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# Nitrogen addition and ecosystem functioning: Both species abundances and traits alter community structure and function

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**Citation:** Tatarko, A. R., and J. M. H. Knops. 2018. Nitrogen addition and ecosystem functioning: Both species abundances and traits alter community structure and function. *Ecosphere* 9(1):e02087. 10.1002/ecs2.2087

**Abstract.** Increased nutrient inputs can cause shifts in plant community composition and plant functional traits, both of which affect ecosystem function. We studied community- and species-level leaf functional trait changes in a full factorial nitrogen (N), phosphorus (P), and potassium (K) fertilization experiment in a semi-arid grassland. Nitrogen was the only nutrient addition to significantly affect leaf functional traits, and N addition increased community-weighted specific leaf area (SLA) by 19%, leaf chlorophyll content by 34%, height by 26%, and leaf dry matter content (LDMC) decreased by 11% while leaf thickness and toughness did not change significantly. At the species level, most species contributed to the community-weighted trait and increased in SLA, chlorophyll, height, and LDMC with N addition. These intraspecific changes in functional traits account for 51–71% of the community-level changes in SLA, chlorophyll, plant height, and LDMC. The remaining change is due to species abundance changes; the two most abundant species (*Bouteloua gracilis* and *Carex filifolia*) decreased in abundance with N addition while subdominant species increased in abundance. We also found annual variation in SLA, chlorophyll, plant height, and LDMC to be as important in influencing traits as N addition, likely due to differences in precipitation. Aboveground net primary productivity (ANPP) did not change significantly with N addition. However, N addition caused a 34% increase in leaf area index (LAI) and a 67% increase in canopy chlorophyll density. We demonstrate that nitrogen-induced changes in both functional traits and species abundances magnify ANPP changes in LAI and canopy chlorophyll density. Therefore, ANPP underestimates N addition-induced ecosystem-level changes in the canopy vegetation.

**Key words:** community structure; community-weighted traits; functional trait; grassland ecology; nutrient addition.

**Received** 7 December 2017; accepted 11 December 2017. Corresponding Editor: Debra P. C. Peters.

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## INTRODUCTION

Human activities are altering the availability of resources in ecosystems worldwide, and environmental change can cause shifts in plant community structure and function (Vitousek et al. 1997, Peters and Meybeck 2000, Baer et al. 2004). Many studies examining the effects of environmental change on plant communities focus on its isolated impact on community composition, functional trait values, or aboveground net primary productivity (ANPP; Stevens et al. 2004,

2015, Yavitt et al. 2011, Fay et al. 2015, Harpole et al. 2016). However, environmental change can simultaneously effect species functional traits and abundances, shifting overall community structure and function (La Pierre and Smith 2014, Siefert and Ritchie 2016). Therefore, environmental change has the potential to indirectly alter ecosystem functions such as the cycling of water, nutrients, and energy by altering the physiology or morphology of individuals, which then scales up to alter community structure and function, and subsequent ecosystem functions (Díaz and

Cabido 2001, Suding et al. 2008, Lavorel and Grigulis 2012). Here, we examine how shifts in both plant functional traits and species abundances contribute to community-level changes in plant resource acquisition–resource use strategies. We examined six, aboveground functional traits, which combined, are key in determining photosynthetic capacity, growth, and productivity: specific leaf area (SLA; Reich et al. 1997, Garnier et al. 2004), leaf chlorophyll content (Chapman and Barreto 1993, Wright et al. 2004), plant height (Tilman 1987, Fonseca et al. 2000, Pérez-Harguindeguy et al. 2013), leaf thickness, leaf toughness, and leaf dry matter content (LDMC; Choong et al. 1992, Cunningham et al. 1999, Pérez-Harguindeguy et al. 2013).

We examined community-level functional traits which weigh species functional traits by species abundances (Grime 1998). Changes in community-level functional traits can be caused by either intraspecific changes in functional traits, changes in species abundance (including species turnover), or both. Ignoring the effects of either of these factors can lead to a mischaracterization of the community response to environmental change and partitioning the effects of each can help us quantify their respective effects on ecological processes (Grime 1998, Bolnick et al. 2011). Studies have shown that intraspecific trait changes due to biotic and abiotic factors can be substantial (Albert et al. 2011). In addition, functional traits have been shown to vary consistently with changes in environmental conditions at multiple scales and across multiple species (Reich et al. 1997, Siefert and Ritchie 2016). The creation of novel environmental conditions may allow certain species may gain a competitive edge, outcompeting resident species and causing diversity loss and declines in species richness (Stevens et al. 2004, Funk 2008, Harpole et al. 2016). This change in abundance may cause a shift in ecosystem functioning by changing which species dominates the community-level response. It is possible that community-weighted traits may only reflect the responses of dominant species, although rare species have been shown to contribute novel traits to measures of community functional diversity and may influence ecosystem function (Jain et al. 2014). Disentangling each of these effects is important to understand the implications of these shifts and to

predict how communities will respond to environmental change.

Using the community-weighted traits and ANPP, we can calculate the leaf area index (LAI) or total leaf area per ground area ( $\text{m}^2/\text{m}^2$ ), and canopy chlorophyll density per square meter ( $\text{mg}/\text{m}^2$ ). Aboveground net primary productivity reflects the net productivity and can be used to examine which nutrients are limiting for productivity, and how nutrient addition influences ecosystem productivity (Tilman et al. 1997, Lebauer and Treseder 2008, Fay et al. 2015). However, LAI and canopy chlorophyll density are more directly linked to photosynthesis, water transpiration, and carbon gain (McWilliam et al. 1993, Chaves et al. 2002, Fitzgerald et al. 2010). Therefore, while ANPP reflects accumulated aboveground biomass, LAI and canopy chlorophyll content better reflect ecosystem consequences of environmental change because they directly influence ecosystem ability to gain carbon and transfer water and energy (McWilliam et al. 1993, Chaves et al. 2002, Chapin et al. 2011). However, how ANPP and trait changes scale to canopy parameters such as LAI and canopy chlorophyll content is rarely examined.

