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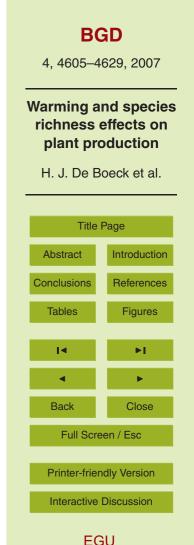
Biomass production in experimental grasslands of different species richness during three years of climate warming

H. J. De Boeck[1], **C. M. H. M. Lemmens**[1], **B. Gielen**[1], **S. Malchair**[3], **M. Carnol**[3], **R. Merckx**[2], **J. Van den Berge**[1], **R. Ceulemans**[1], and **I. Nijs**[1]

[1]Research Group of Plant and Vegetation Ecology, Department of Biology, Universiteit Antwerpen (Campus Drie Eiken), Universiteitsplein 1, 2610 Wilrijk, Belgium
[2]Division Soil and Water Management, Faculty of Bioscience Engineering, Katholieke Universiteit Leuven, Kasteelpark Arenberg 20, 3001 Leuven/Heverlee, Belgium
[3]Laboratory of Plant and Microbial Ecology, Institute of Plant Biology B22, University of Liège, Sart Tilman, 4000 Liège, Belgium

Correspondence to: H. J. De Boeck (hans.deboeck@ua.ac.be)

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Abstract

Here we report on the single and combined impacts of climate warming and species richness on the biomass production in experimental grassland communities. Projections of a future warmer climate have stimulated studies on the response of terres-

5 trial ecosystems to this global change. Experiments have likewise addressed the importance of species numbers for ecosystem functioning. There is, however, little knowledge on the interplay between warming and species richness. During three years, we grew experimental plant communities containing one, three or nine grassland species in 12 sunlit, climate-controlled chambers in Wilrijk, Belgium. Half of these

10 chambers were exposed to ambient air temperatures (unheated), while the other half were warmed by 3°C (heated). Equal amounts of water were added to heated and unheated communities, so that warming would imply drier soils if evapotranspiration was higher. Biomass production was decreased due to warming, both aboveground (-29%) and belowground (-25%), as negative impacts of increased heat and drought stress

15 in summer prevailed. Increased resource partitioning, likely mostly through spatial complementarity, led to higher shoot and root biomass in multi-species communities, regardless of the induced warming. Surprisingly, warming suppressed productivity the most in 9-species communities, which may be attributed to negative impacts of intense interspecific competition for resources under conditions of high abiotic stress. Our

20 results suggest that warming and the associated soil drying could reduce primary production in many temperate grasslands, and that this will not necessarily be mitigated by efforts to maintain or increase species richness.

1 Introduction

As supported by a growing body of observations, the global climate is changing rapidly

25 (IPCC, 2007). Global surface temperatures are projected to increase with 1.8 to 4.0°C by 2100 ("best estimates"), in reaction to rising atmospheric concentrations of green-

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house gases. A number of studies have addressed how plant communities will react to a warmer world, finding numerous possible responses to higher temperatures. Stimulation of primary productivity is possible mainly through altered reaction kinetics (Larcher, 2003), lengthening of the growing season (Myneni et al., 1997; Walther, 2003), and im-

5　proved access to nutrients (Rustad et al., 2001). Adverse effects of climate warming on the productivity of plant communities could, among others, be caused by increased temperature stress (White et al., 2000), water shortage as a result of increased evapotranspiration (ET) (Saleska et al., 1999), and in the long term by a decrease of species richness (S). The issue of declining species numbers has a number of (anthropogenic)

10　causes (Sala et al., 2000), and climate change is but one of these (Klein et al., 2004). Community productivity is generally lower when fewer species are present, both in artificially assembled (Hector et al., 1999; Hooper et al., 2005) and in natural communities (Gillman and Wright, 2006). Two widely debated mechanisms are thought to be involved in altering the community performance in response to changing species num-

