Sensitivity of soil respiration and microbial communities to altered snowfall

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ABSTRACT

Winter respiration is a quantitatively important, yet variable flux of carbon dioxide (CO_2) from soils to the atmosphere. Variability in winter soil respiration may be influenced by the effects of snowfall on microbial communities and their metabolic activities. In this study, we evaluated the importance of snowpack depth on soil respiration and microbial communities in a temperate deciduous forest. Snow removal created relatively dry, frequently frozen, and carbon substrate-poor soils, while snow additions led to wetter, warmer, and relatively carbon substrate-rich soils. Using time-series multiple regression, we observed enhanced sensitivity of respiration to moisture under ambient snow and snow removal; however, this effect was accompanied by a temporal lag suggesting that microorganisms had a delayed response to increases in free-water during soil thawing events. Conversely, soil respiration was only sensitive to temperature in the snow addition treatment when soil temperatures were consistently above 0 °C. The snow-induced respiration dynamics were accompanied by shifts in the structure of wintertime fungal and bacterial communities. We detected an impact of altered snowpack on bacterial richness during the growing season, but our manipulation did not have legacy effects on other features of the soil microbial community at spring thaw. Our results suggest that microbial communities may be "reset" during seasonal transitions from winter to spring, and that soil microorganisms are likely adapted to annual fluctuations in snowpack depth. As snowpack becomes more variable in mid-latitude systems due to climate change, our findings suggest that soil moisture and temperature will co-regulate wintertime respiration through a non-linear relationship surrounding soil freeze–thaw cycles, with snow-mediated changes in microbial community structure likely influencing wintertime respiration dynamics.

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1. Introduction

The exchange of carbon dioxide (CO_2) between soils and the atmosphere is a major component of the global carbon (C) cycle (Raich and Potter, 1995). While most of the C influx to terrestrial ecosystems can be attributed to photosynthesis during the spring and summer months, mineralization processes, such as soil respiration, occur throughout the year. As a result, wintertime soil respiration can be quantitatively important when estimating annual carbon budgets. For example, winter respiration can account for more than half of the C sequestered by higher plants during the growing season (Sommerfeld et al., 1993; Winston et al., 1997; Monson et al., 2002). However, winter respiration is highly variable and may be regulated by fluctuations in environmental variables that covary with the timing and accumulation of a snowpack (Brooks et al., 1997, 2004; Mikan et al., 2002; Liptzin et al., 2009).

Through its effects on temperature and moisture, the depth of a snowpack is an important environmental characteristic that controls wintertime soil respiration. Under a deep snowpack, soils are insulated from colder air temperatures, which can increase heterotrophic respiration (Mariko et al., 1994; Brooks et al., 1997; Rey et al., 2002). Although soil respiration is reduced under

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a shallow snowpack, microorganisms are capable of maintaining catabolic (CO_2 production) and anabolic (biomass synthesis) processes under sub-zero temperatures (Panikov et al., 2006; Drotz et al., 2010; McMahon et al., 2011). Snow-mediated temperature effects on respiration, however, are simultaneously influenced by soil moisture. For example, under a deep snowpack warmer soil temperatures are often associated with wetter conditions, which can promote respiration (Liptzin et al., 2009). Conversely, under a shallow snowpack, soils commonly undergo freeze–thaw cycles (FTCs) where shifts in temperature regulate transitions of water between solid (ice) and liquid phases. As frozen soils thaw, heterotrophic respiration is stimulated by warmer soil temperatures, more free water, and the release of labile C substrates from lysed plant and microbial cells (Brooks et al., 2004; Schimel et al., 2007; Borken and Matzner, 2008).

Winter conditions may influence the sensitivity of soil respiration to moisture and temperature by affecting the composition and activity of soil microbial communities. A number of studies have documented differences in the composition of soil microbial communities collected during summer and winter seasons (Lipson and Schmidt, 2004; Lipson et al., 2009; McMahon et al., 2011). In some instances, these compositional differences correspond with changes in temperature sensitivity. For example, wintertime microbial communities from the soils of a subalpine forest exhibited exponential growth at 0 °C, while summertime microbial communities were unable to grow below 4 °C (Monson et al., 2006). Seasonal shifts in the composition and function of microbial communities may be due in part to the physiological stress associated with FTCs (Schimel et al., 2007), which are thought to select for taxa that can tolerate freezing soil conditions (Sharma et al., 2006; Walker et al., 2006). It remains to be determined if the environmental effects of variable snowfall on microbial communities are transient or if they have the ability to persist into the growing season.

