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Do nutrients and invertebrate herbivory interact in an artificial plant community?

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Abstract

The addition of nutrients has been shown to decrease the species richness of plant communities. Herbivores feed on dominant plant species and should release subdominant species from competitive exclusion at high levels of nutrient availability with a severe competitive regime. Therefore, the effects of nutrients and invertebrate herbivory on the structure and diversity of plant communities should interact. To test this hypothesis, we used artificial plant communities in microcosms with different levels of productivity (applying fertilizer) and herbivory (adding different numbers of the snail, *Cepaea hortensis*, and the grasshopper, *Chorthippus parallelus*). For analyses, we assigned species to three functional groups: grasses, legumes and (non-leguminous) herbs. With the addition of nutrients aboveground biomass increased and species richness of plants decreased. Along the nutrient gradient, species composition shifted from a legume-dominated community to a community dominated by fast-growing annuals. But only legumes showed a consistent negative response to nutrients, while species of grasses and herbs showed idiosyncratic patterns. Herbivory had only minor effects, and bottom–up control was more important than top–down control. With increasing herbivory the biomass of the dominant plant species decreased and evenness increased. We found no interaction between nutrient availability and invertebrate herbivory. Again, species within functional groups showed no consistent responses to herbivory. Overall, the use of the functional groups grasses, legumes and non-leguminous herbs was of limited value to interpret the effects of nutrients and herbivory during our experiments.

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Zusammenfassung

Die erhöhte Verfügbarkeit von Nährstoffen beeinflusst die Diversität von Pflanzengemeinschaften negativ. Durch selektiven Fraß an dominanten Pflanzenarten sollten Herbivore bei hoher Produktivität konkurrenzschwache Arten fördern. Herbivorie sollte daher die Produktivitäts-Diversitätsbeziehung in Pflanzengemeinschaften beeinflussen. Wir testeten den Einfluss verschiedener Stufen von Produktivität und Herbivorieintensität in einem Mikrokosmos-Experiment mit einer künstlichen Pflanzengemeinschaft. Wir analysierten die Reaktion der Pflanzenarten entsprechend ihrer Zugehörigkeit zu den funktionellen Gruppen Gräser, Leguminosen und andere Kräuter.

Unsere Ergebnisse zeigen, dass Düngung einen negativen Einfluss auf die Pflanzendiversität und einen positiven Einfluss auf die Pflanzenbiomasse hatte. Die Artenzusammensetzung veränderte sich von einer leguminosen-dominierten Gemeinschaft bei niedriger Düngung zu einer von schnell wachsenden annuellen Arten dominierten Artengemeinschaft bei hoher Düngung. Nur die Leguminosen zeigten eine konsistent negative Reaktion auf Düngung.

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während Kräuter und Gräser idiosynkratische Muster zeigten. Herbivorie hatte schwächere Effekte und reduzierte die Pflanzenbiomasse der Artengemeinschaft sowie die Abundanz dominanter Arten durch selektiven Fraß und erhöhte die Evenness. Interagierende Effekte von Düngung und Herbivorie durch Wirbellose auf die Pflanzengemeinschaft konnten durch unsere Studie nicht belegt werden. Pflanzenarten innerhalb der funktionellen Gruppen zeigten keine konsistenten Reaktionen auf Herbivorie. Die Einteilung in Gräser, Leguminosen und andere Kräuter hat nur begrenzten Wert für die Interpretation unserer Ergebnisse.

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Keywords: Nutrient availability; Invertebrate herbivory; Microcosms; Productivity; Plant diversity; Plant functional groups; Top-down; Bottom-up

Introduction

Herbivores are important for the structure and diversity of plant communities (Crawley 1989). However, the effects of herbivores are not always consistent across communities. Proulx and Mazumder (1998; see also Bakker, Ritchie, Olf, Milchunas, & Knops 2006) found that species richness of plants increased with herbivory in productive, but decreased in nutrient-poor ecosystems. This switch in the effect of herbivores is attributed to the feeding of herbivores on dominant species with a competitive release of subdominant species at productive sites characterized by a severe competitive regime (Bakker et al. 2006; Huisman & Olf 1998; Pacala & Crawley 1992; Worm, Lotze, Hillebrand, & Sommer 2002). Obviously, productivity and herbivory interact in their effect on the plant community (e.g. Bakker et al. 2006; Frank 2005; Osem, Perevolotsky, & Kigel 2002). Most studies on the interactions between productivity and herbivory consider vertebrates (but see Fraser & Grime 1997, 1999; Schädler, Jung, Auge, & Brandl 2003). However, herbivorous vertebrates as well as invertebrates decrease the abundance of dominant and competitive plant species (Carson & Root 1999, 2000; Schädler, Jung, Brandl, & Auge 2004) and therefore the two groups of herbivores should have similar effects on the plant community.

