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Carbon and Nitrogen Cycling in Snow-Covered Environments

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Abstract

The last two decades have seen significant advances in understanding the cycling of carbon and nutrients in ecosystems characterized by seasonal snow cover. This paper reviews and summarizes work on the interactions between seasonal snow cover, soil physico-chemical characteristics, biological activity, and plot- to ecosystem-scale carbon and nitrogen cycling. The magnitude of winter biogeochemical activity is considerable. For example, including these winter fluxes into annual estimates of net ecosystem exchange reduces annual carbon uptake by 50% or more in many ecosystems. The primary climatic control on these fluxes is the amount and timing of precipitation, especially the formation of a consistent seasonal snow cover. Consistent snow cover limits frost damage and controls both the timing and amount of liquid water in soil and the availability of labile carbon substrates. Together, liquid water and labile carbon control the magnitude of *in situ* activity, exchanges of CO_2 and trace gases, and export of dissolved nutrients. The importance of snow cover to biogeochemical fluxes has led a renewed interest in how spatial variability in vegetation structure influences snow cover through shading, wind sheltering, and interception. Changes in snow cover associated with ongoing changes in both temperature and precipitation have the potential to profoundly impact the soil environment during winter and spring with unclear effects on annual and longer-term patterns of carbon and nitrogen cycling.

Introduction

Approximately 60% of the terrestrial earth surface experiences seasonal snow cover and seasonal soil frost (Zhang et al. 2004), ranging from high latitude tundra and the boreal forests, to mid-latitude forests and grasslands, and many mountain regions (Figure 1). Seasonally snow-covered ecosystems play critical roles in global biogeochemical cycles, particularly the carbon cycle. For example, high latitude regions hold more than half of global organic carbon stores (Hobbie et al. 2000; Tarnocai et al. 2009), and seasonally snow covered mid-latitude zones hold an additional 20% to 30% (Jobbagy and Jackson 2000; Post et al. 1982; Schimel et al. 2001). High and mid-latitude terrestrial ecosystems were accumulating carbon up to the mid-1990s (Schimel et al. 2001); however, ground observations suggest that climate warming subsequently turned higher latitude ecosystems into a net carbon source (Oechel et al. 2000). The effects of changes in climate on nutri-

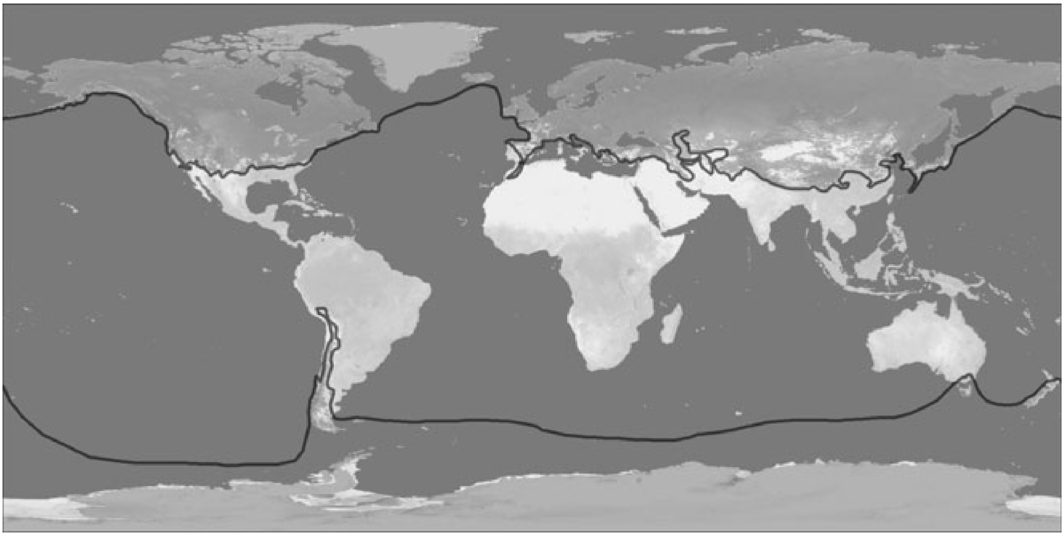

Fig. 1. Light gray-shaded area at higher latitudes denotes the approximate location of seasonal snow cover lasting more than several days. Data are from NASA MODIS. Additionally, many mountain areas (not shown) also are subject to snow accumulation.

ent cycles are even less clear, with some work suggesting that plant available nitrogen may decrease, while hydrologic nitrogen export to lower elevation terrestrial and aquatic ecosystems may increase (Brooks et al. 1999; Christopher et al. 2008; Fitzhugh et al. 2001). The potential importance of these geographic areas to global biogeochemical cycles has led to concerted efforts to understand the controls on biological activity in seasonally snow-covered soils.

Seasonally snow-covered regions are especially susceptible to climate change as small changes in temperature or precipitation may result in large changes in the amount and timing of snow cover. High latitude and high altitude regions are undergoing the most pronounced changes in temperature, with predictions for increases in average temperature between 4°C and 8°C over the next century (IPCC, 2008). Warming in the mid-latitudes is not as extreme, but still expected to significantly impact seasonal snow cover. Climate projections for the end of the 21st century indicate that winter temperatures will warm 2.5–5.3°C in northern Europe and the Northeastern USA (Christensen and Christensen 2007; IPCC, 2007). Increased temperatures likely will result in shorter snow covered seasons due to later accumulation and earlier melt, while lower latitudes may transition from continuous to intermittent winter snowpacks (Hayhoe et al. 2007, 2008; Huntington et al. 2009). A number of mid-latitude, montane ecosystems have already experienced a decrease in maximum snow accumulation and reduction in the duration of snow cover (Mote et al. 2005). Future warming is also likely to result in a decrease in the spatial extent of snow cover, readily observable in an increase in elevation of the rain–snow line (Lundquist et al. 2008). Although most locations will experience reduced duration and spatial extent of snow, feedbacks between local and regional climate are expected to result in an increase in the amount of snowfall in some locations (Rango and Katwijk 1990).

