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Winter soil freeze-thaw cycles lead to reductions in soil microbial biomass and activity not compensated for by soil warming

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ABSTRACT

Air temperatures are rising and the winter snowpack is getting thinner in many high-latitude and high-elevation ecosystems around the globe. Past studies show that soil warming accelerates microbial metabolism and stimulates soil carbon (C) and nitrogen (N) cycling. Conversely, winter snow removal to simulate loss of snow cover leads to increased soil freezing and reductions in soil microbial biomass, exoenzyme activity, and N cycling. The Climate Change Across Seasons Experiment (CCASE), located at Hubbard Brook Experimental Forest, NH (USA) is designed to evaluate the combined effects of growing season soil warming and an increased frequency of winter soil freeze-thaw cycles on a northern forest ecosystem. Soils were collected from CCASE over two years (2014 and 2015) and extractable C and N pool sizes, as well as microbial biomass, exoenzymes, and potential net N mineralization and microbial respiration were measured. Soil warming alone did not stimulate microbial activity at any sampling time. Extractable amino acid N and organic C, proteolytic and acid phosphatase activity, and microbial respiration were reduced by the combination of warming in the growing season and winter soil freeze-thaw cycles during the period following snowmelt through tree leaf out in spring. The declines in microbial activity also coincided with an 85% decline in microbial biomass N at that time. Growing season warming and winter soil freeze-thaw cycles also resulted in a two-fold reduction in phenol oxidase activity and a 20% reduction in peroxidase activity and these declines persisted throughout the snow-free time of the year. The results from this study suggest that positive feedbacks between warming and rates of soil C and N cycling over the next 100 years will be partially mitigated by an increased frequency of winter soil freeze-thaw cycles, which decrease microbial biomass and rates of soil microbial activity.

1. Introduction

Understanding the consequences of climate warming on soil microbial activity is important due to the potential feedbacks to global air temperature rise (Cox et al., 2000; Davidson and Janssens, 2006; Friedlingstein et al., 2006; Melillo et al., 2011). In recent decades, rising air temperatures have reduced the depth and duration of winter snow in temperate ecosystems that have historically experienced a seasonal snowpack (Hamburg et al., 2013; Henry, 2008; Kreyling and Henry, 2011). Winter snow cover plays a critical role in mediating soil nutrient cycling because the physical characteristics of snow, such as high surface albedo and low thermal conductivity, produce an insulating effect that maintains increased soil temperature relative to air temperature during winter (Zhang, 2005). In the northeastern U.S., mean annual air temperatures have risen by approximately 1 °C over the last 50 years (Hamburg et al., 2013), with air temperatures in winter rising at a faster rate (+0.7 °C decade^{-1}) compared to summer (+0.1 °C decade^{-1}; Hayhoe et al., 2007). Increasing winter air temperature over the next 100 years will reduce the depth and duration of winter snow cover, likely causing colder soil temperatures and more frequent soil freeze-thaw cycles in many temperate forest ecosystems (Brown and DeGaetano, 2011; Campbell et al., 2010).

Winter snow and soil temperature conditions are increasingly recognized as critical factors that mediate soil carbon (C) and nitrogen (N) pool sizes and process rates, both overwinter and during the transition between winter and spring (Brooks and Williams, 1999; Giblin et al., 1991; Groffman et al., 2006; Reinmann et al., 2012). Winter snow cover can prevent soils from freezing and thus allows microbial biomass production, exoenzyme synthesis, and nutrient immobilization to be higher compared to when snow is absent and soils freeze (Brooks and

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Williams, 1999; Drake et al., 2013; Kuhnert et al., 2012; Ueda et al., 2013). By contrast, when the winter snowpack is thin or intermittent, soil freezing limits substrate diffusion, increases microbial mortality and reduces microbial population size, and also reduces exoenzyme production following snowmelt in spring (Boutin and Robitaille, 1995; Deluca et al., 1992; Fitzhugh et al., 2001; Matzner and Borken, 2008; Skogland et al., 1988; Sorensen et al., 2016). Thus, an increase in the frequency of soil freeze-thaw cycles due to rising winter air temperature may be associated with reductions in microbial biomass, exoenzyme production, and soil C and N cycle process rates, especially in the spring time following winter snowmelt.

Warmer soil temperatures during snow-free times of the year are known to increase the activity of microbial exoenzymes (Brzostek and Finzi, 2011; Davidson and Janssens, 2006; Schindlbacher et al., 2015), increase the pool sizes of dissolved C and N (Bai et al., 2013; Lu et al., 2013), and are associated with increased rates of net N mineralization and soil respiration in temperate forest ecosystems (Fahey et al., 2005; Giasson et al., 2013; Rustad et al., 2001). Soil warming in temperate forest ecosystems is typically applied with the aim of simulating a projected 2–5 °C increase in mean annual air temperature by the year 2100 (Bai et al., 2013; Melillo et al., 2002). In contrast to soil warming manipulations, other researchers have reduced the winter snowpack to examine the effects of warmer winter air temperatures and increased soil freezing severity on temperate forests (Aanderud et al., 2013; Groffman et al., 2001). Soil freeze-thaw cycles increase dissolved C and N in soil solution in the following growing season (Fitzhugh et al., 2001), which is similar to the effects of soil warming. But in contrast to warming, reductions in winter snow coverage reduce rates of exoenzyme production, net N mineralization, and nitrification in temperate forest ecosystems (Durán et al., 2014; Sorensen et al., 2016). Thus, an increased frequency of winter freeze-thaw cycles may partially offset the stimulatory effect of warmer soils on soil microbial metabolism. Yet effects of winter soil freeze-thaw cycles combined with soil warming during snow-free periods have to date been generally untested. This critical gap in knowledge precludes a comprehensive understanding of the response of soil C and N cycle processes in temperate forests to global air temperature rise.

