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The role of biomass allocation strategy in diversity loss due to fertilization

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Summary

Proposed mechanisms for explaining biodiversity loss due to fertilization include interspecific competition and assemblage-level thinning. The interspecific competition hypothesis (ICH) assumes a link between population changes and species competitive ability, which is related to functional traits such as biomass allocation patterns. Based on a 2-year fertilization experiment in an alpine meadow on the Tibetan Plateau, we attempted to explore the relationships between individual and population responses. Individual response was measured by changes in plant biomass and biomass allocation, and population response was estimated by changes in species abundance. The results suggested that following fertilization (1) changes in individual biomass differ among species and functional groups, (2) reproductive allocation tends to decrease for all species whereas leaf allocation generally increases for grasses but decreases for forbs, (3) a strong positive correlation exists between species relative abundance change and individual biomass response, and (4) species relative abundance change has a positive correlation with leaf allocation response, a negative correlation with stem allocation response, and no significant correlation with reproductive allocation response. We conclude that the individual biomass responses and biomass allocation strategy can partly explain diversity loss due to fertilization, a result consistent with the ICH.

Zusammenfassung

Vorgeschlagene Mechanismen, die den Biodiversitätsverlust erklären, schließen interspezifische Konkurrenz und eine Ausdünnung der Vergesellschaftungsebenen ein. Die interspezifische Konkurrenz Hypothese geht von einer Verbindung zwischen den Populationsänderungen und der Konkurrenzfähigkeit von Arten aus, die mit funktionellen Eigenschaften wie z. B. der Biomassenallokation zusammenhängt. Auf der Basis eines zweijährigen Düngeexperimentes auf einer alpinen Wiese des tibetischen Plateaus versuchten wir die Beziehungen zwischen inviduellen und Populationsreaktionen herauszufinden. Die individuellen Reaktionen wurden durch die Veränderungen in der Biomasse und der Biomassenallokation gemessen, und die Populationsreaktion wurde durch Veränderungen in den Artenabundanzen abgeschätzt. Die Ergebnisse lassen erkennen, dass als Folge der Düngung (1) sich die Veränderungen der individuellen Biomasse zwischen Arten und funktionellen Gruppen unterscheiden, (2) die Reproduktionsallokation bei allen Arten zu einer Abnahme tendiert, während die Blattallokation für Gräser zunimmt

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und für Stauden abnimmt, (3) eine starke positive Korrelation zwischen der relativen Veränderung der Artenabundanz und der individuellen Biomassenreaktion existiert und (4) die relative Veränderung der Artenabundanz eine positive Korrelation zur Blattallokationsreaktion, eine negative zur Stammallokationsreaktion und keine signifikante Korrelation zur Reproduktionsallokationsreaktion hat. Wir schließen daraus, dass die individuellen Biomassenreaktionen und die Biomassenallokations-Strategien den Diversitätsverlust aufgrund von Düngung zum Teil erklären kann. Dies ist ein Ergebnis, das mit der interspezifischen Konkurrenz Hypothese übereinstimmt.

Keywords: Individual biomass; Reproductive allocation; Functional trait; Species relative abundance; Interspecific competition; Alpine Meadow; Tibetan Plateau

Introduction

Ecologists have long observed the effect of fertilization in decreasing plant species diversity (Tilman & Pacala, 1993; Stevens & Carson, 1999a; Hooper et al., 2005). Several hypotheses have been proposed to explain diversity loss, yet understanding the mechanisms remains a challenge (Abrams, 1995; Waide, et al., 1999; Mittelbach et al., 2001).

Plant community ecologists who study the productivity–diversity relationships conclude that competition is the primary cause for diversity loss with nutrient addition (Newman, 1973; Grime, 1973; Tilman, 1988; Goldberg & Miller, 1990; Grace, Allain, & Allen, 2000; Stevens & Carson, 1999b; Rajaniemi, 2002, 2003; Forbes, Schauwecker, & Weiher, 2001). The competition-related hypotheses include the following: (i) the total competition hypothesis predicts that total competitive intensity increases, with superior species depressing the growth of inferior species, which leads to a decrease in species abundance or even the extinction of the inferior species (Grime, 1973). (ii) The light competition hypothesis predicts that total competition intensity remains unchanged, but competition may shift from mainly below ground to above ground (Newman, 1973; Tilman & Pacala, 1993). (iii) The random-loss hypothesis predicts that increased competition causes community-level thinning, with individual species density decreasing due to the death of small individuals of all species. Diversity is reduced in plots of finite area by chance alone (Stevens & Carson, 1999a). (iv) The root competition hypothesis predicts that soil resource heterogeneity increases after fertilization, with larger plants obtaining soil resources, negatively affecting diversity more than size-asymmetric light competition (Rajaniemi, 2002; Rajaniemi, Allison, & Goldberg, 2003). All hypotheses assume that competition has a significant impact on plant growth, resulting in some plant mortality and eventual diversity loss. None of the hypotheses are well supported with experimental data. Further, the mechanism of the productivity–diversity relationship is often dependent on the investigated ecosystem (Waide et al., 1999; Mittelbach et al., 2001).

