

Plant community diversity and composition affect individual plant performance

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Received: 18 November 2008 / Accepted: 7 June 2010 / Published online: 9 July 2010
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Abstract Effects of plant community diversity on ecosystem processes have recently received major attention. In contrast, effects of species richness and functional richness on individual plant performance, and their magnitude relative to effects of community composition, have been largely neglected. Therefore, we examined height, aboveground biomass, and inflorescence production of individual plants of all species present in 82 large plots of the Jena Experiment, a large grassland biodiversity experiment in Germany. These plots differed in species richness (1–60), functional richness (1–4), and community composition. On average, in more species-rich communities, plant individuals grew

taller, but weighed less, were less likely to flower, and had fewer inflorescences. In plots containing legumes, non-legumes were higher and weighed more than in plots without legumes. In plots containing grasses, non-grasses were less likely to flower than in plots without grasses. This indicates that legumes positively and grasses negatively affected the performance of other species. Species richness and functional richness effects differed systematically between functional groups. The magnitude of the increase in plant height with increasing species richness was greatest in grasses and was progressively smaller in legumes, small herbs, and tall herbs. Individual aboveground biomass responses to increasing species richness also differed among functional groups and were positive for legumes, less pronouncedly positive for grasses, negative for small herbs, and more pronouncedly negative for tall herbs. Moreover, these effects of species richness differed strongly between species within these functional groups. We conclude that individual plant performance largely depends on the diversity of the surrounding community, and that the direction and magnitude of the effects of species richness and functional richness differs largely between species. Our study suggests that diversity of the surrounding community needs to be taken into account when interpreting drivers of the performance of individual plants.

Communicated by Peter Reich.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-010-1688-z) contains supplementary material, which is available to authorized users.

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Keywords Biodiversity experiment · Species richness ·
Functional richness · Individual performance ·
The Jena Experiment

Introduction

Over the last decade, consequences of declining plant community diversity for ecosystem processes have received

considerable attention. Among others, increasing plant community diversity was found to increase community biomass production (Naeem et al. 1996; Tilman et al. 1996; Hector et al. 1999; Roscher et al. 2005) to a similar extent as do composition effects due to the presence of particular functional groups such as grasses and legumes (Hooper and Vitousek 1997, 1998; Tilman et al. 1997; Symstad et al. 1998; Spehn et al. 2005). Community diversity effects on ecosystem processes such as biomass production can be attributed to the sampling or complementarity effect or to a combination of the two (Loreau and Hector 2001). The sampling effect accounts for a higher likelihood of including highly productive species in more diverse communities. The complementarity effect may include facilitative interactions and resource use complementarity of species leading to an increased total resource use and thus, to a higher biomass production in more diverse communities. Generally, complementarity is expected to be higher between species of different functional groups than between species of the same functional group, at least to the degree that functional groups differ in plant traits relevant for plant responses to diversity changes. Furthermore, plant community composition can also play an important role. Plant communities with legumes can benefit from their nitrogen fixation (Roscher et al. 2005; Spehn et al. 2005; Temperton et al. 2007) while grasses can negatively affect other species since they are superior competitors for nutrients due to their efficient resource uptake in upper soil layers (Fargione et al. 2003).

Community diversity effects on ecosystem processes have mainly been studied at the level of entire communities. Ultimately, however, community responses and that of single species depend on the performance of individuals (Dimitrakopoulos and Schmid 2004; Scherber et al. 2006). Even when community biomass production increases with increasing community diversity, the responses of the component species may differ greatly (Hector et al. 1999; Troumbis et al. 2000). So far, studies on individual plant performance are restricted to several species in microcosm experiments (Dimitrakopoulos and Schmid 2004) or to single phytometer test species in large field experiments (Scherber et al. 2006; Mwangi et al. 2007; Thein et al. 2008). However, responses of resident species are likely to oppose those of additionally planted test species because more vigorous residents will more negatively affect additional plants. Different responses of different plant species suggest that the study of only one or a few test species may easily result in idiosyncratic conclusions. To date, analyses of individual plant responses comprising all species in a large biodiversity experiment are still missing, which can hamper the mechanistic understanding of community diversity effects.

Plant responses at the community-level are composed of responses at the individual-level. The increasing plant community biomass with increasing diversity (Naeem et al. 1996; Tilman et al. 1996; Hector et al. 1999; Roscher et al. 2005) may be caused by a higher plant density or a higher average individual biomass which can be in turn caused by large positive responses of some species and small responses of others or vice versa. Strong competition for light generally leads to the dominance of tall species (Aerts 1999). Therefore, it might be expected that more diverse plant communities showing higher biomasses than less diverse communities consist of taller individual plants (Spehn et al. 2000). Plant reproductive responses to increased community diversity may include an enhanced inflorescence production as a consequence of increasing individual plant height with increasing diversity. In contrast, inflorescence production can also decrease as a response to the higher competition in more diverse communities since resource allocation to competitive abilities such as vegetative growth can result in lower reproduction (Levins 1968).

Grassland communities are well suited for experimental studies investigating the effects of plant community diversity because they are agriculturally important, their diversity is declining, their small-scale neighbourhood relationships invoke strong species interactions and their diversity can be easily manipulated (Loreau et al. 2002). Our study forms part of a large-scale and long-term grassland diversity experiment, the Jena Experiment (described in detail by Roscher et al. 2004). The experimental communities of different diversities and compositions were established in 2002 and by the time of our investigation in 2005, several diversity effects on community performance had already been observed (Fischer et al. 2008). For example, with increasing species richness, community aboveground biomass increased largely due to complementarity effects (Roscher et al. 2005). This suggests a greater individual aboveground biomass or an increased density in more diverse communities due to increased complementarity among species. The leaf area index (LAI) also increased with increasing species richness and functional richness (Daßler et al. 2008; Weigelt et al. 2010) which may result in higher plants in more diverse communities due to stronger competition for light. To extend the understanding of diversity effects on plant individuals, we examined individual plant performance by measuring height, aboveground biomass, and flower production of plant individuals of all species present in 82 plots of different species richness, functional richness, and composition. We addressed three main questions: (1) How does individual plant performance change with increasing species richness and functional richness, and with the presence or absence of legumes and grasses? (2) Do these changes differ between species

belonging to different functional groups, and (3) between different species within functional groups?