The purpose of the Climate Change Across Seasons Experiment (CCASE), located at Hubbard Brook Experimental Forest (HBEF), New Hampshire, USA is to evaluate the combined effects of elevated soil temperatures in the growing season and an increased frequency of winter soil freeze-thaw cycles in a northern forest ecosystem (Templer et al., 2017). We collected soils in the first two years (2014 and 2015) following initiation of treatments at the CCASE experiment. We tested two hypotheses: (1) soil warming increases potential exoenzyme activity, net N mineralization, and respiration rates during snow-free months of the year. In addition, we hypothesized that (2) winter soil freeze-thaw cycles would offset the stimulatory effect of soil warming on microbial biomass, exoenzyme activity, net N mineralization, and microbial respiration during spring only, but not during later snow-free periods of the year.

2. Materials and methods

2.1. Field site description

The HBEF is a part of the White Mountain National Forest, which is located in central New Hampshire, USA (43.56° N, 71.45° W). The elevation at HBEF ranges from approximately 225 m asl to approximately 1100 m asl. Sites used in this study are located at approximately 225 m asl and are dominated by red maple (*Acer rubrum*) in the canopy with an understory composed of mostly American beech (*Fagus grandifolia*). The soils at Hubbard Brook are acidic (pH 3.9) Typic Haplorthods with an organic layer consisting of leaf-litter (Oi), dense root-mat and decomposing organic material (Oe), and a nutrient-rich humus layer (Oa); all of which together extend to approximately 6.5 cm below the soil surface (Bohlen et al., 2001).

Historically, a snowpack begins to develop in December, reaches a maximum depth of 70–100 cm, and persists until April. In years with below-average snowfall, soil frost can last from December through April or May in this region (Fahey and Lang, 1975). Mean annual soil frost depth is 5.8 cm over the last 50 years, ranging annually from 0 cm to 25 cm below the soil surface (Campbell et al., 2010). Mean air temperature from December to March was −4 °C from 1955 to 2012, and ranges from an average minimum of −12 °C during January to an average maximum of 19 °C during July (Bailey et al., 2003; Bohlen et al., 2001). During the last half century, winter air temperatures have risen by 2.5 °C, the maximum depth of winter snowpack has declined by 26 cm, and the duration of winter snow cover has declined by four days per decade (Bailey et al., 2003; Burakowski et al., 2008; Hamburg et al., 2013).

2.2. Experimental design and climate change treatments

CCASE was established at HBEF in July 2012 and is ongoing (Templer et al., 2017). There are six 11 m x 13.5 m experimental plots, with each plot centered on at least three mature red maple trees and composed of a variety of other hardwood tree species. Two plots serve as reference controls. Four other plots receive one of two experimental treatments: soil warming during the snow-free periods of the year (hereafter referred to as “Warmed” plots; n = 2 plots) or soil warming during snow-free periods plus an increased frequency of winter soil freeze-thaw cycles (hereafter referred to as “Warmed + FTC” plots; n = 2 plots). Large-sized plots were chosen because the main objective of CCASE is to understand both above- and belowground responses to changes in climate. Further, the CCASE experiment is not fully factorial due to the high financial cost associated with establishing and engineering the initial infrastructure and the ongoing cost associated with soil warming. CCASE is similar to other experiments that have not employed a fully-factorial experimental design due to logistical constraints (e.g. Aerts et al., 2004); but rather chosen experimental treatments to most accurately simulate projected changes in climate for the northeastern U.S. region (Campbell et al., 2010).

Buried heating cables were used to achieve soil warming during the growing season in the Warmed and the Warmed + FTC treatment plots, which was intended to simulate soil warming that occurs as a result of an anticipated +5 °C rise in air temperature by the year 2100 (Hayhoe et al., 2007). The heating cables do not warm the air aboveground, thus the heating cables do not fully capture the tree response to warming air temperature and it is possible that we would have observed different plant-soil-microbial feedbacks had the warming been induced using warmed air. Further critical discussions about the advantages and artefacts associated with ecosystem warming methods can be found elsewhere (Aronson and McNulty, 2009; De Frenne, 2015; Henry, 2012; Sanders-DeMott and Templer, 2017).

Warming cables were installed in July and August 2012 in 56 parallel lines across each treatment plot (each 10 cm deep and separated by 20 cm) created using a thin drywall spatula and burying the cable within a thin cut in the soil. We created similar cuts in the Reference treatment, but no cables were installed. Soil temperatures in all six plots were measured throughout the year using thermistors (Betatherm type 10K3A1) buried at 10 cm (n = 6 per plot in heated plots and n = 4 per plot in reference plots) depth below the surface. Additional sensor infrastructure in each plot is described in Templer et al. (2017).

Snow was removed via shoveling from the Warmed + FTC treatment beginning in December 2013 within 48 h of snowfall to induce soil freezing. We left a 3–5 cm layer of packed snow at the soil surface to avoid compacting of the soil during subsequent snow- and shoveling events and to maintain surface albedo. We operationally defined soil freezing as soil temperatures remaining below −0.5 °C at 10 cm depth for 72 h. Following soil freezing, the heating cables were turned on in the Warmed + FTC treatment in order to warm the soils to +1 °C for