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Abstract

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Disciplines

Biodiversity | Climate | Ecology and Evolutionary Biology | Environmental Sciences | Plant Sciences

Comments

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Nutrient addition increases grassland sensitivity to droughts

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Abstract. Grasslands worldwide are expected to experience an increase in extreme events such as drought, along with simultaneous increases in mineral nutrient inputs as a result of human industrial activities. These changes are likely to interact because elevated nutrient inputs may alter plant diversity and increase the sensitivity to droughts. Dividing a system's sensitivity to drought into resistance to change during the drought and rate of recovery after the drought generates insights into different dimensions of the system's resilience in the face of drought. Here, we examine the effects of experimental nutrient fertilization and the resulting diversity loss on the resistance to and recovery from severe regional droughts. We do this at 13 North American sites spanning gradients of aridity, five annual grasslands in California, and eight perennial grasslands in the Great Plains. We measured rate of resistance as the change in annual aboveground biomass (ANPP) per unit change in growing season precipitation as conditions declined from normal to drought. We measured recovery as the change in ANPP during the postdrought period and the return to normal precipitation. Resistance and recovery did not vary across the 400-mm range of mean growing season precipitation spanned by our sites in the Great Plains. However, chronic nutrient fertilization in the Great Plains reduced drought resistance and increased drought recovery. In the California annual grasslands, arid sites had a greater recovery postdrought than mesic sites, and nutrient addition had no consistent effects on resistance or recovery. Across all study sites, we found that predrought species richness in natural grasslands was not consistently associated with rates of resistance to or recovery from the drought, in contrast to earlier findings from experimentally assembled grassland communities. Taken together, these results suggest that human-induced eutrophication may destabilize grassland primary production, but the effects of this may vary across regions and flora, especially between perennial and annual-dominated grasslands.

Key words: diversity loss; drought; fertilization; grasslands; Nutrient Network (NutNet); primary production.

INTRODUCTION

Grassland productivity and biodiversity are being impacted simultaneously by several major elements of global change driven by industrial agriculture and fossil

fuel use: increased frequency of extreme events, exogenous inputs of limiting nutrients, and changes in biodiversity (Weltzin et al. 2003). Grassland and savanna ecosystems cover one-third to one-half of Earth's terrestrial surface and account for 32% of terrestrial gross primary productivity (Beer et al. 2010), with variation in that productivity controlled strongly by precipitation (Beer et al. 2010) and nutrients (Stevens et al 2015). Drought is becoming more frequent as global change

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increases rainfall variation in many regions of the world (Fischer et al. 2013). Many ecosystem functions in grasslands are driven by annual aboveground net primary production (ANPP), the annual amount of aboveground plant biomass produced per unit area (McNaughton et al. 1996, Hector and Bagchi 2007). The response of plant communities to drought can be framed as the sensitivity of ANPP to resource shortage, where water is one of multiple resources limiting grassland productivity (Huxman et al. 2004, Knapp et al. 2015).

Supply of biologically limiting resources and biodiversity loss can shape the sensitivity of ANPP to drought (Weltzin et al. 2003, Hautier et al. 2014), because many grasslands are co-limited by water and mineral nutrients (Huxman et al. 2004, Augustine and McNaughton 2006, Wang et al. 2017). Past research in grasslands has demonstrated that ANPP responds very differently to above-average versus below-average years of precipitation (Knapp and Smith 2001, Wilcox et al. 2017). Thus, it is informative to divide the sensitivity of an ecosystem to an extreme event such as a drought into two broad components—the “resistance” to change during the drought, and the rate of “recovery” after the drought (Hodgson et al. 2015). In addition, plant diversity, which varies with elemental nutrient supply, also has been shown to differ in its effects on resistance and resilience (Isbell et al. 2015). Here, we use a multisite experiment in grasslands to examine the interactions of these global change factors with droughts in two geographical regions. We measured sensitivity as the change in biomass per unit change in rainfall across years. Specifically, we address the following two questions: Does the alleviation of limitation for resources other than water change drought sensitivity across grasslands? Are responses to drought modulated by plant diversity?

If water is one of multiple resources that limits grassland ANPP, we can expect ANPP in arid sites to be more limited by water, and ANPP in mesic sites to be more limited by nutrient or light availability (Sala et al. 1988, Yahdjian et al. 2011). Therefore, we hypothesize that (1) ANPP sensitivity to drought will be higher in more arid systems (Knapp et al. 2015) and that (2) addition of other limiting resources like elemental nutrients will have greater effect on drought sensitivity in mesic rather than arid systems (Huxman et al. 2004). The first hypothesis has found mixed support in grassland systems, with some studies showing higher values of ANPP sensitivity to precipitation in arid sites (Huxman et al. 2004, Knapp et al. 2015), and others finding hump-shaped or weak relationships between sensitivity and mean annual precipitation (Bai et al. 2008, Hsu et al. 2012). The low relative growth rates, density limitation of growth, and high evapotranspiration rates in arid systems can reduce ANPP sensitivity to precipitation variation and nutrient addition compared to what would be expected from a simple hypothesis of multiple resource limitation. (Paruelo et al. 1999, Reichmann et al. 2013). The second hypothesis of multiple resource limitation is amenable to

testing by examining ANPP responses to experimental nutrient addition during years of varying precipitation.