Materials and methods

Experimental design

Our study was integrated into the Jena Experiment (<http://www.the-jena-experiment.de>) for which grassland communities were sown in spring 2002 on former arable land in Jena, Germany (Roscher et al. 2004). The species pool consists of 60 plant species common to Central European mesophilic grassland of the *Arrhenateretum* type. According to multivariate analyses of species traits, the 60 species were classified as 16 grasses, 12 small herbs, 20 tall herbs, and 12 legumes (Roscher et al. 2004). All legumes were characterised by nitrogen fixation (Roscher et al. 2004). To account for a gradient in soil characteristics perpendicular to the course of the adjacent River Saale, the experimental area was grouped into four blocks (Roscher et al. 2004). In these blocks, 82 large plots of 20 × 20 m area were established with different species richness (1, 2, 4, 8, 16 or 60 species per plot) and functional richness (1, 2, 3 or 4 functional groups per plot). There were 16 plots with 1, 2, 4 and 8 species, 14 plots with 16 species and 4 plots with 60 species. 34, 20, 12, and 16 plots represented the 1, 2, 3, and 4 functional richness levels, respectively. For each plot species were randomly selected from the species pool. The plant communities were successfully maintained by weeding twice per year. Plots were mowed twice per year (June and September) as is typical for this type of managed grassland ecosystems. No fertiliser was applied during the experiment. For more details about the experimental design and community establishment in the Jena Experiment, see Roscher et al. (2004, 2005).

Data collection

Between mid-March and mid-June 2005, 2,630 individuals of all species were sampled in all 82 plots. This was done shortly before the sites were completely mowed according to the site management of the Jena Experiment, which is mimicking that of managed grasslands in the region (Roscher et al. 2004). For each species, we selected 6 plant individuals in each of the plots of lower species richness (1, 2, 4, 8 and 16 species) and four in each of the plots of higher species richness (16 and 60 species). Realised species richness was very close to sown species richness, but in some plots not all species were found in the sampling areas. For sampling, the 2 × 4 m sampling area was partitioned into smaller quadrats. After the random selection of sampling quadrats, the individuals nearest to the tip of a

pen randomly thrown into each sampling quadrat were sampled. Selected individuals were clipped 2 cm above ground to simulate the traditional grassland management. We were able to sample whole genets as individuals since, at sampling time, genets could still be recognised even when consisting of several ramets. Sampling was done block-wise and took about 1.5 weeks per block. As measures of individual plant performance, simple morphological and reproductive parameters of each plant individual were recorded: (1) its height indicated by the longest straight length of individuals from the cutting point, including stem, leaves and floral structures; (2) the number of inflorescences per individual; and (3) whether an individual plant was in flower or not. Between the block-wise sampling campaigns, these parameters were measured to avoid decay of individuals. Afterwards, individuals were oven-dried for 48 h at 70°C and weighed to the nearest milligram to measure (4) individual aboveground biomass.

Data analysis

For statistical analyses, performance parameters were averaged per species and plot to avoid pseudo-replications of species within plots. Performance parameters were analysed with mixed-model analysis of variance (ANOVA) with sequential sums of squares (SS) Type 1. Type 3 SS were not possible due to the hierarchical design of the Jena Experiment where, e.g., first fitting plot identity would make tests of species richness effects impossible. For the proportion flowering, the same model was used as a generalised linear model (GLM) with binomial error distribution. Both statistical approaches were implemented in R (version 2.3.1, 2006). Aboveground biomass was log-transformed to achieve normality and homogeneity of variances.

The statistical models contained tests between and within communities, and their interactions. Block, plot identity and species identity were fitted as random effects while functional identity and plot-level treatments (species richness, functional richness, presence of grasses and legumes) were fixed. Each model consisted of the following sequence of factors: block (to account for spatial differences and for block-wise sampling), species richness (logarithm of the sown number of species), functional richness (number of functional groups), presence of legumes, presence of grasses, plot identity (which served as error term for the factors mentioned above), functional identity (FI, error term: FI × plot identity), species identity (SI, error term: SI × plot identity), FI × species richness (error term: SI × species richness), FI × functional richness (error term: SI × functional richness), FI × presence of legumes (error term: SI × presence of legumes), FI × presence of grasses (error term: SI × presence of grasses), SI × species richness, SI × functional richness, SI × presence of legumes,

SI \times presence of grasses, plot identity \times FI, and plot identity \times SI (which served as error term for interactions of mentioned factors with SI). Significance levels remained the same when effects of functional identity (FI) were tested with species identity (SI) as error term instead of the FI \times plot identity interaction as error term. To address potential effects of using Type I SS, we fitted species richness before functional richness and vice versa. In analogy, the interactions of species richness and functional richness with other factors were also fitted in the two different sequences. We mention the few cases of different outcomes of analyses with reversed order of species richness and functional richness in the text. The full model could not be fitted when analysing the likelihood to produce inflorescences because only 68% of the plants produced inflorescences. Therefore, for this variable, we only analysed variation between but not within communities.

Realised species richness in the experiment was very close to sown species richness (linear regression: $R^2 = 0.95$) and analyses using realised species richness yielded the same results as the ones based on sown species richness. Therefore, we present only the latter in this article. In all mixtures, species were grown at maximum evenness (Roscher et al. 2005) and, thus, uneven species abundances within plots are unlikely to play an important role for plant performance.

The presence or absence of a particular functional group may influence individual performance either because individuals of this functional group perform differently from those of others, or because the presence of this group changes the performance of the others. To estimate effects of the presence of legumes and grasses on the individual performance of non-legumes and non-grasses, we calculated mean performance parameters of the latter for plots with legumes and grasses, respectively. We tested these effects of the presence+ (including performance parameter of legumes and grasses), presence– (excluding performance parameter of legumes and grasses although they occurred in the community) and absence of legumes and grasses on the individual parameters height, aboveground biomass, proportion of flowering and number of inflorescences with parametric *t* tests (SPSS, version 15).

Results

Effects of community diversity and composition on average individual plant performance

Plant species richness affected plant height, aboveground biomass and proportion of flowering (Table 1). In plots with higher species richness, individual plants grew taller but weighed less (Fig. 1; Table 1, significant independently

of the fitting sequence of species richness and functional richness) and in plots with higher functional richness plants grew taller (Fig. 1; Table 1, significant when fitted before species richness). Moreover, plants were less likely to flower in plots with higher species richness (Fig. 1; Table 1, significant when fitted before functional richness) and in plots with higher functional richness (Fig. 1; Table 1, significant when fitted before species richness). When monocultures and 60 species mixtures were omitted from statistical analyses to improve orthogonality between species richness and functional richness at the expense of statistical power, effects of functional richness on individual plant height and on the proportion of flowering were not significant.

