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Height and clonality traits determine plant community responses to fertilization

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Height and clonality traits determine plant community responses to fertilization

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Abstract. Fertilization via agricultural inputs and nutrient deposition is one of the major threats to global terrestrial plant richness, yet we still do not fully understand the mechanisms by which fertilization decreases plant richness. Tall clonal species have recently been proposed to cause declines in plant species richness by increasing in abundance in response to fertilization and competing strongly with other species. We tested this hypothesis in a fertilization experiment in a low productivity grassland by using a novel experimental manipulation of the presence vs. absence of clonal species and by examining the role of height within these treatments. We found that fertilization decreased species richness more in the presence than absence of clonal species. We also found that only tall species increased in biomass in response to fertilization. In the absence of clonal species, fertilization increased biomass of tall nonclonal species. However, in the presence of clonal species, fertilization decreased tall nonclonal biomass and only tall clonal biomass increased. Fertilization caused almost all short species to be lost in the presence, but not the absence, of clonal species and caused greater declines in the mean and variance of light levels in the presence of clonal species. These results show that the traits of species in a community can determine the magnitude of species loss due to fertilization. The strongly negative effect of tall clonals on species richness in fertilized plots is likely a result of their capacity to decrease light levels to a greater extent and more uniformly than nonclonal species, and thereby drive the exclusion of short species. These results help clarify the mechanisms whereby fertilization decreases grassland plant species richness and suggest that efforts to prevent the loss of species under fertilized conditions may be most effective when they focus on controlling the biomass of tall clonal species.

Key words: biodiversity; biomass production; functional groups; grassland; nitrogen, phosphorus, potassium fertilization; plant species richness; species traits.

Introduction

A large number of experiments have shown that fertilization leads to a decrease in plant species richness and a shift in species dominance and composition (DiTommaso and Aarssen 1989, Gross et al. 2005). Although these negative effects of fertilization on plant species richness are well documented, the mechanisms responsible for these changes are not well understood (Cleland and Harpole 2010). The magnitude of the response of plant productivity and species richness to fertilization appears to depend on plant species traits (Clark et al. 2007). Traits associated with clonality play an especially important role in the response of plant communities to fertilization (Craine et al. 2001, Grime 2001, Gough et al. 2012).

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Several studies have found that fertilization decreases plant species richness and that species with a clonal growth form (spreading via rhizomes or runners) increase more in response to fertilization than do nonclonal species (Baer et al. 2005, Eilts et al. 2011, Isbell et al. 2013). Theory suggests that the ability of clonal species to have a large foraging footprint and share resources between ramets (integration) gives them a competitive advantage over nonclonal species in heterogeneous environments where resource-rich patches are rare (Golubski et al. 2008, Oborny et al. 2012). However, there is little theoretical or empirical evidence that competition for soil resources explains the greater decline in species richness with fertilization in the presence vs. the absence of clonals (Golubski et al. 2008, Eilts et al. 2011).

Grime (2001) and Craine et al. (2001) propose that plant height and the capacity for clonal spreading may act in concert to increase competitive ability at high soil fertility. By being present at the top of the canopy, tall plants have an obvious competitive advantage when light levels become more limiting in response to fertilization (Hautier et al. 2009). However, it is not

clear how clonal spread will influence competitive advantage for light, and several recent studies show that light competition alone does not fully explain patterns of species loss following nutrient addition (Dickson and Foster 2011, Li et al. 2011). A meta-analysis by Suding et al. (2005) using plant community data from 37 fertilization experiments does not show any individual effects of species' height or clonal growth form on the probability of species loss due to fertilization. However, an analysis by Gough et al. (2012) using the same data set reveals that when both height and clonal traits are analyzed together, fertilization consistently increases the abundance of tall clonal species. Similarly, Dickson and Gross (2013) show that declines in species richness are better predicted by increases in tall clonal biomass than increases in total biomass. Thus, being both tall and clonal appears to lead to a strong increase in biomass in response to fertilization and to an associated decline in overall species richness. However, experimental studies that manipulate the presence of plant growth forms, along with nutrient addition treatments, are needed to better isolate the role of growth form in determining community responses to fertilization.

In 2004, we established an experiment in a low-productivity grassland in Michigan, in which we crossed fertilizer addition (unfertilized or fertilized) with the presence/absence of clonal species (clonal species added or removed) to test the impact of clonal species on plant community responses to nutrient addition. This experiment is the first we are aware of that manipulates the presence of clonal species under fertilized conditions. Results from the sixth year of this study showed that species richness declined more in the presence than in the absence of clonal species (fertilizer $\times$ clonal species interaction; Eilts et al. 2011). We incorporate plant height into our analyses and use new data on community composition, species abundance, and resource availability to test the role of height and clonality in driving community responses to fertilization.