Many studies on the interaction between nutrient availability and herbivory of vertebrates and invertebrates relied on natural gradients. However, across these natural gradients other factors change also, which compromises the interpretation of results (McNaughton, Oesterheld, Frank, & Williams 1989, Oksanen 1990, van der Wal, Egas, Van der Veen, & Bakker 2000). Along natural gradients the composition of the species pool of plants as well as herbivores changes. To overcome the problems of species identity during the interpretation of community data across systems, species are often assigned to functional groups (Diaz & Cabido 2001, Dyer, Goldberg, Turkington, & Sayre 2001). Hawkes and Sullivan (2001) for example showed that herbs and grasses differ in their responses to vertebrate herbivory in correlation to nutrient supply.

With increasing nutrient availability the compensation of losses by herbivory decreased in herbs, but increased in grasses. According to these authors this is a consequence of the location of the meristemes. At productive sites, herbivores promote growth in species with basal meristemes by removing tissue that shades the young leaves (Hawkes & Sullivan 2001). Although there are alternative explanations for this differential response, the specific response of functional groups to certain factors may help to compare results between communities with a different species composition. However, an important assumption for the application of plant functional groups is that all species in a group respond in a similar way to changes in the factor under consideration. Up to now only a few studies evaluated this assumption (Hanley, Trofimov, & Taylor 2004).

We used an outdoor microcosm to explore the interactions between nutrient availability and invertebrate herbivores on the species richness and structure of an artificial plant community. Similar to many ecological experiments (e.g. Bradford et al. 2002; Diemer, Joshi, Körner, Schmid, & Spehn 1997) we used grasses, non-leguminous herbs (simply called herbs henceforth) and legumes as functional groups. Legumes with their ability to fix nitrogen have strong effects in a plant community (Diemer et al. 1997) and may show specific responses to nutrient supply. We posed the following questions: (1) Do nutrients and invertebrate herbivory interact to affect diversity and composition of plant communities? (2) Is it useful to aggregate plant species into functional groups to understand the response of plant communities to nutrient availability and herbivory?

Methods

Microcosms

Plant communities were established in plastic containers (width 40 cm, length 60 cm, height 32 cm). Containers were caged with a mesh attached to two sides of a metal frame (total height of microcosms 1 m; mesh size: 20 µm). The other two sides and the top were covered

with a transparent plastic foil. Microcosms were shaded to avoid heating. The containers were filled with 60 L of a nutrient poor soil (Vulcaterra E extensive roof garden soil; $N_{\min} = 37 \text{ mg/L}$; $P = 57 \text{ mg/L}$; $K = 48 \text{ mg/L}$), consisting of lava, bims and bark mulch.

Plant and herbivore species

We selected 28 plant species (Table 1). All species occur in a wide range of grasslands of Central Europe with different levels of nutrients. These species represent the three functional groups commonly used in community experiments: grasses (10 species), non-leguminous herbs (10 species) and legumes (8 species). In May 2003, 250 seeds from each of the 28 plant species were sown in each microcosm.

We introduced two species of invertebrate herbivores into the microcosms, the white-lipped garden snail (*Cepaea hortensis* [Müller, 1974]) and the common grasshopper (*Chorthippus parallelus* [Zetterstedt, 1821]). Snails are known to feed mainly on herbs (Dirzo 1980), while grasshoppers prefer grasses (Bernays & Chapman 1970). Yet compared to many other herbivores these two species are polyphagous. Individuals of both species were collected around the experimental site.

Experimental layout

The experiment started in May 2003 on an experimental field near Marburg (Hesse, Germany). The design consisted of 15 factorial combinations of five levels of nutrient supply and three levels of herbivory (absent, moderate, high). At the beginning of the

experiment, slow release fertilizer (Plantacote[®] Depot 8 M; 14% N; 9% P₂O₅; 15% K₂O) was added to the soil at concentrations of 0, 1, 2, 4 or 8 g/L soil. Each combination of treatments was replicated five times. The 75 microcosms were arranged in a randomized complete block design.

Microcosms were watered every 2 or 3 days with tap water. The plant community was allowed to develop for 4 weeks. After this time, snails were added to the microcosms by repeated introductions over a period of 2 weeks. In total, the moderate herbivory treatment received 6 snails, whereas the high treatment received 12 snails, resulting in densities comparable to other experiments or the field (e.g. Fraser & Grime 1999). After another 4 weeks, 7 (moderate herbivory) and 14 (high herbivory) grasshoppers were released in the microcosms. Again these densities are similar to natural densities (Köhler 1999). The sequence of introducing the two species of herbivore reflects the natural phenology with snails being active during spring, while grasshoppers are abundant in summer. One microcosm got infected with aphids and we excluded this replicate from subsequent analyses.

