

Do individual plant species show predictable responses to nitrogen addition across multiple experiments?

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A number of experiments have addressed how increases in nitrogen availability increase the productivity and decrease the diversity of plant communities. We lack, however, a rigorous mechanistic understanding of how changes in abundance of particular species combine to produce changes in community productivity and diversity. Single experiments cannot provide insight into this issue because each species occurs only once per experiment, and each experiment is conducted in only one location; thus, it is impossible from single experiments to determine whether responses of particular species are consistent across environments or dependent on the particular environmental context in which the experiment was conducted. To address this issue, we assembled a dataset of 20 herbaceous species that were each represented in at least 6 different fertilization experiments and tested whether responses were general across experiments. Of the 20 species, one consistently increased in relative abundance and five consistently decreased across replicate experiments. A partially-overlapping group of 8 species displayed responses to nitrogen that varied predictably among experiments as a function of geographic location, neighboring species, or a handful of other community characteristics (ANPP, precipitation, species richness, relative abundance of focal species in control plots, and community composition). Thus, despite modest replication and a limited number of predictor variables, we were able to identify consistent patterns in response of 10 out of 20 species across multiple experiments. We conclude that the responses of individual species to nitrogen addition are often predictable, but that in most cases these responses are functions of the abiotic or biotic environment. Thus, a rigorous understanding of how plant species respond to nitrogen addition will have to consider not only the traits of individual plant species, but also aspects of the communities in which those plants live.

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Considerable evidence indicates that terrestrial net primary production is limited by nitrogen availability (Vitousek and Howarth 1991), and that changes in nitrogen availability can dramatically alter local species

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composition and plant community structure (Tilman 1987, Gough et al. 2000, Stevens et al. 2004). Given that anthropogenic activities have greatly increased nitrogen availability globally (Vitousek et al. 1997a, b), it is essential to understand the impacts that increased nitrogen availability will have not only on ecosystem parameters, such as primary production, but also on plant community composition and structure.

In addition to addressing a pressing environmental problem, studies of the impacts of nitrogen availability on plant communities may also reveal the underlying mechanisms that control community diversity, composition and dominance patterns. For example, one hypothesized mechanism to explain changes in species composition with increasing nitrogen availability is a shift from belowground competition for resources to aboveground competition for light (Tilman 1988, Wilson and Tilman 1991, 1993, Milchunas and Lauenroth 1995). Under this scenario, short-statured species are likely to decline as competition for light intensifies. Similarly, one might predict that legumes would decline with increasing nitrogen availability, because they would lose their primary advantage (nitrogen fixation) over other species if nitrogen was not limiting (Suding et al. 2005).

With both these goals in mind, a number of fertilization experiments have been conducted in natural communities in a variety of ecosystems. Literature reviews (DiTomasso and Aarssen 1989) and meta-analyses (Gough et al. 2000) have found relatively similar responses of community biomass and species richness to nutrient additions, with biomass increasing and richness decreasing. Gough et al. (2000) found a consistent increase in aboveground net primary productivity (NPP) in response to nitrogen addition at seven different Long-Term Ecological Research (LTER) sites across North America, with a consistent, but more variable, decrease in species density. Focusing just on species density, however, ignores changes in community composition and the mechanisms underlying these changes. Recent discussion in the literature about the sampling effect (Huston 1997, Loreau and Hector 2001, Wardle 2001, Aarssen et al. 2003) has highlighted the importance of considering the responses of individual species to perturbations. Thus, examining patterns of individual species responses to fertilization might both help illuminate the mechanisms driving the well-documented community changes, and help explain the considerable variation typically observed around the overall diversity decrease (Suding et al. 2005).

Single experiments, however, cannot provide much insight into the responses of particular species, because each species is, by definition, replicated only once in a given experiment. Even if species are grouped into guilds or functional groups, the number of species within a guild in most experiments is modest (or unbalanced), and

therefore it is difficult to make rigorous statements about how particular guilds respond. One solution to this problem is to compare the responses of individual species across multiple experiments. It may be that species respond consistently across experiments, in which case we can develop a predictive understanding of the mechanisms driving the productivity–diversity relationship based upon an understanding of particular species or species with particular traits. Alternatively, the response of species may be context-dependent, a function of the abiotic or biotic environment, in which case our general theory would also have to consider context-dependent responses of different taxa. Finally, species responses to increased nutrient availability might be random, in which case extrapolating from the results of individual studies would be misleading. To evaluate these possibilities we need to search for generalities across experiments.

