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Bessler, H; Temperton, V M; Roscher, C; Buchmann, N; Schmid, B; Schulze, E D; Weisser, W W; Engels, C

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1   Running head: Overyielding and biomass partitioning

2

3   **ABOVEGROUND OVERYIELDING IN GRASSLAND MIXTURES IS ASSOCIATED**

4   **WITH REDUCED BIOMASS PARTITIONING TO BELOWGROUND ORGANS**

5

6   Holger Bessler[1], Vicky M. Temperton[2,3], Christiane Roscher[2], Nina Buchmann[4], Bernhard

7   Schmid[5], Ernst–Detlef Schulze[2], Wolfgang W. Weisser[6] and Christof Engels[1,7]

8

9   [1]Institute of Plant Nutrition, Humboldt–University Berlin, Unter den Linden 6, D–10099 Berlin,

10   Germany

11   [2]Max Planck Institute for Biogeochemistry, PO Box 100164, D–07749 Jena, Germany

12   [3]Phytosphere Institute ICG3, Forschungszentrum Jülich, Leo–Brandt–Str., D–52428 Jülich,

13   Germany

14   [4]Institute of Plant Sciences, ETH Zurich, Universitaetsstr. 2, CH–8092 Zurich, Switzerland

15   [5]Institute of Environmental Sciences, University of Zurich, Winterthurerstrasse 190, CH–8057

16   Zurich, Switzerland

17   [6]Institute of Ecology, University of Jena, Dornburger Str. 159, D–07749 Jena, Germany

18   [7] E–mail: christof.engels@agrar.hu–berlin.de

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Abstract.   We investigated effects of plant species richness in experimental grassland plots on annual above- and belowground biomass production estimated from repeated harvests and in-growth cores, respectively. Aboveground and total biomass production increased with increasing plant species richness while belowground production remained constant. Root to shoot biomass production ratios (R/S) in mixtures were lower than expected from monoculture performance of the species present in the mixtures, showing that interactions among species led to reduced biomass partitioning to belowground organs. This change in partitioning to belowground organs was not confined to mixtures with legumes, but also measured in mixtures without legumes, and correlated with aboveground overyielding in mixtures. It is suggested that species-rich communities invest less into belowground biomass than do monocultures to extract soil resources, thus leading to increased investment into aboveground organs and overyielding.

Key words: Aboveground productivity, belowground productivity, biodiversity, grasslands, plant functional group richness, plant functional group identity, root/shoot ratio, Jena Experiment

38   INTRODUCTION

39   Most biodiversity experiments in grassland ecosystems report increased aboveground biomass

40   production with increasing plant species richness (e.g. Tilman et al. 2001, Niklaus et al. 2001,

41   Spehn et al. 2005, Roscher et al. 2005, van Ruijven and Berendse 2005, Balvanera et al. 2006).

42   This positive biodiversity effect on aboveground productivity has been related to so-called

43   selection and complementarity effects which can be separated statistically by the additive

44   partitioning method developed by Loreau and Hector (2001). Mechanistically, the selection

45   effect is explained by a large contribution to mixture productivity of species with high

46   productivity in monoculture, leading to a potential sampling effect if such species are more often

47   included in more diverse mixtures (Huston 1997). The complementarity effect is explained by

48   niche complementarity or facilitative interactions among species (Tilman 1997). However,

49   despite clear statistical evidence for complementarity effects (Hooper et al. 2005, Spehn et al.

50   2005, Cardinale et al. 2007), evidence for the implied mechanisms of niche complementarity or

51   facilitation is still lacking. It has been proposed that niche complementarity or facilitation may

52   occur because species differ in resource uptake in time, space or chemical form (Kahmen et al.

53   2006, von Felten et al., revised version under review at Ecology [Nr. 08-0802R]) or because they

54   may provide each other with resources (e.g. nitrogen in the case of legumes; Temperton et al.

55   2007) or protection against biotic and abiotic stress factors (Spehn et al. 2005, Kahmen et al.

56   2005).

57   Previous studies focusing on detailed measurement of biomass production in temperate

58   grasslands found that 24–87 % of net primary production can be allocated to belowground plant

59   organs (Sims and Singh 1978, Stanton 1988). In addition to their contribution to net primary

60   production, belowground organs are an important source for organic carbon input into the soil,

61   and thus, for the regulation of heterotrophic soil organisms and soil carbon sequestration.

62   Therefore, it is important to include measurements of belowground biomass production in plant

63   biodiversity experiments to be able to assess the diversity-productivity relationship, and to

64   improve understanding of the mechanisms by which plant biodiversity affects abiotic and biotic

65   soil factors.

66   Studies on the effect of plant biodiversity on belowground productivity have shown

67   contrasting results. In some studies, belowground biomass increased with increasing species

68   richness (Tilman et al. 2001, Reich et al. 2001, Craine et al. 2003, Dimitrakopoulos and Schmid

69   2004) whereas in other studies plant species and functional group diversity did not have

70   significant effects on belowground biomass under natural conditions (Hooper 1998, Wardle et al.

71   1999, Spehn et al. 2000a, Niklaus et al. 2001, He et al. 2002, Gastine et al. 2003, but see Kahmen

72   et al. 2005 for drought response). One possible reason for the contrasting results is the

73   methodological difficulty to measure belowground productivity. In most of these studies,

74   belowground productivity was estimated from measurements of the stock of living and dead

75   belowground biomass in soil cores sampled once or several times per year. However, the stock

76   of living and dead belowground biomass is dependent on belowground biomass production, as

77   well as on longevity and turnover of belowground organs. Root longevity and turnover may

78   substantially vary among species and grassland communities (Gill and Jackson 2000), and are

79   also affected by abiotic and biotic soil factors (Eissenstatt et al. 2000). Therefore, data on the

80   stock of root biomass give only a rough estimate of belowground biomass production.

