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Published on: 20 May 2008 - Perspectives in Plant Ecology Evolution and Systematics (Elsevier)

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Lorentzen, S; Roscher, C; Schumacher, J; Schulze, E D; Schmid, B

Lorentzen, S; Roscher, C; Schumacher, J; Schulze, E D; Schmid, B (2008). Species richness and identity affect the use of aboveground space in experimental grasslands. Perspectives in Plant Ecology, Evolution and Systematics, 10(2):73-87.
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Originally published at:
Perspectives in Plant Ecology, Evolution and Systematics 2008, 10(2):73-87.

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Abstract

Complementary resource use is regarded as a mechanism that contributes to positive relationships between biodiversity and ecosystem functioning. Here, we used a biodiversity experiment composed of nine potentially dominant species (grasses: Alopecurus pratensis, Arrhenatherum elatius, Dactylis glomerata, Phleum pratense, Poa trivialis; legumes: Trifolium pratense, T. repens; non-legume herbs: Anthriscus sylvestris, Geranium pratense) to test for differences among monocultures and mixtures and for effects of species richness and the presence of particular species on the use of aboveground space. The number of rooting shoots determined in a line transect increased from monocultures to mixtures. Particularly, the presence of A. elatius in mixtures caused a higher shoot density at the community level. The number of pin contacts per sampling point (cumulative cover) at the community level, analysed with the point intercept method, was higher in mixtures than monocultures, and higher in mixtures with than without A. elatius. The effect was attributable to increased densities across the strata of the vertical stand profile as well as to an increase in community height. The impact of species richness on the use of aboveground space differed considerably between individual species. A. elatius achieved increased densities across all strata of the stand profile, while D. glomerata reached higher densities with a more pronounced use of space in the upper strata with increasing species richness of mixtures. Cumulative cover of P. pratense and A. pratensis was not affected by species richness, while the remaining species decreased space use mostly in the upper strata with increasing species richness or in mixtures with the competitively superior A. elatius. Our study shows that potentially dominant species are limited in their ability for adaptive responses to canopy shading. Nevertheless, the differential responses to species richness of individual species with regard to vertical niche occupation resulted in positive diversity effects on aboveground space use at the community level.

Species richness and identity affect the use of aboveground space in experimental grasslands

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MS details: 299 words in abstract, 6619 words in full text, 5 figures, 4 tables

Running title: Aboveground space use in experimental grasslands

Abstract

Complementary resource use is regarded as a mechanism that contributes to positive relationships between biodiversity and ecosystem functioning. Here, we used a biodiversity experiment composed of nine potentially dominant species (grasses: *Alopecurus pratensis, Arrhenatherum elatius, Dactylis glomerata, Phleum pratense, Poa trivialis,* legumes: *Trifolium pratense, T. repens*, non-legume herbs: *Anthriscus sylvestris, Geranium pratense*) to test for differences among monocultures and mixtures and for effects of species richness and the presence of particular species on the use of aboveground space. The number of rooting shoots determined in a line transect increased from monocultures to mixtures. Particularly, the presence of *A. elatius* in mixtures caused a higher shoot density at the community level. The number of pin contacts per sampling point (cumulative cover) at the community level, analyzed with the point intercept method, was higher in mixtures than monocultures, and higher in mixtures with than without *A. elatius*. The effect was attributable to increased densities across the strata of the vertical stand profile as well as to an increase in community height. The impact of species richness on the use of aboveground space differed considerably between individual species. *Arrhenatherum elatius* achieved increased densities across all strata of the stand profile, while *D. glomerata* reached higher densities with a more pronounced use of space in the upper strata with increasing species richness of mixtures. Cumulative cover of *P. pratense* and *A. pratensis* was not affected by species richness, while the remaining species decreased space use mostly in the upper strata with increasing species richness or in mixtures with the competitively superior *A. elatius*. Our study shows that potentially dominant species are limited in their ability for adaptive responses to canopy shading. Nevertheless, the differential responses to species richness of individual species with regard to vertical niche occupation resulted in positive diversity effects on aboveground space use at the community level.

Keywords: *Arrhenatherum elatius*, biodiversity effects, complementarity, light competition, The Jena Experiment, vertical structure

Introduction

A number of manipulative biodiversity experiments found positive effects of plant species richness on ecosystem processes such as aboveground productivity (e.g. Hector et al., 1999; Tilman et al., 2001; Spehn et al., 2005; Roscher et al., 2005; van Ruijven and Berendse, 2005; Balvanera et al., 2006). The underlying mechanisms of these experimental results have been discussed controversially (Hooper et al., 2005). The sampling-effect hypothesis describes the mechanism of increasing probability to include a highly productive species in a randomly selected species-rich mixture (Aarssen, 1997; Huston, 1997; Tilman, 1997; Cardinale et al., 2006). The niche-complementarity hypothesis is based on the assumption that differences among species decrease niche overlap in diverse communities and lead to a more efficient use of available resources that finally causes the positive relationship between species richness and productivity (Tilman, 1997; Tilman et al., 1997; Loreau, 1998; Cardinale et al., 2007).

All plant species compete for the same major resources of water, carbon dioxide, mineral nutrients and light. Complementarity in light exploitation has been proposed as one possible mechanism that contributes to the positive effects of plant species richness on aboveground biomass production (Naeem et al., 1994; Spehn et al., 2000, 2005). In addition to morphological and ecophysiological differences among species, individual plasticity may also increase resource-use efficiency of species and contribute to complementarity. This could, for example, occur if species with overlapping vertical distributions of leaves in monoculture would show a segregation of distributions in mixtures allowing the mixture to cover a larger vertical profile than each monoculture by itself. Adaptative changes in response to light availability belong to the best-studied examples of phenotypic plasticity (Schmitt and Wulff, 1993; Valladares et al., 2007). Morphological plasticity in response to light competition includes enhanced internode and petiole extension, reduced leaf development, increased apical dominance with reduced branching, increasing the probability to overtop neighbours

(Smith and Whitelam, 1990; Huber and Wiggerman, 1997; Anten and Hirose, 1999; Weijschedé et al., 2006) and, if these responses are not possible, the formation of shade leaves which can economically use even low levels of light (Corré, 1983; Schmid and Bazzaz, 1994; Evans and Poorter, 2001; Anten, 2005).