Several methods may be used to achieve this goal. One approach is to see if a given species consistently shows similar responses in different experiments within and across ecosystems within its range. For example, the range management literature identifies species that consistently increase or decrease in relative abundance with grazing as “increasers” and “decreasers” (Weaver 1968). If we can identify species that consistently increase or decrease in response to nitrogen addition, this would allow strong predictions in novel situations, and refine a common goal of determining accurate functional group categories based on how species respond to particular perturbations.

Alternatively, some species may not respond consistently in different experiments. Instead, the direction or magnitude of their response may be context dependent (Schade et al. 2003). For example, if other species are present in the community that have a similar inherent ability to respond to increased nutrients, another species might be restricted from increasing via competition, whereas if there were no similar species, it might be able to dramatically change in abundance. Similarly, if environmental conditions cause a particular stress response, a species might not be able to take advantage of increased nutrients for increased growth. If these conditional responses can be understood, this again would allow predictions in novel situations.

To test these hypotheses, we identified a suite of species that occurred in multiple nitrogen addition experiments. We began with a detailed database assembled by a synthesis group focused on nitrogen addition studies, and then supplemented this with additional data on selected species extracted from the literature. We asked two questions. First, do individual species consistently increase or decrease in response to nitrogen addition when examined across a suite of experiments? Second, is variation in the responses of individual species to nitrogen addition predictable based on traits of the sites or the composition of the plant community?

Methods

Species responses to nitrogen fertilization were compiled from 31 experiments at nine different sites (Table 1). The sites were largely herbaceous systems, including arctic tundra, grasslands, old fields and salt marshes. All experiments included in the database involved nitrogen additions, but the amount and form of the nitrogen applied differed among experiments. More than one experiment within a site was included if experiments occurred in different naturally-occurring vegetation types (e.g. dry heath and moist acidic tussock tundra in the arctic site) or if an additional factor was experimentally manipulated (e.g. the effects of nitrogen addition in the presence and absence of annual burns in the tallgrass prairie site). Experiments differed in their duration, ranging from two (in rapidly-responding systems) to 19 years. In most cases the last year available was used in the analyses. Additional details about the experiments and study sites are provided by Suding et al. (2005).

For each species in each treatment of each experiment, we calculated relative abundance based on biomass or percent cover (depending on the study) by dividing the absolute abundance of the species by the abundance of all species and multiplying by 100, yielding relative abundance values that varied from 0 (absent) to 100 (monocultures). We calculated the response ratio for each species in each experiment as $\ln(\text{relative abundance in fertilized treatment}/\text{relative abundance in control})$.

Because this ratio is undefined if the abundance in one of the treatments is zero, we added 0.01 to all relative abundance values prior to calculating the response ratio.

Once this data set was compiled, we identified species that were included in multiple experiments, and searched the literature for additional experiments involving these species to increase replication. We obtained additional data for *Achillea millefolium* (Foster and Gross 1998, Turkington et al. 2002), *Agropyron repens* (Foster and Gross 1998), *Ambrosia artemisiifolia* (Carson and Barrett 1988), *Distichlis spicata* (Levine et al. 1998, Emery et al. 2001, Pennings et al. 2002), *Juncus gerardii* (Levine et al. 1998, Emery et al. 2001), *Juncus roemerianus* (Pennings et al. 2002, McFarlin et al. unpubl.), *Poa pratensis* (Foster and Gross 1998), *Salicornia virginica* (Covin and Zedler 1988, Pennings et al. 2002, McFarlin, unpubl.), *Solidago canadensis* (Bakelaar and Odum 1978, Carson and Barrett 1988), *Spartina alterniflora* (Levine et al. 1998, Emery et al. 2001, Pennings et al. 2002, McFarlin et al., unpubl.), *Spartina patens* (Levine et al. 1998, Emery et al. 2001, Pennings et al. 2002) and *Vaccinium vitis-idaea* (Press et al. 1998). Our final data set consisted of all species (20) that met an arbitrary cutoff of at least six experiments/species (Table 2). No records from the Niwot Ridge or Central Plains sites met our criteria for inclusion in this study.

