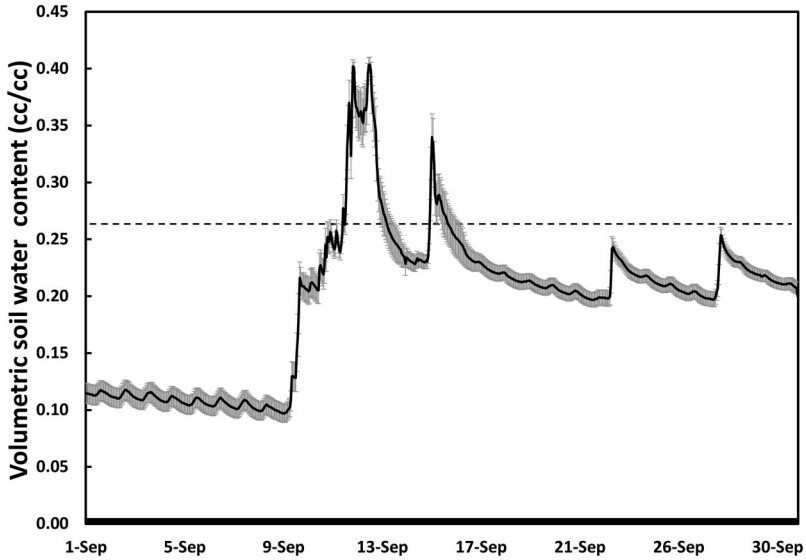

Fig. 2. Mean (±SEM) hourly soil moisture measured on 14 sensors under ambient precipitation conditions at the study site. Dashed line represents estimated field capacity for these soils.

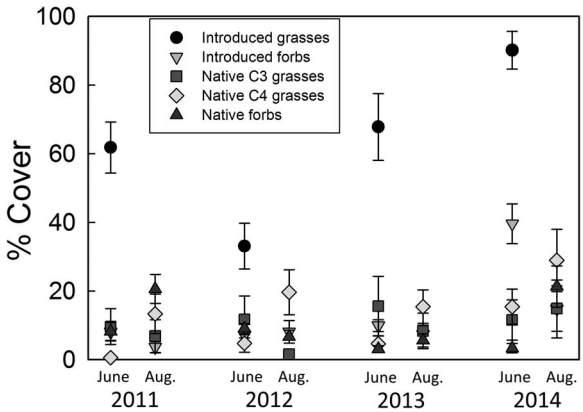

Fig. 3. Absolute cover (±SEM) of plant groups measured in June and August 2011–2014. Values are from a single treatment that received ambient precipitation. Introduced grasses (largely *B. tectorum*) only measured in June of each year.

percent cover in all plots (Fig. 3) and increased in absolute cover when compared to all three previous years of measurements (both $t > 6.14$, $P < 0.0001$). In August 2014, cover of introduced forbs, native warm-season grasses, and cool-season grasses was greater than in August 2011–2013 (all $t > 3.77$, $P < 0.0003$). However, cover of native forbs was not significantly higher in August 2014 ($t = 1.38$, $P = 0.18$)

The effects of the legacies of our precipitation experiment on the response of the plant groups were variable (Fig. 4). The introduced grass response was significantly less in plots that had previously experienced a winter dry treatment ($t = -2.56$, $P = 0.02$; Fig. 4a). Introduced forb response in June 2014 was reduced in the winter wet treatment ($t = -2.42$, $P = 0.02$; Fig. 4c), and the native warm season grasses continued their previous trend of being reduced in winter wet plots relative to the other treatments ($t = -2.23$, $P = 0.03$; Fig. 4b). Native cool season grasses and native forbs showed no precipitation treatment effects, a response continued from what was observed during the 2011–2013 interval (all $P > 0.07$; Fig. 4d, e).

Plots treated with fertilizer in spring of 2014 suggest that the responses seen in Figs. 3 and 4 were amplified by the addition of nitrogen (Fig. 5). All of the plots in the fertilizer experiment had received unmanipulated precipitation inputs during the entire study interval. In the spring of 2014, *B. tectorum* aboveground biomass increased with N fertilization ($t = -3.27$, $P = 0.0034$), while no other group showed significant positive responses. Correspondingly, introduced grasses (mainly *B. tectorum*) increased in relative abundance ($t = -2.37$, $P = 0.026$), while native grasses decreased ($t = 2.54$, $P = 0.019$; Fig. 5a). In late summer after *B. tectorum* senescence, native grasses dominated the aboveground biomass and cover of all plots, but their relative cover ($t = 1.83$, $P = 0.081$; Fig. 5b) and biomass ($t = -2.10$, $P = 0.048$) remained lower in fertilized plots compared to ambient N plots. This was due to an increase in dominance of introduced forbs ($t = 2.4$, $P = 0.025$) with N addition (both relative biomass and cover increased, but only biomass was significantly different by treatment). Native forbs did not show any response to treatments in the spring or summer.