Resource availability, mainly nitrogen (N), limits growth of terrestrial vegetation in many ecosystems, and N limitation of ANPP is particularly widespread (Tilman 1987, Lebauer and Treseder 2008, Vitousek et al. 2010, Stevens et al. 2015). Other nutrients, such as phosphorus and in some cases, potassium and micronutrients, can also limit ANPP in some ecosystems, but N limitation predominates in temperate ecosystems (Fay et al. 2015). Grasslands in particular are unique ecosystems as their productivity in a given year may be limited by nutrient availability (Fay et al. 2015) and also water availability (Heisler-White et al. 2008, Yang et al. 2008). Our study site, Cedar Point Biological Station in eastern Nebraska ( $41^{\circ}0.12' \text{ N}$ ,  $101^{\circ}0.38' \text{ W}$ ), is a relatively dry grassland (precipitation varies between 190 and 565 mm per year), and in a recent study, Wang et al. (2017) found productivity to be limited by precipitation in dry years and N in wet years. This relationship results in large annual variability of ANPP with N addition. Species functional traits have been found to respond to water gradients as well as nutrient availability (Fonseca et al. 2000, Wright et al. 2004, Cornwell

and Ackerly 2009). This allows us to quantify the relative role of precipitation and nutrients in determining community structure and function.

We used a nutrient addition experiment to investigate how community structure and function change with nutrient addition, and determine whether trait plasticity or species abundance changes are more important in driving these changes. We also examined select species functional trait differences across two years that differ in precipitation. This study was carried out within a Nutrient Network (NutNet) site. The NutNet is a global collaboration of grassland sites which examines nutrient limitation and its influences on the diversity-productivity relationship and its stability over time (Borer et al. 2014b). We hypothesized (1) that N alone will cause a shift in community functional traits because of its known site-level importance for ANPP (Wang et al. 2017), while P and K will not have an effect; (2) community-weighted traits will shift under N addition toward traits associated with faster growth rates and higher resource use (increased SLA, chlorophyll, height, and lower thickness, toughness, and LDMC); (3) at the species level, N addition will cause a shift in functional traits in the same direction as the community traits and will not be driven by the dominant species only; (4) if community-weighted SLA and chlorophyll increase as predicted with N addition, LAI and canopy chlorophyll density will also increase, but to a larger degree than community-weighted SLA or chlorophyll alone; and (5) an increase in precipitation will also cause shifts in functional traits toward traits associated with faster growth rates and higher resource use (increased SLA, chlorophyll, height, and lower thickness, toughness, and LDMC).

## METHODS

### Study area

This study was conducted from late May to early August 2015 at Cedar Point Biological Station in Western Nebraska, USA (41°0.12' N, 101°0.38' W). The site is a natural short-grass prairie located on an upland summit south of the Nebraska's Sandhill region in a moderate relief grassland east of Lake McConaughy (Chapman et al. 2001). The elevation of the study site is 965 m above mean sea level, and annual precipitation ranges from 190 to 565 mm from September to

August. In the study year of 2015, the summer was particularly wet, receiving 236 mm of precipitation compared to an average of 185 mm per summer. The summer months of June to August have a relative humidity of 59.1% with average daily temperatures ranging from 15.4° to 30.1°C. In the winter months of December to February, the relative humidity is 65.0% and average daily temperatures range from -7.4° to 5.1°C. All climate data are based on 1996–2016 weather data from Cedar Point HPRCC Weather Station (HPRCC 2017).

Dominant species in this grassland include perennial C4 grasses such as *Bouteloua gracilis*, C3 grasses such as *Hesperostipa comata*, and the perennial sedge *Carex filifolia*. Perennial shrubs *Artemisia frigida* and *Artemisia filifolia* also are abundant species in this grassland, and in some years, annual species such as *Bromus tectorum* and *Helianthus annuus* may become abundant. Species identity and functional type were verified with the USDA PLANTS database (USDA and NRCS 2017), Farrar (2011), and Barnard (2014).

### Experimental design

The plots used in this study are a part of the NutNet and follow the core NutNet protocol (Borer et al. 2014a). The nutrient addition experiment contains 48, 5 × 5 m plots in a three-factorial design consisting of control plots with no manipulation, plots with nitrogen (N), phosphorus (P), and potassium plus micronutrients (K) for a total of eight nutrient addition treatment combinations. Each of the eight fertilizer treatment combinations was replicated six times in a randomized block design for a total of 48 plots. The nutrient treatments have been applied annually in late May or early June since 2008 at 10 g/m<sup>2</sup>. N was applied as time-release urea [(NH<sub>2</sub>)<sub>2</sub>CO], P as triple-super phosphate [Ca(H<sub>2</sub>PO<sub>4</sub>)<sub>2</sub>], and K as potassium sulfate [K<sub>2</sub>SO<sub>4</sub>]. The micronutrient mix, which was only applied in 2008, included Fe (15%), S (14%), Mg (1.5%), Mn (2.5%), Cu (1%), Zn (1%), B (0.2%), and Mo (0.05%), applied as iron sulfate, calcium magnesium carbonate (dolomite), manganese sulfate, copper sulfate pentahydrate, zinc sulfate anhydrous, sodium borate, and sodium molybdate, respectively. The treatments are referred to by their primary nutrient supplements of nitrogen (N), phosphorus (P), and potassium (K). The herbivore exclusion experiment

which exists at this site as a part of the core Nut-Net protocol has two fencing treatments ( $n = 12$  plots); no fencing treatments were utilized in this study.