In previous works, we conducted a series of fertilization experiments in an alpine meadow on the Tibetan Plateau in order to understand the underlying mechanism of species loss due to fertilization (Luo, Qin, & Du, 2006; Niu, Zhao, Luo, & Du, 2006). We showed that the interspecific competition hypothesis (ICH) and the assemblage-level thinning hypothesis (ALT) operate simultaneously. The relative contribution of ALT to the reduction in species diversity after fertilization can be as high as 42.9% (Luo et al., 2006). To further understand how ICH takes place, we attempted to test the importance of biomass and biomass allocation strategy in the changes of community structure. We examined whether the change in species abundance is related to changes in individual biomass and biomass allocation patterns.

Bazzaz (1996) and Tilman (1988) proposed a general theory of change in plant community structure based on resource competition, and the response of plant biomass allocation between leaves, stems, roots, and reproductive structures. The resulting morphology determines a plant's ability to compete for light primarily through leaves and soil nutrients through roots. Based on this theory, we make several predictions regarding plant community composition following fertilization: (1) species abundance will change, and individual biomass response and biomass allocation response will differ among component species and functional groups, (2) individual biomass response will be positively correlated with species abundance change, (3) if a trade-off between competitive ability and reproductive ability occurs when the competitive intensity is enhanced by fertilization (total competition), then one should expect that species reproductive allocation will tend to decrease, and species abundance change will have a negative correlation with the reproductive allocation response, a non-positive correlation predicted by light competition and root competition, (4) as most species are rosette forbs and graminoids, and the primary function of their stems is to support reproductive organs but not directly related to photosynthesis (Niu et al., 2006), species abundance change will not be correlated or negatively correlated with stem allocation response, and (5) finally, species abundance change will have a positive correlation with leaf allocation response (light competition), or with root allocation response (root competition), or, as the total competition hypothesis predicts, an interaction between the two.

In this experiment, we tested the importance of biomass allocation strategy for the loss of diversity due to nutrient addition. We did this by addressing the following questions based on the hypothesis cited above: (1) What changes occur in species abundance, individual biomass and biomass allocation following fertilization? (2) Can the response in individual biomass and biomass allocation explain the change in their abundance? (3) Which hypotheses are supported by biomass responses and their associated change in species abundance?

Material and methods

Study site

The experiment was conducted in a broad, flat alpine meadow in MaQu (N34°00′, E102°08′), Gansu, China, on the eastern Tibetan Plateau, 3500 m above sea level. The average temperature is 1.2, ranging from −10 in January to 11.7 °C in July, with about 270 frost days. Annual precipitation, measured over the last 35 years, is 620 mm; distributed mainly during the short, cool summer. For the years of the study, the annual precipitation was 584.6 mm (2004) and 672.2 mm (2005). The annual cloud-free solar radiation is about 2580 h. The vegetation, typical of Tibetan alpine meadows, is dominated by clonal *Kobresia* sp. (Cyperaceae), *Festuca ovina*, *Poa poophagorum*, *Roegneria nutans*, *Agrostis* sp. (Poaceae), *Saussurea* sp. (Asteraceae), and *Anemone rivularis* (Ranunculaceae). The average above ground biomass is 70–100 g/m^2 (dry mass). Typically, there are 20–30 vascular plant species and 200–500 individual plant per quadrat (0.25 m^2). The site has been fenced since October 1999, with grazing limited to the non-productive winter months.

