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Water availability modifies productivity response to biodiversity and nitrogen in long-term grassland experiments

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Abstract. Diversity and nitrogen addition have positive relationships with plant productivity, yet climate-induced changes in water availability threaten to upend these established relationships. Using long-term data from three experiments in a mesic grassland (ranging from 17 to 34 yr of data), we tested how the effects of species richness and nitrogen addition on community-level plant productivity changed as a function of annual fluctuations in water availability using growing season precipitation and the Standardized Precipitation-Evapotranspiration Index (SPEI). While results varied across experiments, our findings demonstrate that water availability can magnify the positive effects of both biodiversity and nitrogen addition on productivity. These results suggest that productivity responses to anthropogenic species diversity loss and increasing nitrogen deposition could depend on precipitation regimes, highlighting the importance of testing interactions between multiple global change drivers.

Key words: biodiversity–ecosystem-functioning relationship; global change; nitrogen fertilization; nutrient addition; plant biomass; precipitation; species richness; SPEI.

INTRODUCTION

Drivers of plant productivity are of great interest ecologically and societally. It is well established that productivity can respond to both biotic and abiotic factors, including plant species diversity, soil nutrients, and water availability (Chapin 1980, Tilman et al. 2014). However, do the positive effects of species richness (Tilman et al. 1997, Reich et al. 2012) and nitrogen (N) addition (Isbell et al. 2013*a*) on community-level plant productivity hold up across year-to-year variation in water availability? With precipitation and temperature patterns predicted to shift in the future with climate change (Pryor et al. 2014), it is especially important to understand how the effects of these well-established drivers of productivity (i.e., species diversity and N addition) might also shift under different levels of water availability.

Many of the same mechanisms by which diversity increases productivity, e.g., phenological and root partitioning (Fargione and Tilman 2005, Mueller et al. 2013), resource complementarity (Tilman et al. 2001), or selection effects (Loreau and Hector 2001), can similarly be used to hypothesize how water availability may alter diversity–productivity relationships. For example, diverse plots with increased biomass can create microclimate amelioration (Wright et al. 2017), and diverse plots have a higher chance of including species with differential sensitivity to drought (Hoover et al. 2014). Additionally, niche partitioning of roots in more diverse plots results in a greater capacity for the full ecosystem to draw water throughout the entire soil profile (Fornara and Tilman 2009, Mueller et al. 2013). Increased water availability could also magnify the diversity–productivity

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effect. Diverse communities' enhanced ability to take up N (Zak et al. 2003), given facilitative interactions between species (e.g., C4 grasses and legumes as shown in Fornara and Tilman 2008), could be increased with greater water availability and mass flow, particularly in low-nutrient soils (Matimati et al. 2014). Indeed, a global synthesis indicates that increased diversity leads to greater resistance to both extreme drought and heavy rainfall (Isbell et al. 2015). Yet, it is not clear whether water availability can disrupt diversity–productivity relationships over longer timeframes.

Similarly, N addition–productivity relationships may be altered by water availability. In grassland experiments around the globe, N addition has been shown to increase productivity (Fay et al. 2015) and be a key predictor of productivity (Stevens et al. 2015). Yet drought conditions may lessen the stimulatory effect of N addition on productivity (Reich et al. 2014). Indeed, N addition experiments in arid (i.e., low water availability) environments often show no effect of N addition on productivity (Yahdjian et al. 2011), likely because plants are so water-limited that they cannot fully utilize the added N. In contrast, increasing soil moisture to levels below field capacity results in increased N mobility and biological availability, which leads to more efficient utilization of available resources and higher productivity at a fixed total soil N concentration. As a result, increasing water availability could enhance the positive effects of N addition on productivity. However, as with the diversity–productivity relationship discussed above, it is not yet clear how annual changes in water availability can alter N addition–productivity relationships within a site.

Here, we explore whether the impacts on productivity of biodiversity and N addition are sensitive to change in water availability using 17–34 yr of data from three long-term grassland experiments. Specifically, we test whether the experimental effects of species richness and N addition on community-level plant productivity differ across a range of natural variation in precipitation and water availability. We hypothesized that (1) the oft-observed positive effect of species diversity on productivity would increase with total growing season precipitation and water availability; and (2) the common positive effect of N addition on productivity would decline at low levels of precipitation and water availability, but increase at high precipitation and water availability.

