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Recovery in fungal biomass is related to decrease in soil organic matter turnover time in a boreal fire chronosequence

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ABSTRACT

Fire is one of the most important natural disturbances in the boreal forest. It strongly influences boreal forest structure and function, and alters microbial biomass and species composition e.g. by significantly reducing the abundance of decomposing fungi. We measured carbon stocks and estimated fungal biomass and soil carbon turnover in *Pinus sylvestris* stands on a fire chronosequence from 2 to 152 years post-fire. Results show that the turnover time of soil carbon was longest in the area where fire occurred 2 years ago (117 years) and approximately two times shorter (ca. 60 years) in the areas where fire occurred 42, 60 and 152 years ago. The soil carbon turnover time in our study areas was associated with very slow fungal biomass recovery. The fungal biomass (ergosterol content), soil carbon content and soil CO_2 efflux reached the same levels as in the oldest site approximately 60 years after the fire. Our results indicate that the slow multi-decadal post-fire recovery of fungal biomass drives the soil carbon balance of boreal forests, and disturbances such as fires have a profound influence on soil carbon turnover for decades. On the other hand, the longer post-fire residence time of carbon in the soil compared to older forests suggests that fire effects on the soil carbon pool in boreal forests might be less dramatic than previously thought.

1. Introduction

Boreal forests, which cover 15% of the Earth's land area, are a crucial part of the climate system as they contain approximately 60% of the carbon (C) bound in global forest biomes (Bond-Lamberty et al., 2006) and approximately 12–13% of the organic C stocks in the world's soils (Post et al., 1982). The soil organic matter (SOM) pool in boreal forests is a particularly important C storage, with a long turnover time ranging from several decades to millennia. Approximately 80% of the C stored in boreal regions is found in forest soils (Goodale et al., 2002) and most of it is stored in high northern latitudes (Jobbágy and Jackson, 2000). Forest fires have an important influence on the carbon dynamics of boreal landscapes (with regionally varying frequency and severity), and it is expected that the fire frequencies of boreal forests will increase with future climate change because of rising temperatures and more frequently occurring dry periods (Ali et al., 2012; Bond-Lamberty et al., 2006, 2007; Flannigan et al., 2009; Gromtsev, 2002; Pechony and Shindell, 2010). Wildfires strongly influence boreal forests as they can result in combustion-induced aboveground and ground layer biomass losses of 15–35% and 37–70%, respectively (Shorohova et al., 2009; Yarie and Billings, 2002). Circa 0.8% of the total boreal forest area burns yearly, and both high-severity (stand-replacing) and intermediate-severity fires are common in Eurasia (Bond-Lamberty et al., 2006; Conard et al., 2002; Kasischke et al., 2005). In both cases fire functions as a disturbance process that consumes the understorey and moss layer, along with a portion of the humus pool and with a significant portion of the total C stored in the O horizon (DeLuca and Boisvenue, 2012). Contrariwise, mineral soil C remains mostly unchanged (Seedre et al., 2011). Fire directly and indirectly alters the microbial biomass and species composition of soil (Allison and Treseder, 2008; Hart et al., 2005; Holden et al., 2013; Neary et al., 1999). Holden et al. (2013) and Dooley and Treseder (2012) have recently shown that wildfires affect the amount and composition of soil fungal communities by decreasing post-fire litter decomposition. Fungi in boreal forests are particularly important as they can degrade and mineralise the organic material in soils with low soil pH (Högberg et al., 2007). Post-fire ash deposition in acidic soils increases soil pH (Certini, 2005; Peay et al., 2009), which may also cause the post-fire decline in fungal biomass (Dooley and Treseder, 2012; Smith et al., 2008). However, little information exists regarding post-fire fungal and microbial recovery over the long-term period. The recovery of microbial biomass is found to take approximately 10 years (3–17 years) (Dangi et al., 2010; Guénon et al., 2013; Prieto-Fernández et al., 1998; Villar et al., 2004; Waldrop and Harden, 2008) or 40 years (Visser, 1995). The time since fire onset

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may thus be one of the main drivers of several ecosystem functions and also of total stand C content (Brassard and Chen, 2006; Seedre et al., 2011).

Changes in boreal forest soil C storage could significantly alter the global C balance through the soil surface CO_2 efflux. Soil CO_2 efflux increases may thus cause major changes in the net C balance of forests, turning a global C sink into a net C source (Cox et al., 2000). Changes in soil temperature influence the rate of microbial activity in soils and therefore regulate the rate of soil organic C decomposition and soil C turnover times (Carrasco et al., 2006; DeLuca and Boisvenue, 2012; Hakkenberg et al., 2008). Soil C turnover time (also referred to as soil C residence time) is the average time that C resides in a SOM pool (Hakkenberg et al., 2008), and it can be directly inferred from soil CO_2 efflux measurements when the steady state of soil C stocks and the contribution of heterotrophic and autotrophic CO_2 effluxes from the soil are known (Garten and Hanson, 2006).

Abundant levels of fungi reside in boreal forest soils, and have a central role in the decomposition of SOM and C compounds in the soil (Joergensen and Wichern, 2008; McGuire et al., 2013). A more complex and complete understanding of the mechanisms in which fire affects soil fungal communities, and their post-fire recovery, is therefore required for predicting ecosystem C dynamics under future global change. In this study, we characterise the short- and long-term soil fungal biomass responses to fire in boreal Scots pine (*Pinus sylvestris*) forests and its impact on the soil C turnover time. The changes occurring in soil C dynamics (CO_2 efflux, soil C content, soil C turnover times) and fungal biomass were assessed along a fire chronosequence in subarctic Scots pine stands of similar soil type, elevation, and microclimatic conditions. We hypothesised that the post-fire changes in soil fungal biomass affect decomposition (soil C turnover time) in post-fire chronosequence. We expected a post-fire reduction in soil fungal abundance, which will also in turn reduce the decomposition rate of soil C, as previously suggested by Holden et al. (2013). We assume that fungal biomass response to fire is transient and its recovery is associated with the recovery of aboveground plant biomass (Hart et al., 2005). We also hypothesise that the fungal biomass decrease caused by fire disturbance correlates with changes in the CO_2 emissions from soils. We expect that our chronosequence study approach will bring new quantitative information on changes in soil C turnover rates following forest fires and during the forest succession, which may be useful for global C cycle modellers.