The effects of climate change on soil frost, defined as the formation of ice in soil, are difficult to predict, with simultaneous changes in temperature and precipitation leading to counter-intuitive effects on soil ice formation. Subtle shifts in the timing of snow accumulation and variations in air temperatures strongly influence soil frost (Campbell et al. 2010; Dyer and Mote 2006; Henry 2008; Hong et al. 2005; Venäläinen et al. 2001). Reduced and/or intermittent snow cover may result in increased soil frost (Brooks et al. 1995, 1997, 1999) leading to colder soils in a warmer world (Boutin and Robitaille 1994; Decker et al. 2003; Groffman et al. 2001a; Hardy et al. 2001; Isard and Schaetzl 1998; Öquist and Laudon 2008). A shift from snow to rain in the fall and early winter may lead to higher soil water content before soil frost forms (Räisänen et al. 2004). The result is a higher thermal inertia during winter and spring that results in an increase in the extent and duration of frozen soils, even though average air temperatures may be warmer.

The rapid pace of climate change in these regions presents a pressing need to understand the controls on winter biogeochemical processes, and feedbacks to growing season biogeochemistry. The objective of this paper is to review recent research on the subnivean environment, with a focus on how winter biogeochemical cycling is likely to respond to changing climate.

The Subnivean Environment: Soil Temperature and Moisture in Winter

Snow is an excellent thermal insulator and consistent seasonal snow cover of sufficient depth effectively decouples soil temperature from the atmosphere (Edwards and Cresser 1992). Although winter air temperatures in snow-covered environments can be particularly severe and can fluctuate dynamically, soil temperature regimes are always more moderate due to buffering by the overlying snow (Figure 2). In fact, the primary control on winter soil temperature in snow-covered environments is the depth of the overlying snowpack (Edwards and Cresser 1992; Grogan and Jonasson 2006; Sturm et al. 2005). Additionally, the timing of initial snow accumulation has a significant effect on winter soil temperatures because soil exposure to air temperatures prior to snow cover develop-

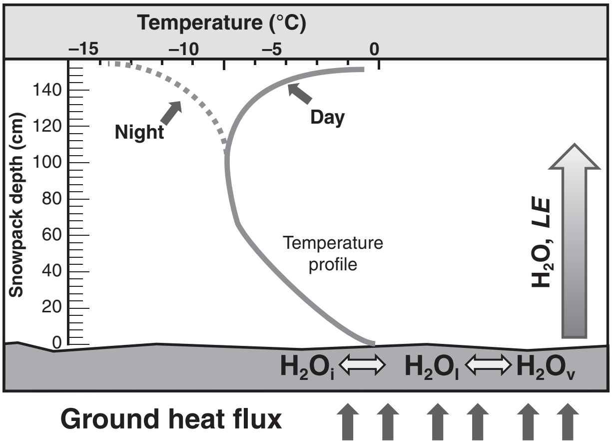

Fig. 2. A representative snowpack temperature profile during a diel air temperature cycle ranging from −15°C to 0°C. Phase change dominates the energy balance of snow-covered soil. In the absence of melt, wet soils experience very little temperature change over winter, while drier soils can slowly warm. In both wet and dry sites, temperature and vapor pressure gradients through the snowpack result in the diffusion of water vapor from soil to snow. H_2O_i is ice, H_2O_l is liquid water, H_2O_v is water vapor, and LE is latent energy.

ment results in substantial cooling (Olsson et al. 2007). Furthermore, the greater heat capacities of soil, water, and ice compared to air, and the latent energy of water, which is present in soils as a liquid, solid, and gas simultaneously, lead to a strong thermal inertia that restricts subsequent warming. Consequently, a simple binary distinction between summer and winter is inadequate to capture the variability in winter biogeochemical activity.

The presence of liquid water in soil is both a prerequisite for biological activity and the most important control on winter biogeochemical cycling (Öquist et al. 2009; Ostroumov and Siegert 1996). 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; Panikov et al. 2006). The partitioning of water between frozen and unfrozen states varies strongly both with temperature (Stähli and Stadler 1997) and with soil characteristics. 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), while, in highly organic soils, matric potential is also a significant factor (Harrysson-Drotz et al. 2009). Furthermore, unfrozen water content is strongly and positively related to soil organic matter quantity, but negatively related to soil organic matter quality (Öquist et al. 2009). Consequently, the amount of liquid water in snow-covered soil at a given temperature may vary significantly based on soil organic characteristics.

The phase transition of water to the solid state during freezing results in an effective reduction in soil water content, comparable to that which occurs during drying. Furthermore, as ice is formed the solute concentration within residual soil liquid water is increased, thereby lowering its osmotic potential and its freezing point. This effect tends to preserve some liquid water within frozen soils, but its bioavailability is reduced. For example, the water potential of liquid water at temperatures below 0°C drops by around 1.2 MPa (Harrysson-Drotz et al. 2009) for each degree of cooling, implying that the water potential of liquid water at −4°C is ca. −4.8 MPa. Thus, the reduction in soil liquid water potential induced by freezing temperatures can be comparable to that of drying beyond the conventional permanent wilting point of most plants (−1.5 MPa). Beyond these temperature effects on liquid water content and availability in soil, soils also dry over winter due to a vapor pressure gradient from warmer soils to the colder overlying snowpack, which has relatively lower saturated vapor pressure (Kane et al. 2001; Figure 2). The reduction in soil ice due to this vapor flux increases soil porosity for gas efflux during winter and for snowmelt water infiltration during spring (Kane et al. 2001).

There is great uncertainty about how climate change will affect soil temperature and moisture in the next 20–50 years. Snowpack manipulations suggest that less snow will produce ''colder soils in a warmer world'' (Brooks et al. 1998; Decker et al. 2003; Hardy et al. 2001; Walker et al. 1999), a prediction consistent with recent observations (Molotch et al. 2009). However, other analyses (Dyer and Mote 2006; Henry 2008; Venäläinen et al. 2001) suggest that warmer temperatures will result in less soil freezing in many areas (Campbell et al. 2010). This critical uncertainty, which is rooted in an incomplete understanding of how snow depth and weather (e.g. cold air fronts, timing of precipitation) interact to produce soil frost, should be a priority for research. Several efforts have attempted to address this knowledge gap by classifying the subnivean environment into four or five classes based on how variability in snow cover and climate affect soil frost and liquid water content (Brooks and Williams 1999; Liptzin et al. 2009; Olsson et al. 2007; Figure 3). Furthermore, it is becoming apparent that although air temperature freeze–thaw cycles are very common in seasonally snow-covered ecosystems, especially in

