

Fertilization effects on species density and primary productivity in herbaceous plant communities

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Gough, L., Osenberg, C. W., Gross, K. L. and Collins, S. L. 2000. Fertilization effects on species density and primary productivity in herbaceous plant communities. – *Oikos* 89: 428–439.

Fertilization experiments in plant communities are often interpreted in the context of a hump-shaped relationship between species richness and productivity. We analyze results of fertilization experiments from seven terrestrial plant communities representing a productivity gradient (arctic and alpine tundra, two old-field habitats, desert, short- and tall-grass prairie) to determine if the response of species richness to experimentally increased productivity is consistent with the hump-shaped curve. In this analysis, we compared ratios of the mean response in nitrogen-fertilized plots to the mean in control plots for aboveground net primary productivity (ANPP) and species density (D ; number of species per plot of fixed unit area). In general, ANPP increased and plant species density decreased following nitrogen addition, although considerable variation characterized the magnitude of response. We also analyzed a subset of the data limited to the longest running studies at each site (≥ 4 yr), and found that adding 9 to 13 g N m⁻² yr⁻¹ (the consistent amount used at all sites) increased ANPP in all communities by approximately 50% over control levels and reduced species density by approximately 30%. The magnitude of response of ANPP and species density to fertilization was independent of initial community productivity. There was as much variation in the magnitude of response among communities within sites as among sites, suggesting community-specific mechanisms of response. Based on these results, we argue that even long-term fertilization experiments are not good predictors of the relationship between species richness and productivity because they are relatively small-scale perturbations whereas the pattern of species richness over natural productivity gradients is influenced by long-term ecological and evolutionary processes.

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The relationship between primary productivity and species richness is often described as a unimodal or “hump-shaped” curve, with a peak of richness at a low to intermediate level of productivity (Grime 1973). Although a number of studies have documented this relationship in herbaceous plant communities (reviewed in Tilman and Pacala 1993, Huston 1994), a unimodal

relationship has been more consistently detected when comparisons are made across community types (e.g., Al-Mufti et al. 1977, Moore and Keddy 1989, Gross et al. 2000; reviewed in Mittelbach et al. unpubl.). Within plant communities, these relationships are frequently positive or unimodal, although with considerable residual variance (Grace 1999, Mittelbach et al. unpubl.).

Accepted 25 October 1999

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ISSN 0030-1299

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Table 1. Experiments at LTER sites that were included in the meta-analysis. Data were included only for certain years for each site ("Years data available" below), with year 1 the initial year of treatment. Nitrogen was added at all sites as $\text{NH}_4\text{-NO}_3$ except as urea-N at NWT. Mammalian exclosures surround the plots at CDR, KNZ, and SGS.

Site	Lat (°N)	Long (°W)	Biome/habitat	Plot size for species density (m ²)	Harvest area (m ²)	Dates of study	Years data available	N added (g m ⁻² yr ⁻¹)	Time of year fertilizer added	Reps*
ARC Arctic Tundra, Toolik Lake, AK	68.6	149.6	Arctic tundra	0.2	0.04 (5)**	1989–present	5, 7, 9	10	early June	4
NWT Niwot Ridge, CO	40.1	105.6	Alpine tundra	4	0.04 (4)**	1990–present	1, 3, 5	25 (10)†	mid-June–early July	5
SGS Shortgrass Steppe, CO	40.8	104.8	short-grass prairie	0.5	0.5	1971–1975	4, 5	10–15	spring	12
JRN Jornada, NM	32.5	106.8	hot desert	0.25	n/a	1983–1987	1, 2, 3, 4	10	summer rains (Aug–Sep.)	11–50
KNZ Konza Prairie Research Natural Area, KS	39.1	94.6	tall-grass prairie	10	0.1	1985–present	4, 9	10	June	4
CDR Cedar Creek Natural History Area, MN	45.4	93.2	old-field	0.3	0.3	1982–present	10, 11, 12, 13	1–27.2‡	mid-May and late June	6
KBS W.K. Kellogg Biological Station, MI	42.4	85.4	old-field	1	1	1989–present	1–6	12.3	early July	6

* Reps indicates the number of replicate quadrats used for the harvest and species number determinations.

** At ARC and NWT, 4–5 0.04-m² subsamples were harvested within each larger block or treatment plot.

† No fertilizer was applied in 1991. In 1993 the fertilizer amount was decreased to 10 g N m⁻² yr⁻¹.

‡ All plots receiving N at CDR also receive a mixture of P, K, Ca, Mg, S, and citrate-chelated trace metals. Lime was also added as necessary to maintain soil pH at control plot levels. See Tilman (1987).

