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Biodiversity and decomposition in experimental grassland ecosystems

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Abstract We examined the impact of biodiversity on litter decomposition in an experiment that manipulated plant species richness. Using biomass originating from the experimental species richness gradient and from a species used as a common substrate, we measured rates of decomposition in litterbags in two locations: in situ in the experiment plots and in an adjacent common garden. This allowed us to separate the effects of litter quality and decomposition location on decomposition. We found that plant species richness had a significant, but minor negative effect on the quality (nitrogen concentration) of the biomass. Neither litter type nor location had a consistent effect on the rate of carbon and nitrogen loss over a 1-year period. Thus, the increased productivity and corresponding lower soil available nitrogen levels observed in high diversity plots do not lead to faster litter decomposition or faster nitrogen turnover. This supports the hypothesis that increased productivity corresponding with higher species richness results in increased litter production, higher standing litter pools and a negative feedback on productivity, because of an increased standing nitrogen pool in the litter.

Keywords Biodiversity · Decomposition · Mixed litterbags · Nitrogen cycling

Introduction

In most ecosystems it is assumed that the dominant plant species control ecosystem processes such as productivity, decomposition and nutrient cycling (Schlesinger 1997). However, recent studies have addressed how the diversity of plant species (Hector et al. 1999; Hooper and Vitousek 1998; Naeem et al. 1994; Tilman et al. 1996, 1997), fungal mycorrhizae (Van der Heijden et al. 1998), herbivores (McNaughton 1993; Mulder et al. 1999), earthworms (Thompson et al. 1993) and microbes (McGrady-Steed et al. 1997; Naeem and Li 1997) influence ecosystem functioning. Several studies have documented that biodiversity influences productivity (Hector et al. 1999; Naeem et al. 1996; Symstad et al. 1998; Tilman et al. 1996), soil nutrient availability (Hooper and Vitousek 1998; Symstad et al. 1998; Tilman et al. 1996), invasion resistance (Knops et al. 1999), system stability (Frank and McNaughton 1991; Tilman and Downing 1994) and reliability (Naeem and Li 1997). In addition to these direct biodiversity effects, plants also have an important “after-life” effect on ecosystem processes. Microbially mediated litter decomposition determines the immobilization and mineralization of nutrients, which in turn feedback to determine net primary productivity. Some studies have shown a relationship between biodiversity and nutrient availability (Hooper and Vitousek 1998; Symstad et al. 1998; Tilman et al. 1996, 1997) and mineralization (Hooper and Vitousek 1998). However, litter decomposition studies have not shown consistent effects of plant species diversity on decomposition rates (Blair et al. 1990; Elliott et al. 1993; Fyles and Fyles 1993; Hart et al. 1993; Klemmedson 1991; Knops et al. 1996; Kochy and Wilson 1997; Taylor et al. 1989; Williams and Alexander 1991). Four recent studies have specifically examined the effect of litter diversity on decomposition (Bardgett and Shine 1999; Finzi and Canham 1998; Hector et al. 2000; Wardle et al. 1997). Finzi and Canham (1998) and Hector et al. (2000) found significant, but non-additive effects and Wardle et al. (1997) found that biodiversity itself was not a significant

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determinant of decomposition rate. In contrast, Bardgett and Shine (1999) studied six herbaceous species and found that increased litter diversity corresponded to increased litter decomposition and increased efficiency of soil biological processes. However, because Bardgett and Shine (1999) used only one specific non-random sequence of species loss, the generality of their results is unclear. Lastly, a microcosm study found a direct diversity effect on the mass loss of dissolved organic matter (Kaunzinger and Morin 1998).

Here we report a study that examines the effects of plant species richness on aboveground litter decomposition. We hypothesized that diversity might have at least two qualitatively different effects: it may influence the quantity and quality of biomass available for decomposition, and it may influence the location in which litter decomposes, by affecting the vegetation biomass and structure, which are likely to change the microclimate. In this study, we examined both.