The plant communities were harvested in September 2003. The living, aboveground biomass was cut at the soil surface. We sorted the material to species and we counted the number of individuals of each species. Since it was impossible to separate root biomass by species, total belowground biomass was sampled in each microcosm with three random soil cores (10 cm × 10 cm, depth 25 cm). Dead plant material was also pooled and used as a measure of litter accumulation. All sampled plant material was dried at 80 °C to constant weight.

Table 1. Plant species used during the microcosm experiments

Grasses	Non-leguminous herbs	Legumes
<i>Alopecurus myosuroides</i>	<i>Capsella bursa-pastoris</i>	<i>Lathyrus pratensis</i>
<i>Arrhenatherum elatius</i>	<i>Centaurea scabiosa</i>	<i>Lotus corniculatus</i>
<i>Brachypodium pinnatum</i>	<i>Chenopodium album</i>	<i>Medicago lupulina</i>
<i>Bromus mollis</i>	<i>Hypericum perforatum</i>	<i>Onobrychis viciifolia</i>
<i>Cynosurus cristatus</i>	<i>Lamium amplexicaule</i>	<i>Trifolium arvense</i>
<i>Echinochloa crus-galli</i>	<i>Leontodon hispidus</i>	<i>Trifolium campestre</i>
<i>Festuca ovina</i>	<i>Matricaria inodora</i>	<i>Trifolium repens</i>
<i>Lolium perenne</i>	<i>Plantago lanceolata</i>	<i>Vicia cracca</i>
<i>Poa annua</i>	<i>Sedum acre</i>	
<i>Vulpia myuros</i>	<i>Stellaria media</i>	

All microcosms started with 250 seeds from each species.

Analysis

If necessary, biomass data were log transformed to achieve normality (Kolmogorov–Smirnov test) and homogeneity of variances (Bartlett's test). Evenness of the plant communities was estimated based on the Shannon-index $J' = \sum(p_i \ln(p_i)) / \ln(S)$; (S = number of species in a microcosm; p_i = proportional biomass of species i in the sample). Relative root biomass was analysed with root biomass as the response variable and shoot biomass as a covariate. The effects of block, nutrient availability and herbivory intensity were analysed using a three-way ANOVA (Proc GLM in SAS/STAT 8.2).

For analyses of treatment effects on functional groups and species, three separate ANOVAs were performed. First, biomass data of species were summed up to yield aggregate values for the three functional groups. Then the effects of block, herbivory and nutrient availability on the biomass of these groups were tested. However, since the effects on total biomass may reflect only the

response of the most common species (Schädler et al. 2004), we also analysed the effect of plant species within a functional group. Only species established in more than a third of the microcosms were used. Significant species \times treatment interactions would indicate differences in the responses of species within a functional group. Finally, separate ANOVAs were used to test for treatment effects on biomass of individual plant species. All interactions with the factor block were pooled in the error sum of squares (Newman, Bergelson, & Grafen 1997).

Results

Community patterns

The number of plant species (Fig. 1A) and the number of individuals (Fig. 1B) decreased with nutrient supply whereas total biomass (Fig. 1C), total aboveground biomass (Fig. 1D) and litter accumulation increased (Table 2). The evenness of the plant community decreased from the treatment without additional nutrients to the treatments with nutrients (Fig. 1E).

The effect of herbivory on the plant community was less obvious than the effect of nutrients. Total and aboveground biomass decreased with herbivory (means \pm standard error across all levels of nutrient treatment: total biomass; without herbivores: 300 ± 8 g, intermediate density: 285 ± 8 g, high density: 266 ± 8 g; aboveground biomass: 264 ± 7 g; 254 ± 7 g; 235 ± 7 g) whereas evenness increased (0.28 ± 0.02 , 0.28 ± 0.02 , 0.34 ± 0.02).

The only significant interaction between herbivory and nutrient supply was found for relative root biomass (Table 2). For all herbivory treatments relative root biomass peaked at 1 g fertilizer/L (Fig. 1F).