15　bers (Hector et al., 2000; Huston et al., 2000). The first is complementarity (lack of niche overlap), which allows for more of the total amount of available resources to be taken up by the community if more species are present. When S is higher, there is also a higher probability for a community to contain one or more productive species that dominate this community. This is the "selection effect", a pure probability effect, occur-

20　ring in both artificially assembled and natural communities (see Hooper et al., 2005 for a review). This implies that higher biomass in species-rich communities can arise from only a few (dominant) species. The complementarity (including facilitation) and the selection effect are thought to operate simultaneously, and can be separated by using the method of additive partitioning (Loreau and Hector, 2001). Roscher et al. (2005) pro-

25　vided experimental evidence that the positive relationships between plant species richness and biomass production are robust, and independent of spatial scale or species pools. It could be expected that species-rich communities are better "equipped" to face negative aspects of climate warming. Higher temperatures would lower the soil water content (unless precipitation increases), which could reinforce the importance

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of complementarity for water. Furthermore, multi-species communities have a larger probability of containing species better adapted to warming and/or drought, and would therefore be better "insured" than species-poor systems (Naeem and Li, 1997). On the other hand, if enhanced productivity in species-rich communities increases canopy
5 transpiration, then soil drying may occur earlier, which would counteract the productivity enhancement (Pfisterer and Schmid, 2002). As dry soils would already be more frequent and severe if ambient temperatures were higher, such a reduction of the positive effect of S on productivity could be more pronounced under heating.

    To uncover both single-factor and interactive effects of climate warming and species
10 richness, we subjected artificially assembled grassland communities of different species richness levels to either ambient temperatures or temperatures that were continuously 3°C higher. Precipitation was identical in the unheated and the heated communities to ensure that warming would also encompass lower soil water contents if ET was higher. The current study investigates biomass production both above- and be-
15 lowground, and how this is affected by warming and species richness over the course of three years. Including root biomass is of significant importance, as root:shoot ratios could increase in response to climate warming and dryer soils (Chaves et al., 2002). We postulate the following questions: (1) is grassland biomass production positively or negatively affected by warming, (2) is productivity higher in multi-species communities,
20 and how important are complementarity and selection, and (3) are there interactions between the two global changes under consideration? In an earlier study (De Boeck et al., 2007a), we reported on productivity in the same communities during the first four months following planting. The results suggested decreased productivity through warming, slightly increased productivity in multi-species systems, and hinted of interac-
25 tion between the two treatments. The current study investigates whether these effects were merely short-term responses, as such transient effects have been found in other treatment studies (e.g. Calfapietra et al., 2003), or whether they were persistent or gained in importance during three years. Importantly, the substantial knowledge gained through process-based studies in the same experimental platform, i.e. on autumn phys-

iology (Gielen et al., 2005), water use (De Boeck et al., 2006a), photochemistry (Gielen et al., 2007) and CO_2 fluxes (De Boeck et al., 2007b) enables us to causally explain observed productivity responses.

2 Material and methods

2.1 Study site and experimental set-up

This study was conducted at the Drie Eiken Campus of the University of Antwerp (Belgium, 51°09′ N, 04°24′ E), where an experimental platform containing 288 artificially assembled grassland model ecosystems in containers was established in 2003. The climate of north Belgium is characterized by mild winters and cool summers, with an average annual air temperature of 9.6°C, and mean monthly air temperatures between 2.2°C (Jan) and 17.0°C (July). Annual precipitation averages 776 mm, equally distributed throughout the year.

At the start of the experiment (2003), the platform consisted of 12 sunlit, climate-controlled chambers (2.25 m^2 ground area) facing south, half at ambient temperatures (unheated) and the other half continuously at ambient temperatures +3°C (heated). Each year in November, two chambers were removed for destructive harvesting and root analysis. Each chamber had an individual air control group with an electrical heating battery, and was linked to a central refrigeration unit by isolated pipes. The conditioned air was evenly distributed throughout the chambers by means of aerators with regulated flow. The aluminium-frame chambers were covered with a colourless polycarbonate plate (4 mm thick), and polyethylene film (200 μm thick) at the sides, both UV transparent and with a total light transmission of 86%.