So far, aboveground space use of the plant community, and particularly of individual plant species, as a function of species richness has received little attention in biodiversity experiments. In the present study, we used the point intercept method (Levy and Madden, 1933) to get detailed information on the spatial arrangement of individual species in a biodiversity experiment with a pool of nine potentially dominant species. The experiment was specifically designed to test for the response of individual species to a species richness gradient ("dominance experiment" of the Jena Experiment; Roscher et al., 2004). The set-up of this experiment was motivated by the criticism that positive effects of biodiversity found in previous experiments were caused by a comparison of species mixtures with monocultures of species that are not able to grow as monospecific plant stands (Huston and McBride, 2002; Thompson et al., 2005). Species used in this experiment were selected on the criterion that they are known for their ability to occur in monospecific patches, to become dominant and to contribute substantially to biomass production in mixtures in semi-natural grassland. The species differ in growth form and height and become dominant under different management regimes, but none of them is normally found in the under-storey of mixed plant communities. Thus, we investigated the following issues: (1) Does species richness increase the use of aboveground space if the species pool of an experiment is restricted to potentially dominant species? (2) Is the use of aboveground space modified by variation in canopy height or density across the canopy profile? (3) How do individual species change the use of aboveground space in response to species richness? Specifically, we address the question whether diversity effects continuously increase with species richness or whether these effects

98 are due to differences between monocultures and mixtures or the inclusion of particular
99 species in mixtures.
100
101 ## Methods
102
103 ***Experimental site***
104 The experimental site is located in the floodplain of the river Saale in Jena (Thuringia,
105 Germany, 50°55`°N, 11°35`°E, 130 m a.s.l.). Mean annual air temperature is 9.3 °C and
106 average annual precipitations are 587 mm (Kluge and Müller-Westermeier, 2000). The Jena
107 Experiment (Roscher et al., 2004) was established in spring 2002 on a formerly fertilized field
108 used for growing cereals and vegetable for at least 40 years up to 2000. The soil is derived
109 from up to 2-m thick, loamy fluvial sediments and almost free of stones. Due to the fluvial
110 dynamics of the river, soil textures ranges from sandy loam to silty clay with increasing
111 distance to the river. Therefore, four experimental blocks were arranged parallel to the river.
112
113 ***Species pool***
114 Typical Central European semi-natural mesophilic grasslands (Arrhenatherion community;
115 Ellenberg, 1988) served as target community to create a species pool for the experiment.
116 These formerly species-rich communities locally lost many species over the past decades due
117 to intensified fertilization and shortened rotation periods. Nine species known to become
118 potentially dominant in these grassland communities were selected for the experiment: five
119 grasses (*Alopecurus pratensis* L.*, Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl et C. Presl*,*
120 *Dactylis glomerata* L.*, Phleum pratense* L. and *Poa trivialis* L.), two legumes *Trifolium*
121 *pratense* L. and *T. repens* L.) and two non-leguminous herbs (*Anthriscus sylvestris* (L.)
122 Hoffm. and *Geranium pratense* L.). Whereas the grass species *A. elatius*, *D. glomerata* and

123 *P. pratense* are characterized by a caespitose growth habit, *A. pratensis* forms belowground
124 stolons and *P. trivialis* grows with creeping aboveground shoots (Beddows, 1959;
125 Pfitzenmeyer, 1962; Mühlberg, 1967). The formation of sterile leafy shoots is a property that
126 distinguishes *A. elatius* from the other grass species. The legumes also differ considerably in
127 their growth habits. *Trifolium repens* produces aboveground creeping shoots rooting at older
128 nodes. Older shoot parts eventually die off leading to fragmentation of ramets, rendering the
129 identification of individuals difficult (Gluch, 1967). In contrast *T. pratense* and the non-
130 leguminous herbs *G. pratense* and *A. sylvestris* have clearly defined individuals. Both non-
131 legume herbs are known to establish slowly from seeds (Roberts, 1979; Nikolaeva et al.,
132 1985). However, during our study carried out in the second year of the experiment all species
133 were present in those plots where they were part of the sown mixtures.
134
135 ***Experimental design***
136 The experiment consisted of 206 plots of 3.5 × 3.5 m size. Species richness varied from
137 one in monocultures to two, three, four, six and the complete set of nine species in mixtures.
138 Each species was present in eight mixtures at each species richness level. Additionally, each
139 possible two-species combination occurred with equal frequency at each species richness
140 level above one. Each monoculture and each particular species combination of mixtures
141 (except for the nine-species mixture) was represented by two replicate plots resulting in the
142 following design: 2 × 9 monocultures, 2 × 36 two-species mixtures (each possible species
143 combination), 2 × 24 three-species mixtures (each pairwise species combination occurring in
144 2 mixtures and 4 plots), 2 × 18 four-species mixtures (each pairwise species combination
145 occurring in 3 mixtures and 6 plots) and 2 × 12 six-species mixtures (each pairwise species
146 combination occurring in 5 mixtures and 10 plots). The nine-species mixture had 8 replicates
147 to ensure that each species was present in eight mixtures at each species richness level (except

148 for the monocultures). Thus, the experimental design combined an equal representation of
149 individual species across the diversity gradient with increasing mixture similarity. For our
150 study we chose randomly one replicate of each monoculture and mixture (and four replicates
151 in case of the nine-species mixture).

152 The experimental communities were sown at an initial density of 1000 viable seeds per m^2
153 (adjusted for germination rates from preliminary laboratory tests) with an equal distribution of
154 seeds among species. The experimental plots were grouped into four blocks and each block
155 contained 51 plots with all species richness levels represented equally. All plots were mown
156 twice a year to 5 cm height. The mown plant material was removed. The plots were weeded
157 regularly to prevent invasion of unwanted species (for details see Roscher et al., 2004).
158
159 ***Data collection***
160 **Horizontal structure.** A line transect of 2 cm width and 250 cm length was used to record
161 density of rooted shoots and their distribution along the plot diagonal in July 2003 when
162 individuals could be easily recognized due to previous mowing. Shoots of each species
163 rooting in the transect were counted in 1-cm intervals. The data were analysed for (1) total
164 and species number of rooting shoots, (2) number of transect sections where no rooting shoots
165 were found, and (3) degree of shoot aggregation estimated as coefficient of variation of shoot
166 density per cm.
167 **Vertical structure.** The point intercept method (Levy and Madden, 1933) was applied to
168 analyse vertical vegetation structure. This method is known to be affected by pin diameter,
169 pin inclination and spatial orientation of plant parts (Warren Wilson, 1959, 1960, 1963). The
170 magnitude of divergence differs among plant species. Nevertheless the point intercept method
171 may provide the most detailed non-destructive information on spatial arrangement of
172 individual species in dense plant stands. A pin frame, consisting of a row of 20 pins with a pin

diameter of 3 mm and a distance of 5 cm between the pins, was inserted vertically through the vegetation down to the soil surface. All contacts of green plant parts (excluding litter) with the pins were counted per species using 5-cm intervals along the pins.

Data were taken at the time of peak biomass before mowing of the plots at the end of May and August 2003. Only monocultures, two-species mixtures and the nine-species mixture were measured in May. In August, all species richness levels, including three-, four- and six-species combinations, were recorded. The two-species mixture of *A. elatius* and *G. pratense* could not be analysed in May because strong rain flattened the vegetation. The following variables were derived from the field data:

(1) *Cumulative cover* per species (and plant stand) was defined as sum of pin contacts per species (or all species) with 20 pins divided by 20, measured at plot level. *Vertical density* was defined as number of pin contacts of plant parts per 5-cm height layer divided by 20. The vertical resolution was considered in seven height strata: 0–5 cm, 5–10 cm, 10–20 cm, 20–30 cm, 30–50 cm, 50–70 cm, >70 cm. The cumulative cover is closely related to the Leaf Area Index (LAI). The difference is only due to the inclusion of non-leaf plant parts (these are also included in optical measurements of LAI).

(2) *Maximum height* (cm) per species (or plant stand) was defined as the highest observed pin contact of plant parts of a species.