Plant functional groups and plant species

Number of grass species showed a significant hump-shaped response to nutrient availability (Fig. 2, Table 3; second-order polynomial contrast: $F_{1,55} = 4.46$, $P = 0.036$). In contrast, the number of herb species decreased with nutrient availability and herbivory with a marginally significant interaction between the two factors (Table 3, Fig. 2). The number of legume species also decreased with nutrient availability. Total biomass of grasses and herbs increased, whereas total biomass of legumes decreased with increasing nutrient availability (Table 3, Fig. 3). However, this pattern was not caused by a concordant response of all species in each functional group (significant interactions between fertilization and species; Table 4). Despite the significant interaction, the biomass of all legume species declined consistently with increasing availability of nutrients (Fig. 3).

Responses of functional groups and individual species to herbivory were again less obvious than responses to nutrient availability. With increasing herbivory, total biomass of grasses decreased while that of herbs increased (Table 3, Fig. 4). These patterns were caused by the dominant species within each functional group (Table 4). Rare species may show quite different

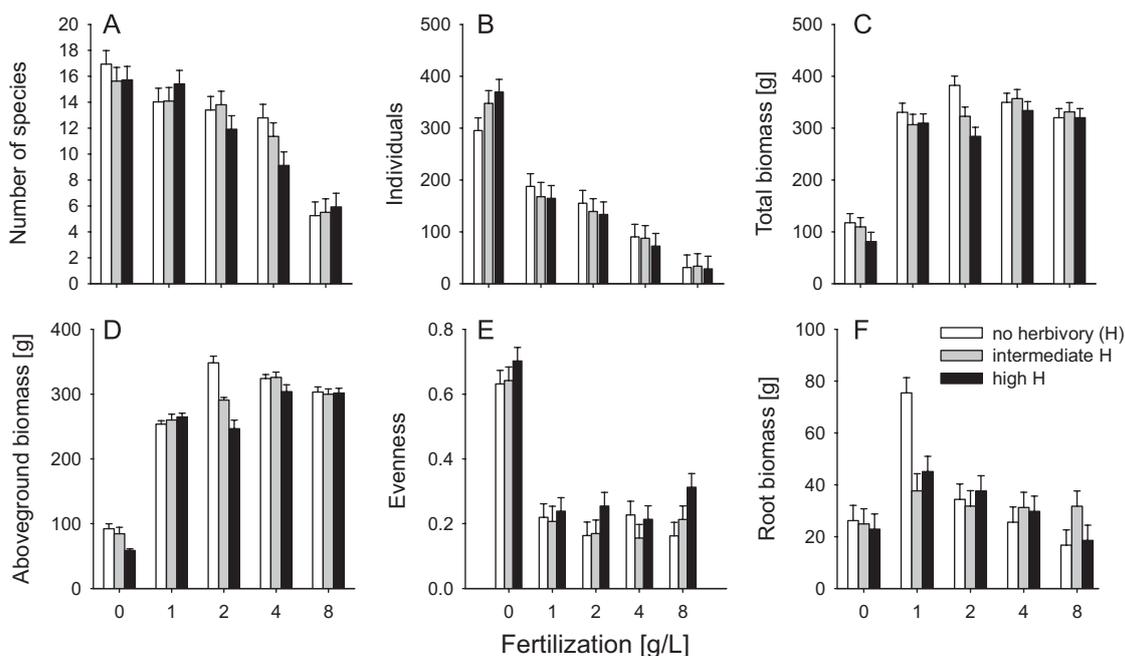


Fig. 1. Effects of nutrients and herbivory on the experimental plant communities (means \pm standard error per microcosm). Root biomass is corrected for shoot biomass and measures the relative allocation of resources to the roots.

Table 2. ANOVA results of the effects of nutrients and herbivory on artificial plant communities

	Nutrients (N)		Herbivory (H)		N × H		Block	
	$F_{4,55}$	<i>P</i>	$F_{2,55}$ a	<i>P</i>	$F_{8,55}$	<i>P</i>	$F_{4,55}$	<i>P</i>
Species richness	66.73	< 0.001	0.91	>0.3	1.50	0.18	14.80	< 0.001
Evenness	68.58	< 0.001	4.02	0.02	0.64	>0.3	1.49	0.21
Shoot biomass	116.57	< 0.001	4.43	0.016	1.98	0.066	5.39	< 0.001
Relative root biomass ^a	11.87	< 0.001	0.51	>0.3	3.31	0.004	1.366	0.26
Total biomass	98.36	< 0.001	4.70	0.013	1.33	0.25	3.39	0.015
Litter accumulation	9.29	< 0.001	0.93	>0.3	1.77	0.10	0.89	>0.3

Significant effects in bold.

^aEffect of shoot biomass as covariate (ANOVA): $F_{1,54} = 1.44$, $P = 0.26$. Error degrees of freedom for root allocation = 54.