To test these hypotheses, we used long-term data from three experiments in the tallgrass prairie at Cedar Creek Ecosystem Science Reserve (central Minnesota, USA) and meteorological data from local weather stations. These experiments manipulated either diversity, N addition, or both for between two and four decades. We used the corresponding precipitation and temperature data to calculate total growing season precipitation and values of the Standardized Precipitation-Evapotranspiration Index, a proxy for water availability (SPEI; Vicente-Serrano et al. 2010). As precipitation and temperature patterns are expected to change with future climate change, understanding how diversity and N addition effects on productivity differ under varying amounts of precipitation and water availability is especially important for predicting future biosphere–atmosphere feedbacks.

METHODS

Site characteristics

The three experiments included in our study were all conducted at Cedar Creek Ecosystem Science Reserve (Minnesota, USA). Cedar Creek is located at the confluence of the boreal forest to the north and the mixed deciduous forest to the south. This is the result of sharp precipitation and temperature gradients across the region; these ecosystems are thus at their fringes and may be particularly sensitive to changes in climate. The soil at Cedar Creek is derived from glacial outwash and is sandy (>90% sand) and nutrient poor (Grigal et al. 1974). Using data collected onsite, the mean annual temperature and mean annual precipitation over the course of the experiments included herein (1984–2018) was 6.8°C (January average −10°C, July average 21.6°C) and 777 mm, respectively. The majority of precipitation occurs in the form of summer convective storms. More precipitation metrics are included as part of the results and described in the methods below.

Precipitation metrics

We utilized two proxies for water inputs and availability for all experiments (Fig. 1). First, we determined total growing season precipitation (April–July, four months), to describe the influx of water into the system prior to biomass sampling in late July and August (see *Long-term experimental data* for details), using Cedar Creek weather station data (CDR Experiment 080). In cases of missing precipitation records (<1.8% of days from 1984 to the present), gaps were filled with data from nearby weather stations in Cambridge and Andover, Minnesota, both within 15 km of Cedar Creek. The second metric was the Standardized Precipitation-Evapotranspiration Index (SPEI), which we used over the April–July growing season to approximate water availability to plants. SPEI is an integrative measure of precipitation and temperature that more precisely assesses water availability than bulk precipitation because it accounts for water losses due to evapotranspiration (Vicente-Serrano et al. 2010). SPEI can therefore be used to determine varying levels of drought (negative values) and water surplus (positive values) and can be used to compare water availability across diverse ecosystems (Slette et al. 2019). SPEI values were extracted from a global gridded database at 1° resolution (database *available online*).[13] For both precipitation and SPEI, we used the duration of the growing season because it more

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[13] http://sac.csic.es/spei/.

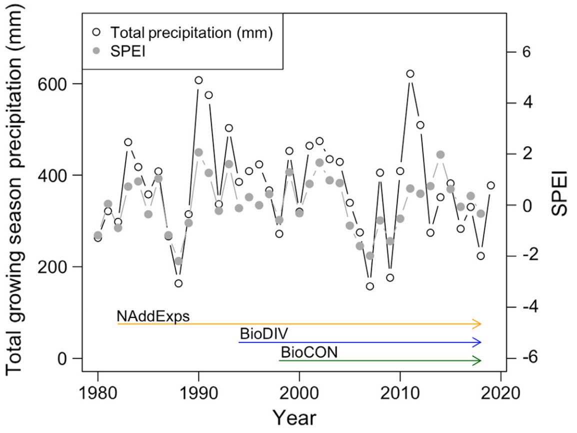

FIG. 1. Total growing season precipitation and SPEI across experiment durations. Total growing season precipitation (mm; April–July, 4 months) is shown as open circles and dark lines. Growing season Standardized Precipitation–Evapotranspiration Index (SPEI) is shown as closed circles and light gray lines. Data included by experiment span the following years: NAddExps (orange line) from 1982 to 2019; BioDIV (blue line) from 1994 to 2019; and BioCON (green line) from 1998 to 2019. No climate change trends were found over time using Mann-Kendall trend tests (Mann 1945) for precipitation or SPEI data sets ($P < 0.001$).

accurately captured what plants experienced in the field. In preliminary analyses, we also considered annual precipitation (12 months prior to biomass harvest), which is correlated with growing season precipitation ($R^2 = 0.67$) and showed similar trends as growing season precipitation, but opted to use growing season precipitation since it most closely reflects water supply when plants are growing. We analyzed the data sets for possible trends due to climate change via Mann-Kendall trend tests (Mann 1945), and found no trends over time in the precipitation or SPEI data sets ($P = 0.37159$ and $P = 0.25856$, respectively).