Each chamber (the blocking variable in the statistical analyses) contained the same series of 24 different grassland communities of varying species richness: nine monocultures, nine S=3 communities and six S=9 communities. These communities are the experimental unit in this study, and were placed in PVC containers (24 cm inner diame-

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ter, 60 cm deep) installed in the soil. Each community contained 30 individuals planted in a hexagonal grid at 4 cm distance, with interspecific interactions maximised. Similar plant densities were used in other experiments (e.g. Van Peer et al., 2004), and are deemed realistic for temperate grasslands. Prior to planting in the containers in June 2003 (which took approximately three weeks), the plants were sown in small seedling pots in April 2003. We opted for species from three functional groups, which were equally represented at each S level: three grass species (*Dactylis glomerata* L., *Festuca arundinacea* Schreb., *Lolium perenne* L.), three N-fixing dicots (*Trifolium repens* L*., Medicago sativa* L*., Lotus corniculatus* L.), and three non-N-fixing dicots (*Bellis perennis* L*., Rumex acetosa* L*., Plantago lanceolata* L.). These C3 species comply with three criteria: presence in European temperate grasslands, perennial life cycle, and preference for clay or loam soil. In addition, they represented different productivities, and different temperature and drought resistances. Species representative of the three functional groups were used to create each of the S=3 communities, with each species combined only once with any other species. Out of the three possible sets of nine different S=3 communities that met these criteria, one randomly chosen set was used. Each of the six S=9 communities had a different internal arrangement, to ensure that each species interacted to the same extent with any other species over the totality of the six S=9 communities.
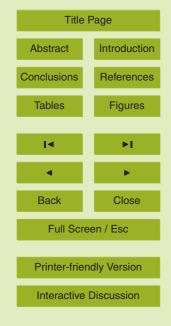
The soil used in the experiment (76.3% silt, 14.8% clay and 8.7% sand; field capacity $0.39\,\mathrm{m^3\,m^{-3}}$; pH 6.45, carbon content 1.6%) was collected from an agricultural field and sieved (0.5 mm mesh size) to remove stones and large organic material. No fertiliser was added to this rich agricultural soil. Plants were treated regularly to avoid fungal infection and insect damage, and weeding was done manually throughout the experiment. Watering was done in accordance with actual outside conditions, and was equal in both temperature treatments so that soil water content would be lower if warming increased evapotranspiration. Further information regarding the experimental set-up and watering regime can be found in De Boeck et al. (2006a).

2.2 Measurements

Aboveground biomass (B_{shoot}) was determined by cutting plants 3.5 cm above the soil surface in all containers. Such harvests were carried out in five periods: late Oct 2003, 2004 and 2005, early June 2004 and late May 2005. Of half of the heated and unheated chambers, biomass was collected per species within community, while the biomass of the other chambers was collected per community. Plant material was then oven dried (one week at 70°C) and weighed. Two chambers (one heated and one unheated) were dismantled each year early November, the stubble biomass (biomass of the lowest 3.5 cm above ground, $B_{stubble}$) was harvested, and all plant containers were removed. Soil slices (4 cm thick) were subsequently cut out of the soil cylinder at depths of 1–5 cm, 6–10 cm, 13–17 cm, 23–27 cm, 35–39 cm and 48–52 cm. These soil samples were subsequently dried during two weeks at 70°C to prevent root decomposition. Later, roots were manually washed from the soil slices, dried at 70°C and weighed.

Belowground biomass (B_{root}) was reconstructed from the slice biomass by regression (the curve chosen per community to best fit the root distribution), followed by a calculation of root biomass for every mm along the depth profile and subsequent summation of these 1-mm biomass values. The root biomass in each layer compared to the total in all layers, provides an estimate of the distribution of roots throughout the soil. For each soil layer, we calculated relative standard deviations (RSDs, the coeffient of variation multiplied by 100) in order to test whether root distributions were similar (low RSD) between communities of a certain S level. Root/shoot (R/S) ratios were calculated from B_{root} and combined B_{shoot} and $B_{stubble}$ in the subsequently dismantled chambers. Selection and complementarity effects were calculated for those chambers in which aboveground biomass was determined up to the species level, using the additive partitioning method formulated by Loreau and Hector (2001). By comparing the observed biomass production in mixtures with the expected production (based on the monoculture productivity of each species in the mixture), we were able to calculate

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over- or underyielding and how complementarity and selection contributed to this.