Materials and methods

The experimental plots used in this study were established in May 1994 at the Cedar Creek Natural History area, which is located on a glacial sandy outwash in east-central Minnesota. For each plot, species were randomly selected from a pool of 24 plant species (Tilman et al. 1996). Plots were 3×3 m with diversity levels of 1, 2, 4, 6, 8, 12 and 24 plant species. Treatments had 20 replicates, except the 12 species treatment which had 23 replicates and the 24 species treatment with 24 replicates, for a total of 147 plots. The species pool consisted of *Agropyron smithii*, *Elymus canadensis*, *Koeleria cristata*, *Poa pratensis*, *Sporobolus cryptandrus*, *Andropogon gerardii*, *Bouteloua gracilis*, *Buchloe dactyloides*, *Panicum virgatum*, *Schizachyrium scoparium*, *Sorghastrum nutans*, *Achillea millefolium*, *Anemone cylindrica*, *Asclepias tuberosa*, *Aster azureus*, *Coreopsis palmata*, *Euphorbia corollata*, *Liatris aspera*, *Rudbeckia hirta*, *Solidago nemoralis*, *Astragalus canadensis*, *Lepedeza capitata*, *Petalostemum purpureum* and *Vicia villosa*. All species are native, or widely naturalized, in native grasslands. The top 8 cm of the soil was removed to reduce the existing seed bank. All plots were weeded 4–6 times throughout the growing season and received about 2.5 cm of water per week (as rainfall or irrigation) from May through September.

Aboveground standing plant and litter biomass were measured with one 10 cm by 1 m strip for each plot, clipped in July 1997, and sorted into the individual species. For each plot two litterbags were filled with a 1 g sample of the standing biomass of all species present in the July clipped biomass sample. The biomass of each species in the sample was proportional to its biomass in the plot. Note that we used standing mid-season biomass rather than senesced litter. Litterbags were made from polyester with a mesh of 0.1 mm and measured 5×10 cm. An aluminum tag was attached to each bag, and each bag was held to the soil surface with a flag in the same location in each plot. Decomposition was estimated as mass loss after each bag was dried to constant dry mass at 50°C. For each plot, one bag was placed back in the original plot to measure in situ decomposition ($n=147$), and one was placed in a common garden ($n=146$); one plot did not have enough biomass for two bags, and a single bag was placed in situ. The common garden area was a *Schizachyrium scoparium* monoculture located 25 m south of the species richness plots. A combined aboveground biomass sample from each plot was ground and analyzed for total nitrogen and carbon, following standard methods on a 1500 NA Carlo-Erba element analyzer (Elan Tech., N.J.). In addition we filled litterbags with senesced *Schizachyrium* litter (0.35% N, SE 0.02, 47.5% C, SE 0.1, $n=10$) obtained from Prairie Restora-

tion (Princeton, Minn.). One common substrate litterbag was placed within each experimental plot ($n=147$) and 25 bags were placed within the common garden. Thus, in total we employed four sets of litterbags; two from the species richness plots, with one bag from each plot placed in situ and one in a common garden, and two sets of a uniform *Schizachyrium* litter, with one set placed within the species richness plots and one set in the common garden.

Bags were placed in the field in the first week of November 1997 and removed in the first week of November 1998. One litterbag was excluded from the analysis, because it had a hole and might have lost mass. Species richness is the average number of vascular plants observed in two visual estimates of areas of 0.5×1 m per plot as measured in mid July of 1997. We present results for the carbon and nitrogen content of the decomposing litter. Litter carbon shows essentially the same pattern as biomass, but is not biased by soil contamination.

Results and discussion

Results obtained in 1995 from the same experiment (Tilman et al. 1996) showed that experimentally imposed increases in plant species richness led to a significant increase in plant cover and biomass and to a significant decrease in soil extractable nitrogen. We found essentially the same pattern in 1997, with a positive relationship between both the experimentally imposed species richness or the achieved species richness and total plant cover, aboveground biomass and aboveground standing litter. We also found a negative relationship between plant species richness and soil available nitrate at 0–20 cm and 40–60 cm depth. Soil total nitrogen did not differ at the beginning of the experiment, i.e. 1994, and remained unaffected by species richness in 1998 (Tilman et al, unpublished data).

The initial nitrogen content of total plot biomass was negatively correlated with species richness (Fig. 1). However, this relationship was non-linear. We found that the initial nitrogen content of decomposing biomass had no significant effect on the rate of carbon loss, either in the plots (simple regression $F=0.51$, $P=0.477$) or in the common garden ($F=3.0$, $P=0.084$). A multiple regression