Studies comparing the effects of experimental nutrient additions across different sites build insight into how co-limitation varies across spatial gradients and plant communities. A recent meta-analysis (Yahdjian et al. 2011) found that the relative effect of nitrogen addition on ANPP increased across an arid to subhumid gradient of mean annual precipitation (50–650 mm/yr). Conversely, we can think about how nutrient addition shifts ANPP sensitivity to precipitation. Plant communities in arid sites have close to maximum values of ANPP sensitivity (Huxman et al. 2004) and should not be much changed by nutrient addition. Mesic sites, however, are not very sensitive to rainfall, and alleviating them from nutrient limitation should lead to changes in rainfall having stronger impacts on plant biomass. Whereas meta-analyses infer patterns from studies using a wide range of methods, standardized experimental nutrient addition treatments combined with identical sampling methods across many sites have potential to offer greater insights into the co-limitation between nutrients and water (Borer et al. 2014).

Biodiversity also may determine ecosystem responses to drought in natural plant communities (Tilman and Downing 1994, Isbell et al. 2015). For example, Tilman and Downing (1994) found that nutrient addition reduced plant diversity and the resulting lower diversity communities had larger reductions in biomass during a severe drought. The confounding of nutrient addition and diversity loss in that experiment motivated field experiments that directly tested the effects of plant diversity on ecosystem stability (van Ruijven and Berendse 2010, Gross et al. 2013, Isbell et al. 2015). More recent studies have shown that loss of plant diversity reduces the temporal stability of ANPP (which can be thought of as the inverse of sensitivity) through loss of compensatory dynamics or asynchronous responses to environmental changes such as variability in precipitation (Gross et al. 2013, Hautier et al. 2015). Across biodiversity experiments, biodiversity loss decreases resistance to drought, but does not affect recovery (Isbell et al. 2015, Craven et al. 2016). In natural grasslands, diversity is one of several drivers of the mean and stability of ANPP (Grace et al. 2016, Flombaum et al. 2017). In a nutrient addition experiment across 41 grasslands, Hautier et al. (2014) found that fertilization weakened the positive effects of biodiversity on stability not through eutrophication-induced species loss, but by increasing temporal variation in productivity and decreasing species asynchrony. However, the effects of nutrient-induced diversity gradients on the drought sensitivity of natural grasslands have only been examined in single sites (Tilman and Downing 1994, Xu et al. 2014), and it remains to be tested if diversity loss induced by nutrient addition remains an important determinant of ecosystem response to drought across a broad range of aridity and plant communities.

In this study, we quantify ANPP sensitivity to precipitation before and after severe regional droughts in 13 identical nutrient addition experiments spread over two biogeographic regions: five sites in annual-dominated California grasslands on the Pacific Coast of North America and eight sites in perennial-dominated grasslands in the Great Plains in the center of the North American continent (see Appendix S1 for site locations). In this work, we use extreme natural droughts that occurred at ongoing nutrient addition experiments. California experienced three consecutive years of extreme drought (2011–2014). During 2013–2014, average winter rainfall was the second driest on record, and average winter temperature was the highest on record since 1895 (Seager et al. 2015). The Great Plains experienced extreme precipitation deficits in 2011–2012; its southern region faced exceptional drought in 2011, and the larger central region faced a sudden, extremely dry summer in 2012, the most severe since at least 1895 (Hoerling et al. 2014).

We examined ANPP responses to these natural droughts and experimental fertilization treatments across precipitation gradients in these two biogeographic regions. We measured ANPP resistance to and recovery from drought by calculating the change in biomass per unit change in rainfall across years (see Fig. 1) as precipitation declined into the drought (resistance) and as precipitation increased after the drought (recovery). We asked three questions about the role of nutrients in mediating drought resistance and recovery:

- Q1. How does resistance of ANPP to drought vary at sites along a broad precipitation gradient, and was this response influenced by nutrient addition? Within a region, we expect that arid sites will be more limited by water than mesic sites, and hence will have a lower resistance (and consequently higher sensitivity) to drought than mesic sites (Huxman et al. 2004, Knapp et al. 2015). We also expect that fertilization will decrease resistance particularly in mesic sites, as productivity in mesic sites is more likely to be limited by nutrients than by water (Yahdjian et al. 2011).
- Q2. How does recovery of ANPP after the drought vary along the precipitation gradient, and how was it influenced by nutrient addition? The recovery should be greater at arid sites, as they are more strongly limited by water availability than mesic sites (Sala et al. 2012). Fertilization should increase recovery rates, particularly in mesic sites, as we expect recovery rates in arid sites to be close to the maximum possible (Huxman et al. 2004).
- Q3. Was drought sensitivity (resistance and recovery) affected by variation in species diversity among plots at a site? We expect that low predrought diversity, including previous losses in response to eutrophication, should decrease resistance of ANPP during the drought (Tilman and Downing 1994, Isbell et al. 2015), and decrease the rate of recovery of ANPP

after the drought (Kreyling et al. 2017; but see Isbell et al. 2015).

METHODS

Study system

The two regions examined in our study, California and the Great Plains, represent large grassland areas in North America. The Great Plains supports three main classes of grassland along a west-to-east precipitation gradient: the tallgrass prairie, the mixed-grass prairie, and the shortgrass steppe (Heisler-White et al. 2009). Both regions have a 4–5-month growing season for vegetation, limited by summer droughts in the California Annual Grasslands, and by freezing winter temperatures in the Great Plains. The Mediterranean climate of California is cool and wet during the region's winter growing season. The continental climate of the Great Plains has a hot summer growing season marked by periods of drought. Our study sites in both regions span a similar range of growing-season precipitation, though the inter-annual variation in precipitation (measured as CV) was much larger in California than in the Great Plains (see Table 1).

