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Plant species diversity as a driver of early succession in abandoned fields: a multi-site approach

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Abstract Succession is one of the most studied processes in ecology and succession theory provides strong predictability. However, few attempts have been made to influence the course of succession thereby testing the hypothesis that passing through one stage is essential before entering the next one. At each stage of succession ecosystem processes may be affected by the diversity of species present, but there is little empirical evidence showing that plant species diversity may affect succession. On ex-arable land, a major constraint of vegetation succession is the dominance of perennial early-successional (arable weed) species. Our aim was to change the initial vegetation succession by the direct sowing of later-successional plant species. The hypothesis was tested that a diverse plant species mixture would be more successful in weed suppression than species-poor mixtures. In order to provide a robust test including a wide range of environmental conditions and plant species, experiments were carried out at five sites across Europe. At each site, an identical experiment was set up, albeit that the plant species composition of the sown mixtures differed from site to site. Results of the 2-year study showed that diverse plant species mixtures were more effective at reducing the number of natural colonisers (mainly weeds from the seed bank) than the average low-diversity treatment. However, the effect of the low-diversity treatment depended on the composition of the species mixture. Thus, the effect of enhanced species diversity strongly depended on the species composition of the low-diversity treatments used for comparison. The effects of high-diversity plant species mixtures on weed suppression differed between sites. Low-productivity sites gave the weakest response to the diversity treatments. These differences among sites did not change the general pattern. The present results have implications for understanding biological invasions. It has been hypothesised that alien species are more likely to invade species-poor communities than communities with high diversity. However, our results show that the identity of the local species matters. This may explain, at least partly, controversial results of studies on the relation between local diversity and the probability of being invaded by aliens.

Key words Biodiversity · Ecosystem functioning · Land use changes · Weed suppression · Invasiveness

Introduction

Growing awareness of the rapid loss of global biodiversity has stimulated the discussion on the functional relationship between species diversity and ecosystem processes (e.g. Schulze and Mooney 1993; Heywood 1995). At local and regional scales, land-use changes are among the most immediate drivers of species diversity. Intensification of land use, especially the conversion of natural ecosystems into agro-ecosystems is supposed to both change the composition and reduce the diversity of biological communities (Burel et al. 1998; Medail et al. 1998; Schläpfer and Schmid 1999; Schläpfer et al. 1999). Therefore, one of the possible ways of counteracting the current loss of biodiversity may be to reduce the

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intensity of land use (in the case of grassland), or to abandon cultivated land (in the case of arable land).

Vegetation development on permanently abandoned arable land (also known as old field succession) has acted as a model for many ecological studies on succession (Lepš et al. 1982; Tilman 1982; Brown and Gange 1989, 1990; Bazzaz 1996; Olff et al. 1997). Changes in plant composition over time depend on the availability of propagules (Bekker et al. 1997; Thompson et al. 1997; S.R. Mortimer, unpublished work), changes in soil fertility (Marrs 1993), above- and belowground herbivore acitvity (Brown and Gange 1989; Bowers 1993; Olff and Ritchie 1998), the presence or absence of mutualistic symbionts (Clay and Holah 1999) as well as feedbacks between plant species and their associated soil communities (Bever et al. 1997; Westover et al. 1997). The final outcome of all these interactions determines which species may, at a certain stage of succession, successfully compete for the available resources.

Ongoing long-term studies show that the development of a species-rich vegetation on abandoned arable land is often constrained even when natural abiotic conditions have been restored (Bakker and Berendse 1999). One of the main reasons is that the seed bank has been depleted (Bekker et al. 1997) and that many late-succession species have poor seed (or propagule) dispersal (Bakker and Berendse 1999). Another constraint, which has received less attention, is that persistent competitive weed species may prevent vegetation development for many years (Lepš and Rejmánek 1991; Burch 1996; Hansson and Hagelfors 1998). The first plant species to become established on abandoned arable land are weedy species that are already present in the seed bank (Bekker et al. 1997). These are opportunists with relatively poor root exploitation capacity (Grime 1979). During the initial stage of land abandonment the initial colonising plant species are replaced by persistent perennials (Hansson and Hagelfors 1998; Kosola and Gross 1999). If plant propagules reach abandoned arable land by the time the vegetation is dominated by persistent perennials, poor establishment conditions can be crucial constraints of succession to species-rich vegetation.