Experimental design

We used a randomized, un-replicated complete block design with two soil resource levels, each level being made up of 10 blocks. Two 5 m × 8 m plots were established in each of the 10 blocks on 25 May 2004, with 2 m buffer strips between plots. Each plot was separated into two parts: a 5 m × 3 m section for vegetation monitoring, and a 5 m × 5 m section for individual plant sampling. Two evenly spaced 0.5 m × 0.5 m quadrants were placed within the 5 m × 3 m section of the plots.

One of the two soil resource treatments was applied to each plot: the control treatment (no resource manipulation) and the fertilized. In the fertilized treatment, 60 g m^{-2} of pelletized fertilizer (pebbles of $(NH_4)_2HPO_4$ fertilizer, 18% N and 46% P, a slow-release fertilizer, manufactured by Tianjin International Trading Company, Tianjin 300 000, China) was hand-broadcasted onto plots once each year (26 May 2004 and 29 May 2005) for 10.8 g N m^{-2} year^{-1} and 27.6 g P m^{-2} year^{-1}. Fertilizer was applied during heavy rain to avoid the need for watering (Luo et al., 2006).

Individual sampling

From our previous studies at this site, we chose 30 common species for measuring species traits. The 30 species were assigned to three functional groups – forbs, grasses, and legumes (Table 1). These 30 species accounted for 85–95% of the aboveground productivity and 80–90% of vegetation cover. Plant aboveground parts were sampled from June through the end of September, taking into account differing phenologies of the 30 species at fruit stage and flower stage. Sampling the roots of individual plants in this dense meadow was deemed impractical. We randomly sampled 2–3 individuals of each species in the larger section (5 m × 5 m) of the plot, to assure that 20 complete individuals were available from each treatment (Niu et al., 2006). For clonal plants, we regarded a ramet as an individual (Cheplick, 1998; Luo et al., 2006). The samples were dried at 80 °C. Plants were dissected into stems, leaves, fruits, and where relevant, flowers, and then weighed with a Sartorius balance accurate to 10^{-4} g.

Vegetation monitoring

At the end of each growing season, one 0.25 m^2 quadrat was harvested from the 5 m × 3 m section of each plot. The aboveground parts of all plant individuals in each quadrat were harvested between 8–12 September 2004 and 8–13 September 2005. Live plants were sorted by species. The number of ramets per species was recorded, and then the ramets were clipped. All samples were dried at 80 °C for 48 h, and weighed accurate to 10^{-4} g. For clonal species, we regarded a ramet as an individual.

Data analysis

For each individual, we calculated the aboveground individual biomass (IB) and the relative biomass allocated to reproductive parts, RA = (flower + fruit biomass)/IB, to stems, SA = stem biomass/IB and to leaves, LA = leaf biomass/IB. We then used these to estimate the species' response to fertilization with the log

Table 1. Species relative abundance change (VRAb) and biomass response after fertilization in 2004 and 2005.