Before the Spanish invasion and colonization, California grasslands were dominated by annual forbs, shrubs, and C3 perennial grasses such as *Stipa pulchra*. The introduction of cattle and forage species from Europe led to a shift in dominance to annual grasses, such as *Taeniatherum*, *Avena*, *Lolium*, and *Bromus* sp. (Seabloom et al. 2006). The Great Plains sites in our study are dominated by perennial C4 grasses such as *Schizachyrium scoparium*, *Andropogon gerardii*, *Sorghastrum nutans*, and *Chondrosium gracilis*, along with some introduced C3 grasses (*Bromus inermis*, *Poa pratensis*) and many perennial forbs. Some sites in the Great Plains have a significant proportion of annual grasses, especially in the drier areas of the western Great Plains. Although large portions of both these regions have been converted to agriculture, much of the remnant native prairie have been extensively managed for cattle grazing over the past 150 yr (Samson et al. 2004). Currently, these study sites have been free of domestic grazing for at least 5 yr before the start of the experiment, though native herbivores are present.

Experimental design and measurements

We use data from the Nutrient Network experiment (NutNet: www.nutnet.org), a distributed research cooperative focused on the study of the diversity, productivity, and composition of grasslands worldwide (Borer et al. 2014). Three nutrient addition treatments (N, P, and K plus micronutrients) were crossed in a factorial design to test for multiple nutrient limitation on plant composition and ecosystem function. Experimental plots were 5 × 5 m in size, one set of all treatment

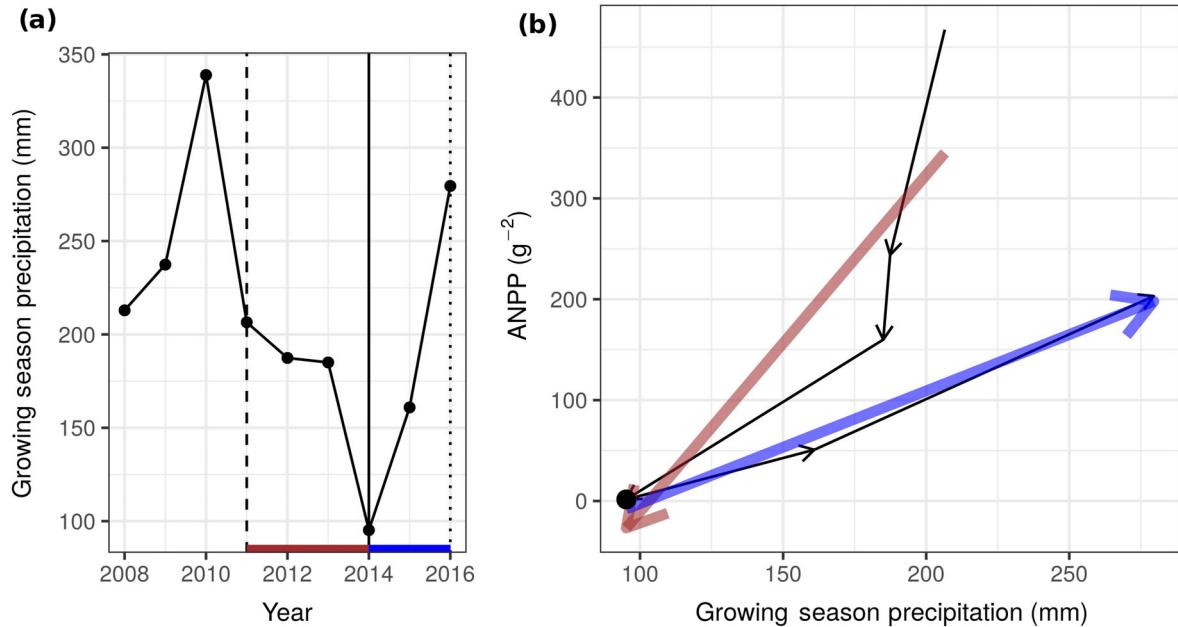


FIG. 1. Measuring rates of resistance to and recovery from drought for a single plot at a site. Data shown are from a plot at site 1, Elliott Chaparral (a) Trace of growing season precipitation over the duration of the experiment at site 1. Vertical lines indicate the normal predrought year (dashed line), year of peak drought (solid line), and normal postdrought year (dotted line). Durations used for measuring resistance are shown in red and recovery is shown in blue. (b) Sensitivity of ANPP to change in rainfall across years. Black arrows trace the change in biomass and rainfall from year to year at one plot, with the year of peak drought indicated by the black point. ANPP sensitivities measured for this plot by linear regression of this relationship are shown by the red line for resistance and blue line for recovery. Slopes of these lines correspond to plot-scale values of S that are reported at the site scale in Figs. 2 and 3.

combinations were arranged in a spatial block, and there were 3–6 blocks per site (see Table 1). Nutrient addition rates and sources are 10 g N·m⁻²·yr⁻¹ as timed-release urea [(NH₂)₂CO], 10 g P·m⁻²·yr⁻¹ as triple-super phosphate [Ca(H₂PO₄)₂], 10 g K·m⁻²·yr⁻¹ as potassium sulfate [K₂SO₄] and 100 g m⁻² of a micronutrient mix of Fe (15%), S (14%), Mg (1.5%), Mn (2.5%), Cu (1%), Zn (1%), B (0.2%), and Mo (0.05%). N, P, and K were applied annually; micronutrients were applied once at the start of the experiment to avoid toxicity (see Borer et al. 2014 for details). The goal of each treatment was to overcome limitation of plant growth by the added nutrients. Experimental treatments were initiated at each site in different years (See column 2 in Table 1).