81   Another possible reason for the contrasting results and the differences in biodiversity effects

82   on above- and belowground productivity is that biomass partitioning between roots and shoots

83   may change with species richness. Biomass partitioning between roots and shoots has been

84   shown to depend on a number of exogenous factors such as light intensity, soil moisture, mineral

85   nutrient availability and on endogenous factors such as plant developmental stage and genotype

86   (e.g., Wilson 1988, McConnaughay and Coleman 1999, Kahmen et al. 2005). Niche

87   complementarity among species should lead to higher supply of individuals with soil resources

88   in diverse plant communities, in which the probability that the neighbour occupies another niche

89   is higher. The theory of functional equilibrium between shoot and roots predicts that better

90   supply with soil resources would lead to lower biomass partitioning to belowground organs

91   (Brouwer 1983, Bloom et al. 1985). In addition, the effect of presence and identity of neighbors

92   on biomass partitioning of target plants is of particular relevance. In this case, biomass allocation

93   to roots and shoots may be related to resource competition or other factors (Callaway et al. 2003,

94   Ninkovic 2003). Evidence from biodiversity experiments themselves indicates that root/shoot

95   biomass ratios in grassland communities can be affected by species evenness (Wilsey and Potvin

96   2000), the identity of species and functional groups present in the communities (Hooper 1998,

97   Wardle et al. 1999, Wardle and Peltzer 2003, Olson and Blicker 2003), or by community density

98   and species richness (He et al. 2005).

99   In this study the effect of species richness on the annual production of above- and

100 belowground biomass in grassland was measured in a biodiversity experiment characterized by

101 an orthogonal design for the presence and absence of four functional groups and large plot sizes

102 ("Jena Experiment" in Germany, Roscher et al. 2004). We used the most detailed measurements

103 of annual belowground biomass production so far to address the following hypothesis:

104 belowground productivity is not influenced by species richness in spite of a positive relationship

105 between species richness and aboveground productivity. This hypothesis is based on the

106 assumption that in species-rich communities the availability of soil resources to plants is

107   increased due to niche complementarity, thus leading to lower biomass partitioning to

108   belowground organs.

109

110   MATERIALS AND METHODS

111   *Study site*

112   The field experiment was located on the floodplain of the river Saale in Jena (Thuringia,

113   Germany, 51°N, 11°E, 135 m a.s.l.). Mean annual air temperature was 9.3 °C, and average

114   annual precipitation was 587 mm. The soil of the experimental site was an Eutric Fluvisol

115   (FAO–Unesco 1997) developed from up to 2-m thick loamy fluvial sediments that were almost

116   free of stones. The experimental site was 100–400 m away from the river. Close to the river, the

117   topsoil consisted of sandy loam, gradually changing into a silt loam with increasing distance

118   from the river. The seasonal depth of water table varied during the experimental period from 0.7

119   m to 2.6 m below surface in (Kreutziger 2006). The site was converted from grassland into

120   arable land in the early 1960s and was used as an arable field for the last 40 years prior to the

121   experiment. Further details of the field site are provided in Roscher et al. (2004).

122

123   *Experimental design*

124   In the Jena Experiment, plant species richness (1, 2, 4, 8, 16 plant species) and plant

125   functional diversity (1, 2, 3, 4 plant functional groups) of experimental grassland stands were

126   varied in a factorial design (Table 1). Sixty plant species were selected from semi-natural

127   species-rich mesophilic grassland common in the regional grassland vegetation. Species were

128   classified into four plant functional groups based on multivariate analysis of 17 traits (Roscher et

129   al. 2004). Two of these functional groups coincided with the well-known functional groups

130   grasses and legumes, the other two could be referred to as small herbs and tall herbs. Species

131   from each functional group were randomly selected to compose monocultures and mixtures

132   according to the factorial design (Table 1). All experimental communities were established in

133   May 2002 by sowing seeds to obtain 1000 seedlings m^{-2}, distributed equally among the species

134   within a community. Plot size was 20 x 20 m. All 60 species sown in the experimental

135   communities were also planted in monoculture on 3.5 x 3.5 m plots. To maintain designed

136   species compositions and richness levels as far as possible all plots were weeded regularly. The

137   plots were mown twice per year (June and September) and the cut biomass was removed

138   (Roscher et al. 2004).

139

140   *Data collection*

141   In principle, there are two direct methods for estimation of the annual belowground biomass

142   production (roots and rhizomes, collectively referred to as roots in the following), (i)

143   measurement of the change of root biomass and necromass during the growing season by

144   sequential coring or (ii) measurement of root in-growth into root free soil zones. In this study the

145   in-growth core technique was used since this method allows assessment of root production when

146   standing root biomass is in equilibrium (i.e. no net change of root biomass and necromass).

147   Furthermore, this method avoids the problem sorting live and dead roots. Since conditions in in-

148   growth cores differ from those in undisturbed soil (e.g. rooting density), it is important to note

149   that the in-growth core method may over- or underestimate actual root production. However, it is

150   assumed that over- or underestimation is similar in all experimental stands. Annual belowground

151   biomass production for all plots (Table 1) was measured by adding up production from June–

152   September 2003 and from September 2003–July 2004. In June 2003, five randomly located soil

153   cores (0.048 m diameter x 0.30 m depth) per plot were removed with a stainless steel corer

154   guided in a tripod. The removed soil was replaced by sieved root-free soil from the field site and

155   care was taken to match the bulk soil density. The root biomass growing into these initially root-

156   free in-growth cores was measured after removing the in-growth cores in September 2003. After

157   withdrawal of the in-growth cores, the holes were re-filled with root-free soil, and the in-growth

158   cores were sampled again in July 2004. For the extraction of roots from the in-growth cores, the

159   cores were cut with scissors until root fragments were less than 1 cm in length. Then the soil was

160   carefully mixed and weighed before taking a subsample of 50 g. The soil was removed from the

161   roots by rinsing over a sieve with 0.5 mm mesh width. Then, organic debris and remaining soil

162   particles were removed. The remaining root biomass was dried at 70 °C and weighed. Separation

163   of roots into plant species using morphological criteria was not possible. Therefore measured

164   annual belowground biomass production represents roots formed by the target plant species

165   community but also by accidental weeds which were not immediately removed by weeding

166   campaigns.

