

REPORT

Overyielding in grassland communities: testing the sampling effect hypothesis with replicated biodiversity experiments

Andy Hector,^{1*}
Ellen Bazeley-White,¹
Michel Loreau,²
Stuart Otway¹ and
Bernhard Schmid³

¹Natural Environmental
Research Council (NERC) Centre
for Population Biology, Imperial
College at Silwood Park, Ascot,
Berkshire GB-SL5 7PY, UK.

²Laboratoire d'Ecologie, UMR
7625, Ecole Normale Supérieure,
46 rue d'Ulm, F-75230 Paris
Cedex 05, France.

³Institut für
Umweltwissenschaften,
Universität Zürich,
Winterthurerstrasse 190, Zürich
CH-8057, Switzerland.

*Correspondence: E-mail:
a.hector01@ic.ac.uk

Abstract

We derive and test some assumptions and predictions of the Sampling Effect Hypothesis (SEH) by examining the relationship between the traits of species in monoculture and their relative abundance in mixture, and by comparing polyculture performance with single-species plots. Although we found a positive relationship between production in monoculture and dominance in mixtures as predicted by the SEH, the relationship had low explanatory power. Counter to predictions, the species with the highest monoculture biomass were not able to strongly dominate all mixtures; instead the dominance of these species decreased with increasing species richness. On average, polycultures did not achieve greater biomass than (transgressively overyield) the species in each mixture, or at each site, that was most productive in monoculture. However, mixture yields did transgressively overyield both the monoculture biomass of the dominant species in the mixtures, and the weighted average of all monocultures (non-transgressive overyielding), both of which were positively related to increasing species richness. The varying responses of different overyielding tests resulted because resource partitioning and positive interactions were often counter-balanced by selection for species with lower biomass than the highest-yielding monocultures. Judging whether or not mixtures overyield therefore depends in part upon which species is the basis for comparison. We present a new general framework for overyielding analysis where every monoculture provides a potential comparison and from which the most relevant tests can be selected.

Keywords

BIODEPTH project, competitive dominance, complementarity effect, niche differentiation, positive interactions, resource partitioning, selection effect, species richness.

Ecology Letters (2002) 5: 502–511

INTRODUCTION

Comparison of the performance of species mixtures with monocultures has become an important tool in the assessment of the effects of changes in biodiversity. In this paper we present a general framework for these comparisons and apply it to data from biodiversity experiments replicated in eight different European grassland systems.

Initial explanations for the effects of biodiversity on ecosystem processes (Naeem *et al.* 1994; Tilman *et al.* 1996) focused on niche differentiation and resource partitioning in space and time, for example via differing rooting depths or phenologies (e.g. Berendse 1982; Bazzaz & Catovsky 2001). However, there is a simpler way, which was initially missed,

in which diversity can affect ecosystem functioning even in the absence of resource partitioning. Under the Sampling Effect Hypothesis (SEH) (Aarssen 1997; Huston 1997; Tilman *et al.* 1997), when communities are assembled at random from a pool of species, more diverse mixtures have a higher probability of containing a species with extreme traits which may drive some ecosystem processes if it becomes dominant. The aim of this paper is to formulate and test various hypotheses we derive from the SEH. Based on the simulation and conceptual models presented in the SEH papers (Aarssen 1997; Huston 1997; Tilman *et al.* 1997), we argue that they work in essentially the same way and share several explicit or implicit assumptions and properties in common.

- 1 Dominance occurs through resource competition.
- 2 Polycultures become dominated by a single species which eventually excludes all others.
- 3 There is a positive correlation between productivity in monoculture and dominance (relative abundance) in polycultures so that mixtures are dominated by the species that is most productive when grown alone, if present, then the next most productive and so on.
- 4 The productivity of a mixture is the same as that of the species with the most highly productive monoculture.

A more general *selection effect* is obtained when some of these assumptions are relaxed (Loreau 1998a, 2000; Loreau & Hector 2001). First, changes in dominance can come about by several processes in addition to resource competition, including differences in growth rates, in resource partitioning and via unequal positive (e.g. facilitation) and negative (e.g. interference, allelopathy) interactions. Second, dominance may be partial, rather than complete, with the persistence of more than one species. Third, dominance need not be positively correlated with monoculture performance. Finally, interspecific interactions could cause the productivity of a mixture to deviate from that of the best-performing monoculture, either negatively or positively. When using this more general approach an additive partitioning method can be applied to separate the overall net change into selection and complementarity effects (Loreau & Hector 2001). The additive partitioning method therefore assesses mixture performance relative to a weighted average of the monoculture yields of all of the component species. However, in some cases we want to know how mixtures perform relative to a single monoculture of particular interest, specifically whether they overyield or not.

There are two categories of overyielding. *Non-transgressive overyielding* occurs when the yield of a mixture is greater than expected based on a weighted average of the monoculture yields of the component species, as indicated by values greater than one for relative yield totals (RYTs) and related measures (Trenbath 1974; Harper 1977; Vandermeer 1989), or by $\bar{D} > 1$ in the scheme of deviations from expected values of Loreau (1998b) and other analyses of biodiversity experiments of this type (Bell 1990, 1991; Wardle *et al.* 1997). *Transgressive overyielding* (Trenbath 1974; Harper 1977; Vandermeer 1989) occurs when a mixture yields more than any monoculture of the component species ($D_{\max} > 0$ following Loreau (1998b)). In agricultural and intercropping research, transgressive overyielding has been of particular interest when the aim is to maximize yields either via monocultures or mixed cropping. However, in the context of changing biodiversity (extinctions and invasions) we argue that a wider range of comparisons is relevant. We therefore propose a new, general framework for overyield-

ing comparisons and demonstrate how and why results vary depending on which species is assumed to be the basis for the test.