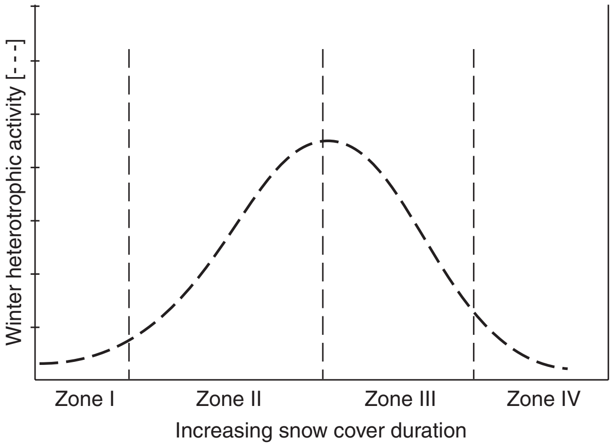

Fig. 3. Conceptual representation of the role of snow cover duration in controlling winter heterotrophic activity: In zone I shallow, intermittent snow cover limits activity; in zone II deeper and earlier snow cover allows heterotrophic communities to continue throughout winter; in zone III substrate limitation begins to reduce activity; in zone IV near permanent snow cover limits carbon supply.

the fall and spring, corresponding soil freeze–thaw fluctuations may be relatively rare because of the large thermal inertia (described above) of many soils (Buckeridge et al. 2010a)

Subnivean Biogeochemical Activity

Many models of soil biogeochemical processes assume that microbial activity is exponentially related to temperature and therefore that biogeochemical activity during winter has negligible impacts on annual fluxes (e.g. Frolking et al. 1998; McGuire et al. 2000; Potter et al. 1996). However, field studies over the past decade have demonstrated high levels of soil heterotrophic activity during winter in a wide variety of seasonally snow-covered ecosystems including arctic tundra (Grogan and Jonasson 2005), alpine tundra (Brooks et al. 1996; Mast et al. 1998), forests (Coxson and Parkinson 1987; Groffman et al. 2006; Monson et al. 2006), peatlands, and grasslands (Wang et al. 2010) at temperatures between 0°C and −39°C (e.g. Elberling and Brandt 2003; Mikan et al. 2002; Panikov et al. 2006). Moreover, upon freezing, there is an abrupt increase in the temperature sensitivity of soil respiration, reflecting changes in the relative dominance of other environmental constraints acting on microbial activity (Elberling and Brandt 2003; Karhu et al. 2010; Mikan et al. 2002; Öquist et al. 2009; Tilston et al. 2010), that is only just beginning to be incorporated into models (Sullivan et al. 2010).

There is a long history of field and laboratory manipulations to evaluate the effects of winter conditions on biogeochemical activity. Laboratory experiments to test specific hypotheses are essential for a deeper mechanistic understanding of winter processes (e.g. Edwards and Cresser 1992). However, they cannot mimic the array of complex interactions among liquid water, ice, roots, organic matter, and microorganisms that complicate scaling results from soil columns to ecosystems (Groffman et al. 2001a). Additionally, many laboratory studies have used rates and severity of soil freezing as treatments that are faster and stronger than what is observed in the field, making conclusions drawn from these experiments limited in their significance (Henry 2007). Field manipulations typically have focused on controlling snow depth as a master driver of winter biogeochemical conditions and activity. Snow fences (Brooks et al. 1995; Nobrega and Grogan 2007; Walker et al. 1993), snow removal (Boutin and Robitaille 1994; Hardy et al. 2001; Hentschel et al. 2008; Öquist and Laudon 2008), and insulation treatments (Austnes et al. 2008; Kaste et al. 2008) have been used to evaluate how changes in snow accumulation affect soil biogeochemistry. Natural gradients in snow accumulation and/or winter climate conditions can be exploited to avoid artifacts associated with manipulation studies (Groffman et al. 2009), but there are always concerns about multiple factor variation along these gradients. In spite of these difficulties, significant progress has been made over the last two decades in identifying the controls on winter biogeochemistry and placing this activity within the context of annual carbon and nitrogen fluxes.

In all regions, winter heterotrophic activity appears to be controlled by interactions among climate, soils, and the physiological potential of the microbial community (Lipson et al. 2002; Monson et al. 2006; Schadt et al. 2003; Schmidt et al. 2007; Walker et al. 2006). The presence of liquid water has been identified as the essential prerequisite for physiological activity of microbes in any environment, including soils at near- or sub-zero temperatures (Coxson and Parkinson 1987; Mikan et al. 2002). As discussed in the preceding section, both climate and soils interact to control liquid water content, implying that available water may differ significantly between soils at the same temperature (Harysson-Drotz et al. 2010). Consequently, highly variable temperature responses (Q_{10}s) in subnivean soils can result from changes in available liquid water, water potential and dissolved substrates, in addition to direct temperature effects on reaction kinetics. Regardless of soil climate conditions, microbial activity is strongly affected by the supply of labile organic carbon (Boddy et al. 2008; Brooks et al. 2005; Buckeridge and Grogan 2008; Feng et al. 2007; Kielland et al. 2006; Nobrega and Grogan 2007; Schimel and Mikan 2005). Snow depth and soil freezing influence labile carbon supply through their effects on litter decomposition and fragmentation (Hobbie and Chapin 1996; Steltzer and Bowman 2005; Sulkava and Huhta 2003), as well as dissolved organic carbon (DOC) fluxes from plant detritus, organic soil layers, and plant roots (Michalzik et al. 2001; Scott-Denton et al. 2006; Wang and Bettany 1993). Although soil frost can increase carbon substrate content, it also decreases substrate diffusion through the soil matrix (Davidson and Janssens 2006), a dual role that highlights the challenges in predicting winter biogeochemical activity.

