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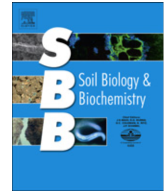

Experimental warming effects on the microbial community of a temperate mountain forest soil

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Soil microbial communities mediate the decomposition of soil organic matter (SOM). The amount of carbon (C) that is respired leaves the soil as CO_2 (soil respiration) and causes one of the greatest fluxes in the global carbon cycle. How soil microbial communities will respond to global warming, however, is not well understood. To elucidate the effect of warming on the microbial community we analyzed soil from the soil warming experiment Achenkirch, Austria. Soil of a mature spruce forest was warmed by 4 °C during snow-free seasons since 2004. Repeated soil sampling from control and warmed plots took place from 2008 until 2010. We monitored microbial biomass C and nitrogen (N). Microbial community composition was assessed by phospholipid fatty acid analysis (PLFA) and by quantitative real time polymerase chain reaction (qPCR) of ribosomal RNA genes. Microbial metabolic activity was estimated by soil respiration to biomass ratios and RNA to DNA ratios. Soil warming did not affect microbial biomass, nor did warming affect the abundances of most microbial groups. Warming significantly enhanced microbial metabolic activity in terms of soil respiration per amount of microbial biomass C. Microbial stress biomarkers were elevated in warmed plots. In summary, the 4 °C increase in soil temperature during the snow-free season had no influence on microbial community composition and biomass but strongly increased microbial metabolic activity and hence reduced carbon use efficiency.

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1. Introduction

Global warming is considered to promote the decomposition of SOM, and thereby to increase the C flux from soil to the atmosphere (Cox et al., 2000; IPCC, 2007; Trumbore et al., 1996). SOM is decomposed by heterotrophic microorganisms, which due to the enormous C fluxes they generate, are one of the main drivers of the global C cycle. How these microorganisms respond to warming, however, is difficult to predict as a set of environmental and biological factors interact during SOM decomposition. The overall warming response of SOM decomposition will be determined by the temperature sensitivity of the decomposers, substrate availability, interactions with aboveground processes and other environmental drivers such as soil moisture, and also by potential adaptations of microbial physiology (Allison et al., 2010; Davidson and Janssens, 2006; De Deyn et al., 2008; Knorr et al., 2005). So far, most effort has been made to understand how increased soil temperature influences the CO_2 efflux from soil. In comparison, physiology and composition of the microbial decomposer community were rarely studied. There is evidence that warming potentially alters decomposer physiology and accordingly the CO_2 efflux from soil (Allison et al., 2010; Balser and Wixon, 2009; Bárcenas-Moreno et al., 2009; Bradford et al., 2008; Zogg et al., 1997). The mechanisms behind temperature adaptations of soil microbes could be physiological adaptations of single species (Malcolm et al., 2008) or species shifts within the microbial community. As various decomposing microbes differ within their ability/strategy to efficiently utilize SOM (Balser and Wixon, 2009; Keiblinger et al., 2010; Lipson et al., 2009; Liptzin et al., 2009; Monson et al., 2006), shifts within the community structure may affect decomposition rates and CO_2 production. Lipson et al. (2009) and Keiblinger et al. (2010), for example, showed that fungi form more biomass from the same amount of added substrate than bacteria, thus they use organic substrates more efficiently. Bacteria on the other hand showed higher growth rates and lower yields suggesting that they were important for determining heterotrophic soil respiration rates. Fungi were further found to dominate during early stages of plant residue decomposition (Berg et al., 1998;

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McMahon et al., 2005). Gram-positive and Gram-negative bacteria showed different patterns in substrate preference. Gram-positive bacteria were found to be dominant in soils with low substrate availability and in deeper soil layers (Fierer et al., 2003), while Gram-negative bacteria were found to dominate soils with high availability of easily decomposable substrate (Kramer and Gleixner, 2006). *Archaea* were found abundant in many soils and important in CH_4 and N dynamics (Leininger et al., 2006). There is evidence that *Archaea* are able to perform heterotrophic or mixotrophic catabolism (Jia and Conrad, 2009) but their role in SOM decomposition is unclear.

Although functional traits (organisms with same physiological pathway) are not strictly related to the taxonomic units mentioned above, the relative abundance of fungi, Gram-positive or Gram-negative bacteria, and other microbial groups can give some insights in the physiological capacity of the soil microbial community. A good example was given by Lipson et al. (2009) who showed that distinct microbial winter- and summer-communities differed in growth kinetics, biomass-specific respiration rates and temperature sensitivity of soil respiration. A temperature difference between winter and summer however is not comparable with the expected temperature increase due to global warming. In order to simulate anticipated global warming (1–5 °C) a large array of field and lab warming studies have been performed. Although microbial assessments were not regularly undertaken, some general patterns were observed. A common finding of most warming studies was that warming did not increase microbial biomass in soil (Biasi et al., 2008; Feng and Simpson, 2009; Rinnan et al., 2007, 2008, 2009; Vanhala et al., 2011; Zhang et al., 2005; Zogg et al., 1997). Depending on the duration of the warming treatment, microbial biomass either remained at steady levels or decreased. Regarding microbial community composition, the picture was more complex. Dependent on the ecosystem observed, the duration of warming and the experimental warming approach, changes in microbial community composition were observed in terms of increased fungal abundance, decreased fungal abundance, increased abundance of Gram-positive bacteria, decreased abundance of Gram-positive bacteria, decreased abundance of Gram-negative bacteria, or not at all (Biasi et al., 2005; Castro et al., 2010; Feng and Simpson, 2009; Frey et al., 2008; Karhu et al., 2010; Rinnan et al., 2007, 2008, 2009; Vanhala et al., 2011; Zogg et al., 1997).