Based on our prior results, we predicted that fertilization would decrease plant species richness more in the presence than absence of clonal species (fertilizer $\times$ clonal species interaction). Because of our novel experimental design, we also made the first experimental tests of the following predictions. We predicted that fertilization would alter the composition of the plant community, with tall species dominating in fertilized plots in both the presence and absence of clonal species. We also predicted that short species would be most likely to be lost from fertilized plots when tall clonal species were present and that fertilized plots would have lower soil and light resources when tall clonal species were present.

Methods

We established the experiment in an 8-ha grassland in the Allegan State Game Area, an approximately 50 000-ha state preserve in southwestern Michigan, USA (see Plate 1). There are few records of the prior use of the experimental site, but the dominance of native perennial grasses and forbs suggests that it was primarily used as pasture before being abandoned in the 1950s. Soils at this site are entisols (suborder psamment; 96:3:1 sand to silt to clay) and are low in nitrogen (total inorganic nitrogen between 4 and 5 μg N/g soil). Before establishing the experiment, we applied nonselective herbicide (Roundup Pro [Monsanto, St. Louis, Missouri, USA]; 23.4 mL/L) to a 50 $\times$ 40 m area of the field three times between October 2002 and July 2003. The herbicide applications killed all of the aboveground vegetation in the study area and reduced variation in initial species composition, especially clonal species (Houseman et al. 2008, Eilts et al. 2011).

Experimental design

We tested our predictions using a subset of the original experiment (see Eilts et al. 2011). We focused on comparing the control (not fertilized) and uniformly fertilized treatments and the treatments in which clonal species were excluded or present (2 $\times$ 2 factorial of fertilization $\times$ clonal species presence). Each of the four treatments were replicated eight times (eight blocks) and were randomly assigned to four 3 $\times$ 3 m plots in each block (randomized block design). All plots were seeded with the same 30 native nonclonal species that are common at our study site and surrounding grasslands (see Appendix A and Eilts et al. 2011). The 30 seeded species were added to all of the plots at a uniform mass (1 g seed$\cdot$m$^{-2}\cdot$species) in the spring of 2004. The nonclonal community treatment was seeded with only these 30 species. To create the mixed community treatment (nonclonal plus clonal species), we added propagules (seeds and ramets) of seven rhizomatous clonal species to half the plots in each block, for a total of 37 species added to the mixed community. The added rhizomatous clonal species included native and introduced grasses and forbs from four plant families common to this site and nearby grasslands. Through time, other native and nonnative species invaded the plots (see Appendix A); we removed sown and nonsown clonal species from the nonclonal treatment and allowed other nonsown species with the appropriate growth form to establish. For our design, we defined clonal species as a spreading (by rhizomes or stolons) growth form. Some species we classified as nonclonal have a bunch or multiple-stem growth form, but do not have long internodes that would expand their foraging footprint. For this reason, we included these species in the nonclonal group, although they might be classified as clonal elsewhere. We define tall species as those that occupy the top one-third of the canopy in the unfertilized (control) communities and short species as those in the bottom two-thirds of the canopy. We determined height from information in McGregor et al. (1986) and through observations of species' height and

PLATE 1. Summer 2010 photograph of plots with unfertilized plot in foreground, fertilized nonclonal plots to left and right, and fertilized mixed plots as darker tall vegetation farther back in the field. Photo credit: Carol Baker.

canopy position in this community (Appendix A). This classification is similar to that used by Suding et al. (2005) and Gough et al. (2012).

By necessity, the nonclonal and mixed communities received some different added species. We recognize that in selecting species for the mixed community treatment, by chance, we may have added species that are especially good competitors or biomass dominants (a species-selection effect [Huston 1997]). However, studies in other habitats have found other tall clonal species increase strongly in response to fertilization (Gough et al. 2012, Dickson and Gross 2013). Still, further experiments testing more species need to be completed to confirm the role of height and rhizomatous growth in the response to fertilization. It should also be noted that all species were added to the nonclonal community as seed whereas some species were added to the mixed community as ramets. However, ramets did not appear to establish differently than seed because the species added as ramets were still at low biomass in 2006 (Eilts et al. 2011). Also, three of the seven clonal species used in the current experiment became biomass dominants in response to fertilization of otherwise unmanipulated intact vegetation (*Elymus repens*, *Rumex acetosella*, and *Rubus flagellaris*; Reynolds et al. 2007, Houseman et al. 2008), thereby suggesting the addition of ramets was not responsible for the eventual dominance of *E. repens* and *R. flagellaris*.

