

Incorporating clonal growth form clarifies the role of plant height in response to nitrogen addition

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Abstract Nutrient addition to grasslands consistently causes species richness declines and productivity increases. Competition, particularly for light, is often assumed to produce this result. Using a long-term dataset from North American herbaceous plant communities, we tested whether height and clonal growth form together predict responses to fertilization because neither trait alone predicted species loss in a previous analysis. Species with a tall-runner growth form commonly increased in relative abundance in response to added nitrogen, while short species and those with a tall-clumped clonal growth form often decreased. The ability to increase in size via vegetative spread across space, while simultaneously occupying the canopy, conferred competitive advantage, although typically only the abundance of a single species within each height-clonal growth form significantly

responded to fertilization in each experiment. Classifying species on the basis of two traits (height and clonal growth form) increases our ability to predict species responses to fertilization compared to either trait alone in predominantly herbaceous plant communities.

Keywords Clonal growth · Competition · Grassland · Nitrogen addition · Productivity

Introduction

Understanding plant traits that are associated with species responses to fertilization is an increasingly important challenge for ecologists as global rates of nutrient deposition, particularly nitrogen (N), are on the rise (Galloway et al. 2008). Fertilization experiments conducted in low-stature, predominantly herbaceous plant communities such as grasslands, tundra, and marshes generally cause increased plant productivity and reduced species richness (Gough et al.

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2000; Suding et al. 2005; recently reviewed in LeBauer and Treseder 2008; Bobbink et al. 2010; De Schrijver et al. 2011). In many systems, species with a clonal growth form (with spreading architecture) appear to respond most positively to nutrient addition (Tilman 1987; Knops and Reinhart 2000; Shaver et al. 2001; Baer et al. 2004; Reynolds et al. 2007; Honsová et al. 2007; Eilts et al. 2011). While sometimes including potentially correlated traits, e.g., lateral spread (Gross et al. 2007), community-level studies rarely focus on clonal growth form directly (but see Sammul et al. 2003; Honsová et al. 2007; Eilts et al. 2011), despite evidence that clonal traits likely affect interactions between individual plants and thus community structure (Herben and Hara 1997; Gough et al. 2002; Zobel et al. 2010). Understanding the role of clonality in community responses to nutrient addition is important given that clonal species often respond significantly to this perturbation.

Shifts in the dominance of particular clonal growth forms have been predicted and observed across productivity and soil fertility gradients in communities dominated by low-stature, herbaceous plant species (e.g., Craine et al. 2001; Sammul et al. 2003). In temperate grasslands, Craine et al. (2001) found that species with low-growing, basal rosette forms were more common at low soil nutrient levels, while species with a taller, runner habit (i.e., rhizomatous growth form) tended to dominate higher productivity sites along both natural and artificial productivity gradients. Height has long been associated with competitive ability in herbaceous plant communities, with the generally accepted idea that light competition becomes more intense at high soil fertility levels when aboveground biomass and the stature of the vegetation increases (Wilson and Tilman 1993). However, there are few direct tests of light as a limiting factor in high fertility environments (Hautier et al. 2009). A recent field experiment by Dickson and Foster (2011) found that light competition is not the only mechanism driving species declines under fertilized conditions in grasslands and suggested that belowground interactions are likely also playing a role (see also Bobbink et al. 2010). We propose, as did Grime (2001) and Craine et al. (2001), that height and the capacity for clonal spreading may act in concert to maximize competitive ability at high soil fertility levels; however, how species with these two traits respond to changes in fertility has rarely been examined simultaneously across sites.

We expect that clonal growth form should affect competitive ability, because clonality creates the potential for local colonization via vegetative growth and can promote resource sharing among ramets that may benefit the entire plant (Stuefer et al. 1994; Herben and Hara 1997; Gough et al. 2002; Golubski et al. 2008). In this analysis, we focus on two simplified categories of clonal growth form distinguished by the distance between ramets of the same indi-

vidual: clumpers with very short spacers (phalanx; sensu Lovett Doust 1981) and runners with longer spacers (guerrilla). We recognize that many clonal species lie on a continuum between these two categories (e.g., Thomas and Hay 2010) and that many more categories of clonal growth can be used if appropriate morphological data are available (Klimešová and Klimeš 2011). Unfortunately, this information is lacking for most North American species. Our goal here was to determine if a simple classification considering only two easily measured or determined traits would be predictive of species responses to fertilization.

These two clonal growth forms have been shown to affect species performance across environments. When grown in competitive conditions, clumper growth forms tend to occupy space more completely over time, while runner growth forms can colonize new areas more quickly (Hartnett and Bazzaz 1985; Schmid and Harper 1985; Humphrey and Pyke 1998). In addition, growth forms may respond differently to a combination of disturbance and altered soil nutrients (e.g., Van Staalduinen et al. 2007). These growth form distinctions may be correlated with bud bank differences (Dalglish et al. 2008), which can be particularly important in determining response to perturbation; the number of meristems both above and below ground can control the initial response to a change in local nutrient availability. Clonal integration, or resource sharing among ramets, may be a crucial trait for plants growing in areas of patchy resources, because ramets in low fertility patches can be supplemented by nutrients from high fertility patches (Grubb 1987; Caraco and Kelly 1991; Stuefer et al. 1994; Oborny et al. 2000; Golubski et al. 2008). The capacity to expand vegetatively may also give clonal species a competitive advantage in high fertility environments, as they can expand in size via both growth of existing individuals and vegetative production of new ramets.