(3) *Mean height* (MH or centre of vertical density) (cm) per species (or plant stand) was used as an integrated measure of the vertical distribution of plant parts. It was computed following Gibson et al. (1987) by multiplying vertical density of each 5-cm wide layer (d_i) with the mean height of the layer (h_i) and dividing the sum of these products by the sum of vertical densities:

196 $$MH = \frac{\sum_{i=1}^{k} h_i d_i}{\sum_{i=1}^{k} d_i}$$

197

198 ***Data analysis***

199 Data analysis was done with S-Plus® 7.0 software (Insightful Corp., 2005). Data were
200 analysed at community and species level. For data recorded with the point intercept method
201 we used repeated-measures analysis of variance (ANOVA), applying the principles described
202 in Schmid et al. (2002). The initial statistical model included species richness decomposed
203 into a contrast to separate monocultures from mixtures and a log-linear contrast for species
204 richness within mixtures. The presence of individual species was used as predictor variable in
205 additional analyses to test for effects of species identity. This was possible because in our
206 design, like in another recent experiment using microbes (Bell et al., 2005), the presence of
207 each individual species was correlated to exactly the same degree with species richness. We
208 found a strong contrast for the presence or absence of *A. elatius* in mixtures. Therefore, we
209 included this effect (presence or absence of *A. elatius*) before entering log-linear species
210 richness in our final statistical models. Together with season (May or August) and their
211 interaction it constituted the treatment model. Composition (= monoculture or mixture
212 identity) and composition within season were used as error term (Table S1, see Schmid et al.,
213 2002). Blocks were not included in the error model because the random selection of one
214 replicate per mixture leads to a confounding of the block term with species richness. The
215 dependent variables were cumulative cover, maximum height and mean height (MH). For the
216 analysis of vertical density, the layer variable, we used a split-plot repeated-measures
217 ANOVA in which the split-plot treatment was height (decomposed into linear contrast and
218 deviation). All other terms were the same as in the above analysis (see Appendix, Table S1

219 for detailled information). For the analysis of species data, the dependent variables were first
220 multiplied with species richness to account for the differences in proportions of sown seeds.
221 This correction transformed these variables to per-individual-sown measures. If necessary,
222 data were log-transformed to meet the assumptions of normality and homogeneity of
223 variances.

224 In further analyses we calculated the differences of mean height for each species pair. The
225 calculation was based on monoculture values from different plots and all species pairs in the
226 two- and nine-species mixtures recorded in May. One-sample t-tests were applied to test each
227 pair for differences between monocultures and mixtures.

228

229 ## Results

230

231 ***Horizontal structure in relation to diversity***

232 **Effects of diversity at community level.** Averaged across all plots, we counted 37 (± 21 s.d.)
233 shoots per metre of transect length. The number of rooting shoots increased from
234 monocultures to mixtures ($F_{1;96} = 7.26$, $P = 0.008$). It was significantly higher in mixtures
235 with *A. elatius* ($F_{1;96} = 25.89$, $P < 0.001$) while a further increase of species richness beyond
236 two had no effect on the number of rooting shoots (Table 1, Fig. 1). The number of gaps (=
237 unoccupied transect sections) as well as the degree of shoot aggregation, estimated as
238 coefficient of variation of shoot density per cm, were significantly lower in mixtures with
239 *A. elatius* (number of gaps: $F_{1;96} = 11.51$, $P < 0.001$; shoot aggregation: $F_{1;96} = 5.85$,
240 $P = 0.017$), but not affected by species richness.

241 **Effects of diversity on individual species.** The number of rooting shoots of individual
242 species was not higher in mixtures than in monocultures. The legumes *T. pratense* and
243 *T. repens* showed a significant decrease of rooting shoots per individual if sown in mixtures

with *A. elatius*. Increasing species richness of mixtures had generally a negative effect on the number of rooting shoots of the herb *A. sylvestris*. *Arrhenatherum elatius* was able to increase the number of rooting shoots per individual sown significantly with the logarithm of species richness of mixtures. The number of rooting shoots per individual sown of the remaining species did not change in response to species richness or the presence of *A. elatius* (Table 1).

Vertical structure in relation to diversity

Effects of diversity at community level. The cumulative cover of the experimental communities was higher in mixtures than in monocultures. This increase was mainly caused by the presence of *A. elatius* in mixtures, and we observed no further increase with increasing species richness of mixtures beyond two species (Table 1, Fig. 2a, b). Cumulative cover was significantly higher in May before first mowing than in August, but the effects of the diversity treatments did not depend on season (Table 1).

While community maximum height was significantly higher in mixtures than monocultures, community mean height did not differ significantly between monocultures and mixtures. Mixtures containing *A. elatius* had significantly higher maximum as well as mean heights (Table 1, Fig. 2c-f). In addition to the effect of this particular species, an increase of species richness affected these parameters in a positive way.

The analysis of strata-level density showed that the higher number of vertical pin contacts in mixtures was due to increased densities per 5-cm height layer across the whole vertical stand profile. Strata-level density was higher in mixtures than in monocultures. Besides positive effects of *A. elatius*, we found a further increase in strata-level densities with increasing species richness of mixtures beyond two species (Table 2, Fig. 3). These increases of strata-level density were most pronounced in the upper height strata (see interactions "Ae × Stratum (linear)" and "SR × Stratum (linear)" in Table 2). All community parameters of

vertical stand structure were higher in May than in August, but the effects of species richness or the presence of *A. elatius* in the plant communities did not change with season (Table 1 and 2).

Effects of diversity on individual species. Changes in spatial arrangement in response to diversity differed strongly among species. Two species, *A. elatius* and *D. glomerata*, were able to increase cumulative cover on a per-individual-sown basis across the species-richness gradient. Cumulative cover of *A. elatius* was higher in mixtures than in monocultures and increased even further with the logarithm of species richness (Table 1). The increasing cumulative cover of *A. elatius* was accompanied neither by changes in maximum height nor in mean height (Table 1). Strata-level analysis confirmed that increased densities of *A. elatius* were not related to a change in vertical distribution of this species (Table 2, Fig. 4a).

The difference between monoculture and mixtures was not significant for the cumulative cover of *D. glomerata*, but cumulative cover of this species increased with the logarithm of species richness after removing variance explained by the presence of *A. elatius* in mixtures (Table 1). The analysis of strata-level density gave evidence that space use of *D. glomerata* in more diverse communities was particularly increased in the upper strata (see interactions "M × Stratum (linear)", "Ae × Stratum (linear)" and "SR × Stratum (linear)" in Table 2, Fig. 4b), although we did not find a significant increase of mean or maximum height of this species with increasing species richness of mixtures (Table 1).

Cumulative cover of *A. pratensis* and *P. pratense* did not differ significantly between monocultures and mixtures and was not affected either by the presence of *A. elatius* in mixtures or an increasing species richness of mixtures beyond two species (Table 1, Fig. 4c, d). Whereas we found a significant decrease in maximum and mean height of *A. pratensis* with a log-linear increase in species richness, these parameters did not change in response to species richness in *P. pratense*. However, the analysis of strata-level density indicated that

aboveground space use of *P. pratense* in the upper canopy layers increased more strongly in mixtures with *A. elatius* and with increasing species richness of the plant communities (see interactions "Ae × Stratum (linear)" and "SR × Stratum (linear)" in Table 2).