Winter Carbon Cycling

Both CO_2 and CH_4 flux studies during winter demonstrate active carbon cycling under seasonal snowpacks in sub-alpine wetlands (Mast et al. 1998; Sommerfeld et al. 1993) high alpine tundra (Brooks et al. 2005), arctic tundra (Fahnestock et al. 1998; Grogan and Chapin 1999; Grogan and Jonasson 2006; Oechel et al. 1997; Zimov et al. 1996), fens (Aurela et al. 2002; Jackowicz-Korczynski et al. 2010), peatlands (Alm et al. 1999; Lafleur et al. 2003), and forests (Groffman et al. 2006; Kurganova et al.2003). Winter fluxes of CO_2 from snow-covered soils are highly variable, and are not a simple function of soil temperature (Figure 4). Instantaneous flux rates range from negligible to values similar to those observed during the growing season (Brooks et al. 1997; Groffman et al. 2006; Grogan and Jonasson 2005; Jones et al. 1999; Mariko et al. 2000; McDowell et al. 2000; Sommerfeld et al. 1993; Wickland et al. 2001). Until recently, relatively few flux towers maintained continuous records throughout both summer and winter seasons, which has hampered evaluating the potential importance of winter fluxes to annual ecosystem carbon exchange. Current estimates of net overwinter CO_2 efflux range from

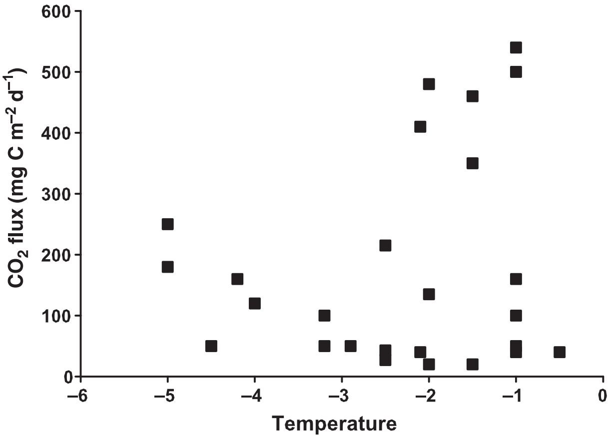

Fig. 4. Carbon dioxide fluxes beneath winter snowpacks are weakly related to temperature across a range of ecosystems. The simultaneous presence of water in winter soil as ice, liquid, and gas complicates the relationship between winter CO_2 flux and soil temperature resulting in large and variable Q_{10}s that result from both temperature and water limitation. Data are a compilation of previously published work by P.D. Brooks and include alpine and arctic tundra, subalpine forests, and meadows throughout North America.

5–10% of net ecosystem exchange (NEE) in eastern deciduous forests of the USA (Groffman et al. 2006, 2009, 2010), to 60% or more of annual NEE in western coniferous forests (Monson et al. 2002). A comparison of winter CO_2 fluxes to growing season NEE from flux towers in Europe and North America suggests that failing to account for winter CO_2 fluxes would result in an overestimation of annual NEE of 71% in deciduous forests (244 vs. 65 g C m^{-2}) and 111% in coniferous forests (167 vs. 79 g C m^{-2}) (Brooks et al. 2005). There are fewer continuous measurements in other ecosystems, but estimates of wintertime processes to annual CO_2 exchange are in the same range. In tundra and boreal systems for example, winter fluxes appear to range from 10% to 30% of annual ecosystem respiration and may account for 33% to >90% of summer uptake (Brooks et al. 1997; Lafleur et al. 2003; Nilsson et al. 2008; Nobrega and Grogan 2007; Sagerfors et al. 2008).

Although the absolute importance of winter CO_2 fluxes appears to vary based on ecosystem type, the sensitivity of fluxes to small changes in seasonal snow cover is quite high in all systems. Both snowpack manipulations and laboratory experiments have demonstrated that winter heterotrophic activity and CO_2 efflux increases following freeze–thaw events due to an increase in labile carbon substrates (Brooks and Williams 1999; Brooks et al. 1997; Coxson and Parkinson 1987; Groffman et al. 2001b; Neilson et al. 2001; Schimel and Clein 1996). For example, direct glucose additions to snow-covered soil increased respiration up to 160% 24 hours after addition, and fluxes remained significantly higher than controls a month after addition demonstrating the soil microbial communities' ability to utilize readily available carbon sources during winter (Brooks et al. 2005).

An emerging area of uncertainty in winter biogeochemistry is the effect of variation in snow cover on DOC dynamics. The DOC pool in soil is the net result of numerous sorption and desorption processes, such as electrostatic repulsion in aqueous solutions, cation exchange, decomplexation, and displacement of sorbed organic ions, which act selectively on different molecules (Reetsma et al. 1999). During winter, labile simple sugars and amino acids increase by approximately 8 to 40-fold relative to summer (Ivarson and Sowden 1966, 1970; Scott-Denton et al. 2006), presumably as a result of freeze damage to roots and microbial cells. It appears that seasonal differences in carbon availability and lability result in preferential utilization of labile substrates by soil microorganisms at subzero temperatures (Biasi et al. 2005; Clein and Schimel 1995a,b). Furthermore, solutes in soil solution may be preferentially taken up by soil microorganisms for osmoregulation to prevent ice damage and maintain cell turgor, and for continued functioning of intracellular enzymes (Jefferies et al. 2010; Schimel et al. 2007).

Several studies have identified links between microbial respiration (an index of labile, actively cycling carbon) and DOC production (Brooks et al. 1999; Jandl and Sollins 1997), consistent with indications that DOC production is related to soil heterotrophic activity (Christ and David 1996; Scott et al. 1998; Tipping et al. 1999), although it remains unclear if DOC increases respiration or if respiration increases mobile DOC. If soil freezing mobilizes DOC, it can have significant effects on other biogeochemical processes including hydrologic and gaseous nitrogen losses and CO_2 flux (Goodale et al. 2005; Hafner and Groffman 2005; Hafner et al. 2005; Sobczak et al. 2003). While some studies have shown marked DOC responses to soil freezing, others have not. In field and laboratory experiments with Norwegian heathland soils, frost increased DOC, dissolved organic N (DON) and NH_4^+ concentrations, and either decreased or had no effect on NO_3^- concentrations (Austnes and Vestgarden 2008; Austnes et al. 2008; Kaste et al. 2008; Vestgarden and Austnes 2009). The decreased NO_3^- losses may have been linked to the increase in DOC, which may have increased immobilization and/or denitrification. However, denitrification can also be increased by ice blockage of oxygen diffusion (Miller et al. 2007; Öquist et al. 2004). Soil freezing induced an increase in DOC in laboratory experiments with German forest soils at temperatures of −8°C and −13°C, but not at −3°C, a much more common field temperature (Hentschel et al. 2008); no response was observed in field experiments (Hentschel et al. 2009). In contrast, Haei et al. (2010) found that prolonged soil frost enhanced DOC concentrations in an adjacent stream during snow melt and that soil water DOC concentrations were elevated during the subsequent summer. A 2-year study of snow removal in New Hampshire, USA, indicated marked variation in DOC response to soil freezing, and potential links to nitrogen losses, that is, sites with high DOC response had low nitrogen loss response (Fitzhugh et al. 2001; Groffman et al. 2010). There is a clear need for further research on the factors regulating DOC response to soil freezing disturbance and on how this response regulates NO_3^- loss following this disturbance.