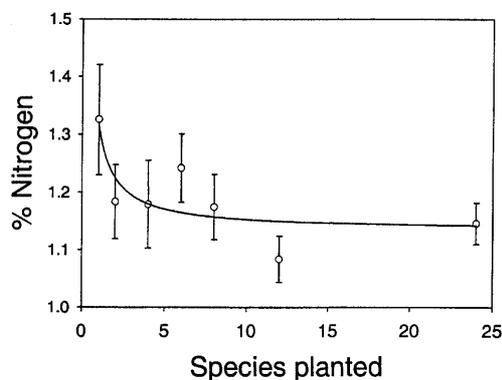


Fig. 1 Experimentally imposed plant species richness in relation to percentage nitrogen in the July plot biomass. Data are the means±1 SE, $n=20$, except 23 for the 12 species and 24 for the 24 species. Fitted curve is $y=1.14+0.179/x$, $F=8.97$, $R^2=0.642$ and $P=0.030$

Table 1 Type III GLM, univariate analysis of variance of litter origin (either from the biodiversity experiment or *Schizachyrium scoparium*) and litter location (in situ or in a common garden *Schizachyrium scoparium* monoculture). Sample size is 147 for each treatment, except experimental litter in the *Schizachyrium* common garden, $n=146$ and *Schizachyrium* in the common garden, $n=25$. Dependent variables are carbon loss ($R^2=0.853$) and nitrogen loss ($R^2=0.696$)

| Source | df | Carbon loss | | Nitrogen loss | |
|--------------------|-----|-------------|-------|---------------|-------|
| | | F | P | F | P |
| Corrected Model | 3 | 895 | 0.000 | 350 | 0.000 |
| Intercept | 1 | 6,141 | 0.000 | 279 | 0.000 |
| Location | 1 | 4 | 0.057 | 18 | 0.000 |
| Origin | 1 | 1,750 | 0.000 | 543 | 0.000 |
| Location by origin | 1 | 2 | 0.119 | 1 | 0.306 |
| Error | 456 | | | | |

with carbon loss as the dependent variable, and the actual plant species diversity (e^h) and initial plant tissue nitrogen content as independent variables was not significant in the common garden ($P=0.228$, $F=1.49$, $n=145$) and was marginally significant in the plots ($P=0.042$, $F=3.25$, $n=146$, with e^h $P=0.066$ and initial plant tissue nitrogen $P=0.082$).

We found no interaction between the litter origin (e.g. *Schizachyrium* versus species richness plots) and litter decomposition location (i.e. species richness plots versus the *Schizachyrium* monoculture) (Table 1). On average, 46% of the carbon was lost within one year for biomass from the experimental plots, with no difference between the common garden and the species richness plots (Fig. 2A, one-way ANOVA, $df=1,287$, $F=0.1$, $P=0.708$). In contrast there was a significant difference in nitrogen loss as the biomass only lost 5% of its nitrogen while decomposing in situ, whereas it lost 15% of its nitrogen while decomposing in the common garden (Fig. 2B, one-way ANOVA, $df=1,287$, $F=18.8$, $P<0.000$). *Schizachyrium*, the species used as a common substrate, was also present in 57 out of the 147 plots. However, the presence of *Schizachyrium* within these plots did not impact either C loss (one-way ANOVA, $F_{1,145}=0.1$ $P>0.7$) or nitrogen immobilization ($F_{1,145}=1.5$ $P>0.2$).

Schizachyrium showed a significant location effect for both carbon and nitrogen, with litter losing more carbon (15% versus 13%, one way ANOVA, $df=1,168$, $F=15.0$, $P<0.000$) and immobilizing more nitrogen (68% versus 51%, $F=5.4$, $P=0.022$) in the experimental plots. Note that the initial litter quality of the common litter was much lower than that from the species richness plots (e.g. 0.35% nitrogen versus 1.19% on average) and immobilized nitrogen during decomposition, whereas the plot litterbags lost nitrogen. Thus, decomposition was faster in the experimental plots, perhaps because of repeated watering of the experimental plots; increased water availability can increase litter decomposition (Austin and Vitousek 2000). This response is more important for the *Schizachyrium* litter, which decomposes much more slowly than the plant mixtures from the experimental plots.