In March 2004, we began to add slow-release fertilizer (14:14:14 NPK; Osmocote NH_4NO_3-N, Scotts-Sierra Horticultural Products, Marysville, Ohio, USA) twice a year (spring and midsummer) at a rate of 20 g $N \cdot m^{-2} \cdot yr^{-1}$ to the fertilized plots. In 2007, we began to add lime (80 $g \cdot m^{-2} \cdot yr^{-1}$) to these plots to prevent shifts in pH expected with long-term fertilizer addition. To maintain the nonclonal only community treatment, we checked the plots regularly (two to three times during each growing season) and removed clonal species by clipping stems just beneath the soil surface. The average clonal biomass weeded from the plots was typically 5% of the nonclonal biomass harvested during vegetation sampling, but in 2008 there was strong recruitment of the clonal species, *Rumex acetosella*, into the nonclonal only plots (likely from seed dispersal from the surrounding area), and this increased average clonal biomass weeded from the plots to 27% of the mass of harvested nonclonal biomass (Eilts et al. 2011). To reduce disturbance from clonal species removal, clipping was done from mounted boards that spanned the plots. To avoid removing soil nutrients and organic matter, clonal biomass removed from plots was dried, weighed, and then returned to the plots.

TABLE 1. The response of species richness and biomass to fertilization and the presence or absence of clonal species.

Response variable	Nonclonal unfertilized	Nonclonal fertilized	Mixed unfertilized	Mixed fertilized	*P*		
					Fertilization (F)	Clonality (C)	F × C
Species richness							
Total†	$22.0^{a} \pm 3.7$	$11.9^{b} \pm 2.5$	$24.5^{a} \pm 5.4$	$5.5^{c} \pm 1.2$	<0.001	0.132	0.002
Nonclonal species	$22.0^{a} \pm 3.7$	$11.9^{b} \pm 2.5$	$19.1^{a} \pm 5.4$	$3.4^{c} \pm 0.9$	<0.001	<0.001	0.030
Biomass (g/m^2)							
Total	$285^{a} \pm 61$	$464^{b} \pm 83$	$270^{a} \pm 8$	$503^{b} \pm 55$	<0.001	0.700	0.358
Most abundant species‡	$58^{a} \pm 44$	$364^{b} \pm 113$	$108^{a} \pm 68$	$408^{b} \pm 59$	<0.001	0.144	0.930

Notes: Values are mean ± SD; standard deviation is calculated from data after removing blocking effects. Different letters indicate Bonferroni-corrected post hoc contrasts showing significantly different means.

† Both nonclonal and clonal species were sown into mixed plots; clonal species were removed from the nonclonal treatment. Nonsown species of the appropriate growth form were allowed to establish in both communities (see Appendix A for species list and abundance in each treatment).

‡ *Elymus repens* in mixed fertilized treatment; *Centaurea stoebe* in other treatments.

We mimicked the disturbance effect from biomass removal in the nonclonal treatments by creating similar disturbance (but no biomass removal) in the mixed community (see Eilts et al. 2011).

Data collection

We determined how these treatments impacted species composition and abundance based on biomass harvested in July 2011. We harvested all aboveground biomass from 12 randomly selected 25 × 25 cm subplots within each treatment plot and separated biomass into species or litter (prior years' production not sorted to species). Plant and litter biomass was dried at 60°C to constant weight and weighed with 0.01-g accuracy. Harvested biomass was returned to the field in late fall to prevent nutrient and organic matter loss. Light, soil nitrogen, and soil moisture levels in these treatments were determined in 2010 to provide estimates of how the treatments affected above- and belowground resources. Light measures were taken in July within two hours of solar noon under clear skies using an AccuPAR LP-80 ceptometer (Decagon Devices, Pullman, Washington, USA). We placed the ceptometer in eight locations in each plot and recorded light measurements at ground level (beneath vegetation and litter). Full sunlight levels were measured above canopy in each plot and used to calculate percentage light penetration (%PAR) to the ground. We also collected light data from 2013 to estimate how light levels changed across years, and we found a strong correlation between 2010 and 2013 light levels ($r = 0.661$; Appendix B; all other light data presented are from 2010). For soil nitrogen, soils were sampled in September to 10 cm depth from 10 randomly selected points within plots. Two cores collected from each point were combined, kept at 5°C, and processed in the lab within 36 h of collection. After soils were passed through a 2-mm sieve, a 20-g sample was extracted in 50 mL of 1 mol/L KCl, shaken for 1 min, and stored at room temperature for 24 h. The solution was filtered through an A/E glass fiber filter and frozen until analyzed on a Flow Solution IV analyzer (OI Analytical, College Station, Texas, USA) for NO_3-N and NH_4-N levels, which were summed to estimate total plant available nitrogen. Soil moisture also was measured gravimetrically from 10 cm deep soil cores from 10 selected points within plots sampled in July and September (average for the two months used for analysis).