METHODS

The EU-funded BIODDEPTH project (Hector *et al.* 1999) simulated the loss of plant species in grassland ecosystems by removing the existing vegetation and seed bank and re-establishing plant communities from seed. Using standardized protocols we established field sites in the UK at Silwood Park (Hector *et al.* 2000a; Hector *et al.* 2001) and Sheffield, and at single localities in Germany (Scherer-Lorenzen 1999), Ireland, Greece (Troumbis *et al.* 2000), Portugal (Caldeira *et al.* 2001), Sweden (Mulder *et al.* 1999) and Switzerland (Spehn *et al.* 2000). We summarize the relevant points here. The experiment manipulated plant diversity by varying the richness (numbers) and composition (types) of plant species and functional groups (we categorized our species into graminoids, nitrogen-fixing legumes and other herbaceous species, "herbs"). We assembled experimental communities, by constrained random selection from the local pools of grassland species to form partially crossed gradients of species richness and functional group richness where polycultures contained at least one grass. At each site, five levels of species richness ranged from monocultures to higher-diversity assemblages that approximately matched estimated background levels of diversity in comparable unmanipulated semi-natural grasslands. To replicate plant species richness, each of the five levels at each site was represented by several plant assemblages with different compositions. In addition, to quantify the overall effect of species composition, each assemblage, including monocultures of many of the species involved, was replicated in a minimum of two plots at each site. In total, the experiment comprised 480 plots, in which various ecosystem properties were measured. To help maintain the composition of the experimental communities all unsown species were periodically removed from the plots as required. We recorded species numbers over time (observed levels of diversity). For our analysis here, we use data on above-ground plant biomass production (plots were cut to 5 cm once or twice a year depending on site fertility) measured 2 years after establishment of the experimental communities (Hector *et al.* 1999; Loreau & Hector 2001; Spehn *et al.* 2002). We report analyses with planned levels of diversity here since these are more consistent with our experimental design, matched observed levels closely and produce the same results, but actually have greater explanatory power (Hector *et al.* 1999, 2000b; Schmid *et al.* 2002a).

We performed a variety of comparisons of the yields of mixtures relative to monocultures of different species.

Deviation (D) values (following Loreau 1998b) from the yield of a selected monoculture (D_{mono}) follow the general form:

$$D_{\text{mono}} = \frac{O_T - M_i}{M_i}$$

where O_T = the observed total yield of a selected polyculture and M_i = the monoculture yield of the species chosen for comparison. In principle every monoculture provides a potential comparison but here we examine the following three cases:

- 1 ' D_{site} ' – vs. the maximum monoculture yield of any of the species at a site (whether present in a mixture or not);
- 2 ' D_{mix} ' – vs. the maximum monoculture yield of any of the species in a mixture at a site;
- 3 ' D_{dom} ' – vs. the monoculture yield of the dominant species in a mixture at a site.

We also calculated a similar weighted average proportional deviation from expected values:

$$\bar{D} = \sum p_i D_i$$

where p_i is the proportion of species i in a mixture, and:

$$D_i = \frac{O_i - M_i}{M_i}$$

where O_i = the observed yield of species i in mixture and E_i = the expected yield: simply the monoculture yield times the initial proportion of the species in the mixture. D -values were transformed to meet the assumptions of analyses using natural logarithms after adding 1.1 to make all values positive (the minimum possible value of D is -1).

RESULTS

There was a wide range in above-ground biomass production by different species grown in monoculture at each location and by the same species grown at different sites. *Trifolium pratense* however, was an exception, achieving high biomass at three sites. Figure 1 shows the identity of the highest-yielding monoculture at each site, i.e. the species predicted by the SEH to dominate mixtures.

The relationship between biomass production in monoculture and dominance of polycultures was positive in Germany, Ireland, Sweden and Sheffield. However, there were notable deviations from this general pattern: in Portugal, Switzerland, Greece and Silwood, species of intermediate or low-to-intermediate monoculture biomass were most dominant in mixtures on average (Fig. 2a–h). We regressed dominance against monoculture biomass after adjusting for site differences in productivity by normalizing monoculture biomasses to proportions of the maximum value observed at each location, following a similar

methodology to Austin (1982); see Fig. 2 for details). The sample size was large (308 polycultures with between two and 32 species each, $N = 1090$) and therefore the analysis powerful, with any term always highly significant; therefore we focus on differences in explanatory power. The relationship between biomass production in monoculture and dominance in polycultures was positive and accounted for 9% of the total variation (Fig. 2i). To quantify the linear trend and deviation from it we performed contrast analysis (Rosenthal & Rosnow 1985) analogous to the log-linear species richness effect and deviation term in Hector *et al.* (1999). We used a general linear model which combined the regression reported above with a categorical variable with a level, 86 in total, for each normalized monoculture biomass (this amounts to performing the ANOVA after first removing the linear regression effect). The deviation from linearity explained a much larger amount of the variation, 44%, with 47% remaining as the unexplained residual.

We next tested the SEH assumption that the species with the highest-yielding monoculture at each site would dominate the mixtures it was present in, by regressing the dominance of the species (its biomass as a proportion of total community biomass) against plot species richness (Fig. 3). We tested two null hypotheses. First, we used F -tests from the regressions to test for strong dominance across the species richness gradients, as would be shown by regression slopes close to zero. Second, we performed t -tests on the regression slopes to compare the observed proportions of polyculture biomass with the slope of minus one given by the initial sowing proportions. We used a substitutive design with equal representation of all species in a mixture, so that the expected proportion for a species based on initial values was $1/N$, where N is the number of species in an assemblage (e.g. $1/2$ in a two-species assemblage). On a \log_2 scale a regression of the proportion of a species in a mixture would therefore have a slope of minus one. The relative abundance in mixture of the most productive monoculture species did not differ significantly from the initial relative abundance in the seed mixtures at half of our sites: in Portugal, Switzerland, Sweden and Silwood (Table 1). Further, in Greece the regression slope was significantly more negative, indicating that at high diversity *Bromus* had actually slightly declined in abundance since sowing. Similarly, in Silwood *Agrostis* (the species most productive in monoculture) was frequently found at lower than its initial abundance. Contrary to the predictions of the SEH, the proportional biomass of the most dominant species declined with increasing species richness at all sites. At five of the eight locations the negative regression slopes were significantly different from zero (Table 1). At the three other sites, Portugal, Sweden and Silwood, they were not significantly different from zero but they could also not be distinguished from the slope for initial abundance of minus