Winter Nitrogen Cycling

Roughly concurrent with the early reports of CO_2 fluxes from beneath snow referenced above, research in both deciduous and coniferous forests indicated that ecosystem nitrogen retention was higher, and export was lower in years with deeper snow cover (Brooks et al. 1998; Lewis and Grant 1980; Mitchell et al. 1996; Peters and Leavesley 1995). Subsequent plot scale research in a variety of forest and tundra ecosystems confirmed that increased snow cover insulated soils from cold air temperatures and allowed higher levels of microbial nitrogen immobilization under snow (Brooks et al. 1999; Buckeridge and Grogan 2010), while shallower snowpacks were associated with higher nitrogen export (Boutin and Robitaille 1994; Brooks et al. 1996; Brooks et al. 1999; Callesen et al. 2007; Fitzhugh et al. 2003; Groffman et al. 2001b; Groffman et al. 2006; Lipson et al. 1999; Neilson et al. 2001). Nitrogen mineralized under deeper snow cover initially is immobilized by microbial biomass (Brooks et al. 1996, 1999) and presumably later taken up by vegetation at the beginning of the growing season (Socci and Templer 2010). Consequently, variability in seasonal snow cover may indirectly affect ecosystem carbon storage by controlling the amount of nitrogen available to vegetation after melt. However, in some cases, nitrogen mineralization in soils is not affected by variation in snowpack (Groffman et al. 2001b, 2009, 2010). Further, over-winter root mortality (Cleavitt et al. 2008; Tierney et al. 2001) caused by a smaller snow-pack and greater soil frost can lead to reduced nitrogen uptake by trees (Templer and Socci 2010), which could potentially contribute to greater nitrogen export from forests.

A critical factor regulating wintertime nitrogen cycling in tundra is a shift in microbial physiology with the onset of winter (Schimel and Mikan 2005). Acid tussock tundra soils are intensely nitrogen-limited during the summer (Weintraub and Schimel 2003) and do not show positive rates of net mineralization (Giblin et al. 1991). However, as temperatures drop, microbes shift to carbon limitation and mineralize nitrogen (Giblin et al. 1991); in a snow-fence experiment that maintained soil temperatures at −5°C or above, wintertime net mineralization was sufficient to support the entire annual plant demand for aboveground growth (Schimel et al. 2004). The fate of nitrogen mineralized during the winter, however, is unclear as the ability of vegetation to take up nitrogen from under arctic snowpacks appears limited, but may be much more significant in the relatively warm soils of many alpine ecosystems (Bilbrough and Welker 2000; Grogan and Jonasson 2003).

Active nitrogen cycling under seasonal snow cover also affects N_2O fluxes (Matzner and Borken 2008). Winter N_2O fluxes appear to be related to the depth and duration of seasonal snow cover and the amount of heterotrophic activity (Brooks et al. 1997; Maljanen et al. 2010), consistent with increasing levels of denitrification in soils that become progressively anaerobic as the winter season proceeds. Winter N_2O flux rates in alpine systems can be an order of magnitude higher than those observed during the growing season (Brooks et al. 1997; Sommerfeld et al. 1993), while in temperate regions the winter emissions may account for more than one half of the annual emission (Röver et al. 1998; Shurmann et al. 2002; Teepe et al. 2000). These high winter emissions presumably result from both increased anoxia and reduced competition for nitrate from vegetation during the winter.

Ultimately, the balance of microbial nitrogen production and consumption processes is strongly affected by the supply of labile organic carbon, which as noted above is influenced by snow depth and soil freezing through changes in litter decomposition and fragmentation and by DOC flux from plant detritus and organic soil layers.

Snow Cover and Vegetation Activity

In the last several years, research on seasonally snow-covered forest ecosystems has found that coniferous trees, similar to microbes in snow-covered soil, respond to soil water availability, even when temperatures are near 0°C. Plant roots are protected from cold air temperatures in winter by the insulating layer of snow. In fact, some plant species can fix carbon under snow (Starr and Oberbauer 2003; Steenberg Larsen et al. 2007) or take up nutrients during snowmelt (Bilbrough and Welker 2000). For example, in high altitude mixed-conifer forests in Colorado, maximum rates of carbon fixation occur during spring while snow covers the ground and soil temperatures are buffered by snowmelt water at 0°C (Monson et al. 2002, 2005). Winter warming is projected to increase the growing season length and rates of plant productivity, but these could be counteracted by the negative effects of increased soil frost or by water stress later in the growing season (Monson et al. 2005). Warming is expected to shift the ranges of plant species to higher latitudes, alter plant species composition and reduce frost-hardiness of vegetation (see review by Kreyling 2010). Together, these changes could alter the biogeochemistry of soils through effects on carbon fluxes (photosynthesis and autotrophic respiration) and nutrient uptake and assimilation by plants. Compared to our understanding of the impact of an altered winter snowpack on belowground microbial processes, much less is known about the response of plants (Kreyling 2010) and their role in biogeochemical cycles in winter.

With a reduced snowpack, tree roots can experience frost damage and increased mortality (Cleavitt et al. 2008; Tierney et al. 2001). Plants exposed to below-freezing air temperatures can adapt through changes in phenology, morphology or growth, and can also lower the freezing point of their tissues by increasing solute concentrations to prevent ice crystallization. However, increased freeze–thaw cycles caused by warming (Henry 2008) could make plants vulnerable to frost damage. Typically, plants develop frost hardiness following sustained exposure to cold temperatures (Thomashow 1999). With sudden shifts in temperatures, plant tissues may be unprepared (Cannell and Smith 1986; Leinonen 1996). Additionally, plants experiencing multiple freeze–thaw events within a season can form xylem embolisms, which reduce conductivity and can lead to crown dieback (Sperry et al. 1994; Zhu et al. 2000). Plants can also be severely damaged by extreme weather events such as warm fronts during winter (Bokhurst et al. 2009) and spring freezing fronts during earlier growing seasons (Gu et al. 2008;). All of these changes in winter climate can expose plants to cold temperatures that their tissues cannot tolerate. Plant nutrient uptake (Templer and Socci 2010) and canopy carbon uptake could be reduced in plant tissues damaged by freezing, soil freeze–thaw events or abrupt changes in air temperature in the early growing season, which could in turn impact carbon and nitrogen fluxes and storage.