Each treatment plot was sampled annually for above-ground biomass, clipped from two 0.1-m² quadrats per plot, dried to constant mass at 60°C and weighed to the nearest 0.01 g. Cover of each species was measured concurrently with ANPP sampling in 1-m² subplots in which no destructive sampling occurred. Across all our plots, woody biomass made a very small fraction of annual biomass (interquartile range of 0 to 0.001, maximum of 0.1), and was excluded in these analyses to ensure that biomass only reflected production of the current year.

For the analysis of biomass sensitivity and nutrient addition (questions 1 and 2), we used data only from the control and NPK + added plots in each block, to

compare the control condition to the condition where all nutrient limitation was alleviated. For the analysis of species diversity and biomass sensitivity (question 3), we used data from all the nutrient addition treatments, as this question required the among-plot variation in species richness caused by the different nutrient treatments (Harpole et al. 2016).

Meteorological data and site selection

Thirteen NutNet sites located in the California grasslands and Great Plains regions experienced severe drought, defined as the lowest tenth percentile of the Standardized Precipitation Evapotranspiration Index since 1901 (SPEI; Vicente-Serrano et al. 2010; see Appendix S1 for details). The SPEI is a normalized metric that considers both water supply (precipitation) and loss (potential evapotranspiration [PET]), and standardizes water availability against the climate history of the site, thus enabling consistent comparison of drought intensity among sites. We obtained meteorological data of monthly precipitation and temperature from nearby weather stations with at least 30 yr of data for each site. We used the knowledge of the lead scientist at each site to determine the first and last month of the growing season for their site, and aggregated our metrics of water availability accordingly.

TABLE 1. Descriptions of sites involved in this study and the extent of drought.

No.	Site and first fertilization year	Region	Blocks†	Mean GSP (mm)	CV of GSP	SPEI at peak drought	GSP at peak drought (mm)	Duration of resistance‡	Duration of recovery§
1	Elliott Chaparral—2009	California	3	258	0.54	−1.85	95	2011–2014	2014–2016
2	Sedgwick Reserve UCNRS—2008	California	3	375	0.59	−1.93	109	2011–2014	2014–2016
3	Sierra Foothills REC—2008	California	5	604	0.34	−1.33	395	2012–2014	2014–2016
4	Mclaughlin UCNRS—2008	California	3	640	0.49	−1.54	373	2011–2014	2014–2015
5	Hopland REC—2008	California	3	772	0.40	−1.52	423	2011–2014	2014–2016
6	Sevilleta LTER—2008	Great Plains	5	159	0.33	−1.57	81	2008–2011	2011–2012
7	Shortgrass Steppe LTER—2008	Great Plains	3	225	0.28	−1.55	121	2010–2012	2012–2013
8	Cedar Point—2008	Great Plains	6	281	0.28	−1.68	134	2011–2012	2012–2013
9	Saline Experimental Range—2008	Great Plains	3	369	0.28	−1.94	226	2010–2012	2012–2013
10	Temple—2008	Great Plains	3	487	0.33	−3.06	144	2010–2011	2011–2012
11	Konza LTER—2008	Great Plains	3	562	0.28	−1.44	321	2010–2012	2012–2014
12	Chichaua Bottoms—2010	Great Plains	6	568	0.33	−1.57	424	2011–2012	2012–2013
13	Trelease Prairie—2009	Great Plains	3	594	0.25	−1.25	363	2010–2012	2012–2013

Note: Years in column 2 denote the first year of sampling at each site.

CV, coefficient of variation; GSP, growing-season precipitation; SPEI, standardized precipitation evapotranspiration index.

† Blocks denote the number of spatial replicate plots for each experimental treatment.

‡ The duration of resistance runs from a year of normal rainfall preceding the drought to the year of peak drought.

§ The duration of recovery runs from the year of peak drought to the first year of normal rainfall subsequent to the drought.

We used three metrics to describe water availability over time within and across sites. The first metric was growing season precipitation (GSP), the total rainfall received each year over the growing season at each site, as an absolute metric of water availability at a site. GSP is generally found to predict ANPP better than total annual precipitation (Robinson et al. 2013). The second metric considered was SPEI measured over the growing season (SPEI_{gs}), which identifies periods of drought and recovery in a standardized manner across sites. We calculated PET at a monthly time scale using the Hargreaves method, and SPEI over each growing season and water year (using the package `spei` in R). Third, we used mean GSP, the average GSP across years, to quantify the location of sites along regional gradients of aridity.

For our analyses, we identified at each site a pre-drought year of normal or above-normal rainfall, then a 1–3-yr period of declining rainfall to the “drought” year, followed by a 1–2-yr period of rise in rainfall to a “recovery” year that fell within the normal range of precipitation, determined by SPEI_{gs} (see Appendix S1: Fig. S2).

Measuring biomass sensitivity

Ecosystems and plant communities have different sensitivity to extreme climate events such as drought. Because the results of studies can depend on the way sensitivity was estimated, it is important to select and interpret sensitivity indices carefully (Smith et al. 2017). Comparing sensitivity across sites with very different precipitation regimes requires that changes in the output

(ANPP) are relativized to change in inputs (rainfall) (Verón et al., 2005, Smith et al. 2017).