One of the main questions concerning succession is to which extent the trajectory may be predictable or not. In particular, could succession be enhanced, if dominance of the weedy species in the early stage of vegetation development is suppressed? How should weed suppression be achieved? What will be the consequence of the different succession pathways for ecosystem processes, such as productivity and resource utilisation, as well as species composition of both above- and belowground communities? What will be the subsequent effects of feedback to vegetation development through initial manipulation of vegetation after land abandonment? And, finally, how general may results be when obtained in specific conditions? These questions were addressed by an international project team (CLUE: changing land usage, enhancement of biodiversity and ecosystem development) under the Fourth Framework Environment and Climate Program of the European Commission. In the present paper, we present the approach and first results of the CLUE project.

The general aim of CLUE was to examine whether manipulation of above- and/or belowground species diversity on abandoned arable land could influence initial vegetation development, diversity and abundance of non-manipulated species groups, as well as ecosystem processes (productivity, nutrient uptake). This paper focuses on the suppression of early-successional (arable weed) species by more or less diverse species mixtures of later-successional plant species. The diversity treatments contained 4 (low diversity) or 15 (high diversity) plant species. Low-diversity assemblages varied between replicates to take account of sampling effects (see comments by Huston 1997 and others on initial diversity studies of Naeem et al. 1994; Tilman 1996; and replies by Tilman 1997a; Lawton et al. 1998). We did not test for effects of different functional groups (as shown to be important in serpentine grassland, Hooper and Vitousek 1998; and for Minnesota prairie ecosystems, Tilman 1997b), as there may be many different and possibly opposing functions of plant species during secondary succession. However, in order not to exclude dominants from the mixtures (Grime 1998) or plant species with special traits (such as legumes), plants were stratified to three species groups (grasses, legumes and other forbs), all of which were present in both diversity treatments.

We tested the hypothesis that high-diversity mixtures of later-successional plant species are better able to suppress early successional (arable weed) species than low-diversity species mixtures. Arguments for this hypothesis may be derived from the hypothesis of Elton (1958) on invasiveness. According to Elton (1958) exotics will be more likely to invade areas with low species diversity than areas with high species diversity. At continental scales, Elton’s hypothesis is generally supported (Rejmánek 1996), and several studies, e.g. of species-poor islands (Vitousek et al. 1996), have shown that species-poor vegetation may be sensitive to invasions. In addition to the work on invasiveness, which concerns non-native species, Tilman (1997b) showed that diverse prairie plant communities are less well invaded by sown mixtures of native species than species-poor communities. There are, however, also many arguments that do not support Elton’s hypothesis (e.g. Robinson and Quinn 1988; Rejmánek 1996), so that our alternative hypothesis is that plant species diversity does not matter for suppressing early-successional species.

The hypothesis was tested using a standard experimental design at five field sites in different European countries. As the five field sites differed in climate, soil type, and cropping history, later-successional plant species chosen for the experiment differed from site to site (with some overlap). The experimental design, therefore, enables testing of the robustness of results for a fairly wide range of conditions and species.

Table 1 Description of experimental sites

	Netherlands	Sweden	United Kingdom	Spain	Czech Republic
Name	Mossel	Trolleholm	Bradenham	Muñovela	Benešov
Coordinates	52°04′N 05°45′E	55°45′N 13°15′E	51°40′N 0°48′W	40°54′N 5°45′W0	49°20′N 15°00′E
Altitude[a]	30	85	140	840	659
Slope (%)	0	0	15–20	2	0
Mean temperature	9.4	7.5	9.6	10.8	6.4
Warmest month[b]	July (22.1)	July (17.1)	July (16.5)	Aug (29.9)	July (16.4)
Coldest month[b]	Jan (4.3)	Jan (–0.9)	Jan (3.6)	Jan (0.8)	Jan (–2.7)
Average rainfall[c]	0.84	0.7	0.75	0.5	0.68
Wettest month[c]	Aug (0.13)	July	Oct (0.065)	Nov (0.099)	Jul (0.078)
Driest month[c]	Feb (0.075)	Feb	Feb (0.041)	June (0.017)	Feb (0.036)
Soil type	Sandy loam	Clay	Brown rendzina (chalk)	Loamy clay	Brown soil on ground rock
Last crop (1995)	Maize	*Lolium perenne*	*Hordeum vulgare*	*Medicago sativa*	*Hordeum vulgare*
Other crops	Sugar beet, potatoes, oats, *Lolium perenne*	Winter wheat, spring rape	Winter wheat, *Brassica napus*, set-aside	*Triticum sativum*, *Hordeum vulgare*, set-aside	*Solanum tuberosum*, *Pisum sativum*
Surrounding vegetation	Heath, mixed forest, abandoned arable land	Deciduous forest, cultured field	Chalk grassland, deciduous forest	*Dehesa*-like woodland (*Quercus rotundifolia* Lam)	Arable land and recently established species-poor grassland

[a] m above sea level
[b] Long-term data: mean (°C)
[c] m year^{-1}

Table 2 Chemical and physical soil characteristics (country codes as in Table 3)