Statistical analysis

We used SPSS 13.0 (Chicago, Illinois, USA) for Mann-Whitney tests of extremely nonnormal data and for logistic regressions, and we used PCOrd 5.10 (Gleneden Beach, Oregon, USA) for nonmetric multidimensional scaling (NMDS) to compare differences in plant community composition among treatments. We compared differences between light, nitrogen, and soil moisture distributions using the *G* test for goodness of fit with an intrinsic hypothesis (similar to a chi-square test) as described by Sokal and Rohlf (1995). All other statistical analyses were completed in SAS 9.2 (Cary, North Carolina, USA) using PROC MIXED with block as a random effect and the clonality treatments and fertilization treatments as fixed effects. We conducted multivariate analysis of variance (MANOVA) using PROC MIXED with the two axes of NMDS data as response variables. For analyses using PROC MIXED, we transformed the data to improve normality, and we do not report block effects. For logistic regressions, we included only nonclonal species because these were the only species included in all four treatments. Data were summed across all plots within a treatment to determine species presence/absence and to determine the biomass of each species in unfertilized plots. We used a level of significance of $\alpha = 0.05$.

RESULTS

Plant species richness

Consistent with our prediction, fertilization decreased both total and nonclonal species richness significantly more in the mixed (with clonal species present) than the nonclonal treatment (fertilization × clonal interaction; Table 1). Furthermore, height and clonality groups

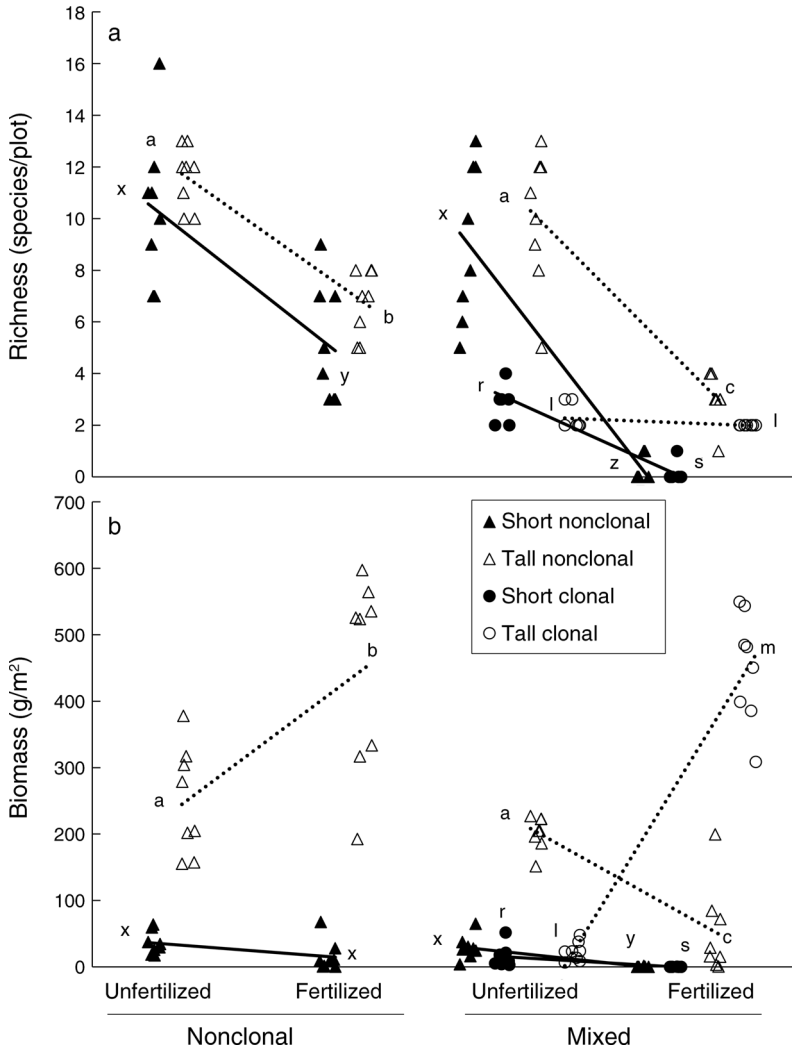

FIG. 1. The effects of treatments on (a) species richness and (b) biomass of the four height-clonality functional groups. Letters indicate post hoc contrasts (Bonferroni corrected) within each functional group (different letters denote significant differences between treatments). Data are jittered on the *x*-axis and the endpoints of regression lines indicate treatment means.

responded differently to fertilization in the nonclonal and mixed treatments. In the nonclonal only community, fertilization decreased the number of tall and short nonclonal species approximately equally (Fig. 1a). In contrast, fertilization did not significantly decrease the number of tall clonal species in the mixed community, but strongly decreased the number of short species (Fig. 1a).

Plant community composition

We predicted that fertilization would alter the composition of the plant community, with tall species increasing in dominance (biomass) in response to fertilization in both nonclonal and mixed treatments. Although neither total biomass nor the biomass of the most abundant species differed significantly between the nonclonal and mixed community treatments (Table 1), community type had a significant effect on which species groups increased and decreased in biomass in response to fertilization. We found that fertilization in the nonclonal treatment led to large increases in tall nonclonal biomass without significantly decreasing short nonclonal biomass, whereas fertilization in the mixed treatment led to large increases in tall clonal biomass with significant decreases in the biomass of every other group of species (Fig. 1b).

