Resistance of microbial and soil properties to warming treatment seven years after boreal fire

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ABSTRACT

Boreal forests store a large fraction of global terrestrial carbon and are susceptible to environmental change, particularly rising temperatures and increased fire frequency. These changes have the potential to drive positive feedbacks between climate warming and the boreal carbon cycle. Because few studies have examined the warming response of boreal ecosystems recovering from fire, we established a greenhouse warming experiment near Delta Junction, Alaska, seven years after a 1999 wildfire. We hypothesized that experimental warming would increase soil CO_2 efflux, stimulate nutrient mineralization, and alter the composition and function of soil fungal communities. Although our treatment resulted in 1.20 °C soil warming, we found little support for our hypothesis. Only the activities of cellulose- and chitin-degrading enzymes increased significantly by 15% and 35%, respectively, and there were no changes in soil fungal communities. Warming resulted in drier soils, but the corresponding change in soil water potential was probably not sufficient to limit microbial activity. Rather, the warming response of this soil may be constrained by depletion of labile carbon substrates resulting from combustion and elevated soil temperatures in the years after the 1999 fire. We conclude that positive feedbacks between warming and the microbial release of soil carbon are weak in boreal ecosystems lacking permafrost. Since permafrost-free soils underlie 45–60% of the boreal zone, our results should be useful for modeling the warming response during recovery from fire in a large fraction of the boreal forest.

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1. Introduction

Increasing emissions of atmospheric CO_2 are expected to affect high-latitude climate disproportionately (IPCC, 2007). Tundra and boreal ecosystems in northern latitudes have already experienced >1 °C warming, and may warm by 4–7 °C over the next century (Moritz et al., 2002; ACIA, 2004). Climate warming in these systems may have biogeochemical consequences because they contain large stocks of soil organic matter. Recent estimates place these stocks at >1600 Pg carbon (C), more than double the amount of C in the atmosphere (Schuur et al., 2008). As the climate warms in high latitudes, rates of decomposition may also increase, leading to greater soil CO_2 respiration, increased nutrient mineralization, and a positive feedback to global warming (Lükewille and Wright, 1997; Rustad et al., 2001; Schuur et al., 2009).

One potential impact of climate change in boreal ecosystems is increased frequency of wildfire (Kasischke and Stocks, 2000). In boreal Asia and North America, fires burn an average of 11.1 million ha yr^{-1} (Giglio et al., 2006) and drive major ecosystem impacts such as increased albedo, reduced C storage, and drastic changes in vegetation and microbial communities (Bond-Lamberty et al., 2004; Randerson et al., 2006; Waldrop and Harden, 2008). In Alaskan boreal forest, wildfire triggers rapid ecological succession and further changes in ecosystem properties (Mack et al., 2008). Within a few years after fire, grasses and shrubs dominate the vegetation, followed by deciduous *Populus tremuloides* trees that dominate the canopy ~15–50 years post-fire (Treseder et al., 2004; Mack et al., 2008). After >80 years, black spruce (*Picea mariana*) becomes the dominant canopy tree, with an understory of primarily shrubs and mosses. If fire frequency increases with climate change, a larger fraction of the landscape will be occupied by early-successional systems, and it becomes important to understand their responses to environmental changes, such as climate warming.

Losses of soil C are primarily determined by the metabolic rates of decomposer microbes, which often increase with rising

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temperature (Lloyd and Taylor, 1994). In boreal ecosystems, fungi are important drivers of soil C loss because they tolerate acidic soils and, along with bacteria, produce extracellular enzymes required to degrade recalcitrant litter inputs of the dominant plant species (Högberg et al., 2007; Allison et al., 2009). Additionally, most of the dominant plants in boreal forests associate with symbiotic mycorrhizal fungi that contribute to soil CO_2 efflux, and may drive turnover of soil organic C through the production of extracellular enzymes (Read et al., 2004; Talbot et al., 2008; Bödeker et al., 2009).

Although microbial metabolic rates usually increase with warming, the impact of climate change on boreal C cycling is far from certain. For example, soil drying or reductions in snow depth may counteract warming effects on microbial metabolism (Monson et al., 2006; Allison and Treseder, 2008). In addition, microbial communities may adapt to warming through physiological mechanisms (Malcolm et al., 2008) or changes in community composition (Clemmensen et al., 2006), such that temperature effects diminish over time. This uncertainty is compounded by a paucity of direct experimental manipulations of soil temperature in boreal ecosystems. Only two boreal sites were included in a 2001 meta-analysis of soil warming studies (Rustad et al., 2001), and there have been few recent studies (Bergner et al., 2004; Niinistö et al., 2004; Allison and Treseder, 2008; Bronson et al., 2008). There is considerable variability in the warming response across these studies, with most showing higher rates of soil CO_2 efflux but some showing lower rates (Allison and Treseder, 2008; Bronson et al., 2008).