We tested for consistent responses across experiments in two ways. First, we tested whether a species increased

Table 1. Species responses were synthesized from 31 experiments at 9 sites throughout North America. Multiple values are listed for duration of the study, and the year used for each experiment, if experiments within a site varied in protocols (the order follows the order in which the experiments are listed within each site). Details on experiments and sites can be found for ARC (Shaver et al. 1996, Gough et al. 2002, Gough and Hobbie 2003), CRP (unpubl.), CDR (Inouye et al. 1987, Tilman 1987, Wedin and Tilman 1996), GCE (Pennings et al. 2002), JRG (Shaw et al. 2002, Zavaleta et al. 2003), KBS (Huberty et al. 1998), KNZ (Seastedt et al. 1991, Collins et al. 1998), NWT (Bowman et al. 1995, Theodose and Bowman 1997, Seastedt and Vaccaro 2001), and SGS (Lauenroth et al. 1978, Milchunas and Lauenroth 1995).

Community type and location	Experiments within each site	Duration	Year used
ARC. Arctic tundra, Toolik Lake, AK	5 sites: dry heath (2 locations), moist acidic tussock, moist nonacidic tussock, moist tussock tundra	1985, 89, 89, 97, 85-present	14, 10, 10, 5, 14
SBC. Coastal salt marsh, Carpenteria, CA	5 zones dominated by different species	1999-present	3
CDR. Old field, Cedar Creek Natural History Area, MN	3 sites abandoned from agriculture in 1968 (last crop = soybean), 1957 (last crop = soybean), 1934 (last crop = corn) and 1 site of native oak savannah	1982-present	Avg 17–19†
GCE. Coastal salt marsh, Sapelo Island, GA	5 zones dominated by different species	1996–1997	2
JRG. Annual grassland, Jasper Ridge Biological Reserve, CA	1 site, dominated by naturalized European species	1998-present	4
KBS. Old field, Kellogg Biological Station, MI	2 sites, both abandoned from agriculture 1989, annually tilled or untilled	1989-present	Avg 10–12†
KNZ. Tallgrass prairie, Konza Prairie Research Natural Area, KS	4 lowland sites: burned and annually mowed, burned only, mowed only, or neither	1986-present	13
NWT. Alpine dry meadow tundra, Niwot Ridge, CO#	3 sites: one dry, two mesic, with and without additional snow	1990-2002; 1993-present	10, 4
SGS. Upland shortgrass steppe, Central Plains Experimental Range, CO#	2 sites: one with increased water. Both ungrazed.	1997-present	3

† three-year averages of relative abundance measures were used in these studies because destructive biomass sampling produced high variability across years (the same area was never sampled twice).

no records from the Niwot Ridge or Central Plains sites met the criteria for use in this paper.

or decreased more often than would be expected by chance with a two-tailed binomial test. Second, we tested whether each species' response ratio was significantly different from zero with a one-sample t-test.

We then selected a subset of these species and explored variation in response within a species in two ways. First, for six salt marsh species, which had most of their records obtained from the literature, we typically had little information on site properties, but did have information on geographic location and most abundant neighbor (because salt marsh plant communities are low in diversity, there always was an unambiguous "most abundant neighbor" in control plots). For these six species (*Distichlis spicata*, *Juncus gerardii*, *J. roemerianus*, *Salicornia virginica*, *Spartina alterniflora*, *S. patens*) we examined variation as a function of geography and/or neighbor identity, depending on the distribution of the experiments across space or neighbors, using ANOVA or t-tests.

Second, for one of the salt marsh species, *Salicornia virginica*, and for eight terrestrial species (Table 3), we had data from a number of experiments on site traits and community composition. For these species we regressed their response ratio against six predictor variables: annual net primary production (typically estimated as standing biomass), annual precipitation, estimated species richness at the 10 m² scale, the relative abundance of the species in the control treatment, and plant community principle components PCA1 and PCA2. PCA1 and 2 were derived from a rotated, principle components analysis that described the differences in functional group abundance across the control plots in the different experiments. Functional groups that were the inverse of other groups (i.e. natives compared to non-natives) were

omitted from the analysis, leaving 11 functional group descriptors. PCA1 explained 29% of the variation and PCA2 explained an additional 22% of variation. Clumper-clonal growth had high positive loadings and runner-clonal growth and evergreen-shrub growth-form had high negative loadings on PCA1. Non-native origin and annual life history had high positive loadings on PCA2. Thus, PCA1 explained differences among sites in clonality and woody growth, and PCA2 described differences among sites in life history and invasability. We selected the best regression model based on Mallows' Cp statistic and adjusted R² values. This process may retain variables that are not individually significant but improve the fit of other variables. We only retained variables with P < 0.15. Because we did not have site trait data for every replicate, sample sizes in regressions (Table 3) were often less than in t-tests (Table 2). For one species (*Salicornia virginica*) we were able to use both the geographic and the site trait analytical approaches.