	Country				
	NL	SE	UK	SP	CZ
Soil characteristic					
pH H_2O	6.42	6.61	7.98	7.84	5.88
pH KCl	5.81	5.75	7.59	7.27	4.95
pH $CaCl_2$	5.88	6.06	7.51	7.41	5.41
%$CaCO_3$	0.15	0.11	73.8	0.07	0.11
%Organic matter	4.5	5.76	5.94	2.14	4.88
Electrical conductivity (μS m^{-2})	7.26	7.09	18	194	146
Available P (mg per 100 g)	110	32	22.8	24.6	24.3
P total (mg per 100 g)	1127	718	1326	298	803
N total (mg per 100 g)	1330	1850	2000	731	1538
Na (mEq per 100 g soil)	8.15	11.8	7.31	39.6	3.75
K (mEq per 100 g soil)	75.1	83.4	28.8	56.3	95.3
Mg (mEq per 100 g soil)	62.9	65.1	11.5	260	90
$CaCl_2$ (mg per 100 g soil)	2.76	2.56	4.6	16	1.99
Grain size distribution (μm)[a]					
<2	3.44	15.6	15	20.2	14.0
<63	17.3	60.6	59.7	38.7	43
>63	79.7	34.2	13	61.3	60

[a] <63 includes <2

Materials and methods

Site description and soil analyses

Field experiments were set up at five sites in Europe, representing a gradient from Boreal to Mediterranean: Sweden (SE), United Kingdom (UK) and the Netherlands (NL), Spain (SP) and a gradient from Atlantic to Continental: UK, NL, Czech Republic (CZ). All sites were on former agricultural land where arable crops had been grown, in most cases according to a crop rotation scheme, until the experiment was started. The experimental fields were installed in spring 1996 (data on field site characteristics are given in Table 1).

At the start of the experiment, soil samples were collected from the top 0–15 cm layer (100 cores; a total of 100 kg of each

Table 3 Plant species used for the sowing experiments

	Netherlands (NL)	Sweden (SE)	United Kingdom (UK)	Spain (SP)	Czech Republic (CZ)
Grasses	*Festuca rubra*	*F. rubra*	*F. rubra*	*F. rubra*	*F. rubra*
	Phleum pratense	*P. pratense*	*P. pratense*	*P. pratense*	*P. pratense*
	Poa pratensis	*Agrostis capillaris*	*Cynosursus cristatus*	*Bromus inermus*	*C. cristatus*
	A. capillaris	*C. cristatus*	*Holcus lanatus*	*Poa trivialis*	*H. lanatus*
	Anthoxanthum odoratum	*A. odoratum*	*Trisetum flavescens*	*P. pratensis*	*Trisetum flavescens*
Forbs	*Plantago lanceolata*	*P. lanceolata*	*P. lanceolata*	*P. lanceolata*	*P. lanceolata*
	Tanacetum vulgare	*Leontodon hispidus*	*Centaurea nigra*	*Sanguisorba minor*	*Centaurea jacea*
	Hypericum perforatum	*Galium verum*	*G. verum*	*Achillea millefolium*	*G. verum*
	Hypochaeris radicata	*Prunella vulgaris*	*L. hispidus*	*G. verum*	*Lychnis flos-cuculi*
	Linaria vulgaris	*Campanula rotundifolia*	*Sanguisorba minor*	*Matricaria chamomilla*	*Prunella vulgaris*
Legumes	*Lotus corniculatus*	*L. corniculatus*	*L. corniculatus*	*L. corniculatus*	*L. corniculatus*
	Trifolium pratense	*Anthyllus vulneria*	*A. vulneraria*	*T. pratense*	*Lathyrus pratensis*
	T. dubium	*T. pratense*	*Medicago lupulina*	*M. lupulina*	*M. lupulina*
	T. arvense	*T. repens*	*T. dubium*	*T. subterraneum*	*T. dubium*
	Vicia cracca	*M. lupulina*	*T. pratense*	*T. fragiferum*	*T. pratense*

50×100 m^2 field). The chemical analyses were performed according to Novozsamsky et al. (1984). Details of chemical soil characteristics, and climate, co-ordinates, and cropping history are given in Table 2.

The NL site was situated on a sandy loam soil with a relatively high fraction of soil particles larger than 63 µm and a relatively high amount of available phosphorus (Table 2). The SE, SP and CZ sites were on clay soils all with a relatively large fraction smaller than 63 µm, whereas the UK site was on chalk soil. The soils of the NL, SE and CZ sites were slightly acid, whereas the UK and SP soils had the highest pH. Most soils were within the same range of organic matter content. The SP soil contained relatively little organic matter, total nitrogen and total phosphorus, whereas sodium and magnesium concentrations were relatively high.