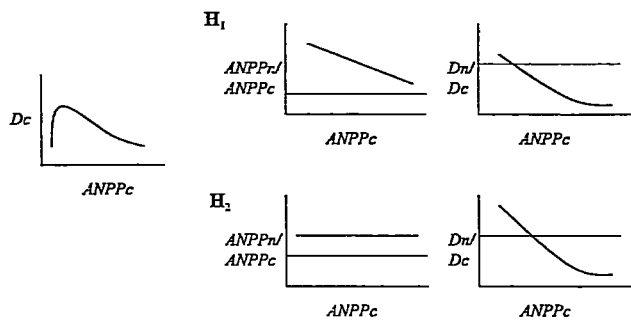


Fig. 1. Conceptual figure representing the relationship between control level ANPP and control level species density, the two alternative hypotheses examined for the response of ANPP to fertilization [represented as the ratio of ANPP in fertilized plots ($ANPP_n$) to ANPP in control plots ($ANPP_c$)], and the two possible outcomes for species density (D) response [represented as the ratio of D in fertilized plots (D_n) to D in control plots (D_c)]. Dotted line represents no change in fertilized plots relative to control plots.

The mechanisms that may generate the “hump” are currently disputed, particularly the role of competition along productivity gradients (Rosenzweig and Abramsky 1993, Tilman and Pacala 1993, Abrams 1995, Oksanen 1996, Goldberg and Novoplansky 1997, Stevens and Carson 1999). Results of nutrient enrichment studies in plant communities are frequently interpreted in light of a hump-shaped relationship because fertilization is expected to increase species richness at sites with low initial productivity and decrease species richness in more productive communities. DiTommaso and Aarssen (1989) summarized responses of herbaceous plant communities to resource additions and concluded that the addition of nutrients generally increased productivity and decreased species richness as documented in more recent studies (e.g., Wilson and Tilman 1993, Chapin et al. 1995). They argued, however, that low fertility communities were relatively unresponsive to nutrient addition. Our goal was to assemble a data set to quantify responses of species density (number of species in a plot of fixed area, our measure of species richness) to nutrient addition across a broad range of sites that differ in initial productivity and species composition, and to examine this relationship in more detail.

We assembled data from fertilization studies conducted in predominantly herbaceous plant communities at seven U.S. Long-Term Ecological Research (LTER) sites that represent a broad scale productivity gradient. In a companion paper we have also examined the pattern of plant species density across natural productivity gradients at these sites (Gross et al. 2000). The sites represent a broad gradient in latitude and climate across North America, and range from arctic tundra to desert communities (Table 1). We focus on LTER sites because of the somewhat similar methods employed, relatively long duration of the experiments (> 4 yr), and most importantly, the availability of raw data.

Although some authors have suggested that an index of species diversity which incorporates measures of evenness is a more responsive measure of the effects of fertilization (e.g., Theodose and Bowman 1997), we were not able to obtain data on changes in species abundance from most sites and therefore focus here on changes in species numbers per plot (species density, D).

Our initial hypothesis was that the direction and magnitude of change in species density response to fertilization would be related to the initial productivity of each community. We assumed that the magnitude of aboveground net primary productivity (ANPP) change along with initial ANPP would determine the degree of change in species density according to an underlying hump-shaped relationship. To test this hypothesis we used the ratio of the response in fertilized plots to the mean in control plots and examined two alternative hypotheses regarding the change in ANPP in response to fertilization: 1) low productivity sites would show a greater relative increase in ANPP than high productivity sites (because of greater nutrient limitation, see Fig. 1), or 2) the change in ANPP would be similar in all communities regardless of initial productivity. Although in previous research at these sites, ANPP increased with nitrogen (N) addition (Dodd and Lauenroth 1979, Tilman 1993, Chapin et al. 1995, Theodose and Bowman 1997, Collins et al. 1998, Huberty et al. 1998), we could not compare the magnitudes of ANPP and species density response among sites without examining the methods and raw data in detail. Both scenarios of ANPP increase predict a similar pattern in species density response (Fig. 1), but the slope of this relationship and the number of communities predicted to gain species differ between the two depending on magnitude of response of ANPP. In very low productivity communities we predicted an increase in species density relative to controls, and in high productivity communities we predicted a decrease, with perhaps no response at intermediate levels of productivity (Fig. 1).

We used qualitative and quantitative meta-analytical approaches to answer the following questions: 1) Does plant species density respond to an increase in productivity caused by N fertilization as predicted by the “hump-shaped” curve? 2) What accounts for differences in the direction and magnitude of response among sites? 3) Do other factors limit the response of productivity and species density to N fertilization?

Methods

Assembled data set

We selected data from seven U.S. LTER sites for this analysis based on the availability of raw data and

metadata, duration of study, and similarity of experimental treatments (Table 1). At six of these sites patterns of species density across natural productivity gradients have been examined in a companion paper (Gross et al. 2000). The communities and fields used to examine natural productivity–species richness relationships at these sites were generally different than those used for the experimental studies reviewed here (see Gross et al. 2000). We limited the data set to communities dominated by herbaceous species because of comparability of data and similarity of experimental designs. In addition, most published studies examining the productivity–species richness relationship have been conducted in herbaceous communities, allowing us to directly compare our results with others (e.g., DiTommaso and Aarssen 1989, Grace 1999). This analysis is directed at patterns in response among community types as these sites represent communities within Michigan old fields, Minnesota old fields, tall- and short-grass prairie, desert, and arctic and alpine tundra.