167   Annual aboveground biomass production for all plots (Table 1) was measured by adding up

168   production from June to September 2003, and from September 2003 to June 2004. Aboveground

169   biomass was cut 3 cm above ground on four randomly selected sample areas of 0.2 x 0.5 m per

170   large plot. In small plots with monocultures only two such samples were harvested per plot.

171   Sampled aboveground plant material was sorted into biomass of each sown target species and

172   dead plant material before drying at 70 °C and weighing. In addition, annual aboveground

173   biomass production of non target species (weeds) was determined separately. For comparability

174   with measured belowground biomass production, aboveground biomass production included

175   weeds as well as target species. According to this calculation, on average 92 % of the reported

176   annual aboveground biomass production was formed by the target species in the communities.

177

178   *Data analysis*

179   To assess the effect of plant functional group identity on annual biomass production and

180   biomass partitioning between belowground and aboveground organs (termed R/S-ratio), we first

181   tested whether *a priori* defined plant functional groups (legumes, grasses, tall herbs, small herbs)

182   differed in the annual production of total, aboveground and belowground biomass or in the R/S-

183   ratio when grown in monocultures. Differences between plant functional groups were tested with

184   a one-way ANOVA and the Tukey test. Second, we tested the effect of the presence/absence of

185   each plant functional group on the annual biomass production and R/S-ratio in all experimental

186   communities of the Jena Experiment (see below for statistical method).

187   To assess the effect of plant species richness and plant functional group richness on annual

188   biomass production and the R/S-ratio, we used general linear models. Since plant species

189   richness and plant functional group richness were not fully orthogonal, sequential sum of squares

190   were used (Schmid et al. 2002). Consequently the order in which the terms were entered in the

191   model influenced the amount of variation explained by a term. The effect of the

192   presence/absence of each plant functional group was tested with separate models for each plant

193   functional group fitted after plant species richness and plant functional group richness.

194   To assess whether R/S-ratios in mixed plant communities were influenced by species

195   interactions, an expected R/S-ratio was calculated for each mixture from the measured R/S-ratio

196   of each component species in monoculture and the species contribution to the aboveground

197   biomass production in mixture according to the formula:

198
$$R/S_e = \sum_{i=1}^{n} R/S_{i,mono} \times \frac{S_{i,mix}}{S_{mix}} \ ,$$

199   where $R/S_{i,mono}$ is the R/S-ratio measured in monoculture of species i; $S_{i,mix}$ is the aboveground

200   biomass production of species i in the mixture and S_{mix} is the aboveground biomass production of

201   the mixture. If R/S-ratios are modified by interactions among species in mixtures, measured R/S-

202   ratios in mixtures should differ from expected R/S-ratios. We used a paired t-test to assess if this

203   difference was significantly larger or smaller than zero.

204   To test whether aboveground overyielding in mixtures was related to alterations of the

205   community-wide R/S ratio, aboveground overyielding was quantified in a more restrictive way,

206   by calculation of relative yield totals (RYT, Hector 1998). The relative yield (RY), i.e. a species'

207   aboveground biomass production in mixture divided by its aboveground biomass production in

208   monoculture, was calculated for each species. The RYT of a mixture is the sum of RYs of all

209   species growing in a mixture. Using this relative-yield approach, overyielding is indicated by

210   RYT > 1 (Hector et al. 2002). Alterations of the R/S-ratio in mixtures were quantified by the

211   quotient of measured/expected R/S-ratio. A quotient > 1 indicates higher relative biomass

212   partitioning to belowground organs in mixture than expected from component species in

213   monocultures. To test whether aboveground overyielding in mixtures was related to alterations

214   of biomass partitioning to belowground organs, the Spearman rank correlation between RYT and

215   the quotient of measured/expected R/S-ratio was calculated.

216

217   RESULTS

218   *Effect of plant functional group identity on annual biomass production and R/S-ratio in*

219   *monocultures*

220   In the monocultures, total annual biomass production tended to be higher for legumes and

221   grasses compared to small herbs (Table 2). The contribution of aboveground and belowground

222   organs to total annual biomass production was significantly affected by plant functional group.

223   Legumes had the highest annual aboveground biomass production but the lowest annual

224   belowground biomass production among the four plant functional groups. For legumes,

225   belowground biomass production was less than 50% of aboveground biomass production,

226   whereas for the other plant functional groups belowground biomass production was similar or

227   slightly higher than aboveground biomass production. Consequently, the ratio of annual

228   belowground production to annual aboveground production (R/S-ratio) of legumes was less than

229   half than that of grasses, tall herbs and small herbs.

230

231   *Effect of plant species richness on annual biomass production and R/S–ratio*

232   The annual total biomass production varied between 582 and 2321 g m^{-2} y^{-1} (Fig. 1a). The

233   annual aboveground biomass production varied between 337 and 1610 g m^{-2} y^{-1} (Fig. 1b). The

234   maximum total biomass and aboveground biomass that was produced annually in each level of

235   sown species diversity by specific plant communities was very similar among all levels of

236   diversity. However, on average of all plant communities, annual total biomass and aboveground

237   biomass production significantly increased with increasing species richness (Fig. 1a, b),

238   regardless whether species richness in the ANOVA was fitted prior to or after plant functional

239   group richness (Table 3). Plant functional group richness had a significant positive effect on

240   annual total biomass and aboveground biomass production when fitted prior to species richness

241   but not when fitted after species richness (Table 3). The annual total biomass production and

242   aboveground biomass production were decreased by the presence of small herbs, whereas the

243   presence of legumes increased annual aboveground biomass production (Table 3, model 3).