In plots with grasses, individuals of all plant species (including grasses) grew taller (Fig. 2; $P < 0.001$), tended to be more in flower (Fig. 2; $P = 0.109$) and had more inflorescences (Fig. 2; $P = 0.024$) than in plots without grasses. When only the performance of non-grasses was considered, this effect was only significant for the proportion of flowering (Fig. 2; $P = 0.009$). Thus, fewer non-grass individuals were in flower in plots with grasses. Plant height (Fig. 2; $P < 0.001$), proportion of flowering (Fig. 2; $P < 0.001$) and number of inflorescences (Fig. 2; $P < 0.001$) differed between grasses and non-grasses in plots with grasses. This reflects that grass individuals grew taller than plants of other functional groups, were more in flower and had more inflorescences (Table 2).

In plots with legumes, individuals of all plant species (including legumes) grew taller (Fig. 2; $P < 0.001$) and weighed more (Fig. 2; $P < 0.001$) than in plots without legumes. When only the performance of non-legumes was considered, these effects remained although they were less pronounced for aboveground biomass (Fig. 2; $P = 0.043$). This indicates that the presence of legumes stimulated individual height and aboveground biomass of non-legumes. In plots containing legumes, individuals of all species (including legumes) weighed more than non-legumes (Fig. 2; $P = 0.003$) which reflects that legume individuals weighed more than plants of other functional groups (Table 2).

Species-specific effects of community diversity and composition on individual plant performance

Individual plant height, aboveground biomass and number of inflorescences per plant differed between functional groups (Tables 1 and 2; all $P < 0.001$). Moreover, effects of species and functional richness on individual plant performance differed between plants of different functional groups (Table 2).

The magnitude of the positive effect of species richness on individual plant height (Fig. 3) increased from tall herbs (slope of the regression line = 1.24, i.e. plant height

Table 1 Sequential ANOVA table (Type 1 SS) on the relationships between individual plant performance parameters (height, aboveground biomass, proportion of flowering and number of inflorescences) and main experimental factors

Source of variation ^a	Height			Log (aboveground biomass)			Proportion of flowering			No. of inflorescences		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Block	3	4.39	0.007	3	0.53	0.660	3	3.94	0.012	3	1.14	0.340
Species richness (log linear)	1	14.05	<0.001	1	7.54	0.008	1	6.57	0.012	1	0.12	0.733
Functional richness (linear)	1	1.24	0.269	1	3.38	0.070	1	0.43	0.515	1	0.03	0.869
<i>Functional richness (linear)</i>	<i>1</i>	<i>11.15</i>	<i>0.001</i>	<i>1</i>	<i>0.25</i>	<i>0.620</i>	<i>1</i>	<i>4.86</i>	<i>0.030</i>	<i>1</i>	<i>0.01</i>	<i>0.919</i>
<i>Species richness (log linear)</i>	<i>1</i>	<i>4.14</i>	<i>0.045</i>	<i>1</i>	<i>10.67</i>	<i>0.002</i>	<i>1</i>	<i>2.14</i>	<i>0.148</i>	<i>1</i>	<i>0.14</i>	<i>0.715</i>
Presence of legumes	1	11.06	0.001	1	29.99	<0.001	1	1.71	0.195	1	1.32	0.254
Presence of grasses	1	23.42	<0.001	1	2.38	0.127	1	9.99	0.002	1	5.75	0.019
Plot identity	75	11.35	<0.001	74	6.25	<0.001	75			70	6.46	<0.001
Functional identity (FI)	3	448.40	<0.001	3	69.08	<0.001				3	95.15	<0.001
Species identity (SI)	55	38.50	<0.001	55	30.64	<0.001				48	30.42	<0.001
FI × species richness (log linear)	3	7.00	<0.001	3	6.09	0.001				3	1.39	0.261
FI × functional richness (linear)	3	4.17	0.010	3	1.57	0.208				3	0.30	0.827
<i>FI × functional richness (linear)</i>	<i>3</i>	<i>11.26</i>	<i><0.001</i>	<i>3</i>	<i>3.88</i>	<i>0.014</i>				<i>3</i>	<i>1.08</i>	<i>0.370</i>
<i>FI × species richness (log linear)</i>	<i>3</i>	<i>2.08</i>	<i>0.114</i>	<i>3</i>	<i>3.98</i>	<i>0.013</i>				<i>3</i>	<i>0.21</i>	<i>0.891</i>
FI × presence of legumes	2	0.28	0.756	2	1.01	0.373				2	0.43	0.658
FI × presence of grasses	2	2.75	0.080	2	0.97	0.394				2	2.40	0.125
SI × species richness (log linear)	53	2.18	<0.001	53	1.98	0.002				40	1.63	0.033
SI × functional richness (linear)	53	1.22	0.173	51	1.77	0.009				39	4.01	<0.001
<i>SI × functional richness (linear)</i>	<i>54</i>	<i>1.45</i>	<i>0.040</i>	<i>54</i>	<i>1.65</i>	<i>0.011</i>				<i>42</i>	<i>2.63</i>	<i><0.001</i>
<i>SI × species richness (log linear)</i>	<i>52</i>	<i>1.96</i>	<i>0.001</i>	<i>50</i>	<i>2.12</i>	<i><0.001</i>				<i>37</i>	<i>3.00</i>	<i><0.001</i>
SI × presence of legumes	39	1.17	0.247	37	1.39	0.090				26	1.06	0.411
SI × presence of grasses	29	1.09	0.350	26	1.53	0.063				15	0.57	0.892
Plot identity × FI	65	1.46	0.028	54	1.31	0.110				39	1.10	0.358
Plot identity × SI (residuals)	170			133						81		

P values indicating significant effects of the factor on the performance parameter are in bold

^a To assess potential effects of the fitting order, species richness was fitted before functional richness and vice versa (see [Materials and methods](#)) and results of both fitting sequences are given in the text. Main factors in italics indicate the second fitting sequence

increased by 1.24 cm per doubling of species richness) to small herbs (1.49) to legumes (3.23) to grasses (5.78). This functional identity × species richness interaction was highly significant when fitted before the functional identity × functional richness interaction (Table 1). The pattern of the effect of functional richness on individual height of species belonging to different functional groups (data not shown) was very similar to the one of the effect of species richness. The functional identity × functional richness interaction was significant independent of the sequence in which it was fitted in the statistical model (Table 1).