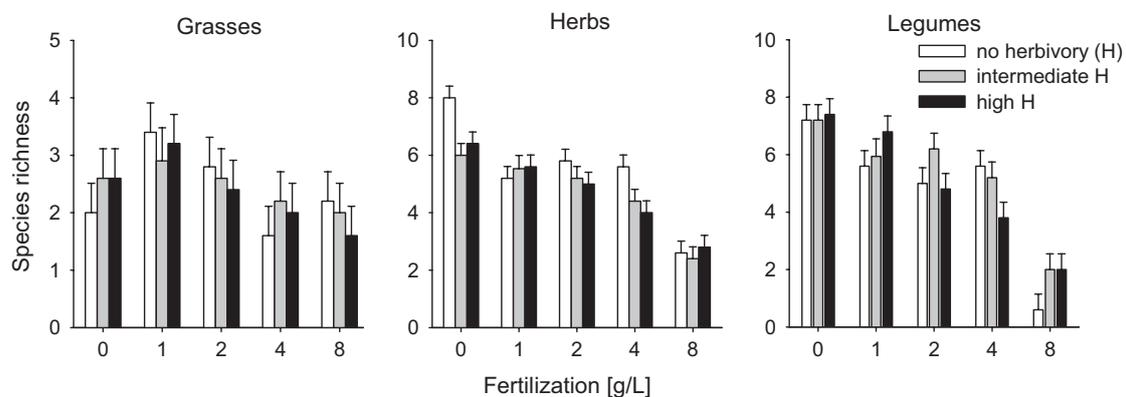


Fig. 2. Effects of nutrients and herbivory on the species richness of the three functional groups (grasses, herbs and legumes; means ± standard error).

Table 3. ANOVA results of the effects of nutrients and herbivory on species richness and total aboveground biomass of functional groups

	Nutrients (N)		Herbivory (H)		N × H		Block	
	$F_{4,55}$	<i>P</i>	$F_{2,55}$	<i>P</i>	$F_{8,55}$	<i>P</i>	$F_{4,55}$	<i>P</i>
<i>Species richness</i>								
Grasses	2.99	0.026	0.24	>0.3	0.31	>0.3	3.24	0.018
Herbs	41.91	< 0.001	4.91	0.011	1.82	0.093	18.11	< 0.001
Legumes	46.57	< 0.001	1.10	>0.3	1.82	0.094	3.51	0.013
<i>Total aboveground biomass</i>								
Grasses	104.50	< 0.001	6.04	0.004	1.50	0.18	3.74	0.009
Herbs	6.82	< 0.001	3.76	0.03	1.84	0.09	1.04	>0.3
Legumes	51.24	< 0.001	0.39	>0.3	0.44	>0.3	2.74	0.04

Significant effects in bold.

responses (see Fig. 3). Herbivory had no effect on legumes (Table 3, Fig. 4).

Fifteen species occurred in a sufficient number of microcosms to allow individual analyses (three grasses, six herbs and six legumes; Table 5, Figs. 3 and 4). Nutrient availability had clear but idiosyncratic effects on the biomass of all analysed species. Only three species were significantly influenced by herbivory: the biomass

of *Echinochloa crus-galli* and *Capsella bursa-pastoris* decreased while the biomass of *Chenopodium album* increased with herbivory (Table 5; Fig. 4). The grass *E. crus-galli* was the dominant plant species in the microcosms with additional nutrients and the overall response of the community and the functional group of grasses were dominated by *E. crus-galli*. The significant increase in total biomass with nutrient availability and

