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Seasonal changes in the soil microbial community in a grassland plant diversity gradient four years after establishment

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ABSTRACT

Aboveground plant diversity is known to influence belowground diversity and ecosystem processes. However, the knowledge on soil microbial succession from an agricultural field to grassland varying in plant diversity is scarce. Therefore, we investigated the effects of vegetation cover, varying plant biodiversity and season on soil microbial parameters in a temperate grassland ecosystem. In May and October 2006 mixed soil samples were taken from the field site from The Jena Experiment: a large biodiversity experiment in Germany which was established in 2002 on a former agricultural field. Sampled plots differed in plant species richness (0, 4, 8, 16), number of plant functional groups (0, 1, 2, 3, 4), and plant functional group composition. We measured basal respiration (BR) and microbial biomass ($C_{mic/CFE}$; chloroform fumigation extraction method), phospholipid fatty acids (PLFA), and substrate induced respiration (SIR). We found distinct seasonal variations in the microbial community structure; BR and amount of PLFAs were higher at the end of the vegetation period than in spring, which was primarily due to increased biomass of fungi and Gram negative bacteria. Furthermore, BR and the amount of PLFAs were higher on vegetated plots than on bare ground plots. Although the number of plant functional groups had no effect on microbial parameters, plant species richness affected the amount of PLFAs at the end of the vegetation period with higher biomass in 4 than in 8 and 16 species mixtures. Moreover, the proportion of Gram negative bacteria was increased whereas the proportion of fungi was decreased in presence of legumes. The present study showed distinct seasonal changes in the soil microbial community composition, which is probably driven by the availability and quality of organic resources. Further, our results highlight the time-lag of belowground responses to aboveground vegetation manipulations with only few significant changes four years after the establishment of the experiment.

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1. Introduction

Biodiversity is known to impact ecosystem processes such as net primary productivity due to complementarity and sampling effects (Hector et al., 1999; Tilman et al., 2001). It is increasingly recognized that changes in plant diversity also affect the belowground system (Wardle et al., 2004). Above and belowground components of terrestrial ecosystems essentially depend on each other since plants provide carbon sources for the soil fauna and microflora. On the other hand, microorganisms and detritivore animals decompose organic matter, thereby increasing the availability of nutrients for plants and enhancing plant growth (Porazinska et al., 2003). The impact of aboveground biodiversity on soil biota may alter the functioning of microorganisms and therefore result in changes in the decomposition of organic matter (Orwin et al., 2006). Increasing plant species richness may beneficially affect the diversity of soil biota by including plants differing in root morphology, root chemical composition, and temporal variability of resource inputs. The increased morphological, chemical and temporal variability of belowground structures and resources is likely to result in increased diversity of niches supporting more diverse assemblages of soil biota (Lavelle et al., 1995; Hooper et al., 2000). We hypothesized that changes in plant diversity modify resource availability for heterotrophic microbial communities in soil, and thus modify their activity, biomass and composition.

Studies investigating the effects of plant diversity on soil microbial communities are scarce and mostly restricted to gross

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parameters such as microbial biomass, culturable microbes or single functional groups of microorganisms (Spehn et al., 2000; Stephan et al., 2000; Porazinska et al., 2003; Zak et al., 2003). Additionally, there is the need to follow changes in microbial community composition and functioning with time after establishment of biodiversity experiments (Maly et al., 2000; Balser and Firestone, 2005).

Using The Jena Experiment field site (Roscher et al., 2004) we assessed changes in microbial community composition and functioning four years after establishment of a plant diversity gradient. We hypothesized that food supply over the season is more variable in communities with low plant species richness due to a decreased overlap of different phenologies in time. A reduction in plant species richness can therefore have considerable effects on soil microbial communities via differences in the chemical composition of plant residues or via the timing of residue availability.

In order to test the proposed hypotheses we asked whether (1) season and aboveground plant biodiversity influence the amount of soil microorganisms four years after the establishment of the experiment; (2) soil microbial communities are more diverse on vegetated plots than under bare ground conditions; and (3) soil microbial community composition differs in presence of plants from certain functional groups.