The magnitude of the effect of species richness on individual aboveground biomass (Fig. 3) increased from negative for tall herbs (slope = −0.31, i.e. individual aboveground biomass decreased by 0.31 g per doubling of species richness) to slightly negative for small herbs (−0.05) to slightly positive for grasses (0.06) to positive for

legumes (0.12). This functional identity × species richness interaction was significant independent of the fitting sequence (Table 1). Moreover, effects of functional richness on individual aboveground biomass differed significantly between functional groups when these were fitted before functional identity × species richness (Table 1).

Responses to the presence or absence of legumes and grasses did not significantly differ between individuals of different functional groups (Table 1).

Individual plant height, aboveground biomass and number of inflorescences also differed between species belonging to the same functional group (Table 1; all $P < 0.001$). Moreover, individual species within functional groups responded differently to increasing species richness (Fig. 4) and to functional richness (data not shown). Except for two interactions, all species identity × species richness and species identity × functional richness interactions were significant for plant height, aboveground biomass, and number of

Fig. 1 The effect of sown species richness (\log_2 scale, *left*) and functional richness (*right*) on average individual plant performances. *Solid regression lines* represent significant relationships, *dotted lines* non-significant ones. *P* values are from ANOVA models

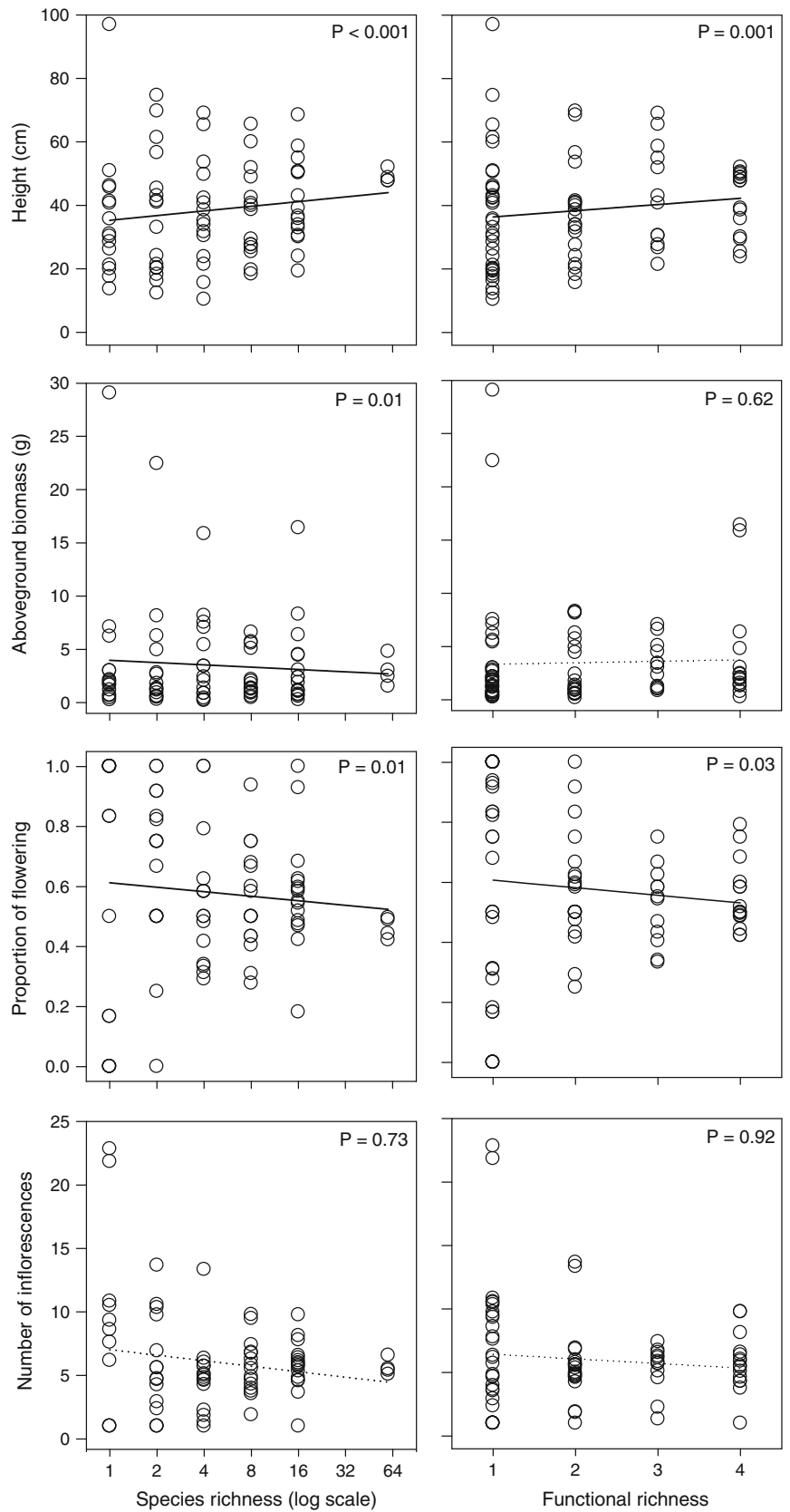
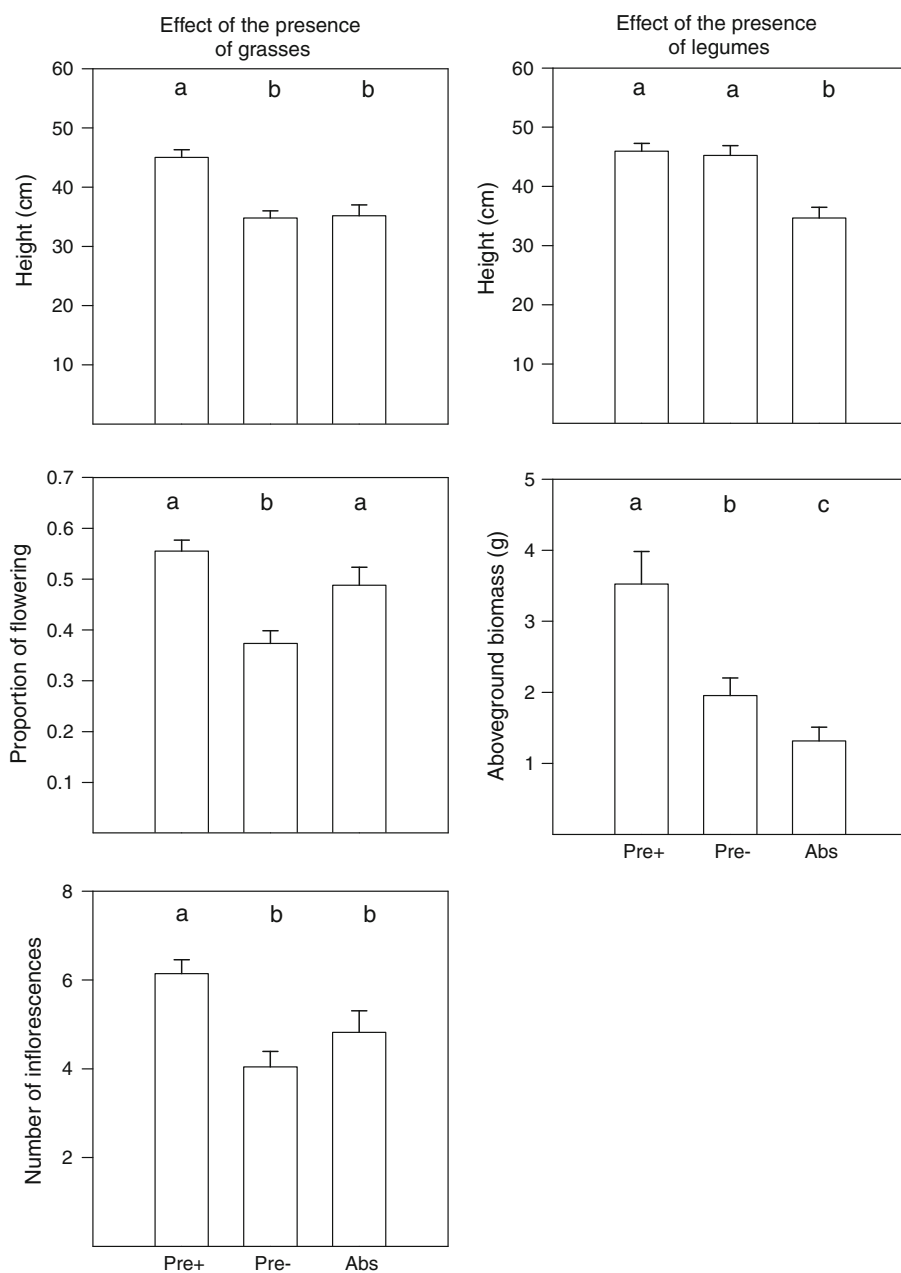