Long-term experimental data

We included three long-term data sets of aboveground biomass from ongoing Cedar Creek experiments – one that experimentally manipulated nutrient availability (NAddExps), one that manipulated plant species richness (BioDIV), and one that manipulated both nutrients and diversity (BioCON). Jointly, these experiments allowed for multiple examinations of how water availability alters the impact of global change factors on productivity. We utilized two tests for biodiversity and two for N addition across the three experiments.

The first data set was from a long-term N addition experiment in a restored grassland, established in 1982, with two sub-experiments (e001 and e002, together referred to herein as "NAddExps"). The first sub-experiment, e001, included 48 4 × 4 m plots in each of three fields. The second sub-experiment, e002, included 24 4 × 4 m plots in each of the same three fields. The e002 sub-experiment, also included a disking treatment (soil disturbance) at the establishment, but initial plant communities recovered very rapidly in the year or two following disking, and to-date no significant differences in response to N between the experiments have been documented. Since 1982, these existing grassland communities have received one of nine N addition treatments: 0 (control), 1, 2, 3.4, 5.4, 9.5, 17, or 27 g $\mathrm{N \cdot m^{-2} \cdot yr^{-1}}$, all with micronutrients P, K, Ca, Mg, S and trace metals simultaneously added to ensure primary limitation by N. Another control with no N or micronutrients added (0 N, 0 micros) showed no differences with the 0 N control (0 N, + micros), so was included in the control, following Wedin and Tilman (1996). Most plots included a diverse mixture of native warm season (C_4) grasses, non-legume forbs, and a few legume species at establishment, however, across all fields and both experiments, N addition led to shifts in functional group composition in favor of a small number of cool season (C_3) grasses, such that at the highest N addition rates, plots were dominated by just one or two such species (Tilman 1987, Inouye and Tilman 1995, Isbell et al. 2013*b*). For both e001 and e002, aboveground biomass was collected in late July or early August using a 10 cm by 3 m long quadrat that was positioned in a new location each year, dried, and weighed (see Clark and Tilman [2008] for more methods details). In total, 34 yr of data were used from e001 and 17 yr of data were used from e002. The difference in time span was due to the uneven biomass sampling of the two experiments, as well as the need to drop the first two years of e002 as the system equilibrated following the disking treatment. (For more details and other findings from these experiments, see Tilman 1987, Wedin and Tilman 1996, Clark and Tilman 2008, Isbell et al. 2013*a*).

The second data set came from a grassland biodiversity experiment (e120, "BioDIV") established at Cedar Creek in 1993. The BioDIV experiment manipulated planted species richness in 168 9 × 9 m plots. Prior to establishment, the top 6–8 cm of topsoil was removed to reduce the seedbank and promote successful establishment of planted species. In 1993, plots were seeded with random combinations of prairie plant species ranging from one to 16 species (1, 2, 4, 8, and 16 species) from a pool of 18 species, which included C_3 grasses, C_4 grasses, legumes, non-leguminous forbs (four species each), and woody plants (two species). Species richness has been maintained since establishment via hand weeding. Aboveground biomass was collected in August using a quadrat that was positioned in a new location within each plot each year, dried, and weighed. Following previous work from this experiment, we utilized the 154 plots, of the original 168 plots, that have been continuously maintained. (For prior results and more methods, see Tilman et al. 2001, Reich et al. 2012).

The third data set was from the biodiversity, CO_2, and nitrogen experiment (e141: "BioCON") that manipulated both N addition and planted species diversity.

BioCON also has a CO_2 enrichment treatment, however, the plots receiving CO_2 were not included in these analyses. BioCON employed a fully factorial randomized block design with four levels of species richness (1, 4, 9, and 16 species) and two levels of N addition (ambient or +4 g $N \cdot m^{-2} \cdot yr^{-1}$) divided into three blocks. Species were selected from a plant species pool of 16 species, which included C_3 grasses, C_4 grasses, legumes, non-leguminous forbs (four species each), 13 of which were the same species as those planted in BioDIV. Species richness has been maintained since establishment via hand weeding. Prior to establishment, soils were fumigated to reduce the seedbank and promote successful establishment of planted species. Aboveground biomass was collected in August using a 10 cm by 1 m long quadrat that was positioned in a new location within each plot each year, dried, and weighed (for more methodological details and other results, see Reich et al. 2001, 2012).

These long-term experiments, all with similar soils and weather, yielded two data sets each for biodiversity and N addition. Combined with weather data over the same period, we were able to test whether natural variation in water availability moderated species and N effects on plant productivity. The experiments have obvious differences in set up and maintenance (see Table 1 and *Discussion*), but, by addressing them collectively, we increased the potential for understanding ways in which water availability may moderate the effects of other global change drivers.