Thus, while fertilization increased the biomass of tall species in both nonclonal and mixed treatments, we found that tall nonclonals dominated in the nonclonal treatment, but only tall clonal species dominated in the mixed treatment (fertilizer × clonal treatment MANOVA interaction: $P < 0.001$; Fig. 2). Although the mixed treatment had seven more species added at the start of the experiment (clonal species added; see Appendix A), there was no significant difference in community composition between the nonclonal and

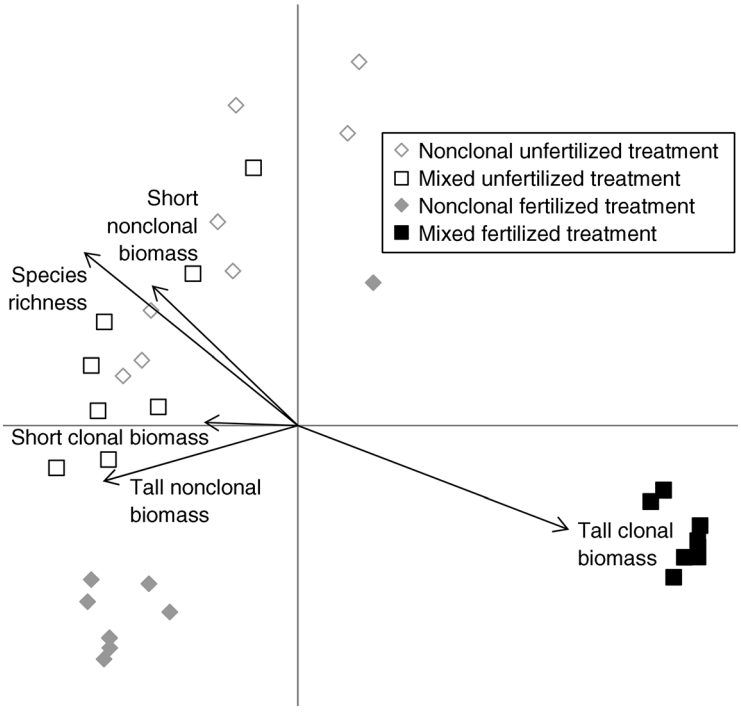

FIG. 2. Variation in plant community composition among four treatments based on nonmetric multidimensional scaling (NMDS) of the biomass of each species. Results are shown for each replicate plot ($n = 8$) of the four treatments. The arrows denote the correlation of the biomass of the four functional groups and total species richness with NMDS data (longer arrows along a particular axis denote a higher degree of correlation between the variable and the axis).

mixed treatments in the unfertilized plots (MANOVA: $P = 0.099$; Fig. 2). However, there was a large difference in community composition between the nonclonal and mixed treatments in the fertilized plots (MANOVA: $P < 0.001$; Fig. 2). In the nonclonal treatment, *Centaurea stoebe* was the most abundant species in both fertilized and unfertilized plots, and fertilization significantly increased the biomass of this tall species six-fold (from 58 to 364 g/m^2; Appendix A). In the mixed treatment, *C. stoebe* was the most abundant species in unfertilized plots, but fertilization significantly decreased the biomass of *C. stoebe* 98% in mixed plots (from 108 to 2 g/m^2; Appendix A). In contrast, the tall clonal species *Elymus repens* significantly increased in biomass over 200-fold in response to fertilization in the mixed treatment (from 2 to 408 g/m^2; Appendix A).

Species loss

We predicted that short species would be most likely to be lost from fertilized plots when tall clonal species were dominant. We found support for this prediction because the probability of a species being present in the fertilized plots varied in relation to height and differed in the nonclonal vs. mixed treatments (Fig. 3). Overall, species that were rare (low biomass) in the unfertilized plots were less likely to be present in the fertilized plots (unfertilized biomass: $P < 0.001$). Species height was also a significant predictor of presence in the fertilized plots (height, $P = 0.031$), but the effect varied in the nonclonal and mixed treatments (height × clonality interaction, $P = 0.017$; Fig. 3). Almost no short-statured species were present in the fertilized plots in the mixed treatment ($P = 0.016$), however, plant height did not significantly affect the loss of species in fertilized plots in the nonclonal treatment ($P = 0.139$). There was no significant main effect of nonclonal vs. mixed treatments (clonality: $P = 0.665$).