In the present study, we took the opportunity to sample soil from the forest soil warming experiment in Achenkirch, Austria, (Schindlbacher et al., 2009). Soil was warmed 4 °C above ambient throughout growing seasons since 2004. CO_2 flux rates were regularly measured. To assess microbial biomass and community composition, repeated soil sampling from control and warmed plots took place in the fourth and fifth year of artificial warming. According to enzyme kinetics (Davidson and Janssens, 2006), we hypothesized that (I) soil warming strongly enhanced microbial metabolic activities. We further hypothesized that (II) increased soil temperatures generated advantages for specific microbial groups better adapted to warmer conditions and hence caused shifts in the microbial community composition. A decrease in fungal abundance, as observed in related studies (Frey et al., 2008; Vanhala et al., 2011) was anticipated.

2. Materials & methods

2.1. Site description

The study site was located at 910 m a.s.l. in the North Tyrolean Limestone Alps, near Achenkirch, Austria (11°38′21″ East; 47°34′50″ North). The 130 year-old mountain forest consists of Norway spruce (*Picea abies*) with inter-spread of European beech (*Fagus sylvatica*) and silver fir (*Abies alba*). Climate at the site was cool, humid, with maximum precipitation during summer. Snow-free periods were typically from April or May to November or December. Mean annual air temperature and precipitation were 5.7 °C and 1480 mm, respectively (1987–2007, ZAMG). Soils were shallow Chromic Cambisols and Rendzic Leptosols with high spatial variability. The dominant humus form was mull followed by thick A-horizons that reach up to 10–20 cm in Chromic Cambisols and 60 cm in Rendzic Leptosols. Dolomite formed the bedrock. The soil pH was slightly above 6 and the C/N ratio was 15–18. A detailed site description is given in Herman et al. (2002).

2.2. Soil warming and soil respiration measurements

Three experimental plots with 2 × 2 m warmed- and control-subplots were installed in 2004. Within the heated plots resistance heating cables (Etherma, Salzburg) were installed at 3 cm soil depth and with 7.5 cm space between the cable lines. To account for potential disturbance effects, the same cables were installed in control plots but not heated. The temperature difference between control and warmed plots was set to 4 °C at 5 cm soil depth. Soil was warmed during snow-free seasons. Soil temperature and moisture of each subplot were measured year-round at 5 and 15 cm soil depth and data were stored on data-loggers at half-hourly intervals. Soil respiration was measured manually every second week during the growing seasons and every third week during snow-cover. A detailed description of the experimental setup and soil respiration measurements is given in Schindlbacher et al. (2009) and Schindlbacher et al. (2007).

2.3. Soil sampling

For soil analysis the Ah horizon (0–5 cm) was sampled with a 3 cm diameter soil-corer. At warmed plots, soil samples were taken exactly half way between two heating-cable lines to assure that all samples received the same heat input. In order to represent different seasonal conditions the samples were taken on the following dates in 2008: 14 February, 6 May, 29 June, 23 September, 18 November, and in 2009: 18 March, 17 June, 10 August and 22 September. The last samples were taken on 23 March 2010. Three replicates from each of the six 2 × 2 m subplots (three warmed and three controls) were analyzed for the sample dates 6 May, 29 June, 18 November 2008 and 18 March 2009. Because within-subplot variability was low, we pooled the three randomly taken samples across each subplot to one mixed sample for analysis during subsequent sampling dates. The samples were stored in cooling boxes and transported to the laboratory in Vienna where the soil samples were homogenized with 5 mm mesh sized sieves and frozen at −20 °C. Prior to laboratory analysis, soil water content was determined gravimetrically by drying soil samples at 105 °C for 24 h (Schinner et al., 1996). For qPCR analysis two samples of about 100 g fresh soil were collected from each subplot and homogenized. Aliquots were immediately frozen in liquid nitrogen and stored at −80 °C.

2.4. Microbial analysis

Microbial analysis focused on the total microbial biomass and the abundance of specific microbial groups. To assess microbial biomass C and N, we applied chloroform-fumigation-extraction. Specific microbial groups were separated by PLFA analysis and alternatively by qPCR. Microbial activity was estimated according to respiration to biomass ratios and RNA to DNA ratios.

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