Statistical analysis

Statistical analyses were conducted using the nlme package (Pinheiro et al. 2019) in R (version 4.0.2; R Core Team 2013). Due to the repeated measures for all experiments, we included a random intercept that varied with plot. Due to the nested blocking structure of BioCON, we additionally included a plot within block random intercept. For simplicity, we incorporated any spatial and temporal autocorrelation due to the repeated measures or nesting as random effects instead of correlation structure, as tests with the correlation structure included showed no significant improvement in model fit. For the NAddExps, we included experiment (e001 and e002) and field identity (A, B, or C) as fixed effects in the model.

We ran separate models for each precipitation metric and global change experiment. The response variable for all models was aboveground biomass (square-root transformed to meet model assumptions, as assessed prior to analyses and via visual inspection of model residuals). For fixed effects, each model included experiment year (1 through length of experiment, continuous), global change factor (N, continuous for NAddExps, ambient/elevated factor for BioCON; diversity, planted species richness as continuous for both BioDIV and BioCON), experiment year × global change factor,

Table 1. Experimental information for each Cedar Creek global change experiment included in this study.

Experiment name	Cedar Creek experiment codes	Treatment(s)	Treatment levels	Plot size	Year started (years of data used)	Notes	References
NAddExps	e001 and e002	+N	0, 1, 2, 3.4, 5.4, 9.5, 17, or 27 g $N \cdot m^{-2} \cdot yr^{-1}$	4 × 4 m	1982 (34, 17)	P, K, Ca, Mg, S and trace metals added with N addition	Clark and Tilman (2008)
BioCON	e141	+N, biodiversity	4 g $N \cdot m^{-2} \cdot yr^{-1}$; 1, 4, 9, 16 species	2 × 2 m	1998 (21)	soil treated with methyl bromide at beginning of experiment; no micronutrients added in addition to N; annual weeding to maintain biodiversity treatments	Reich et al. (2001)
BioDIV	e120	Biodiversity	1, 2, 4, 8, 16 species	9 × 9 m	1994 (25)	topsoil removed at beginning of experiment; annual weeding to maintain biodiversity treatments	Tilman et al. (2001)

Note: Treatments include those assessed here: nitrogen addition (+N) and biodiversity manipulation (biodiversity).

precipitation metric, and precipitation metric × global change factor. For BioCON, where both N and diversity were manipulated, we included both terms in the same model, with no interactions between the global change factors or higher order interactions, as these were not significant in preliminary analyses. In order to standardize the interpretation of estimates, precipitation metrics were scaled prior to analyses, so that the scale of the impact of a change in total precipitation matched that of SPEI. The global change factors were not standardized in this way as it is difficult to impossible to say what is an equivalent change in diversity loss and N addition.

Because existing statistical packages for linear mixed effects modelling are unable to simultaneously account for changes in degrees of freedom associated with treatments changing across space (e.g., diversity, N) and treatments changing across time (e.g., precipitation, SPEI), we calculated by hand the significance of each parameter using the estimated correct degrees of freedom (corresponding to the number of years minus the number of parameters estimated). These corrections do slightly change the significance but not the interpretations of results and serve as a check against any possible false positives due to pseudo-replication in repeated measures across years (Arnqvist 2020; see Appendix S1).

As the focus of our analyses was to ascertain how precipitation metrics affected the relationship between the global change factor and productivity, our variable of interest was the interaction between the precipitation metric and the global change factor. The experiment year main effect and interaction with the global change factors are included in the models, as previous work has shown that the effect of global change factors on productivity increases with time over the course of these experiments (e.g., Reich et al. 2012).

Results

Diversity–precipitation interactions

Water availability metrics altered the effect of biodiversity on productivity, although not universally. In BioDIV, the positive biodiversity effects on productivity were generally magnified with more water availability during the growing season (Figs. 2a, b, 3; Appendix S1: Table S1). The positive effect of biodiversity on productivity was greater both in years with more growing season total precipitation ($\chi^2 = 11.8$; $P = 0.02$) and with increasing SPEI ($\chi^2 = 3.8$; $P = 0.11$). In contrast, BioCON displayed no biodiversity–total-precipitation interaction effect ($\chi^2 = 0.9$; $P = 0.39$), but did show a surprising negative interaction between SPEI and diversity ($\chi^2 = 6.3$; $P = 0.06$), where the effect of diversity on productivity was diminished under a water surplus (Figs. 2c, d, 3; Appendix S1: Table S3).

