Increased productivity in wet years drives a decline in ecosystem stability with nitrogen additions in arid grasslands

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Abstract. Adding nutrients to nutrient-limited ecosystems typically lowers plant diversity and decreases species asynchrony. Both, in turn, decrease the stability of productivity in the response to negative climate fluctuations such as droughts. However, most classic studies examining stability have been done in relatively wet grasslands dominated by perennial grasses. We examined how nutrient additions influence the stability of productivity to rainfall variability in an arid grassland with a mix of perennial and annual species. Of the nutrients, only nitrogen increased productivity, and only in wet years. In addition, only nitrogen decreased the stability of productivity. Thus, nutrient addition makes ecosystem productivity less stable in both wet and arid grasslands. However, the mechanism is very different. In contrast to wet grasslands, adding nitrogen to an arid grassland did not decrease diversity. Rather, stability decreased with nitrogen addition due to an increase in annual species that increased productivity. In other words, in our arid grassland, nitrogen addition decreased ecosystem stability because of increased ecosystem responsiveness to positive climate fluctuations. These climate fluctuations were facilitated by annual species that take advantage of wet years and can escape dry years as seeds. Our data support the conclusion that nutrient additions decrease the stability of productivity in both wet and arid grasslands. Nutrient enrichment increases the sensitivity of productivity to low rainfall years in wet grasslands, whereas nutrient enrichment in arid grasslands increases the sensitivity of productivity to high rainfall years.

Key words: arid grassland ecosystem; community stability; diversity; eutrophication; fluctuating limiting resource; mechanism; productivity; species composition.

INTRODUCTION

Observational and experimental biodiversity and ecosystem functioning studies have identified that diversity begets stability (Tilman and Downing 1994, Ives et al. 2000, Pfisterer and Schmid 2002, Tilman et al. 2006, Isbell et al. 2009, Hautier et al. 2014). High diversity can buffer ecosystem productivity from negative perturbations caused by disturbances such as droughts and eutrophication (Tilman and Downing 1994, Hautier et al. 2014). Asynchronies in how species respond to variation in climate and resources is one common mechanism causing increased ecosystem stability with increased diversity (Hector et al. 2010, Loreau and Mazancourt 2013). Hence, decreases in diversity can lead to lower stability of productivity and negative consequences for ecosystem functioning, either because fewer species are present or because of a decrease in species asynchrony (Hautier et al. 2014).

Eutrophication has been identified as one of the major factors decreasing stability because eutrophication lowers diversity and induces species composition and dominance changes (Tilman and Downing 1994, Vitousek et al. 1997, Downing and Leibold 2002, Haddad et al. 2002, Srivastava and Vellend 2005, Ives and Carpenter 2007, Borer et al. 2014). Temporal stability of productivity, commonly calculated as the ratio of the temporal mean of productivity to the temporal standard deviation of productivity, can increase because of either an increase in the mean, a decrease in the standard deviation, or both (Hautier et al. 2014). Hautier et al. (2014) found that, across 41 grassland sites, higher diversity decreased the temporal variability of productivity because species asynchrony was positively correlated with plant diversity and stability, whereas the productivity mean was not related to plant diversity. Fertilization within these grassland sites not only reduced plant diversity and increased productivity, but also increased the temporal variation of productivity because of a decrease in species asynchrony. As a result, the positive effect of diversity on stability was weakened. Implicit in all these diversity–stability studies is the notion that increased stability with higher diversity has positive effects for ecosystem functioning (Cardinale et al. 2013). Directly or indirectly, this view is largely based on evidence from relatively wet grasslands limited mainly by nitrogen or other nutrients (Tilman et al. 2006, Hautier et al. 2014, Fay et al. 2015).

In contrast to wet, productive grasslands, many grasslands worldwide are located in relatively dry, arid environments where either water is the key factor limiting productivity or where water, along with nutrients, colimits its productivity (Sala et al. 2012). This is the case for our study site, in western Nebraska, USA. In a normal year, water limits productivity. In a wet year, nutrients limit productivity (Hooper and Johnson 1999). Because rainfall in arid grasslands varies strongly over time, the limiting resource for ecosystem productivity also varies strongly over time (Huston 1997). Furthermore, species composition differs between grasslands. Long-lived perennial grasses dominate relatively wet, nutrient-limited grasslands. In contrast, annual species can be an important component of the vegetation in arid grasslands (Eurasian Dry Grassland Group ; Papanastasis 1999). Many of these annuals respond to different germination cues, often linked to the amount and timing of precipitation; thus species composition can fluctuate over time (Knapp and Smith 2001).