244   The annual belowground biomass production in 0–0.3 m soil depth varied between 168 and

245   1515 g m^{-2} y^{-1}. Annual belowground biomass production was not affected by sown species

246   richness and plant functional group richness (Fig. 1c, Table 3). The presence of legumes in the

247   plant communities negatively affected belowground biomass production, whereas grasses had a

248   positive effect on annual belowground biomass production (Table 3, model 3). The contribution

249   of annual belowground biomass production to annual total biomass production varied between

250   10 and 77 %. On average, 44 % of annual total biomass production was below ground for all

251   communities. The R/S ratio was negatively affected by plant species richness (Fig. 1d) and plant

252   functional group richness when these model terms were fitted first (Table 3). The negative

253   relationship between sown species richness and the R/S ratio was due to significant decreases in

254   mixtures in comparison to monocultures, whereas R/S ratios did not significantly differ among

255   the mixtures containing 2, 4, 8 or 16 species ($F_{1,51} = 0.61$; $P = 0.438$). The presence of legumes in

256   the plant communities decreased the R/S-ratio, whereas the presence of grasses increased the

257   R/S-ratio (Table 3, model 3).

258

259   *Test for possible mechanisms leading to reduced R/S ratios in mixtures*

260   The expected R/S ratio in mixtures was not significantly lower than the average R/S ratio in

261   monocultures (Table 4, $P = 0.527$, t–Test), indicating that mixtures were not dominated by

262   species with inherently low R/S ratios. The measured R/S ratio in mixtures was significantly

263   lower than the expected R/S ratio (Table 4). This indicates that in mixtures the biomass

264   partitioning to roots relative to biomass partitioning to shoots was reduced.

265   The R/S ratio of legumes grown in monocultures was significantly lower than that of other

266   plant functional groups (Table 2). Accordingly, the expected R/S ratios were lower in mixtures

267   containing legumes than in mixtures without legumes (Table 4). However, in mixtures

268   containing legumes, and in mixtures without legumes, the measured R/S ratios were lower than

269   the R/S ratios expected from the monoculture performance. This shows that species interactions

270   leading to reduced biomass partitioning to belowground organs in 0–0.3 m soil depth can not

271   only be explained with legume effects leading to additional nitrogen supply to non-legumes.

272

273   *Correlation between aboveground overyielding and reduction of R/S ratios*

274   The RYT of the mixtures varied from 0.4 to 2.7 (Fig. 2), showing that in some species

275   mixtures aboveground biomass production was lower (RYT < 1, "underyielding") and in some

276   mixtures it was higher (RYT > 1, "overyielding") than the sum of expected relative aboveground

277   yields of the component species. However, on average, the RYT was significantly larger than 1

278    $(1.31 \pm se\ 0.07; P<0.01)$. The quotient of measured/expected R/S ratio in mixtures varied

279   between 0.3 and 2.0, showing that in some species mixtures the biomass partitioning to

280   belowground organs (0–0.3 m soil depth) was lower and in some mixtures it was higher than

281   expected. There was a significant negative correlation between RYT and the quotient of

282   measured/expected R/S ratio $(r_s = -0.492; P < 0.01)$. To avoid problems with spurious

283   correlations between the two variables which both involved the same aboveground biomass

284   production data as component variable (mean of the four sample areas in which aboveground

285   biomass was harvested), RYT and the quotient of measured/expected R/S ratio were also

286   calculated from independent data sets (mean of two sample areas for the calculation of RYT, and

287   mean of two other sample areas for the calculation of measured/expected R/S ratio). However,

288   the correlation remained significant $(r_s = -0.308; P < 0.05)$. This indicates that with increased

289   aboveground overyielding biomass partitioning to belowground organs (0–0.3 m soil depth) was

290   continually reduced in comparison with monocultures.

291

292   DISCUSSION

293   *Effect of plant functional group identity on biomass production*

294   Under the environmental conditions of the Jena Experiment, both, biomass production, and

295   biomass partitioning between belowground and aboveground organs differed among plant

296   functional groups (Table 2). In monocultures, total biomass production was lowest for small

297   herbs. In accordance with the low productivity of small herbs in monocultures, the presence of

298   small herbs decreased total productivity and aboveground productivity of plant communities

299   (Table 3). Even if the monocultures were excluded from the analysis, and only mixed plant

300   communities are regarded, total productivity decreased with increasing proportion of small herbs

301   in aboveground biomass production ($r = -0.54$; $P < 0.001$). Little is known about plant traits

302   relevant to productivity which are common to this functional group except low canopy height

303   (Roscher et al. 2004). In mixed plant communities containing species with tall stature, low

304   canopy height of small herbs is associated with low light availability. Small herbs react to low

305   light availability in mixed plant communities by production of leaves with higher specific leaf

306   area and leaf area ratio (Daßler et al. 2008). However, in the Jena-Experiment, these

307   ecophysiological adaptations to low light availability did not lead to higher shoot biomass in

308   mixtures than expected from monocultures (Daßler et al. 2008). Annual belowground biomass

309   production was not significantly correlated with the proportion of small herbs in aboveground

310   biomass production ($r = -0.08$; $P = 0.568$). Furthermore, there is no evidence for lower rooting

311   depth of small herbs in monocultures (Bessler and Engels, unpublished results), and thus, lower

312   ability for foraging of soil resources.

313   Legumes had the highest annual aboveground productivity (Table 2), whereas total

314   productivity of legumes was not significantly higher than that of grasses, small and tall herbs.

315   Most legumes were actively fixing N_2 in our experiment (Temperton et al. 2007; Thein et al.

316   2008,), and their tissue N concentrations were markedly higher than those of non-legumes (data

317   not shown). However, the ability of legumes to obtain additional nitrogen from symbiotic N_2

318   fixation did not lead to higher productivity, presumably because in the initial phase after

319   conversion of fertilized crop land to non-fertilized grassland nitrogen was not limiting plant

320   growth.

321   In mixtures, increasing percentage of legumes was positively correlated with aboveground

322   productivity (r = 0.57; P < 0.001), but only a marginally positive correlation with total

323   productivity was found (r = 0.23; P = 0.094). The important role of legumes for control of

324   aboveground productivity in mixtures is supported by other studies (Tilman et al. 1997, Mulder

325   et al., 2002, Spehn et al. 2002, Lambers et al. 2004, Hooper and Dukes 2004, Palmborg et al.