N-precipitation interactions

Water availability magnified the effect of N addition on productivity, however, not all experiments demonstrated this interaction. Higher levels of both total growing season precipitation ($\chi^2 = 4.7$; $P = 0.09$) and SPEI ($\chi^2 = 9.0$; $P = 0.04$) increased the positive effect of N addition on productivity in BioCON (Figs. 2e, f, 3; Appendix S1: Table S3). However, the other N addition experiments (NAddExps) did not exhibit any N-precipitation interactions (total precipitation $\chi^2 = 0.2$, $P = 0.66$; SPEI $\chi^2 = 0.15$, $P = 0.71$; Figs. 2g, h, 3; Appendix S1: Table S2).

Discussion

Here we provide evidence that productivity responses to two common global change factors (biodiversity and N addition) can depend on growing season precipitation and net water availability. Although these responses are likely mediated by local site conditions and management history, theory supports the ideas that biodiversity–ecosystem-functioning relationships depend on variability in precipitation and temperature (e.g., Knapp and Smith 2001). Additionally, there is ample support in the literature for multiple-nutrient co-limitation of community productivity (e.g., Fay et al. 2015). The findings presented here not only further suggest that productivity response to global change should be climate dependent, but also that responses to global change could shift in the future with climate-change-induced shifts in water availability. While there were not meaningful changes in precipitation in central Minnesota during the duration of the studies included here, the region is expected to experience extreme rainfall events and prolonged droughts in the upcoming decades (Pryor et al. 2014).

The finding that water availability can alter the positive effect of biodiversity on productivity helps put the biodiversity–ecosystem-functioning field into a broader context. The vast number of biodiversity–ecosystem-productivity experiments, performed in many different climates, suggests that biodiversity's positive impact on productivity is robust across different levels of water availability (e.g., see universality of responses in Cardinale et al. [2013]). In dryland systems, for example, species diversity is known to be vital to maintaining ecosystem productivity and functionality, particularly with increased environmental stressors due to climate change (Maestre et al. 2012), likely due to microclimate amelioration (Wright et al. 2017). Across climates, temporal variation in precipitation also offer insights. For example, prior work at Cedar Creek demonstrated that, under drought conditions, communities with high diversity maintain productivity better than those with low diversity (Tilman and Downing 1994). Findings from the long-term biodiversity experiment in Jena, Germany also suggest relatively minor effects of flooding on species composition and biodiversity–productivity