Species abundance data were collected annually in a  $1 \times 1$  m subplot in late June. Species abundances were visually estimated to the nearest 1% percent vegetation cover within the  $1 \times 1$  m subplot using a modified Daubenmire method (Daubenmire 1959). All aboveground standing biomass was clipped in two  $10 \times 100$  cm strips in each plot at the peak of standing aboveground biomass, in late June. All species, except for *A. filifolia*, *Corypantha vivipara*, and *Opuntia polyacantha*, have annual aboveground tissues only. *Artimisia filifolia* has a woody base, and we included only the annually produced leaves in our estimation of ANPP. For the cacti, we only collected biomass produced within the study year. Thus, similar to many other grassland studies, we used the peak standing biomass as an estimate of ANPP (Sala and Austin 2000, Scurlock et al. 2002). Collected biomass samples were dried at  $60^\circ\text{C}$  to constant dry weight and were weighed to the nearest 0.01 g to estimate ANPP. Light interception was estimated by taking two measurements at ground level from opposite corners of the  $1 \times 1$  m subplot and one measurement above the canopy with a 1-m LI-191R Line Quantum sensor (LI-COR; Lincoln, Nebraska, USA).

Functional traits were measured from plants in the remaining plot area in the summer of 2015. We collected one sample from each species present in each plot. Each sample contained leaves from 1 to 15 individual plants to obtain at least 1 g fresh weight. This was due to the imprecision of measuring leaf area and dry weights measurements on very small leaf samples. For species with large leaves, such as *Helianthus annuus*, only one leaf was collected, whereas up to 103 leaves were included for small-leaved species such as *C. filifolia*. Of the 51 species collected, 17 were early season species sampled in late May and June whereas the remaining 34 were late season species sampled in July and early August. The functional traits measured for each species include SLA, chlorophyll content, height, leaf thickness, leaf toughness, and LDMC. Canopy height (cm) was recorded for 1–15 individuals in a plot. Leaf functional traits were obtained by collecting the last, fully expanded leaves from several mature and

undamaged individuals of that species. Leaves were scanned using a LI3000 (LI-COR, Lincoln, Nebraska, USA) to determine leaf area ( $\text{cm}^2$ ). Measurements were also taken for chlorophyll ( $\text{mg}/\text{m}^2$ ) using Chlorophyll Content Meter Model CCM-300 (Opti-Science, Hudson, New Hampshire, USA), leaf thickness (mm) using Digimatic Micrometer Series 293 MDC-MX Lite (Mitutoyo, Aurora, Illinois, USA), and toughness (g) using 516–1000M Push Pull Gauge (Chatillon, Largo, Florida, USA). The leaves were then dried in a forced air oven at  $60^\circ\text{C}$  to constant dry weight. Specific leaf area was recorded as leaf area per dry mass ( $\text{cm}^2/\text{g}$ ), and LDMC was recorded as dry mass per fresh mass ( $\text{mg}/\text{g}$ ). Trait values were pooled by species for each plot to obtain an average trait value for each species within a plot.

To assess annual variation in functional traits, we collected functional trait data in 2016 using the same field methods. Whereas 2015 was a wet summer (236 mm of precipitation), 2016 was much drier, only receiving 116 mm of precipitation. We used a subset of 12 species which were common in both years, occurring in at least three N added and three non-N added plots in both years to evaluate functional trait plasticity across these two years.

### Analyses

In total, we measured abundance for 51 species in all 48 plots at the site (463 observations  $\times$  plot combinations). Functional trait data were not collected for every species observation in each plot. Of 463 occurrences of species in the 48 plots, we did not collect functional trait data for 207 occurrences, which accounts for an average 17.5% cover per plot (0.5–69.5%). Missing traits were substituted with the average trait values for the same species occurring in plots with the same fertilizer treatment combination or, where this was not possible due to lack of observations, missing traits were replaced with average values across all plots in which the species was found or from data collected in 2016 using the same methods. Differences between the substituted and raw datasets were assessed with a generalized linear model and were insignificant (Appendix S1: Table S1).

Community-weighted traits were used to make comparisons across plots with different species compositions (Grime 1998). Using this method, changes in the resulting community-weighted



trait from plot to plot can be due to either species abundance changes (including species turnover) or intraspecific trait changes. To partition the effects of each of these two components, we used fixed community traits following methods from Lepš et al. (2011). The fixed-community-weighted trait assigns each species a fixed trait value, which was the mean trait value in the control plots for a species. Any change in the fixed-community-weighted trait under fertilizer addition, for example, can only be due to species abundance changes. Therefore, this fixed-community-weighted trait can quantify how much of the community-weighted trait change is due to abundance changes and intraspecific trait changes.

Multivariate analysis of variance (MANOVA) was used to assess the effects of fertilization on the suite of community-weighted functional traits (see *Methods* for community-weighted trait below). The Pillai test statistic was used to assess the MANOVA's goodness of fit. Nitrogen was the only fertilizer to effect community-weighted traits (MANOVA,  $F = 17.31$ ,  $P < 0.001$ , Table 1). Therefore, all fertilizer treatments were combined into two groups, with N addition (N+) and without N addition (N–). Note that both the N– and the N+ treatments include the treatment plots with P and K additions. Linear mixed-effects models with Gaussian distribution were then used to determine whether N addition predicts the community-weighted trait, LAI, canopy chlorophyll density, and ANPP. Addition of N fertilizer was included as a fixed effect (coded as 1 or 0 for with and without N addition), and

block was included as a random effect to account for natural variation between blocks. Models were checked for heteroscedasticity, and no transformations were needed. Type II Wald chi-square tests were used to assess the goodness of fit of each model.

Finally, individual species responses were assessed by observing the change in average trait value between treatments. Species that occurred in two or fewer plots or that required traits to be replaced with the average (as described above) in over half of their observations were not included in this analysis. A generalized linear model with Gaussian distribution was then used to determine whether the change is best explained by unique groups of species. Predictor variables were percent of total abundance, flowering (early or late), duration (annual or perennial), and growth habit (graminoid, forb, shrub, etc.; Appendix S1: Table S2). We did not distinguish between C3 and C4 grasses or annual and biennial due to lack of sample size of C4 and biennial species. Predictor variables were also checked for correlation to avoid including highly correlated variables in the same model. No variables were highly correlated, though growth habit and duration were slightly correlated ( $r = 0.48$ ). We also assessed species evenness in the fertilized and unfertilized plots using Pielou's evenness index. Functional trait data were also collected in 2016 using the same field methods. To evaluate functional trait plasticity across these two years, we used a subset of 12 species which were common in both years, occurring in at least three N fertilized and three non-N fertilized plots in both years. We used linear

Table 1. Results of a MANOVA with community-weighted traits (specific leaf area, chlorophyll, thickness, toughness, height, leaf dry matter content) as the response variable and the fertilizer treatments N, P, K, their interactions, and block as predictor variables.