326   2005). In mixed communities, legumes may improve nitrogen supply of non-legumes either due

327   to their lower competitive ability for nitrogen uptake from soil, or transfer of symbiotically fixed

328   N_2 (Corre-Hellou et al. 2006, Temperton et al. 2007, von Felten et al., revised version under

329   review at Ecology [Nr. 08-0802R]). In our study, the proportion of legumes in aboveground

330   biomass was negatively correlated with belowground productivity (r = –0.47; P < 0.001) and

331   R/S-ratio (r = –0.62; P < 0.001). This shows that also the high biomass partitioning to

332   aboveground organs is contributing to the positive effect of legumes on aboveground

333   productivity. This indicates that the role of legumes for total productivity is overestimated from

334   measurements of aboveground productivity only.

335

336   *Effect of plant species richness on annual biomass production*

337   In this study, we observed that annual aboveground and total biomass production significantly

338   increased with species richness (Fig. 1 a, b) and plant functional group richness (Table 3). This is

339   consistent with results from other experiments (e.g. Tilman et al. 1997; Spehn et al. 2005), and

340   the positive relationship between plant species richness and aboveground biomass production

341   found at our study site in the first year after plot establishment (Roscher et al. 2005), where

342   weeds and belowground parts were not included in the biomass production measurements. The

343   species richness effect on aboveground and total biomass production was significant despite the

344   large variability among our plots containing communities with different species or functional-

345   group compositions. Differences in productivity among communities of the same species-

346   richness level but with different species or functional-group composition are typically observed

347   in biodiversity experiments (Tilman et al. 1996, Hooper 1998, Hector et al. 1999). Our data on

348   biomass production of functional groups in monocultures (Table 2), and correlations between the

349   proportions of specific functional groups in mixed plant communities and biomass production of

350   these communities suggest that in the environmental context of the Jena Experiment the

351   differences in total and/or aboveground productivity within levels of species diversity can be

352   attributed at least in part to the proportion of legumes and small herbs.

353   In contrast to aboveground and total biomass production, belowground biomass production in

354   0–0.3 m soil depth was not related to species richness and plant functional group richness. This is

355   consistent with several studies in which the standing belowground biomass rather than

356   belowground biomass production was measured (Spehn et al. 2000a, Niklaus et al. 2001, He et al.

357   2002, Gastine et al. 2003). However, in other studies the standing belowground biomass

358   increased with increasing species richness (Tilman et al. 2001, Reich et al. 2001, Craine et al.

359   2003, Dimitrakopoulos and Schmid 2004). In the present study, belowground biomass

360   production was assessed by measuring the belowground plant biomass that was newly produced

361   within initially root-free soil cores during 3-month periods. From observations using mini-

362   rhizotrons we have evidence that decomposition of the newly formed belowground biomass

363   within three months is negligible (Bessler and Engels, unpublished data), making it unlikely that

364   our data on belowground biomass production are confounded by potential plant diversity effects

365   on decomposition. It should be noted that, similar to other studies, belowground biomass

366   production was assessed in the top 0.3 m of the soil profile. There is good evidence that in

367   temperate grasslands most of the roots are located in this soil zone, but 10–20% of the roots

368   growing deeper than this (Jackson et al. 1996). In the Jena Experiment, the standing root biomass

369   in 0–1.5 m soil depth was measured in the year 2006. We found that the percentage of roots

370   growing below 0.3 m ranged from 4–53% (mean = 19%; median = 17%) and was not correlated

371   with species richness (P = 0.793). Therefore, we believe that our results from the top 0.3 m of the

372   soil would not be substantially changed if we would have used the first 1.5 m instead.

373   Our data suggest that the differential effect of plant diversity on aboveground and

374   belowground biomass production (Fig. 1, Table 3), which is in line with other European

375   biodiversity experiments (Schmid & Pfisterer 2003, Spehn et al., 2005), can be attributed at least

376   in part to differences among plant functional groups in biomass allocation to aboveground and

377   belowground organs. Legumes which often strongly contribute to the positive plant biodiversity-

378   aboveground productivity relationship have low belowground productivity. Furthermore, as

379   discussed in more detail in the next section, species interactions leading to reduced biomass

380   allocation to belowground organs relative to aboveground organs also contribute to the

381   differential effect of plant diversity on aboveground and belowground productivity.

382

383   *Reduced R/S ratio in mixtures: dominance of species with low R/S ratio or reduced biomass*

384   *partitioning to roots?*

385   R/S ratios of species grown in monoculture ranged from 0.1–3.4 (see Fig. 1d). A similar range

386   of R/S ratios was also measured in an investigation including 59 species from the Great Plains

387   grasslands in the USA (Johnson and Biondini 2001). This shows that large interspecific

388   variability of R/S ratios exists in grassland species. In our experiment, R/S ratios were

389   significantly higher in monocultures than in mixtures, whereas R/S ratios in mixtures were not

390   significantly affected by species richness (Fig. 1d; $F_{1,51} = 0.61$; $P = 0.438$). Two mechanisms that

391   may contribute to the reduced R/S ratios in mixtures as compared with monocultures are: (i)

392   dominance of species with low R/S ratio in mixtures, and (ii) interactions among species leading

393   to reduced biomass partitioning to roots. To assess the role of both mechanisms, we calculated

394   the expected R/S ratio with the assumption that biomass partitioning between roots and shoots is

395   not affected by interactions among species. The expected R/S ratio of mixtures was not lower

396   than the average R/S ratio of monocultures (Table 4) indicating that the mixtures were not

397   dominated by species with inherently low R/S ratio. Similar to the study of Hooper (1998), the

398   measured R/S ratios in some mixtures were lower and in other mixtures were higher than

399   expected from the performance in monoculture. However, on average, the measured R/S ratio

400   was lower than the expected R/S ratio (see Table 4), indicating that the lower R/S ratios in

401   mixtures in comparison with monocultures were due to interactions among species leading to

402   reduced biomass partitioning to roots. Belowground biomass production was measured only in

403   the top 0.3 m of the soil profile. However, our data on standing root biomass in 0–1.5 m soil

404   depth in 2006 showed that the percentage of roots below 0.3 m did not differ between

405   monocultures and mixtures (P=0.397). This indicates that monocultures and mixtures did not

406   differ in biomass partitioning to roots in various soil depths and that our conclusions would not

407   be altered if deeper soil layers would be included into the analyses.