Discussion

Extreme events concurrently alter resource availability and the potential of the specific biotic community to respond to those alterations (Diez et al. 2012). For example, at our site, vegetation in lowland meadows and riparian communities adjacent to our monitoring plots was scoured by surface runoff, removing both vegetation and topsoil, thereby initiating secondary succession. At our upland site discussed here, the biotic system survived largely unscathed, although we do not know the extent to which propagules were added or subtracted by surface water movements. Our results indicate that diverse groups of plants can exploit this event, but that responses of each group are related to how the extreme event was filtered by the extant abiotic and biotic status of the community.

Our research area, like many others in western North America, has experienced warming over recent decades (Ray et al. 2008). This warming, alone, is likely affecting community dynamics at our site (White et al. 2014*a*). In addition, changes caused by carbon dioxide fertilization and nitrogen deposition are likely as well (e.g., Bowman et al. 2012, Zelikova et al. 2014). Finally, we are also confident that potential changes in the seasonality of rainfall, in conjunction with the presence of introduced species pre-adapted to these climate changes, are also affecting commu-

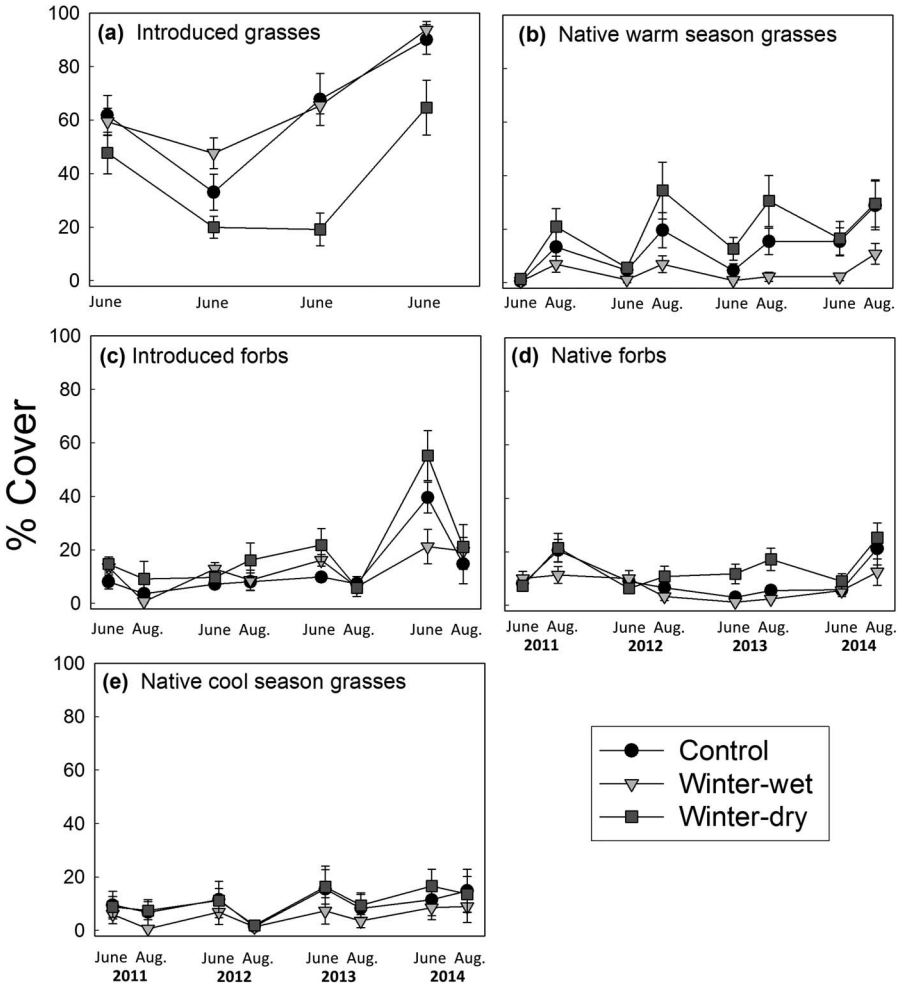

Fig. 4. Legacy effects of previous precipitation treatments on absolute cover (±SEM) of various plant groups. Introduced grasses show that plots previously affected by reduced winter precipitation do not have equal cover with plots that received either ambient or additional winter water. In contrast, introduced forbs (in June only) or native warm season grasses (June and August) showed reduced response from plots treated with winter precipitation, i.e., the treatment that enhanced winter annual grasses during the 2011–2013 interval.