The data we obtained from each LTER site included duration of the study, size of plot, metadata related to the timing and levels of nutrient addition, and responses of ANPP and vascular plant species composition to fertilization (Table 1). All experiments were conducted for a minimum of four years, with fertilizer treatments applied each year. We analyzed the response of species density (*D*) and ANPP to nutrient addition, focusing primarily on N addition studies. Because the communities were dominated by herbaceous species, ANPP was estimated by a harvest at peak growing season of all live and standing dead aboveground biomass (vascular species only). The only exception to this was at the arctic tundra site, where new secondary growth of dwarf shrubs was calculated at each harvest by including estimates of new woody stem growth (Shaver 1986, Chapin et al. 1995). Productivity estimates were not available for the experimental plots at the desert site, but we include species density responses from that site in appropriate figures, with control level ANPP estimated from nearby plots within those communities (L. F. Huenneke pers. comm.). We also include results of phosphorus (P) and water (H₂O) additions conducted in a factorial manner with N additions from a subset of sites (Table 2).

Data analysis

We used two basic meta-analytic approaches to examine responses to nutrient addition. First, we summarized the responses using a vote-count method where we recorded whether the plots with added nitrogen had a mean response (in ANPP or *D*) greater or less than the control plots. We also used a second meta-analytic technique that measured the magnitude of response to fertilization (for general discussion of meta-analysis, see Hedges and Olkin 1985, Gurevitch and Hedges 1999, Osenberg et al. 1999). Choosing an appropriate measure of magnitude of response to an experimental treatment is not always straightforward (Osenberg et al. 1997, Englund et al. 1999). We used the response ratio [i.e., the ratio of *D* (or ANPP) in the fertilized plots relative to the control plots], in part because many biological processes act multiplicatively and because ecologists often find proportionate changes more meaningful than absolute changes (see also Hedges et al. 1999).

We constructed response ratios that isolated the response to the N addition treatment in each community within each site. In general, we simply divided the mean response in the N addition treatment by the mean in control plots. However, at the Minnesota old-field site all N addition treatments included several other trace elements (Tilman 1987); therefore, we used results from the trace element additions (with no N added) as the control values, to isolate the effects of N alone (Table 1). In a few studies, P (at three sites) and H₂O (at one site) were also added, in combination with N. Therefore, we also calculated a response ratio for the N + P (or N + H₂O) plots relative to N-alone plots to isolate the effects of P (or H₂O) when N was also added.

We treated the data in an exploratory mode, emphasizing relationships in the data by plotting them and providing some summary analyses. We used the observed within-study variances of the control and fertilized plot means to estimate the variance of each log-transformed response ratio (Hedges et al. 1999). A weighted mean for a group of studies was estimated using a random effects meta-analysis procedure with MetaWin software (Rosenberg et al. 1997). Means and 95% confidence intervals were back-transformed for

Table 2. LTER studies involving factorial additions of N plus P or N plus H₂O. All P was applied in the form of P₂O₅. See Table 1 for site abbreviations and other metadata.

Site	Dates of study	Years data available	N added (g m ⁻² yr ⁻¹)	P added (g m ⁻² yr ⁻¹)	H ₂ O added (mm yr ⁻¹)	Time of year fertilizer added
ARC	1989–present	5, 7, 9	10	5		early June
SGS	1971–1975	4, 5	10–15		586*	spring
NWT	1990–present	1, 3, 5	25 (10)**	25 (6)**		mid-June–early July
KNZ	1985–present	4, 9	10	1		June

* This is the average value for the 5 yr of treatments and includes rainfall. An irrigation system applied water throughout the growing season (Lauenroth et al. 1978).

** No fertilizer was applied in 1991. In 1993 the fertilizer amount was decreased to 6 g P m⁻² yr⁻¹.

Table 3. Direction of effect of fertilization on vascular plant species density (no. of species/quadrat) from fertilization experiments conducted at LTER sites. Response is zero if the difference between the control and treatment means was less than one species; arrows do not necessarily represent significant responses. Mean ANPP and species density were calculated for control plots over all available years. The table includes unpublished data from all sites (see Table 1 for metadata and plot sizes). '—': data needed for comparisons unavailable.

Site	Community	Duration (yr)	N	P	N+P	Mean ANPP (g m ⁻² yr ⁻¹)	Mean species density	Citations
ARC	tussock	15	—	—	↓	140	11.7	Chapin et al. (1995)
	dry heath	7	↓	↓	↓	75	7.7	
	wet sedge	5/9	0	0	0	60	7	Shaver et al. (1998)
NWT	dry meadow	5	↑	0	↑	150	23.1	Bowman et al. (1993), Theodose and Bowman (1997)
	wet meadow	5	↓	0	↓	260	14.5	
SGS	short-grass prairie	5	0	—	—	100	6.6	Lauenroth et al. (1978), Milchunas et al. (1990)
JRN	basin grassland	4	↓	—	—	146*	7.9**	
	piedmont grassland	4	0	—	—	346	5.7	
	creosote shrub	4	↓	—	—	192	3	
KNZ	burned prairie	9	↓	0	↓	315	14.2	
	unburned prairie	9	↓	↑	↓	250	15.5	
CDR	old-field, 1968† (A)	13	↓	—	—	140	9.7	Tilman (1987, 1993)
	old-field, 1957 (B)	13	↓	—	—	150	8.0	
	old-field, 1934 (C)	13	↓	—	—	230	14.5	
	native savanna (D)	13	↓	—	—	310	15.8	
KBS	annually tilled	6	↓	—	—	480	8.4	Huberty et al. (1998)
	successional	6	0	—	—	390	11.2	