Here, we used data from a set of long-term fertilization experiments in low-stature plant communities across North America [see Electronic Supplementary Material (ESM) 1; Gough et al. 2000; Suding et al. 2005; Clark et al. 2007] to examine how clonal growth form and height together determine species changes in abundance in response to fertilization. A prior analysis of these data (see Suding et al. 2005), showed that aboveground net primary production (NPP) increased on average about 1.5× and species richness decreased on average 30% in these sites in response to fertilization (usually 10–12 g N m⁻² year⁻¹). However, there was variation among sites in the magnitude of the NPP increase; sites with greater NPP increases had greater species losses (see also Clark et al. 2007). A trait-focused analysis found that some traits expected to be less advantageous under higher fertility (e.g., capacity for N-fixation) were predictive of species loss in fertilized plots (Suding et al. 2005), but neither ‘clonality’ (either clonal or not) nor

height (relative position in the canopy) predicted probability of local extirpation in fertilized plots. This is contrary to empirical observations and theoretical predictions mentioned earlier that both height and lateral spreading should confer competitive advantage under increased soil nutrient conditions. However, Suding et al. (2005) only looked at species that were lost from fertilized plots. We focus here on how changes in abundance may be predicted by a combination of two traits: height and clonal growth form.

To examine the combined effects of clonal growth form and height on species response to fertilization, we created six height-clonal growth form categories based on the morphology of species growing in plots that did not receive added N in each experiment (data published in Cleland et al. 2008). Each species was classified into one of three clonal growth forms that reflected differences in lateral spread (non-clonal, runner, or clumper) and one of two height categories [tall (the top third of the canopy relative to the maximum in that community) or short (the bottom two-thirds of the canopy)]. We then examined how the relative abundance of species in these six height-clonal growth forms changed in response to fertilization and explored the following questions: (1) Do “tall-runners” (species that occur in the canopy and have a runner growth form) increase at the expense of other growth forms in response to added soil N across communities? (2) Does the initial abundance or number of species of a growth form affect the response to fertilization? We pose this question to determine if our observations are evidence for growth form differences or a sampling effect (*sensu* Huston 1997). (3) Do all species within a growth form respond similarly to added soil N? We pose this final question to test whether or not the growth form categories are predictive across species.

Materials and methods

The data used here include individual species responses to N addition and traits for each species for over 380 species and 37 experiments (Cleland et al. 2008). All trait data in this dataset were contributed by investigators involved in the experiments and by consultation with appropriate floras based on the characteristics of species in plots that did not receive added N. The experiments were conducted in a range of low-stature, predominantly herbaceous plant communities spanning a broad geographic gradient in North America including arctic and alpine tundra, coastal salt-marsh, and a variety of grasslands (ESM 1). Most of the communities are dominated by clonal perennials where recruitment from seed is infrequent, although the desert grassland and California annual grassland sites were exceptions to this pattern.

NPP measured as live annual or peak biomass in plots without added N ranged from <100 to more than 700 g m⁻² year⁻¹ across sites. Although the experiments varied in duration (4–19 years), the amount, form and method of N fertilizer added were similar across sites (7–12 g N m⁻² year⁻¹ with higher amounts in coastal marshes to compensate for loss into the water column; ESM 1). All of the experiments included an estimate of individual species relative abundance in control and fertilized treatments allowing us to compare how species changed in abundance (not just presence/absence) in response to N-addition. At some sites, fertilization experiments were conducted in multiple community types or additional manipulations such as water addition or mowing were included as separate “experiments” in the study design, allowing us to evaluate the effects of fertilization across a wide range of environmental parameter space. In all comparisons, we were examining how species abundances changed in response to N-addition and compare results to the appropriate “control” treatment to which no N was added (details in ESM 1 and Cleland et al. 2008). Although species richness and composition differ across sites, species of all six growth forms occurred in almost all sites and experiments (ESM 1).

In the published dataset (Cleland et al. 2008), species were assigned to one of three height categories based on relative position in the canopy in control plots: upper, middle, and bottom. For this analysis, we categorized species into two height classes: tall (previously “upper”) or short (either “middle” or “bottom” previously; see Cleland et al. 2008 for metadata). For clonal architecture we used the three categories included in the published dataset: non-clonal or two categories of clonal: clumper or runner. Species with vegetative offspring produced adjacent to parents were categorized as “clumpers.” Species with vegetative offspring produced farther away from parents were categorized as “runners.” Almost all the species included in the dataset are rhizomatous; only a few spread via stolons. Species that do not naturally produce vegetative ramets and all annuals were categorized as non-clonal. Each species in the dataset was then assigned to one of six height-clonal growth forms: tall-non-clonal, tall-clumper, tall-runner, short-non-clonal, short-clumper or short-runner. Because height was determined relative to the entire community, the growth form of each species in a particular experiment or site was determined based on its growth form in plots with no added N for each particular experiment and site. Thus, some widespread species that occurred in multiple sites were categorized differently for height (but not clonal growth form) in this analysis if their height relative to the rest of the community differed across experiments.

For most sites, we used the final year for which we had data in the published dataset; many of these experiments

are ongoing. For two sites, Michigan and Minnesota old fields (KBS and CDR, respectively), which had greater inter-annual variation in species richness than other sites, we used the average species abundance over the last 3 years of data in the analysis (see Clark et al. 2007). Because sites measured species abundance in different ways (percent cover or biomass; ESM 1), we used relative abundance as our estimate of abundance; this allowed us to include data from all 37 experiments in the analysis.

For each experimental plot, the relative abundance of each of the six height-clonal growth forms was calculated by summing the relative abundance of each species in that growth form category. We used MANOVA with site, experiment nested in site, fertilization, and appropriate interactions with the six growth form relative abundance values as the dependent variables to see how the main effects altered distribution among the growth forms. We also tested if relative abundance of the six growth forms individually were affected by fertilization and if this differed among sites and experiments.