408

409   *Possible explanations for the lower than expected biomass partitioning to belowground organs*

410   *in mixtures*

411   The R/S ratios were lower in mixtures with than in those without legumes (see Table 4). Root

412   biomass of legumes is lower than that of grasses and forbs (Gastine et al. 2003). Our own data

413   also show that in monocultures R/S ratios of legumes are smaller than R/S ratios of non–legumes

414   (Table 2). In mixtures containing legumes, R/S ratios were lower than expected from R/S ratios

415   in monocultures of the involved species (see Table 4), indicating that species interactions led to

416   reduced biomass partitioning to roots. In mixed plant communities, legumes may contribute to

417   improved N nutrition of associated non-legumes because of lower N uptake of legumes from soil,

418   and transfer of biologically fixed N_2 to non-legumes (Mulder et al. 2002, Spehn et al. 2002,

419   Palmborg et al. 2005). It is well documented that biomass partitioning to roots is reduced by

420   increased N supply. At our study site, soil nitrate concentrations (Oelmann et al. 2007) and shoot

421   N concentrations of non-legume phytometer species (Temperton et al. 2007) were significantly

422   higher in plots with legumes than in plots without legumes, suggesting that the reduced biomass

423   partitioning to roots was due to improved N nutrition of non-legumes. This suggestion should be

424   further substantiated by identifying roots at the species level in future studies.

425   In mixtures without legumes, the R/S ratios were also lower than expected, indicating that

426   species interactions leading to modification of biomass partitioning were not confined to

427   mixtures containing legumes. We know of one further study (Wardle and Peltzer 2003), carried

428   out with potted non-legume grassland species, which also found lower biomass partitioning to

429   roots in mixtures than in monocultures.

430   The R/S ratio of plants is often reduced by environmental conditions that reduce specific

431   shoot activity, e.g. by low light intensity, or that increase specific root activity, e.g. by high soil

432   nutrient content (Brouwer, 1983, Wilson 1988, Callaway et al. 2003, Kahmen et al. 2005). Light

433   absorbance within the canopy may be increased in mixtures as compared with monocultures

434   (Spehn et al. 2000b, Fridley 2003). This reduces light intensity for short species growing in the

435   shade of tall species, and may lead to a decrease in R/S ratio of short species in mixtures. Similar

436   to the utilization of light, also the utilization of soil resources such as nitrate can be increased in

437   mixtures in comparison with monocultures (Tilman et al. 1996, Niklaus et al. 2001, Scherer-

438   Lorenzen et al. 2003, Palmborg et al. 2005). However, in contrast to light, where competition

439   between tall and short species is asymmetric, competition for nutrients may be reduced between

440   species if they take up nutrients at different depths or in different chemical form. Thus,

441   aboveground asymmetric competition for light and belowground niche complementarity,

442   respectively, may reduce availability of light and increase availability of soil resources for

443   individual species in mixtures and thus allow lower biomass partitioning to roots.

444

445   *Why is lower than expected biomass partitioning to belowground organs associated with*

446   *overyielding?*

447   Aboveground overyielding in mixtures was negatively correlated with the quotient of

448   measured/expected R/S ratio (see Fig. 2). This indicates that species interactions leading to lower

449   than expected biomass partitioning to belowground organs relative to biomass partitioning to

450   aboveground organs were associated with increased productivity of mixtures. Why an alteration

451   of biomass partitioning at the expense of plant organs responsible for acquisition of soil

452   resources and in favour of plant organs responsible for light interception and photosynthesis was

453   associated with increased productivity? Our suggestion is that in 0–0.3 m soil depth root

454   production was excessive, and thus, species interactions leading to an altered biomass

455   partitioning in favor of aboveground organs increased productivity. From model calculations in

456   which homogenous distribution of actively absorbing roots are assumed, it can be predicted that

457   root length densities > 1 cm root length cm^{-3} soil are sufficient for complete spatial exploitation

458   of mobile soil resources such as nitrate (Claassen and Steingrobe 1999). At our study site we

459   measured annual root length growth of about 40 cm root length cm^{-3} soil in 0–0.3 m soil depth.

460   We have no information about the distribution and activity of the roots in the Jena-Experiment,

461   however this high root-length density indicates that there is more root growth than needed for

462   exploitation of soil resources even if their mobility is lower than that of nitrate. Formation of

463   high root-length densities is associated with high competitive ability of plant individuals (Hodge

464   2004). But at the plant community level, any increase of root length density in the range of 40

465    $cm\,cm^{-3}$ is not expected to enhance acquisition of soil resources. Under these circumstances, any

466   decrease of biomass partitioning to roots in favor of biomass partitioning to roots should increase

467   productivity, at least when it is assumed that the net cost for tissue maintenance is higher for

468   belowground organs than for aboveground organs which yet in a dense stand make some gross

469   photosynthesis. In a "tragedy of the commons" scenario in pot experiments, it has been shown

470   that in soil compartments which are shared by several individual plants, competition among

471   plants may induce excessive root production leading to lower total productivity (Gersani et al.

472   2001).

473   Our analysis of both above- and belowground biomass production and its ratio shows that

474   there can be balancing effects between biodiversity effects related to above- and belowground

475   resource use. Looking only at one side of the biomass production may lead to biased conclusions,

476   because the response of one side to biodiversity can depend on the response of the other side.

477

487

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668 **Table 1** Number of sown plots in the Jena Experiment and number of plots analyzed in this

669 study (in parenthesis). In this study a lower than the originally sown number of plots was

670 included due to (i) the exclusion of monocultures with low plant establishment and (ii) the

671 exclusion of mixed plant communities where species not included in monocultures contributed

672 more than 5% to the community aboveground biomass production.