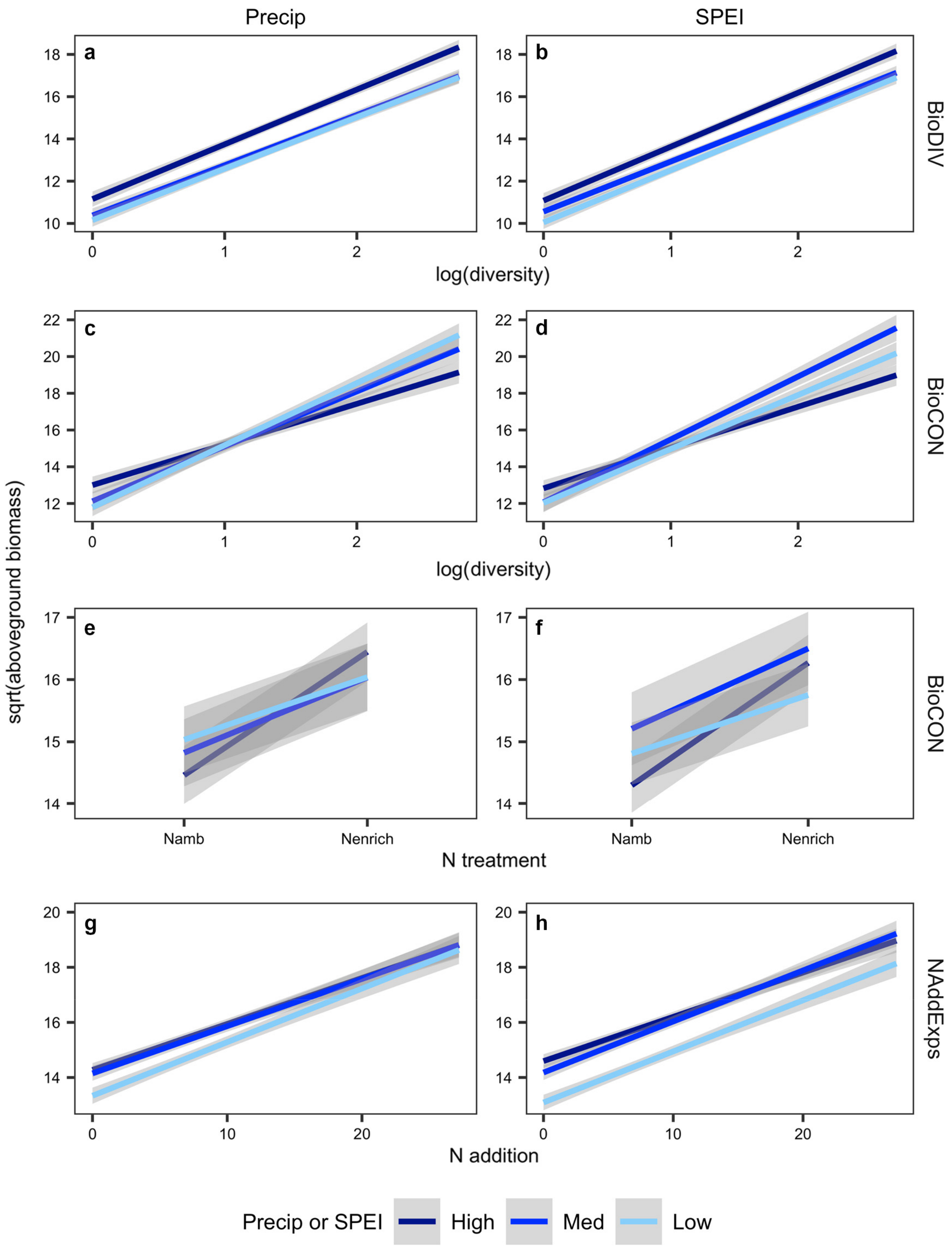

FIG. 2. Aboveground biomass response to biodiversity and N addition for low, medium, and high levels of water availability. Figures show square-root-transformed (sqrt) aboveground biomass by experimental treatment: (a–d) species diversity level (log-transformed), (e–f) N addition factor (ambient or enriched, 4 g N·m^{-2}·yr^{-1}, for BioCON), or (g–h) N addition level (g N·m^{-2}·yr^{-1}for NAddExps). Water availability is shown as high, medium, low classes (determined as the lower, middle, and upper third) for both total growing season precipitation (Precip_Level; a, c, e, g) and growing season Standardized Precipitation–Evapotranspiration Index (SPEI_Level; (b, d, f, h). Gray bands around lines represent ± 1SE from the mean. Precip and SPEI were analyzed as continuous variables in all statistical models, but are shown in the figure as binned categorical variables to depict these effects.