To determine the individual species responses to fertilization, analyses were performed for each experiment separately and focused on the individual species not the growth forms. Relative abundance was analyzed as a function of species, fertilization, and their interaction, with appropriate blocking factors for that experimental design. Plot-level means were then compared using Scheffe's posthoc tests.

For each growth form at the experiment level, we further calculated a natural log response ratio as used in other meta-analyses based on the relative abundance (RA) of the growth form at the plot-level: $\lnRR = \ln(RA + N/RA \text{ control})$. A similar ratio was calculated for plot-level species richness and NPP to examine how responses of a particular growth form were correlated with these plot-level variables. For presentation, plot values were averaged according to the experimental design (some studies used blocks while others did not). All statistical analyses were carried out in SAS (v.9.2; SAS Institute, Cary, NC, USA).

Results

Effects of site and fertilization on growth form relative abundance

We examined the response to fertilization first with log response ratios calculated across the entire dataset. In this analysis, only the tall-runner growth form had a significantly positive \lnRR (0.38, 95% CI: 0.14–0.62) indicating that this growth form consistently increased in relative abundance with fertilization (Fig. 1). The response ratios for the two non-clonal growth forms were not significantly different from zero. For the remaining three growth forms,

the response to fertilization was significantly negative (tall-clumpers, -0.91 , 95% CI -1.62 to -0.19 ; short-runners, -0.37 , 95% CI -0.68 to -0.06 ; short-clumpers, -0.65 , 95% CI -1.26 to -0.04), indicating that these groups consistently declined with fertilization (Fig. 1).

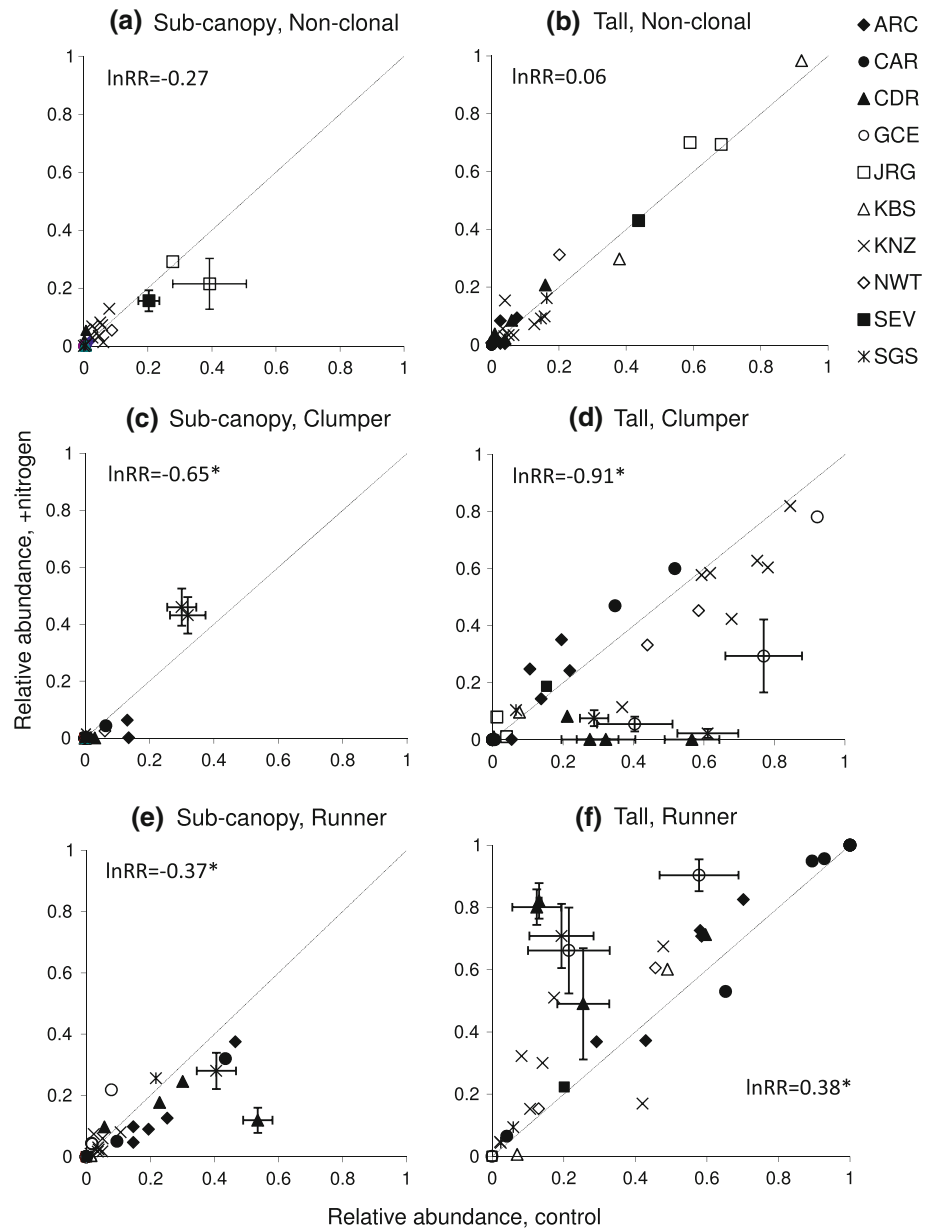
In the overall MANOVA, the interaction between fertilization and experiment (nested in site) was significant (Table 1), showing that fertilization affected relative abundance of the growth forms differently across the experiments. This was true for each growth form individually, except for tall-non-clonal. Similar to the log response ratios reported above, tall-clumpers, tall-runners, and short-runners had significant main effects of fertilization when analyzed in individual ANOVAs, suggesting that the response of these growth forms was driving the significant main effect of fertilization in the overall MANOVA.