The criteria for including species in the above two analyses were based on our ability to construct a geographic or neighbor contrast, and/or on a sample size ≥ 7 for use in regressions. Fifteen species met one or both of these criteria.

Results

Consistent responses

Six of 20 species responded consistently across multiple experiments (Table 2). The binomial test and t-test identified the same six species as consistent responders,

Table 2. Patterns of response of plant species to nitrogen addition. Consistent increasers or decreasers are indicated in bold.

Species	Number of experiments	Relative abundance in control plots (range)	Pattern (no. of experiments in which increased or decreased)	Binomial test, 2-tailed	Response ratio, t-test vs zero
<i>Achillea millefolium</i> *	12	0.02–5.8	Decr 7 of 12	P = 0.78	P = 0.11
<i>Agropyron repens</i>	7	0.04–15.2	Incr 6 of 7	P = 0.12	P = 0.07
<i>Ambrosia artemisiifolia</i>	9	0–11.4	Incr 7 of 9	P = 0.18	P = 0.06
<i>Andropogon gerardii</i> *	10	0–72.9	Decr 8 of 10	P = 0.11	P = 0.39
<i>Apocynum cannabinum</i>	7	0–12.8	Decr 4 of 7	P = 1.00	P = 0.46
<i>Asclepias syriaca</i>	10	0–1.4	Incr 6 of 10	P = 0.75	P = 0.65
<i>Asclepias tuberosa</i>	8	0–0.39	Incr 4 of 8	P = 1.00	P = 0.95
<i>Distichlis spicata</i> #	10	0.16–47.4	Incr 7 of 10	P = 0.24	P = 0.12
<i>Eragrostis spectabilis</i>	6	0–0.53	Incr 4 of 6	P = 0.68	P = 0.38
<i>Erigeron strigosus</i> *	8	0.003–0.79	Decr 7 of 8	P = 0.07	P = 0.02
<i>Juncus gerardii</i>	6	47.1–82.5	Decr 6 of 6	P = 0.03	P = 0.0009
<i>Juncus roemerianus</i> #	28	10.1–95.9	Decr 26 of 28	P < 0.00001	P < 0.0001
<i>Lespedeza capitata</i> *	10	0.004–5.9	Decr 9 of 10	P = 0.02	P = 0.01
<i>Poa pratensis</i>	9	0.004–45.9	Decr 5 of 9	P = 1.00	P = 0.40
<i>Salicornia virginica</i>	12	0–90.2	Incr 6 of 12	P = 1.00	P = 0.47
<i>Solidago canadensis</i>	13	0–55.0	Decr 7 of 13	P = 1.00	P = 0.44
<i>Solidago rigida</i> *	8	0.13–13.14	Decr 8 of 8	P = 0.008	P = 0.0004
<i>Spartina alterniflora</i>	32	6.9–80.4	Incr 32 of 32	P < 0.00001	P < 0.0001
<i>Spartina patens</i> #	8	26.3–79.3	Decr 5 of 8	P = 0.72	P = 0.47
<i>Vaccinium vitis-idaea</i>	6	0.24–18.9	Decr 5 of 6	P = 0.22	P = 0.32

* response predictably varied as a function of site traits (Table 2).

response predictably varied as a function of geography or neighbor (Fig. 1).