Here, we used a long-term grassland nutrient addition study located at Cedar Point Biological Station in Western Nebraska, part of the Nutrient Network Global Research Cooperative, to examine nutrient addition effects on productivity and the stability of productivity. We hypothesized that. within this arid, relatively dry grassland (1) species diversity does not change as a result of nutrient additions because nutrients are not influencing productivity in the frequent dry years; (2) species composition fluctuates over time because annual species composition and abundances vary with rainfall; (3) nutrient addition decreases the stability of productivity because of a stronger increase in productivity in wet years due to increased annual species abundance rather than a decline of productivity in dry years; (4) species asynchrony increases with nutrient addition because of an increase in annual species dominance in wet years; and (5) longer-term, annual species seed production increases in wet years in nutrient fertilized treatments, leading to an increased seed bank that magnifies the annual responsiveness in wet years with nutrient additions.

MATERIALS AND METHODS

Study site and experimental design

Our study site is located (41°.12′ N, 101°.38′ W, 965 m above sea level) in Western Nebraska, USA, which has a dry, continental climate. Annual rainfall varies from a low of 168 mm to a high of 601 mm with ~80% falling during April–September (1997–2014). Potential annual evapotranspiration averages 1885 mm and varies from 1,631 to 2,301 mm. July is the warmest month with an average low of 17°C and a high of 32°C. December is the coldest month with an average low of −8°C and a high of 5°C. The shallow and rocky soils are part of the Tassel series formed from calcareous sandstone (Scheinost et al. 1995), containing, on average,

1.3% carbon ($n = 60$, range 0.8–2.7%) and 0.11% nitrogen ($n = 60$, range 0.08–0.21%) at 0–10 cm depth. The vegetation is dominated by a perennial sedge *Carex filifolia*; perennial grasses such as *Stipa comata*, *Bouteloua gracilis*, and *Buchloe dactyloides*; and, in wet years, annual species such as *Bromus tectorum* and *Helianthus annuus*.

The experimental design and nutrient addition protocols follows the Nutrient Network Global Research Cooperative (Borer et al. 2014, Hautier et al. 2014). Cattle grazing was excluded from the entire site. Nitrogen (N), phosphorus (P), and potassium (K) plus micronutrients were added in a three-way factorial design, with an N addition rate of 10 g N m^{-2}, P at 10 g m^{-2}, and K at 10 g m^{-2}, for a total of eight treatment combinations. The eight treatments were placed in a randomized block design of six blocks, for a total of 48 plots. Herbivory from animals such as deer, rabbits, and field mice was examined with two additional fenced treatments included in each block, one without nutrient addition and one with NPK addition, for a total of 12 additional plots. Each of the 60 5 × 5 m plots was separated by a 1-m buffer zone, and setup with initial sampling started in 2007. All nutrients were added once annually starting in 2008. N was added as time release urea, P as triple super phosphate, and K as potassium sulfate. Micronutrients were added to the K treatment only in 2008.

Vegetation sampling

Plant cover by species and total productivity were collected every year in one permanently marked 1-m^2 subplot at peak plant productivity in either the last week of June or the first week of July during 2008–2014. Plant cover to the nearest 1% was recorded for each plant species using a modified Daubenmire method (Daubenmire 1959). The percent cover of litter and bare soil were also estimated. Community-level productivity was measured destructively by clipping all aboveground biomass of individual plants rooted within two 10 × 100 cm strips at ground level; different areas were clipped over time. All plant samples were weighed to the nearest 0.01 g after drying at 60°C to constant dry mass. Weather data from a weather station located <1 km from the site were used (High Plains Regional Climate Center; data *available online*).[4]

Data analyses

The temporal stability of productivity was defined for each plot as μ/σ (Tilman 1996), where μ is the mean of productivity and σ is the standard deviation of productivity over the seven years from 2008 to 2014. Species asynchrony equals $1 - \sigma^2/(\sum_{i=1}^{S} \sigma_i)^2$, where σ has already been defined, σ_i is the temporal standard

[4] http://www.hprcc.unl.edu/

deviation of the cover of species i, and S is the total species in the plot (Hautier et al. 2014).