Fig. 2 Effects of the presence+ (*Pre+*, including performance parameter of legumes and grasses), presence– (*Pre–*, excluding performance parameter of legumes and grasses although they occurred in the community) and absence (*Abs*) of grasses (*left*) and legumes (*right*) on height, aboveground biomass, proportion of flowering, and number of inflorescences per plant. Columns show mean performance parameters and error bars indicate standard errors (SE). *a, b, c* indicate significant differences among treatments ($P < 0.05$)



inflorescences independent of the fitting sequence (Table 1). The two exceptions were the species identity × functional richness interaction for height (significant only when fitted after species identity × functional richness interaction; Table 1) and species identity × functional richness interaction for aboveground biomass (significant only when fitted after species identity × species richness interaction; Table 1).

Individuals of species belonging to the same functional group showed a similar response in height and aboveground biomass to diversity, both in terms of species and functional richness, except for one case of grasses. While almost all grasses showed a negative relationship between

individual aboveground biomass and species richness (Fig. 4), the opposite pattern was found for the effect of functional richness on aboveground biomass of the grasses (data not shown).

Due to the experimental design of the Jena Experiment, not all species occurred at all levels of species richness and functional richness. The following examples illustrate responses of two species which were present at least at four species richness levels. Within grasses, the strongest positive effect of species richness on individual height was observed for individuals of the potentially dominant grass *Arrhenatherum elatius*. While the aboveground biomass of *A. elatius* and that of two other grasses increased with

Table 2 Mean height, aboveground biomass, proportion of flowering, and number of inflorescences of plants belonging to different functional groups averaged over all plots (\pm standard error)

	Grasses	Small herbs	Tall herbs	Legumes
<i>Height (cm)</i>	63.92 \pm 2.23	22.64 \pm 0.09	36.01 \pm 1.52	47.60 \pm 2.10
Species richness	5.77 \pm 1.38	1.49 \pm 0.56	1.24 \pm 0.94	3.23 \pm 1.23
Functional richness	8.14 \pm 1.74	1.65 \pm 0.79	2.85 \pm 1.27	3.33 \pm 1.88
<i>Aboveground biomass (g)</i>	3.04 \pm 2.31	0.79 \pm 0.10	1.16 \pm 0.15	6.94 \pm 1.30
Species richness	0.06 \pm 0.27	-0.06 \pm 0.06	-0.31 \pm 0.08	0.12 \pm 0.76
Functional richness	0.84 \pm 0.34	-0.04 \pm 0.08	-0.28 \pm 0.12	0.42 \pm 1.15
<i>Proportion of flowering</i>	0.89 \pm 0.02	0.48 \pm 0.03	0.33 \pm 0.03	0.45 \pm 0.04
Species richness	0.00 \pm 0.01	-0.03 \pm 0.02	-0.03 \pm 0.03	-0.03 \pm 0.02
Functional richness	0.00 \pm 0.02	-0.06 \pm 0.03	-0.02 \pm 0.03	0.00 \pm 0.04
<i>Number of inflorescences</i>	8.28 \pm 0.42	4.05 \pm 0.50	5.46 \pm 0.57	3.74 \pm 0.38
Species richness	0.07 \pm 0.30	0.10 \pm 0.27	-0.32 \pm 0.02	-0.24 \pm 0.18
Functional richness	0.13 \pm 0.38	0.25 \pm 0.38	-0.45 \pm 0.32	0.14 \pm 0.28

Responses of individual performance parameter to increased species richness (\log_2 scale) and functional richness are indicated as slopes of linear regression (\pm standard error)

increasing species richness, those of the other grass individuals decreased. Responses of individual plant aboveground biomass were very variable among legume species and ranged from strong decrease through indifference to a strong increase of the species with the heaviest and tallest individuals, *Onobrychis viciifolia*.