Not surprisingly, the overall MANOVA revealed different relative abundances of the six growth forms across sites and experiments (Table 1). The six height-clonal growth forms were present in control plots in most experiments and were often represented by multiple species (ESM 1). Notable exceptions were the highest productivity saltmarsh sites which had low species richness overall compared to the other sites and only one or two growth forms (ESM 1). Site differences in abundance or number of species in different growth forms were not consistent across biomes. For example, tall-runners made up greater than 50% of the community in control plots for both coastal marshes (CAR and GCE) and some arctic tundra (ARC) communities, while tall-clumpers dominated control plots at tall-grass prairie (KNZ) and alpine tundra (NWT) sites.

In the overall MANOVA, five of the ten sites (CDR, KNZ, GCE, SEV and SGS) had a significant response of growth form relative abundance to fertilization. In multiple experiments in Minnesota old fields, Georgia coastal marsh, and tall-grass prairie (CDR, GCE, KNZ), tall-runners significantly increased in relative abundance, while tall-clumpers significantly declined (Fig. 1d, f). This trend of increasing relative abundance of tall-runners and decreasing relative abundance of tall-clumpers was evident, but not significant, in other experiments (Fig. 1).

Experiment-level NPP (in control plots) was not predictive of the type of growth form nor the magnitude of each growth form's response to fertilization (data not shown). Tall-runners significantly increased and tall-clumpers significantly decreased in experiments ranging from near $200 \text{ g m}^{-2} \text{ year}^{-1}$ (CDR) to almost $3,000 \text{ g m}^{-2} \text{ year}^{-1}$ (GCE). In two sites with low NPP ($\leq 165 \text{ g m}^{-2} \text{ year}^{-1}$), short-clonal growth forms were the strongest responders to fertilization. At the short-grass steppe site (SGS), short-clumpers significantly increased with N addition, while short-runners declined (Fig. 1c, e). In the desert grassland site (SEV), short-non-clonal species decreased in response

Fig. 1 Mean relative abundance of each height-clonal growth form in control plots plotted against their mean relative abundance in nitrogen addition plots by experiment; most sites had multiple experiments hence multiple data points per site (see ESM 1). *Error bars* represent the 95% confidence interval around the mean and are only plotted for growth forms with a significant response (significantly different from the 1:1 line). Significant natural log response ratios are indicated with an *asterisk* (see text for details)



to N addition (Fig. 1a). In higher productivity California annual grasslands with no water additions (JRG-NW; $475 \text{ g m}^{-2} \text{ year}^{-1}$), short-non-clonal species also significantly decreased. SEV and JRG-NW were the only site/experiments (out of 37) where non-clonal species had a significant change in relative abundance in response to fertilization; these sites have a greater proportion of annuals (non-clonal) than the others in this analysis.

Initial abundance and richness of growth forms versus magnitude of response

The relative abundance of species within a growth form in control plots generally had no effect on the response to fertilization. For the tall-runner growth form, which overall

showed the strongest positive response to fertilization, abundance in the control plots was not related to the magnitude of response to fertilization (Fig. 1f). In fact, experiments in which tall-runners were relatively low in abundance in control plots, such as several in Minnesota old fields (CDR), often had the strongest response to fertilization. Although tall-clumpers had similar ranges of abundance as tall-runners in control plots across experiments, tall-clumpers more often decreased in abundance in response to fertilization (Fig. 1d). These results suggest that initial abundance of a growth form is not a strong predictor of the magnitude or direction of response to fertilization.

Similarly, the number of species within a growth form was not related to the magnitude of abundance change (measured as lnRR) in response to N addition (Fig. 2). For

Table 1 MANOVA results analyzing the change in relative abundance with N addition overall and within each of the six height-clonal growth forms

Source	Overall			Short-clumpers			Short-runners		Short-non-clonal	
	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Site	54, 6,220	148.37	<0.0001	9	142.70	<0.0001	49.52	<0.0001	260.00	<0.0001
Experiment (site)	162, 7,171	14.79	<0.0001	27			7.86	<0.0001	1.86	0.005
Fertilization	6, 1,219	31.49	<0.0001	1			4.47	0.03		
Fert × exper (site)	216, 7,236	4.33	<0.0001	36	1.81	0.0026	1.92	0.001	3.08	<0.0001
Source	Tall-clumpers		Tall-runners		Tall-non-clonal					
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>				
Site	117.81	<0.0001	408.29	<0.0001	258.21	<0.0001				
Experiment (site)	36.66	<0.0001	74.15	<0.0001	17.70	<0.0001				
Fertilization	86.54	<0.0001	154.34	<0.0001						
Fert × exper (site)	11.32	<0.0001	12.91	<0.0001						

Degrees of freedom (*df*) are reported for numerator and denominator for overall results, numerator alone for individual growth forms, with 1,224 *df* used for the denominator (error) for all tests within individual growth forms. Only results significant at 0.05 are reported

example, although tall-runners and tall-clumpers showed the strongest response to fertilization (positive and negative, respectively), differences in the magnitude of the response to fertilization across experiments was not related to the number of species in these growth forms. Although sites differed in a number of environmental and biotic characteristics, there was not a consistent site specific signal in the number of tall-runner or tall-clumper species in an experiment or the magnitude of response to fertilization (Fig. 1; ESM 1). Nor were there any consistent differences within a site in how strongly the tall-runner group responded that related to the number of species in that group. For example, there were eight fertilization experiments from the tall-grass prairie (KNZ) in our dataset (ESM 1). Across these experiments, the number of species in the tall-runner growth form ranged from 2 to 15, and the magnitude of change in relative abundance (cover) by this growth form varied from none to a 4-fold increase. However, the number of species and the magnitude of relative change in abundance were not related in these experiments (Fig. 2a). Thus, species richness of a growth form was not predictive of the response of a community or growth form to fertilization.