The temporal stability of productivity and species asynchrony were analyzed using a general linear model; all other data were analyzed using linear mixed-effects models with year and plot as random effects to account for the repeated measure across time.

The three nutrients (N, P, and K) were considered as fixed factors, and we used rainfall as a covariance factor to examine productivity, species richness, and annual abundance. The six blocks were included as a random factor; however, we removed the block factor because it had no significant effect on either productivity or stability. The relationship between plant diversity, species asynchrony, and annual abundance with temporal stability of productivity were analyzed using correlations. All hypothesis testing used a two-tails approach. All the analyses were performed in R V.3.3.1 (R Foundation for Statistical Computing, Vienna, Austria) using glm or lmer in library lmerTest, along with type 2 comparisons from library car. The library MuMIn was used to report model-level marginal R^2 values, which represent the variation explained by the fixed effects (Nakagawa and Schielzeth 2013).

RESULTS

Nitrogen was the only nutrient that significantly increased productivity over the seven years; however, there was a significant interaction between N addition and rainfall (Table 1). Compared to the control, the N addition treatment increased productivity significantly more with increased rainfall (Table 1, Fig. 1a; nitrogen slope = 2.57, control slope = 1.02, nitrogen × rainfall interaction $F_{1,281.9} = 44.96$, $P < 0.001$). Similar to productivity, the temporal stability of productivity across years was only significantly, negatively influenced by N addition (Table 2, Fig. 2a). Alternative methods to quantifying

stability with resistance or resilience (sensu Isbell et al. 2015) showed qualitatively the same results: N was the only significant nutrient (Appendix S1: Fig. S2).

Nitrogen addition and its interaction with rainfall significantly influenced annual species abundance (Table 1, Fig. 1c). In both the control and the N addition treatments, annual species abundance changed only with rainfall; the change was much stronger in the N addition treatment (Fig. 1c, Fig. 3). Across the 48 plots, the temporal stability of productivity was not correlated with the average species richness ($r = 0.107$, $P = 0.470$) nor with species asynchrony across years ($r = -0.140$, $P = 0.343$). However, the temporal stability of productivity was related to the average abundance of annual species ($r = -0.309$, $P = 0.033$). *Bromus tectorum*, *Panicum capillare*, *Chenopodium album*, *Conyza ramosissima*, *Helianthus annuus*, and *Lepidium densiflorum* mainly drove the annuals' response (Fig. 3). Note that all the dominant species in both the annual and perennial functional groups are native, except for *Bromus tectorum* (Keller et al. 1980). However, the response of annuals to climate and N addition was only partly driven by *Bromus*, as demonstrated by the variable importance of non-*Bromus* annuals in different years, for example 2010 vs. 2013 (Fig. 3).

Species richness varied among the years, driven by rainfall differences (Table 1, Fig. 1b). However, in contrast to productivity and the temporal stability of productivity, N additions did not significantly change species richness (Table 1, Fig. 1b, Appendix S1: Table S1, Fig. S1) or species asynchrony (Table 2, Fig. 2b; Appendix S1: Table S2). Fencing did not influence productivity or the temporal stability of productivity (Appendix S1: Tables S1, S2). Furthermore, fencing did not influence either species richness, species asynchrony or annual species abundance (Appendix S1: Tables S1, S2).

TABLE 1. Model results of productivity, species richness and annual species abundance with nitrogen (N), phosphorus (P), and potassium (K) additions and their interactions.