Experimental design

At each field site, the effects of sowing low- and high-diversity seed mixtures of later-successional plant species (LD and HD, respectively) on arable soil were compared with natural colonisation (NC) and continued agricultural rotation (CA). The CA treatment will not be further discussed. The experiment was organised according to a randomised block design with five blocks as replicates. Within each block, there were four plots of 10×10 m^2 and each of the four treatments was randomly assigned to one plot. All plots were separated by border rows of 2 m.

The choice of plant species to be used for the low- and high-diversity treatments depended on the following considerations:

1. Each diversity treatment and each replicate should include potentially dominant and subordinate plant species (Grime 1998). We chose grasses as potential dominant species and forbs as potential subordinate species. Legumes were regarded as a separate group of forbs because of their association with nitrogen-fixing symbionts.
2. The plant species to be used should occur naturally in later stages of secondary vegetation succession at the specific experimental sites.
3. The seeds should originate from natural plant populations and should be obtainable commercially or by local collecting.
4. Considering 1, 2, and 3, the total species pool available for the experiment was limited. Therefore, all replicates of the high-diversity plots were sown with the same combination of 15 species (5 per species group).
5. As there is more chance of incorporating highly productive species in high-diversity assemblages than in low-diversity assemblages (Huston 1997), we randomly chose different species mixtures of two grass species, one legume and one other forb species for each of the five LD replicates. Two grass species were chosen to avoid the risk of losing the potential dominants from a replicate in case one of the grass species failed to establish. Within field sites, different LD replicates never had the same forb or legume in common. None of the different LD-replicates had the same combination of two grass species.
6. In view of the geographical differences and the previous considerations (especially 2), not all species could be used in common at all experimental sites. We were, nevertheless, able to find two grass species (*Festuca rubra*, *Phleum pratense*), one legume (*Lotus corniculatus*) and one forb (*Plantago lanceolata*) that could occur at all sites. At each field site, one of the low-diversity replicates was planted with that particular species mixture. A list of species and sites where they were used is presented in Table 3.

Installing the treatments

The seed batches used for establishing the low and high diversity mixtures consisted of the same amounts of seeds (grasses: 2500 seeds m^{-2}, legumes and other forbs: 500 seeds m^{-2} seeds m). One species with heavy seeds (*Vicia cracca*) was reduced to 100 seeds m^{-2} to avoid their becoming dominant. In the high diversity treatments, every grass species was sown at a density of 500 seeds m^{-2}, and every legume and forb as 100 seeds m^{-2}. In the low-diversity treatments each of the two grass species was sown at a density of 1250 seeds m^{-2} and the forb as well as the legume at 500 seeds m^{-2}. The treatments were installed in April–May 1996. The seeds were either hand-sown or mixed with sand/soil to facilitate equal spreading. Subsequently, the plots were cultivated by harrows to bring the seeds into the surface layer.

Site management

The Spanish site was watered initially to ensure germination. Irrigation was stopped after the first growing season. The Dutch site was situated in an area exposed to natural grazing by horses, deer, wild boar, and rabbits, and a fence was erected to exclude these herbivores. All other fields were unprotected against herbivores. The border rows in between the plots were mown or cultivated.

Table 4 Summary of ANOVA results (Country as fixed factor) on the number of naturally colonizing plant species with *NC* (natural colonization), *LD* (sowing later-successional plant species at low diversity, i.e. 4 species) and *HD* (sowing later-successional plant species at high diversity, i.e. 15 species). The *numerals* in the model column refer to the error terms used for calculating the *F*-values, given in parentheses after the source of variation

	NC, LD and HD						LD and HD only				
Year			1996		1997			1996		1997	
Source of variation	Model	*df*	*F*	*P*	*F*	*P*	*df*	*F*	*P*	*F*	*P*
Country (1)	2	4	90.9	***	15.5	***	4	91.9	***	6.4	**
Block (within Country) (2)	3	20	7.45	***	16.8	***	20	5.18	***	15.2	***
Subplot (within Block) (3)		275					275				
Treatment (4)	6	2	1.42	Ns	97.6	***	1	1.26	Ns	18.6	***
Country×Treatment (5)	6	8	1.56	Ns	6.32	***	4	1.44	Ns	0.98	Ns
Block×Treatment (6)	7	40	3.36	***	10.6	***	20	4.35	***	17.2	***
Residuals (7)		550					275				

**P*<0.05, ***P*<0.01, ****P*<0.001

Plants that colonised naturally (weeds) were not removed. At the end of each growing season, the aboveground vegetation of all plots and border rows was mown and removed in September.