Cumulative cover of the remaining species was negatively affected either by growing in mixtures (*A. sylvestris, G. pratense*), the presence of *A. elatius* in the mixtures (*G. pratense, T. pratense*, *T. repens*) or an increasing species richness of mixtures (*P. trivialis*) (Table 1, Fig. 4e-i). The lower cumulative cover was accompanied by reduced maximum and mean heights. Maximum and mean heights of *A. sylvestris* and *G. pratense* decreased from monocultures to mixtures and even further with increasing species richness of mixtures (except for maximum height of *G. pratense*). Both variables also decreased significantly with increasing species richness for *P. trivialis*. The legumes *T. pratense* and *T. repens* had lower maximum (only *T. repens*) and mean heights in mixtures with *A. elatius*, while species richness had no significant effect on vertical space use of these species. Analysis of strata-level densities confirmed that species whose vertical density was affected negatively by community diversity had a more pronounced decrease in space use in the upper layers of the plant stands when they were growing in mixtures, in mixtures with *A. elatius* or with increasing species richness of mixtures (Table 2).

Pairwise differences in mean height. Pairwise comparisons of species mean heights gave further insight how species combinations affected vertical space use of individual species. *Arrhenatherum elatius*, the species with the largest mean height in monoculture, achieved in general relatively larger values in mixtures. In contrast, the difference between mean height of *A. pratensis*, which nearly had the same mean height as *A. elatius* in monoculture, and other species decreased in mixtures. The relation even reversed in the comparisons of *A. pratensis* with *P. pratense* or *D. glomerata* which obtained relatively larger values of mean height in mixtures. Significant relative changes of mean height were also found for other species pairs

(Table 3). The variety of response patterns to interspecific competition demonstrates that species height in monoculture was a poor predictor for the probability that a species reaches the upper strata of the vertical profile in mixtures (Fig. 5).

Discussion

Similar to a number of biodiversity experiments (see Hooper et al., 2005), we have shown in previous analyses that aboveground biomass production increases with species richness in our experiment composed of nine potentially dominant grassland species (Roscher et al., 2005). In the present study we analysed the relationship between biodiversity and aboveground space use and how individual species change their spatial arrangement to contribute to the response at the community level. Our analyses gave evidence that the use of aboveground space measured as community shoot density and as cumulative cover of the plant stands increased from monocultures to mixtures. The higher cumulative cover was attributable to both, an increase in vertical densities across the whole stand profile and increased height of the plant stands. In addition, we could show that the presence of individual species, in particular *A. elatius*, led to a further increase in cumulative cover, while an increase of species richness within mixtures did not result in significant changes of community vertical and horizontal density.

Spatial complementarity of plant species in natural grasslands is known from stands where subordinate species exploit successfully less favourable microhabitats such as under-storey vegetation (Grime, 1998). Tall-statured species obtain a higher fraction of incident photon flux density, but short-statured species use their biomass more efficiently to capture photons (Werger et al., 2002; Anten, 2005). We hypothesized that such mechanisms of complementary light use should be less important among potentially dominant species that normally do not grow as under-storey species. Our results confirmed this prediction: among

344 the selected potentially dominant species there was none that could assume the role of a
345 subordinate in mixture with even more dominant species. Rather, only those of the nine
346 species that could respond to competition by placing their parts into the upper canopy layers,
347 and overtop neighbouring species that could not do so, were able to reach a high cumulative
348 cover in mixtures.

349 In plant monocultures, the relative height of neighbouring individuals can predict the
350 outcome of competition (Ford and Diggle, 1981), because larger plants receive a
351 disproportionate share of light and are more likely to outcompete smaller plants (Weiner,
352 1990). Our results indicate that this mechanism is important in our species pool as well.
353 However, while canopy height is an important predictor for competitive dominance (Gaudet
354 and Keddy, 1988; Mitchley, 1988; Mitchley and Willems, 1995), the relative height of species
355 in mixtures was not predictable from their height growth in monocultures (Table 3, Fig. 5). In
356 contrast to our results, Vojtech et al. (2007) found that levels of light intercepted in grass
357 monocultures were a good indicator for competitive outcomes between species pairs, but this
358 findings may be due to the shorter duration of their experiment (18 weeks).

359 *Arrhenatherum elatius* was able to overtop neighbours in mixtures and its vertical
360 distribution of aboveground plant parts was characterized by the highest mean values in
361 monocultures and mixtures (Fig. 5). This species was the only one that increased its
362 abundance (number of rooting shoots) across the whole species richness gradient formed by
363 the others, reaching the highest biomass values and overyielding in many mixtures (Roscher
364 et al., 2007). The superiority of *A. elatius* could be explained by the exceptional growth form
365 of this grass that forms sterile leafy stalks with elevated meristems (Pfitzenmeyer, 1962).
366 Many grass species are characterized by a basal position of meristems on sterile shoots which
367 limits their potential for vertical light foraging by leaves (Grime and Mackey, 2002).

368 A rich literature exists on the effects of light quality and quantity on adaptive changes of
369 plant growth form. Gradients of light availability (photon flux density) and spectral light
370 quality are developed within closed canopies (Monsi and Saeki, 1953; Jones, 1992). Changes
371 in light quality perceived by phytochrome may control the activity of axillary buds, tillering
372 and the formation of reproductive shoots in grass species (Deregibus et al., 1985; Casal et al.,
373 1986). Abundance and height growth of the creeping legume *T. repens*, and the non-
374 leguminous herbs *A. sylvestris* and *G. pratense* with predominantly horizontal leaves were
375 affected negatively by species richness in our experiment. Plastic responses of individuals of
376 herbaceous plants established under canopy shade conditions may be less pronounced than in
377 individuals grown under sunlit conditions (McLaren and Smith, 1978). This effect could also
378 apply for *A. sylvestris* and *G. pratense*, whose establishment was delayed in the experimental
379 communities. Individuals often developed only basal rosettes. Radiation filtered by plant
380 canopies reduces branching frequency and the number of nodes in *T. repens* (Solangaarachchi
381 and Harper, 1987; Thompson and Harper, 1988; Markuvitz and Turkington, 2000) and other
382 stoloniferous species (Schmid, 1986) and would consequently lead to decreased abundances
383 of such species. Thus, light quality does not only induce shade-avoidance reactions. It is also
384 important for density regulation of plant populations and could be a reason why we found no
385 effect of species richness on the number of rooting shoots within mixtures.

386 Spehn et al. (2000) showed in another biodiversity experiment (Swiss site of BIODEPTH
387 study) that height growth of individuals of several species increased with increasing species
388 richness, while Dimitrakopoulos and Schmid (2004) and Mwangi et al. (2007) found little
389 effects of species richness on height growth. In our study species richness did not affect
390 maximum or mean height of individual species in a positive way. In contrast, height growth
391 of five out of nine species was affected negatively either by species richness or the presence
392 of *A. elatius* in mixtures. This result could be a consequence of species selection. Whereas

both potentially dominant and subordinate species occurred in the species pool of previous experiments, we only used potential dominants that proved to have a low ability for adaptive morphological changes in response to vegetation shade.

Recently Yachi and Loreau (2007) presented a model of light competition in multi-species plant communities. They emphasized the importance of competitive balance among species for a positive net effect of complementary resource use. In our experiment, the most competitive species, *A. elatius*, and increasing species richness had negative effects on inferior species. However, the beneficial effects of competitive release for *A. elatius* itself in mixtures with interspecific neighbors overcompensated for negative effects of competitive imbalance on some species, while other species showed little response to species richness. In conclusion, changes in vertical niche occupation in mixtures are either the result of competitive release for the superior species or of competitive suppression. These effects lead to an enhanced and complementary use of available space at the community level although the potential for alternative strategies of light exploitation appeared to be limited among potentially dominant species.