Treatment	df	Pillai	F	Numerator df	Denominator df	P
N	1	0.713	14.069	6	34	<0.001***
P	1	0.167	1.134	6	34	0.364
K	1	0.115	0.733	6	34	0.627
Block	1	0.161	1.087	6	34	0.390
N × P	1	0.121	0.777	6	34	0.594
N × K	1	0.123	0.793	6	34	0.582
P × K	1	0.186	1.293	6	34	0.287
N × P × K	1	0.216	1.564	6	34	0.188

*Notes:* Community-weighted traits were calculated summing the product of individual species trait values and species abundance in a plot and dividing by the total abundance of a plot. Here, we use the Pillai test statistic to determine goodness of fit of each model. Significant *P*-values are denoted with asterisks (\*\*\*)  $P < 0.001$ .

mixed-effects models with Gaussian distribution to see whether N addition (coded as 0 or 1), year (coded as 0 for 2015 and 1 for 2016), and their interaction could predict SLA, chlorophyll, and plant height. Species and block were included as a random effect to account for their natural variation.

All statistical analyses were carried out in R version 3.3.1 (Development Core Team 2014) using the lmer function from the lme4 package (Bates et al. 2014), type II ANOVAs from the car package (Fox and Weisberg 2011), and glht function from the multcomp package (Hothorn et al. 2008).

## RESULTS

### Community-level traits

Nitrogen addition significantly influenced the community-weighted traits (MANOVA,  $F = 17.3$ ,  $P < 0.001$ ), but P, K, and all other pairwise combinations did not have any effect (Table 1). Therefore, we combined all nutrient addition treatments into two groups, with and without N addition. Nitrogen addition had a

significant effect on four of the six community-weighted traits measured in this study (Fig. 1). Community SLA increased by 19% with N addition ( $\chi^2 = 6.3$ ,  $P = 0.012$ ). Nitrogen addition also caused a 32% increase in community-weighted chlorophyll and a 26% increase in community-weighted plant height ( $\chi^2 = 65.5$ ,  $P < 0.001$  and  $\chi^2 = 23.6$ ,  $P < 0.001$ , respectively). Community LDMC decreased by 11% with the addition of N ( $\chi^2 = 11.5$ ,  $P < 0.001$ ). Community leaf thickness and leaf toughness did not respond significantly to N addition ( $\chi^2 = 1.3$ ,  $P = 0.251$  and  $\chi^2 = 2.8$ ,  $P = 0.094$ , respectively).

We found that 51–71% of the change in community-weighted traits was due to intraspecific trait changes and the remaining 29–49% to abundance changes. Community-level chlorophyll concentration had the largest change in intraspecific traits. When N was added, the community-weighted chlorophyll increased by 111 mg/cm<sup>2</sup> whereas only 31.9 mg/cm<sup>2</sup> (or 29%) was attributed to abundance changes. The remaining increase of 71.9 mg/cm<sup>2</sup> or 71% was attributed intraspecific trait changes. Of the 15.1 cm<sup>2</sup>/g increase in

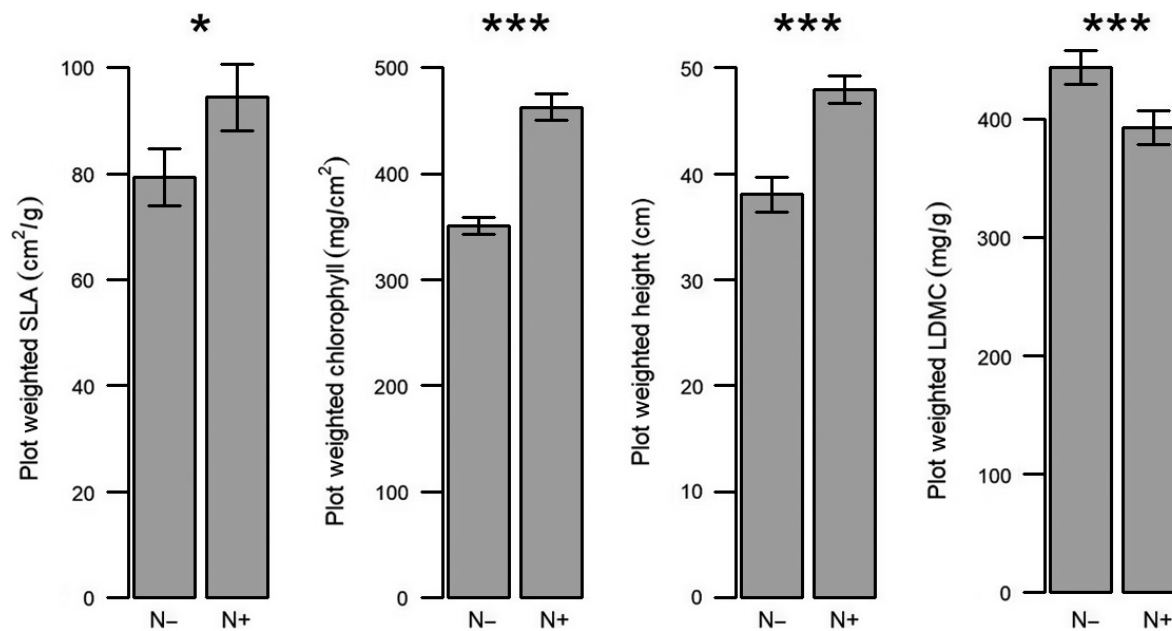


Fig. 1. Mean community-weighted specific leaf area (SLA), chlorophyll, plant height, and leaf dry matter content (LDMC) in the plots with no nitrogen added (N-) and the nitrogen added (N+) plots. Community-weighted traits were calculated summing the product of individual species traits and species abundance in a plot and dividing by the total abundance of a plot. Significant  $P$ -values are denoted with asterisks (\*\*\* $P < 0.001$ , \* $P < 0.05$ ), and the error bars represent the standard error of the mean of each treatment.