Feedbacks Between Vegetation and Snow Cover

A critical, yet relatively uninvestigated, linkage between changes in climate, snow cover, and winter soil biogeochemical activity is the role of vegetation in controlling snowpack depth and duration. Forest vegetation can reduce snow accumulation via interception and subsequent sublimation, yet may also increase snow depth and prolong melt by shading, decreasing wind speeds, and reducing energy input to the snowpack through reduced turbulent heat exchange (Barry et al. 1990; Gelfan et al. 2004; Harding and Pomeroy 1996; Hardy et al. 1997; Hedstrom and Pomeroy 1998; Link and Marks 1999a,b; Molotch et al. 2007; Musselman et al. 2008; Pomeroy et al. 1998a,b; Storck et al. 2002; Stottlemyer and Troendle 2001; Wigmosta et al. 1994; Yamazaki and Kondo 1992). The net effect is that forest snowpacks tend to be shallower than in open areas, due to sublimation of intercepted snow. By contrast, tundra vegetation patches of relatively tall plants such as shrubs and open birch stands enhance local snowpack depths due to interception and trapping of windblown snow (Grogan and Jonasson 2006; Sturm et al. 2005). Differences in plant density between forests and tundra explain these patterns – even small canopy openings within forested areas hold more snow, and hold it longer, than either open areas or dense forests (Golding and Swanson 1978). Although dense forest and tundra shrub vegetation differ in their effects on winter snowpack accumulation, they both shade the snow in spring, slowing ablation and extending the duration of snow cover compared to low vegetation and open areas.

As climate changes, interactions between vegetation structure and seasonal snow cover are likely to become increasingly important in determining the depth, duration, and spatial extent of soils insulated by continuous snow cover. Warmer temperatures and increased precipitation in a warmer climate may result in greater spatial heterogeneity in seasonal snow cover in forest stands (Veatch et al. 2009), creating a patchwork in soil moisture, soil frost, and winter biogeochemical activity which may effect large scale ecosystem structure. Similar interactions between snow accumulation and biogeochemical cycling have been used to explain ongoing shrub expansion across the low Arctic (Goetz et al. 2005). Deepened snow directly around shrubs increases winter soil temperatures, promoting decomposition and nutrient availability to shrubs (Sturm et al. 2005). This positive feedback between shrubs, snow, and nutrient availability may provide a competitive advantage to shrubs in these nutrient limited systems (Buckeridge et al. 2010b).

Synthesis and Conclusions

Seasonal snow cover provides a unique soil environment capable of supporting high levels of biogeochemical activity that significantly impacts annual carbon and nutrient cycles. A prerequisite for biological activity in snow-covered soil is the presence of liquid water, the amount of which is controlled by interactions between the depth and timing snow cover development, antecedent climate, and soil physical characteristics. Once this prerequisite is met, the controls on the amount of activity are less clear, but include carbon substrate availability, microbial community structure and physiology, and soil moisture changes over winter. Given the importance of snow cover in insulating soil and promoting winter biological activity, an emerging area of research involves quantifying the feedbacks between vegetation structure, snow cover development, and growing season nutrient availability and carbon uptake. The need to quantify these interactions is exacerbated by ongoing changes in both climate and vegetation structure. Improved understanding and representation of winter processes and how they are linked to the growing season represents a significant knowledge gap in our ability to predict biogeochemical cycling in seasonally snow-covered systems, and should be a priority for research in the coming decade.

Short Biography

Paul Brooks' research is focused on the interactions between Hydrology, Biogeochemistry, and Ecosystem Science. He has authored papers for a diverse set of peer-reviewed publications including Arctic, Antarctic, and Alpine Research, Biogeochemistry, Ecosystems, Eastern Snow Conference, Global Biogeochemical Cycles, Global Change Biology, Hydrologic Processes, Hydrometeorology, International Association of Hydrological Sciences, Journal of the American Water Resources Association, Journal of Geophysical Research, Journal of Hydrometeorology, Oecologia, and Water Resources Research among others. He currently serves as the director for the Center for the Sustainability of Semi-Arid Hydrology and Riparian Areas (SAHRA) and as a professor in the Department of Hydrology and Water Resources, University of Arizona. He has been actively involved in national and international efforts to develop interdisciplinary environmental observatories. He holds a BS from Florida State University and a PhD from the University of Colorado.

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References

Alm, J., et al. (1999). Winter CO_2, CH_4 and N_2O fluxes on some natural and drained boreal peatlands. *Biogeochemistry* 44, pp. 163–186.

Aurela, M., Laurila, T. and Tuovinen, J. P. (2002). Annual CO_2 balance of a subarctic fen in northern Europe: importance of the wintertime efflux. *Journal of Geophysical Research-Atmospheres* 107 (D21), pp. 4607, doi: 10.1029/2002JD002055.

Austnes, K., Kaste, O., Vestgarden, L. S. and Mulder, J. (2008). Manipulation of snow in small headwater catchments at Storgama, Norway: effects on leaching of total organic carbon and total organic nitrogen. *Ambio* 37, pp. 38–47.

Austnes, K. and Vestgarden, L. S. (2008). Prolonged frost increases release of C and N from a montane heathland soil in southern Norway. *Soil Biology & Biochemistry* 40, pp. 2540–2546.

Banin, A. and Anderson, D. M. (1974). Effects of salt concentration changes during freezing on the unfrozen water content of porous materials. *Water Resources Research* 10, pp. 124–128.

Barry, R., Prevost, M., Stein, J. and Plamondon, A. P. (1990). Application of a snow cover energy and mass balance model in a balsam fir forest. *Water Resources Research* 26 (5), pp. 1079–1092.

Biasi, C., et al. (2005). Temperature-dependent shift from labile to recalcitrant carbon sources of arctic heterotrophs. *Rapid Communications in Mass Spectrometry* 19 (11), pp. 1401–1408, doi: 10.1002/rcm.1911.

Bilbrough, C. J. and Welker, J. M. (2000). Early spring nitrogen uptake by snow-covered plants: a comparison of arctic and alpine plant function under the snowpack. *Arctic, Antarctic, and Alpine Research* 32, pp. 404–411.

Boddy, E., et al. (2008). Turnover of low molecular weight dissolved organic C (DOC) and microbial C exhibit different temperature sensitivities in Arctic tundra soils. *Soil Biology & Biochemistry* 40, pp. 1557–1566.