Table 3. Relationship of species responses to site characteristics. Species with significant regression models are indicated in bold. ANPP = annual net primary production, PCA1 and PCA2 = first and second principal component descriptors of plant community composition in control plots (PCA1 = clonality/woody growth; PCA2 = annual/non-native), PRECIP = annual precipitation, RACON = relative abundance in control treatment, SP10 = estimated species richness in a 10 m² plot. For predictor variables, # = 0.05 < P < 0.15, * = P < 0.05, ** = P < 0.01, *** = P < 0.001

Species	Predictor variables	Model
<i>Achillea millefolium</i>	+ANPP*, -PCA1**, +RACON**	n = 8, adj r² = 0.93, P = 0.003
<i>Andropogon gerardii</i>	-ANPP**, -PCA2**, -SP10*, -RACON**	n = 8, adj r² = 0.89, P = 0.03
<i>Apocynum cannabinum</i>	No significant model	n = 7
<i>Asclepias syriaca</i>	No significant model	n = 8
<i>Erigeron strigosus</i>	-ANPP**, -PRECIP*	n = 7, adj r² = 0.82, P = 0.01
<i>Lespedeza capitata</i>	-ANPP*, -PCA1*	n = 8, adj r² = 0.57, P = 0.051
<i>Salicornia virginica</i>	No significant model	n = 8
<i>Solidago canadensis</i>	No significant model	n = 8
<i>Solidago rigida</i>	+PCA1#, +SP10*	n = 8, adj r² = 0.70, P = 0.02

although in one case with modest replication (*Erigeron strigosus*) the binomial test was only marginally significant (P = 0.07). One species (*Spartina alterniflora*) consistently increased and five (*Erigeron strigosus*, *Juncus gerardii*, *J. roemerianus*, *Lespedeza capitata*, *Solidago rigida*) consistently decreased. Four other species showed strong trends towards increasing (*Agropyron repens*, *Ambrosia artemisifolia*, *Distichlis spicata*) or decreasing (*Andropogon gerardii*) that might have attained statistical significance with a few more replicate experiments.

Geographic and neighbor contrasts

Three of the six species examined had responses that varied with geography or neighbors. The response of *Distichlis spicata* differed between the northeast and southern (southeast, gulf coast, southwest) USA sites, with stronger increases in the northeast (Fig. 1A, t-test, P = 0.02). The response of *J. roemerianus* differed between the southeast and Gulf coasts of the United States, with strongest decreases on the southeast coast (Fig. 1B, t-test, P = 0.006). The response of *Spartina patens* differed significantly as a function of which species it was paired with in experiments (Fig. 1C). *S. patens* decreased when paired with *S. alterniflora* or *D. spicata*, but increased when paired with *Juncus gerardii* (ANOVA, P = 0.008, response with *Juncus gerardii* neighbors significantly different from other two neighbor types, which did not differ from each other, P < 0.05, Tukey test). The responses of the remaining three species examined did not vary with geography or neighbors. The response of *Juncus gerardii* did not differ as a function of which species it was paired with in experiments (*D. spicata*, n = 3, vs *S. patens*, n = 3; t-test, P = 0.56). The response of *Salicornia virginica* did not differ between experiments in the southeast (n = 5) and southwest (n = 7) of the United States (t-test, P = 0.65). The response of *Spartina alterniflora* did not differ among geographic regions of the