community-weighted SLA with the addition of N, 4.6 cm<sup>2</sup>/g (30%) of the change was attributed to variation in species abundances and the remaining increase of 10.5 cm<sup>2</sup>/g (70%) was caused by intraspecific change in SLA. Community-weighted plant height increased by 9.9 cm under N addition, 3.8 cm (38%) was attributed to species abundance changes, and the remaining 6.1 cm (62%) is due to species-level changes in height. Finally, community-weighted LDMC decreased by 50.6 mg/g with N addition with 24.6 mg/g (49%) of this decrease was caused by abundance changes and the remaining 24.0 mg/g (51%) was caused by intraspecific trait changes.

### Species-level changes

Neither abundances changes nor trait changes were predicted by any functional groups of species ( $P > 0.05$ , Fig. 2). The two most dominant species *Bouteloua gracilis* and *Carex filifolia* declined in their abundance with N fertilization. All other species, with the exception of *Dichanthelium oligosanthes*, increased in abundance with the addition of N. There was an increase in plot evenness with the addition of N, but the trend was not significant ( $J' = 0.75$  without N, and  $J' = 0.73$  with N,  $P = 0.10$ ). Most species increased in SLA with the addition of N with an average increase of 6.7 cm<sup>2</sup>/g within the 15 species with sufficient sample size. Only four moderately abundant to rare species declined in SLA. Notably, most species increased substantially in chlorophyll concentration, except for *Agropogon smithii* and *Helianthus annuus*. The average change in chlorophyll with N was an increase of 74.4 mg/cm<sup>2</sup> within the 15 species examined. Plant height under the addition of N also increased across species with the exception of *Hesperostipa comata* and four, predominantly rare, species. Overall, plants increased by an average of 6.4 cm with N fertilization. Finally, 10 of 15 species decreased in LDMC with an average decrease of 10.4 mg/g with the addition of N.

In both 2015 and 2016, N had a significant effect on species-level SLA, chlorophyll, plant height, and LDMC (Fig. 3). The year and N addition interaction significantly influenced SLA, but no other functional traits. Nitrogen addition had the strongest effect on SLA in 2015, and a Tukey post hoc comparison did not find a difference between the N and non-N plots in 2016

( $P = 0.16$ ). On average, N addition caused an 11% increase in SLA or an increase of 9.4 cm<sup>2</sup>/g, a 29% increase in chlorophyll or 94.0 mg/cm<sup>2</sup>, a 28% increase in height or 10.3 cm, and a 7% decrease in LDMC or an average decrease of 27.2 mg/g. However, from 2015 to 2016, there was an 11% decrease in average SLA (11.1 cm<sup>2</sup>/g), a 26% decrease in average chlorophyll (108.1 mg/cm<sup>2</sup>), a 14% decrease in average plant height (5.8 cm), and an average increase of 8% in LDMC (29.0 mg/g).

### ANPP, LAI, and canopy chlorophyll density

Aboveground net primary productivity did not have a significant response to N addition ( $\chi^2 = 2.133$ ,  $P = 0.144$ ; Fig. 4). Both the LAI and the canopy chlorophyll density increased significantly under the addition of N ( $\chi^2 = 5.307$ ,  $P = 0.021$  and,  $\chi^2 = 5.953$ ,  $P < 0.001$ , respectively). The magnitude of change in LAI and canopy chlorophyll density was greater than those of community-weighted SLA and chlorophyll. Community-weighted SLA increased by 19% and the community-weighted chlorophyll increased by 32%, whereas the LAI showed a 34% increase and the canopy chlorophyll density nearly doubled with a 67% increase.

## DISCUSSION

### Nutrients at cedar point

Nitrogen addition was the only fertilizer treatment to significantly affect the suite of community-weighted functional traits. This is consistent with the findings of Wang et al. (2017) which demonstrated that N was the only nutrient limiting ANPP across years at Cedar Point. Cedar Point contains shallow and rocky soil which are part of the Tassel series formed from calcareous sandstone which are high in cations and potassium (Scheinost et al. 1995), which may explain why K addition had no effect. Furthermore, Cedar Point's shallow soil is young and may have relatively high weathering, preventing P limitation (Scheinost et al. 1995). Thus, these sources of soil P, K, and cations may have led to stronger N limitation. However, other experiments within the NutNet have found other nutrients to be important. For example, Fay et al. (2015) found N to limit ANPP at 11 sites out of 31 which showed some nutrient limitation while