2.3 Statistical analysis

Statistics were performed using SPSS 10.0 (SPSS Science, Woking, UK) and SAS 8.2 (SAS Institute Inc., Cary, NC, USA). To test for effects of heating, species richness level, rooting depth, period and interactions, we used general linear model (GLM) univariate analysis. Adding chamber numbers as a random factor in a mixed analysis revealed that there were no chamber effects. Post-hoc tests (Games-Howell) were used to separate multiple means. To test whether complementarity or selection was significantly different from 0, we used one-sample t-tests. All data were tested for normality with the Shapiro-Wilk statistic, and were square root transformed if not normally distributed. The significance level for all tests was 0.05.

3 Results

3.1 Biomass production

Grassland communities growing at elevated temperatures for three growing seasons, produced significantly less biomass (Fig. 1), with productivity being reduced by 29% aboveground ($p<0.001$), and 25% belowground ($p<0.05$) on average for all periods and S levels together. Reductions were consistently observed throughout the course of the study, with no significant period × temperature treatment interaction. Productivity was generally stimulated by S, both above- ($p<0.001$) and belowground ($p<0.005$). A significant period × S interaction aboveground ($p<0.05$) likely reflects the difference between the first and consecutive periods (Fig. 1a). Although an interactive effect between species richness and temperature treatment only proved significant aboveground ($p<0.05$), a similar trend towards increased differences in biomass production at S=9 between the two temperature treatments was observed belowground (Fig. 1b).

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3.2 Complementarity and selection

Differences in aboveground production between S=3 and S=9 were generally small and non-significant (post-hoc tests). In line with this result, we found that neither complementarity nor (net) selection differed significantly between these two richness levels. The net effect of selection did not change as a result of warming, whereas complementarity was generally lower in heated communities ($p<0.05$, Fig. 2). Because the period had a clear effect ($p<0.01$), we performed one-sample t-tests for each period separately. Complementarity proved positive in 8 out of 10 cases, while selection had no effects, with the exception of one period in which it stimulated productivity (Table 2). Although no significant interaction was found between S and temperature treatment, data were consistent with biomass data by showing the largest differences between heated and unheated communities at S=9.

3.3 Root distribution

Root biomass was highest near the soil surface, with 48% of the roots located in the 1–5 cm layer, and gradually declined with increasing depth in the soil ($p<0.001$). The same general pattern was found in all years, but in the last year, less roots were found near the soil surface (39% in the 1–5 cm layer) versus more deeper down when compared with the other two years ($p<0.001$). No effects of either warming or S were detected, but the significant interaction between species richness and depth ($p<0.005$) indicates that the root distribution pattern was influenced by S, although differences were small (Fig. 3). Differences in root distribution between individual species were small and statistically undetectable. When comparing RSDs, the differences in root distribution between communities proved smallest at S=9 (post-hoc, $p<0.05$ for both the comparison with S=1 and S=3).

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3.4 Root/shoot ratio

Neither warming nor species richness affected the ratio belowground versus aboveground biomass. This R/S ratio increased sharply from 0.8 in the start-up year to 3.5 in the third year (with the year influence being significant; $p<0.001$), in line with a much higher B_{root} observed in year three (Fig. 1b). It is remarkable that, when comparing B_{shoot} with $B_{stubble}$, an effect of temperature treatment ($p<0.05$) and a temperature treatment × year interaction ($p<0.01$) was found. This reflected a strong increase in stubble biomass and stubble versus aboveground biomass in the heated communities in the third year (Fig. 4). No effects of S were detected here.