Acknowledgements

This study was funded by grants from the German Science Foundation (FOR 456) and the Swiss Science Foundation (grant no. 31-65224-01) with support by the Friedrich Schiller University of Jena and the Max Planck Society. E. Machalett, S. Manthej, S. Müller and C. Pfister assisted with data collection in the field. We gratefully acknowledge M. Scherer-Lorenzen for cooperation. Special thank to the gardeners S. Eismann, O. Foitzik, S. Junghans, B. Lenk, H. Scheffler and U. Wehmeier and numerous student helpers for their careful management of the experimental plots.

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590

591 **Appendix**

592 The number of plots entering in different levels of the ANOVA is not equal because all
593 species-richness levels were studied in August and data in monocultures, two- and nine-
594 species mixtures only were recorded in May. The main effects (monoculture vs. mixture,
595 presence of *A. elatius*, species richness as log-linear term) were tested across all species
596 richness-levels (including monocultures, 2-, 3-, 4-, 6- and 9-species mixtures). This part of the
597 analysis comprises 103 plots (= 100 different compositions because we analysed 4 identical
598 replicates of the 9-species mixture) in total. The total number of compositions (= 100) served
599 as error term. The analysis of seasonal effects is complicated because not all compositions
600 were measured in May. Thus, 49 plots (= 46 different compositions because we analysed 4
601 identical replicates of the 9-species mixture) had data for May and August, whereas the
602 remaining ones only had data for August. As a consequence of this imbalance, the effects of
603 "season" and their interaction with the diversity treatments appear at different levels of the
604 ANOVA table. According to Heiberger (1989) we used the lower level of appearance of these
605 variables to test for significance. Nevertheless, the appearance of these variables affects the
606 mean squares of the error term at the upper level. We excluded these terms from the upper
607 level. The variable height "stratum" was fitted as linear term and as deviation from linearity
608 (factor). It has seven factor levels according to the following height strata: 0–5 cm, 5–10 cm,
609 10–20 cm, 20–30 cm, 30–50 cm, 50–70 cm, >70 cm. Mean values per height level were used
610 for the linear term (2.5, 7.5, 15.0, 25.0, 40.0, 60.0, 100.0). The effects were tested across all
611 species-richness levels (including monocultures, 2-, 3-, 4-, 6- and 9-species mixtures). The
612 mean squares of the error terms (C1, C2, C3) of the different analysis strata were calculated in
613 the hierarchical ANOVA with treatment and error model (see e.g. Schmid et al. 2002). The
614 residuals come from the use of 4 (out of 8) identical replicates of the 9-species mixtures
615 (during each sampling campaign), while we did not analyse identical replicates of the other
616 mixtures (= compositions).

Table S1: Skeleton analysis of variance for community and species data analyzed at stand level (center) or at the level of vertical height strata (right); (a) degrees of freedom (d.f.) for analyses of community data, (b) d.f. for analyses of species data. For the analysis on the right d.f.s for terms including height stratum were lower for species which did not occur in all strata.

	Stand analysis				Strata level analysis			
Source of variation	d.f. (a)	d.f. (b)	Mean square	Variance ratio	d.f. (a)	d.f. (b)	Mean square	Variance ratio
Mixture (M)	1	1	MS_M	MS_M/MS_{C1}	1	1	MS_M	MS_M/MS_{C1}
Presence of *Arrhenatherum elatius* (Ae)	1	1	MS_{Ae}	MS_{Ae}/MS_{C1}	1	1	MS_{Ae}	MSA_e/MS_{C1}
Species richness (log-linear) (SR)	1	1	MS_{SR}	MS_{SR}/MS_{C1}	1	1	MS_{SR}	MS_{SR}/MS_{C1}
Composition (C1)	96	30	MS_{C1}		96	30	MS_{C1}	
Season (S)	1	1	MS_S	MS_S/MS_{C2}	1	1	MS_S	MS_S/MS_{C2}
Mixture x Season (M x S)	1	1	MS_{MxS}	MS_{MoxS}/MS_{C2}	1	1	MS_{MxS}	MS_{MxS}/MS_{C2}
A. elatius x Season (Ae x S)	1	1	MS_{AexS}	MS_{AexS}/MS_{C2}	1	1	MS_{AexS}	MS_{AexS}/MS_{C2}
Species richness (log-linear) x Season (SR x S)	1	1	MS_{SRxS}	MS_{SRxS}/MS_{C2}	1	1	MS_{SRxS}	MS_{SRxS}/MS_{C2}
Composition (C2) (nested within season)	41	6	MS_{C2}		41	6	MS_{C2}	
Stratum (H1) as linear contrast					1	1	MS_{H1}	MS_{H1}/MS_{C3}
Stratum (H2) as deviation from linearity					5	≤ 5	MS_{H2}	MS_{H2}/MS_{C3}
Mixture x stratum (linear) (M x H1)					1	1	MS_{MxH1}	MS_{MxH1}/MS_{C3}
Mixture x stratum (deviation from linearity) (M x H2)					5	≤ 5	MS_{MxH2}	MS_{MxH2}/MS_{C3}
A. elatius x stratum (linear) (Ae x H1)					1	1	MS_{AexH1}	MS_{AexH1}/MS_{C3}
A. elatius x stratum (deviation from linearity) (Ae x H2)					5	≤ 5	MS_{AexH2}	MS_{AexH2}/MS_{C3}
Species richness (log-linear) x stratum (linear) (SR x H1)					1	1	MS_{SRxH1}	MS_{SRxH1}/MS_{C3}
Species richness (log-linear) x stratum (deviation from linearity) (SR x H2)					5	≤ 5	MS_{SRxH2}	MS_{SRxH2}/MS_{C3}
Season x stratum (linear) (S x H1)					1	1	MS_{SxH1}	MS_{SxH1}/MS_{C3}
Season x stratum (deviation from linearity) (S x H2)					5	≤ 5	MS_{SxH2}	MS_{SxH2}/MS_{C3}
Composition (C3) (nested within season and stratum)					840	≤ 234	MS_{C3}	
Residuals	6	6	MS_R		42	42	MS_R	

Table 1: Effects of species richness and season on horizontal density and measures of vertical stand architecture of entire plant communities and of individual species within these mixtures.
Listed are F ratios and the levels of significance, where *: $P \leq 0.05$, **: $P < 0.01$, and ***: $P < 0.001$. Arrows indicate significant increase (↑) or decrease (↓) of the measures in mixtures compared with monocultures (M), in mixtures with compared with mixtures without *A. elatius* (Ae) or with a logarithmic increase in species richness (SR). M after season means significantly higher values of the measure in May than in August.