Species		VRAb		VIB		VRA		VSA		VLA	
		2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
Trigonella ruthenica	L	0.03	0.19	**0.41**	**0.44**	**−0.45**	**−0.65**	**0.35**	**0.04**	**−0.07**	
Gueldenstaedtia diversifolia	L	−1.27	−1.10	0.10	−0.17	**−0.90**	−0.28	**0.27**	−0.12	0.07	**0.09**
Delphinium kamaonense var. *glabrescens*	F	0.14	1.37	0.76	0.10	−0.04	**−0.49**	**0.11**	0.11	**−0.22**	−0.12
Allium beesianum	F	−0.68	1.02	−0.51	−0.01	−0.19	−0.13	**0.18**	**0.14**	−0.17	−0.30
Gentianopsis banbata	F	−0.61		−0.12		**−0.25**		**0.28**		−0.16	
Halenia corniculata	F	1.31	−2.16	0.38	−0.13	**−0.28**	−0.19	**0.22**	0.17	−0.15	0.19
Veronica eriogyne	F	−0.32	−0.10	1.03	0.39	**−0.17**	**−0.47**	**0.34**	**0.24**	**−0.51**	−0.00
Potentilla fragarioides	F	−0.02	−0.12	0.45	0.39	0.03	0.03	0.10	**0.12**	−0.14	**0.12**
Anemone rivularis var *floreminors*	F	0.35	0.25	−0.21	−0.10	**−0.78**	**−0.42**	−0.06	0.16	0.12	0.02
Euphorbia pekinensis	F	−0.13	0.10	0.40	0.03	**−0.26**	**−0.57**	**0.24**	**0.35**	**−0.12**	**−0.01**
Taraxacum mongolicum	F	−0.41	−0.92	−0.02	−0.25	**−0.21**	**0.12**	0.06	**−0.03**	0.13	−0.05
Ligularia virgaurea	F	−1.89	0.13	−0.16	−0.11	−0.08	−0.03	**0.17**	0.14	**−0.24**	−0.02
Geranium pratense	F	0.24	0.19	0.25		**−0.20**		**0.24**		−0.07	
Saposhnikovia divaricata	F	0.96	−0.61	0.22	0.21	**−0.27**	−0.30	**0.15**	0.38	0.04	−0.31
Ajania tenuifolia	F	−0.27	−0.25	0.60	0.07	−0.12	−0.09	0.26	0.02	−0.27	
Bupleurum smithii var *.parvifolium*	F	0.11	−1.44	0.13	**−0.61**	−0.04	0.07	**0.36**	**0.63**	**−0.46**	**−0.66**
Galium verum	F	−0.50	1.95	0.22	0.36	−0.08	−0.97	0.50	**−0.04**	−0.04	
Anemone obtusiloba	F	0.18	−0.04	**0.64**	−0.05	**−0.47**	−0.00	0.05	0.15	0.12	−0.07
Ranunculus tanguticus var *.nematolobus*	F	−0.22	1.85	**0.58**	**0.71**	−0.08	−0.18	**0.23**	0.12	**−0.63**	0.03
Ranunculus tanguticus	F	−0.55	−0.21	0.87	**0.69**	−0.19	−0.04	0.40	**0.12**	−0.58	**−0.38**
Kobresia capillifolia	G	−0.04	0.59	**0.77**	0.79	−0.36	**−0.44**	**−0.57**	**−0.04**	**0.37**	**0.10**
Stipa aliena	G	−0.60	−1.19	−0.34	0.00	0.13	0.07	0.01	−0.03	−0.03	−0.00
Koeleria cristata	G	0.77	1.38	**1.75**	**1.90**	**−0.43**	**−0.30**	**−0.44**	**−0.41**	**0.97**	**0.69**
Poa botryoides	G	1.19	1.00.	**1.23**	**0.78**	−0.14	**0.71**	**0.08**	−0.02	**−0.24**	**−0.33**
Poa pratensis	G	0.63	2.03	0.29		0.04		**−0.09**		**0.33**	
Festuca sinensis	G	1.36	1.99	**1.23**	0.26	**−0.23**	0.07	−0.12	0.11	**0.56**	−0.23
Agrostis trinii	G	2.33	−0.81	1.36	−0.34	**−0.12**	0.12	-0.07	0.07	0.36	−0.20
Agrostis gigantea	G	0.67	−0.39	**0.09**	1.36	−0.47	−0.51	0.15	−0.36	**0.10**	0.53
Elymus nutans	G	1.15	1.15	**0.82**	0.93	−0.19	**−0.19**	−0.13	−0.03	**0.31**	0.11
Roegneria nutans	G	1.17	0.09	**0.99**	**1.36**	0.12	−0.01	−0.07	0.00	0.01	−0.01

The biomass response measured in term of individual biomass response (VIB), reproductive allocation response (VRA), stem allocation (VSA) response, and leaf allocation response (VLA). The value is the mean log response ratio of abundance or biomass, refer to the Method. Bold types indicate a significant difference between the mean of fertilized and control plots assessed by a *t*-test ($p < 0.05$, df = 20). Species are grouped according to functional groups (F: forbs L: legumes G: grasses)

response ratio (LRR). We calculated the individual biomass response as follows, $\mathrm{VIB} = \ln(\mathrm{IBf}/\mathrm{IBc})$, where IBf and IBc are the mean biomass of 20 individuals sampled in fertilized and controlled plots, respectively. Thus, a positive VIB value indicates that fertilization increased the individual biomass of a given species. Similar calculations were done for reproductive allocation response ($\mathrm{VRA} = \ln(\mathrm{RAf}/\mathrm{RAc})$, stem allocation response ($\mathrm{VSA} = (\ln \mathrm{SAf}/\mathrm{SAc})$), and leaf allocation response ($\mathrm{VLA} = \ln(\mathrm{LAf}/\mathrm{LAc})$).