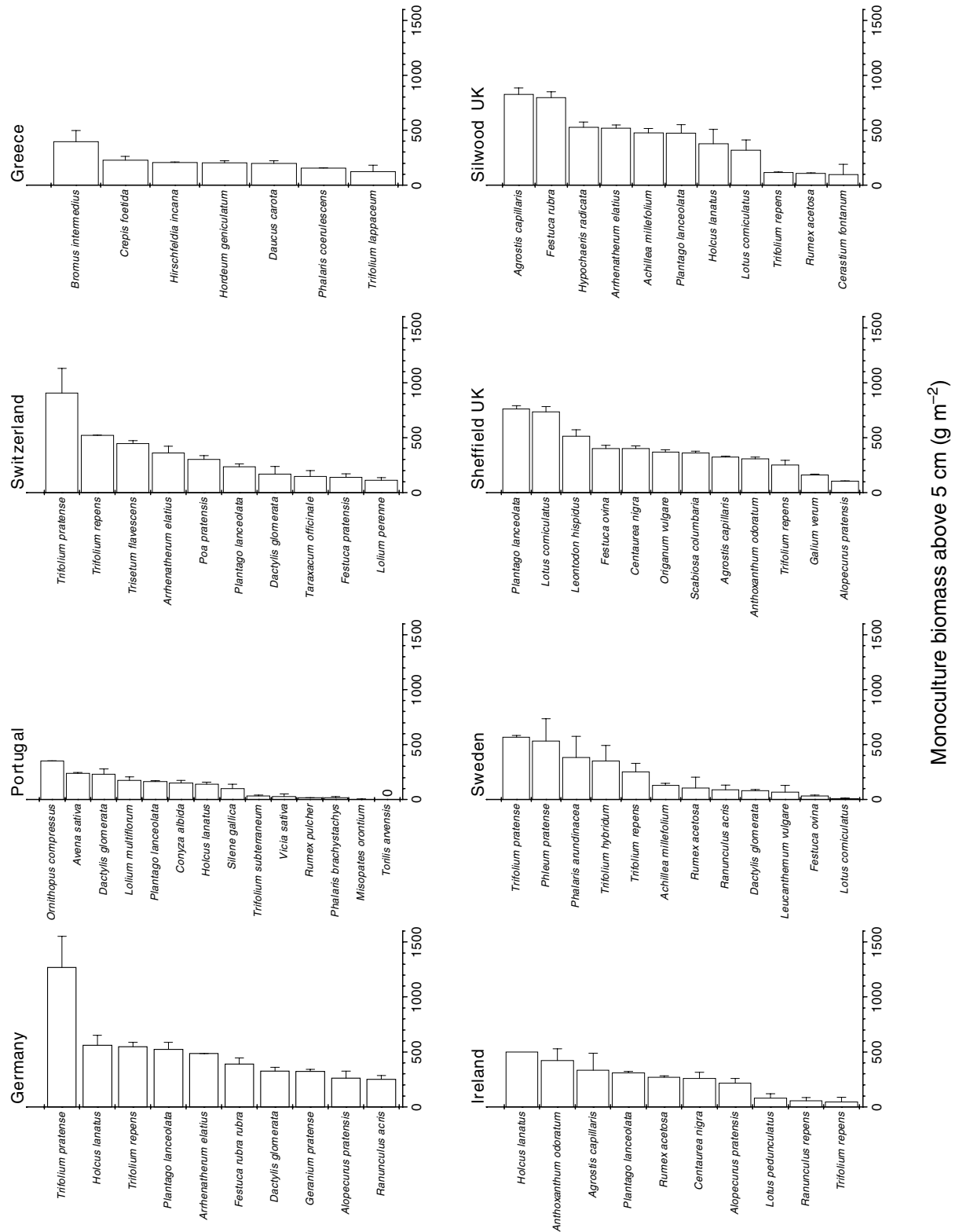


Figure 1 Above-ground biomass of species grown in monoculture at each site. The mean yield of replicate monocultures are shown with SEMs. Biomass depends on the interactive effects of species identity and location.