Bokhurst, S. F., et al. (2009). Winter warming events damage sub-Arctic vegetation: consistent evidence from an experimental manipulation and a natural event. *Journal of Ecology* 97 (6), pp. 1408–1415, doi: 10.1111/j.1365-2745.2009.01554.x.

Boutin, R. and Robitaille, G. (1994). Increased soil nitrate losses under mature sugar maple trees affected by experimentally induced deep frost. *Canadian Journal of Forest Research* 25, pp. 588–602.

Brooks, P. D., Campbell, D. H., Tonnessen, K. A. and Heuer, K. (1999). Natural variability in N export from headwater catchments: snow cover controls on ecosystem N retention. *Hydrological Processes* 13 (14–15), pp. 2191–2201.

Brooks, P. D., McKnight, D. and Elder, K. (2005). Carbon limitation of soil respiration under winter snowpacks: potential feedbacks between growing season and winter carbon fluxes. *Global Change Biology* 11, pp. 231–238.

Brooks, P. D., Schmidt, S. K. and Williams, M. W. (1997). Winter production of CO_2 and N_2O from alpine tundra: environmental controls and relationship to inter-system C and N fluxes. *Oecologia* 110, pp. 403–413.

Brooks, P. D. and Williams, M. W. (1999). Snowpack controls on nitrogen cycling and export in seasonally snow-covered catchments. *Hydrological Processes* 13 (14–15), pp. 2177–2190.

Brooks, P. D., Williams, M. W. and Schmidt, S. K. (1996). Microbial activity under alpine snowpacks, Niwot Ridge, Colorado. *Biogeochemistry* 32, pp. 93–113.

Brooks, P. D., Williams, M. W. and Schmidt, S. K. (1998). Inorganic nitrogen and microbial biomass dynamics before and during spring snowmelt. *Biogeochemistry* 43 (1), pp. 1–15.

Brooks, P. D., Williams, M. W., Walker, D. A. and Schmidt, S. K. (1995). The Niwot Ridge snow fence experiment: biogeochemical responses to changes in the seasonal snowpack. In: Tonneseen, K. A. (ed.) *Biogeochemistry of seasonally snow-covered catchments*. Boulder, CO: IAHS, pp. 293–302.

Buckeridge, K. M., Cen, Y. P., Layzell, D. B. and Grogan, P. (2010a). Soil biogeochemistry during the early spring in low arctic mesic tundra and the impacts of deepened snow and enhanced nitrogen availability. *Biogeochemistry* 99 (1–3), pp. 127–141, doi: 10.1007/s10533-009-9396-7.

Buckeridge, K. M. and Grogan, P. (2008). Deepened snow alters soil microbial nutrient limitations in arctic birch hummock tundra. *Applied Soil Ecology* 39 (2), pp. 210–222, doi: 10.1016/j.apsoil.2007.12.010.

Buckeridge, K. M. and Grogan, P. (2010). Deepened snow increases late thaw biogeochemical pulses in mesic low arctic tundra. *Biogeochemistry* 101 (1–3), pp. 105–121, doi: 10.1007/s10533-010-9426-5.

Buckeridge, K. M., Zufelt, E., Chu, H. Y. and Grogan, P. (2010b). Soil nitrogen cycling rates in low arctic shrub tundra are enhanced by litter feedbacks. *Plant and Soil* 330 (1–2), pp. 407–421, doi: 10.1007/s11104-009-0214-8.

Callesen, I., Borken, W., Kalbitz, K. and Matzner, E. (2007). Long-term development of nitrogen fluxes in a coniferous ecosystem: does soil frost trigger nitrate leaching? *Journal of Plant Nutrition and Soil Science* 170, pp. 189–196.

Campbell, J. L., et al. (2010). Past and projected future changes in snowpack and soil frost at the Hubbard Brook Experimental Forest, New Hampshire, USA. *Hydrological Processes* 24, pp. 2465–2480.

Cannel, G. H. and Gardner, W. H. (1959). Freezing-point depressions in stabilized aggregates, synthetic soil, and quartz sand. *Soil Science Society of America Proceedings* 23, pp. 418–422.

Cannell, M. G. R. and Smith, R. I. (1986). Climatic warming, spring budburst and frost damage on trees. *Journal of Applied Ecology* 23, pp. 177–191.

Christ, M. J. and David, M. B. (1996). Temperature and moisture effects on the production of dissolved organic carbon in a spodosol. *Soil Biology & Biochemistry* 28 (9), pp. 1191–1199.

Christensen, J. H. and Christensen, O. B. (2007). A summary of the PRUDENCE model projections of changes in European climate during this century. *Climatic Change* 81, pp. S7–S30.

Christopher, S. F., et al. (2008). The effect of soil freezing on N cycling: comparison of two headwater subcatchments with different vegetation and snowpack conditions in the northern Hokkaido Island of Japan. *Biogeochemistry* 88 (1), pp. 15–30, doi: 10.1007/s10533-008-9189-4.

Cleavitt, N. L., et al. (2008). Effects of soil freezing on fine roots in a northern hardwood forest. *Canadian Journal of Forest Research* 38, pp. 82–91.

Clein, J. S. and Schimel, J. P. (1995a). Microbial activity of tundra and taiga soils at subzero temperatures. *soil Biology & Biochemistry* 27 (9), pp. 1231–1234.

Clein, J. S. and Schimel, J. P. (1995b). Nitrogen turnover and availability during succession from alder to poplar in alaskan taiga forests. *Soil Biology & Biochemistry* 27 (6), pp. 743–752.

Coxson, D. S. and Parkinson, D. (1987). Winter respiratory activity in aspen woodland forest floor litter and soils. *Soil Biology & Biochemistry* 19, pp. 49–59.

Davidson, E. A. and Janssens, I. A. (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440 (7081), pp. 165–173, doi: 10.1038/nature04514.

Decker, K. L. M., Wang, D., Waite, C. and Scherbatskoy, T. (2003). Snow removal and ambient air temperature effects on forest soil temperatures in Northern Vermont. *Soil Science Society of America Journal* 67, pp. 1234–1242.

Dyer, J. L. and Mote, T. L. (2006). Spatial variability and trends in observed snow depth over North America. *Geophysical Research Letters* 33, L16503, doi: 10.1029/2006GL027258.