	Community	*A. pratensis*	*A. sylvestris*	*A. elatius*	*D. glomerata*	*G. pratense*	*P. pratense*	*P. trivialis*	*T. pratense*	*T. repens*
Horizontal density (line transect data)										
Mixture (M)	7.26** ↑	<0.01	2.32	0.13	3.15	1.11	0.05	0.10	0.14	0.89
Presence *A. elatius* (Ae)	25.86*** ↑	2.33	0.59		0.20	0.31	0.80	0.11	9.07** ↓	12.92*** ↓
Species richness (SR)	0.01	0.07	5.37* ↓	9.25** ↑	3.46	0.29	0.11	2.43	2.45	0.71
Cumulative cover (point intercept data)										
Mixture (M)	15.92*** ↑	0.03	18.35*** ↓	11.92** ↑	2.00	9.75** ↓	0.44	<0.01	0.18	1.99
Presence *A. elatius* (Ae)	37.77*** ↑	0.01	0.81		1.02	4.79* ↓	2.61	1.45	6.89* ↓	25.49*** ↓
Species richness (SR)	1.73	2.29	3.28	15.18*** ↑	13.32*** ↑	2.86	2.54	4.32** ↓	0.02	2.38
Season	67.94*** M	9.95* M	0.16	16.39*** M	0.55	0.22	217.53*** M	162.44*** M	9.95* M	11.77* M
M x Season	2.29	0.66	<0.01	1.82	0.20	<0.01	14.14**	0.04	0.17	0.14
Ae x Season	0.09	0.01	0.11		2.65	1.27	72.17***	12.12*	0.14	1.32
SR x Season	0.05	2.90	<0.01	10.22*	15.95**		16.59**	4.42	0.02	0.06
Maximum height										
Mixture (M)	6.84**↑	2.24	6.95* ↓	0.57	1.35	5.44* ↓	0.54	1.27	1.79	2.10
Presence *A. elatius* (Ae)	84.00***↑	0.21	0.74		0.05	1.63	1.80	0.05	2.80	26.32*** ↓
Species richness (SR)	7.65**↑	16.05*** ↓	7.33* ↓	2.09	1.62	3.92	0.80	5.68* ↓	0.57	2.48
Season	80.69***M	106.70***M	0.21	73.11*** M	1175.35*** M	0.38	205.92*** M	78.59*** M	2.08	30.81*** M
M x Season	0.06	1.23	0.02	2.13	12.22*	0.06	1.84	0.28	0.29	0.07
Ae x Season	1.62	3.79	0.02		<0.01	0.71	2.77	5.42	10.54*	4.80
SR x Season	0.06	0.13	0.15	0.04	2.95		3.17	1.84	2.49	0.22
Mean height										
Mixture (M)	2.17	1.69	5.82* ↓	<0.01	1.23	4.87* ↓	0.24	0.89	0.31	1.22

Presence *A. elatius* (Ae)	62.12***↑	0.19	0.88		0.13	2.18	0.55	<0.01	6.18* ↓	13.79*** ↓
Species richness (SR)	11.50***↑	9.98** ↓	6.55* ↓	0.14	1.42	5.40* ↓	0.80	4.28* ↓	2.30	1.18
Season	92.55***M	228.74***M	0.34	151.26*** M	729.50***M	0.54	372.06*** M	59.01*** M	17.69** M	14.73** M
M x Season	0.19	2.01	0.04		0.16	0.04	0.07	0.42	11.43*	0.44
Ae x Season	0.33	3.87	0.04	0.23	7.80*	0.12	3.46	5.24	12.70*	4.00
SR x Season	<0.01	0.32	0.23	1.01	0.19		0.47	0.93	4.44	0.03

Table 2: Effects of species richness, season and height stratum on vertical density of the community and of individual species.
Listed are F ratios and the levels of significance, where *: $P \leq 0.05$, **: $P < 0.01$, and ***: $P < 0.001$. Arrows indicate significant increase (↑) or decrease (↓) of the measures in mixtures compared with monocultures (M), in mixtures with compared with mixtures without *A. elatius* (Ae) or with a logarithmic increase in species richness (SR). M after season means significantly higher values of the measure in May than in August.

	Community	*A. pratensis*	*A. sylvestris*	*A. elatius*	*D. glomerata*	*G. pratense*	*P. pratense*	*P. trivialis*	*T. pratense*	*T. repens*
Strata-level interval density										
Mixture (M)	13.21** ↑	0.22	16.95*** ↓	6.52* ↑	0.07	17.09*** ↓	<0.01	0.27	0.64	3.38
A. elatius (Ae)	79.89*** ↑	1.04	0.85		1.88	5.64* ↓	3.77	0.98	8.25** ↓	30.85*** ↓
Species richness (SR)	6.21* ↑	8.53** ↓	4.68* ↓	3.91	1.88	3.58	0.27	2.32	0.63	4.25* ↓
Season (S)	142.48*** M	51.03***	0.07	35.17*** M	48.18*** M	<0.01	228.85*** M	264.46*** M	15.95** M	26.15** M
M x Season	3.99	0.41	<0.01	1.40	0.06	0.01	6.43*	0.17	0.70	0.10
Ae x Season	0.08	1.90	0.12		4.27	0.70	8.17*	17.13**	0.44	2.63
SR x Season	0.01	2.20	0.04	17.47**	6.02*		15.02**	1.33	0.01	0.31
Stratum (linear) (H1)	1420.28***	322.88***	11.47***	192.44***	870.86***	12.85***	300.83***	179.64***	196.56***	271.73***
Stratum (deviation from linearity) (H2)	40.58***	30.28***	0.35	56.32***	56.76***	6.96***	12.30***	17.64***	15.22***	4.28**
M x Stratum (linear) (H1)	3.77	3.09	21.61*** ↓	1.02	7.82** ↑	3.72	0.57	0.37	0.14	4.31* ↓
M x Stratum (deviation from linearity) (H2)	0.97	0.06	3.49	0.29	0.66	0.37	0.18	0.19	0.20	0.28
Ae x Stratum (linear) (H1)	46.57*** ↑	1.19	0.71		6.01* ↑	3.50	20.32*** ↑	0.66	8.19** ↓	68.51*** ↓
Ae x Stratum (deviation from linearity) (H2)	33.01***	2.38*	0.41		2.29*	0.38	3.04*	0.40	0.73	1.30
SR x Stratum (linear) (H1)	28.76*** ↑	0.02	4.73* ↓	2.13	21.81*** ↑	1.33	5.57* ↑	16.25*** ↓	0.07	5.56* ↓
SR x Stratum (deviation from linearity) (H2)	6.30***	1.00	0.21	0.97	3.60**	1.06	1.85	0.90	1.50	0.15
S x Stratum (linear) (H1)	151.78***	78.74***	0.24	300.86***	277.89***	0.47	63.24***	50.33***	0.04	1.28
S x Stratum (deviation from linearity) (H2)	18.44***	13.61***	0.90	9.35***	37.18***	0.35	53.85***	8.43***	0.68	5.92***

Table 3: Differences of mean height (MH) for each species pair. Values are based on data recorded in monocultures, two- and nine-species mixtures in May 2003. Differences between species monocultures were used to compare average height differences between species in mixture. Negative values indicate that species in the respective column achieved a lower mean height in comparison to the species in the respective row. Asterisks indicate significant differences between monocultures and mixtures (*: $P \leq 0.05$, **: $P < 0.01$; t-tests). Arrows show significant increase (↑) or decrease (↓) of the measures in mixtures compared to monocultures.