Discussion

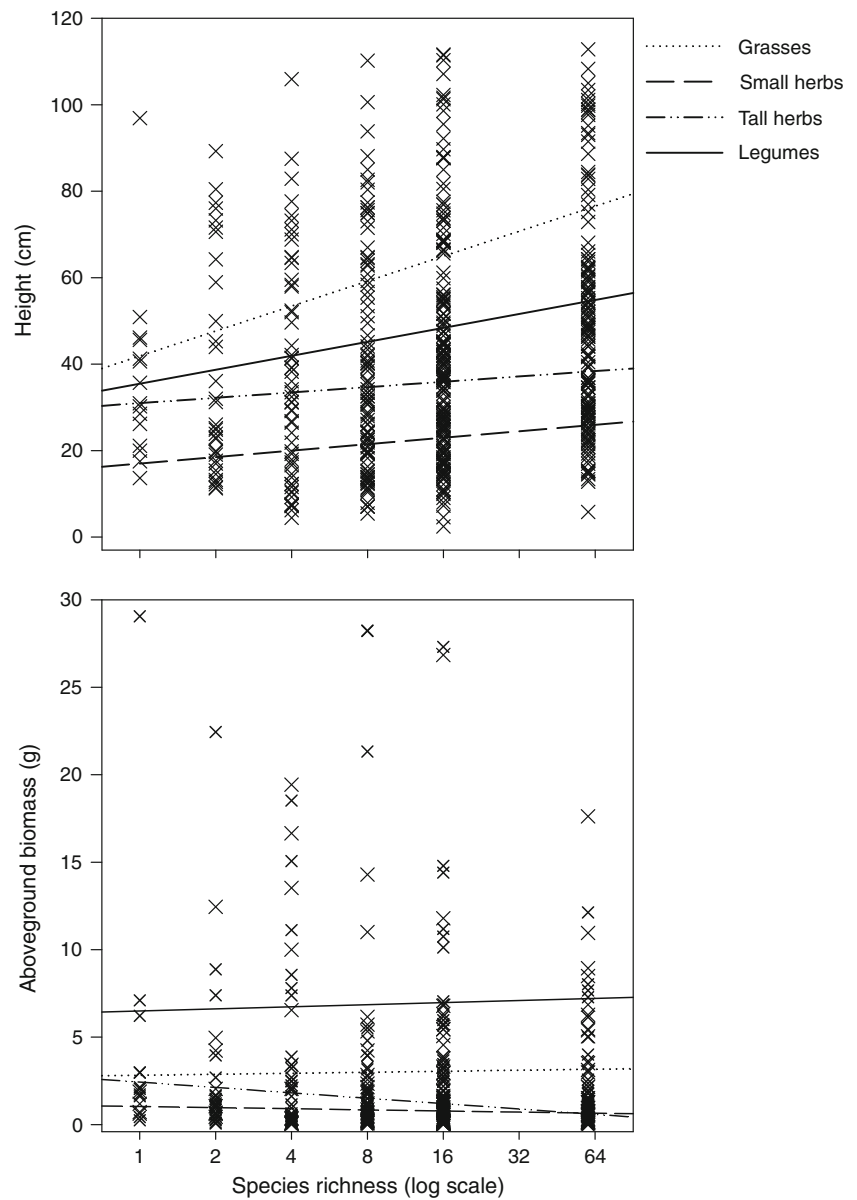
Effects of community diversity and composition on average individual plant performance

Due to potentially higher complementarity among species in more diverse communities, a greater individual aboveground biomass could have been expected when species are growing at higher functional richness (e.g. Fargione et al. 2003). In contrast, our results showed that average individual plant aboveground biomass was not strongly affected by functional richness and even decreased with increasing species richness. This suggests that the higher community biomass at higher species richness in the Jena Experiment (Roscher et al. 2005) was either due to an increase in plant density in more species-rich plots or due to the occurrence of species whose response opposes the average trend of decreasing individual aboveground biomass with increasing species richness in our study. Lower individual aboveground biomass in plots of higher community diversity had not previously been found for resident individuals but was reported for experimental invaders (Kennedy et al. 2002). This may be explained by increased competition, since the community LAI increased with increasing species richness and functional richness (for more details, see below). Our finding of decreased individual aboveground biomass with

increasing species richness might have been caused by the decreased soil nitrate concentrations observed in more species-rich communities of the Jena Experiment (Oelmann et al. 2007). However, the reduced soil nitrate concentrations in more diverse communities might indicate more efficient resource use of more diverse communities rather than reduced supply due to resource depletion. This is supported by the fact that diversity effects on community aboveground biomass do not diminish over time in the Jena Experiment (Roscher et al. 2005) and other biodiversity experiments (Pfisterer et al. 2004), which would be expected when resources become depleted. Therefore, a lack of soil nitrogen is unlikely to be the main underlying mechanism of reduced individual aboveground biomass in more diverse communities. Rather, increased LAI (for more details, see below) may mechanistically explain reduced individual performance at higher species richness, which should be tested by direct experimental manipulation in the future.

Moreover, we found a positive relationship between individual plant height and species richness. Such greater average plant height in more diverse communities had been reported for the community-level by Spehn et al. (2000). At the time of our sampling, community LAI was positively affected by species richness (when fitted before functional richness, $F = 32.40$, $P < 0.001$) and functional richness (when fitted before species richness, $F = 20.07$, $P < 0.001$) in the Jena Experiment (Alexandra Weigelt, University of Leipzig, personal communication). Mean LAI increased from 1.81 for the lowest species richness level to 3.90 for the highest one with an increase of 0.36 per doubling of species richness (Weigelt et al. 2010). It was significantly positively related to individual plant height in our study (data not shown), supporting stronger light competition in

Fig. 3 The effect of sown species richness (\log_2 -scale) on height and aboveground biomass for different functional groups. The single functional groups are represented by different types of fitted regression lines: *dotted* grasses, *dash* small herbs, *dash-dot-dot* tall herbs, and *solid* legumes