nity composition (Prevéy and Seastedt 2014). Thus, the extreme event was delivered to a community already undergoing directional change.

Zhang et al. (2013) presented results suggesting that grasslands will not respond as might be predicted by current models of production-precipitation relationships because of a reduction in water use efficiency. However, grasslands also appear to differ in their sensitivity to enhanced precipitation as a function of their soil water status and the extent to which water limits seasonal productivity (Huxman et al. 2004, Zeppel et al. 2014). That said, the northern mixed grass prairies in particular appear relatively insensitive to precipitation manipulations (White et al. 2014*b*, Wilcox et al. 2014), a finding also previously observed for the native vegetation at our site (Prevéy and Seastedt 2014).

The availability of soil N is known to affect the production response of grasslands to disturbances such as fire (Seastedt et al. 1991), and we hypothesized that it would affect plant community response to this extreme event. We know from monitoring inorganic N flux with ion-exchange resins that N leaching at our site was

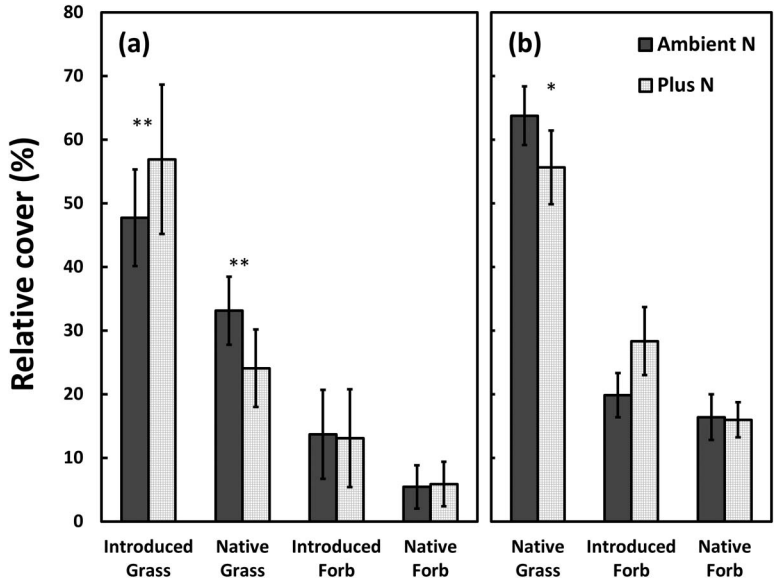

Fig. 5. Relative abundance of plant groups (±SEM) in plots experiencing ambient levels of N compared to supplemental N in the spring (a) and summer (b) season. Introduced grasses had senesced by the summer sampling period and are therefore not included. Significant differences by N treatment within each plant group are denoted by asterisks ($n = 24$ plots, paired t tests; * $P \leq 0.1$, ** $P \leq 0.05$, *** $P \leq 0.01$).

enhanced by the extreme event, and these losses or movements to deeper soil horizons may have influenced plant responses. For example, this N captured at 5 cm depth should not have been available for seedlings that germinated following the rainfall event. At the same time, however, N mineralized from the litter and dead roots during the warm, wet period during and following the extreme event may have compensated for leaching losses of N in the uppermost soil horizon. Further, we know that species composition can affect N availability, and our site is rather patchy with areas of near-monoculture of cheatgrass and native-dominated patches.