	A. elatius	*A. pratensis*	*D. glomerata*	*P. pratense*	*G. pratense*	*P. trivialis*	*T. pratense*	*T. repens*
Alopecurus pratensis								
Monoculture	0.57							
Mixture	31.72* ↑							
Dactylis glomerata								
Monoculture	4.65	4.08						
Mixture	21.65* ↑	-9.15						
Phleum pratense								
Monoculture	8.40	7.83	3.75					
Mixture	21.18* ↑	-10.23* ↓	-0.16					
Geranium pratense								
Monoculture	19.09	18.52	14.44	10.69				
Mixture	54.74* ↑	18.07	31.15** ↑	28.48** ↑				
Poa trivialis								
Monoculture	25.65	15.08	21.01	17.25	6.57			
Mixture	34.14	6.21	14.73	14.47	-12.46			
Trifolium pratense								
Monoculture	27.55	26.98	22.90	19.15	8.46	1.89		
Mixture	43.69	11.97* ↓	22.07	21.07	-10.64** ↑	8.25		
Trifolium repens								
Monoculture	30.97	30.39	26.32	22.57	11.88	5.31	3.42	
Mixture	52.39* ↑	19.03	29.64	29.35	1.38* ↓	16.22	10.83	
Anthriscus sylvestris								
Monoculture	35.22	34.65	30.57	26.82	16.13	9.56	7.67	4.25
Mixture	56.41* ↑	27.00	35.58	35.79** ↑	5.41** ↓	21.24* ↑	12.72	4.11

Figure captions

Figure 1: Number of rooting shoots as function of species richness (log-scale). Plots with *A. elatius* are shown with filled circles; plots without *A. elatius* are shown with open circles. The lines connect arithmetic means calculated for each species-richness level (solid line = plots with *A. elatius*, broken line = plots without *A. elatius*).

Figure 2: Cumulative cover (a, b), maximum height of pin contacts (c, d), and mean height of pin contacts (e, f) recorded in May (left panel) and August 2003 (right panel) as a function of species richness (log-scale). Plots with *A. elatius* are shown with filled circles; plots without *A. elatius* are shown with open circles. The lines are arithmetic means for all assemblages per diversity level (solid line = plots with *A. elatius*, broken line = plots without *A. elatius*).

Figure 3: Vertical density (number of pin contacts per 5-cm height layer per pin) for the three species-richness levels measured both in May (a) and August 2003 (b): monocultures = dotted lines, two-species-mixtures = broken lines, nine-species-mixtures = solid lines. Horizontal lines show average mean height.

Figure 4: Vertical density (number of pin contacts per 5-cm height layer per pin, corrected for reduced species proportions in mixtures by multiplication with species richness) for individual species in May: monocultures = dotted lines, two-species mixtures = broken lines, nine-species mixtures = solid lines. Horizontal lines show average mean height.

Figure 5: Species mean height in mixtures plotted against species mean height in monoculture for data recorded in May in monocultures, two- and nine-species mixtures. Points above the

broken line indicate cases where individual species obtained larger mean heights in mixtures than in monoculture.

Abbreviations of species names: ae = *Arrhenatherum elatius*, ap = *Alopecurus pratensis,* as = *Anthriscus sylvestris*, dg = *Dactylis glomerata*, gp = *Geranium pratense*, pp = *Phleum pratense*, pt = *Poa trivialis*, tp = *Trifolium pratense*, tr = *Trifolium repens.*

Figure 1

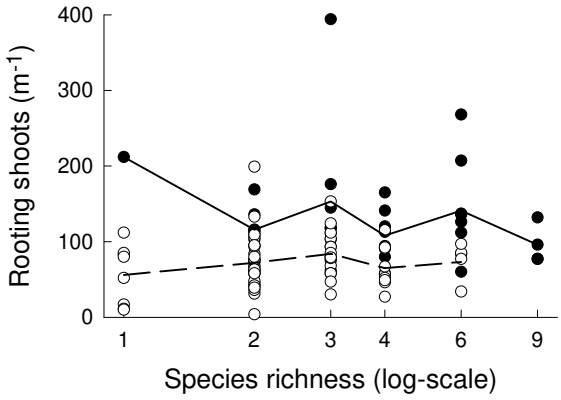

400
300
200
100
0
Rooting shoots (m-1)
1
2
3
4
6
9
Species richness (log-scale)

Figure 2

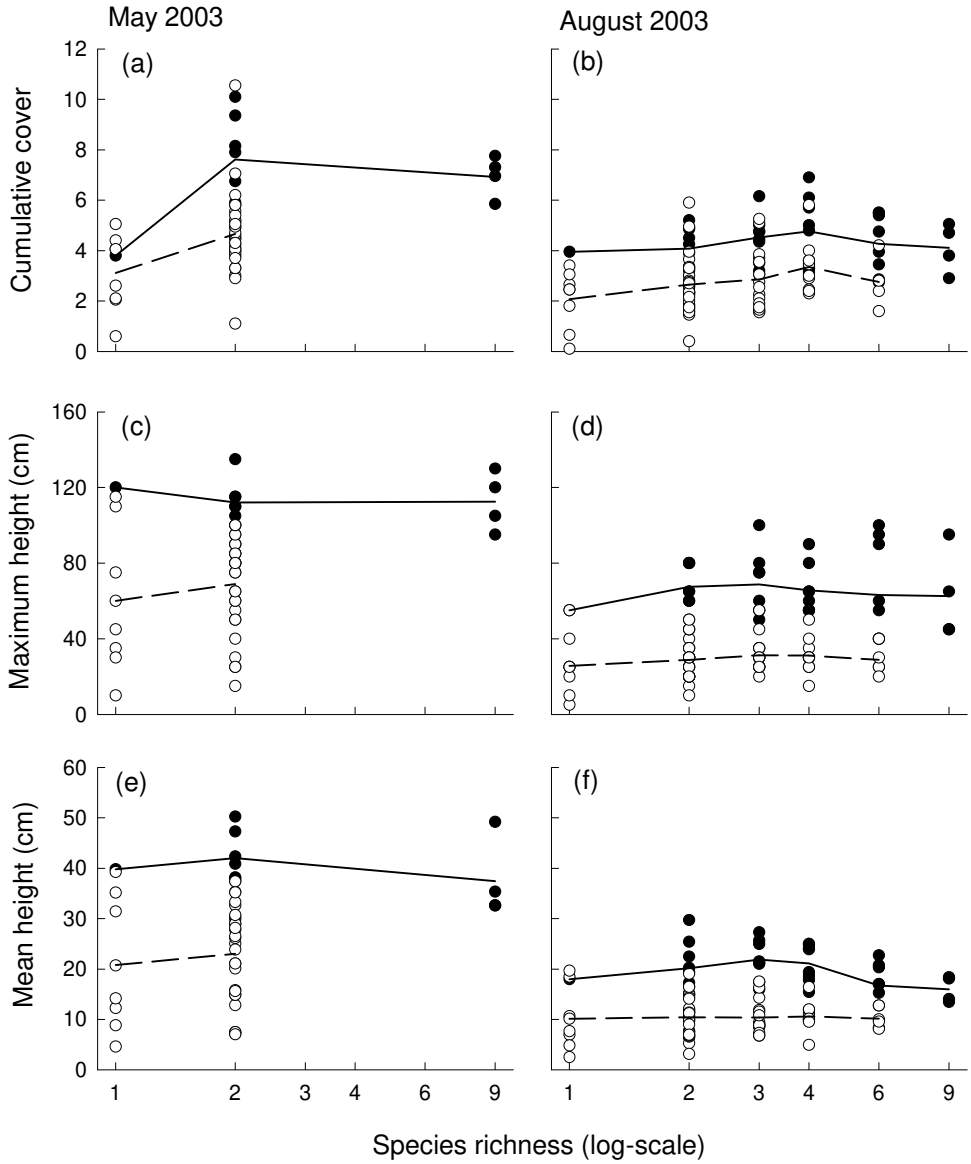

May 2003
August 2003
(a)
(b)
(c)
(d)
(e)
(f)
Cumulative cover
Maximum height (cm)
Mean height (cm)
Species richness (log-scale)
0
2
4
6
8
10
12
40
80
120
160
10
20
30
40
50
60
1
2
3
4
6
9