		Plant species richness				
		1	2	4	8	16
Plant functional	1	60 (42)	8 (6)	4 (4)	4 (4)	2 (2)
group richness	2		8 (6)	4 (3)	4 (3)	4 (4)
	3			4 (4)	4 (4)	4 (4)
	4			4 (4)	4 (3)	4 (3)
	all	60 (42)	16 (12)	16 (15)	16 (14)	14 (13)

673

674 **Table 2** Annual biomass production and biomass partitioning between belowground and aboveground organs (termed R/S-ratio) of

675 plant functional groups in monocultures. N is the number of species per plant functional group. Shown are means ± 1 SE. Effect of

676 plant functional group identity was tested with a one-way ANOVA (P-values are shown in the last row). Different letters within

677 columns mark significant differences between specific plant functional groups determined by the Tukey test (P<0.05).

Plant functional group	N	Annual total biomass production [g m^{-2} year^{-1}]	Annual aboveground biomass production [g m^{-2} year^{-1}]	Annual belowground biomass production [g m^{-2} year^{-1}]	R/S-ratio
Legumes	6	1497 ± 142	1082 ± 130 [a]	415 ± 64 [a]	0.42 ± 0.08 [a]
Grasses	14	1407 ± 79	653 ± 60 [b]	754 ± 45 [b]	1.27 ± 0.13 [b]
Tall herbs	15	1242 ± 119	601 ± 60 [b]	642 ± 90 [ab]	1.16 ± 0.20 [b]
Small herbs	7	1070 ± 62	530 ± 43 [b]	541 ± 40 [ab]	1.05 ± 0.10 [ab]
P		0.116	0.002	0.040	0.028

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682   **Table 3** Effects of plant species richness, plant functional group richness and the presence of specific plant functional groups (legumes,

683   grasses, small herbs, tall herbs) on annual biomass production and biomass partitioning between belowground and aboveground

684   organs (termed R/S-ratio). Effects were tested with general linear models. Model terms were entered hierarchically, whereas plant

685   species richness was fitted first in model 1 and plant functional group richness was fitted first in model 2. The effect of each plant

686   functional groups was tested in separate models where the presence of each plant functional group was fitted after plant species

687   richness and plant functional group richness. The results are summarized as model 3. Shown are F-values, significance levels (*

688    $P<0.05$, ** $P<0.01$, *** $P<0.001$) and the direction of significant effects ($\uparrow$ increase, $\downarrow$ decrease).

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Model term	Annual total biomass production	Annual aboveground biomass production	Annual belowground biomass production	R/S-ratio
Model 1				
Plant species richness (log-transformed)	$F_{1,93}=14.93^{***}\uparrow$	$F_{1,93}=18.35^{***}\uparrow$	$F_{1,93}=0.11$	$F_{1,93}=7.98^{**}\downarrow$
Plant functional group richness	$F_{1,93}=0.23$	$F_{1,93}=1.06$	$F_{1,93}=0.33$	$F_{1,93}=0.63$
Model 2				
Plant functional group richness	$F_{1,93}=8.33^{**}\uparrow$	$F_{1,93}=12.80^{***}\uparrow$	$F_{1,93}=0.05$	$F_{1,93}=5.99^{*}\downarrow$
Plant species richness (log-transformed)	$F_{1,93}=6.82^{*}\uparrow$	$F_{1,93}=6.61^{*}\uparrow$	$F_{1,93}=0.40$	$F_{1,93}=2.62$
Model 3				
Plant species richness (log-transformed)	$F_{1,92}=15.01^{***}\uparrow$	$F_{1,92}=24.27^{***}\uparrow$	$F_{1,92}=0.14$	$F_{1,92}=10.30^{**}\downarrow$
Plant functional group richness	$F_{1,92}=0.23$	$F_{1,92}=1.40$	$F_{1,92}=0.41$	$F_{1,92}=0.82$
Presence of legumes	$F_{1,92}=1.51$	$F_{1,92}=31.04^{***}\uparrow$	$F_{1,92}=21.76^{***}\downarrow$	$F_{1,92}=28.11^{***}\downarrow$
Presence of grasses	$F_{1,92}=2.35$	$F_{1,92}=0.98$	$F_{1,92}=13.50^{***}\uparrow$	$F_{1,92}=7.49^{**}\uparrow$
Presence of tall herbs	$F_{1,92}=0.17$	$F_{1,92}=<0.01$	$F_{1,92}=0.40$	$F_{1,92}=<0.01$
Presence of small herbs	$F_{1,92}=11.04^{**}\downarrow$	$F_{1,92}=12.99^{**}\downarrow$	$F_{1,92}=0.16$	$F_{1,92}=2.27$

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701 **Table 4** Biomass partitioning between belowground and aboveground organs (termed R/S-ratio) in monocultures and mixed plant

702 species communities. Expected R/S-ratio in mixture was calculated as mean of the R/S-ratio measured in monocultures of the

703 component species, whereas the R/S-ratio of each species was weighed by its proportion to the mixture aboveground biomass

704 production. Shown are means ± 1 SE. Different letters within rows mark significant (paired t-test, $P<0.05$) differences between

705 expected R/S-ratio and measured R/S-ratio. NA: not applicable.