Stark and Norton (2015) demonstrated that cheatgrass could increase soil carbon storage in surface soils and increase inorganic N cycling relative to similar plots containing native species. Those results are in agreement with our measurements of N in soil beneath cheatgrass compared with those beneath the native *Pascopryum smithii*, suggesting that cheatgrass may have initiated a similar plant-soil N feedback at out site. We also know from previous studies that nutrient limitation can inhibit the ability of introduced annual species to exploit opportunities created by disturbances (Paschke et al. 2000, James et al. 2008, Cherwin et al. 2009). Finally, we found that cheatgrass was one of the only species that responded to fertilizer additions with increased productivity (hence the only species to exhibit N-limitation in our experiment). However, cheatgrass was also the "biggest winner" after the extreme event. Our findings would therefore support the contention that, despite the N leaching that we observed, severe N limitation was not an outcome of this extreme event, and that N availability influenced the introduced species responses to some unknown degree. The fertilizer additions confirm that additional N would have further enhanced the response of introduced species.

The species that benefited most from this extreme precipitation event was the introduced winter-active grass, cheatgrass. This was in agreement with past research at the site, which found that cheatgrass responds strongly to increased winter precipitation (Prevéy and Seastedt 2014), even though the magnitude of the precipitation increase was greatly amplified over past experimental manipulations. Introduced forbs, dominated by the winter annual species *Erodium cicutarium* and *Alyssum parviflorum,* also clearly benefited from the rainfall event but their

response was more limited in winter wet plots favored by cheatgrass. Likewise, in N addition plots where cheatgrass dominated, introduced forbs were not able to take advantage of this excess resource until the late summer sampling period when cheatgrass had senesced. Previously, we had not seen these forbs exploit winter wet conditions (Prevéy and Seastedt 2014). We also had found that suppression of cheatgrass by mowing could increase the abundance of these introduced forbs (Prevéy et al. 2014). Thus, we see a positive response of one group of introduced species being constrained by the response of another opportunist. Prevéy and Seastedt (2014) had shown that the warm season grasses benefited from a winter-dry, summer-wet scenario, but not from a winter-wet, summer wet scenario. The interpretation was that early growth by the introduced cool-season species suppressed the warm season grasses. Here, we see that the warm season grasses could benefit from a precipitation event that occurred almost 11 months earlier, but the response appeared muted in plots where other species (and the introduced winter annuals in particular) were stimulated by the rainfall event as well. Thus, while winter annuals may be thought of as occupying a different temporal niche than the warm season grasses, they appear to impact the productivity of the latter group by making solar radiation, nitrogen, or both of these resources less available. This was also apparent in the N-addition experiment where warm season grasses still showed decreased dominance in +N plots long after cheatgrass had senesced.

The answer to the question regarding which species benefit from extreme events produces mixed outcomes, and as Diez et al. (2012) noted, context matters. No plant groups appeared harmed by this event, but some clearly benefited more than others. Here we emphasize that the response we observed is consistent with expectations based upon the life history traits of the species, as impacted by the abundances of plant groups prior to the event. Clearly, species capable of opportunistic growth are first in line to benefit. However, we know that the timing of the event also often matters in terms of which species benefit (Prevéy and Seastedt 2014).

Enhanced N deposition, along with the (probable) increased N feedback generated by the plant-soil system found in areas of cheatgrass abundance, facilitated this plant's ability to exploit extreme precipitation events. However, other introduced winter annuals, not known to exhibit the competitive interactions observed for cheatgrass, can also exploit the increase in water availability as can a subset of native species represented here by the warm season grasses. Both of these latter groups showed legacy constraints imposed by the dominant opportunist. In contrast, while the native cool season grasses and all native forbs maintained their absolute cover in 2014, they did not perform significantly better than growth measured in previous years. To date, those species showing the greatest positive responses to extreme events are the same as those with life history strategies that benefit from other global change drivers. The response to the combination of global change drivers, including extreme precipitation events, argues that that introduced winter annuals have high probabilities of becoming more dominant on these prairies in the coming decades.

Acknowledgments

This research was funded by grants from the USDA, EPA, and NSF (DEB 1120390) to the University of Colorado. We thank Robin Reibold, Shivani Ehreunfelt, Jeremy Arkin, Summer Sugg, Michael Mann, Oren Rabinowitz, Nohal Amir, David Knochel, Samantha Weintraub, and Joseph Knelman for help with field sampling and lab analysis. The first three authors contributed equally to the study.

Literature Cited

Beals, S., L. M. Hartley, J. S. Prevéy, and T. R. Seastedt. 2014. The effects of black-tailed prairie dogs on plant communities within a complex urban landscape: An ecological surprise? Ecology 95:1349–1359.

Binkley, D., and P. Matson. 1983. Ion exchange resin bag method for assessing forest soil nitrogen availability. Soil Science Society of America Journal 47:1050–1052.