Data recording and statistical analyses

In every replicate 10×10 m^2 plot, the vegetation was recorded in 12 permanent subplots of 1 m^2 each. Every year at peak standing biomass (May/June in Spain and July/August in the other countries) the number of plant species was counted for both sown and non-sown species. The numbers of colonising species were statistically analysed for 1996 and 1997 separately. ANOVA was used with block nested within country and subplot nested within treatment. Block and Subplot were regarded as random factors; Treatment as fixed.

Four ANOVAs were carried out with non-transformed data (after testing homogeneity of variances by Cochran's *Q* using Block as the lowest level of observation). With respect to Country, analyses were performed in two ways: with Country as fixed or as a random factor (ANOVAs 1 and 2). When Country was regarded as a random factor, the treatment effect was tested against Country×Treatment and the latter against Block×Treatment. Considering Country as a fixed factor resulted in a simpler design, testing the effects of Block against Subplot (within Block) and of both Treatment and Country×Treatment against Block (within Country)×Treatment. When Country was assumed to be a fixed factor, the results may only be interpreted in relation to the actual choice of the field sites. This test will be least conservative, however, results may not be extrapolated to other areas (in Europe). When Country is regarded as a random factor the results may be extrapolated to a wider scale in Europe, which maximises the advantage of the multi-site approach. However, assuming a random distribution of the field sites (countries) over Europe will make the test more conservative. The second comparison (ANOVAs 3 and 4) varied the number of treatments. One analysis was performed with natural colonisation (NC), low diversity (LD) and high diversity (HD) to compare the effect of sowing with spontaneous development of vegetation. A second analysis concerned LD and HD only, to examine the effect of diversity as such. In all four cases, since Block was nested within Country, the effect of Country was tested against Block. All treatment means were compared by Tukey's HSD.

Results

In 1996, the first year of the experiment, there was no significant effect of treatment (Table 4; ANOVA-results shown for Country as fixed factor). There was only a significant effect of Country. In 1997, the second year of the experiment, the number of colonising species was significantly affected by the treatment (i.e. sowing LD or HD species mixtures). Significance of the Treatment effect was stronger when Country was regarded as a fixed factor (*P*<0.001) than when Country was random (*P*<0.01; data notshown).

After 2 years (in 1997) the sown mixtures of plants with characteristics of later-successional species had suppressed the number of colonising species (Fig. 1). When natural colonisation (NC), LD and HD were compared, the effect of treatment depended on Country (*P*<0.001; *P*<0.01 when Country was regarded as a random factor). However, when LD and HD were compared the interaction of country and treatment was not significant (Table 4). Therefore, the differences between the NC plots were responsible for the significant interaction with country. Part of the interaction was probably due to the relatively low numbers of natural colonisers at the Czech site in 1997 (Fig. 1).

In both analyses (with three and two vegetation treatments) of the 1997 data using the design with country as either a fixed or a random factor there was a significant effect of Block, as well as significant interaction of Block and Treatment (Table 4). Besides NC, at least one other treatment contributed to this interaction, as the interaction remained when LD and HD were compared excluding NC. The Block effect also remained significant when NC was omitted from the analysis. The LD treatment gave most weight to the Block×Treatment interaction, as the different replicate blocks showed quite variable suppression of the numbers of colonising species as compared to the HD replicates (Fig. 1).

When the treatment effect of the ANOVA with LD and HD was analysed by Tukey's HSD, plots sown with a HD mixture of later-successional plant species contained fewer colonising plant species than plots with a LD mixture. Figure 1 demonstrates that some LD combinations were as effective in suppressing the numbers of colonising plant species as the most effective HD plots.