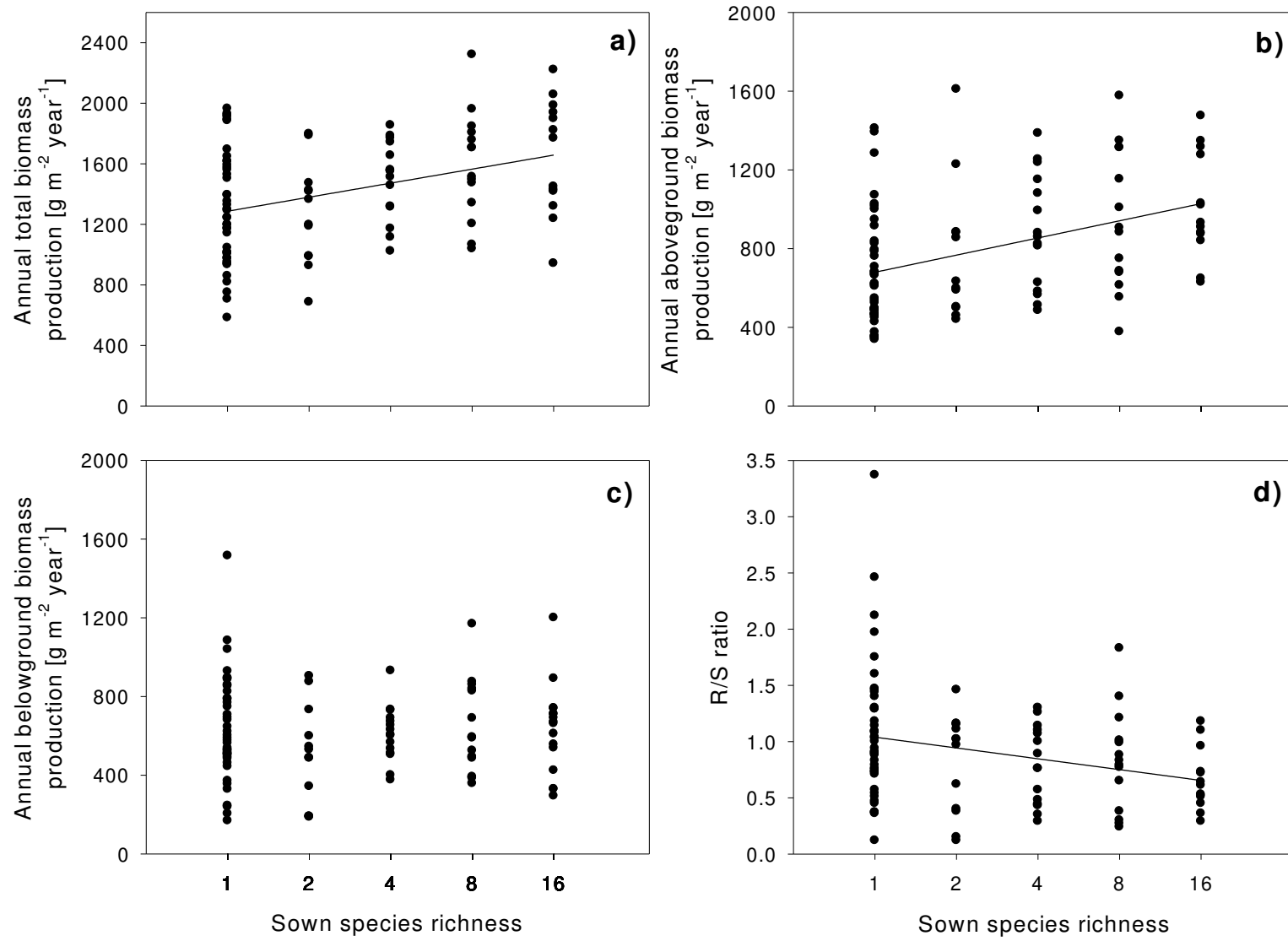|	N	Expected R/S-ratio	Measured R/S-ratio
Monocultures	42	NA	1.08 ± 0.10
Mixtures	54	1.00 ± 0.07 a	0.77 ± 0.05 b
Mixtures with legumes	30	0.79 ± 0.07 a	0.59 ± 0.06 b
Mixtures without legumes	24	1.26 ± 0.12 a	1.00 ± 0.07 b

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710   **FIGURE LEGENDS**

711   **Figure 1** Annual production of (a) aboveground biomass, (b) total biomass, (c) belowground

712   biomass and (d) belowground / aboveground biomass production (R/S ratio) as functions of the

713   number of sown plant species in experimental grassland communities. Lines show predicted

714   values from regression models.

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716   **Figure 2** Correlation between RYT for annual aboveground biomass production and the quotient

717   of measured/expected R/S ratio in mixtures. Expected R/S ratio was calculated from R/S ratio

718   measured in monocultures and the aboveground biomass proportion of the component species in

719   mixtures. Quotient of measured/expected R/S ratio < 1 indicates lower than expected relative

720   biomass partitioning to belowground organs. RYT > 1 indicates overyielding of aboveground

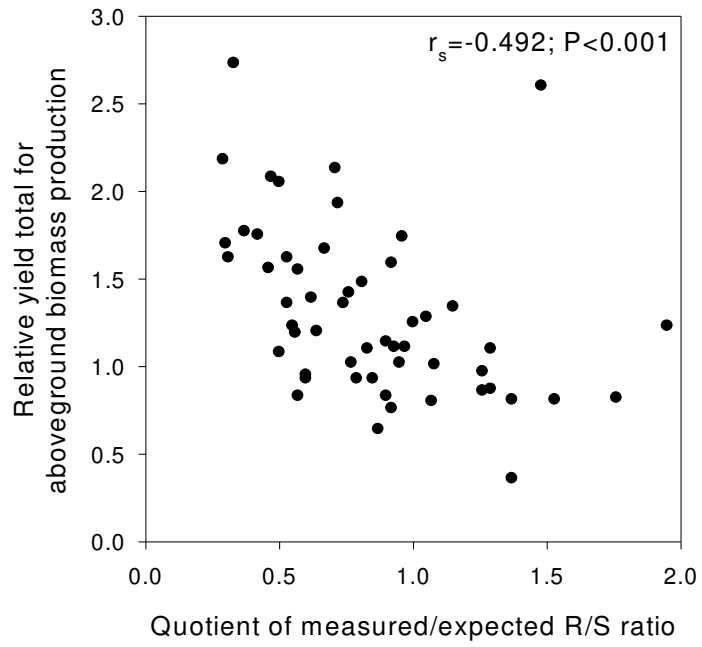721   biomass production. Spearman rank correlation coefficient (r_s) = –0.492; P<0.001.

722   Figure 1.

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724 Figure 2.

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