* ANPP values for JRN are estimates calculated as 5-yr averages from adjacent plots (L. F. Huenneke pers. comm.).

** Species density values for JRN are seasonal averages (fall and spring), not annual averages.

† Date of old-field abandonment.

presentation. We also used MetaWin to decompose the variance of each log(response ratio) into the between-“study” and average within-“study” variances in effect size to determine the extent to which the magnitude of response varied among studies. We use “study” to refer to individual estimates of effect size; this corresponded to an effect for each year data was collected, N level, and community.

The assembled data contained multiple observations for each community because of multiple years (all sites) and levels of N addition (one site). Because this non-independence complicates our interpretation, we conducted an additional analysis on a restricted data set reduced to one observation per community. We used the available data to guide our data restriction by

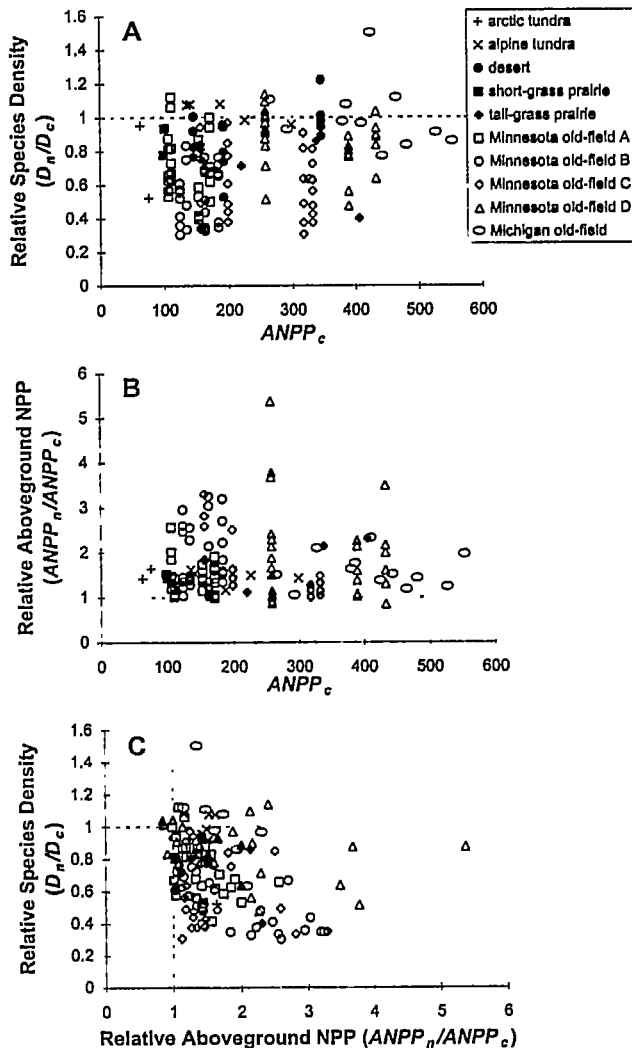


Fig. 2. Response ratios for N treatments relative to controls plotted for all data (all N treatments and all available dates) from all communities in seven LTER sites (see Table 1 for description) for A) species density vs mean ANPP of control plots, B) ANPP vs mean ANPP of control plots, and C) species density vs ANPP. Dashed lines indicate a response ratio of one where the N treatment showed no difference from control plots. Mammalian exclosures surround the plots at the short- and tall-grass prairie and Minnesota old-field sites.