4 Discussion

4.1 Is grassland biomass production positively or negatively affected by warming?

Exposing experimental grassland communities to a warmer climate resulted in a substantially lower biomass production, both above- and belowground. The decrease in productivity was consistently observed in all periods, which negates the possibility of a transient response, at least in the medium term. A positive effect of warming recorded on the same communities by Gielen et al. (2005), was an increased efficiency of the electron transport chain. However, the same study detected no warming-induced delay of senescence at the end of the growing season, while (unpublished) data of spring growth likewise do not show substantial earlier growth. This suggests that any production-enhancing effects of a lengthening of the growing season were small. In contrast, several negative effects of heating were recorded.

Lower soil moisture levels (5% relatively) recorded in warmed communities (De Boeck et al., 2006a) triggered a decrease in stomatal conductance (Lemmens et al., 2006) ensuring that transpirative losses were dampened (De Boeck et al., 2006a). The decreased stomatal conductance contributed to lower photosynthetic rates, while

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plant respiration was also decreased, but by a lower amount (De Boeck et al., 2007b). This subsequently resulted in the decrease of biomass production reported here. Our study on carbon fluxes on these same communities revealed that the adverse effects of warming were concentrated and likely confined to late spring and summer (De Boeck et al., 2007b). Apart from indirect effects of (summer) drought, direct negative effects of increased temperatures were also found, with summer fluorescence measurements indicating an increased intensity of midday stress as a result of heating, causing down-regulation of photosystem 2 (Gielen et al., 2007).

Although plants can invest in expanding their root system to increase water uptake (Chaves, 2002), leading to an increase in R/S, we found no evidence of such increases, and the distribution of roots also remained unchanged under heating. However, higher temperatures could have counteracted any drought-induced R/S increases, with Edwards et al., (2004) reporting that warming without soil drying had a negative effect on root biomass in temperate grasslands through increased root death. The root system in both temperature treatments became more extensive as the communities matured, with R/S values well above 1, in accordance with other studies on temperate grasslands (Mokany et al., 2006). The markedly higher stubble versus aboveground biomass under heating in year three highlights that especially the amount of photosynthetic tissue, which is mostly located higher than 3.5 cm above the soil surface, was reduced by heating. The amount of data is, however, too limited to confidently ascribe this to a drought-avoidance strategy.

Changes in precipitation are one of the least certain aspects of climate change (IPCC, 2007). In line with other reports (Eatherall, 1997; De Valpine and Harte, 2001), this study suggests that unless precipitation increases, the productivity of many grasslands could significantly decline under climate warming. Indeed, grassland productivity is often limited by precipitation (Weltzin et al., 2003; Nippert et al., 2006). However, if productivity is limited most by low temperatures or low nutrient concentrations, such as in polar and alpine regions, warming may be beneficial through alleviation of these constraints either directly through higher temperatures or indirectly via in-

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creased nutrient mineralization rates (Riedo et al., 2001; Rustad et al., 2001; Aerts et al., 2006). In precipitation-limited grasslands, we expect considerable variation in productivity changes in the next decades, depending on future local precipitation regimes, although it is possible that drought-effects will be alleviated by rising atmospheric CO_2
⁵ concentrations (Norby and Luo, 2004).

4.2 Is productivity higher in multi-species communities, and how important are complementarity and selection?

More biomass was produced in mixtures than in monocultures, in line with similar experimental studies (Hector et al., 1999; van Ruijven and Berendse, 2005), while pro-
¹⁰ ductivity differences between 3- and 9-species were small or absent as predicted from theory (De Boeck et al., 2006b). As expected (De Boeck et al., 2007a), S effects were smallest in the first growing season, as plant-plant interactions generally grow stronger in time (van Ruijven and Berendse, 2005). The method of additive partitioning revealed that the increase from monocultures to multi-species communities could be attributed
¹⁵ almost exclusively to complementarity effects, with selection effects small and mostly non-significant. As illustrated by Lemmens et al. (2005), this does not imply that all plants were equal competitors, but merely that the net effect of selection on community biomass was close to zero.