Response of individual species

Despite the presence of multiple species within each of the six height-clonal growth forms, in almost all cases a single species at each site drove the significant response to fertilization (Table 2). Interestingly, the same species often had a consistent response to fertilization across multiple experiments within a site. For example, the positive response by tall-runners in Minnesota old-fields (CDR) was caused by

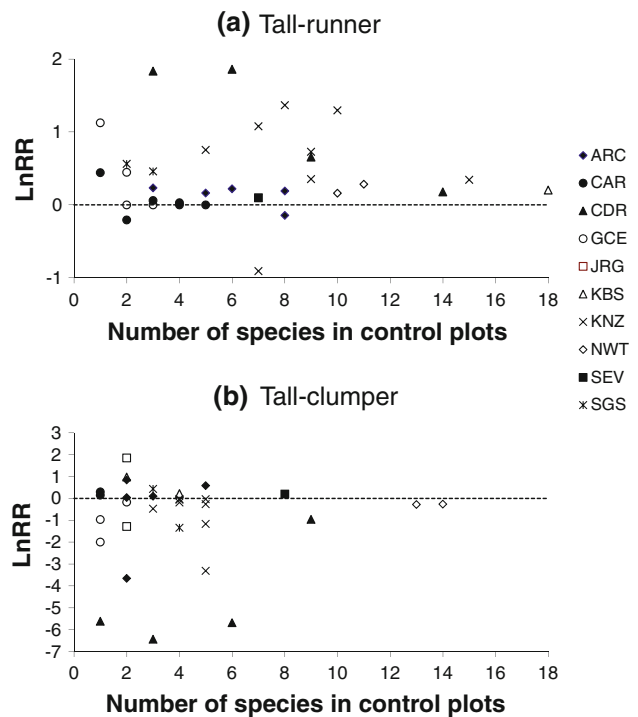


Fig. 2 Abundance response to added nitrogen (LnRR) in relation to species richness in control plots for **a** tall-runner and **b** tall-clumper. The dotted line indicates a log response ratio of 0, or no difference in relative abundance between control and N added plots. Site abbreviations in ESM

Elymus (Agropyron) repens at the expense of the tall-clumper *Schizachyrium scoparium* in three experiments (Fields A, B, C; Table 2). Similarly, in Georgia saltmarsh (GCE), *Spartina alterniflora* (a tall-runner) increased in relative abundance at the expense of tall-clumpers. In the tallgrass prairie site (KNZ), the tall-runner *Panicum virgatum*

Table 2 Individual species that responded significantly to added N

Species	Growth form	Site	Exper	Growth form richness	Growth form response	Species response	Detailed life form	Native	Family
Positive responders									
<i>Elymus repens</i>	TR	CDR	A	3	+66%	0.12–0.78	C3	Non-native	Poaceae
			B	6	+70%	0.01–0.67			
			C	9	+55%	0.01–0.40			
<i>Panicum virgatum</i>	TR	KNZ	BU	10	+41%	0.16–0.70	C4	Native	Poaceae
<i>Spartina alterniflora</i>	TR	GCE	SB	2	+32%	0.58–0.90	C4	Native	Poaceae
			SJ	1	+45%	0.21–0.66			
<i>Bouteloua gracilis</i>	SC	SGS	W	2	+16%	0.30–0.46	C4	Native	Poaceae
			NW	1	+9%	0.32–0.43			
Negative responders									
<i>Andropogon gerardii</i>	TC	KNZ	BU	5	–60%	0.28–0.02	C4	Native	Poaceae
<i>Aristida longiseta</i>	TC	SGS	W	4	–21%	0.26–0.06	C4	Native	Poaceae
<i>Borrichia frutescens</i>	TC	GCE	SB	1	–34%	0.40–0.06	DS	Native	Asteraceae
<i>Juncus roemerianus</i>	TC	GCE	SJ	1	–48%	0.77–0.29	C4	Native	Poaceae
<i>Schizachyrium scoparium</i>	TC	CDR	A	1	–28%	0.32–0.001	C4	Native	Poaceae
			B	3	–56%	0.54–0.001			
			C	6	–28%	0.25–0.001			
			KNZ	BU	5	–60%			
<i>Buchloe dactyloides</i>	SR	SGS	NW	3	–12%	0.28–0.19	C4	Native	Poaceae
<i>Poa pratensis</i>	SR	CDR	A	1	–42%	0.54–0.12	C3	Non-native	Poaceae

For site and experiment (*Exper*) abbreviations, please see ESM 1. *Growth form richness* is the number of species of that growth form recorded in control plots. *Growth form response* is the net change in relative abundance for the growth form while *species response* gives the mean relative abundance of that species in control plots and the value in +N plots. *Detailed life form* provides the photosynthetic pathway for grasses or *DS* for deciduous shrub

Growth forms: *TR* tall-runners, *TC* tall-clumpers, *SR* short-runners, *SC* short-clumpers

increased, but only significantly so in one experiment; in several experiments, tall-clumper relative abundance declined. In burned, unmowed tall grass prairie, two tall-clumpers significantly decreased: *S. scoparium* and *Andropogon gerardii* (Table 2). In unburned, unmowed tall grass prairie (KNZ), tall-clumper relative abundance declined by 24% with fertilization, but this was not caused by a significant individual response of any one of the five species within this growth form.