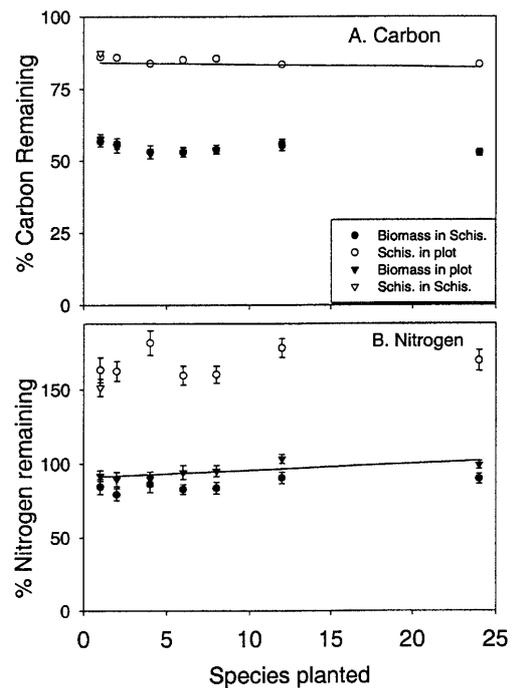


Fig. 2 Decomposition loss of carbon (A) and nitrogen (B) in relation to plant species richness. Data are means \pm 1 SE of mass loss of litterbags, decomposed from November 1997 through November 1998. **A** Carbon, litterbags from the species richness plots placed into the *Schizachyrium* common garden, regression $F=1.4$, $P=0.239$, species richness litterbags placed in situ, regression $F=1.5$, $P=0.218$, *Schizachyrium* common litter placed in the *Schizachyrium* monocultures, *Schizachyrium* common litter in the species richness plots, regression $F=8.1$, $P=0.005$, $R^2=0.046$; **B** Nitrogen, litterbags from the species richness plots placed into the *Schizachyrium* common garden, regression $F=2.7$, $P=0.101$, species richness litterbags placed in situ, regression $F=5.1$, $P=0.025$, $R^2=0.034$, *Schizachyrium* common litter placed in the *Schizachyrium* monocultures, and *Schizachyrium* common litter in the species richness plots, regression $F=0.5$, $P=0.494$

Plant species richness can influence decomposition by impacting the quality of the litter and the microclimate in which the litter decomposes. However, we found that both the quality of the biomass as influenced by the species richness treatments and the decomposition location had only a minor influence on decomposition. Only one set of litterbags showed a significant correlation between carbon loss and the species richness gradient, e.g. the common substrate, *Schizachyrium*, in the species richness plots. Similarly only one set showed a significant effect of species richness on the nitrogen loss rate, e.g. biomass decomposition in situ (Fig. 2). However, both regressions were weak, with an R^2 of less than 0.05, and the actual change in loss rate from 1 to 24 plant species was 2.6% for carbon and 7% for nitrogen. Thus, the legacy effect of plant species richness in the decomposing litter had only a minor effect on decomposition and nitrogen release from decomposing litter. Decomposing plant biomass seems to average the qualities of the plants and has no predictable interactions as related to plant species richness. Note that we used mid-season green

biomass and this might have magnified any species richness treatment effects because of its higher quality, e.g. standing July biomass had 1.19% nitrogen, whereas standing July litter had 0.69% nitrogen. We also found that the species richness gradient only marginally influenced the common *Schizachyrium* litter decomposition. Thus, in total, the plant species richness gradient had, at best, only a marginal influence on litter decomposition.

This biodiversity experiment shows strong effects of plant species richness on available soil nitrate levels (Tilman et al. 1996, 1997). These available soil nitrate differences, which are present in the rooting zone, are likely to influence the long term sustainability of these plots, as there are also differences below the rooting zone, e.g. 40–60 cm depth, indicating that there are differences in leaching losses. Thus, higher species richness results in lower levels of soil nitrate, indicating that higher species richness increases the uptake and/or immobilization of soil nitrate and lowers nitrate leaching losses, thereby increasing the efficiency of nitrogen use (Tilman et al. 1996). However, decomposition of above-ground plant biomass was not influenced by plant species richness and the retention of nitrogen from the decomposing litter is not likely to be an important factor influencing the sustainability of prairie ecosystems as biodiversity declines. Species differ in aboveground litter quality, but the pattern of soil mineral nitrate availability along the species richness gradient is only weakly reflected in the aboveground litter quality gradient. Thus, higher species richness results in an averaging of the species differences in aboveground litter quality without significant interactions along a species richness gradient, as reported by Wardle et al. (1997) and Hector et al. (2000). This supports the hypothesis that litter production increases with higher plant species richness because of increased productivity. This results in an increase in the amount of standing litter and an increased nitrogen pool in standing litter, because litter decomposition does not change with plant species richness. This suggests that decomposition and nitrogen turnover within high diversity plots, rather than contributing to higher nitrogen availability and productivity, may actually have a negative effect on productivity. Consequently, the increase of nitrogen within the standing litter may lead to a negative feedback through nitrogen cycling on productivity within the high diversity plots. This is in contrast with nutrient uptake by plants, where higher plant species richness allows vegetation to exploit soil resources more efficiently.

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