Covariate	Productivity		Species richness		Annual species abundance	
	df	F	df	F	df	F
N	1, 327.8	7.55**	1,213.0	0.10	1,176.0	0.77
P	1, 327.8	0.12	1,213.0	1.29	1,176.0	0.01
K	1, 327.8	0.50	1,213.0	0.63	1,176.0	0.54
Rainfall	1, 7	11.90*	1,6.6	55.64***	1,6.9	6.25*
N × P	1, 47.1	0.005	1,47.9	0.04	1,47.5	1.00
N × K	1, 47.1	0.142	1,47.9	0.64	1,47.5	0.04
P × K	1, 47.1	0.012	1,47.9	0.001	1,47.5	0.04
N × Rainfall	1, 281.9	44.96***	1,281.7	1.5	1,281.9	11.31***
P × Rainfall	1, 281.9	0.000	1,281.7	0.48	1,281.9	1.36
K × Rainfall	1, 281.9	1.84	1,281.7	0.20	1,281.9	1.01
N × P× K	1, 47.1	5.79*	1,47.9	0.08	1,47.4	1.54

Notes: Models include rainfall as a covariate. Replication is 48 plots repeated across seven years for productivity, with random effects for plot and year. For productivity, the marginal $R^2_{GLMM} = 0.440$; for species richness, the marginal $R^2_{GLMM} = 0.246$; for annual species abundance, the marginal $R^2_{GLMM} = 0.213$. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
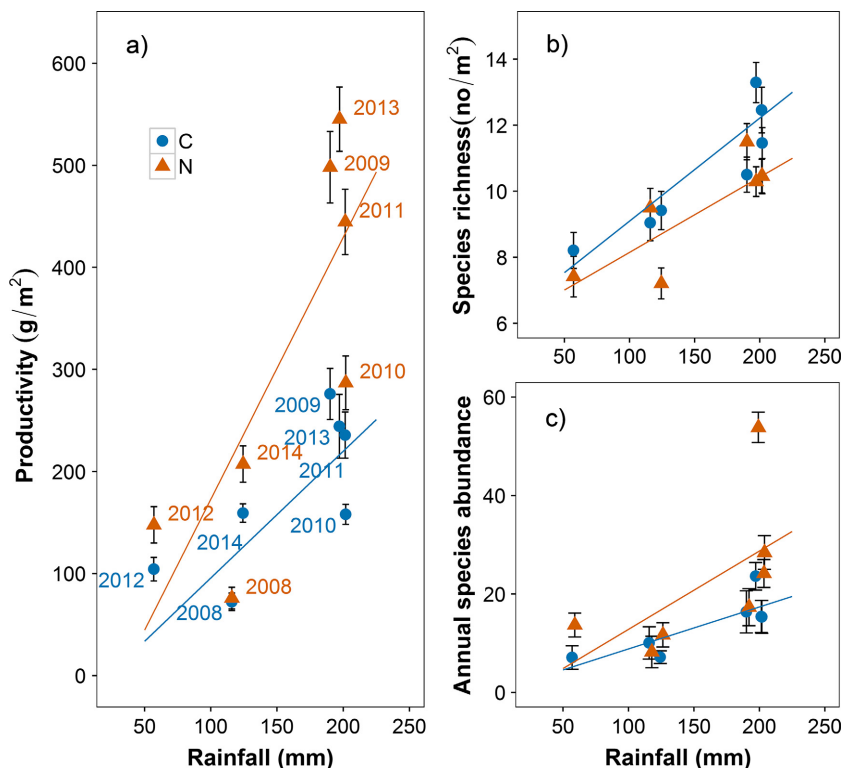
Fig. 1. Relationships among (a) productivity, (b) species richness, and (c) annual species abundance vs. rainfall (May–June), combining 24 plots with nitrogen addition (N) vs. 24 plots without nitrogen addition (C). We found a significant interaction between N and rainfall for productivity and annual species abundance, while only a main effect of rainfall for species richness (Table 1). Data are presented as mean ± SE. [Color figure can be viewed at wileyonlinelibrary.com]

DISCUSSION

Productivity and its temporal stability

Nutrients, especially N, are commonly important limiting factors for productivity in many types of grasslands (Fay et al. 2015). Much of our current understanding of

TABLE 2. Model results of species asynchrony with nitrogen (N), phosphorus (P), and potassium (K) additions and their interactions.