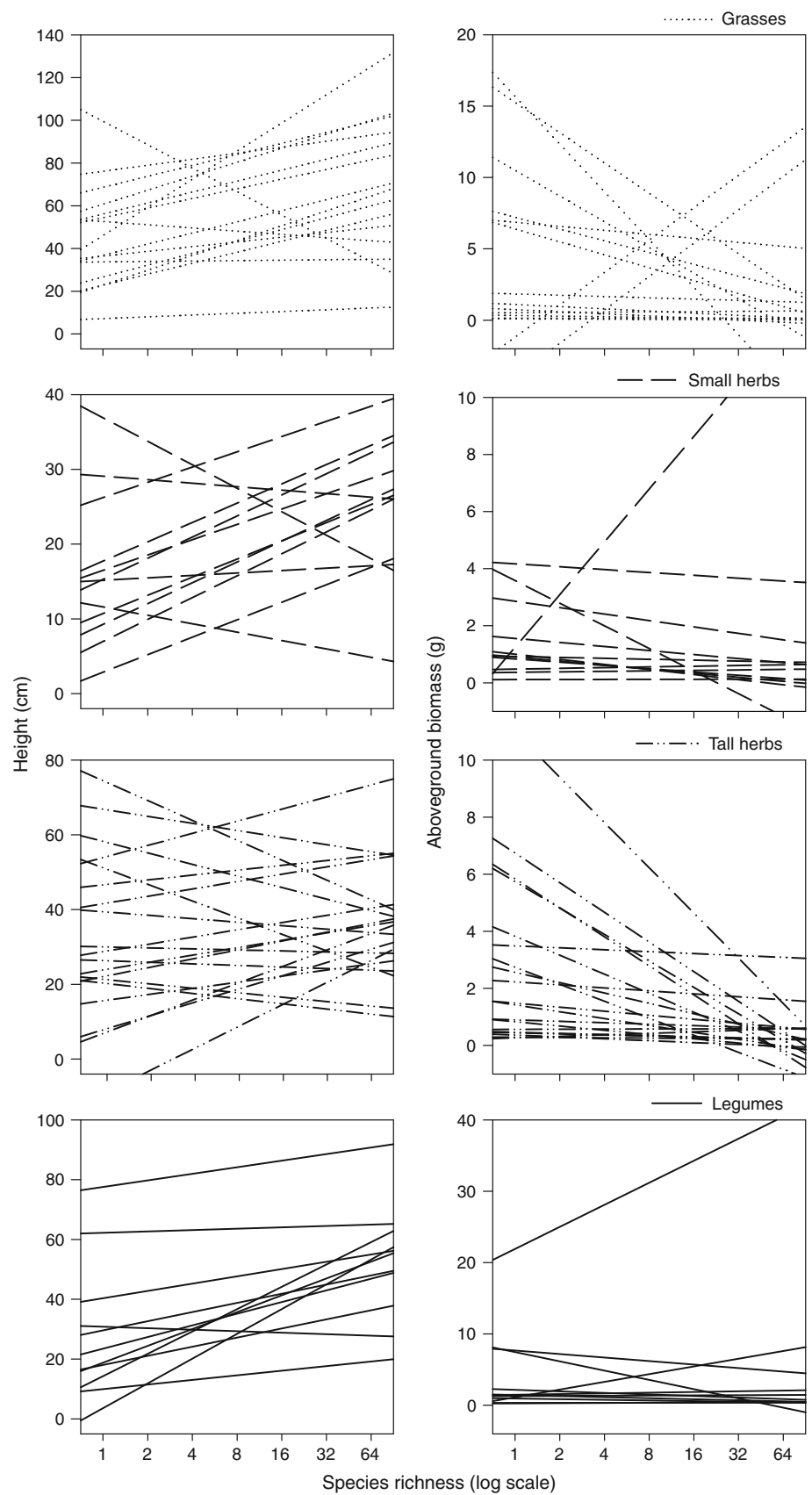


more diverse communities. Therefore, the greater individual plant height observed in more diverse communities in our study is likely to be an allometric response of plants to increased competition for light (Weiner 1990). At the same time, the proportion of flowering decreased with increasing species richness. This may result from a trade-off between resource allocation to vegetative height growth and to reproduction (Levins 1968). Individuals were harvested in late spring mimicking agriculturally managed grasslands, and, thus, harvesting affected the proportion of flowering. On average, grasses were more likely to be in flower (0.89 ± 0.02 SD) than non-grasses (0.41 ± 0.02). Nevertheless, a negative effect of species richness on the proportion of flowering was observed only for non-grass individuals ($F = 8.53$, $P = 0.005$ when fitted before functional richness, and $F = 5.79$, $P = 0.02$ when fitted after

functional richness) while it was not observed for grass individuals. Counting seeds and monitoring seedling establishment were beyond the scope of our study, but it remains to be seen whether reduced flowering in more species-rich communities is related to reduced seed production and seedling establishment. In the Jena Experiment, rates of flower visitation by insects increased with species richness (Ebeling et al. 2008) which may compensate for the reduced number of inflorescences per plant reported here.

Plant performance can be positively affected by the presence of legumes due to their nitrogen fixation. At the community-level, this has been reported for several biodiversity experiments (Roscher et al. 2005; Spehn et al. 2005; Temperton et al. 2007). On the other hand, the presence of grasses can negatively affect other species because they are superior competitors for nutrients (Fargione et al. 2003).

Fig. 4 The effect of sown species richness (\log_2 -scale) on height and aboveground biomass for single species belonging to grasses, small herbs, tall herbs, and legumes. Species are represented by different types of fitted regression lines: *dotted* grasses, *dash* small herbs, *dash-dot-dot* tall herbs, and *solid* legumes



Such effects of the presence and absence of legumes and grasses were also apparent in experimental plant communities with different arrival times of different functional types (Körner et al. 2008), underlining their generality. In plots with legumes, individual non-legumes of our study weighed on average 1.5 times more than in plots without legumes. Thus, the presence of legumes stimulated individual aboveground biomasses of other plant individuals. Similarly, Mwangi et al. (2007) who planted individuals of four species as test invaders into the Jena Experiment, and Scherber et al. (2006) who planted *Rumex acetosa*, found positive effects of legume presence for all test species. Our study extends these findings to all species resident in the experiment and adds the conclusion that legume presence increases individual aboveground biomass of all species contained in the community, first because legumes themselves weigh more than non-legumes, and second because non-legumes weigh more when legumes are present in the community.