For this study, we have chosen a common approach to measure ANPP sensitivity to precipitation change: the change in biomass per unit change in rainfall across years (henceforth abbreviated *S*, the slope of the relationship between ANPP and annual rainfall across years at a site). This commonly employed metric has also been referred to as the Precipitation Marginal Response (Verón et al. 2005) or ANPP_{sens} (Wilcox et al. 2016). It is a rate measure in biologically relevant units (grams of biomass change per millimeter of rainfall change) that is easy to relate across different plant communities, and relates to existing literature on the sensitivity of ANPP to precipitation (Smith et al. 2017). This metric measures rates of resistance when calculated during years of declining precipitation leading to drought, and measures rates of recovery for years of increasing precipitation after the drought.

We define *S* as the slope of a linear regression of annual biomass measured at a single plot against GSP across years. For resistance, we measured change from a normal predrought year until the year of peak drought. For recovery, we measured change from the year of peak drought until the first normal postdrought year (see Fig. 1 and Appendix S1). The duration of both these periods are shown in Table 1; sites with a longer period of drought have more data points to estimate *S*. In sites where there is only a 1-yr period of resistance and recovery, calculating *S* is mathematically equivalent to point-based metrics of sensitivity (van Ruijven and Berendse

2010). Resistance is the ability to withstand perturbation; thus a lower value of S corresponds to higher resistance rate. Recovery is the rate at which biomass increases after the drought; thus a higher value of S corresponds to higher recovery. S is in units of $\text{g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$, the biomass change per millimeter of rainfall change. All statistical analyses were performed in R version 3.4.2 (R Development Core Team 2017).

Effect of nutrients on biomass sensitivity along regional aridity gradients

We examined the effects of fertilization on sensitivity across the aridity gradient in each region. We did this by fitting linear mixed-effects models (using R packages *lme4* and *lmerTest*; Bates et al. 2015, Kuznetsova et al. 2017) with plot-scale resistance or recovery rates as the response variable; mean GSP for a site, nutrient treatment, and the interaction between the two as predictors; and random intercepts for blocks nested within sites. We compared models with and without the interaction term using likelihood ratio tests and retained the interaction term only if it significantly improved model fit ($P < 0.05$).

Species diversity and biomass sensitivity

We used species richness as our measure of diversity, calculated from annual estimates of species cover in 1-m² permanent plots. To evaluate correlations between richness and biomass sensitivity, we fit linear mixed-effects models to explain variation in resistance and recovery. Predrought species richness and site mean GSP were fixed effects in each model. Richness was log-transformed to meet modeling assumptions. Models included random slopes for richness at every site and random intercepts for sites and blocks within site. This allowed the effect of the richness gradient on S to vary among sites, enabling us to examine if within each site, richness of plots changes their resistance to or recovery from drought. We determined whether richness was important in the models through likelihood ratio tests between the full model and models with richness removed as a predictor (both as a main effect and as random slopes for richness at every site). The difference in deviance between the two nested models follows a chi-squared distribution with degrees of freedom equal to the difference in number of parameters between the two models.

RESULTS

Q1. Resistance to drought, and the effect of fertilization

Increases in the sensitivity metric S indicates declines in drought resistance. Fertilization and the regional aridity gradient (site mean GSP) had no consistent effects on resistance rate in the California grasslands. In the Great Plains, fertilization decreased resistance rate by

$0.46 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ ($P < 0.01$) and that effect did not vary significantly across the aridity gradient (Table 2, Figs. 2 and 4).

Q2. Recovery from drought, and the effect of fertilization

At the regional scale, fertilization increased drought recovery rates by $1.35 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ in the Great Plains ($P < 0.001$) but had no consistent effect in California (Table 2, Fig. 3). In California, recovery rate declined as site mean GSP increased, from a value of $3.2 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ at the most arid site to a value of $0.32 \text{ g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$ at the mesic end of the aridity gradient (Table 2, Figs. 3 and 5). S values in both regions were generally higher during the recovery period than during the resistance period (intercept values in Table 2).

Q3. Effect of diversity on resistance and recovery

The gradients of predrought species richness existing at each site, or across sites, were not correlated with any of our metrics of sensitivity (Appendix S2: Fig. S2). The AIC values of models with and without predrought diversity, and the results of likelihood ratio tests for the effects of diversity, are shown in Appendix S2: Table S2.

DISCUSSION

In our study of the effects of severe drought on grassland biomass at 13 sites, we found that the rates of ANPP resistance to and recovery from drought differed in the two regions. Grassland sites in the Great Plains were generally more sensitive to drought than the sites in the California grasslands. In the Great Plains, chronic nutrient fertilization reduced drought resistance rate and increased postdrought recovery rate across the precipitation gradient. In the California grasslands, recovery was higher in arid as compared to mesic sites, and fertilization had no consistent effects on resistance or recovery. Contrary to our hypotheses, we found no correlation between predrought plant diversity and rates of resistance to or recovery from the drought. Our results are methodologically robust to different choices of drought sensitivity metrics from the literature (see Appendix S2).

We did not find site mean GSP to be a good predictor of resistance or recovery in the Great Plains, contrary to our hypotheses shaped by previous work (Huxman et al. 2004, Knapp et al. 2015). Knapp et al. (2015) quantified ANPP responses to the 2012 drought at five sites in the Great Plains and concluded that more arid sites had lower resistance (higher S values) during the drought. Their data support a model in which arid sites are more limited by water than other factors and hence have a higher sensitivity to precipitation (Huxman et al. 2004), a pattern we do not see when we include sites across a wider gradient of precipitation in the Great Plains. Instead, our results match those of other cross-site studies that find precipitation sensitivity to have a flat or

TABLE 2. Results of linear mixed-effects models fit at each region explaining resistance and recovery rates by mean GSP (growing season precipitation) at each site, fertilization treatments, and their interaction.