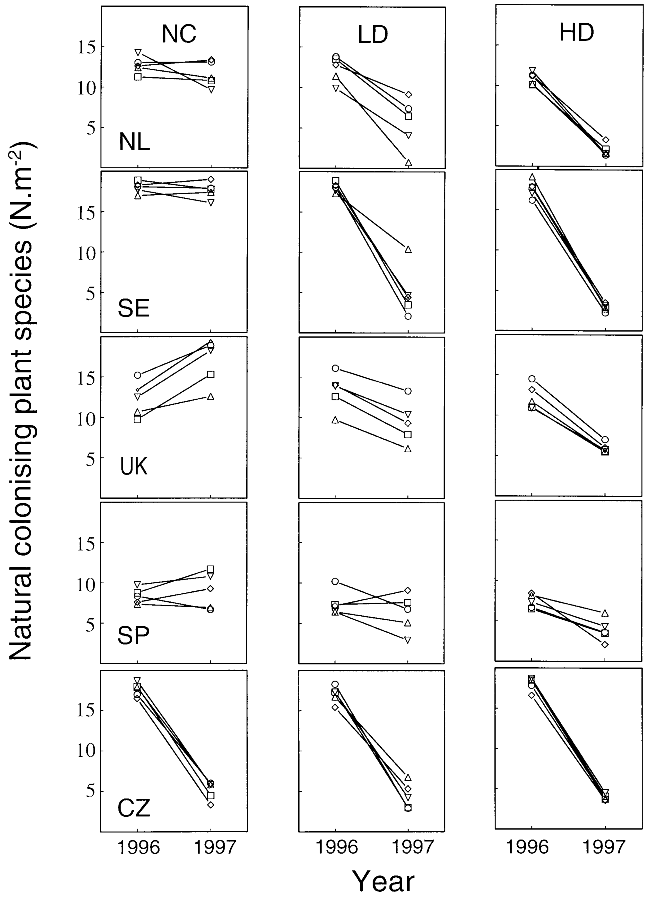

Fig. 1 Numbers of naturally colonising plant species in each different block (5 blocks indicated by different *symbols*) for natural colonisation (*NC*; no later-successional plant species sown), and for sowing later-successional plant species in low-diversity (*LD*; 4 species sown) and high-diversity (*HD*; 15 species sown) treatments. The *x*-axis shows the two years 1996 and 1997. The experiment (though with partly different sets of sown plant species, soil types, and so on) was carried out in five different countries: Netherlands (*NL*), Sweden (*SE*), United Kingdom (*UK*), Spain (*SP*), and Czech Republic (*CZ*)

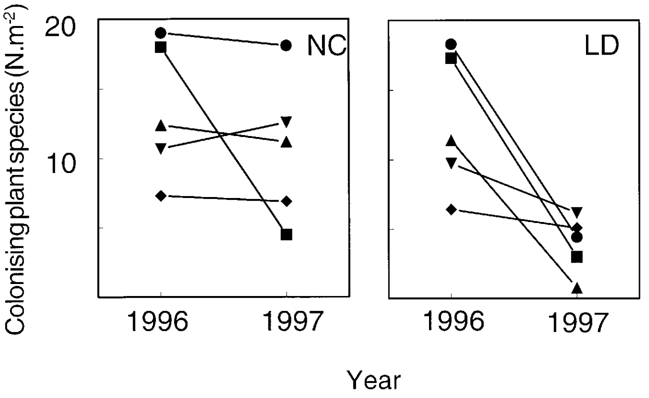

Fig. 2 Numbers of naturally colonising plant species (*vertical axis*) in low-diversity (*LD*) blocks of the five different field sites with the same plant species mixture, and in natural colonisation (*NC*) plots of the corresponding blocks in two years (*horizontal axis*). *Symbols* indicate the different field sites: ▲ Netherlands, ● Sweden, ▼ United Kingdom, ◆ Spain, ■ Czech Republic

Thus, on average there was a significant diversity effect on the suppression of naturally colonising plant species, but the same effect could also be equally well obtained with some LD plant species mixtures. The strong suppression of natural colonisers in the Czech natural colonisation treatment was due to two unsown rhizome-forming plant species, *Trifolium repens* and *Elymus repens*, which suppressed all others.

One of the LD replicates of each country was sown with a mixture of the same four plant species. This treatment cannot be analysed statistically because of the absence of independent replicates within a country (the 12 permanent subplots cannot be considered as replicates). However, the trend observed in the five countries shows some interesting contrasts when compared to the numbers of colonizing plant species in the NC plots from the same blocks. In the NL and SE fields, the species mixture appeared to be far more suppressive than in the UK and SP fields (Fig. 2). In the CZ field the LD species mixture performed similarly to the NC treatment, which was most likely due to the two naturally colonising rhizome-forming species (Fig. 2). Therefore, results of this plant species mixture indicate that the effect of a certain combination of later-successional plant species on natural colonisers at one site may not be a good predictor of results at other sites.

In order to identify the possible mechanism of suppression of naturally colonising plant species by the later-successional species, numbers of colonising plant species were correlated with average total aboveground biomass production (which included biomass of both sown and non-sown plants). Treatment averages were used for each country. The scatter plots of biomass against numbers of colonizing species showed site-specific patterns in 1996 (Fig. 3a). The Czech site was relatively the most productive and the UK site the lowest. The Swedish, Dutch and Spanish sites had intermediate amounts of biomass, but were different in the average numbers of colonizing plant species. There was no significant overall correlation between biomass and the numbers of colonising plant species (r^2=0.0062, n=15, P>0.36).