2. Material and methods

2.1. Study sites

The study area was located in Värriö Strict Nature Reserve (67°46′ N, 29°35′ E), Finnish Lapland, in northern boreal subarctic coniferous forests (Fig. 1). The reserve's lowlands are covered by taiga, where the main tree species is Scots pine and the ground vegetation consists of *Vaccinium myrtillus*, *Vaccinium vitis idaea*, *Empetrum nigrum* and *Cladina* sp. An average fire return interval of 50–150 years is generally stated for boreal forests and Fennoscandia for the last one thousand years (Johnstone and Chapin, 2006; Toivanen and Kotiaho, 2007).

The soils in the area are classified as haplic podsols (FAO, 1990) with sand tills. The top layer contains a mixture of litter and decomposing organic layer (F-horizon) and the thickness of layer varies between 0 and 2.5 cm (Table 1). Next is the humus layer (O-horizon) in a mixture with some mineral soil, with a thickness varying between 0 and 1.2 cm (Table 1). The mineral soil consists of an eluvial horizon (A-horizon) (thickness 1–4.5 cm) that is low in clay, organic compounds and iron (Fe) oxides, which accumulate in the illuvial horizon (B-horizon) (thickness 1–6 cm) (Table 1). The mineral soil mostly consists of sand. Average soil pH in the mineral soil and humus layer is 4.4 and 3.6–4.0, respectively (Table 1). The area's annual mean precipitation is approximately 592 mm, and annual evapotranspiration from May until September (snow-free period) is approximately 330 mm (Korhonen and Haavanlammi, 2012). Average annual mean temperature at Värriö research station (altitude 380 m) is approximately −1 °C (Susiluoto et al., 2008). The climate is subcontinental and the soil has no underlying permafrost. Snow covers the ground ca. 200 to 225 days per year (the average snow cover period ends on May 20th), and the length of the growing season is 105–120 days (Pohjonen et al., 2008). The growing season (mean monthly temperature > 5 °C) lasts for four months and the average temperature during that period (June to September) is approximately 12 °C.

2.2. Field measurements

In the summer of 2011 we identified eight sample plots that were spatially separated by at least 500 m and had burned within the last 150 years (study area of 18 km^2). The sample plots form a chronosequence of four age classes: (i) fire occurrence 2 years ago, (ii) fire occurrence 42 years ago, (iii) fire occurrence 60 years ago, and (iv) fire occurrence 152 years ago. Each age class was represented by two sample plots. None of the fires detected on the sample plots were completely stand-replacing, as a lot of trees survived in areas where the fire occurred 2, 42 and 60 years ago (Table 2) and in the area where the fire occurred 152 years ago we found some trees that were older than 152 years (Table 2). To characterise the stands we established circular sample plots in the study area, with a surface area of 400 m^2. Diameter at 1.3 m height, tree height, crown height and crown diameter were measured. Trees on the sample plot were divided into five diameter classes and two trees were randomly selected as sample trees from each diameter class. Tree age and time since the last fire occurred was determined from core samples taken from the sample trees (a total of 10 trees per sample plot) and analysed using WinDENDRO (Regent Instruments Inc., Canada). Ground vegetation biomass was determined from five small sample plots (0.2 × 0.2 m in size) located systematically inside the circular sample plots.

Soil CO_2 efflux was measured from all sample plots using a portable chamber (0.24 m in height and 0.22 m in diameter) made of Plexiglas and covered with aluminium foil. CO_2 concentration was recorded with a four-minute chamber deployment time with a diffusion-type CO_2 probe (GMP343, Vaisala Oyj, Vantaa, Finland). The CO_2 exchange rate was estimated from a linear regression fitted to the CO_2 readings. Measurements were performed on six measurement collars at each sample plot between June and August 2011 (six times per collar). CO_2 efflux measurements were performed concurrently with air humidity and temperature measurements taken from within the chamber with a relative humidity and temperature sensor (HM70, Vaisala Oyj, Vantaa, Finland).

Continuous temperature and soil water content measurements were taken from one sample plot at 15-min intervals. Soil temperature was measured using silicon temperature sensors (Philips KTY81-110, Philips semiconductors, Eindhoven, the Netherlands) and water content was measured using soil moisture sensors (Thetaprobe ML2x, Delta-T Devices Ltd., Cambridge, UK) connected to a datalogger (DataTaker DT80, Thermo Fisher Scientific Australia Pty Ltd., Victoria, Australia). Soil temperature was additionally measured in three-hour intervals at individual sample plots with iButton® temperature sensors (Maxim Integrated, San Jose, CA, US) installed permanently beneath the moss layer.

From each sample plot, 10 soil cores for soil chemical analyses and incubation studies were taken in early summer (June) using a soil corer. The soil samples were 150 mm in length and 50 mm in diameter and were stored at +4 °C. A total of four soil cores (100 mm in length and 50 mm in diameter) were also taken from each sample plot in late summer (August), for gravimetric soil water content measurements.

2.3. Laboratory measurements

Soil respiration was also measured in a laboratory incubation experiment, to exclude root respiration. In the laboratory, soil cores were