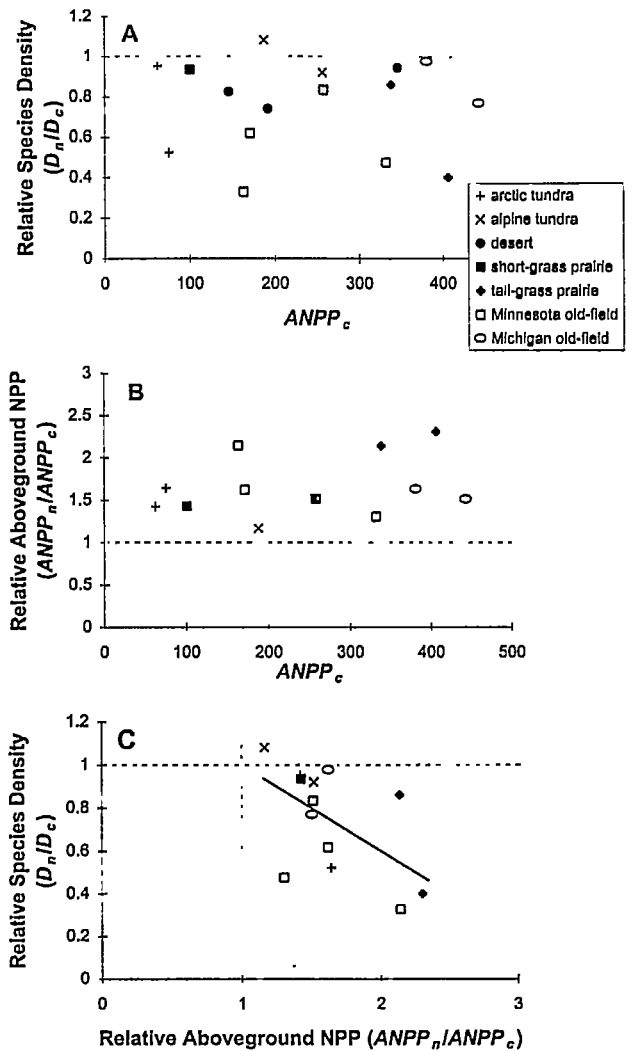


Fig. 3. Response ratios plotted for the last year of data for each site and restricted to nitrogen additions between 9 and 13 $\text{g m}^{-2} \text{yr}^{-1}$ for: A) species density vs mean ANPP of control plots, B) ANPP vs mean ANPP of control plots, and C) species density vs ANPP. Dashed lines indicate a response ratio of one where the N treatment showed no difference from control plots. Mammalian exclosures surround the plots at the short- and tall-grass prairie and Minnesota old-field sites.

examining how responses of ANPP and species density varied with two critical (and variable) features of these experiments: duration of study, and the amount of N added at the one site where multiple levels of N were applied (Minnesota old fields).

Results

Qualitative responses to fertilization

Qualitative examination of the data showed that species density declined as a result of fertilization in most communities, and the response was not related to initial productivity of the site (Table 3). Overall, 11 of 16 comparisons showed a decrease in species density in

response to N fertilization. There was no change in four communities: wet sedge tundra (arctic), successional old fields (Michigan), piedmont grasslands (desert), and short grass prairie. Only in the dry meadow at the alpine tundra site did species density increase after N addition (though not significantly; see Theodose and Bowman 1997). These exceptions to the general pattern were not concentrated in communities characterized by a particular range of productivity, biome or location along a climatic gradient.

Quantitative responses to fertilization

The species density response ratio generally decreased with fertilization, but the magnitude of response was not correlated with initial productivity (Fig. 2A). Just as decreases in species density occurred over a range of productivity, the few increases in species density also occurred at several productivity levels (Fig. 2A). Averaged across all available data ($n = 162$ comparisons), species density declined 28% (95% C.I.: 24–31%; however, these observations were not all independent so this C.I. should be interpreted with caution) in response to N addition. The average within-study variance in the log response ratio accounted for only 34% of the total variance, suggesting there was appreciable variation in the species density response among studies.

Plot sizes used for these experiments differed among sites (Table 1), and this could affect the magnitude of the species density response (see Oksanen 1996, Stevens and Carson 1999). However, when we examined the magnitude of species density response relative to plot size, we found no relationship (data not shown). We also examined in a preliminary analysis how species richness response was related to the species density response. We calculated species richness over larger scales (up to 40 m²) from available sites and found that the response ratios of species richness and small scale species density (D) were highly correlated [$r = 0.84$, $n = 16$, $p < 0.0001$; although some degree of correlation is expected, see discussion by Zobel (1997)], further suggesting that our patterns were not scale dependent.

Much of the observed variation in the response of species density might be explained by variation in the response of ANPP to fertilization (e.g., greater increases in ANPP might have intensified competition for light and thus caused a greater decline in species density). As with species density, we observed no consistent relationship between productivity response and initial productivity; responses differed among and within sites, although in almost all cases productivity increased (Fig. 2B). The largest ANPP response ratios occurred at the Minnesota old-field site at the highest levels of N addition, but the magnitude of response varied from year to year. Averaged across all observations ($n = 138$ comparisons), ANPP increased 53% (95% C.I.: 45–

62%) in response to N addition. Within-study variance accounted for only 38% of the total variation in ANPP, suggesting appreciable differences in ANPP response among studies. There was a negative relationship, with considerable variation, between the species density response and the productivity response across these sites (Fig. 2C) indicating that some variation in species density response was likely due to site-to-site variation in overall productivity response following fertilization.

Some of the variation in the data in Fig. 2 could be ascribed to the duration of the study, particularly for those studies for which we had multiple years of data. Although ANPP responses to fertilization may be rapid, it is likely that the magnitude of the species density response to this manipulation increases over time. Tilman (1993) found that the decline in species density in fertilized plots in Minnesota old fields varied over time but stabilized after four to five years. Variation among studies in the amount of N applied also could contribute to variation in ANPP response, and thus the response in species density. The Minnesota old-field site was the only site where multiple N levels were applied; other sites used a single level of N addition between 10 and 13 g m⁻² yr⁻¹. At the Minnesota site, two old fields showed a larger ANPP increase at the higher levels of N than the other two fields (data not shown).