In 1997, there was a larger gradient in productivity among the field sites (Fig. 3b). The rank order of peak standing biomass of the different field sites was generally in line with that of 1996, except for the Spanish site. This site had been irrigated in spring 1996 in order to get the plots established, which may explain the relatively high peak biomass in 1996 as compared to 1997. In 1997, the most productive site (CZ) showed the largest proportional loss of natural colonisers, whereas one of the least productive sites (UK), retained the highest numbers of natural colonisers (Fig. 3). Over all, there was a significant negative correlation (r^2=0.50, n=15, P=0.0029) between peak standing biomass and the numbers of naturally colonising species. Thus, the productivity of the

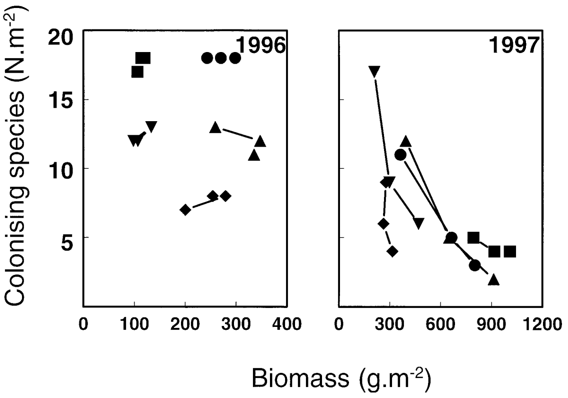

Fig. 3 Correlation of above-ground biomass against numbers of colonising plant species (both as country treatment averages) in five different countries in two years: **a** 1996, **b** 1997. For each country: treatments are connected by a *line* and the *lefthand* point is always *NC* (natural colonisation), *LD* (low diversity) is in the *middle* and *HD* (high diversity) is on the *right*. *Symbols* indicate the different field sites: ▲ Netherlands, ● Sweden, ▼ United Kingdom, ◆ Spain, ■ Czech Republic

low- and high-diversity stands may have contributed to the suppression of non-sown plant species.

Discussion

Functional consequences of diversity?

A major difference between this study and many other biodiversity experiments (Naeem et al. 1994; Tilman 1996; Hooper 1998; Hooper and Vitousek 1997, 1998; Diemer et al. 1997; Hector et al. 1999) is that in this study no topsoil was removed, no soil sterilisation was applied and no hand-weeding was done. The naturally colonising plants were mainly weedy species from the seed bank resulting from previous agricultural use of the sites (T. Len, S.R. Mortimer and G.W. Korthals, unpublished work). Some additional colonisation from other sources cannot be completely excluded. We considered the suppression of early-successional plant species (arable weeds) by later-successional species as a function of the species diversity in the sown mixtures.

First, the suppressing effect of the high diversity treatment showed more homogeneity among replicates than of the low-diversity mixtures. This demonstrates that the different low-diversity mixtures had variable effects on weed suppression (to be considered as an aspect of ecosystem function), which supports the view of Huston (1997) that species-specific effects (especially in low-diversity treatments) may matter in diversity experiments.

A major methodological decision concerned the total amount of seeds used, as well as the amounts of seeds per species group. In the high-diversity treatment every grass species was sown at the same density of 500 seeds m^{-2}, whereas the legumes and other forbs were sown at 100 seeds m^{-2}. In the low-diversity treatment, there were two grass species sown at 1250 seeds m^{-2} each and a legume and other forb at 500 seeds m^{-2} each. In total, each treatment (both low and high diversity) was planted with 2500 grass seeds m^{-2}, 500 legume seeds m^{-2} and 500 other forb seeds m^{-2}. Seed number of one plant species (*Vicia cracca*) was reduced, because of the heavy seed weight. So, in all treatments the total number of seeds was constant for each species group (except for one species with heavy seeds) and there was no check with monocultures or additional treatments on possible consequences of the choice of equal numbers of seeds, or of the sown densities applied. Initial numbers of individuals should have been fairly constant, as most species germinated well (data not shown).

The conclusions on weed suppression have been based on the numbers of naturally colonising species recorded in the diversity treatments. There could have been an over-estimation of the treatment effects if the natural colonisers were the same species as the species in the sown mixtures. However, as later successional plant species were used for sowing, there was little overlap between the plant species in the seed bank and the plant species in the sown mixtures. For example, in the 2nd year, in the UK field, 6 of the 15 sown plant species occurred in the natural colonisation treatments, but the proportion of plots colonised by these species was low: *Centaurium nigrum*, *Festuca rubra* and *Trifolium dubium* were registered in 1, *Holcus lanatus* and *Plantago lanceolata* in 3, and *Medicago lupilina* in 9 out of 60 permanent quadrats (S.R. Mortimer, unpublished work). Since the number of naturally colonising plant species of each replicate was calculated as the average of 12 permanent quadrats, these species did not introduce any substantial error, irrespective their origin (from the seed bank or dispersed from the sown stands).