Resource levels and species richness

We predicted that fertilized plots would have lower soil and light resources when tall clonal species were dominant. In support of this prediction, we found that average light levels (%PAR) were reduced by fertilization more in the mixed than nonclonal treatment (Fig. 4a) despite the fact that aboveground biomass production did not significantly differ between the mixed and nonclonal treatment (Table 1). Also, we found that the distribution of light levels was slightly different between the nonclonal and mixed treatment in unfertilized plots ($P = 0.048$), but very different in fertilized plots (fewer sunflecks in mixed treatment; $P < 0.001$; Fig. 4b). Different from our prediction, we found that the increase in soil nitrogen availability due to fertilization was significantly higher in the mixed than in the nonclonal fertilized treatment (Fig. 4c). The distribution of soil nitrogen was not significantly different between

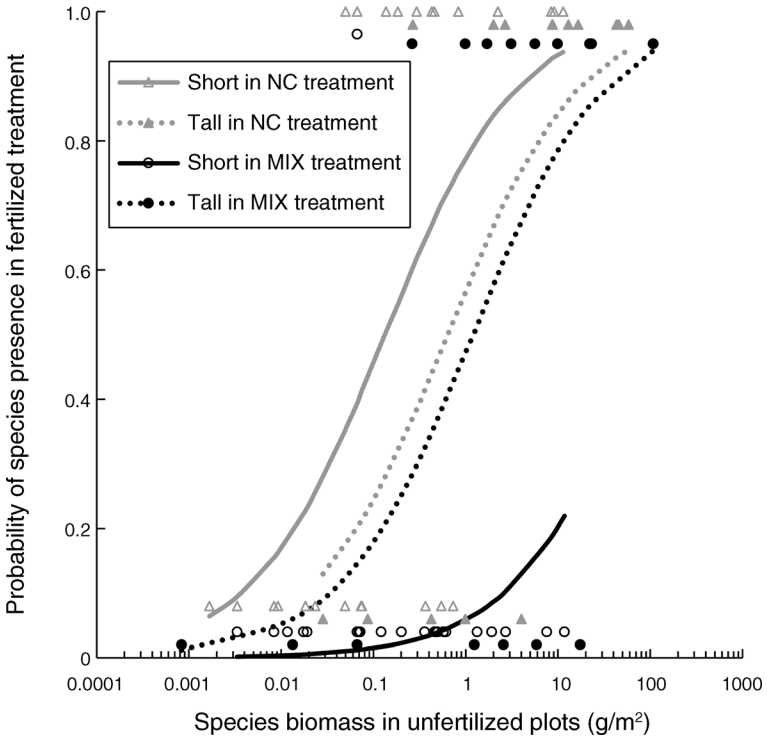

FIG. 3. Probability that a species observed in the unfertilized plots of the nonclonals only (NC) or mixed (MIX) treatment was present in fertilized plots of that treatment. Probability functions (lines) are plotted separately for tall (top one-third) and short species and are statistically fitted with logistic regression to presence/absence data in the fertilization treatments. Points near 0 on the *y*-axis are species that were absent in fertilized plots but present in control plots.

the nonclonal and mixed treatment in the unfertilized plots ($P = 0.403$), but there were more high nitrogen patches in the mixed treatment than the nonclonal treatment in the fertilized plots ($P < 0.001$; Fig. 4d). Soil moisture was slightly lower in fertilized treatments (Fig. 4e), and the distribution of soil moisture was not significantly different between the nonclonal and mixed treatments ($P = 0.771$ unfertilized; $P = 0.909$ fertilized; Fig. 4f). We also found that species richness was positively correlated with light availability across all treatments (Fig. 5).

DISCUSSION

Through a novel manipulation of clonal species presence/absence and fertilization under field conditions, our experiment provides new insight into the mechanisms of species loss following nutrient enrichment. We found that plant species richness was decreased by fertilization more in the presence than absence of clonal species and that this response was driven by a subset of the clonal species that were tall (occurring in the top third of the canopy). Our results are consistent with observational studies documenting increases in tall clonal species with fertilization (Gough et al. 2012, Dickson and Gross 2013), suggesting that height and clonality comprise a key set of traits driving the plant community dynamics in response to nutrient inputs.

In the nonclonal treatment, we found that tall nonclonal species increased in biomass and that species loss was not dependent on height (tall and short species were equally likely to be lost from the fertilized plots). In contrast, in the mixed treatment, we found that only tall clonal species increased in biomass (tall nonclonal and short species decreased in biomass) and that species loss in this community was dependent on height (short species were much more likely to be lost from the fertilized plots than tall species). These results indicate that height alone cannot account for diversity declines with nutrient enrichment and that height and clonality together constitute a trait combination that drives species loss after fertilization.

We attribute the differences between the nonclonal and mixed treatments to the presence of tall clonal species, although it is possible that these effects were driven by other traits. We feel that the combined traits of plant height and clonality provide the most likely interpretation, given that none of the nonclonal species in our study had the same effects as tall clonal species and given that tall clonal species have been shown to respond positively to fertilization at many other sites, often at the expense of other species (Gough et al. 2012, Dickson and Gross 2013). Still, further experimental tests are warranted with more species that vary in height and clonality.