Restricted data set

Based on these preliminary analyses, we created a subset of the data by focusing on studies that added between 9 and 13 g N m⁻² yr⁻¹, and examining only the last year (> 4 yr) for which we had data from each LTER site (Table 1). Analyses run on this restricted dataset, containing one observation per community at each site, generally supported the patterns revealed by the initial exploration of the entire data set.

In the restricted data set there was no clear pattern among sites, or among communities within sites, of species density response (Fig. 3A). Overall, D decreased 26% (13–38%; $n = 16$) in response to N addition. Even with this restricted data set, there was still considerable variation among studies in the species density response ratio; the between-study variance accounted for 72% of the remaining variance (comparable to the 66% for the entire data set). ANPP increased an average of 52% (39–66%; $n = 13$), but this response again appeared to be independent of initial productivity (Fig. 3B). Because this relationship involves two variables whose errors are not independent (i.e., the independent variable, $ANPP_c$, is measured with error and is used to calculate the productivity response ratio), we regressed $ANPP_n$ on $ANPP_c$. This relationship was linear (slope = 1.8 ± 0.2 ; a quadratic term did not explain additional variance), with an intercept that did not

differ from zero (-38.0 ± 65.3), and explained 83% of the variance ($p < 0.001$) in ANPP response to fertilization. This alternative (unweighted) analysis provides further support for the conclusion that the proportional response of ANPP was constant across the initial productivity gradient.

Interestingly, we could detect no statistically significant differences among sites in their responses (i.e., using communities within sites as replicate observations, and using a mixed effects model) with respect to either species density or ANPP. Thus, there was as much variation among communities within a particular site in response to N addition as observed across all the sites included here (e.g., see Minnesota old-field data in Fig. 3B). The response in species density was, however, negatively correlated with the magnitude of response in ANPP ($r = -0.56$, $n = 13$, $p < 0.05$; Fig. 3C), suggesting again that a larger increase in ANPP resulted in a larger decrease in species density.

Other limiting factors

The lack of predictable variation in species density response and the presence of variation in the ANPP response may imply that other resources limit ANPP at some sites and may affect community response to N addition. Simultaneous factorial experiments of N and P addition have been conducted at three of the sites included here (tall-grass prairie, arctic and alpine tundra) whereas at one site (short-grass prairie) an experiment adding H₂O, with and without N, was conducted for five years (Table 2). Factorial H₂O and N additions have also been conducted at the Michigan old-field and desert sites, but were not appropriate for this analysis. The Michigan study only lasted one year and added much higher amounts of N ($80 \text{ g m}^{-2} \text{ yr}^{-1}$; Goldberg and Miller 1990), and the desert experiment did not measure community-level ANPP.

Adding H₂O to short-grass prairie communities had more dramatic effects on species density than did adding N. Water additions significantly increased both ANPP [by 89% (95% C.I.: 36–164%)] and species density [by 71% (42–107%)] over control values after five years of treatment. The N + H₂O addition treatments in short-grass prairie resulted in an ANPP increase almost twice that of N alone [i.e., a 93% (47–155%) increase]; however, species density did not change relative to N alone [i.e., a 3% (–21% to 34%) increase]. The H₂O addition treatments eliminated succulent species, while other functional groups increased in dominance and species numbers. These shifts in species composition and functional groups were still evident eleven years after cessation of the treatments (Milchunas et al. 1990). During dry years at the desert site there was very little difference between D_n and D_c in the N-only treatments (Table 1), while during

wet years $D_n < D_c$ (visible as seasonal variation in Fig. 2A).

Phosphorus additions alone had a negligible effect on ANPP, except in wet sedge tundra at the arctic site, where ANPP doubled in response to P addition (Shaver et al. 1998). However, P additions had no significant effect on species density at any site in our data set. N + P increased ANPP more than N alone in arctic and alpine tundra, but not in tall-grass prairie; species density in N + P fertilized plots did not change consistently among these sites (data not shown).

Discussion

We discerned patterns in response to fertilization across these seven sites that had not been detailed in previous reviews, perhaps because by using raw data we could better evaluate quantitative effects (also see Osenberg et al. 1999, Gross et al. 2000) and compare magnitudes of response. Ideally, a meta-analysis of experimental studies combines data from a coordinated, planned, consistent set of experiments, but such efforts have rarely been undertaken [for two notable exceptions see results of the International Tundra Experiment in Arft et al. (1999) and a cross-site decomposition experiment (LIDET 1995)].