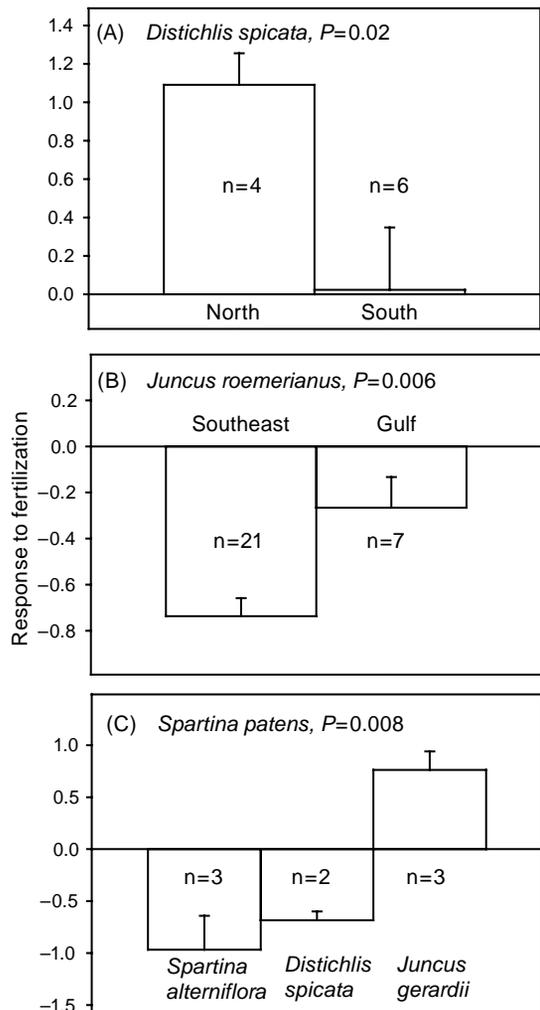


Fig. 1. Intraspecific variation in response to nitrogen. Data (response ratios) are means + 1 SE. (A) *Distichlis spicata* in two geographic regions. (B) *Juncus roemerianus* in two geographic regions. (C) *Spartina patens* when paired with increasers in New England (*Spartina alterniflora* and *Distichlis spicata*) vs a decreaser (*Juncus gerardii*).

United States (northeast, n = 3; southeast, n = 23; Gulf Coast, n = 6; ANOVA, P = 0.88).

Regressions versus site traits

Five (*Achillea millefolium*, *Andropogon gerardii*, *Erigeron strigosus*, *Lespedeza capitata*, *Solidago rigida*) of nine species examined had responses that predictably varied as a function of site characteristics (Table 3). Three of these five species are forbs (*Achillea*, *Erigeron*, *Solidago*) that are rare to moderately abundant in control plots, one (*Andropogon*) is a C4 grass dominant in old-field succession in Minnesota, and one (*Lespedeza*) is a common Midwestern legume. The most important predictor variables of the responses of these species were ANPP (1 positive and 3 negative relationships) and plant community composition, as described by principal components 1 (2 negative relationships) and 2 (1 negative relationship). Of these five, only the response of the grass (*Andropogon*) was (negatively) related to PCA2 (abundance of native/non-native species), while both the forb (*Achillea*) and the legume (*Lespedeza*) were negatively related to PCA1 (abundance of runner/clumper growth forms). In addition, the relative abundance of the species in control plots, species richness and precipitation entered into 2, 2 and 1 regression model(s) respectively. All inland species that had no significant models were forbs.

Discussion

We found that some species (6 of 20) consistently responded to nitrogen addition, and an additional four species showed strong trends towards consistent responses. Of the six significant responders, one increased and five decreased in abundance in fertilized plots (Table 2), consistent with the observation that species diversity is reduced in most fertilization studies (Gough et al. 2000). In addition, a partially-overlapping group of species (8 of 15) had variable responses which were predictable but context-dependent. In total, we were able to identify predictable patterns in the response to fertilization of 10 out of 20 species (Table 2). Given that our sample sizes for these analyses were quite modest (only 2 of 20 species occurred in n > 13 experiments), that we considered a limited number of predictor variables, and that the only trait uniting the 20 species that we studied was that they occurred in multiple experiments (i.e. they were not necessarily species that would be expected to show a strong response to nitrogen), we consider this to be a surprisingly strong result. Below, we first discuss the group of species that consistently responded, and then discuss variation in responses within species.

Consistent responders

One species, *Spartina alterniflora*, increased in response to nitrogen addition in each of 32 experiments. This salt-marsh grass can attain over 2 m in height under ideal conditions but is typically constrained to heights of < 1 m by the stressful soil conditions that prevail across most of the saltmarsh landscape, and which limit nitrogen availability (Mendelssohn and Morris 2000). Adding nitrogen frees *S. alterniflora* from the constraints imposed upon it by the physical environment, and allows it to attain more of its potential height. With added nitrogen, *S. alterniflora* is able to over-top and out-shade all of the species with which it normally co-occurs. Consequently, increases in *S. alterniflora* are likely to be a robust indicator of eutrophication in coastal habitats (Levine et al. 1998, Emery et al. 2001, Bertness et al. 2002, Pennings et al. 2002). Similarly, the increase in abundance of *Agropyron repens* with fertilization at most sites is likely due to its ability to rapidly fill light gaps and overtop its competitors (Tilman 1987, Tilman and Wedin 1991).