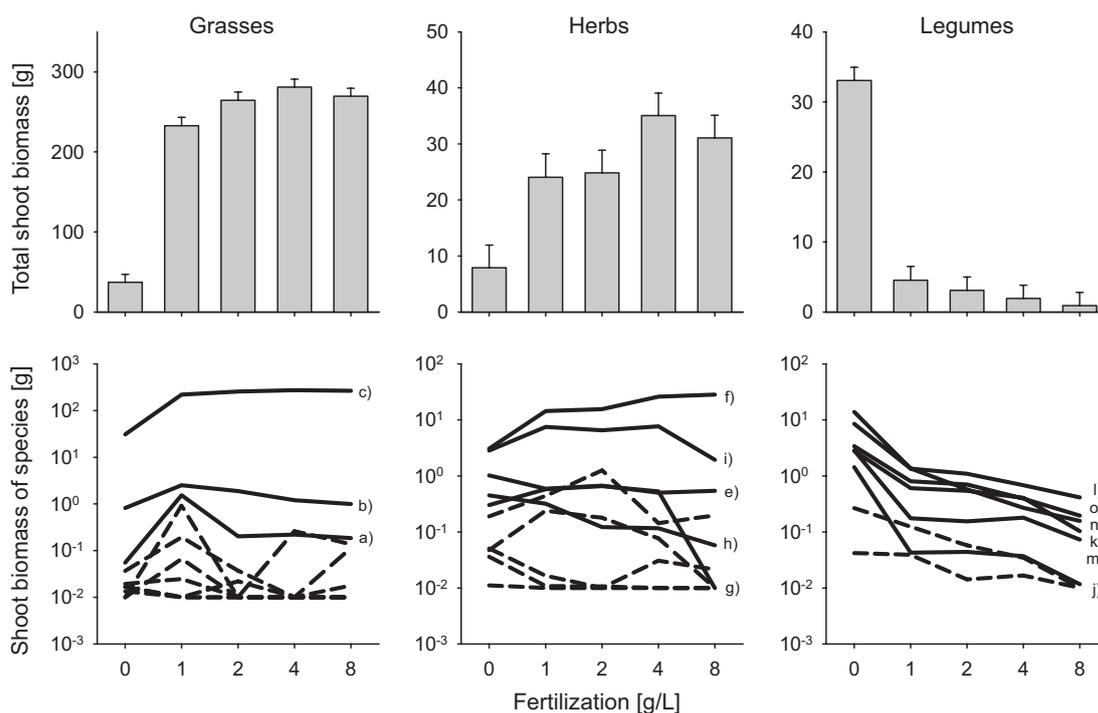


Fig. 3. Effects of nutrients on the aboveground biomass of the three functional groups (top row, means \pm standard error) and individual species within these groups (bottom row). Solid lines refer to species which occurred in at least one-third of all microcosms (see Table 5). Shoot mass of species is presented on a log scale to allow comparisons of abundant and rare species.

Table 4. ANOVA results of the effects of nutrients, herbivory and species identity on aboveground biomass within the three functional groups of plants

Source	Grasses			Herbs			Legumes		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Nutrients (N)	4	84.56	<0.001	4	6.64	<0.001	4	267.04	<0.001
Herbivory (H)	2	3.74	0.026	2	3.83	0.023	3	0.35	>0.3
Species (SP)	2	1729.56	<0.001	5	85.33	<0.001	5	51.03	<0.001
N \times H	8	1.11	>0.3	8	1.85	0.067	8	0.68	>0.3
N \times SP	8	83.59	<0.001	20	6.82	<0.001	20	4.34	<0.001
H \times SP	5	3.31	0.012	10	3.12	<0.001	10	0.22	>0.3
N \times H \times SP	16	1.09	>0.3	40	1.42	0.055	40	1.06	>0.3
Block	4	4.49	0.002	4	1.13	>0.3	4	9.28	<0.001
Residuals	173			350			350		

Degrees of freedom differ between the groups since only species occurring in more than a third of the microcosms were used. Significant effects in bold.

the decrease with herbivory disappeared when this grass species was removed from the analysis (nutrient availability: $F_{4,55} = 0.67$, $P > 0.3$; herbivory: $F_{2,55} = 1.64$, $P = 0.20$).

Discussion

Our results are in line with the many studies that report a decrease in species richness with increased availability of nutrients and therefore increased produc-

tivity (Gough, Osenberg, Gross, & Collins 2000; Gross, Willig, Gough, Inouye, & Cox 2000; Waide et al. 1999). Two mutually non-exclusive processes may explain this effect. First, diversity decreases with nutrient availability because dominants lead to a competitive exclusion of certain species at high levels of nutrient supply (Rajaniemi 2002, 2003). In our experiment, the addition of nutrients increased aboveground biomass. This effect was due to one fast-growing annual species, *E. crus-galli*. Second, the decrease of diversity with nutrient availability may be a by-product of increased plant size