Blumenthal, D. M. 2009. Carbon addition interacts with water availability to reduce invasive forb establishment in a semi-arid grassland. Biological Invasions 11:1281–1290.

Bowman, W. D., J. Murgel, T. Blett, and E. Porter. 2012. Nitrogen critical loads for alpine vegetation and soils in Rocky Mountain National Park. Journal of Environmental Management 103:165–171.

Cherwin, K. L., T. R. Seastedt, and K. N. Suding. 2009. Effects of nutrient manipulations and grass removal on cover, species composition, and invasibility of a novel grassland community in Colorado. Restoration Ecology 17:818–826.

Denslow, J. S. 2014. Plant community assembly. Bulletin of the Ecological Society of America 95:334–336.

Diez, J. M., et al. 2012. Will extreme climatic events facilitate biological invasions? Frontiers in Ecology and the Environment 10:249–257.

Dukes, J. S., and H. A. Mooney. 1999. Does global change increase the success of biological invaders? Trends in Ecology and Evolution 14:135–139.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6:324–37.

Huxman, T. E., et al. 2004. Convergence across biomes to a common rain-use efficiency. Nature 429:651–654.

James, J. J., K. W. Davies, R. L. Sheley, and Z. T. Aanderud. 2008. Linking nitrogen partitioning and species abundance to invasion resistance in the Great Basin. Oecologia 156:637–648.

Jentsch, A., J. Kreyling, and C. Beierkuhnlein. 2007. A new generation of climate-change experiments: events, not trends. Frontiers in Ecology and Environment 5:365–374.

Knapp, A. K., et al. 2008. Consequences of more extreme precipitation regimes for terrestrial ecosystems. BioScience 58:811–821.

Lajtha, K. 1988. The use of ion-exchange resin bags for measuring nutrient availability in an arid ecosystem. Plant and Soil 105:105–111.

MacDougall, A. S., B. Gilbert, and J. M. Levine. 2009. Plant invasions and the niche. Journal of Eoclogy 97:609–615.

NOAA. 2014. Preliminary precipitation totals map. September 9–16, 2013 for Denver/Boulder. , Colorado, USA. http://www.crh.noaa.gov/bou/?n=stormtotals_092013

Paschke, M. W., T. McLendon, and E. F. Redente. 2000. Nitrogen availability and old-field succession in a shortgrass steppe. Ecosystems 3:144–158.

Prevéy, J. S. 2014. Precipitation change in a semi-arid grassland: plant community responses and management strategies. Dissertation. University of Colorado, Boulder, USA.

Prevéy, J. S., D. G. Knochel, and T. R. Seastedt. 2014. Mowing reduces exotic annual grasses but increases exotic forbs in a semiarid grassland. Restoration Ecology 22:774–781.

Prevéy, J. S., and T. R. Seastedt. 2014. Seasonality of precipitation interacts with exotic species to alter composition and phenology of a semi-arid grassland. Journal of Ecology 102:1549–1561.

Pyšek, P., and D. M. Richardson. 2007. Traits associated with invasiveness in alien plants: where do we stand? Pages 97–125 *in* W. Nentwig, editor. Biological invasions. Springer, Berlin, Germany.

Ray, A. J., J. J. Barsugli, K. B. Averyt, et al. 2008. Climate change in Colorado: a synthesis to support water resources management and adaptation. Report for the Colorado Water Conservation Board. University of Colorado, Boulder, Colorado, USA. http://wwa.colorado.edu/publications/reports/WWA_ClimateChangeColoradoReport_2008.pdf

R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Seastedt, T. R., J. M. Briggs, and D. J. Gibson. 1991. Controls of nitrogen limitation in tallgrass prairie. Oecologia 87:72–79.

Seastedt, T. R., and P. Pyšek. 2011. Mechanisms of plant invasions of North American and European Grasslands. Annual Review of Ecology, Evolution, and Systematics 42:133–153.

Seastedt, T. R., and K. N. Suding. 2007. Biotic constraints on the invasion of diffuse knapweed (*Centaurea diffusa*) in North American grasslands. Oecologia 151:626–636.

Stark, J. M., and J. M. Norton. 2015. The invasive annual cheatgrass increases nitrogen availability in 24-year-old replicated field plots. Oecologia 177:799–809.

Thompson, R. M., J. Beardall, J. Beringer, M. Grace, and P. Sardina. 2013. Means and extremes: building variability into community-level climate change experiments. Ecology Letters 16:799–806.