Of the three main forms of complementarity, namely temporal, nutrient-type, and
²⁰ spatial complementarity (Fridley, 2001), it is likely that the first two contributed the least in the total complementarity effect. Indeed, these temperate grassland species have a similar phenology with only limited seasonal activity differences between them, and resources other than water were abundant in this rich agricultural soil, making strong nutrient-type effects unlikely. Multi-species communities generally are able to capture
²⁵ more light and hence photosynthesize more, as their canopy structure is less uniform than monocultures and fills the three-dimensional space more completely (Cernusca, 1976; Middelboe and Binzer, 2004). The decrease in wind speed caused by better canopy filling would at the same time limit the increases in transpiration accompany-

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ing higher green biomass (Larcher, 2003). Lower than expected ET increases with S were indeed observed in these communities (De Boeck et al., 2006a). The combination of increased light interception and restrained evapotranspiration through aboveground spatial complementarity could thus have contributed to the observed increased biomass production in mixtures.

The fact that monoculture root profiles did not differ significantly between species, suggests that belowground spatial competition in multi-species communities was potentially strong. Such intense interspecific competition between neighbouring plants could cause a relocation of roots to avoid overlap (Mou et al., 1995; Nobel, 1997; Wardle and Peltzer, 2003). Roots seemed more evenly distributed across the soil profile in mixtures, which could confirm this assertion, although differences with monocultures were small (Fig. 3). Soil water measurements suggest more water was taken up in mixtures (De Boeck et al., 2006a), making it more probable that spatial complementarity in multi-species communities was indeed taking place also belowground. The higher biomass production observed in mixtures could also have triggered higher water uptake and use, but at least initially, increased water uptake (through complementarity) would have been necessary to support higher biomass production.

4.3 Are there interactions between the two global changes under consideration?
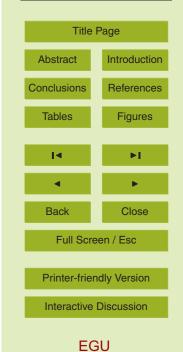
Biomass data show that the response of plant communities to warming depended on the species richness level. Both above- and belowground data indicate that negative impacts of heating on biomass production were highest in 9-species communities (Fig. 1). This greater discrepancy between both temperature treatments at S=9 was observed in almost all periods, and is supported by similar observations for other measurements such as carbon exchange (De Boeck et al., 2007b). These findings seem in contradiction with the "insurance hypothesis" (Naeem and Li, 1997), as the negative impact of warming became more, rather than less, pronounced at the S=9 level.

One possible explanation for the observed interaction is the fact that evapotranspiration increased slightly with rising S (De Boeck et al., 2006a), which may have limited

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productivity through ET-induced drought in multi-species communities (Pfisterer and Schmid, 2002). This would have been more evident in heated communities, where drought was already more pronounced. Complementarity was lowered significantly under warming, but the effect was especially pronounced at S=9 (Fig. 2). Possibly,
5 drought stress limited niche separation in heated multi-species ecosystems as a result of decreased plant vigour (Wardle and Peltzer, 2003), thereby lowering the drought-avoidance potential. In a study on natural ecosystems, Callaway et al. (2002) showed that plant-plant interactions are largely positive when abiotic stress is high, whereas competitive interactions prevail under less physically stressful conditions. These find-
10 ings have more recently been confirmed by Michalet et al. (2006) using a modelling approach. As the grassland species used in the current experiment normally coex-ist in mild, temperate conditions, it is safe to assume that competition among them is substantial. Exposed to abiotic stress, as was measured primarily under heated condi-tions, these mainly competitively oriented interactions would then hamper community
15 productivity. If we had performed our experiment on communities in more stressful biomes (where mutualistic relationships prevail), the interaction effect we observed un-der heating may not have occurred. As this is the first experiment studying effects of climate warming in communities varying in species number, we are unable to compare our findings. A number of questions remain unanswered, such as why the interaction
20 was not detected at S=3. It is obvious, however, that studying global changes simulta-neously is essential, as the responses to single changes are likely not additive.