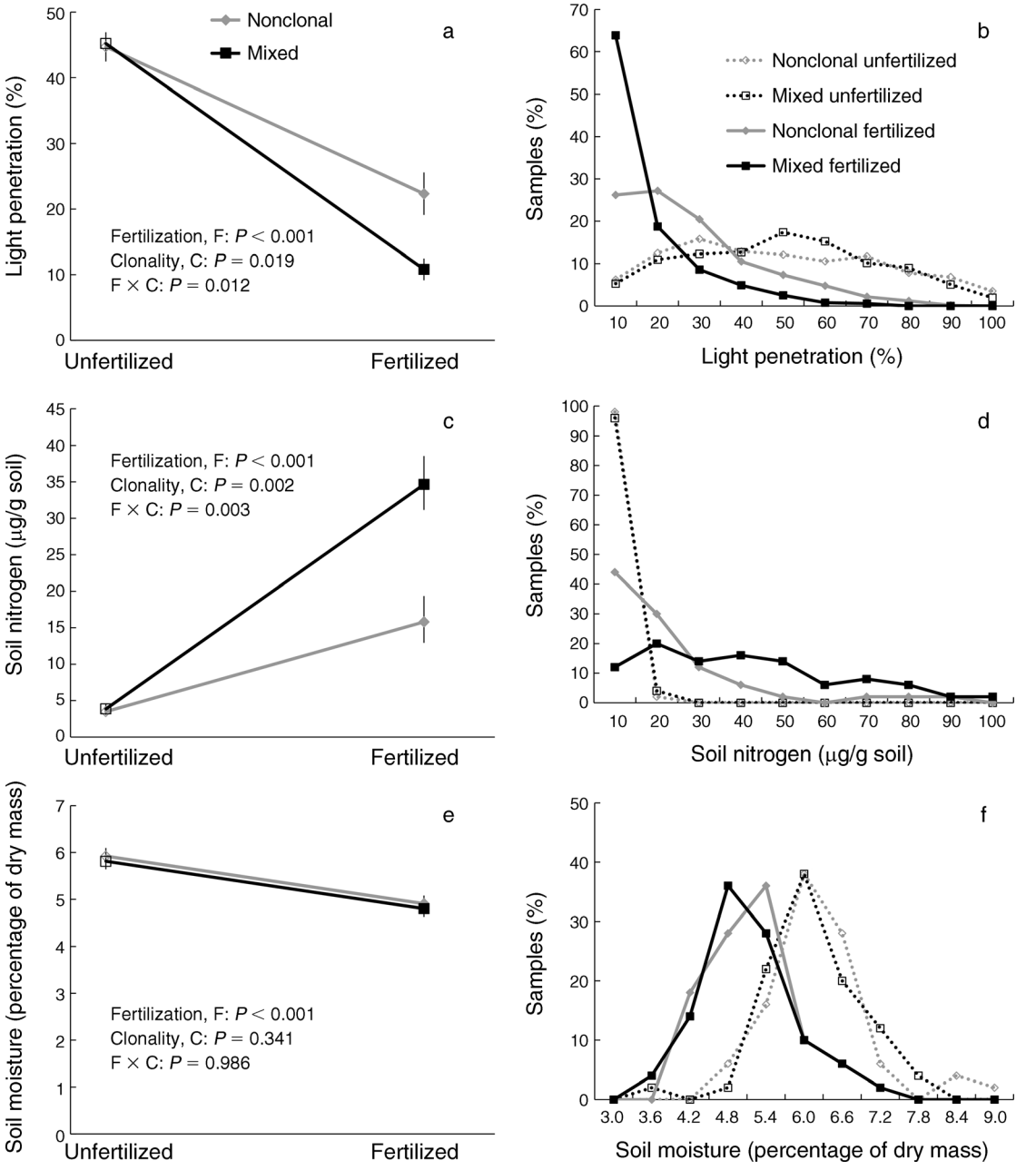

FIG. 4. The effects of treatments on (a) mean light, (b) frequency distribution of light, (c) mean soil nitrogen, (d) frequency distribution of soil nitrogen, (e) mean soil moisture, and (f) frequency distribution of soil moisture. Error bars are ±SE and data points in panels b, d, and f are the percentage of total samples that have light penetration between the value shown on the *x*-axis and the next smaller value.

Interestingly, even though most studies predict that species losses due to fertilization should correlate directly with biomass increases (Suding et al. 2005), total biomass and biomass of tall species did not differ in the fertilized mixed and nonclonal communities, but species loss was greater in the mixed community. This raises the question of which mechanism(s) caused species richness to be lower in the fertilized plots when clonal species were present. As a potential explanation, we examined how resource levels differed in the response to fertilization in the presence and absence of clonal species. We found that mean light levels were significantly lower in fertilized plots in the mixed community (clonals present) than in the nonclonals only treatment. Also, light levels were reduced more uniformly in the fertilized mixed community than the nonclonal community (fewer sunflecks in fertilized mixed community). We also found a strong positive relationship between light

levels and species richness that accounted for most of the variation in richness between treatments.

