Soil Biology & Biochemistry 91 (2015) 248–257

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Temporal dynamics and variation with forest type of phospholipid fatty acids in litter and soil of temperate forests across regions

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A R T I C L E I N F O

Article history:
Received 23 February 2015
Received in revised form
24 August 2015
Accepted 28 August 2015
Available online 21 September 2015

Keywords:
PLFA
Microbial community composition
Fungal-to-bacterial ratio
Management intensity
Forest types
Temporal variability

A B S T R A C T

Microorganisms form the basis of soil food webs and represent key control points of carbon cycling and sequestration. Virtually all central European forests are managed and land-use regimes likely impact microbial abundance and community composition. Consequently, knowledge on how land-use intensity and abiotic variables, such as pH, C-to-N ratios, moisture regimes and concomitantly different stress levels, affect microbial communities is needed. We investigated phospholipid fatty acid (PLFA) profiles of leaf litter and soil from four forest types differing in foliage, age and management intensity, replicated in three regions across Germany. To account for temporal variation, samples were taken twice in the same season, but with an interval of three years. Total microbial biomass and microbial community composition differed between years, presumably due to between year variations in weather conditions. The litter layer was more prone to effects of drying, with a reduction of almost 30% of total PLFAs in the drier year. In soil effects of weather conditions depended on soil type and therefore differed between regions, with microorganisms in the sandy soils of the Schorfheide being more susceptible to water-stress, as evidenced by a ten-fold increase of the stress indicator cy/pre ratio in the drier year. Despite temporal variations in microbial biomass and community composition, the balance between the fungal and bacterial energy channel, as measured by fungal-to-bacterial ratios, remained rather constant in particular in soil. While total microbial biomass did not differ between forest types, microbial community composition differed significantly between beech and coniferous forests. Despite more acidic conditions, the fungal energy channel was less pronounced in leaf litter of coniferous forests than in broad-leaved forests, whereas the proportion of bacterial fatty acids was the highest in coniferous forests. Increasing management intensity presumably fosters the bacterial energy channel in the exposed litter layer. Supporting this assumption coniferous forests featured significantly higher values of the stress indicators cy/pre and SAT/MONO ratio. Bacterial community structure and biomass closely correlated with pH, with particular PLFAs dominating at high and low pH, respectively, indicating pH-specific microbial communities. In contrast, fungal abundance in leaf litter was correlated with C-to-N ratio. The results suggest that leaf litter and soil need to be considered separately when investigating changes in microbial community composition, since susceptibility of microorganisms to environmental stressors differs markedly between these layers. This, and repeated sampling events, may be particularly important when investigating subtle effects such as those related to climate change.

1. Introduction

Temperate forest ecosystems form an important component of global carbon cycling and climate control, storing about half of the total terrestrial carbon, predominantly in forest soils (Dixon et al., 1994). The functioning of forest ecosystems is intricately linked to soil microbial processes driving decomposition and mineralization processes (Brussaard, 1997; Carney and Matson, 2005) and thereby forest productivity. Soil microorganisms form key control points for carbon sequestration and carbon cycling (Drake et al., 2011). Further, microorganisms form the basis of soil food webs representing the major food resource for a variety of soil animals

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http://dx.doi.org/10.1016/j.soilbio.2015.08.035

channelling carbon to higher trophic levels (Hunt et al., 1987). Consequently, knowledge on the structure of soil microbial communities and their variation due to anthropogenic land use is essential for predicting effects of climate changes on soil processes (Jones et al., 1998) as well as for understanding the functioning of soil food webs (Tylianakis et al., 2008).

The way carbon is channelled through soil food webs, i.e. the relative contribution of bacterial and fungal energy channels, is assumed to significantly affect ecosystem properties. The bacterial pathway is associated with water filled pore spaces, whereas the fungal pathway is confined to air-filled pore spaces. Due to fast generation times of bacteria, the bacterial channel is assumed to be associated with fast carbon cycling, whereas the fungal channel presumably is associated with slow carbon cycling (Moore et al., 2005). These differences affect nutrient fluxes, excretion and respiration rates, but also ecosystem properties such as resilience and stability. The fungal energy channel dominates in infertile and unproductive ecosystems, whereas the bacterial energy channel is more prominent in fertile, productive ecosystems (Wardle et al., 2004). The two channels are assumed to exist in dynamic equilibrium that fluctuate seasonally, but persist in time (Moore et al., 2005). However, anthropogenic or natural disturbances may cause shifts in the relative importance of the two channels with the bacterial energy channel likely being more resistant against disturbances than the fungal energy channel (Wardle, 2002; Hedlund et al., 2004).

Virtually all central European forests are or have been managed to some degree. While effects of forest management on aboveground communities have been investigated extensively (Niemelä, 1997; Carey, 2000; Werner and Raffa, 2000; Battles et al., 2001; Paillet et al., 2010), effects on the belowground system are less well known. Although belowground communities often are more resilient to disturbances caused by management practices (Johnson and Curtis, 2001; Cruz-Martínez et al., 2009), different land-use intensities may result in altered partitioning of energy between the bacterial and fungal energy channel. Older stands, for instance, have been shown to exhibit increased fungal-to-bacterial phospholipid fatty acid (PLFA) ratios (Pennanen et al., 1999; Moore-Kucera and Dick, 2008). Shifts between the relative strength of these energy channels may impact resistance and resilience of the soil food web (De Vries et al., 2012).