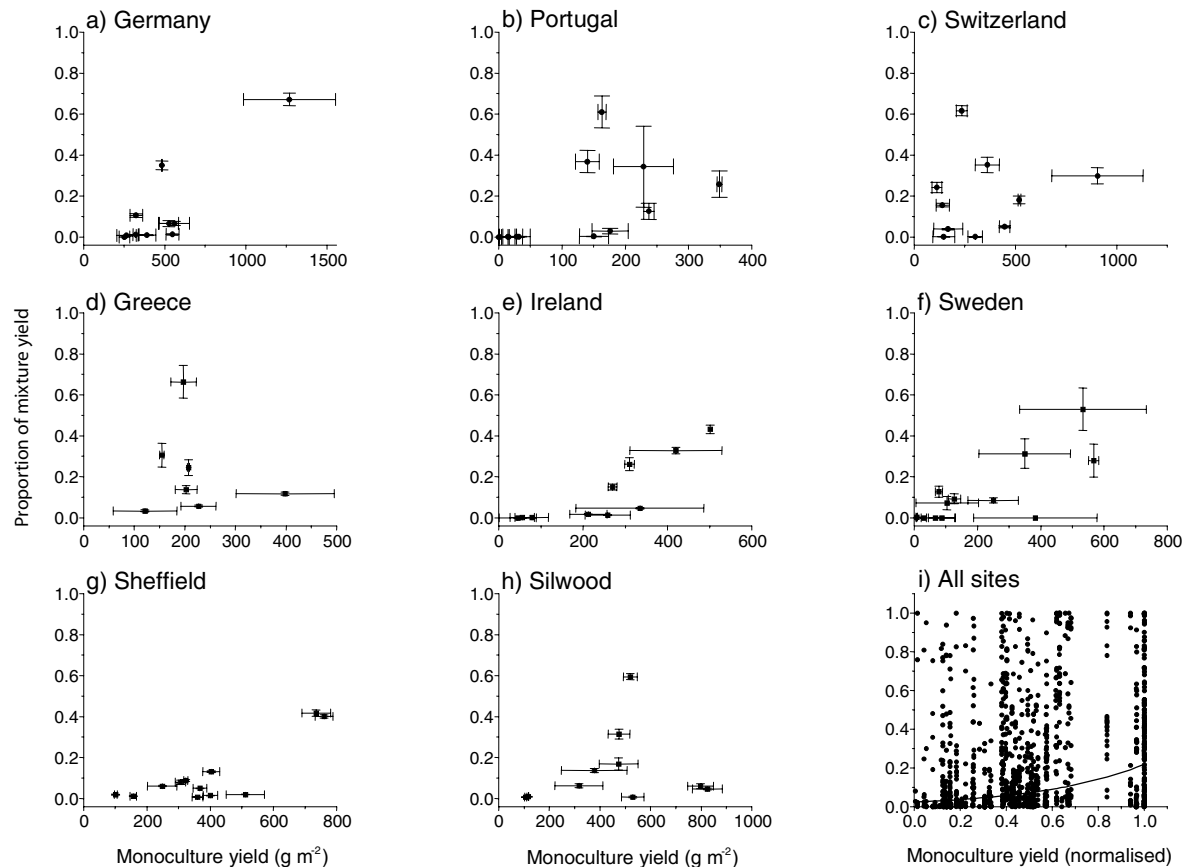


Figure 2 Dominance of mixtures (proportion of total above-ground biomass) as a function of monoculture biomass. (a–h) Average yield of paired monoculture plots and the average dominance across replicate polycultures (with SEMs) for each location (monoculture species identities available from Fig. 1). (i) Dominance of species in individual mixtures (points) vs. average monoculture yields normalized to the maximum at each location, for all sites combined. The line is the back-transformed slope from a regression of dominance (log-transformed to improve residual plots) on normalized monoculture yield. Regression: $r^2 = 0.09$, $P < 0.001$; deviation: $r^2 = 0.44$, $P < 0.001$; $N = 1090$.

one. In other words, the degree of scatter at these three sites was large and a wide range of slopes lay within the confidence intervals including both zero and minus one. However, although nonsignificant, the slopes in Portugal, Sweden and Silwood were negative. Similarly, even when species lay above the line of initial abundance, as in Germany, Ireland and Sheffield, dominance declined with increasing diversity. Therefore, in general we found little support for the prediction of the SEH that species that produce the highest yield in monoculture should dominate mixtures.

When compared to the most productive monoculture at a location, whereas many individual plots transgressively overyield, overall our mixtures generally underyield: the grand mean of D across all polycultures was significantly negative (Table 2; Fig. 4a). There was a significant effect of location and positive effects of both species and functional group richness on overyielding, with Ireland having both a

positive slope and intercept. As with all of the following comparisons, species composition had a highly significant effect on D . However, because our mixtures were selected at random (with some constraints) from the species pools at each location, many of the mixtures did not contain the species which was most productive in monoculture at a site. To avoid confounding differences in species composition (absence of the species with the highest-yielding monoculture at a site) with differences in species richness (see also Hector *et al.* 2000b), we also compared the yield of each mixture with the maximum monoculture yield of any species present in that mixture. Highly significant effects of composition and location remained, as did a slightly negative grand mean, although values at many sites were now close to zero and there was no significant effect of species richness on average, only the functional component was significant (Table 2; Fig. 4b). Therefore, both of these tests for what we call “agricultural overyielding” (producing more than the

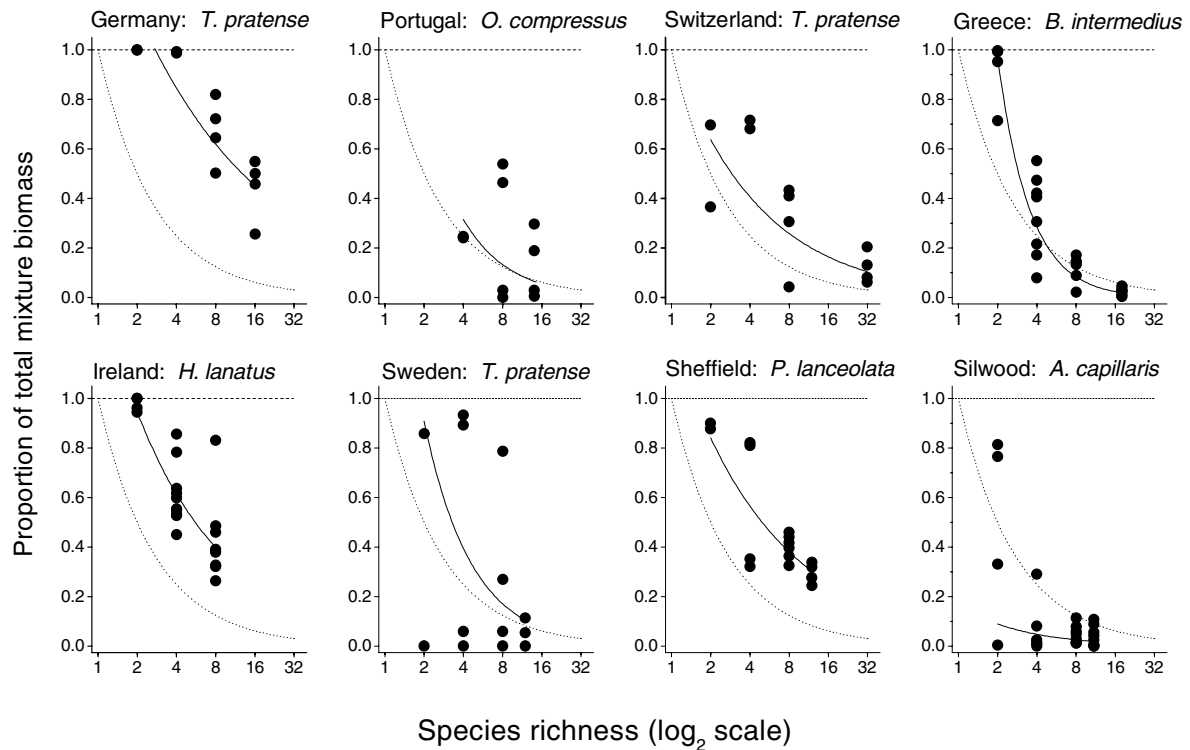


Figure 3 Dominance of mixtures by the species that was most productive in monoculture at each site in relation to species richness. Complete dominance is shown by the dashed horizontal line and initial proportions in the seed mixtures by the curved dashed line.