From the vegetation harvest data, we calculated the relative abundance of each species (RAb = number of individuals of a given species in a quadrat/total number of individuals for all species in a quadrat) for the controlled and fertilized plots. We then calculated the change in species relative abundance using LRR ($\mathrm{VRAb} = \ln(\mathrm{RAbf}/\mathrm{RAbc})$), where RAbf and RAbc are the mean of species relative abundance in 10 quadrats of fertilized and controlled plots, respectively.

To test for the effect of the two treatments on species's abundance and species' biomass, we used an independent-sample *t*-test. We examined the relationships between the change in species' relative abundance and the change in species' biomass by calculating kendall's tau-b correlation coefficients. Data for each growing season (2004 and 2005) were analyzed separately.

The mean LRR of each functional group was calculated for relative abundance, aboveground individual biomass, and biomass allocation. To test for differences among groups, we performed non-parametric Kruskal–Wallis tests because the normality assumption of the data was not met. For post-hoc comparisons, we ran Mann–Whitney *U* tests on each pair of groups and adjusted the *P* value with the Bonferroni method, i.e. the *P*-values were multiplied by the number of comparisons.

Results

Following fertilization, the relative abundance of all grass species tends to increase (positive LRR) though the effect is never significant (Table 1). The response of forbs and legumes species is more idiosyncratic with positive or negative responses to fertilization. At the level of functional groups, there is a significant difference between the response of grasses and forbs in 2004 (Fig. 1A) and the same trend is observed in 2005. Overall, the fertilization appeared to favour grasses.

For individual biomass, most grass species showed a significant increase whereas forbs species exhibit no significant changes (Table 1). All, three functional groups increased after fertilization in 2004 and 2005 (Fig. 1B). The response of the grasses is more pronounced though not significantly different from the other groups.

In terms of biomass allocation, many species showed a significant reduction in reproductive allocation in one or both years (Table 1). This negative response to fertilization is the same for all the functional groups (Fig. 1C). By contrast, stem allocation response to fertilization varied within and between groups. The difference between grasses (with a negative LRR) and forbs (with a positive LRR) is significant for both years (Fig. 1D). Finally, leaf allocation response to fertilization was opposite to stem allocation response, with most grass species showing a significant increase and most forbs exhibiting decrease (Fig. 1E and Table 1). The effects of fertilization on species response were similar in both years. We could not find enough fruited individuals for some species (*Gentianopsis banbata, Geranium pratense*) in fertilized plots and *Poa pratensis* was absent because of missing fruit stage in 2005. Overall, biomass response was weaker in the second year of fertilization (Table 1).

Changes in species relative abundance showed a strong correlation with changes in the individual biomass response for both years (Fig. 2A). On the contrary, yet we found no relationship between abundance and reproductive allocation (Fig. 2B) and a weak negative correlation between abundance and stem allocation in 2004 only (Fig. 2C). A positive correlation between relative abundance change and leaf allocation response was observed in 2004 (Fig. 2D). A strong negative correlation was found between stem and leaf allocation for both years (Fig. 2E), suggesting a trade-off in the allocation strategy.

Discussion

Can biomass allocation response explain diversity loss due to fertilization?

Our previous work on Tibetan alpine meadows showed an increase in the community productivity and a decline in species biodiversity after fertilization (Luo et al., 2006). Here, we examined to what extent one could relate individual responses (biomass and biomass allocation) and population responses (relative abundance) to fertilization.

Plant strategies are the most important predictors for each species within a particular environment, especially, when plant communities experience environmental changes (Tilman, 1988). Functional traits, such as biomass allocation patterns and relative growth rate can determine competitive ability, survivability, and reproductive ability (Suding, Collins, Gough, et al., 2005). However, field evidence that biomass allocation patterns measured at the individual level influence species abundance at the population level is rare.

Maximizing fitness requires an optimal allocation of limited resources. Plants are able to respond to resource limitations by adjusting the allocation to functional organs (Bazzaz & Grace, 1997). When a plant community experiences fertilization, species should adjust their resource allocation patterns. This leads to changes in competitive ability among species, which in turn results in changes in relative abundance (Wilson & Tilman, 1993). It is, therefore, important to look for the mechanisms responsible for the change in structure of fertilized community by studying the functional strategies of the component species. Many studies predict species abundance from plant traits at population level (Suding et al., 2005), but studies at population level cannot answer the questions at the community level. Suding et al. (2005) recently summarized the functional traits for 967 plant species recorded in 34 N-fertilization experiments to study the mechanisms influencing diversity loss, and found that the functional traits are very important in all ecosystems. Our study found that the change in species abundance is a positively correlated with individual biomass response and leaf allocation response, and negatively with stem allocation response. This suggests that the biomass allocation strategy can partially predict the change in species abundance due to fertilization.