USDA. 2001. Web soil survey. Natural Resources Conservation Center. http://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx

White, S. R., J. F. Cahill, and E. W. Bork. 2014*a*. Implications of precipitation, warming, and clipping for grazing resources in Canadian prairies. Agronomy Journal 106:33–42.

White, S. R., E. W. Bork, and J. F. Cahill. 2014*b*. Direct and indirect drivers of plant diversity responses to climate and clipping across northern temperate grassland. Ecology 95:3093–3103.

Wilcox, K. R., J. C. von Fischer, J. M. Muscha, M. K. Petersen, and A. K. Knapp. 2014. Contrasting above-and belowground sensitivity of three Great Plains grasslands to altered rainfall regimes. Global Change Biology 21:335–344.

WRCC [Western Regional Climate Center]. 2014. Recent climate in the West. http://www.wrcc.dri.edu/

Zelikova, T. J., D. M. Blumenthal, D. G. Williams, L. Souza, D. R. LeCain, J. Morgan, and E. Pendall. 2014. Long-term exposure to elevated CO_2 enhances plant community stability by suppressing dominant plant species in a mixed-grass prairie.

Proceedings of the National Academy of Sciences 111:15456–15461.

Zeppel, M. J. B., J. V. Wilks, and J. D. Lewis. 2014. Impacts of extreme precipitation and seasonal changes in precipitation on plants. Biogeosciences 11:3083–3093.

Zhang, Y., et al. 2013. Extreme precipitation patterns and reductions of terrestrial ecosystem production across biomes. Journal of Geophysical Research: Biogeosciences 118:148–157.

Supplemental Material

Appendix

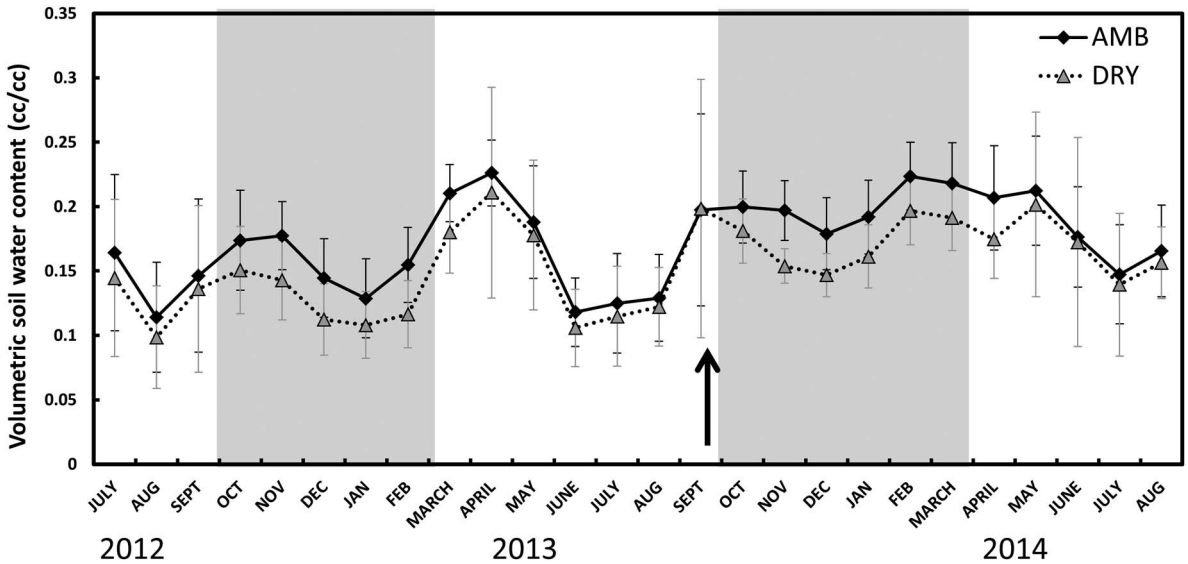

Fig. A1. Mean (±SEM) monthly soil moisture in ambient precipitation and winter dry treatments between 2012 and 2014. Measurements were made hourly in 14 ambient and 14 dry plots. Gray areas represent the times when shelters were covering winter dry plots, and the arrow points to September 2013 when the site experienced an extreme precipitation event.

Supplement

R scripts for conducting the statistical analyses described in the *Methods* section (*Ecological Archives*, http://dx.doi.org/10.1890/ES15-00073.1.sm).