To identify traits typical of “increasers” and “decreasers” in fertilization experiments, Suding et al. (unpubl.) analyzed the response to nitrogen addition of 967 species records from 34 fertilization records using 19 functional groupings. Traits identified as typical of increasers include 1) non-leguminous, 2) monocot, 3) runner morphology, and 4) height (present in the upper third of the canopy). *Spartina alterniflora* has all four of these traits. The five species that consistently decreased in response to nitrogen additions each have some mixture of “increaser” and “decreaser” traits. *Erigeron strigosus* is an herbaceous dicot that does not occupy the upper third of the canopy (decreaser traits), but is non-leguminous (increaser trait). *Lespedeza capitata* is a leguminous dicot (decreaser traits), but it occupies the upper third of the canopy and has a runner morphology (increaser traits). *Solidago rigida* is a low-stature dicot that typically does not grow beyond the bottom third of the canopy (decreaser traits), but it is non-leguminous and has short rhizomes and so was classified as having a runner morphology (increaser traits). For these three species, it may have been that the presence of one or two decreaser traits was sufficient to “cancel out” the advantage of one or two increaser traits.

The final two consistent decreasers, *Juncus gerardii* and *J. roemerianus*, each have three increaser traits (they are monocots, non-leguminous, and occur in the upper third of the canopy) and only one decreaser trait (clumped morphology). These two *Juncus* species, however, usually co-occurred with other species, such as *Distichlis spicata* and *Spartina alterniflora*, that shared all their increaser traits and had the more favorable (under high nitrogen conditions) runner morphology. Thus, they may have been prevented from increasing in the nitrogen addition treatment by the presence of other

species that responded even more strongly. Alternatively, it may be, as we argued above, that the presence of even one “decreaser trait” is sufficient to prevent a species from increasing strongly following nitrogen addition.

Variation in responses within species

Although the early grazing literature described some species as “increasers” or “decreasers”, depending on their response to grazing (Weaver 1968), additional work has clarified that these responses to grazing are not always consistent. Instead, the responses of many species to grazing are dependent on environmental context (Milchunas et al. 1988, 1989, Vesk and Westoby 2001). Similarly, we found that the responses of many species to nitrogen addition were context-dependent, varying with geography, neighbor identity, or other environmental factors.

For three species, the response to nitrogen additions depended upon geographic location or neighbor. *Distichlis spicata* increased in all four of the experiments conducted in New England (Levine et al. 1998, Emery et al. 2001), but decreased in three of six experiments conducted at lower latitudes (Pennings et al. 2002, McFarlin, unpubl., Pennings, unpubl.). In two of the low-latitude experiments *Distichlis* was paired with *Spartina alterniflora*, which was a consistent and strong increaser. In general, low latitude salt marshes support greater biomass than high-latitude marshes, and plants at low latitudes may experience greater competition than plants at high latitudes (Pennings et al. 2003). Thus, better performance of *Distichlis* at high latitudes may reflect either that it was not paired with *Spartina alterniflora*, that competition is generally less intense at high latitudes, or both.

Juncus roemerianus decreased more strongly in experiments conducted on the southeast Atlantic coast than in experiments conducted on the Gulf coast. These two geographic regions differ strongly in physical forcing: the southeast Atlantic coast experiences large-amplitude (ca 3 m) lunar tides, whereas the Gulf coast experiences small-amplitude (ca 50 cm) weather-driven tides with an irregular periodicity (Pennings and Bertness 2001). Studies of zonation patterns of *J. roemerianus* in the two regions have suggested that competitive interactions between *J. roemerianus* and *S. alterniflora* are stronger in the southeast Atlantic than in the Gulf coast (Stanton 1998, Pennings et al. 2005). We speculate that nitrogen additions had smaller effects on *J. roemerianus* on the Gulf coast because of the weaker competitive interactions prevailing in this geographic region. Alternatively, many aspects of marsh soils and biogeochemistry likely differ between these geographic regions and may explain the different experimental results.

The responses of *Spartina patens* depended on the other species present in the community (Levine et al. 1998, Emery et al. 2001). *Spartina patens* always increased when paired with *Juncus gerardii*, a consistent decreaser (n=3 experiments), but always decreased when paired with *Spartina alterniflora*, a consistent increaser (n=3 experiments) or with *Distichlis spicata*, a consistent increaser at the New England sites where it overlapped with *Spartina patens* (n=2 experiments). Thus, the variable responses of *Spartina patens* simply reflected community context: whether *S. patens* increased or decreased depended on the nature and strength of response of its neighbors (and perhaps also on the underlying abiotic conditions that created these different plant mixtures).