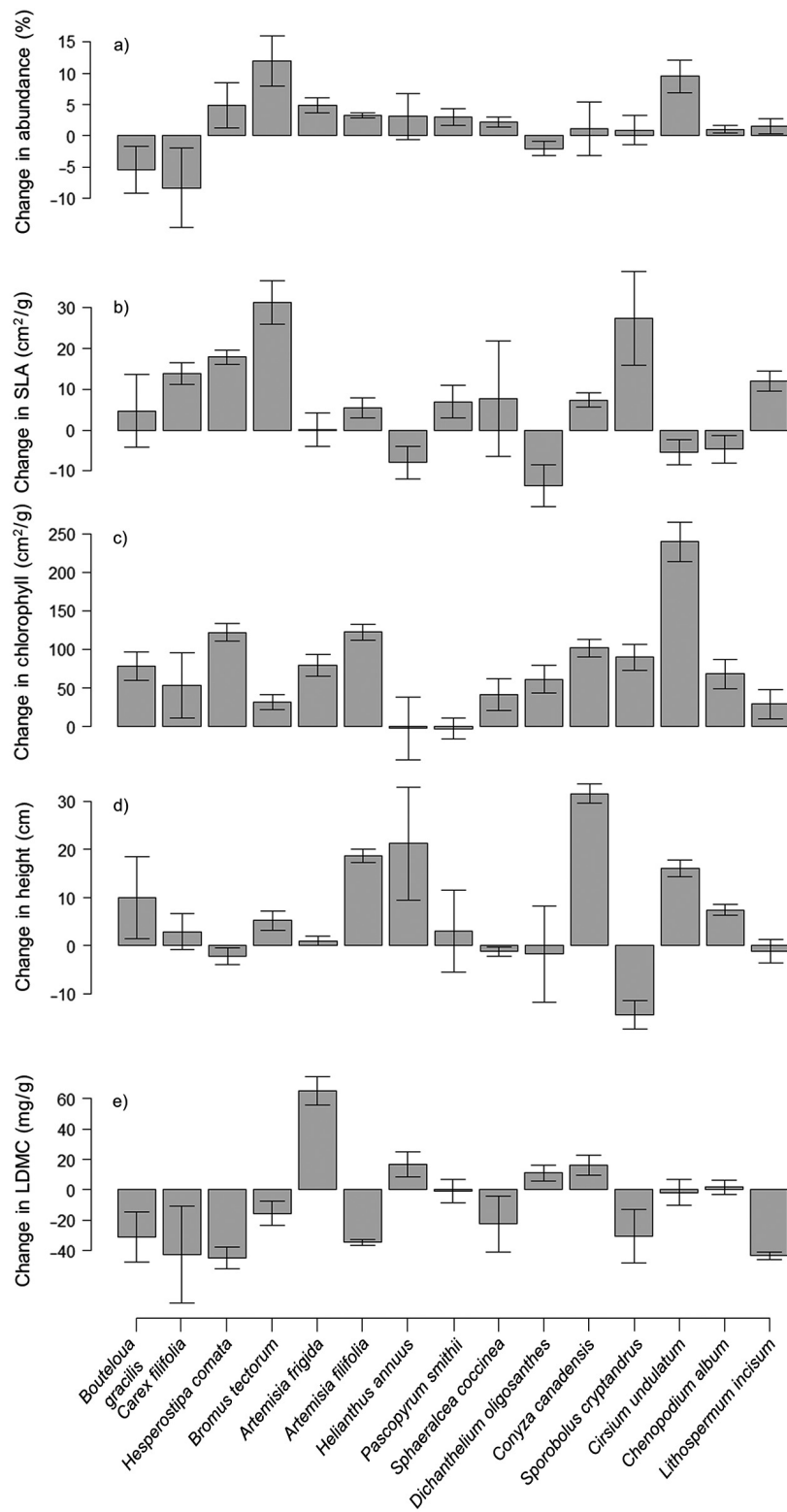


Fig. 2. Change in species average (a) abundance, (b) specific leaf area, (c) chlorophyll, (d) plant height, and

(Fig. 2. *Continued*)

(e) leaf dry matter content (LDMC) in the plots without nitrogen added and plots with nitrogen fertilization. Species are arranged by site-level dominance with dominant on the left to rare on the right. The error bars represent the standard error of the difference between the nitrogen plots and the mean of the non-nitrogen plots.

P and K were limiting at 12 and five sites, respectively, often this limitation occurred in the form of co-limitation. Other studies have reported that P, K, and cations can have effects on individual traits or other metrics of community structure and function (Fonseca et al. 2000, Vitousek et al. 2010, La Pierre and Smith 2014, Fay et al. 2015). Thus, how communities and functional traits

respond to nutrient addition may vary across sites if different nutrients are limiting.

#### *Community-weighted functional traits*

Nitrogen had significant effects on community-weighted SLA, chlorophyll, height, and LDMC. This is consistent with other studies of the effect of nutrient addition on these functional traits