Covariate	Temporal stability of productivity		Species asynchrony	
	df	F	df	F
N	1,40	30.34***	1,40	3.11
P	1,40	1.71	1,40	0.002
K	1,40	0.03	1,40	0.53
N × P	1,40	1.00	1,40	0.05
N × K	1,40	0.02	1,40	1.56
P × K	1,40	0.65	1,40	1.35
N × P × K	1,40	0.02	1,40	2.01

Notes: Replication is a single measure for each of 48 plots because data across years is used to create the single metric. For temporal stability of productivity, $R^2 = 0.418$; for species asynchrony, $R^2 = 0.155$. ***$P < 0.001$.

how plant diversity influences ecosystem functioning is based on nutrient-limited grasslands (Tilman et al. 2006, Hautier et al. 2014). However, the distribution of different types of grasslands in North America, i.e., tall grass, mixed grass and short grass prairies, is driven by gradients in precipitation. Additionally, many grasslands worldwide are located in relatively dry, arid environments where water is, in many years, the primary factor limiting productivity (Knapp and Smith 2001). Current consensus is that nutrient additions increase productivity and decrease temporal stability of productivity (Tilman et al. 2006, Bezemer and van der Putten 2007, Isbell et al. 2009, Cardinale et al. 2013, Hautier et al. 2014). However, this consensus is largely based on studies in primarily nutrient-limited, relatively wet grasslands, and does not fit the data of our arid, primarily water-limited grassland. Our study site is part of the network of 41 sites in the Nutrient Network Global Research Cooperative where stability in grasslands has been examined (Hautier et al. 2014). The majority of these sites (32 out of 41) are located in relatively wet areas with annual precipitation between 521 to 1,898 mm; only nine sites have precipitation of <450 mm annually (Hautier et al. 2014). Furthermore, the response of nutrient additions increases with rainfall (Lee et al. 2010). Many, if not the majority, of the world's grasslands are water limited
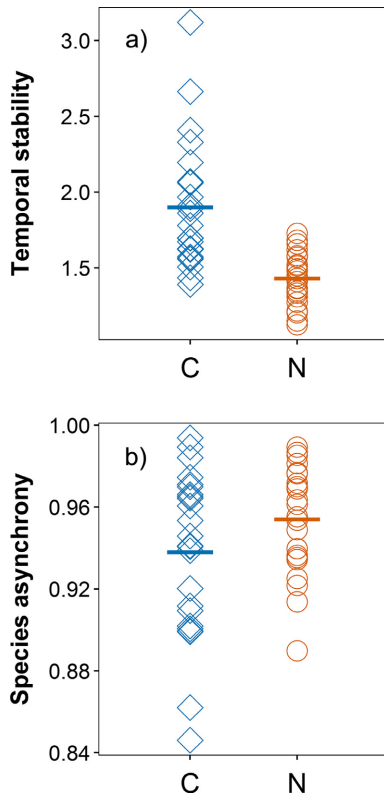
Fig. 2. (a) Temporal stability and (b) species asynchrony response of 48 plots across seven years of nitrogen addition (N) vs. without nitrogen addition (C). Heavy lines show mean values. The main effect of nitrogen on temporal stability was the only significant response across all nutrient addition treatments (Table 2). [Color figure can be viewed at wileyonlinelibrary.com]

(Sala et al. 2012). Therefore, this skew in research locations is a major limitation of studies examining overall patterns in grasslands.

In the arid, relatively dry grassland we studied, rainfall is the primary limiting factor for productivity in most years, and N limitation is a secondary factor during wet years. The temporal stability of productivity also decreased with N addition, consistent with other studies (Tilman et al. 2006, Isbell et al. 2009, Hautier et al. 2014). However in contrast to other studies, we found no significant change in species richness or species asynchrony. Species composition strongly fluctuated over time, linked with an increase in annual species abundance in wet years. Thus consistent with our hypothesis for this arid grassland, N addition does not lead to a decline in plant diversity, nor does it change species asynchrony. Productivity in dry years does not increase with N addition. However, in wet years, annual species abundance increases more in the N addition treatment. Hence, N fertilization increases the responsiveness of productivity to rainfall driven by a plastic response of annual species. This pattern became stronger over the seven years of N additions, likely because of increased seed production and an increase in the annual seedbank (Fig. 3).