In this study, we evaluated the sensitivity of soil respiration to snowpack-induced fluctuations in temperature and moisture in a temperate deciduous forest. We compared soil respiration sensitivity (i.e., CO_2 evolved per unit change in moisture or temperature) in a replicated field experiment where snowpack levels were directly manipulated. In addition to measuring soil properties, including organic C availability, which are often influenced by a snowpack (Groffman et al., 2001; Schimel et al., 2004; Brooks et al., 2004), we evaluated the effects of our manipulations on the structure of soil microbial communities. Bacterial and fungal responses measured throughout winter season allowed us to identify potential links between microbial communities, snow, and our observed winter CO_2 dynamics. Furthermore, we tested whether or not snowpack induced shifts in bacterial community structure persisted beyond spring–thaw, which could potentially have legacy effects on springtime soil processes.

2. Materials and methods

2.1. Site description

We conducted our study at the W. K. Kellogg Biological Station (KBS) Long-Term Ecological Research (LTER) site located in southwestern Michigan, USA. The experiment was performed in a native maple-hickory deciduous forest (KBS LTER treatment DF3) (DeGryze et al., 2004). Dominant tree species include *Acer saccharum* (Marsh.), *Carya glabra* (Mill.), and *Quercus alba* (L.). Average annual precipitation at the site is 890 mm ($\pm$148.0 SD, $n = 21$) with approximately half falling as snow, and the mean annual temperature is 9.0 °C ($\pm$0.81 SD, $n = 21$) (http://www.kbs.msu.edu/

databases). All soils are fine-loamy, mixed, mesic Typic Hapludalfs with a total C of 1.6%, total soil N of 0.10%, and pH of 5.3.

2.2. Snow manipulation

To investigate the effects of a variable snowpack on ecosystem processes and soil microbial structure, we created three treatments where snow was removed (Snow removal, $-S$), added (Snow addition, $+S$) or left in place (Ambient). Treatments were assigned in a complete randomized block design ($n = 3$) for a total of nine experimental units. We constructed three blocks (5 m $\times$ 13 m), subdivided the blocks into three plots (3 m $\times$ 3 m), and randomly assigned one treatment to each plot. We left a 1 m buffer strip around each plot to control for edge effects. The treatments were created and maintained over four months (20 December–5 April 2008) by removing the snowfall from the $-S$ treatment with a shovel and redistributing this removed snow evenly across replicates in the $+S$ treatment. Snow was removed from the $-S$ treatment following any snowfall event greater than 20 mm. When removing the snow from the $-S$ treatment, we left approximately 20 mm of snowfall to minimize physical disturbance to the litter and soil surface.

2.3. C substrate availability and chemistry

We quantified soil dissolved organic carbon (DOC) and inorganic nitrogen (N) concentrations in the snow treatments, as these variables can affect soil respiration and microbial communities. DOC (mg C g soil^{-1}), dissolved organic N (DON, mg C g soil^{-1}), and inorganic N (NH_4^+ and NO_3^-, µg N g soil^{-1}) were measured on at least a monthly basis (3 snow manipulations $\times$ 3 replicates $\times$ 6 time points = 36 samples) over the four-month experiment. Each soil sample represented a composite of three subsamples removed from each plot with a soil probe (diameter = 2 cm, 0–5 cm depth). After each soil core was removed, we placed a 12 cm piece of PVC pipe, capped with a rubber stopper, into the hole made by the soil probe to prevent preferential water flow from snow melt. Within 24 h of sampling, soils were water-extracted (1:2 w/v), passed through a 0.2-µm nylon filter (Millipore, Billerica MA, USA), and analyzed for DOC and DON using a total organic C and total N analyzer (Shimadzu, Columbia MD, USA). For inorganic N, soils were extracted within 48 h via a 1 M KCl extraction (1:10 w/v), passed through a Whatman #1 filter, and measured on an OI Analytical Flow Solution IV analyzer (OI Analytical, College Station TX, USA). DON was estimated as the difference between total N and total inorganic N. All soil variables were expressed on a soil dry-weight basis by correcting for gravimetric water content (subsample dried at 105 °C for 48 h). We tested for the effect of the snow treatments on our response variables (i.e., DOC, DON, NH_4^+ and NO_3^- concentrations) using repeated measures (RM) ANOVA (SAS PROC MIXED) with covariance structures selected using Bayesian Information Criterion (Keselman et al., 1999).

2.4. Soil CO_2 concentrations, temperature, and moisture

To determine the effects of a snowpack on respiration, we measured real-time soil CO_2 concentrations, soil moisture, and soil temperature in a single replicate of each snow treatment. We measured near-surface CO_2 concentrations (ppmv) as a proxy for soil respiration. It has been shown that near-surface CO_2 concentrations generated with our sensor technology provide accurate estimates of soil respiration (Daly et al., 2008). By placing the sensor close to the soil surface, one is able to capture an integrated CO_2 response before the gas is released to the atmosphere (Daly et al., 2008; Aanderud et al., 2011). Specifically, we placed sensors at