The objective of our current study was to determine how climate warming would affect soil properties and the fungal community in a boreal ecosystem recovering from wildfire. Our work follows up on the Bergner et al. (2004) study, which assessed warming responses immediately after a 1999 wildfire near Delta Junction, Alaska. We hypothesized that warming would increase the metabolic rates of decomposer microbes, thereby increasing soil CO_2 efflux and the mineralization of organic nutrients (Rustad et al., 2001). In turn, we expected that greater C and nutrient mineralization would support more microbial biomass and extracellular enzyme production. Finally, we predicted that warming would alter the composition of fungal communities because laboratory studies suggest that higher nutrient availability should favor the growth of Ascomycete and Zygomycete fungi over Basidiomycetes (Zadražil and Brunnert, 1980; Fog, 1988).

2. Materials and methods

2.1. Site description

We conducted our experiment in an upland boreal ecosystem that experienced a severe fire that killed all of the canopy trees in 1999. The site is located on the Fort Greely military base (63° 55′ N, 145° 44′ W) near Delta Junction, Alaska. Permafrost is discontinuous in this region and was not present in the site. The dominant plants were herbaceous perennials, deciduous trees, and shrubs; major plant taxa included Betula, Calamagrostis, Festuca, Ledum, Lupinus, Populus, Salix, and Vaccinium as described by Mack et al. (2008). Before the 1999 fire, a forest of P. mariana occupied the area. The climate is dry and cold, with a precipitation rate of 303 mm y^{-1} and a mean annual temperature of -2 °C (http://weather.noaa.gov/). Soils are well-drained and consist of a shallow organic horizon ($<$5 cm depth) underlain by a silt-loam mineral soil (A horizon) derived from gravelly glacial till and outwash (Harden et al., 2006; Waldrop and Harden, 2008). The 1999 fire removed $\sim$60% of the surface organic C, leaving behind an unburned forest floor horizon approximately 0–3 cm thick (King et al., 2002). The unburned organic horizon (where present) was

overlain by several centimeters of char and ash immediately after the fire, but little of this burned material remained by 2006.

For the warming manipulation (see Allison and Treseder, 2008 for details), we established 5 pairs of 2.5 m × 2.5 m plots in a $\sim$1 km^2 area of burned forest. One plot in each pair served as a control, and was located in a visually similar area within 10 m of the treatment plot to minimize any effects of spatial variability. The treatment plot was passively warmed with a greenhouse constructed of two-by-fours in an A-frame covered with clear 6 mil plastic sheeting (AT Plastics, Inc, Edmonton, Canada). The plastic transmits 60–70% of photosynthetically active radiation (Krizek et al., 2005). The dominant plants at the site (i.e. mosses, grasses, forbs, shrubs) were fully enclosed in the greenhouses. We applied the warming treatment from mid May to mid September each year (starting in 2006) by attaching a top plastic panel to the greenhouse frame. Therefore snowfall could reach the greenhouse plots during the winter. Precipitation during the growing season was captured with gutters on the greenhouses and redistributed via tubing to the plot surface at 8 locations separated by at least 50 cm. Gaps between the plastic and the frame or ground allowed air to circulate within the greenhouses. Large animals occasionally added additional air vents to the plastic panels. We did not include a chamber control (i.e. frames with no plastic) because a prior open-top chamber study at this site showed there was no chamber effect (Bergner et al., 2004).

2.2. Temperature and soil water content

We measured soil temperatures using Onset HOBO dataloggers placed 5 cm beneath the soil surface in control and warmed plots. Temperatures in 4–5 experimental blocks were recorded every 30 min during 3 growing seasons: May 13–September 18, 2006; May 10–September 18, 2007; and May 30–September 15, 2008. Soil water content was determined gravimetrically (oven-dry, 65 °C) on samples collected for extracellular enzyme assays. These cores generally included 1–3 cm of organic soil from the surface with the remainder derived from the mineral A horizon.

2.3. Soil CO_2 efflux

Soil CO_2 effluxes were measured with chambers and an infrared gas analyzer (PP Systems EGM-4) as described previously (Allison and Treseder, 2008). Chamber bases 25 cm in diameter were inserted 2 cm into the soil in May 2006. At 3–4 time points during the 2006–2008 growing seasons, we placed an opaque lid on the chamber base and measured the rate of increase in CO_2 concentration in the chamber for 5–10 min. We also measured soil temperature next to the chamber with a temperature probe. Fluxes were calculated according to the ideal gas law using the chamber volume, ambient air temperature, and 1 atm pressure. Litter, grasses, mosses, and other plants were generally left in the chambers to avoid disrupting root and litter inputs, except that we clipped aboveground plant biomass in chambers on August 21, 2006. However, before and after measurements indicated that clipping had no significant effect on soil CO_2 efflux.

2.4. Resin nutrients and microbial biomass

The availabilities of NH_4^+, NO_3^-, and PO_4^{3-} were measured as reported previously using resin bags (Allison et al., 2008). We placed 4 anion and 4 cation bags 5 cm below the soil surface and at least 25 cm apart in each warmed and control plot. One set of bags was placed in the field from May 14, 2006 to September 17, 2006, and a second set was placed in the field from May 11, 2007 to September 19, 2007. After collection, bags were rinsed in deionized