Interspecific competitive exclusion hypothesis supported by study's results

The ALT assumes that mortality is equal for all species, and that all species are functionally equivalent (Stevens & Carson, 1999b). In contrast, the interspecific

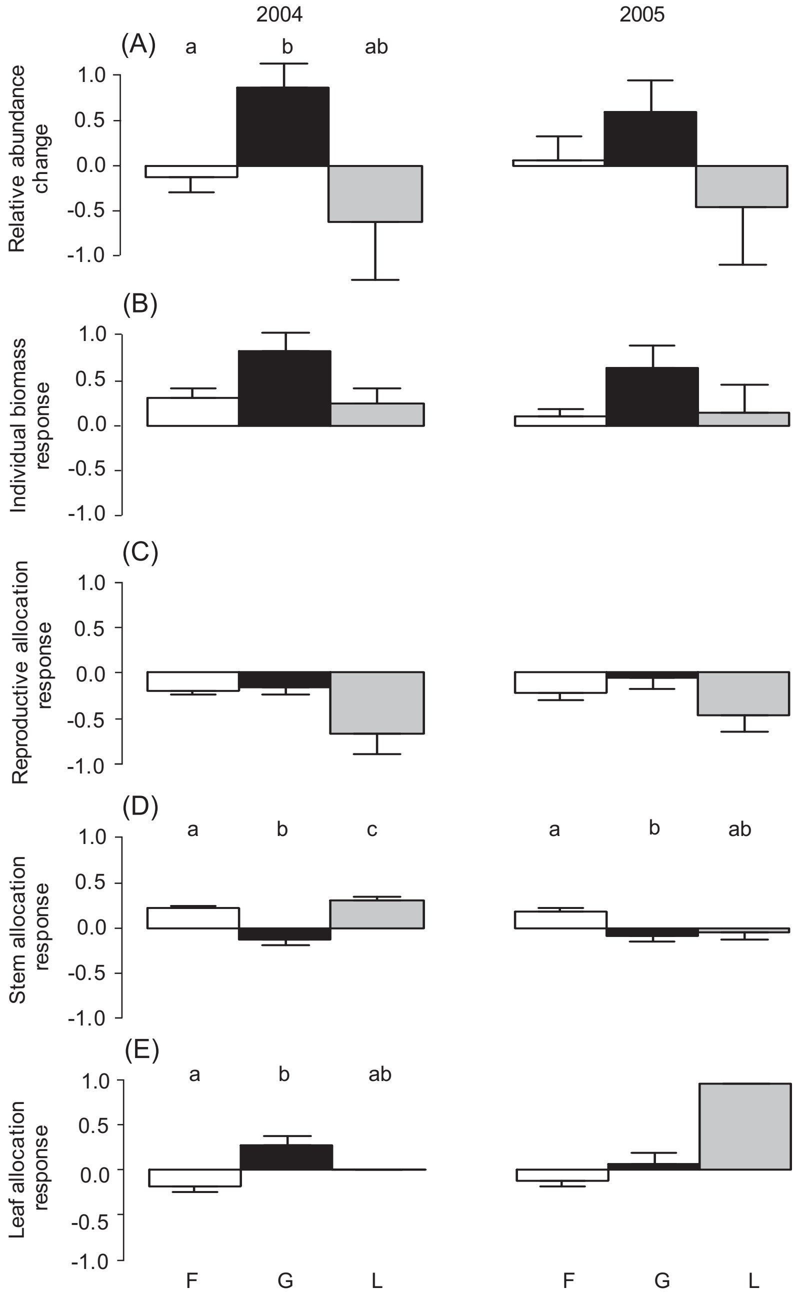

Figure 1. The effect of fertilization on the change in the relative abundance (A), the biomass (B), and the biomass allocation (C–E) in functional groups. The mean and standard error of log response ratio are shown for the years 2004 and 2005. Functional groups are as follows, F: forbs ($n = 18$), G: grasses ($n = 10$), and L: legumes ($n = 2$). Groups of bars without letters indicate a non-significant effect of functional group on LRR using Kruskal–Wallis test. Different letters above the bars indicate significant differences between pairs of functional groups in a Mann–Whitney post-hoc comparison test with P-values adjusted by Bonferroni correction.