5 Conclusions

Our data suggest that warming could cause a significant non-transient decline of pri-mary production in many temperate grasslands through increased heat and drought
25 stress, and that such a negative impact may not necessarily be alleviated at higher species richness. While single factor studies have provided better mechanistic under-standing of the response of plant communities to several predicted global changes,

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their results can be confounded by co-occurring global changes. Future studies should therefore address multiple global changes simultaneously, which requires large-scale and long-term experiments to be able to entangle the multitude of interactions.
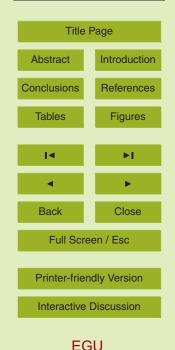
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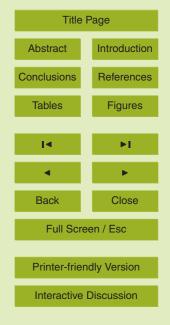
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Table 1. Results of GLM univariate analysis on above- and belowground biomass production and complementarity and selection effects in all periods (see text for details). Significance (sgn) of effects of temperature treatment (T), species richness (S), period, and their interactions (×) are indicated as ns, not significant; $*P<0.05$; $**P<0.01$; $***P<0.001$. F-values, nominator (ndf) and denominator (ddf) degrees of freedom are also shown.

	aboveground biomass				belowground biomass				complementarity				selection effect			
	ndf	ddf	F	sgn	ndf	ddf	F	sgn	ndf	ddf	F	sgn	ndf	ddf	F	sgn
T	1	1083	54.8	***	1	126	4.4	*	1	304	4.3	*	1	304	0.0	ns
S	2	1083	49.1	***	2	126	5.9	**	1	304	0.1	ns	1	304	1.2	ns
Period	4	1083	11.0	***	2	126	64.9	***	4	304	5.5	***	4	304	3.2	*
TxS	2	1083	3.3	*	2	126	1.3	ns	1	304	1.2	ns	1	304	1.3	ns
TxPeriod	4	1083	1.2	ns	2	126	0.6	ns	4	304	0.6	ns	4	304	1.3	ns
SxPeriod	8	1083	2.2	*	4	126	1.6	ns	4	304	2.1	ns	4	304	0.8	ns
TxSxPeriod	8	1083	0.4	ns	4	126	0.1	ns	4	304	1.3	ns	4	304	0.5	ns

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Table 2. Results of one-sample t-tests (test value=0) on data of complementarity and selection in five different periods: (1) June-Oct 2003, (2) Nov 2003-June 2004, (3) June-Oct 2004, (4) Nov 2004-May 2005, (5) June-Oct 2005. Data of 3- and 9-species communities combined are separated per temperature treatment (unheated or heated) when significant in univariate analysis. Significant p-values ($p<0.05$) are indicated in bold and averages are expressed as g community $^{-1}$ with overyielding >0 and underyielding <0.

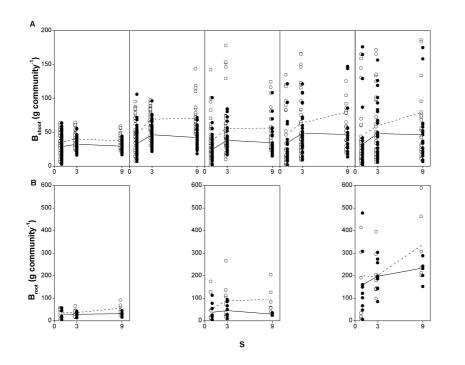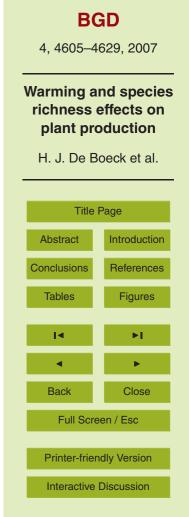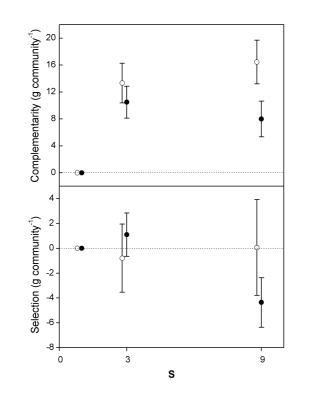| | complementarity | | | | selection | |
| | unheated | | heated | | | |
period	average	p-value	average	p-value	average	p-value
1	3.82	0.044	1.03	0.542	−0.05	0.917
2	15.45	0.000	7.53	0.010	5.00	0.001
3	22.59	0.001	10.59	0.004	−2.24	0.256
4	18.03	0.002	21.24	0.001	−4.89	0.270
5	18.32	0.023	11.35	0.054	−2.21	0.672