Predictor	California grasslands			Great Plains		
	estimate	SE	<i>P</i> value	estimate	SE	<i>P</i> value
Resistance rate						
Intercept†	1.55	0.98	0.22	0.24	0.80	0.77
Mean GSP	-0.0038	0.0030	0.28	0.0015	0.0027	0.60
Fertilization	0.09	0.19	0.62	0.46	0.17	0.01
Interaction‡	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Recovery rate						
Intercept†	3.17	0.58	0.00	0.56	0.53	0.32
Mean GSP	-0.0055	0.0017	0.03	-0.0004	0.0017	0.84
Fertilization	0.22	0.42	0.61	1.35	0.29	<0.001
Interaction‡	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

† The value of the intercept is the sensitivity estimated at the most arid site in a region.
 ‡ Interactions that were not significant by likelihood ratio tests (*P* > 0.1) are denoted by n.s. in the table; only fits from additive models are reported.

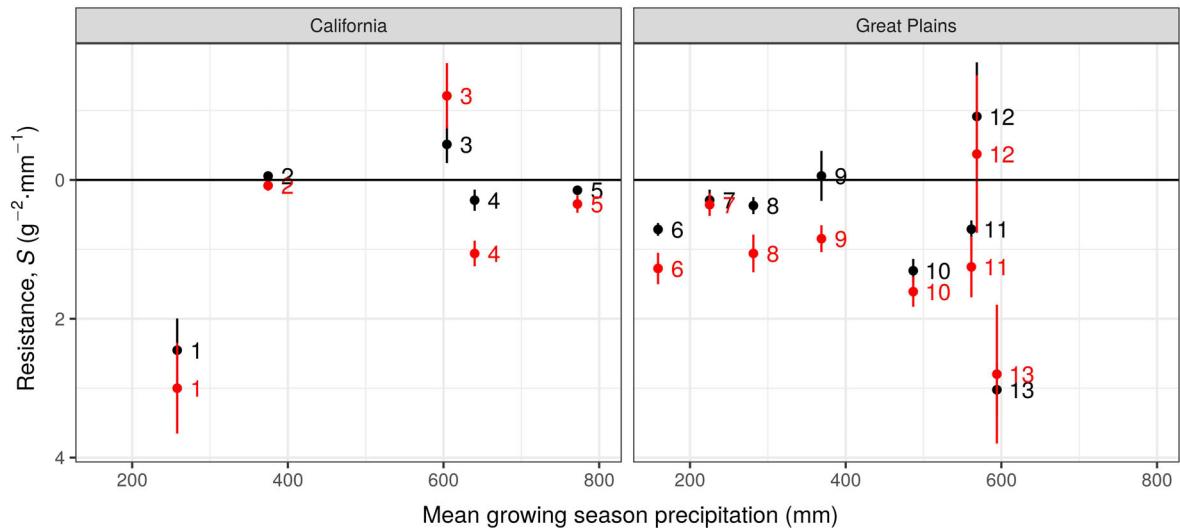


FIG. 2. Resistance of biomass to drought (*S*, $g^{-2} \cdot mm^{-1}$) across sites in two regions, in relation to nutrient fertilization treatments and mean growing season precipitation (GSP) at each site. *S* is the change in biomass per millimeter change in rainfall from before the drought until the year of peak drought. The direction of the y-axis is switched to show that higher values of *S* correspond to lower resistance rates. Plots that received nutrient fertilization are shown in red, and control plots are in black. Points and vertical lines denote the mean and standard error of plot level *S* estimates for a site. Numbers correspond to sites as listed in Table 1.

unimodal relationship with site mean annual precipitation (Bai et al. 2008, Hsu et al. 2012). It is possible that the hypotheses of multiple limitation shaping ANPP variation in nonextreme years (Huxman et al. 2004) does not apply to years of extreme precipitation (Knapp et al. 2017). Mediterranean grassland ecosystems in Eurasia, which have a combination of long-term high variability in rainfall and long grazing history, are highly resistant to variation in precipitation, which could account for the low sensitivity of sites in California (Tielbörger et al. 2014, Sternberg et al. 2017). Further, in both regions, *S* was higher postdrought than during the drought. This pattern of grassland biomass being buffered against decreased rainfall and responding strongly to increased rainfall (Knapp et al. 2017, Griffin-Nolan et al. 2018) is

consistent with those found in a meta-analysis of precipitation manipulation experiments (Wilcox et al. 2017), and in cross-site observational studies (Knapp and Smith 2001, Bai et al. 2008). It is, however, surprising that this holds even in the extreme droughts analyzed in this study (Griffin-Nolan et al. 2018).