2. Materials and methods

2.1. Site description, soil and biomass sampling

Soil samples were collected from the field site of The Jena Experiment in the north of the city of Jena, Germany. This long-term experiment containing species, which are common to Central European Molinio-Arrhenatheretum grasslands, was established in 2002 to investigate the role of biodiversity for element cycling and trophic interactions (Roscher et al., 2004). Before experiment establishment, the site was used as an arable field for the last 40 years and ploughed and fertilized regularly. The soil of the field site is classified as Eutric Fluvisol (FAO, 1998) developed from up to 2 m-thick loamy fluvial sediments (Roscher et al., 2004). The texture ranges from sandy loam to silty clay. Due to the varying soil texture the field site was subdivided into four blocks with homogenous soil properties. After sowing plots varying in plant diversity no fertilizer was applied. The chosen grassland species were classified into four functional groups (small herbs, tall herbs, grasses and legumes) according to their physiological, phenological and above- and belowground morphological traits. The plant diversity gradient established in The Jena Experiment ranges from 1 (2, 4, 8, 16) to 60 plant species and 1 (2, 3) to 4 plant functional groups, respectively. Species number and number of functional groups were varied as independently as possible when compiling the plot mixtures. Thus, the experimental design allows to test between sampling and complementarity effects and to attribute processes to species or functional group richness. In addition to the vegetated plots bare ground plots were kept free of vegetation. Further information on the experimental set-up including the plant species and soil characteristics is given in Roscher et al. (2004) and Steinbeiss et al. (in press), respectively. For analysis of microbial parameters, 27 plots were chosen representing a gradient in plant species diversity (from 0 to 16) and in the number of plant functional groups (from 0 to 4). Accounting for the block design of the experiment, two replicates with 4, 8 and 16 plant species were sampled from each of the four blocks. However, bare ground plots (no plant species sown) could only be sampled in three blocks.

In May and October 2006, eight soil samples per plot were taken with a core cutter (inner diameter: 5.6 cm) to a depth of 5 cm and pooled separately for the two sampling dates. Mixed samples were placed in cooling boxes immediately after sampling and stored at 4 °C. Soil samples were sieved (2 mm) within 48 h after sampling and shared for the different analyses. Sub-samples for PLFA analysis were frozen at −20 °C until analysis. Sub-samples for the other analyses were analyzed within four weeks from the stored material.

Soil samples for organic carbon and total nitrogen measurements were taken in April 2002 and 2006 as a paired sampling using a split tube sampler (inner diameter 4.8 cm). Samples were dried at 40 °C, sieved to 1 mm, ground and analyzed for soil organic carbon and nitrogen using an elemental analyzer at 1150 °C (Elemetaranalysator vario Max CN, Elementar Analysensysteme GmbH, Hanau, Germany).

Aboveground biomass was harvested in May and August 2006 on three randomized sites (20 cm × 50 cm) per plot by cutting standing biomass 3 cm above ground. The biomass of the sown species was dried at 70 °C to constant weight. Plant material was chaffed and ground to fine powder. Carbon and nitrogen were analyzed at 20 mg sub-samples with an elemental analyzer (see above) and C/N ratio was determined.

2.2. PLFA analysis

PLFAs were extracted according to Bligh and Dyer (1959) and modified by Kramer and Gleixner (2006). Briefly, soil lipids were extracted by a mixture of chloroform, methanol and 0.05 M phosphate buffer (pH 7.4) and split up into phospholipids by eluting with chloroform, acetone and methanol from a silica-filled solid phase extraction column. Subsequently, the phospholipids were hydrolyzed and methylated by a methanolic KOH solution and the PLFA-methyl esters were identified and quantified by GC-AED (Agilent, Böblingen, Germany) and GC/MS (Thermo Electron, Dreieich, Germany). PLFA 19:0 was used as internal standard. PLFA concentration was calculated as mg PLFA per g soil dry weight. Among 27 recorded PLFAs the following represented bacterial biomass: 14:0, 15:0, 15:0br iso, 15:0br anteiso, 16:0, 17:0, 18:0 and 20:0. PLFA 18:2ω6 was a marker for saprophytic fungal biomass according to Zelles (1997). Gram negative bacteria were represented by 16:1, 17:1, 17:1(2), 18:1, 18:1(2), 18:1n9, 18:1n11, 19:1, 18:0 cyclo, and 20:1 and Gram positive bacteria were represented by 16:0br, 17:0br, 17:0br(2), 17:0br(3) and 17:0br(4). PLFA 14:0 could not be assigned to a bacterial group (Zelles, 1997).

2.3. Microbial biomass carbon ($C_{mic/CFE}$)

Microbial biomass carbon was determined using the chloroform fumigation extraction (CFE) method as described by Vance et al. (1987) using 10 g fresh soil samples. Non-fumigated samples were extracted with 50 ml 0.5 M K_2SO_4 for 1 h at 130 rev min^{-1} and filtered subsequently. Extracted samples were kept frozen until analysis. Samples for fumigation were placed in a vacuum desiccator and fumigated with ethanol-free chloroform for 24 h. Fumigated samples were extracted with 0.5 M K_2SO_4 under the same conditions as non-fumigated samples. The C content of the K_2SO_4 extracts was measured on a high TOC elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany). Microbial biomass carbon was calculated as $C_{mic/CFE} = E_c/k_{ec}$, with E_c the difference between organic C extracted from fumigated soils and organic C extracted from non-fumigated soils, and k_{ec} the efficiency constant 0.45 (Joergensen, 1996).

2.4. Basal respiration (BR) and substrate induced respiration (SIR)

BR and SIR were measured using an O_2 microcompensation apparatus (Scheu, 1992). The microbial respiratory response was measured at hourly intervals for 24 h at 22 °C. BR (μl O_2 g^{-1} soil dry weight h^{-1}) was determined without addition of substrate and measured as mean of the O_2 consumption rates of hours 12–22

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