Table 1 Species richness and the relative abundance in mixture of the species with the highest monoculture biomass at each site. “Slope” gives estimates of linear regressions of proportion of total above-ground biomass vs. species richness, both on a \log_2 scale. Observed slopes are tested for significant differences from the slope of minus one for initial abundances (by t -test) and from a model of complete dominance with a slope of zero (by F -test from regressions). N , sample size for the regressions (excluding zero values). Significant values ($P < 0.05$) are highlighted in bold

Site	Species	Test vs. -1 slope of initial abundance					Test vs. 0 slope of complete dominance	
		Slope	SE	N	t	P	F	P
Germany	<i>Trifolium pratense</i>	-0.45	0.096	12	5.73	< 0.001	21.85	< 0.001
Portugal	<i>Ornithopus compressus</i>	-1.24	1.020	9	-0.24	0.821	1.49	0.262
Switzerland	<i>Trifolium pratense</i>	-0.65	0.210	12	1.67	0.126	9.51	0.012
Greece	<i>Bromus intermedius</i>	-1.76	0.171	26	-4.44	< 0.001	106.11	< 0.001
Ireland	<i>Holcus lanatus</i>	-0.62	0.105	22	3.62	0.002	34.67	< 0.001
Sweden	<i>Trifolium pratense</i>	-1.20	0.667	9	-0.30	0.773	3.22	0.116
Sheffield	<i>Plantago lanceolata</i>	-0.57	0.113	16	3.81	0.002	25.68	< 0.001
Silwood	<i>Agrostis capillaris</i>	-0.89	0.591	25	0.19	0.854	2.25	0.148

highest-yielding monoculture in a particular mixtures or at a site in general, both forms of transgressive overyielding) show that although particular high-yielding mixtures often overyield, overall polycultures did not outperform the highest-yielding monocultures.

However, one limitation of these tests for transgressive overyielding is that, as demonstrated above (Figs 2 and 3),

they often compare the yield of a mixture with the monoculture yield of a species that is not dominant in that mixture and which is sometimes only a minor component. An alternative test that we performed was to compare the total yield of a mixture with the monoculture yield of the dominant species in that mixture (Hector *et al.* 1999, 2000b). If the SEH was supported this would amount to

Table 2 Summary of overyielding analyses comparing polyculture and monoculture yields with either the highest-yielding monoculture at a site (D_{site}), the highest-yielding monoculture in a mixture (D_{mix}), the monoculture yield of the dominant species in each mixture (D_{dom}), or the weighted average of all species (\bar{D}). “Grand mean” tests the average deviation across all polycultures vs. the null expectation of zero and later lines test the effects of location and diversity components. Values were transformed using natural logarithms for analysis after adding 1.1 to make all values positive (we subtracted the natural log of 1.1 from all values to re-scale them so that the analysis tested the grand mean vs. zero)

Source	D_{site}			D_{mix}			D_{dom}			\bar{D}		
	d.f.	MS	<i>F</i>	d.f.	MS	<i>F</i>	d.f.	MS	<i>F</i>	d.f.	MS	<i>F</i>
Grand mean	1	34.87	116.21***	1	7.64	28.09***	1	4.17	12.8***	1	14.53	65.37***
Location	7	4.95	16.49***	7	3.46	13***	7	1.05	3.22**	7	0.46	2.06(*)
Block	6	0.28	4.09***	7	0.54	5***	7	0.36	2.39*	8	0.30	3.40**
Species richness (\log_2)	1	6.70	22.33***	1	0.79	2.9	1	1.68	5.16*	1	1.91	8.58**
Deviation	8	0.36	1.21	8	0.32	1.2	8	0.34	1.03	5	0.20	0.89
Functional richness	1	3.53	11.77***	1	1.48	5.4*	1	1.23	3.78(*)	1	1.28	5.75*
Deviation	1	0.13	0.42	1	0.05	0.2	1	0.53	1.62	1	0.65	2.91(*)
Location × species richness	7	0.40	1.32	7	0.19	0.7	7	0.38	1.16	6	0.18	0.82
Location × functional richness	6	0.29	0.98	7	0.26	1	7	0.27	0.81	7	0.17	0.75
Species composition	117	0.30	4.43***	112	0.27	2.5***	105	0.33	2.16***	87	0.22	2.51***
Residual	152	0.07		147	0.11		129	0.15		81	0.09	
Total	306	0.33		298	0.28		273	0.27		204	0.19	

(*) means $0.05 < P < 0.1$; * $P < 0.05$; ** $P < 0.01$, *** $P < 0.001$.

the same test as performed above (Fig. 4b), but because the most-productive monoculture species do not always dominate mixtures it produces a different answer. When compared to the monoculture yield of the dominant species in a mixture the presence of additional species does cause mixtures to transgressively overyield; the grand mean is significantly positive and although locations again differ there are positive effects of species and (marginally) functional group richness on overyielding (Table 2; Fig. 4c). Non-transgressive overyielding showed the same qualitative pattern as for the comparison with the dominant species yields: a positive grand mean, significant effects of location and composition and positive slopes for both species and (marginally) functional group richness (Table 2; Fig. 4d).

DISCUSSION

Our results indicate that the relationship between production in monoculture and in mixtures is more complex than the simple positive relationship predicted by the SEH. Similar results have been found in experiments on a Californian serpentine grassland (Hooper & Vitousek 1998; Dukes 2001) and in experimental wetland communities (Engelhardt & Ritchie 2001). In biodiversity experiments in glasshouses, mixture yields are well predicted in some cases (e.g. Spaekova & Leps 2001) but not others (e.g. Naeem *et al.* 1996).