competitive exclusion hypothesis (ICH) emphasizes that there are differences among species in terms of plant strategy. According to ALT, species mortality should be equal among component species, and therefore that component species relative abundances should not change after fertilization. Our data indicate that the relative abundance responses strongly differ among species after fertilization suggesting that individual mortality is not equal among species. The decrease in some species abundance (*Gentianopsis banbata* and *Geranium pratense*) was such that it was difficult to find 20 fruited individuals in fertilized plots during the second year. We found that individual biomass and biomass allocation response to fertilization perturbation are very different among species and functional groups. Size of dominant grass individuals became larger with

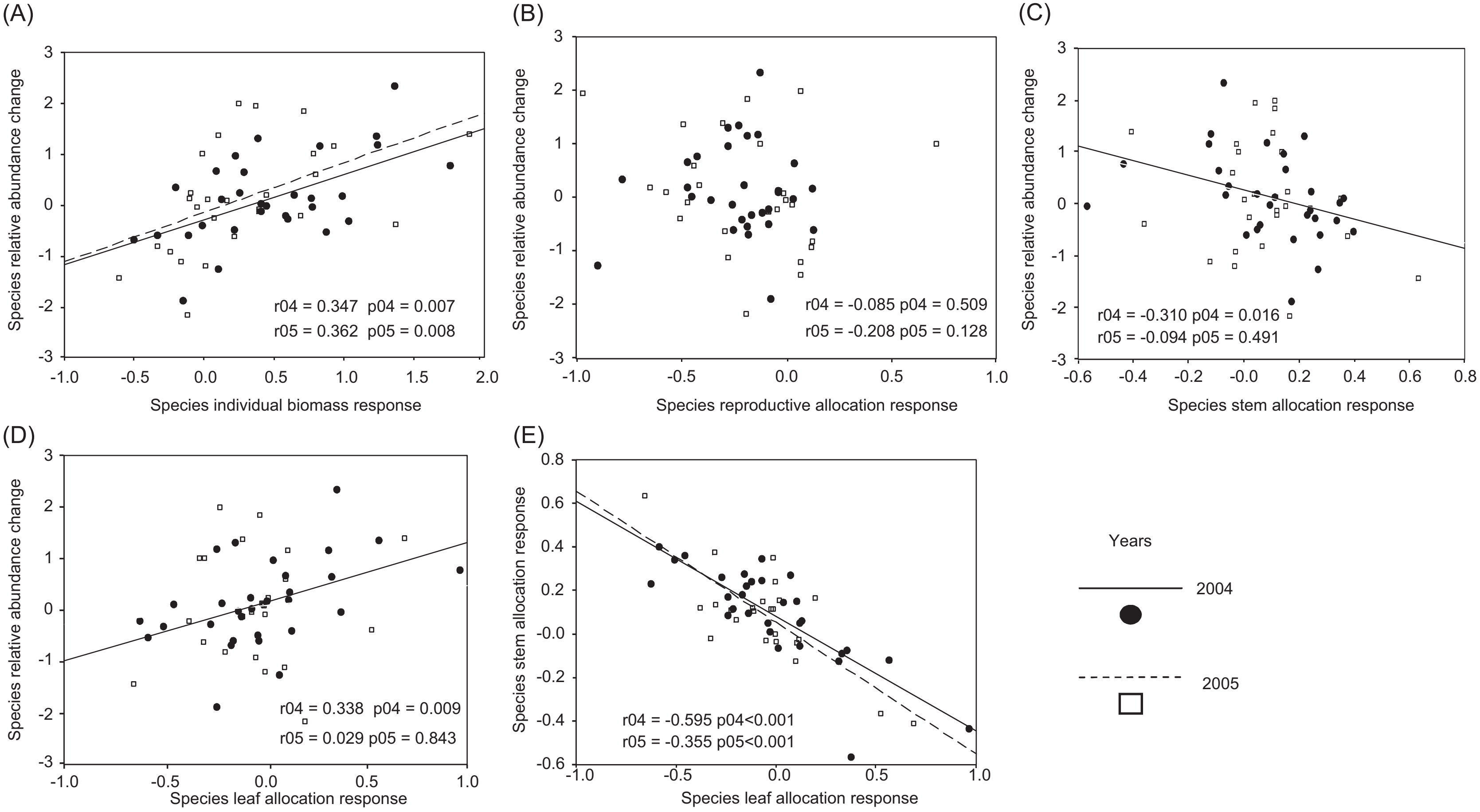

Figure 2. The relationships between change in species abundance and individual biomass response (A) or biomass allocation responses (B–D), and between change in stem and leaf allocation response (E). Each symbol is for the LRR of one species in 2004 (black circle and filled line) and 2005 (open square and broken line). The kendall's tau-b correlation coefficient (*r*) is reported for each year.

increasing fertility, whereas the biomass of subordinate species significantly decreases, as suggested in ICH. It is likely that dominant grasses depressed the growth of subordinate species after fertilization. Species are also very different in their biomass allocation patterns, a result that also fits with the expectations of the ICH hypothesis (Stevens & Carson, 1999a; Luo et al., 2006).

Total competition hypothesis was best supported by the biomass response and its relationship to species abundance change

Although light competition may be an important mechanism to explain diversity loss in a fertilized plant community, few experiments have tested this hypothesis (Rajaniemi, 2003). We found a positive correlation between species relative abundance change and leaf allocation response. This suggests that the increased light competition leads to changes in relative abundance. A small increase in leaf allocation gives a plant an advantage in competing for light. Species with increased leaf allocation will out-compete species allocating less to leaves in shaded habitats, and their relative abundance will increase after fertilization. As noted in other studies, height is a very important trait in pre-empting light (Tilman 1988; Tilman & Pacala, 1993; Gleeson & Tilman, 1990; Suding et al., 2005). In our study site, most species are rosette forbs and graminoids. We consider that the function of stems is primarily to support reproductive organs rather than for supporting photosynthesis-related structures. A strong negative correlation between leaf allocation and stem allocation suggests that there is a trade-off between leaf allocation and stem allocation (Fig. 2E). Most species increased leaf allocation at the expense of stem allocation, and even at the cost of reproductive allocation. We believe this explains the negative correlation with stem allocation response, and even the weak negative correlation with reproductive allocation response. The results of this study were not in agreement with predictions of stem function found in other studies but further confirm the role of light competition in diversity loss due to fertilization.