The only instances in which a short growth form responded positively to N addition were in short-grass steppe (SGS). There, *Bouteloua gracilis*, a short-clumper, increased relative abundance with fertilization in two experiments. The species and growth form that declined in relative abundance at this site depended on whether the N addition was conducted with or without a manipulation of water. *Aristida longiseta*, a tall-clumper, declined when fertilized plots were watered, and *Buchloe dactyloides*, a short-runner, declined when N was added without additional water (Table 2). At one of the least productive sites, the desert grassland (SEV), there were 10 species in the short-non-clonal growth form, and although overall relative abundance of this group decreased with fertilization

(Fig. 1a), no one species had a large enough response to be significant individually.

We did not find strong evidence that other plant traits included in our dataset were predictive of which species within a growth form would be a positive or negative responder to fertilization. All four species that significantly increased in response to added N are grasses; three are native, C_4 grasses and one (*E. repens*) is an introduced C_3 grass that is invasive in many Midwestern grasslands. Of the seven species that significantly declined in fertilized plots, five are native C_4 grasses, one is a non-native C_3 grass, and one is a deciduous shrub (Table 2). Although C_4 grasses (which make up approximately 12% of the species records in our dataset) were more likely to respond to increased N, whether they increased or decreased in relative abundance depended on their height-clonal growth form.

Discussion

Across the 37 experiments at ten sites that are included in this dataset, the most common positive response to added N was an increase in the relative abundance of species with a

tall-runner growth form. In only a very few cases did this height-clonal growth form decline in response to N fertilization. This significant increase in tall-runner relative abundance was unrelated to site productivity or other environmental factors. There also appeared to be no relationship between the tall-runner response and the number of plant species overall (ESM 1) or the number of tall-runner species (Fig. 2a) in control plots in a particular experiment, suggesting that neither site conditions nor a ‘sampling effect’ (sensu Huston 1997) drove this pattern.

Somewhat surprisingly, the increase in tall-runner relative abundance with N addition was not correlated with the magnitude of decline in species richness or increase in NPP at the plot level (ESM 1). We would have expected this if growth forms that were strong responders to N addition were driving community level patterns. Most likely, the absolute effect on NPP may be somewhat masked by our use of relative abundance as a response variable. For example, in Minnesota old fields (CDR) where biomass was used to calculate abundance, the magnitude of response of *E. repens* (a tall-runner) to fertilizer addition was correlated with both community-level NPP increase and species loss (Tilman 1987; Collins et al. 2008). Eilts et al. (2011) found, in an experiment where the presence of clonal species with a runner morphology was manipulated, that the magnitude of species loss in response to fertilization was correlated with the absolute and relative increase in biomass of this growth form. Similarly, Reynolds et al. (2007) found that the diversity loss in a low-productivity grassland was related to the magnitude of biomass increase by tall-runner clonal species (herbaceous and shrubby) to N fertilization (see also Houseman et al. 2008).

Although height is expected to give species a competitive advantage in high fertility environments (Wilson and Tilman 1993), our analyses have shown that height alone is not sufficient to predict a species’ probability of extinction (Suding et al. 2005) or change in relative abundance in response to N fertilization (see above). Short-statured species (those observed in the lower canopy in control plots) infrequently demonstrated a significant response to fertilization. Of the 37 experiments in our dataset, short-statured growth forms significantly declined in relative abundance in four experiments (short-runners at CDR-A and SGS-NW; short-non-clonals at SEV and JRG-NW) and significantly increased in two experiments (short-clumpers in two SGS communities). Some of the general lack of response may relate to the relatively low abundance of these growth forms in many of the communities (Fig. 1), but short plants make up approximately 70% of the species records in the dataset, so it is not likely that there were too few species with this trait included in our analysis to be able to detect a response.

Similarly, being “tall” was not a sufficient predictor of abundance increases in response to fertilization. In fact, species with a tall-clumper growth form declined in abundance, whereas those with a tall-runner form consistently increased. This pattern appears to hold whether we conduct these analyses based on change in absolute or relative abundance. For example, in several Minnesota old fields (CDR), tall-runners increased and tall-clumpers significantly decreased in both absolute and relative abundance (measured as biomass). As described earlier, it is unlikely that this response to fertilization is a result of a statistical sampling effect. Perhaps the ability of a runner species to escape localized light competition by placing new ramets in areas of greater light availability facilitates this growth form’s increase in relative abundance when soil N is no longer limiting. Clumping of ramets has been shown to reduce competitive ability under certain environmental conditions (Lenssen et al. 2005), but this likely depends on the growth form of the competitors (Cheplick 1997) and thus is neighborhood dependent. Manipulative garden or pot experiments that have explicitly focused on competition between clonal growth forms are rarely repeated in the field (Callaghan et al. 1992; Gough et al. 2002), thus extrapolating to natural conditions remains difficult.

Interestingly, in our analyses, a significant growth form response (positive or negative) was driven by the response of a single species to fertilization. Clonal demography of only a few of the species included in our dataset is understood well enough to begin to delineate how growth pattern differences among species within a growth form might contribute to this response (e.g., *S. scoparium*; Briske and Butler 1989; Welker and Briske 1992). We suspect that some of the differences in response within growth form are driven by meristem availability (bud bank) and flexibility in growth that facilitate rapid response to increased nutrients. Specific leaf area (SLA) could play a role in response, based on correlations of SLA along soil fertility gradients (e.g., Knops and Reinhart 2000; Wright et al. 2001). In a previous analysis of this dataset, however, SLA poorly predicted the loss of individual species (Spasojevic, M.J. and Suding, K.N., unpublished data). Environmental context is also an important factor in terms of whether or not a particular species can respond in a particular setting (see also Pennings et al. 2005). Additional trait and environmental data are likely necessary to predict which species within a growth form will be the strong responder.