Examining the effects of nutrient fertilization in conjunction with drought gives us insight into the nature of multiple resource limitation of biomass in these grasslands. As we expected, fertilization led to increased sensitivity of biomass to precipitation change, reducing resistance to and increasing recovery from a drought. If limitation by water is determined by spatial gradients of aridity, then we would expect nutrient addition to have stronger effects on primary production at mesic rather

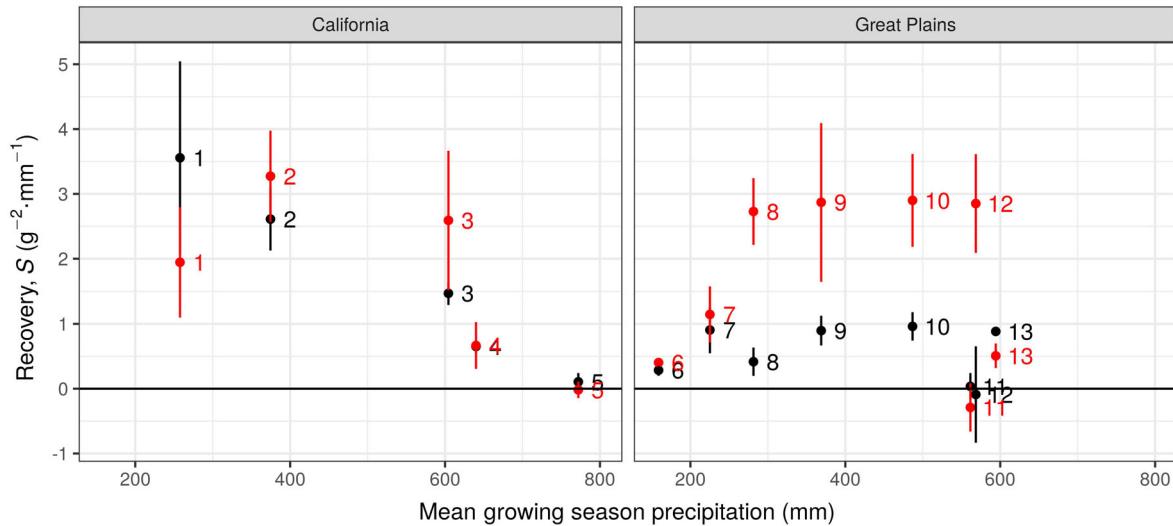


FIG. 3. Change in grassland ANPP during droughts in two regions. Lines denote ANPP (y-axis) in years of declining precipitation (x-axis) leading to the year of peak drought from linear regressions fit at each site. Arrows denote the direction of change of biomass and precipitation during the drought. Control plots are in black, nutrient added plots are in red.

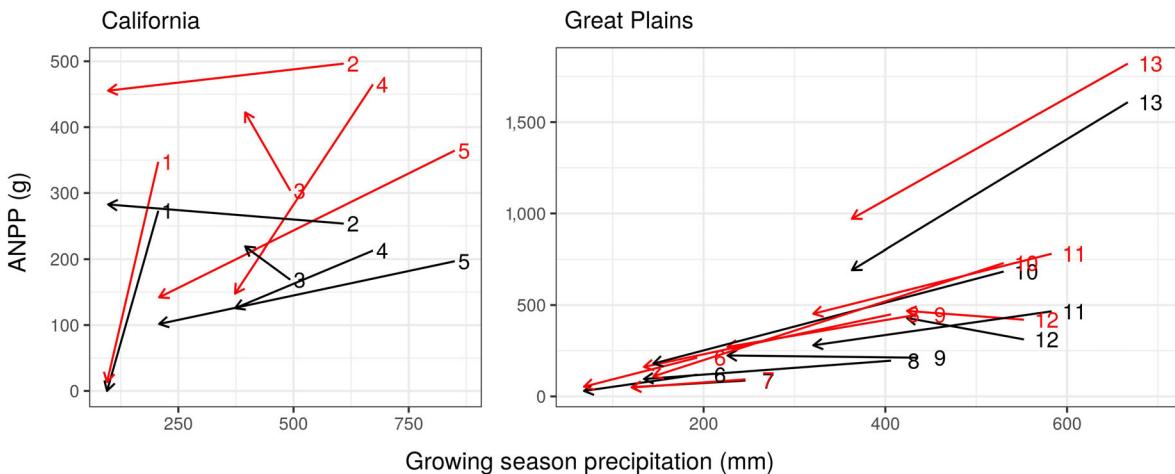


FIG. 4. Recovery of biomass postdrought (S , $\text{g}\cdot\text{m}^{-2}\cdot\text{mm}^{-1}$) across sites in two regions, in relation to nutrient fertilization treatments and mean growing season precipitation (GSP) at each site. S is the change in biomass per millimeter change in rainfall from the year of peak drought to the first year of normal rainfall postdrought. Higher values of S correspond to higher recovery rates. Labels and points are as described in Fig. 2.

than arid sites (Yahdjian et al. 2011). Fertilization increased recovery rates across the Great Plains, accelerating the rate at which biomass recovered with increasing rainfall. In the California grasslands, nutrient addition increased mean ANPP, but did not consistently affect resistance or recovery rates. Sensitivity to precipitation and nutrients was similar for all sites across the aridity gradient in the Great Plains, pointing to grassland biomass being co-limited by water and nutrients.

We found that local plant diversity was not associated with drought resistance or recovery rates within or among sites. Studies in systems that have experimentally manipulated diversity show consistently that diversity

increases temporal stability (Tilman et al. 2014) and resistance to drought (Isbell et al. 2015, Craven et al. 2016). Studies in naturally occurring grasslands also have demonstrated that chronic nutrient addition decreases local diversity across a wide range of environments (Harpole et al. 2016), which can erode nutrient driven enhancement of productivity (Isbell et al. 2013). This also may lead to declines in the temporal stability of ANPP, not only through the effects of biodiversity, but also through direct impacts of increased variability in ANPP and decreased species asynchrony (Hautier et al. 2014, Hautier et al. 2015, Zhang et al. 2016). In an examination of the effects of local plant diversity on