As light decreased in fertilized plots (Luo et al., 2006), reproductive allocation tended to decrease in all species. If there is a trade-off between competitive ability and reproductive ability, according total competition, reproductive allocation should decline with increasing allocation to competitive structures. With increasing allocation to competitive structures such as leaves suggests that the total competitive intensity increased with fertilization. Reproductive allocation decreased to varying extent among species (Table 1). This suggests size-dependent asymmetric competition for light among species also increased. Several species were significantly diminished in the fertilized plots, a result consistent with the prediction of total competition hypotheses. No correlation existed between species reproductive allocation response and species relative abundance. This supports the recent suggestion that seedling recruitment limitation is not due to propagule limitation (Henry, Stevens, Bunker, Schnitzert, & Carson, 2004; Foster, 2001; Foster & Tilman, 2003).

Most species in this study are perennials and can reproduce clonally, with the ramets possibly sharing resources. Our results were consistent with other fertilization experiments in clonal plant communities (Rajaniemi, 2002). The individual biomass response was enhanced, and the biomass allocation response was generally weakened in the second year of fertilization. The correlation between change in species relative abundance and individual biomass response was stronger, but no significant relationship was found between change in relative abundance and stem allocation response (or leaf allocation response) in the second year of fertilization. This might be related to a limited plasticity in biomass allocation for the species (Bazzaz & Grace, 1997). The plasticity of biomass allocation is partly attributed to the response to nutrient addition, and to plant allometric strategies (Müller, Schmid, & Weiner, 2000). In our study, the plant biomass response was consistent with the plasticity of biomass allocation. The changes in biomass allocation were not only a direct effect of fertilization, but also an indirect effect of altered individual plant size (Niu et al., 2006).

In summary, the individual biomass response and its allocation strategy are important in explaining diversity loss due to fertilization. There are some relationships between species abundance change in population level and biomass response in individual level. We thus conclude that the ICH, and more precisely the total competition hypothesis, is supported by our study.

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