Figure 3

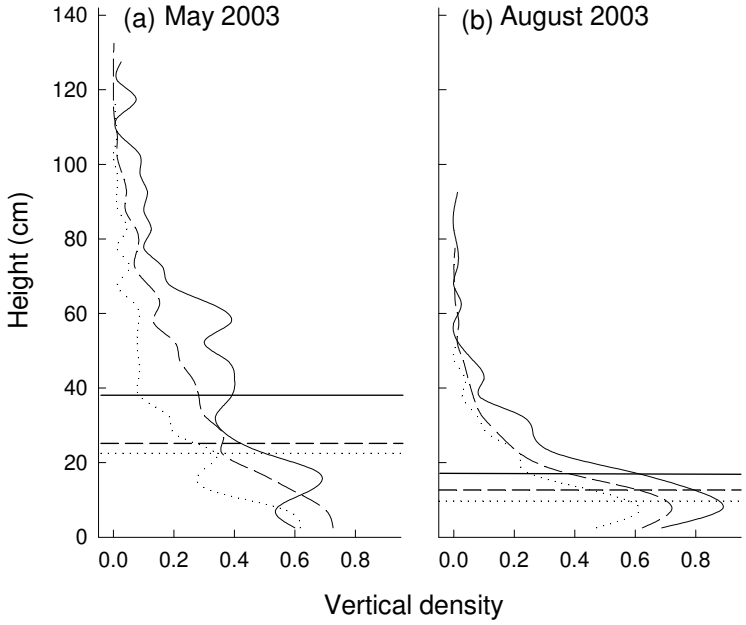

(a) May 2003
(b) August 2003
Height (cm)
140
120
100
80
60
40
20
0
0.0
0.2
0.4
0.6
0.8
Vertical density

Figure 4

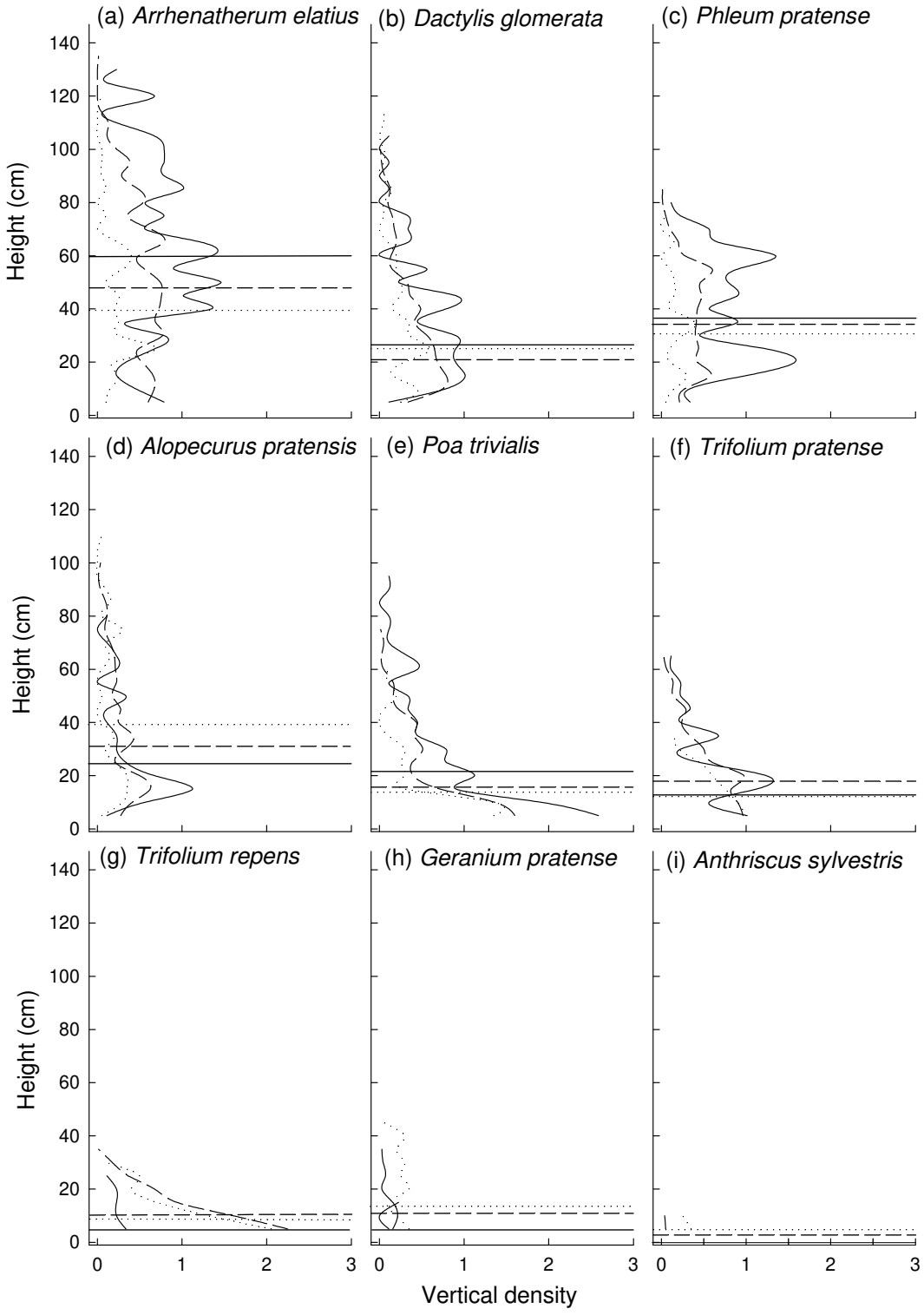
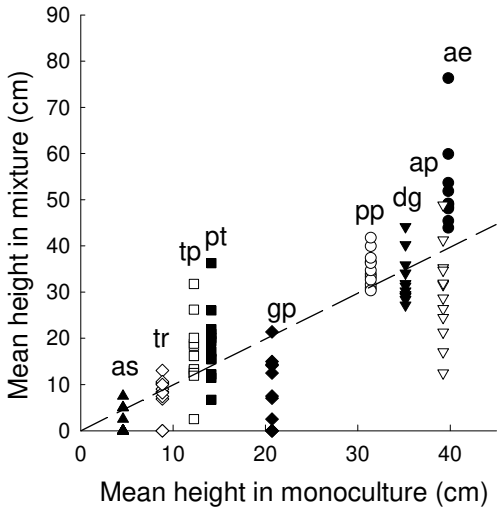

(a) Arrhenatherum elatius
(b) Dactylis glomerata
(c) Phleum pratense
(d) Alopecurus pratensis
(e) Poa trivialis
(f) Trifolium pratense
(g) Trifolium repens
(h) Geranium pratense
(i) Anthriscus sylvestris
Height (cm)
Vertical density
0
20
40
60
80
100
120
140
1
2
3

Figure 5


Mean height in mixture (cm)
Mean height in monoculture (cm)
0
10
20
30
40
50
60
70
80
90
as
tr
tp
pt
gp
pp
dg
ap
ae