A mechanistic understanding of species interactions will be needed to explain the lack of a simple positive relationship between monoculture and mixture yields. We predict that this arises due to trade-offs within species between allocation to growth and competition (e.g. leaves vs. stems; Tilman 1988) or between competitive abilities for different resources (e.g. nitrogen vs. phosphorous) and due to variation in which resources are being competed for in a given environment. Therefore different plant traits can be associated with competitive dominance (Trenbath 1974). For example, consider the situation where there is strong competition for light. In this case, a plant's ability to overtop and shade its neighbours before they overtop it may be a better predictor of competitive success than annual above-ground production observed in monoculture. To quickly establish a tall canopy a plant must allocate more resources to stems, some of which could otherwise have gone into leaves which have a higher return relative to their cost. In other words, to be a successful competitor for light in a mixture a plant must sacrifice some of its potential production when growing in monoculture. For example, the experimental communities at Silwood were dominated by *Arrhenatherum elatius* (Figs 2 and 3) whereas the potentially more productive *Agrostis capillaris* and *Festuca rubra* (Fig. 1) were subordinate within many mixtures (Figs 2 and 3). Although *Arrhenatherum* had much lower monoculture productivity than these other species, it was able to quickly elevate its canopy higher than them, a trait which correlated with its dominance better than its

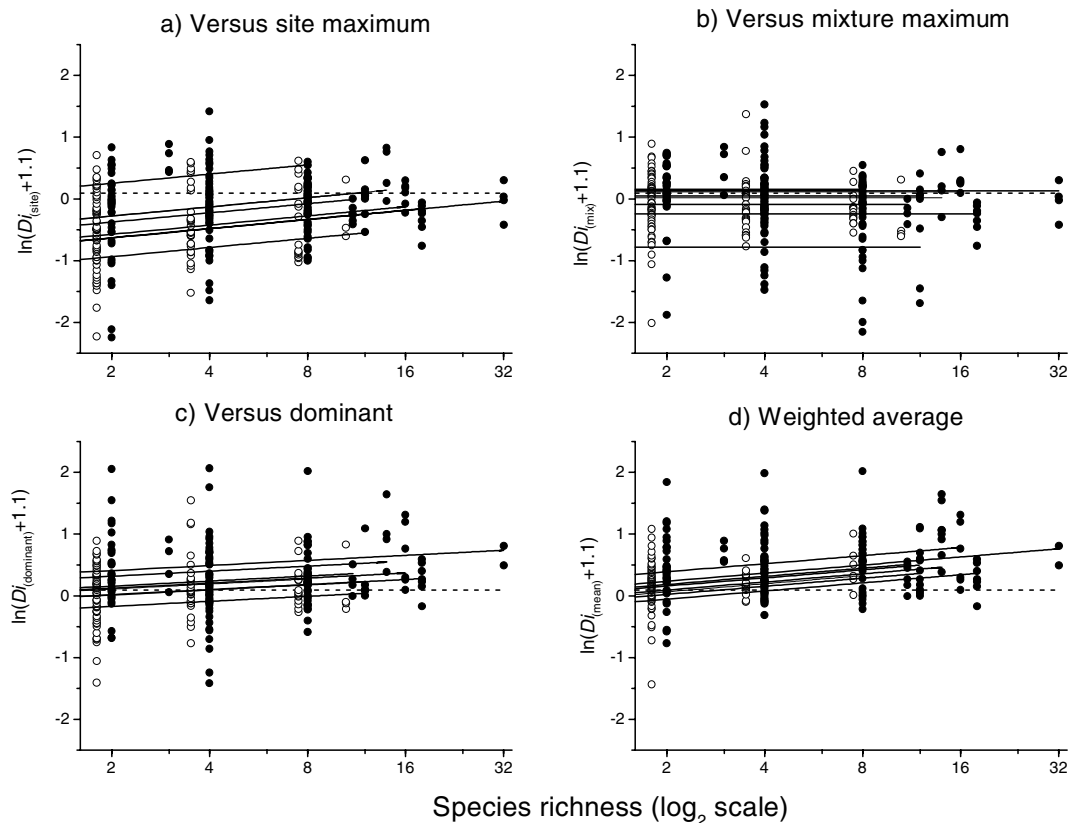


Figure 4 Comparison of four different overyielding tests. Polyculture yields were compared with the monoculture yields of either: (a) the highest-yielding monoculture at a site (D_{site}); (b) the highest-yielding monoculture of the species in a mixture (D_{mix}); (c) the monoculture yield of the dominant species in each mixture (D_{dom}); or (d) the weighted average of all species (\bar{D}) – see Methods for details of calculations. The dotted line shows the null prediction of $\ln[0 + 1.1]$ (for analysis values were rescaled to zero by subtracting $\ln[1.1]$ – see Table 2). Closed circles, polycultures with legumes, and open circles, those without, have been staggered slightly for clarity.

biomass and several other traits as measured in monoculture. In general, we predict that the resource competition component of the selection effect will depend in large part upon which resources are being competed for and therefore on which traits are associated with competitive dominance, given the inevitable trade-offs in resource allocation that organisms face (e.g. Bloom *et al.* 1985; Tilman 1988; King 1990; Schmid & Bazzaz 1994).