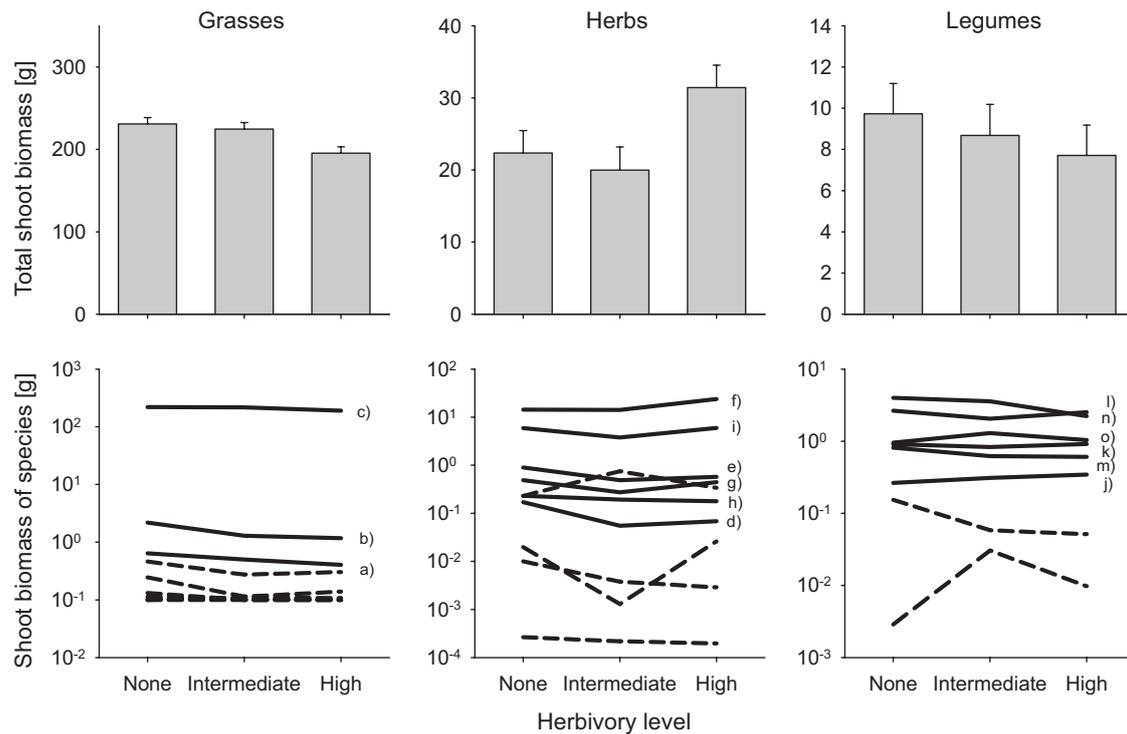


Fig. 4. Effects of herbivory on the pooled aboveground biomass of the three functional groups (top row, means \pm standard error) and individual species within these groups (bottom row). Solid lines refer to species which occurred in at least one-third of the microcosms (see Table 5). Shoot mass of species is presented on a log-scale to allow comparisons of abundant and rare species.

Table 5. ANOVA results (*P*-values) of the effects of nutrients (N) and herbivory (H) on aboveground biomass of frequent plant species in the microcosms

	N	H	N \times H
Grasses			
<i>A. myosuroides</i> ^a	<0.001	>0.3	>0.3
<i>B. mollis</i> ^b	0.020	>0.3	>0.3
<i>E. crus-galli</i> ^c	<0.001	0.017	0.24
Herbs			
<i>C. bursa-pastoris</i> ^d	0.004	0.048	>0.3
<i>C. scabiosae</i> ^e	0.009	>0.3	>0.3
<i>C. album</i> ^f	<0.001	0.043	0.18
<i>L. amplexicaule</i> ^g	0.021	>0.3	0.14
<i>M. inodora</i> ^h	<0.001	>0.3	0.05
<i>P. lanceolata</i> ⁱ	<0.001	>0.3	>0.3
Legumes			
<i>L. pratensis</i> ^j	<0.001	>0.3	>0.3
<i>L. corniculatus</i> ^k	<0.001	>0.3	>0.3
<i>M. lupulina</i> ^l	<0.001	>0.3	0.15
<i>O. viciifolia</i> ^m	<0.001	>0.3	>0.3
<i>T. repens</i> ⁿ	<0.001	>0.3	0.22
<i>V. cracca</i> ^o	<0.001	>0.3	>0.3

Letters refer to the curves of mean biomass of these species in Figs. 3 and 4.

and therefore lower numbers of individuals (the sampling effect of Oksanen 1996). We found a decrease in the number of plant individuals with nutrient availability. Thus, sampling effects and competitive exclusion may operate simultaneously within a community (Chiarucci, Carmela, & Bastow 2004).

In our experiment we found only minor effects of herbivores on the composition and diversity of plant communities. In particular we found no interaction between herbivory and nutrients. This may have two reasons: First, Turkington, John, Watson, and Secombe-Hett (2002) reported from a study on vertebrates that the interaction between herbivory and productivity depends on the density of herbivores. We used densities of invertebrates up to the higher range of natural densities. Therefore our experiment mimics natural situations and our results should be representative for such situations. At outbreak densities, however, the situation quite different (Carson & Root 2000). Second, across several years, Brown and Gange (1992) as well as Schädler et al. (2004) found substantial effects of herbivorous invertebrate herbivores on plant communities in field experiments. Given the short time scale of our experiment, our results refer to the impact of herbivores during the early establishment of plant

communities. Of course this compromises the generality of our conclusions.