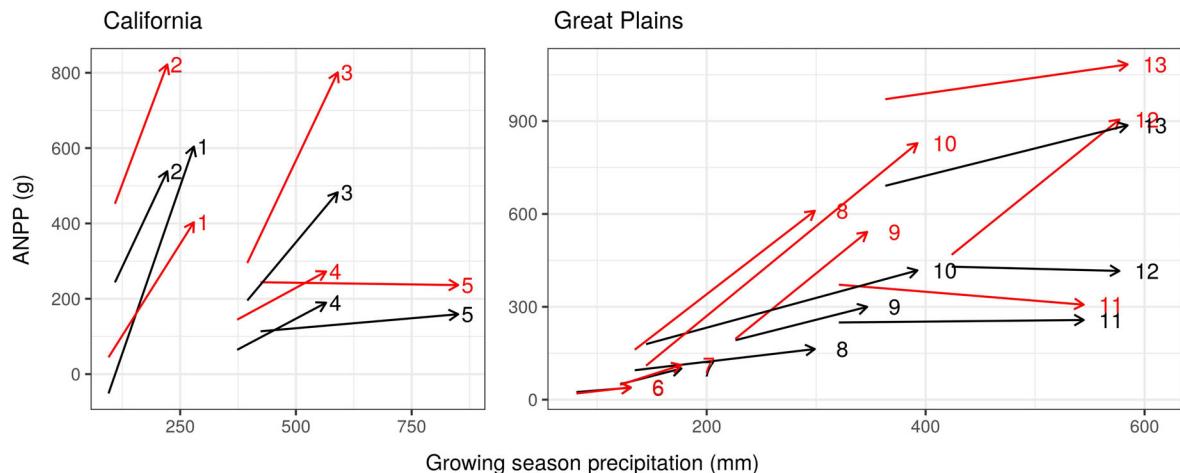


FIG. 5. Change in grassland ANPP during recovery from drought. Lines denote ANPP change in years of increasing precipitation postdrought, from linear regressions fit at each site. Labels and lines are described in Fig. 4. Arrows denote the direction of change in biomass and precipitation during recovery.

grassland drought sensitivity at a single site in the Great Plains, Tilman and Downing (1994) demonstrated that nutrient-induced diversity loss can lead to reduced drought resistance. Our investigation of the generality of the relationship between diversity loss and drought responses across 13 grassland sites found no significant relationship between diversity and drought sensitivity. Consistent with our work, several recent studies that have examined the joint effects of nutrient addition and drought in grasslands have found that species diversity does not consistently increase stability (Xu et al. 2014, 2015, Zhang et al. 2016). Thus, the phenomenon demonstrated by Tilman and Downing (1994) appears to be context-dependent, suggesting that the effects of diversity on ecosystem function in natural grasslands may be masked by environmental factors varying within and among sites (Loreau 1998, Grace et al. 2016).

Asynchrony in species responses to environmental drivers, or compensatory dynamics among plant species with different resource-use traits, can drive stability of ANPP (Hautier et al. 2014, La Pierre et al. 2016), and these dynamics might differ because of regional climate and floristic composition. Thus, differences in plant community dynamics may help explain why California grasslands behave markedly differently from grasslands in the Great Plains in response to drought (Smith et al. 2009, La Pierre et al. 2016, Wilcox et al. 2016). The lower sensitivity of California grasslands to drought may be due to faster turnover in annual plant communities in response to environmental change (Figuroa and Davy 1991), rapidly shifting the community to more drought-tolerant species that are able to maintain ANPP in dry years. In contrast, the stability of perennial-dominated grasslands of the Great Plains might depend upon compensatory dynamics among species (as seen in sites 7, 9, and 11 by La Pierre et al. 2016). At some of our Great Plains sites, annual grass biomass had a greater

sensitivity to precipitation than perennials, and the responsiveness of annuals was further amplified by nutrient addition (Wang et al. 2017, conducted at site 8). In addition, herbivores vary in identity and density between the Great Plains and California. They are a major force structuring grasslands and limiting ANPP; their role can buffer or exacerbate the effects of drought on plant communities (Augustine and McNaughton 2006, Irisarri et al. 2016, Staver et al. 2019). In terms of climate, the growing season in California occurs during the cooler winter months, in contrast to the hot summer growing seasons of the Great Plains, which could make water availability more consistently limited to ANPP in the Great Plains. California grasslands also have greater variation in precipitation than the sites in the Great Plains (Table 1), which could select for species adapted to tolerate wide variation in water availability among years. Although out of the purview of the current study, an analysis of traits influencing water and nutrient use efficiency could inform this hypothesis. With increasing frequency and severity of drought expected in the future (Fischer et al. 2013), the pronounced differences between the two regions in this study point to the need for studies of community dynamics and resource co-limitation of ANPP spanning more grassland regions of the world, to identify and test the generality of mechanisms controlling drought responses.

Our multisite experiment demonstrates that nutrient addition strongly affects the sensitivity of ANPP to drought, indicating that ongoing human-induced eutrophication may destabilize grassland primary production. We found diversity loss induced by nutrients is not consistently correlated with drought resistance or recovery rates in naturally assembled grasslands, and site aridity also was a poor predictor of grassland resistance to and recovery from drought. In particular, grasslands in the Great Plains did not follow simple expectations of

arid sites being more limited by water and mesic sites being more limited by nutrients, suggesting that productivity of grassland communities is simultaneously co-limited by both of these changing factors across a wide range of precipitation. This work provides a step toward a general understanding of co-limitation of ANPP by water and nutrients in grassland communities, which will help generalize site-scale mechanistic experiments to an understanding of ANPP stability across regions and flora in a future of increasingly variable supply of nutrients and water in ecosystems.

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