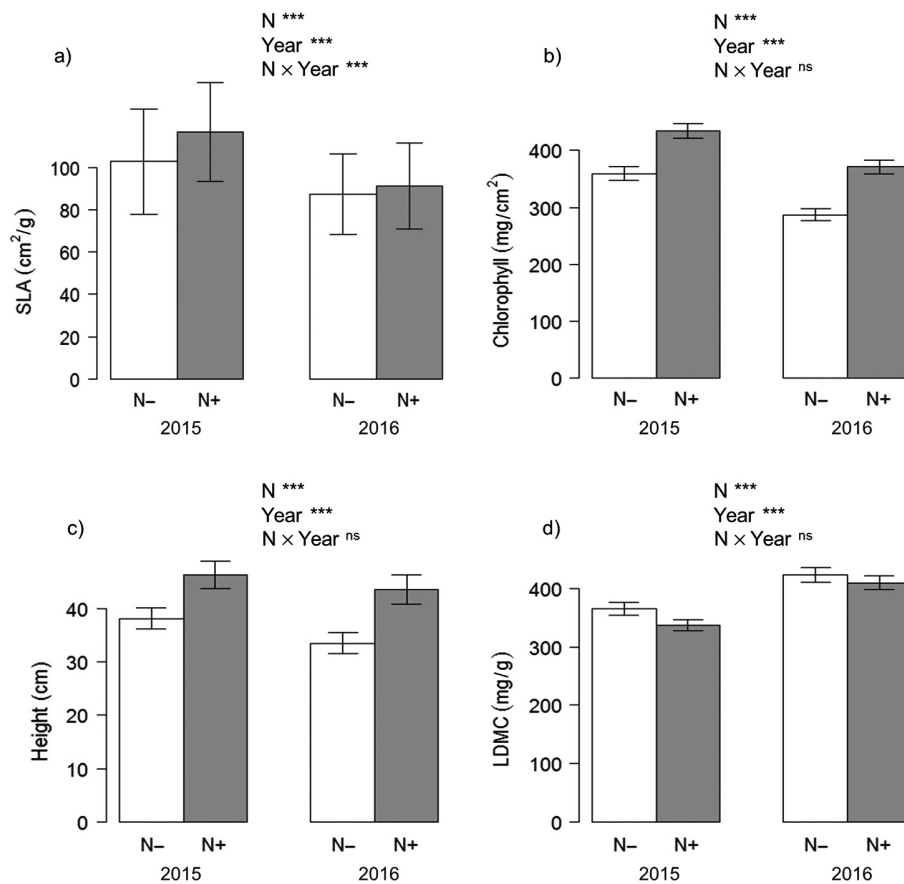


Fig. 3. Change in mean (a) specific leaf area (SLA), (b) chlorophyll, (c) height, (d) leaf dry matter content (LDMC) between the plots with no nitrogen added (N-) and the nitrogen fertilized (N+) plots in 2015 and 2016. The two study years had markedly different precipitation (236 mm in 2015 and 116 mm in 2016). We used linear mixed-effects models with functional traits (SLA, chlorophyll, height, and LDMC) as the response variable and the fertilizer treatments N, year, and their interaction as predictor variables. We use type II ANOVA to determine goodness of fit of each model. Significant *P*-values are denoted with asterisks (\*\*\**P* < 0.001, \*\**P* < 0.01, \**P* < 0.05). The error bars represent the standard error of the mean of each treatment.

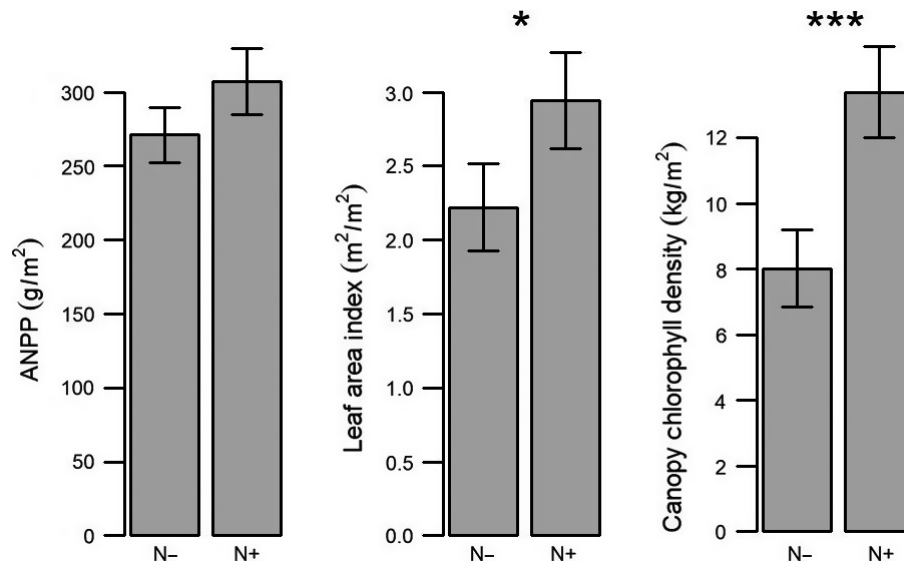


Fig. 4. Mean Aboveground net primary productivity (ANPP), leaf area index, and canopy chlorophyll density in the plots with no nitrogen added (N-) and the nitrogen added (N+) plots. Leaf area index (LAI), or the total leaf surface area per square meter, is the product of community-weighted specific leaf area and ANPP. Canopy chlorophyll density, or total number of chlorophyll molecules per square meter, is the product of community-weighted chlorophyll and LAI. Significant *P*-values are denoted with asterisks (\*\**P* < 0.001, \**P* < 0.05), and the error bars represent the standard error of the mean of each treatment.

(Tilman 1987, Knops and Reinhart 2000, Wright et al. 2004, Al Haj Khaled et al. 2005). La Pierre and Smith (2014) did a similar study within the NutNet at a tallgrass prairie site in Kansas (USA) examining functional trait response to nutrient addition. They found an increase in traits like SLA and plant height with P addition and a decrease in LDMC with N addition, but no relative change in leaf thickness or toughness. According to Fay et al. (2015), productivity at this site is co-limited by N and P, which may explain these differences in functional trait response to nutrient additions. Although leaf thickness and toughness may not be directly related to nutrient availability, leaf thickness and toughness are generally highest when nutrients are low and leaves are costly to replace such as when risk of herbivory is high and there is much aboveground competition for light (Choong et al. 1992, Cunningham et al. 1999, Westbrook et al. 2011). However, the effects of herbivory are moderate at our site, and the herbivore-excluding fences do not have any influence on ANPP (Wang et al. 2017). Furthermore, Cedar Point has relatively low ANPP and is unlikely to have large

aboveground competition for light. However, the strength of light competition and herbivory varies across grasslands and Borer et al. (2014b) reported strong impacts of herbivory and light levels on ANPP in most NutNet sites. Therefore, trait change in response to nutrient addition may vary depending on the degree to which herbivory, light competition, and/or water availability influence vegetation. Finally, Cedar Point is a dry grassland and may have naturally high leaf thickness and toughness relative to other sites, although there are few studies with which to compare. Overall, these results suggest a shift in plant strategy with increasing nutrient availability toward higher resource acquisition and use, and lower resource storage (Lavorel and Garnier 2002, Collins et al. 2016) which could have implications for biogeochemical cycling and precipitation regimes (Lavorel and Garnier 2002, Reichstein et al. 2014).

Many studies have documented that nutrient addition may cause change in plant community composition (Borer et al. 2014b, Craven et al. 2016). However, response of community-weighted traits can be due to two factors: species

abundance changes and intraspecific trait changes. We demonstrate that intraspecific trait changes contribute substantially to the community functional response, even after eight years of nutrient addition. In fact, several previous studies have shown that intraspecific trait changes were more important than abundance changes under fertilization (Lepš et al. 2011, La Pierre and Smith 2014, Siefert and Ritchie 2016). However, this relationship may vary over time. La Pierre and Smith (2014) observed stronger changes in community composition in a 14-yr fertilization experiment than in a nine-year experiment. Wang et al. (2017) also found abundance changes to be increasingly important over time at Cedar Point, partially due to an increase in annual species abundance over time. Furthermore, these results are not limited to nutrient manipulation experiments. Jung et al. (2014) simulated an extreme drought event and found intraspecific variation drove the community functional trait response. However, Lepš et al. (2011) found species abundance changes were more important in some community traits in response to disturbances such as mowing. Therefore, the type of environmental change a community is exposed to will likely influence the mechanisms of community response. Together, these findings demonstrate that both species composition and intraspecific trait changes can influence community-weighted traits and the relative importance of each can vary over time.