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Fig. 1. Community biomass production -A- aboveground (>3.5 cm above the soil surface, B_{shoot}) in five consecutive periods (panels from left to right: June–Oct 2003, Nov 2003–June 2004, June–Oct 2004, Nov 2004–May 2005, June-Oct 2005) and -B-belowground (B_{root}) in three consecutive years (panels from left to right: Nov 2003, Nov 2004, Nov 2005), at ambient temperatures (o) and ambient temperatures +3°C (•). Each symbol represents a different community, and 9 out of 1113 symbols for B_{shoot}, and 1 out of 144 symbols for B_{root} are not depicted because their values exceed the Y-axis range deemed the limit for preserving clarity. Averages for unheated (- -) and heated (–) communities are connected with a straight line. Symbols are slightly shifted with respect to the X-axis for clarity.
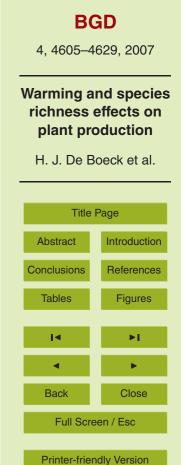
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Fig. 2. Average 2003–2005 aboveground (>3.5 cm above the soil surface) biomass overyielding (if >0) or underyielding (if <0) due to complementarity or selection, at ambient temperatures (o) and ambient temperatures +3°C (•). Only averages and standard errors for each of the three species richness (S) levels are shown. Symbols are slightly shifted with respect to the X-axis for clarity.
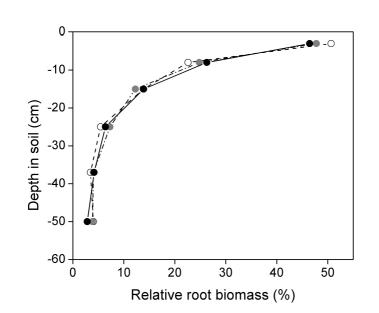
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Fig. 3. Average 2003-2005 root profiles for communities of different species richness (S) levels, S=1 (o and −) S=3 (● and --) and S=9 (● and −). Data from 48 communities at ambient temperatures and ambient temperatures +3°C were combined. Only average percentages of root biomass in each soil slice are shown (see text for details).

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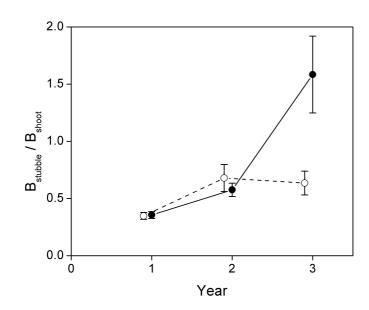**Fig. 4.** Ratio of stubble biomass ($B_{stubble}$, the biomass <3.5 cm above the soil surface) and shoot biomass (B_{shoot}, the biomass >3.5 cm above the soil surface) at ambient temperatures (o and - -) and ambient temperatures +3°C (• and –). Data from harvests in October 2003, 2004 and 2005, for all three species richness levels combined. Only averages (24 communities) and standard errors are shown. Symbols are slightly shifted with respect to the X-axis for clarity.