



Unfrozen water content moderates temperature dependence of sub-zero microbial respiration

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ABSTRACT

Abrupt increases in the temperature sensitivity of soil respiration below 0 °C have been interpreted as a change in the dominance of other co-dependent environmental controls, such as the availability of liquid-state water. Yet the relationship between unfrozen water content and soil respiration at sub-zero temperatures has received little attention because of difficulties in measuring unfrozen water contents. Using a recently-developed semi-solid ²H NMR technique the unfrozen water content present in seasonally frozen boreal forest soils was quantified and related to biotic CO₂ efflux in laboratory microcosms maintained at temperatures between −0.5 and −8 °C. In both soils the unfrozen water content had an exponential relationship with temperature and was increased by addition of KCl solutions of defined osmotic potential. Approximately 13% unfrozen water was required to release the dependence of soil respiration on unfrozen water content. Depending on the osmotic potential of soil solution, this threshold unfrozen water content was associated with temperatures down to −6 °C; yet if temperature were the predictor of CO₂ efflux, then the abrupt increase in the temperature sensitivity of CO₂ efflux was associated with −2 °C, except in soils amended with −1500 kPa KCl which did not show any abrupt changes in temperature sensitivity. The KCl-amendments also had the effect of decreasing Q₁₀ values and activation energies (E_a) by factors of 100 and three, respectively, to values comparable with those for soil respiration in unfrozen soil. The disparity between the threshold temperatures and the reductions in Q₁₀ values and activation energies after KCl amendment indicates the significance of unfrozen water availability as an environmental control of equal importance to temperature acting on sub-zero soil respiration. However, this significance was diminished when soils were supplied with abundant labile C (sucrose) and the influences of other environmental controls, allied to the solubility and diffusion of respiratory substrates and gases, are considered to increase.

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1. Introduction

Measurable microbial physiological activity below 0 °C provides strong evidence that microbial activity slows, but does not cease, in frozen soils at temperatures between 0 and −39 °C (e.g. Mikan et al., 2002; Elberling and Brandt, 2003; Panikov et al., 2006). Moreover, on freezing, there is an abrupt increase in the temperature dependence of soil respiration, reflecting changes in the relative dominance of other environmental constraints acting on soil respiration (Mikan et al., 2002; Elberling and Brandt, 2003; Karhu et al., 2010). The lack of detailed mathematical models that explicitly consider

the seasonality of soil CO₂ production and respiration severely limits predictions of the susceptibility of soil respiration to e.g. climate change (Bond-Lamberty and Thomson, 2010). This situation is particularly undesirable for high latitude (above 45–50°N) systems because empirical flux measurements of greenhouse gases show that significant exchange occurs during the winter. More than 20% of annual CO₂ emissions (e.g. Zimov et al., 1993; Clein and Schimel, 1995; Alm et al., 1999; Kim et al., 2007; Sullivan et al., 2008) occur during the long winters and the cumulative CO₂ production in surface layers of boreal forest soils during the winter (Harrysson-Drotz, 2010) accounts for a significant fraction of annual net ecosystem productivity in boreal forests (Lindroth et al., 2008). Climate change scenarios indicate that for northern Europe significant warming, in the order of 2.5–4 °C, will be most pronounced in the winter (Christensen and Christensen, 2007). The warming is not anticipated to manifest as general warming, but as higher temperatures on cold days, thus decreasing winter temperature variability

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and the depth of soil frost (Alcamo et al., 2007). Other possible climate-related perturbations include reduced snow cover resulting in deeper and more prolonged soil frost (Maljanen et al., 2010) and increased winter precipitation leading to greater water-logging of soil (Räsänen et al., 2004). Thus, it seems likely that in the future wetter boreal soils will still be frozen for much of the year, but will be subject to higher temperatures in the frozen state.

The boreal forest occupies approximately 10% of global land area and contains nearly 19% of terrestrial C stocks (UNEP-WCMC, 2008); approximately 65% of which is contained in soil rather than plant biomass (Malhi et al., 1999; Amundson, 2001). Boreal systems are characterized by long, severe winters; and in conjunction with limiting nitrogen availability and low quality organic matter inputs, net primary production currently exceeds decomposition and the soils are a C sink (Van Cleve et al., 1983; Jarvis and Linder, 2000). If the prevailing climate conditions change as predicted then this status could be reversed (Alcamo et al., 2007). The relationship between temperature and CO₂ flux to the atmosphere is particularly uncertain for boreal soils (Alcamo et al., 2007); thus, it is important that our understanding of the physico-chemical controls acting on microbial activity during this time is improved.