Recognition that species differences in clonal growth form can predict their response to environmental perturbations has been a long (and strong) focus of many European plant ecologists. A recent compilation of clonal plant traits for northern Europe (the CLO-PLA3 database; Klimešová and Klimeš 2011), that defines clonal syndromes on the basis not only of morphology but also the mode of

persistence and ramet connectivity, has shown that these traits can work in concert to predict species abundance across community types. For example, Sammul et al. (2003) determined that the species lost from plots with added nutrients were those with longer ramet life spans and higher patch-holding capacity, so that clumped species tended to be excluded by faster turnover runner species. In addition to soil fertility gradients, clonal growth forms have been found to shift in abundance along other gradients such as soil moisture, e.g., clumped species can be more common in dry habitats than mesic (Halassy et al. 2005; Rusch et al. 2010). These individual studies point to the idea that traits associated with clonal growth are often important in competitive interactions and persistence, but require further study (Zobel et al. 2010).

Such detailed knowledge of clonal traits for the North American flora is lacking. However, we have shown that even using relatively coarse categories to categorize species into growth forms provides a good predictor of relative abundance responses to increased soil nutrients. By including clonal spread and height simultaneously in one growth form category, we are able to capture the combination of traits that are important for competitive response to perturbations like added nutrients. The fact that this result holds across a broad range of low stature, predominantly herbaceous communities which vary broadly in primary production and other environmental variables, suggests that the pattern is widespread and robust and can be useful in forecasting changes in community composition in response to increased nutrient load. Based on our results, tall-runner species should be examined first for responsiveness to fertilization, especially within areas of high nitrogen deposition.

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References

- Baer SG, Blair JM, Collins SL, Knapp AK (2004) Plant community responses to resource availability and heterogeneity during restoration. *Oecologia* 139:617–629
- Bobbink R, Hicks K, Galloway J, Spranger T, Alkemade R, Ashmore M et al (2010) Global assessment of nitrogen deposition effects on terrestrial plant diversity effects of terrestrial ecosystems: a synthesis. *Ecol Appl* 20:30–59
- Briske DD, Butler JL (1989) Density-dependent regulation of ramet populations within the bunchgrass *Schizachyrium scoparium*: interclonal versus intraclonal interference. *J Ecol* 77:963–974
- Callaghan TV, Carlsson BÅ, Jónsdóttir IS, Svensson BM, Jonasson S (1992) Clonal plants and environmental change: introduction to the proceedings and summary. *Oikos* 63:341–347
- Caraco T, Kelly CK (1991) On the adaptive value of physiological integration in clonal plants. *Ecology* 72:81–93
- Cheplick GP (1997) Responses to severe competitive stress in a clonal plant: differences between genotypes. *Oikos* 79:581–591
- Clark CM, Cleland EE, Collins SL, Fargione JE, Gough L, Gross KL et al (2007) Environmental and plant community determinants of species loss following nitrogen enrichment. *Ecol Lett* 10:596–607
- Cleland EE, Clark CM, Collins SL, Fargione JE, Gough L, Gross KL et al (2008) Species responses to nitrogen fertilization in herbaceous plant communities, and associated species traits (Data Publication). *Ecology* 89:1175
- Collins SL, Suding KN, Cleland EE, Batty M, Pennings SC, Gross KL et al (2008) Rank clocks and community dynamics. *Ecology* 89:3534–3541
- Craine JM, Froehle J, Tilman GD, Wedin DA, Chapin FS (2001) The relationships among root and leaf traits of 76 grassland species and relative abundance along fertility and disturbance gradients. *Oikos* 93:274–285
- Dalgliesh HJ, Kula AR, Hartnett DC, Sandercock BK (2008) Responses of two bunchgrasses to nitrogen addition in tallgrass prairie: the role of bud bank demography. *Am J Bot* 95:672–680
- De Schrijver A, De Frenne P, Ampoorter E, Van Nevel L, Demey A, Wuyts K et al (2011) Cumulative nitrogen input drives species loss in terrestrial ecosystems. *Glob Ecol Biogeogr*. doi:10.1111/j.1466-8238.2011.00652.x
- Dickson TL, Foster BL (2011) Fertilization decreases plant biodiversity even when light is not limiting. *Ecol Lett* 14:380–388
- Eilts JA, Mittelbach GG, Reynolds HL, Gross KL (2011) Resource heterogeneity, soil fertility and species diversity: impacts of clonal species on plant communities. *Am Nat* 177:574–588
- Galloway JN, Townsend AR, Erisman JW, Bekunda M, Cai ZC, Freney JR et al (2008) Transformation of the nitrogen cycle: recent trends, questions and potential solutions. *Science* 320:889–892
- Golubski AJ, Gross KL, Mittelbach GG (2008) Competition among plant species that interact with their environment at different spatial scales. *Proc R Soc Lond B* 275:1897–1906
- Gough L, Osenberg CW, Gross KL, Collins SL (2000) Fertilization effects on species density and primary productivity in herbaceous plant communities. *Oikos* 89:428–439
- Gough L, Goldberg DE, Hershock C, Pauliukonis N, Petru M (2002) Investigating the community consequences of competition among clonal plants. *Evol Ecol* 15:547–563
- Grime JP (2001) Plant strategies, vegetation processes, and ecosystem properties, 2nd edn. Wiley, New York
- Gross N, Suding KN, Lavorel S (2007) Leaf dry matter content and lateral spread predict response to land use change for six subalpine grassland species. *J Veg Sci* 18:289–300
- Grubb PJ (1987) Some generalizing ideas about colonization and succession in green plants and fungi. In: Gray AJ, Crawley MJ,