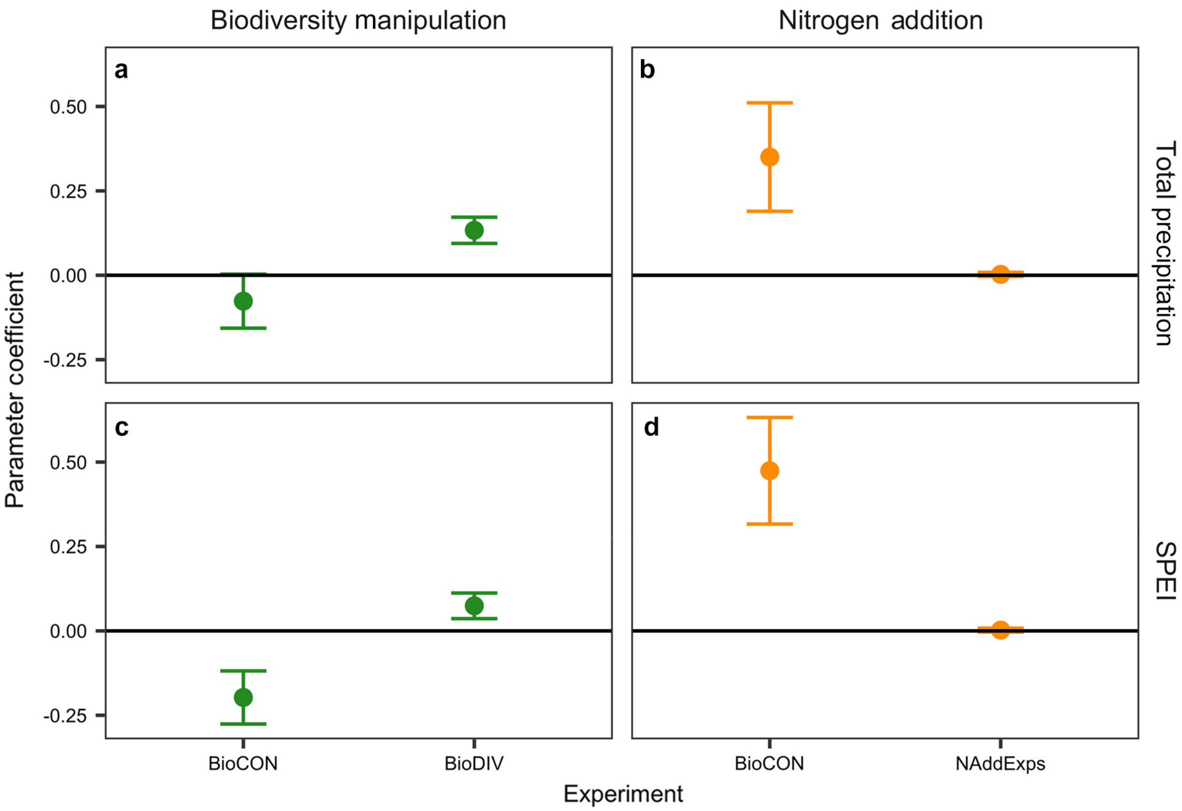

Fig. 3. Parameter estimates for interaction effects between global change treatment and water availability metric. Mean parameter estimates are shown with ±SE, such that values above zero reflect positive interaction effects between global change factor (i.e., diversity or nitrogen addition) and water availability proxy (total precipitation or SPEI), and values below zero reflect negative interaction effects. Diversity parameters (from BioDIV and BioCON experiments) are in green in the left panel (a, c) and N addition parameters (from NAddExps and BioCON) are in orange in the right panel (b, d). The top panel (a, b) shows parameters for total growing season precipitation (April-July) and the bottom panel (c, d) shows parameters for the growing season Standardized Precipitation–Evapotranspiration Index (SPEI), both of which are scaled between 0 and 1 for comparable results. Parameter estimates non-overlapping with zero are significant (i.e. $P < 0.05$).

relationships (Wright et al. 2015, Weisser et al. 2017), although diverse communities appear to recover from flooding better than those with fewer species (van Moorsel et al. 2020). Indeed, an analysis of grassland systems globally found highly diverse communities to be more resistant than less diverse communities to both extreme wet and extreme dry years (Isbell et al. 2015). Although there are many other factors at play in these different ecosystems including, but not limited to, soil texture, soil fertility, plant community composition, and meteorological conditions, the general patterns offer insight into how water availability may influence the effects of biodiversity on productivity.

Diversity experiments where water availability is manipulated are also increasing (e.g., TeRaCON and droughtnet; see Knapp et al. [2017]), and offer additional evidence on the role of species diversity under variable and changing precipitation. Drought by diversity experiments have shown that positive effects of diversity on grassland productivity are sustained during drought (Vogel et al. 2012), despite lower absolute productivity (Craven et al. 2016) and that the negative impacts of drought are less strong at higher diversity (Wagg et al. 2017).

The second finding that N addition effects on productivity can be enhanced at high water availability is broadly supported by literature on multiple-element limitation (e.g., Harpole et al. 2011). For example, the co-limiting effects of N and water availability on ecosystem productivity have been documented in a California grassland, where sites with both N and water enhancement experienced greater productivity and also exhibited shifts in species richness and abundance (Harpole et al. 2007). Findings from a global meta-analysis of grassland community response to experimental additions of N, water, and both N and water highlight the prevalence of this N and water co-limitation, as well as the heterogeneity in responses across different studies (DeMalach et al. 2017). As our results also demonstrate, multiple nutrient or resource limitation is not always straightforward and can rely heavily on the individual species and site conditions, as well as current and past weather conditions (Zavaleta et al. 2003).