Advances in molecular and physiological techniques, such as community DNA profiling, community level physiological profiles (CLPP; Campbell et al., 1997; Garland, 1997) and PLFA profiles, have facilitated the analysis of soil microbial communities. Recently, nucleic acid-based methods such as microarrays (Sessitsch et al., 2006) and high-throughput sequencing (454 sequencing, Illumina; Baldrian et al., 2012; Hirsch et al., 2010; Urbanová et al., 2015) are on the rise and can offer detailed information on microbial community composition. However, PLFA analyses are still a powerful tool to trace changes in microbial communities (Grayston et al., 2004; Ramsey et al., 2006) and are widely used, e.g. to investigate microbial community dynamics during land-use change (Smith et al., 2015), to track priming effects in organic matter decomposition (Xiao et al., 2015) and to follow the flux of labelled carbon into oil microorganisms (Kaiser et al., 2015). PLFAs are major components of bacterial and fungal cell walls. Since they are rapidly degraded after cell death, they represent a reliable quantitative measure for living microorganisms in soil. Using the ratio of fungal and bacterial PLFA biomarkers therefore allows to deduce the relative abundance of fungi vs. bacteria in soils and consequently the balance between the fungal and bacterial energy channel (Frostegård and Bååth, 1996; Bååth and Anderson, 2003; Högberg et al., 2007). Additionally, the ratios of cyclopropyl PLFAs to their monoenoic precursors and of saturated to monounsaturated PLFAs can be used as indicators for physiological stress (Bossio and Scow, 1998; Moore-Kucera and Dick, 2008).

We used PLFA profiles to investigate microbial communities of four forest types differing in foliage (needles vs. broad leaves), age (~30, ~70 and ~120 years) and concomitantly in management intensity. As effects of forest management likely vary with soil depth we considered both the leaf litter and upper mineral soil layer. To allow insight into large-scale variations, the different forest types were replicated in three regions across Germany. To account for temporal variation, samples were taken twice with an interval of three years, but in the same season (spring).

We hypothesized that (1) increased management intensity strengthens the bacterial energy channel in particular in broad-leaved forests, (2) due to low pH the fungal energy channel is more pronounced in coniferous forests, (3) the microbial community in leaf litter is more prone to disturbances and fluctuations in environmental conditions than in the mineral soil, and consequently is more variable in time, and (4) stress (as measured by PLFA stress indicators) is higher for microbial communities in more intensively managed forests.

2. Materials and methods

2.1. Study sites

The study sites comprised three regions across Germany, i.e. the Swabian Alb, Hainich-Dün (Hainich) and Schorfheide-Chorin (Schorfheide), and were part of the “Biodiversity Exploratories”, a large project serving as open platform for biodiversity and ecosystem research (www.biodiversity-exploratories.de; Fischer et al., 2010). The Schorfheide is a young glacial landscape with an altitude of 3–140 m a.s.l., a mean annual temperature of 8.0–8.5 °C and a mean annual precipitation of 500–600 mm. Soils in the Schorfheide are mainly cambisols. The Hainich is based on calcareous bedrock and varies in altitude from 285 to 550 m a.s.l. Soils in the Hainich are mainly luvisols with few stagnosols. The mean annual temperature is 6.5–8.0 °C and the mean annual precipitation is 600–800 mm. The Swabian Alb also has calcareous bedrock, but with karst phenomena. Its soils are cambisols and leptosols. For detailed information on soil types see Table S1 in Appendix. The altitude of the Swabian Alb varies between 460 and 860 m a.s.l., the mean annual temperature is 6–7 °C and the mean annual precipitation is 700–1000 mm.

In each region four forest types with four replicates each were sampled (for details see Klarner et al., 2014). The forest types included coniferous forests, age class stands of young beech (*Fagus sylvatica*; age ~30 years, young managed beech), mature beech age class stands (age ~70 years, old managed beech) and mature beech stands that were left unmanaged for at least 60 years (age ~120 years, unmanaged beech), representing a gradient of decreasing management intensity. Coniferous forests consisted of spruce (*Picea abies*) in the Swabian Alb and Hainich, and pine (*Pinus sylvestris*) in the Schorfheide and were classified as the most intensively managed forests since they had been planted to replace naturally occurring beech forests (Schall and Ammer, 2013). The study sites were located within 100 × 100 m grid plots established as core sampling sites of the Biodiversity Exploratories. The plots were at least 200 m apart from each other and had a minimum distance of 100 m to the next forest edge.

2.2. Sampling

Samples were taken in spring (April and May) 2008 and 2011. In 2008 April featured high precipitation and low temperatures (mean precipitation 30–75 mm, mean temperature ~10 °C),