- Edwards PJ (eds) Colonization, succession and stability. Blackwell, Oxford, pp 81–102
- Halassy M, Campetella G, Canullo R, Mucina L (2005) Patterns of functional clonal traits and clonal growth modes in contrasting grasslands of the central Apennines, Italy. *J Veg Sci* 16:29–36
- Hartnett DC, Bazzaz FA (1985) The integration of neighborhood effects by clonal genets in *Solidago canadensis*. *J Ecol* 73:415–427
- Hautier Y, Niklaus PA, Hector A (2009) Competition for light causes plant biodiversity loss after eutrophication. *Science* 324:636–638
- Herben T, Hara T (1997) Competition and spatial dynamics of clonal plants. In: de Kroon H, van Groenendael J (eds) The ecology and evolution of clonal plants. Backhuys, Leiden, pp 331–358
- Honsová D, Hejman M, Klaudivová M, Pavlů V, Kocourková D, Hák J (2007) Species composition of an alluvial meadow after 40 years of applying nitrogen, phosphorus and potassium fertilizer. *Preslia* 79:245–258
- Houseman GR, Mittelbach GG, Reynolds HL, Gross KL (2008) Perturbations alter community convergence, divergence, and formation of multiple community states. *Ecology* 89:2172–2180
- Humphrey LD, Pyke DA (1998) Demographic and growth responses of a guerilla and a phalanx perennial grass in competitive mixtures. *J Ecol* 86:854–865
- Huston MA (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110:449–460
- Klimešová J, Klimeš L (2011) CLO-PLA3—database of clonal growth of plants from Central Europe. [WWW document] URL <http://clopla.butbn.cas.cz/>
- Knops JMH, Reinhart K (2000) Specific leaf area along a nitrogen fertilization gradient. *Am Midl Nat* 144:265–272
- LeBauer DS, Treseder KK (2008) Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* 89:371–379
- Lenssen JPM, Hershock C, Speck T, During HJ, de Kroon H (2005) Experimental ramet aggregation in the clonal plant *Agrostis stolonifera* reduces its competitive ability. *Ecology* 86:1358–1365
- Lovett Doust L (1981) Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*). I. The dynamics of ramets in contrasting habitats. *J Ecol* 69:743–755
- Oborny B, Kun A, Czarán T, Bokros S (2000) The effect of clonal integration on plant competition for mosaic habitat space. *Ecology* 81:3291–3304
- Pennings SC, Clark CM, Cleland EE, Collins SL, Gough L, Gross KL et al (2005) Do individual plant species show predictable responses to nitrogen addition across multiple experiments? *Oikos* 110:547–555
- Reynolds HL, Mittelbach GG, Darcy-Hall TL, Houseman GR, Gross KL (2007) No effect of varying soil resource heterogeneity on plant species richness in a low fertility grassland. *J Ecol* 95:723–733
- Rusch GM, Wilmann B, Klimešová L, Evju M (2010) Do clonal and bud bank traits vary in correspondence with soil properties and resource acquisition strategies? Patterns in alpine communities in the scandinavian mountains. *Folia Geobot*. doi:10.1007/s12224-010-9072-7
- Sammul M, Kull K, Tamm A (2003) Clonal growth in a species-rich grassland: results of a 20-year fertilization experiment. *Folia Geobot* 38:1–20
- Schmid B, Harper JL (1985) Clonal growth in grassland perennials. I. Density and pattern dependent competition between plants with different growth forms. *J Ecol* 73:793–808
- Shaver GR, Bret-Harte SM, Jones MH, Johnstone J, Gough L, Laundre J et al (2001) Species composition interacts with fertilizer to control long-term change in tundra productivity. *Ecology* 82:3163–3181
- Stuefer JF, During HJ, de Kroon H (1994) High benefits of clonal integration in two stoloniferous species in response to heterogeneous light environments. *J Ecol* 82:511–518
- Suding KN, Collins SL, Gough L, Clark C, Cleland EE, Gross KL et al (2005) Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proc Natl Acad Sci USA* 102:4387–4392
- Thomas RG, Hay MJM (2010) The role of nodal roots in prostrate clonal herbs: ‘phalanx’ versus ‘guerilla’. *Evol Ecol* 24:1489–1504
- Tilman D (1987) Secondary succession and the pattern of plant dominance along experiment nitrogen gradients. *Ecol Monogr* 57:189–214
- Van Staalduin MA, During H, Werger MJA (2007) Impact of grazing regime on a Mongolian forest steppe. *Appl Veg Sci* 10:299–306
- Welker JM, Briske DD (1992) Clonal biology of the temperate, caespitose graminoid *Schizachyrium scoparium*: a synthesis with reference to climate change. *Oikos* 63:357–365
- Wilson SD, Tilman D (1993) Plant competition and resource availability in response to disturbance and fertilization. *Ecology* 74:599–611
- Wright IJ, Reich PB, Westoby M (2001) Strategy-shifts in leaf physiology, structure and nutrient content between species of high and low rainfall, and high and low nutrient habitats. *Funct Ecol* 15:423–434
- Zobel M, Moora M, Herben T (2010) Clonal mobility and its implications for spatio-temporal patterns of plant communities: what do we need to know next? *Oikos* 119:802–806