The relationship between light availability and species richness in this experiment suggests that light levels may drive the effects of fertilization and clonal species on species loss. However, recent field studies have shown that declines in plant diversity due to fertilization can be caused by more than just decreased light levels (Dickson and Foster 2011, Li et al. 2011, but see Hautier et al. 2009). The most parsimonious explanation for the difference in species richness between nonclonal and mixed fertilized plots is that lower light levels reduced the number of short statured species. Still, it is not clear why tall nonclonal species richness and biomass were strongly decreased in the fertilized mixed treatment because tall nonclonal species have the potential to escape light limitation by reaching the top of the canopy. Our data suggest there is something about the combination of height in the canopy (tall) and a spreading, clonal growth form that is favored under fertilized conditions (Gough et al. 2012). It may be that the capacity for horizontal spread and integration between ramets is critical for taking advantage of high fertility environments (van Groenendael et al. 1996). The ability of clonal species to provide resources to new shoots under low light conditions and other stressful conditions should be further studied as another potential mechanism whereby tall clonal species are able to dominate under fertilized and other high productivity conditions.

Fertilization also led to decreased heterogeneity of light levels, especially in mixed plots, and this decreased heterogeneity in light may also have led to decreases in species richness. Heterogeneity in resources has been argued to be one of the main factors allowing species coexistence in many theoretical models (Chesson 2000). However, one of the few studies to experimentally test the role of light heterogeneity on species richness found that light heterogeneity did not significantly affect species richness whereas mean light levels did significantly affect richness (Stevens and Carson 2002). Although we cannot separate the effects of changing mean light levels and changing heterogeneity of light in our study, we suggest that a combination of these two factors played an important role in decreasing species richness under fertilized conditions, especially in the presence of clonal species. While soil nitrogen heterogeneity was greater in the mixed than nonclonal fertilized plots, this likely had little effect due to light being the more limiting resource. Soil nitrogen levels may have been lower in the fertilized nonclonal than mixed plots due to the low nitrogen use efficiency of *Centaurea stoebe*, the dominant species in fertilized nonclonal plots (Blicker et al. 2002). We also found lower soil moisture levels in fertilized than unfertilized plots, but soil moisture was not significantly affected by clonality and soil moisture does not appear to explain the greater declines in richness in fertilized mixed than nonclonal plots.

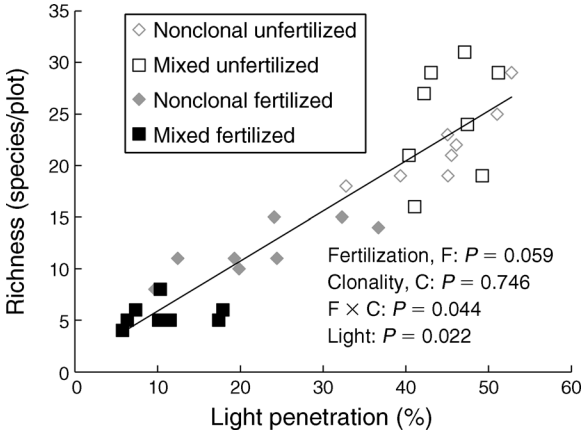

FIG. 5. The relationship between light penetration and species richness showing the statistical results of the treatment effects and the covariate (light penetration).

Our results have implications for understanding long-term shifts in community dynamics and ecosystem functioning with sustained nutrient enrichment. Recent work from long-term grassland experiments at Cedar Creek in Minnesota, USA demonstrates that chronic fertilization results in nonrandom loss of species over time and that initial productivity gains with fertilization diminish over time, in part due to nonrandom species losses (Isbell et al. 2013). Our results suggest that tall clonal species are an important component in these dynamics, as tall clonal species, particularly *Elymus repens*, rose to dominance with fertilization in both our study and the Cedar Creek experiments (Isbell et al. 2013). However, unlike the Cedar Creek results, we have not seen a corresponding decline in productivity over time with species loss from the community (similar to Eilts et al. 2011, Dickson and Gross 2013).

Our study is the first we are aware of that manipulates the presence and absence of clonal species and examines the mechanism by which fertilization affects nonclonal and mixed communities differently. Overall, the presence of clonal species in our experiment dramatically altered the effects of fertilization on plant species composition and richness. Our data suggest that tall clonal species are able to reduce the abundance of and presence of all other species in fertilized plots because tall clonal species strongly reduce the mean and variance of light levels and thereby exclude short-statured species (clonal and nonclonal). While further work is needed to uncover how tall, clonal species reduce light levels to a greater extent than other species with a similar increase in biomass, the results suggest that losses of species due to fertilization may be minimized by managing the abundance of tall clonal species.

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Supplemental Material

Appendix A

The average biomass per treatment of each individual species harvested from the experiment, along with information about their height and clonality and whether each species was added (*Ecological Archives* E095-217-A1).

Appendix B

Scatterplot showing the correlation between 2010 and 2013 light levels (*Ecological Archives* E095-217-A2).

Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.6rp18