#### *Species-level trait plasticity*

At the species-level, functional trait responses varied, but most species shifted from trait values toward trait values associated with higher resource use and acquisition. These trait changes were consistent with the community trend and were not seen in a few dominant species only. Abundance of the two most dominant species declined as the subdominant species increased in abundance. The dominant plasticity hypothesis states that species gain a competitive advantage when they can exhibit plasticity in their resource use (Ashton et al. 2010). This was observed in *Bromus tectorum* and *Cirsium undulatum*, which had the largest increases in abundance. *Bromus tectorum* also had the largest increase in SLA under N addition and accompanied by slight increases in chlorophyll and height. Of the species studied, *C. undulatum* had the largest increase in chlorophyll, a moderate increase in

height, and a slight decline in SLA. Combined, this plasticity in resource use suggests that these species gained a competitive edge with N addition as seen by their increase in abundance. However, there was no correlation between trait plasticity and abundance changes of all species overall (analysis not shown). Thus, it may be that only a few annual/biannual species are more plastic than the majority of species.

We sampled 12 species in both 2015 and 2016 and combined these species showed that SLA, chlorophyll, and plant height were significantly lower in 2016 than in 2015. However, LDMC was significantly higher in 2016 than in 2015. Of these traits, SLA showed a significant year by N addition interaction, whereas the other traits did not. The summer of 2016 was much drier than 2015, only receiving 116 mm of precipitation in June and July while 2015 received 236 mm. Water availability has been shown to affect these traits in other studies and to limit plant growth in general (Fonseca et al. 2000, Chaves et al. 2002, Chapin et al. 2011). Thus, annual fluctuations in climate can be just as important as nutrient availability in influencing species functional traits. This clearly highlights that the importance of nutrient-induced trait changes varies among years, likely influenced by precipitation differences.

#### *Scaling ANPP and community-weighted traits to LAI and canopy chlorophyll density*

Studies seeking to quantify the effect of changing biotic and abiotic factors on ecosystem function often measure shifts in ANPP (Tilman et al. 1997, Fay et al. 2015). However, LAI and canopy chlorophyll density are more directly related to photosynthesis and carbon gain (McWilliam et al. 1993, Chaves et al. 2002, Fitzgerald et al. 2010). In 2015, ANPP did not increase significantly and species richness was not significantly different with N addition; however, LAI and canopy chlorophyll density increased by 34% and 67%, respectively. In addition, even with no ANPP changes, N addition increases light interception in the canopy by 19% ( $N- 62 \pm 2\%$  SE,  $N+ 74 \pm 3\%$  SE,  $n = 48$ , J. M. H. Knops, unpublished data). Given this, ANPP can underestimate N-induced changes in aboveground competition for light and ecosystem carbon gain as we saw an increase in light interception and chlorophyll content which are directly related to photosynthetic rates.



Nutrient addition can cause a shift in allocation from root to shoot biomass as competition aboveground for light increases and belowground competition for nutrients decreases (Nadelhoffer et al. 1985). However, a shift in root-to-shoot ratio is not likely at our site for several reasons. First, we did not find a significant increase in aboveground biomass, and Wang et al. (2017) only showed increased aboveground biomass in wet years. Aboveground net primary productivity at our site is primarily precipitation limited (Wang et al. 2017), and therefore, a shift in root-to-shoot ratio as seen in sites that are primarily nutrient limited may not occur. Second, the increased aboveground biomass is largely driven by increased annual species abundances at our site (Wang et al. 2017), and annual species typically have lower root-to-shoot ratio. However, we did not find an increase in annual species abundances in 2015. Finally, the observed shift in functional traits with N addition is associated with faster growth rates and higher maintenance costs which require increased cellular respiration (Penning De Vries 1975). Therefore, carbon may have been lost to respiration rather than assimilated into ANPP. We have no direct estimate of belowground root biomass, however, which is difficult to measure at our site due to the shallow and rocky soil.

Precipitation in June and July of 2015 was 236 mm which was the highest precipitation of the past 10 yr. However, ANPP did not increase significantly with N addition in 2015. Wang et al. (2017) found that ANPP at Cedar Point was primarily limited by precipitation, but in years when precipitation was not limiting, N was limiting. Therefore, with the high precipitation in 2015, a larger increase in ANPP with N addition was expected. Wang et al. (2017) also found that annual species productivity drove the responses to N fertilizer in wet years. However, here we found that annual species did not differ significantly from the perennial species in their abundance change, or trait change, with N addition. Although total precipitation is an important factor determining ANPP variation, the timing of precipitation events is also important as it may serve as a crucial germination cue for annual plant species (Philippi 1993). Therefore, the timing of precipitation events may be equally as important as quantity of precipitation in influencing community-level productivity.

We found that both N addition and annual precipitation to be important in determining relative species abundance and species functional traits. Canopy parameters such as LAI and canopy chlorophyll content are the product of ANPP, relative species abundances, and species functional traits. Therefore, ecosystem-level changes in canopy structure can be strongly influenced by species abundance changes and species functional trait changes, even when ANPP does not change. We also found large annual variation in species functional traits, likely induced by precipitation differences. Further, this annual variation can be just as important as nutrient addition in determining functional traits. Therefore, annual trait variability combined with annual variability in ANPP and species composition can lead to even larger variation in LAI and canopy chlorophyll content. To understand the ecosystem consequences of N addition, we need to examine not only ANPP, but also annual differences in species composition and functional traits, as they are crucial in determining canopy structure.

#### ACKNOWLEDGMENTS

We would like to thank the University of Nebraska, Lincoln School of Biological Sciences, and Cedar Point Biological Station for financial support. We are also grateful to Dai Shizuka, Chad Brassil, and Sabrina Russo for comments on this manuscript.

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