In our experiment, the biomass of the dominant species *E. crus-galli* decreased with herbivory. This is most likely due to the feeding by *Ch. parallelus*, since this species is known to prefer grasses (Bernays & Chapman 1970), and we observed repeatedly grasshoppers feeding on *E. crus-galli*. Snails are active during the night and we have no direct observations on feeding. Molluscs, however, are known to feed on *C. bursa-pastoris* (Dirzo 1980) and the decrease of this species with herbivory may be due to the snails. Despite the effect of herbivores on the dominant species, herbivory had no effect on species richness of plants. Herbivores increased only the evenness of the plant community (see also Buckland & Grime 2000). Reports from natural communities agree with our experiment in that invertebrate herbivores have only small effects on the richness of plant species (del Val & Crawley 2005; Schädler et al. 2004).

In our microcosms, relative root biomass showed a peak at intermediate levels of nutrient availability. The decrease in relative root biomass at the high end of our nutrient gradient may be due to the competition for light which favours plants that allocate relatively more resources to the shoots (Tilman 1988; Wilson & Tilman 1991). The low relative root biomass without additional nutrient supply may be due to the high proportion of legumes in these communities (see below). An effect of herbivory on root biomass was only visible at fertilization level 2 with a higher root biomass in the herbivore-free microcosms. A reduction of root biomass has been repeatedly shown for vertebrates (see Bardgett, Wardle, & Yeates 1998 for review) but few studies report this effect for invertebrate herbivores (Choudhury 1984, Inbar, Eshel, & Wool 1995). Roots could not be identified to species, which compromises the detailed analysis and understanding of the mechanisms behind the effects of herbivory on root allocation in our experiment.

Nutrient availability influenced the composition of the community. The most striking change occurred between the first two levels of nutrient availability. Legumes dominated the microcosms with no additional nutrients while the addition of nutrients favoured *E. crus-galli* and, to a lesser extent, *Ch. album*. The decrease of species with N-fixing symbionts with increasing nutrient availability is a common pattern in terrestrial ecosystems (Suding, Collins, Gough, Clark, Cleland et al. 2005). This symbiosis is the main reason for the competitive advantage of legumes on nutrient poor soils (De Wit, Tow, & Ennik 1966).

Obviously the relative composition of functional groups changed with nutrient availability in our experiment. Plant species can be classified into functional groups in many different ways (Smith, Shugat, &

Woodward 1997). Here we adopted the coarse classification in grasses, non-leguminous herbs and legumes, which is often used in ecological experiments (Bradford et al. 2002; Diemer et al. 1997), to test whether such a classification helps to understand the effects of nutrient supply and herbivory. Although the aboveground biomass of grasses and non-leguminous herbs increased with increasing nutrient availability, the effect was due to the response of a few dominant plant species. Other species showed quite different patterns. Only the biomass of legumes decreased consistently with nutrient availability. Herbivores decreased the absolute and relative biomass of grasses and increased the absolute and relative biomass of herbs. This general response was again generated by the responses of the dominant plant species within each group. In contrast to Hawkes and Sullivan (2001), we found therefore no evidence for a general difference between grasses and herbs in their responses to herbivory under different levels of nutrient availability. The idiosyncratic responses of species of a functional group during our experiment do not necessarily reflect the response of these species in natural communities. The responses of species depend on the identity of the competitors. In our experiment competitors were from a pool of randomly selected species. Natural communities consist of a co-adapted species pool and therefore responses to a factor may be more consistent than in artificial communities (Buckland & Grime 2000). With respect to the effects of herbivory, early-successional species may show a decreased allocation of resources to defence compounds and may therefore be more susceptible to herbivory than late-successional species (Briner & Frank 1998; Cates & Oriens 1975). We grouped plants into annual and perennial species as a rough approximation of life history strategy (see De Deyn et al., 2003), but again the dominant species dominated the results of each group.

Conclusions

First, our study showed a clear bottom–up control of vegetation by nutrient availability and a weak top–down control by invertebrate herbivores. Furthermore, our results did not support the hypothesis that invertebrate herbivory and nutrient availability interact to affect plant diversity in plant communities. Second, we found that species in functional groups did not respond consistently to variations of nutrient availability or herbivory. Conclusions based on the responses of the total biomass of species aggregated into such coarse functional groups are biased by the response of the most common species (see also Schädler et al. 2004). Legumes are an exception: they are the only functional group in which the categorization reflects a common trait (N-fixation) with a clear ecological impact, suggesting

that functional groups should be defined by traits with a clear-cut ecological meaning.

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