Consistent with our results, several other studies in arid grasslands also found that species diversity is not the primary factor influencing the stability of productivity (Sankaran and McNaughton 1999, Grime et al. 2000, Bai et al. 2004). These studies identified compensatory interactions among dominant species (Grime 1998, Sasaki and Lauenroth 2011) or among functional groups, in particular between annuals and perennials (Bai et al. 2004) as mechanisms influencing community-level stability. Grman et al. 2010 also found that human-driven disturbances such as N fertilization can shift community composition towards species with shorter lifespans and greater seed production. Whereas the response of the plant community in our study was driven by annual species, different mechanisms may drive a similar response in other arid grasslands.

Temporal stability of productivity in wet vs. arid grasslands

Here, we propose a different conceptual framework for the temporal stability of productivity in arid grasslands (Fig. 4). In wet grasslands (Fig. 4a) most years are relatively wet (gray area) and occasional climate fluctuations result in dry years, i.e., droughts (Tilman and Downing 1994). During the "normal" wet years, nutrient additions increase productivity, enhancing competition for light, which in turn decreases plant diversity and species asynchrony. As a result of nutrient additions, this decreased plant diversity and species asynchrony increases the sensitivity to climate fluctuations. Hence, a sharper decline in productivity occurs in dry years with nutrient additions (Haddad et al. 2002).

In arid grasslands (Fig. 4b), a "normal" year is relatively dry (gray area) and water limits productivity. Therefore, there is no increase in productivity with nutrient enrichment. Consequently, nutrient enrichment does not affect light competition or any other competitive interactions among plant species, resulting in unchanged plant diversity. In wet years, the productivity in both control and fertilized treatments increases. However, because arid grasslands are nutrient-limited (Huston 1997) rather than water-limited in wet years, nutrient enrichment more strongly increases productivity compared to the control (Hooper and Johnson 1999). Furthermore, arid grasslands can contain a large pool of annual plant species that depend on germination cues linked to the timing and amount of precipitation. These species are opportunistic in their development and growth patterns (Beatley 1974, Yan et al. 2015). Vegetation composition differs in wet years because of differences in the abundance of annual species. Within arid ecosystems, annual species can be a strong driver of how such ecosystems respond to climate fluctuations. However, because such annual species retreat to the soil seed bank in subsequent frequent dry years, such nutrient-induced vegetation changes disappear in the short term, and patterns of diversity may not capture this storage
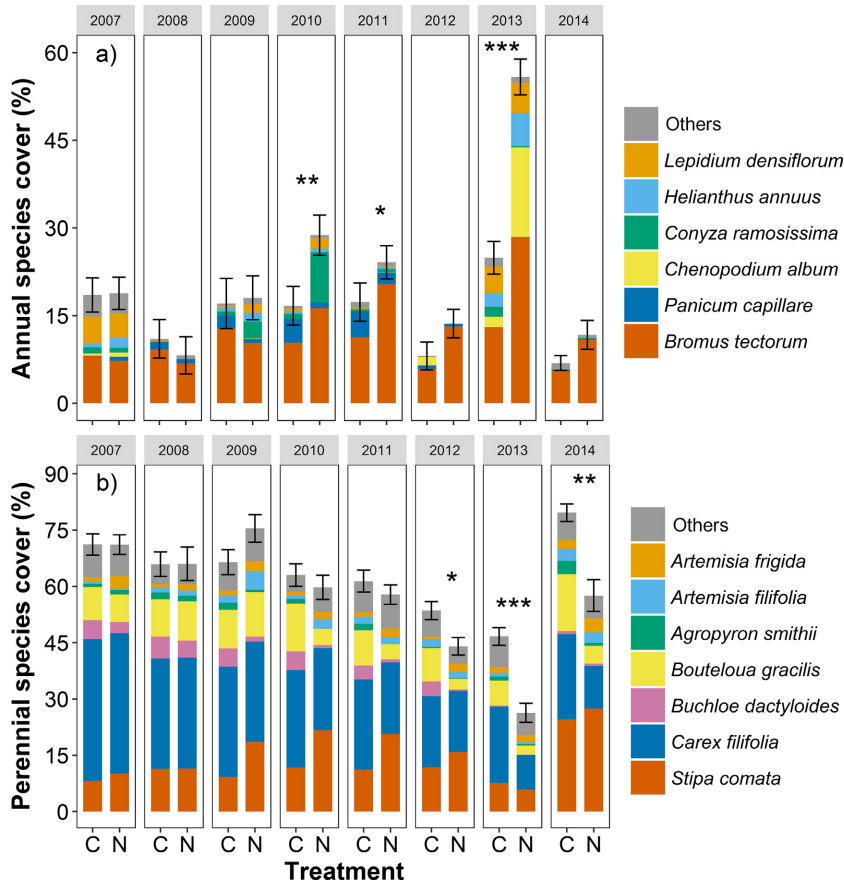
FIG. 3. Cover of the most abundant (a) annual species and (b) perennial species in control (C) and nitrogen addition (N) treatments. Data are presented as mean $\pm$ SE (n = 24) for each year from 2007 through 2014. $*P < 0.05$; $**P < 0.01$; and $***P < 0.001$. [Color figure can be viewed at wileyonlinelibrary.com]
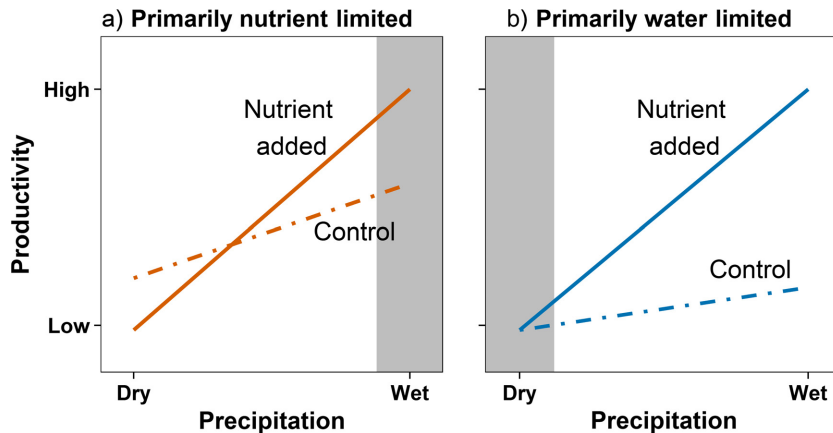