In plots with grasses which are on average taller than other functional groups, all individuals grew on average 1.3 times taller than in plots without grasses. However, this effect disappeared when only the individual height of non-grasses was compared between plots with and without grasses. This indicates that the presence of grasses did not affect the height of other species. In contrast, grass presence reduced the proportion of flowering of non-grasses which may be caused by their efficient resource uptake which depletes resources for the other plant species (Fargione et al. 2003). In the above-mentioned phytometer studies adding test invaders to our communities, resident grasses showed a strong negative effect on aboveground biomass of all test invaders (Scherber et al. 2006; Mwangi et al. 2007). This contrasts with the neutral effect of grasses on aboveground biomass of resident species detected in our study and potentially shows constraints of phytometer approaches for drawing conclusions on resident species. Our findings illustrate that it is important to separate contributions of the sheer presence of legumes or grasses to average performance from contributions of their effects on individuals of other plants.

Differential community diversity responses of individuals belonging to different functional groups

We found differences in plant height, aboveground biomass and number of inflorescences between grasses, legumes, tall and small herbs which supported the a priori classification of species—based on multivariate analyses of their characteristics—into these functional groups in the Jena Experiment (Roscher et al. 2004). Moreover, the species richness and functional richness responses of individual plant height and aboveground biomass differed significantly

between plants of different functional groups. In contrast, responses to the presence or absence of grasses and legumes did not differ between individuals of different functional groups. This indicates that it is easier to predict plant performance responses to changes in plant composition than to changes in species richness and functional richness.

Grasses and legumes, the two functional groups with the tallest plants, showed the strongest increase of average plant height with increasing species richness, whereas individuals of small and tall herbs showed a less pronounced increase of average plant height with increasing species richness. This corresponds well with the idea that plastic responses to shading of smaller plants growing constantly under canopy shade are less pronounced than that of larger plants growing under sunny conditions (McLaren and Smith 1978), and with the idea that larger and smaller plants have different mechanisms to capture or use light (Werger et al. 2002; Anten 2005).

The response of individual aboveground biomass to increasing plant community diversity has so far not been addressed for resident species, but only for phytometer species planted into established communities as test invaders. Plant aboveground biomass of four phytometers declined from monocultures to 16-species mixtures and this effect was stronger for small and tall herbs than for grasses and legumes (Mwangi et al. 2007). In our study, individual aboveground biomass of tall herbs decreased pronouncedly with increasing species richness whereas the weak increase of the aboveground biomass of legumes and grasses opposed this pattern. Thus, aboveground biomass response of tall herbs can be responsible for the average decrease of individual aboveground biomass with increasing species richness across all species, whereas grasses and legumes may play a key role for the positive relationship between species richness and community aboveground biomass in the Jena Experiment.

Differential community diversity responses of individuals belonging to different species of the same functional group

In our study, species richness responses of individual plant height, aboveground biomass and number of inflorescences differed significantly between species of the same functional group. Moreover, species of the same functional group also responded differently in plant aboveground biomass and number of inflorescences to functional richness. A priori classifications of species into functional groups are very common and are often correlated with above- and belowground morphological, phenological and physiological traits. However, classifications into functional groups can be very coarse (Lavorel et al. 1997) and, therefore, species of the same functional group can still differ markedly

in characteristics relevant for resource uptake and plant performance (Craine et al. 2001).

In our study, responses to the presence or absence of grasses and legumes did not differ between species of the same functional group. Thus, species richness and functional richness, but not species composition, were the important factors causing species-specific responses within functional groups. Our results on individual plant performance generalise previous findings of species-specific contributions to community biomass in large field experiments (Hector et al. 1999; Lorentzen et al. 2008) and of species-specific responses in pot experiments (Dimitrakopoulos and Schmid 2004) and phytometer studies (Mwangi et al. 2007). We found that the potentially dominant grass *Arrhenaterum elatius* was strongly positively affected by species richness. In the Jena Experiment, *A. elatius* showed the greatest relative increase in aboveground biomass of all species in mixtures (Roscher et al. 2005), and it overtopped neighbours in mixtures (Lorentzen et al. 2008) of the so-called dominance experiment, a smaller experiment within the Jena Experiment involving only nine dominant species in the regional grassland of the *Arrhenaterum* type (Roscher et al. 2004). Thus, *A. elatius* appears to be competitively superior to other species. The relatively tall legume *O. viciifolia* was also remarkable in our study. Due to its height, its position in the competition for light was expected to be better in more diverse communities with various species of different heights than in less diverse communities with more tall conspecifics. *O. viciifolia* showed a strong positive effect of aboveground biomass to species richness possibly caused by such reduced light competition in more diverse communities in combination with its indifference to lower soil nitrogen levels in more diverse communities. Since *O. viciifolia* was the only species reaching aboveground biomasses above 20 g per individual, its contribution to community aboveground biomass was very large and its positive response contrasting with most other species may have largely contributed to the positive effect of species richness on community biomass in the Jena Experiment (Roscher et al. 2005). These results support earlier community-based conclusions of Troumbis et al. (2000) that relationships between community diversity and biomass production in grasslands are strongly influenced by species-specific performances in mixtures.

Conclusions

So far, the effect of community diversity on individual plant performance has received little attention. However, our experimental study clearly showed strong effects of diversity, both in terms of species richness and functional richness, and of species composition, on individual plant

height, aboveground biomass, likelihood to flower and the number of inflorescences. Such effects, and their deviation from community means, contribute to a more mechanistic understanding of how increased community diversity affects ecosystem processes. Moreover, we found that individuals of species belonging to the same or to different functional groups responded differently to species richness and functional richness. In the context of our biodiversity experiment, these differential responses of individual plants suggest that community composition will change over time in favour of taller grasses and taller legumes in combination with some smaller but shade-tolerant herbs. This exemplifies that assessing individual plant performance, including the traits examined in this study, as well as further morphological, physiological and fitness traits, is highly important to elucidate mechanisms underlying community dynamics. In more general terms, our study indicates that drivers of the performance of individual plants can be better understood when the diversity of the corresponding community is taken into account.

Acknowledgments We thank the management team, the gardeners of the Jena Experiment, Lena Kloss, Konstanze Gebauer and Christoph Scherber for help in the field and with measuring plants and Alexandra Weigelt for providing LAI information. Christiane Roscher and Bernhard Schmid provided very helpful comments on an earlier draft. Andrea Schmidtke conducted this work as part of her PhD thesis in a project funded by the Deutsche Forschungsgemeinschaft DFG (Grant FI1246/1-2) as part of the DFG Research Unit 456 Jena Experiment. The experiments conducted comply with current German laws.

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