For five terrestrial species, the response to nitrogen addition depended upon site traits, most typically ANPP and community composition (as described by PCA1 and 2). Of the four species that included ANPP in their final model, three were negatively associated with this site trait. These species cover a broad range of functional groups, including a common legume (*Lespedeza capitata*), a common forb (*Erigeron strigosus*) and a dominant C4 grass (*Andropogon gerardii*). We speculate that this broad distribution of species function may suggest a general relationship between the productivity of a site (estimated as control ANPP), and a species' response following fertilization, with greater decreases (in species that tend to decrease overall) following nitrogen addition at sites with high ANPP.

Sites of low productivity (e.g. ARC, CDR) in this dataset tend to have lower species richness (Suding et al. unpubl.) than sites of high productivity (e.g. KNZ). Low-productivity sites may also be more strongly limited by multiple resources than high-productivity sites. Hence, nitrogen addition may have more of an effect at high-productivity sites due to two mechanisms. First, a productive site may be more amenable to growth in general, with limitation primarily the result of N availability (Vitousek and Howarth 1991). Release from this limitation via nitrogen addition sets the system up for radical change. This change is amplified by the presence of species able to capitalize on these newfound conditions. A species-rich pool, though not necessarily a prerequisite, makes this more likely, whether by the higher statistical likelihood of having an opportunistic species present (e.g. sampling effect, Huston 1997), or by more complete coverage of “niche space” (niche complementarity effect, Tilman 1997, Loreau 2000). In addition, a low-productivity site will probably be dominated by species adapted to harsher conditions, with longer-lived tissues and slower overall growth rates (Aerts 1999), thereby making the number of opportunistic species in the already-small species pool even lower. However, teasing apart these poorly understood,

yet related, effects of productivity and species richness is difficult at best (Diaz and Cabido 2001).

For three terrestrial species, the response to nitrogen additions also depended in part on community composition (as described by PCA1 and 2). This result presumably reflects how responses to nitrogen addition by these species were mediated by other species. In the case of several salt marsh plants discussed above, we were able to explain variability as a function of community composition (neighbor identity) in some detail because the biology of those widely-distributed species is well known and the communities in which they occur are biologically simple, with low species richness. The terrestrial species occur in communities that are much more diverse both within and among sites, making it difficult to unambiguously identify the effects of neighbors. We suspect, however, that similar mechanisms are at work in salt marsh and terrestrial systems — the response of particular species to nitrogen is a function of both abiotic conditions and the responses of their neighboring species — but that these mechanisms are easier to identify in simpler communities.

Do plants show predictable responses to nitrogen addition?

Our results suggest that the response of individual plant species to nitrogen addition is often predictable. Given modest sample sizes (number of experiments) and a limited number of predictor variables, we were able to identify predictable aspects of species responses to nitrogen in half of the species we studied. It is reasonable to expect that, if we had had larger sample sizes and/or more predictor variables, we would have been able to identify predictable responses in a larger fraction of the species.

In only two cases, however (*Juncus gerardii* and *Spartina alterniflora*), were the responses of species completely independent of community context. In all other cases, species responses to nitrogen were context-dependent. The response of species was a function of site productivity, species richness and functional composition, and of how abundant the target species was to begin with. In part, this is a consequence of the fact that we used relative abundance, rather than absolute abundance, as a metric. Given the use of relative abundance, a strong increase in one species mathematically creates a decrease in relative abundance of others, even if they do not change in absolute abundance. We used this metric because the different methods that were employed in different experiments precluded use of absolute abundance, and also because it facilitates comparisons across systems that vary in richness and production. Nevertheless, examination of individual studies indicates that in fact particular species may either increase or decrease in absolute abundance following nitrogen addition depending upon who their

neighbors are (Levine et al. 1998, Emery et al. 2001). Thus, whether we look at relative or absolute abundance, it is likely that the response of many species to nitrogen additions will be context-dependent, a function of abiotic and/or biotic factors that differ among sites. This context-dependency is not surprising. Rather, it is exactly what would be expected if plants are adapted to particular environments and are competing with each other: whether a particular species can respond positively to a new environment will be a function of how its traits match the new environment and the degree to which other species are benefited by the new conditions. Experimental studies that directly pursue an understanding of this variation in response would greatly add to our ability to predict the responses of plant communities to nitrogen addition.

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