The relationship between mixture and monoculture yields, particularly the occurrence or not of overyielding, has become a critical issue in interpreting biodiversity experiments. However, the fact that the species with the most productive monocultures often do not dominate mixtures has important consequences for the assessment of whether mixtures transgressively overyield or not. In our experiment, when compared to monocultures of the species dominant in each mixture, on average the polycultures did overyield transgressively. This was because the species that dominated many mixtures were not those that were highest-yielding in monoculture, and resource partitioning was strong enough

to significantly increase mixture yield relative to these monocultures. However, some of the subordinate species in mixtures were high-yielding in monoculture and resource partitioning and positive interactions were not strong enough to increase yields above these levels. That is, our mixtures did not show what we have called “agricultural” (transgressive) overyielding on average, even though it was clearly possible in some cases at every site both with and without legumes (Fig. 4). This lack of widespread agricultural overyielding, in spite of the presence of resource partitioning and positive interactions, is due to negative selection effects and is similar in qualitative terms to the results discussed above (Hooper & Vitousek 1997; Dukes 2001; Engelhardt & Ritchie 2001). Reviews of agricultural (Vandermeer 1989) and ecological experiments with species mixtures have found that overyielding frequently occurs but is by no means the rule: non-transgressive overyielding occurred in 53% of cases and transgressive overyielding in 24% in the first major reviews of these data (Trenbath 1974; Harper 1977) and a more recent review estimated the average strength of

non-transgressive overyielding at 12% (Jolliffe 1997). In contrast, the long-term biodiversity experiment at Cedar Creek shows marked transgressive overyielding after seven years (Tilman *et al.* 2001). This raises the question of whether the reviewed literature accurately reflects the occurrence of niche differentiation and overyielding or whether some of this work was conducted under conditions where resource partitioning is not fully developed (Jolliffe 1997; Hector *et al.* 2000b). In regard to our results, it is important to point out two things. First, that we report patterns from only the second year of our experiment and both selection and complementarity would no doubt change somewhat over time (although the general results of the BIODEPTH project over three to five years, depending on site, appear to remain fairly consistent). Second, that although, overall, our mixtures did not overyield the highest-yielding monocultures, this test is very demanding in that it compares the average over all mixtures against the single highest monoculture yield. However, if we instead focus on the highest-yielding polycultures then many mixtures did transgressively overyield even the best monocultures (Fig. 4).

The results presented here are consistent with related analyses that we have presented elsewhere; in particular, the average weighted deviation, \bar{D} , shows a similar positive log-linear relationship as did the complementarity effect presented by Loreau & Hector (2001) for the same data set. Our new results should also help resolve apparently contradictory analyses presented in the literature (Hector *et al.* 2000b; Huston *et al.* 2000). We have shown how a difference between agricultural overyielding (vs. the maximum monoculture yield) and comparisons with dominant species yields in monoculture can arise when the species that are most productive in monoculture do not dominate mixtures. Furthermore, comparisons of mixture yields with the monoculture yields of species that they do not even contain (Fig. 4a), as may be the case for some plots in Huston *et al.* (2000), is likely to produce more negative values than when considering species that are present in mixtures, particularly at low diversity where the most productive species are more likely to be absent (Fig. 4b). It is also essential to distinguish between these tests for transgressive overyielding compared to single species, as opposed to non-transgressive overyielding which considers a weighted average of all species in a mixture (Garnier *et al.* 1997; Hector 1998; Hooper & Vitousek 1998; Loreau 1998b). In addition, it is essential to remember that it is also possible for mixtures with RYTs of 1–2 to yield less than the highest-yielding monoculture depending on how strongly the higher- and lower-yielding species differ in monoculture yields and experience resource partitioning and positive and negative interactions (Schmid *et al.* 2002b).

To summarize, we found that, counter to the SEH, species which yielded most in monocultures often did not

dominate mixtures. Because of this, mixture yields did not equal or exceed the highest-yielding monocultures on average despite the presence of positive interactions and resource partitioning that caused many mixtures with particular compositions to overyield. On the other hand, because the highest-yielding monoculture species were not dominant, it is not clear that they are the most relevant comparison for mixtures. Compared to the yield of the dominant species grown alone, the presence of resource partitioning and positive interactions did increase the yields of mixtures. Thus, just as the response of ecosystem processes to changes in diversity depends on exactly which species are lost, the judgement of whether mixtures transgressively overyield also depends on which species are chosen for comparison. We therefore propose a new general framework for overyielding analyses where every monoculture provides a potential comparison and from which the most relevant can be selected.

ACKNOWLEDGEMENTS

Our thanks to our BIODEPTH colleagues and to Mike Austin, Jan Leps, Shahid Naeem, Andy Wilby and Owen Petchy for their advice and suggestions.

REFERENCES

- Aarssen, L.W. (1997). High productivity in grassland ecosystems: effected by species diversity or productive species? *Oikos*, 80, 183–184.
- Austin, M.P. (1982). Use of a relative physiological performance value in the prediction of performance in multispecies mixtures from monoculture performance. *J. Ecol.*, 70, 559–570.
- Bazzaz, F.A. & Catovsky, S. (2001). Resource partitioning. In: *Encyclopedia of Biodiversity*. Academic Press, San Diego.
- Bell, G. (1990). The ecology and genetics of fitness in *Chlamydomonas*. 2. The properties of mixtures of strains. *Proc. R. Soc. London B*, 240, 323–350.
- Bell, G. (1991). The ecology and genetics of fitness in *Chlamydomonas*. 4. The properties of mixtures of genotypes of the same species. *Evolution*, 45, 1036–1046.
- Berendse, F. (1982). Competition between plant populations with different rooting depths III. Field experiments. *Oecologia*, 53, 50–55.
- Bloom, A.J., Chapin, F.S.I. & Mooney, H.A. (1985). Resource limitation in plants – an economic analogy. *Ann. Rev. Ecol. Syst.*, 16, 363–392.
- Caldeira, M.C., Ryel, R.J., Lawton, J.H. & Pereira, J.S. (2001). Mechanisms of positive biodiversity–production relationships: insights provided by ^{13}C analysis in experimental Portuguese grassland plots. *Ecol. Lett.*, 4, 439–443.
- Dukes, J.S. (2001). Productivity and complementarity in grassland microcosms of varying diversity. *Oikos*, 94, 468–480.
- Engelhardt, K.A.M. & Ritchie, M.E. (2001). Effects of macrophyte species richness on wetland ecosystem functioning and services. *Nature*, 411, 687–689.