In any meta-analysis, there are several crucial issues to consider, two of which are spatial scale and temporal scale of the experimental studies. Unfortunately, investigators at most of these sites have not documented species-area relationships in these communities, and this hampered our ability to compare spatial patterns of species density among sites. Also, we did not have good estimates of the regional (large-scale) species pool at these sites, and this can also influence the local (small-scale) species pool (Pärtel et al. 1996, Zobel 1997). Clearly, our understanding of small-scale dynamics is incomplete if we do not also know the species that are available to colonize a site. As for temporal scale, duration of the study can affect response to nutrient addition, with long-term studies frequently showing different effects from short-term studies (reviewed in DiTommaso and Aarssen 1989, Chapin et al. 1995). Within sites, levels of ANPP can vary over time based on previous and current year's precipitation, as well as other factors (Walker et al. 1994, Briggs and Knapp 1995, Huenneke and Noble 1996, Huberty et al. 1998), as can species density. Unfortunately we did not have data collected in consecutive years for the complete duration of any study, so we were limited to those years for which data were available. Despite these limitations, our results represent a summary of a valuable data set from several different biome types that showed surprisingly similar results in direction of response to a consistent amount of N addition.

General findings

Our initial hypotheses, and the questions we posed in the Introduction, were based on the assumption that differences in initial productivity among sites would determine the magnitude and direction of change in species density in response to nutrient additions that increase productivity. Instead, we found that plant species density did not respond to increased productivity as predicted by the hump-shaped curve. All sites showed similar changes in both productivity and species density, regardless of initial productivity levels.

Recently, Stevens and Carson (1999) proposed that the decrease in species density along an artificial productivity gradient may be caused by certain plants increasing in size, but that the species identity of the plants that are excluded is relatively random. This suggests that the magnitude of response to a fertilizer perturbation depends on the spatial scale of the experiment and the analysis (see also Oksanen 1996). However, we found that species richness calculated at larger scales (e.g., summed over all plots) indicated the same species consistently were excluded from the fertilized plots within a community, suggesting that exclusion was not random and that species identity is important in determining response to fertilization. Further, in our data set, plot size used for the manipulations did not appear to affect differences in magnitude of response to fertilization.

The magnitude of productivity response did appear to affect the magnitude of species density response, but with some variation. Sites in which there was a large ANPP increase in response to fertilization demonstrated large decreases in D . The extent to which other limiting resources, such as H_2O or P, limited productivity at these sites also may have contributed to some of the variation in magnitude of response we observed. However, our data was too limited to generalize across all sites included. We discuss these results in detail below.

All communities increased ANPP and decreased species density in response to added N

When $9\text{--}13\text{ g N m}^{-2}\text{ yr}^{-1}$ was added, ANPP increased by approximately 50% over control levels across the full range of productivity examined, supporting our second hypothesis that ANPP should increase similarly across communities and sites regardless of their initial productivity (H_2 in Fig. 1). In low productivity sites this may represent a small absolute change in biomass, and therefore may be more difficult to detect statistically than an equivalent proportional increase observed at a high fertility site. This may explain the difference between our results and those reported by DiTommaso and Aarssen (1989) who concluded in their review that

low fertility communities were less responsive to increased nutrients than intermediate or high fertility communities (see also Chapin et al. 1986).

Species density decreased in response to fertilization in almost all the communities and sites we examined. For our results to be consistent with a hump-shaped relationship between species density and productivity, D_n/D_c should have been greater than (or equal to) one at low productivity and less than one at higher productivity levels (Fig. 1). Although D_n/D_c was variable both among communities within a site and among sites, it was consistently less than one and was not related to initial productivity or biome type. Even within our restricted data set, we found no relationship between species density response and initial productivity.

Our initial hypothesis was based on the assumption of a hump-shaped relationship between ANPP and D within and among these sites. Although we found there was a unimodal relationship across these sites (see Gross et al. 2000), the relationship was weak ($R^2 = 0.26$, $p = 0.007$). In only one of the sites included in this analysis was there a significant relationship between species density and natural productivity; in unperturbed old fields at the Minnesota site, species density declined with increasing productivity (see Inouye et al. 1987, Gross et al. 2000). However, the results of fertilization studies at this site were similar to those observed at sites in which there was no relationship between species density and initial productivity (see Fig. 3 and Gross et al. 2000).

Variation in response among communities within biomes as large as across biomes

Despite a consistent proportional increase in ANPP across sites, and a general decrease in species density, N addition affected communities differently. There was as much variation among communities within a particular site in response to N addition as was observed across all the sites included here. This result suggests that although the direction of response to N addition was consistent, we cannot generalize across sites or within biomes and must seek community-specific mechanisms to explain differences in magnitude of response.

Our analysis focused on the effect of N addition on these communities, but other resources may constrain the magnitude of response to N additions. For example, H_2O limitation is likely an important controlling variable in community dynamics in arid and semi-arid communities, particularly in terms of productivity (Lauenroth et al. 1978). Phosphorus limitation may also affect responses to N addition. From the experiments conducted at these LTER sites, it is difficult to determine if there is a general relationship between N and P additions because different amounts of P were added, and only three studies appropriate for this analysis were conducted.