The numbers of naturally colonising plant species is a robust measure but, the few species that persisted in the high diversity sowing plots could have had a disproportional contribution to cover and biomass. The way cover was recorded (on a five-point scale) does not allow detailed accurate comparisons for all sites. In fact, there was only one case where a few non-sown plant species dominated the stands. This was in the Czech field, which was widely colonised by *Elymus repens* and *Trifolium repens*. In general, it may be assumed that low numbers of natural colonisers corresponded with low percentage cover.

Weed suppression was correlated with above-ground biomass (Fig. 3b). As weeds also contributed to the total stand biomass, the regression analysis did not reveal the real relationship between productivity of the sown mixtures and weed suppression. Most probably, if only the biomass of the sown species had been used, the correlation between biomass and weed suppression would have been stronger.

The correlation between biomass and weed suppression does not reveal mechanisms, as suppression may have been due to prevention of seed germination or competition for a specific resource (water, nutrients, light)

(Tilman 1982). Because weed suppression became obvious in the 2nd year (1997), germination limitations may have been a major cause of weed suppression in the sown stands.

Succession, soil processes and invasiveness

Sowing later-successional species essentially changed the initial stage of vegetation development on abandoned arable land, confirming previous work by e.g. Burch (1996) and Hansson and Hagelfors (1998). As weed suppression depended on the number of species in the sown stands, the diversity of plant species at a certain stage may affect the course of succession at least temporarily. The experimental period was too short to assess to what extent succession may be affected in the longer term.

In addition to changing dominance patterns in vegetation, the sowing treatments may also change patterns of plant-soil feedback. Conceptual models of plant-soil feedback (Bever et al. 1997; Van der Putten and Van der Stoel 1998) predict that low-diversity plots may be more susceptible to self-induced changes in the rhizosphere community than plots with diverse species mixtures. As a consequence, in the long term low-diversity plots might be less stable than plots with high species diversity, which could as well enhance possibilities for other later-succession species to become established. Effects on nutrient pools, fluxes, and trophic levels in soil may also be expected (Bardgett et al. 1998; Roy 2000), although Wardle et al. (1999) observed few effects on decomposer communities of experimental plant removal from New Zealand pasture unless all plants were removed. In the Dutch site of the present study, after the second growing season Malý et al. (2000) found no effect of the diversity treatments on net mineralisation, short-term nitrification, respiration and arginin ammonification, microbial biomass C and N or colony-forming units of the major microbial groups of soil organisms. While the plant community may show fast responses to plant diversity treatments, the soil community (if responding) will lag behind. So far, following plant diversity treatments lengths of lag periods in the response of the soil community and consequences for further ecosystem development are unknown.

Different from succession, invasion usually concerns species that reach beyond their previous range (Williamson 1996). However, the basic ecological principles are similar to succession. Translating the present results into conclusions on invasiveness implies that the specific characteristics of communities to become invaded affect their invasibility. Some low-diversity species combinations turned out to be severely suppressive to natural colonisers, which could also occur in natural communities. Why would results on invasibility of diverse communities be so contradictory? In the present study, in some fields (UK, SP), high-diversity mixtures appeared to be less suppressive than in other fields (NL, SE; Fig. 1). The sowing of the same low-diversity species mixture at the five different field sites also showed considerable variation in weed suppression (Fig. 2). Apparently, the characteristics of the environment (including productivity), as well as the nature of the species (both the ones to invade and the species in the communities that were invaded) may affect the invasibility of plant communities. The present results are in line with conclusions of e.g. Stohlgren et al. (1999) and indicate why the hypothesis of Elton (1958) may not be generally valid.

Multi-site comparison

The five sites used for this experiment were a random sample of European examples of land abandonment or land use change. All field sites differed in most respects (soil type, climate, history), except for their recent agricultural usage (although even crop rotation schemes were different: see Table 3). When all treatments (natural colonisation, low and high diversity) were included, interactions of country and treatment were significant. As significance disappeared when only low and high diversity were considered as treatments, the interaction was most likely the result of the influence of the natural colonisation plots. Therefore, in the present case five sites across Europe were already sufficient to demonstrate effects of low versus high diversity, even when country was regarded as a random factor.

Conclusion

In the short term, succession on abandoned arable land may be enhanced by the introduction of later-successional plant species. Moreover, the results suggest that at some stages of succession the plant species diversity present may determine how succession proceeds. The results hold generally in a multi-site comparison across Europe. However, local conditions and species identities affect the suppressive capacity of plant communities towards other species, which complicates the generalisation of any relationship between the diversity of communities and their susceptibility to invasions.

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