The findings presented here highlight the potential importance of other site-specific factors related to experimental design and management history. Despite their close physical proximity (<5 km) and similar soil type and species pools, the two diversity experiments assessed here showed different responses with water availability (a positive interaction in BioDIV and negative interaction in BioCON). BioDIV (started in 1994) is a longer running experiment than BioCON (started in 1998) and has experienced greater variations in precipitation (Fig. 1). However, our results were qualitatively similar when we subset BioDIV data to only include the years in which BioCON was running (1998–2018), although, in doing so the SPEI effect in BioDIV was lost. Last, the management histories of the two experiments are different: the BioDIV experiment had topsoil removed as part of its establishment in 1994, whereas the BioCON experiment retained its topsoil (which was instead fumigated to minimize plot to plot differences in microbial communities). As a result, BioDIV plots lost carbon initially, which has been re-established in high-diversity plots but not in species poor plots (Yang et al. 2019). The more carbon-rich soils in the higher biodiversity plots likely have greater water-holding capacity than the species-poor plots with less organic matter (Hudson 1994). And, compared to BioCON, the difference in soil fertility between the low and high diversity plots may be greater in BioDIV as a lasting legacy of the experimental setup, thus magnifying the interaction between diversity and water availability. If this holds true, it would suggest that especially degraded or low-fertility soils may be more likely to show an interaction between water availability and biodiversity, which could be especially relevant given current and expected soil degradation worldwide (FAO 2015).

Similar to the two biodiversity experiments included in this study, the two N addition experiments assessed also showed different patterns with water availability despite their close proximity, and similar soil type, climate, and species pools. However, differences in experiment maintenance could have played a role in their different responses. For example, one difference between the experiments was how they were maintained: in BioCON, where we found a positive interaction between N addition and water availability, planted species richness was maintained through weeding, whereas in NAddExps, where we found no interaction, the plant community was unmanipulated. Given the influence that plant community composition, including functional group composition, can have on biomass production (Marquard et al. 2009) and that communities show varying degrees of co-limitation by N and water (DeMalach et al. 2017), the difference in how experiments were maintained could have affected the degree of resource limitation observed. However, prior work has shown N addition leads to a reduction in species richness and an increase in relative abundance of C_3 grasses, with concomitant declines in C_4 grasses and legumes, in both BioCON (Reich 2009) and NAddExps (Isbell et al. 2013*b*). Another difference between BioCON and NAddExps is whether or not plots are burned. A lack of burning in NAddExps, and the shift in dominance to *Elymus repens*, has resulted in the buildup of a thick litter layer in N addition plots (Isbell et al. 2013*b*), which may have led to greater soil water retention thus minimizing the impacts of precipitation. In contrast, plots in BioCON have been burned either every year or every other year since establishment, limiting the amount of litter build up and potentially increasing the sensitivity to water availability. Although the prevalence of N and water co-limitation has been well documented (DeMalach et al. 2017), and shown to depend on soil nutrient status (Eskelinen and Harrison 2015), further work that explores additional biotic and abiotic controls could help inform variability in degrees of co-limitation observed (DeMalach et al. 2017), including from this study.

CONCLUSION

The finding that water availability can magnify the net positive effects of biodiversity and N addition on productivity has implications for understanding how climate change will impact ecosystems. With global change, plant species diversity, N addition, and water availability are all in flux (e.g., Willis and Bhagwat 2009, IPCC 2014, Wieder et al. 2015). Specifically, precipitation (and water availability, by proxy) is projected to increase in some places and decrease in others, with widespread increases in intra-annual variability (Pryor et al. 2014). Although we did not explicitly assess impacts of drought (Cedar Creek experienced just two droughts during the duration of these experiments), the findings from BioCON described here suggest that high-diversity communities can buffer themselves against water limitation in drier years. During the study period, Cedar Creek also likely did not experience precipitation conditions that resulted in frequent or long-term soil saturation, which is partly due to the coarse-structured soils found at the site. However, soil saturation could decrease the otherwise positive effects of biodiversity or N addition on productivity if plants are waterlogged and function is diminished. Future work could explore the potential dependency of the positive interactions observed here on the degree of drought or wetness. In particular, experimental manipulations of water availability could test the hypothesis that the positive interaction effect between diversity or N addition and water availability would reach a point of diminishing return. However, absent extensive global change experiments to test these interactions, long-term experiments paired with precipitation records create the opportunity to test important questions on the combined effects of water and nutrient availability on ecosystem function and productivity.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2363/full

Open Research

Data are available from the Environmental Data Initiative. Aboveground biomass data are available from Tilman (2020*a*) at https://doi.org/10.6073/pasta/13940d0f82389887764ab8142a11ce69, Tilman (2020*b*) at https://doi.org/10.6073/pasta/03f58013909c3ce4482d1333dc813279, Tilman (2021) at https://doi.org/10.6073/PASTA/7EF2DE3865062D7352F7B20753ECD39B, and Reich (2020) at https://doi.org/10.6073/pasta/ec929b4fec86eaf676d2a293694175d2. Weather data are available from Seeley (2020) at https://doi.org/10.6073/pasta/81cabf5e01842aa1464dee3dcf6f2860.