A key factor in the response of a community to nutrient additions is initial species composition. A species that can respond quickly to increased nutrients will likely come to dominate the area and exclude other species when fertilized (e.g., Tilman 1993). This effect may be particularly strong in communities that include different life forms or functional groups. For example, in moist tussock and dry heath arctic tundra at Toolik Lake, Alaska, one or two species of a particular growth form, deciduous shrub and graminoid, respectively, came to dominate fertilized plots; species density decreased in these plots after several years of fertilization (Chapin et al. 1995, L. Gough and G. R. Shaver unpubl.). However, in another arctic community (wet sedge tundra), where most species are of the same growth form (rhizomatous graminoids), fertilization did not cause a shift in dominant life form. Although species abundance was altered, no changes in species density occurred even after nine years of treatment (Shaver et al. 1998). Similar results have been found in other systems (Tilman 1993, Collins et al. 1998, Gough and Grace 1998, Huberty et al. 1998), suggesting that initial species composition and the composition of the local species pool likely account for some of the variation in response to fertilization we observed in this survey.

Litter accumulation is another important mechanism that can affect species composition in terrestrial plant communities and may cause species density to decrease with resource addition (reviewed in Facelli and Pickett 1991; Tilman 1987, Carson and Peterson 1990, Tilman 1993, Foster and Gross 1998). Results from several studies indicate seedling emergence is inhibited by increased litter production and that species recruiting from seed, particularly dicots, are most likely to be excluded (Foster and Gross 1998, Gough and Grace 1998). In the short-grass prairie, species density differed in watered plots relative to controls for many years following cessation of treatments, with no clear correlation with precipitation. Litter accumulation due to increased aboveground production in the watered plots maintained these differences in species numbers (Milchunas and Lauenroth 1995). In unburned tall-grass prairie, however, species richness is highest in the presence of litter (Collins et al. 1995). These studies and others suggest that the importance of litter accumulation in controlling species numbers may differ among communities, depending on the effect of litter on moisture and light availability, and the adaptation of species in the community to such conditions.

Interpretation of richness responses to nutrient addition

Local plant species richness is determined by many factors in addition to soil N availability, including

availability of other resources, land use history, various stresses, and the species pool available to colonize a site. We focused in this paper on the effects of manipulation of one resource, N, that is commonly limiting in terrestrial plant communities to determine how added N influences plant species density across a productivity gradient. From our detailed comparisons of the results of fertilization experiments from seven different habitats, we conclude that nutrient enrichment studies can tell us much about local, within-community processes, but may be of limited value in interpreting an across community pattern, such as the hump-shaped relationship between productivity and species richness. Nutrient addition experiments reveal a great deal about community nutrient limitation, which plant species are better adapted to high artificial and natural fertilities, and other important aspects of plant-nutrient dynamics. They also may help us predict responses of natural vegetation to increasing atmospheric N deposition that has already caused shifts in species composition, particularly in heathlands in northern Europe (Bobbink et al. 1998).

However, interpreting experimental results from a local-scale experiment in terms of a broad hump-shaped pattern can be misleading; the forces acting to cause the hump-shaped pattern include long-term processes (succession, colonization, adaptation, feedbacks/linkages to soil microbial communities, etc.) that are not likely to be mimicked by experimentally increasing fertility at one small area over relatively short time spans (Rosenzweig and Abramsky 1993, Mittelbach et al. unpubl.). In particular, it may be easier for species to be lost from a plot than for species to be gained, because of limitations on the dispersal and colonization abilities of individual species and the traits of species present in the regional species pool (Tilman 1993, Marrs et al. 1996, Zobel 1997). For the sites examined in this study, an underlying hump-shaped relationship (Gross et al. 2000) had little effect on the response to fertilization of ANPP, suggesting similar nutrient limitation among sites despite different productivity levels. The consistent decrease in species density among sites with variation in the magnitude of this response indicates local, community-specific mechanisms are operating within and among biomes to cause changes in community structure as a result of N addition.

Acknowledgements – We gratefully thank many LTER investigators who went to great lengths to provide us with unpublished and published data sets, including Laura Huenneke and John Anderson (JRN), Bill Bowman and Terry Theodose (NWT), Danny Milchunas and Bill Lauenroth (SGS), Jim Laundre and Gus Shaver (ARC), and Clarence Lehman and Dave Tilman (CDR). Helpful comments on earlier versions of the manuscript were provided by Bill Bowman, Stanley Dodson, Laura Huenneke, Danny Milchunas, Gary Mittelbach, John Moore, Sam Scheiner, Gus Shaver, Bob Waide, Mike Willig, Bob Peet, Mike Huston, and Martin Zobel. This work resulted from a workshop organized by Bob Waide and Mike Willig entitled “Analysis of the Relationship Between Produc-

tivity and Diversity Using Experimental Results from the Long-Term Ecological Research Network" conducted at the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant DEB-9421535), the Univ. of California at Santa Barbara, and the State of California. We thank all the participants of the workshop for their valuable comments and insight. The LTER Network Office provided additional financial support for the completion of this paper. Salary support for L. Gough was provided by NSF grant OPP-9415411 to the Marine Biological Laboratory.

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