- Garnier, E., Navas, M.-L., Austin, M.P., Lilley, J.M. & Gifford, R.M. (1997). A problem for biodiversity–productivity studies: how to compare the productivity of multispecific plant mixtures to that of monocultures? *Acta Oecologica*, 18, 657–670.
- Harper, J.L. (1977). *Population Biology of Plants*. Academic Press, London.
- Hector, A. (1998). The effect of diversity on productivity: detecting the role of species complementarity. *Oikos*, 82, 597–599.
- Hector, A., Beale, A., Minns, A., Otway, S. & Lawton, J.H. (2000a). Consequences of loss of plant diversity for litter decomposition: mechanisms of litter quality and microenvironment. *Oikos*, 90, 357–371.
- Hector, A., Dobson, K., Minns, A., Bazeley-White, E. & Lawton, J.H. (2001). Community diversity and invasion resistance: an experimental test in a grassland ecosystem and a review of comparable studies. *Ecol. Res.*, 16 (Supplement), in press.
- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., *et al.* (1999). Plant diversity and productivity experiments in European grasslands. *Science*, 286, 1123–1127.
- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., *et al.* (2000b). No consistent effect of plant diversity on productivity? Response. *Science*, 289, 1255a.
- Hooper, D.U. & Vitousek, P.M. (1997). The effects of plant composition and diversity on ecosystem processes. *Science*, 277, 1302–1305.
- Hooper, D.U. & Vitousek, P.M. (1998). Effects of plant composition and diversity on nutrient cycling. *Ecol. Monogr.*, 68, 121–149.
- Huston, M.A. (1997). Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, 110, 449–460.
- Huston, M.A., Aarssen, L.W., Austin, M.P., Cade, B.S., Fridley, J.D., Garnier, E., Grime, J.P., Hodgson, J., Laurenroth, W.K., Thompson, K., Vandemeer, J.H. & Wardle, D.A. (2000). No consistent effect of plant diversity on productivity? *Science*, 289, 1255a.
- Jolliffe, P.A. (1997). Are mixed populations of plant species more productive than pure stands? *Oikos*, 80, 595–602.
- King, D.A. (1990). The adaptive significance of tree height. *Am. Nat.*, 136, 809–828.
- Loreau, M. (1998a). Biodiversity and ecosystem functioning: a mechanistic model. *Proc. Nat. Acad. Sci. USA*, 95, 5632–5636.
- Loreau, M. (1998b). Separating sampling and other effects in biodiversity experiments. *Oikos*, 82, 600–602.
- Loreau, M. (2000). Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos*, 91, 3–17.
- Loreau, M. & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412, 72–76 [erratum: 413, 548].
- Mulder, C.P.H., Koricheva, J., Huss-Danell, K., Högberg, P. & Joshi, J. (1999). Insects affect relationships between plant species richness and ecosystem processes. *Ecol. Lett.*, 2, 237–246.
- Naeem, S., Håkansson, K., Lawton, J.H., Crawley, M.J. & Thompson, L.J. (1996). Biodiversity and plant productivity in a model assemblage of plant species. *Oikos*, 76, 259–264.
- Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1994). Declining biodiversity can alter the performance of ecosystems. *Nature*, 368, 734–737.
- Rosenthal, R. & Rosnow, R.L. (1985). *Contrast Analysis*. Cambridge University Press, Cambridge.
- Scherer-Lorenzen, M. (1999). Effects of plant diversity on ecosystem processes in experimental grassland communities. *Bayreuther Forum Ökologie*, 75, 1–195.
- Schmid, B. & Bazzaz, F.A. (1994). Crown construction, leaf dynamics, and carbon gain in two perennials with contrasting architecture. *Ecol. Monogr.*, 64, 177–203.
- Schmid, B., Hector, A., Huston, M.A., Inchausti, P., Nijs, I., Leadley, P.W. & Tilman, D. (2002a). The design and analysis of biodiversity experiments. In: *Biodiversity and Ecosystem Functioning* (eds Loreau, M., Naeem, S. & Inchausti, P.). Oxford University Press, Oxford. in press.
- Schmid, B., Joshi, J. & Schläpfer, F. (2002b). Empirical Evidence for Biodiversity-Ecosystem Functioning Relationships. In: *Functional Consequences of Biodiversity: Experimental Progress and Theoretical Extensions* (eds Kinzig, A., Tilman, D. & Pacala, S.P.). Princeton University Press, Princeton, NJ, 71–95.
- Spakova, I. & Leps, J. (2001). Procedure for separating the selection effect from other effects in diversity-productivity relationships. *Ecol. Lett.*, 4, 585–594.
- Spehn, E.M., Joshi, J., Schmid, B., Diemer, M. & Körner, C. (2000). Aboveground resource use increases with plant species richness in experimental grassland ecosystems. *Funct. Ecol.*, 14, 326–337.
- Spehn, E.M., Scherer-Lorenzen, M., Schmid, B., Hector, A., Caldeira, M.C., Dimitrakopoulos, P.G., Finn, J.A., Jumpponen, A., O'Donovan, G., Pereira, J.S., Schulze, E.-D., Troumbis, A.Y. & Körner, C. (2002). The role of legumes as a component of biodiversity in a cross-European study of grassland biomass nitrogen. *Oikos*, in press.
- Tilman, D. (1988). *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, NJ.
- Tilman, D., Lehman, C.L. & Thomson, K.T. (1997). Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Nat. Acad. Sci. USA*, 94, 1857–1861.
- Tilman, D., Reich, P.B., Knops, J.M.H., Wedin, D., Mielke, T. & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science*, 294, 843–845.
- Tilman, D., Wedin, D. & Knops, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, 379, 718–720.
- Trenbath, B.R. (1974). Biomass productivity of mixtures. *Adv. Agron.*, 26, 177–210.
- Troumbis, A.Y., Dimitrakopoulos, P.G., Siamantziouras, A.-S.D. & Memtsas, D. (2000). Hidden diversity and productivity patterns in mixed Mediterranean grasslands. *Oikos*, 90, 549–559.
- Vandermeer, J. (1989). *The Ecology of Intercropping*. Cambridge University Press, Cambridge.
- Wardle, D.A., Bonner, K.I. & Nicholson, K.S. (1997). Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos*, 79, 247–258.

Editor, S. Naeem

Manuscript received 14 December 2001

First decision made 25 January 2002

Manuscript accepted 27 February 2002