FIG. 4. Conceptual diagram of primarily nutrient limited vs. primarily water limited productivity in grasslands. (a) In wet grasslands, most years are relatively wet (gray area) and occasional climate fluctuations result in dry years. Because of the reduced diversity from nutrient enrichment, in a dry year there is a steeper decline in productivity resulting in decreased stability. (b) In arid grasslands, a "normal" year is relatively dry (gray area), productivity is water limited, and nutrient enrichments does not change productivity. However, because of the response from annual species, in a wet year there is a steeper increase in productivity resulting in decrease stability via a different mechanism than in wet grasslands. [Color figure can be viewed at wileyonlinelibrary.com]

effect of annuals. Thus, ecosystems where annuals are an important component of diversity and productivity behave much differently than ecosystems dominated by perennials (Isbell et al. 2015, Craven et al. 2016). Longer term, increased seed production may lead to a greater representation of annual species in fertilized grasslands.

In summary, with nutrient enrichment, the temporal stability of productivity decreases in both wet and arid grasslands. However, the underlying mechanisms and their implications for ecosystem function are very different. In wet grasslands, nutrient enrichment increases productivity in "normal" wet years (Lee et al. 2010); however, because of the much stronger decrease in productivity due to nutrient enrichment in subsequent dry years (Grime et al. 2000, Haddad et al. 2002), ecosystem functioning is negatively influenced by nutrient enrichment (Cardinale et al. 2013, Hautier et al. 2014). In contrast, in arid grasslands ecosystem functioning is positively influenced by nutrient enrichment because of the steeper increase of productivity with increased precipitation in wet years. Adding a secondary limiting resource, nitrogen, in a primarily water-limited grassland decreases ecosystem stability because of increased responsiveness to annual variability. Thus, how ecosystems respond to resource enrichment depends on whether the resource enrichment is a primary or secondary limiting factor for productivity.

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