The relationship between temperature and unfrozen water content in soil shows profound physico-chemical co-dependency, such that Spaans and Baker (1996) introduced a single term “soil freezing characteristic” to describe all the effects. Temperature exerts a strong control on soil water content in frozen soils, with the phase transition of water from the liquid to solid state on freezing resulting in an effective reduction in soil water content, comparable to that occurring during drying beyond permanent wilting point (−1.5 MPa), but not to the extent of air-dried soil (−100 MPa). Furthermore, the presence of unfrozen water has been identified as an essential pre-requisite for physiological activity of microbes at sub-zero temperatures (Coxson and Parkinson, 1987; Mikan et al., 2002). Water in soil can exist in the liquid-state at temperatures significantly below the equilibrium freezing point of pure water through a variety of mechanisms (Cannel and Gardner, 1959). While the unfrozen water content of mineral soils (excluding clay soils) is principally determined by the osmotic potential of soil solution (Banin and Anderson, 1974; Harrysson-Drotz et al., 2009); in highly organic soils, matric potential makes a significant additional contribution to the unfrozen water content (Harrysson-Drotz et al., 2009). Matric potential also determines the distribution of water in pore spaces; and thus has both direct and indirect influences on soil processes (Young and Ritz, 2000). Furthermore, the partitioning of water between frozen and unfrozen states is dynamic over a range of temperatures (Stähli and Stadler, 1997) and thus, the abundance of unfrozen water is another constraint on sub-zero microbial activity (Ostroumov and Siegert, 1996; Öquist et al., 2009). Öquist et al. (2009) also report strong relationships between unfrozen water content and soil organic matter, the correlation with the amount of organic matter being positive and that with the quality is negative.

High latitude soils generally contain a large pool of plant detritus (Weintraub and Schimel, 2003) and in addition freeze–thaw related damage to microbial cells and tree roots occurring before and during the prolonged winter freeze increases the concentrations of labile simple sugars, such as sucrose, and amino acids in soil by approximately 8–40-times more than those present in spring or summer (Ivarson and Sowden, 1966, 1970; Scott-Denton et al., 2006). In addition to their role in respiration, the seasonal additions of solutes from disrupted organisms may also be taken up by soil microorganisms for osmoregulation. During the formation of ice in soil the extracellular osmotic potential experienced by soil microorganisms increases, to maintain cell turgor and for continued functioning of

intracellular enzymes an increase in intracellular osmotic potential is required, which can be achieved through the loss of water and the accumulation of compatible solutes (Jefferies et al., 2010). Rather than using the same substrates as those used in summer more slowly, as suggested by Clein and Schimel (1995), it appears that seasonal differences in input availability and lability result in preferential utilization of labile substrates by soil microorganisms at sub-zero temperatures (Grogan et al., 2001; Biasi et al., 2005). While the influence of important confounding effects, such as N availability, has received some attention (see Schimel et al., 2003; Schimel and Mikan, 2005), the effect of water availability at sub-zero temperatures remains poorly characterized being hampered by the difficulty of measuring the unfrozen water content of soil. Conventional methods for measuring soil moisture content, such as gravimetry, neutron thermalization and gamma densitometry, are unable to distinguish between liquid water and ice and time-domain reflectometry-based methods require cumbersome calibration procedures (Sparrman et al., 2004). Consequently there is still no consensus on the temperature dependence of soil organic matter decomposition (Kirschbaum, 2006).

In this paper we describe laboratory incubations of boreal forest soils with contrasting physico-chemical properties to quantify the temperature dependence of soil respiration over an environmentally-relevant temperature range for boreal systems and to investigate physico-chemical controls acting on that dependence, i.e. unfrozen water content and the availability of labile substrates. We used the ²H NMR-based technique developed by Sparrman et al. (2004) to quantify the amount of unfrozen water present in soils at incubation temperatures, which has the advantage over methods detecting ¹H because soil contains many ¹H species other than water. Soils from under different vegetation communities were amended with osmotically-defined solutions of KCl or labile C (sucrose) and N (NH₄Cl) sources providing further empirical evidence for the hypotheses that microbial activity in frozen soils is limited by the availabilities of both liquid-state water and labile substrates.

2. Materials and methods

2.1. Sites and soils

The organic horizons from haplic podzols (FAO classification) comprising organic matter in the full range of decomposition states (slight – high) states of decomposition were collected in September 2005 from two boreal forest sites in northern Sweden. At Vindeln (64° 10' N, 19° 35' E, 275 m asl), the soil was a podzolized alluvial sand and the dominant tree species was spruce (*Picea abies* (L.) Karst); while at Hössjö (63° 48' N, 19° 45' E, 170 m asl), predominantly pine (*Pinus sylvestris* L.) was growing on a podzolized loamy-sand. Further details can be found in Öquist et al. (2009); site 3.1 being Vindeln and site 1.2 Hössjö. Soil moisture contents were determined gravimetrically (105 °C, 24 h). Organic matter content was determined by loss on ignition (550 °C, 2 h) and total C and N contents were determined using an ANCA-NT elemental analyser (Europa Scientific, Crewe, U.K.).

2.2. Soil processing

On collection, roots and contemporary (i.e. green) plant debris were removed manually and the soils were homogenized by passing through a cutting sieve (6 × 3.5 mm mesh) in the field-moist state. Soils were stored at +4 °C until sieving was completed, thereafter at −20 °C (Mikan et al., 2002; Panikov et al., 2006) for not more than three months in the case of the sub-samples used for the KCl-amended experiment and for three to six months for the sub-samples

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