Edwards, A. C. and Cresser, M. S. (1992). Freezing and its effect on chemical and biological properties of soil. *Advances in Soil Science* 18, pp. 61–79.

Elberling, B. and Brandt, K. K. (2003). Uncoupling of microbial CO_2 production and release in frozen soil and its implications for field studies of arctic C cycling. *Soil Biology & Biochemistry* 35, pp. 263–272.

Fahnestock, J. T., et al. (1998). Winter and early spring CO_2 efflux from tundra communities of northern Alaska. *Journal of Geophysical Research-Atmospheres* 103 (D22), pp. 29023–29027.

Feng, X. J., Nielsen, L. L. and Simpson, M. J. (2007). Responses of soil organic matter and microorganisms to freeze-thaw cycles. *Soil Biology & Biochemistry* 39, pp. 2027–2037.

Fitzhugh, R. D., et al. (2001). Effects of soil freezing disturbance on soil solution nitrogen, phosphorus, and carbon chemistry in a northern hardwood ecosystem. *Biogeochemistry* 56, pp. 215–238.

Fitzhugh, R. D., et al. (2003). Soil freezing and the acid-base chemistry of soil solutions in a northern hardwood forest. *Soil Science Society of America Journal* 67, pp. 1897–1908.

Frolking, S. E., et al. (1998). Comparison of N_2O emissions from soils at three temperate agricultural sites: simulations of year-round measurements by four models. *Nutrient Cycling in Agroecosystems* 52, pp. 77–105.

Gelfan, A. N., Pomeroy, J. W. and Kuchment, L. S. (2004). Modeling forest cover influences on snow accumulation, sublimation, and melt. *Journal of Hydrometeorology* 5 (5), pp. 785–803.

Giblin, A. E., et al. (1991). Biogeochemical diversity along a riverside toposequence in arctic Alaska. *Ecological Monographs* 61 (4), pp. 415–435.

Goetz, S. J., Bunn, A. G., Fiske, G. J. and Houghton, R. A. (2005). Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. *Proceedings of the National Academy of Sciences of the United States of America* 102 (38), pp. 13521–13525, doi: 10.1073/pnas.0506179102.

Golding, D. L. and Swanson, R. H. (1978). Snow accumulation and melt in small forest openings in Alberta. *Canadian Journal of Forest Research – Revue Canadienne De Recherche Forestiere* 8 (4), pp. 380–388.

Goodale, C. L., Aber, J. D., Vitousek, P. M. and McDowell, W. H. (2005). Long-term decreases in stream nitrate: successional causes unlikely; possible links to DOC? *Ecosystems* 8, pp. 334–337.

Groffman, P. M., Hardy, J. P., Driscoll, C. T. and Fahey, T. J. (2006). Snow depth, soil freezing, and fluxes of C dioxide, nitrous oxide and methane in a northern hardwood forest. *Global Change Biology* 12, pp. 1748–1760.

Groffman, P. M., et al. (2001a). Colder soils in a warmer world: a snow manipulation study in a northern hardwood forest ecosystem. *Biogeochemistry* 56 (2), pp. 135–150.

Groffman, P. M., et al. (2001b). Effects of mild winter freezing on soil nitrogen and carbon dynamics in a northern hardwood forest. *Biogeochemistry* 56 (2), pp. 191–213.

Groffman, P. M., et al. (2009). Climate variation and soil carbon and nitrogen cycling processes in a northern hardwood forest. *Ecosystems* 12, pp. 927–943.

Groffman, P. M., et al. (2010). Snow depth, soil freezing and nitrogen cycling in a northern hardwood forest landscape. *Biogeochemistry* 102, pp. 223–238, doi: 10.1007/s10533-10010-19436-10533.

Grogan, P. and Chapin, F. S. III. (1999). Arctic soil respiration: effects of climate and vegetation depend on season. *Ecosystems* 2 (5), pp. 451–459.

Grogan, P. and Jonasson, S. (2003). Controls on annual nitrogen cycling in the understory of a subarctic birch forest. *Ecology* 84 (1), pp. 202–218.

Grogan, P. and Jonasson, S. (2005). Temperature and substrate controls on intra-annual variation in ecosystem respiration in two sub-arctic vegetation-types. *Global Change Biology* 11, pp. 465–475.

Grogan, P. and Jonasson, S. (2006). Ecosystem CO_2 production during winter in a Swedish subarctic region: the relative importance of climate and vegetation type. *Global Change Biology* 12, pp. 1479–1495.

Gu, L., et al. (2008). The 2007 Eastern US spring freeze: increased cold damage in a warming world? *BioScience* 58, pp. 253–262.

Haei, M., et al. (2010). Cold winter soils enhance dissolved organic carbon in stream water. *Geophysical Research Letters* 37, Art. no. L08501, doi: 10.1029/2010GL042821.

Hafner, S. D. and Groffman, P. M. (2005). Soil nitrogen cycling under litter and coarse woody debris in a mixed forest in New York State. *Soil Biology & Biochemistry* 37, pp. 2159–2162.

Hafner, S. D., Groffman, P. M. and Mitchell, M. J. (2005). Leaching of dissolved organic carbon, dissolved organic nitrogen, and other solutes from coarse woody debris and litter in a mixed forest in New York State. *Biogeochemistry* 74, pp. 257–282.

Harding, R. J. and Pomeroy, J. W. (1996). Energy balance of the winter boreal landscape. *Journal of Climate* 9 (11), pp. 2778–2787.

Hardy, J. P., et al. (1997). Snow ablation modeling at the stand scale in a boreal jack pine forest. *Journal of Geophysical Research-Atmospheres* 102 (D24), pp. 29397–29405.

Hardy, J. P., et al. (2001). Snow depth manipulation and its influence on soil frost and water dynamics in a northern hardwood forest. *Biogeochemistry* 56 (2), pp. 151–174.

Harrysson-Drotz, S., et al. (2009). Contributions of matric and osmotic potentials to the unfrozen water content of frozen soils. *Geoderma* 148, pp. 392–398.

Harrysson-Drotz, S., et al. (2010). Effects of soil organic matter composition on unfrozen water content and heterotrophic CO_2 production of frozen soils. *Geochimica et Cosmochimica Acta* 74, pp. 2281–2290.

Hayhoe, K., et al. (2007). Past and future changes in climate and hydrological indicators in the US Northeast. *Climate Dynamics* 28, pp. 381–407.

Hayhoe, K., et al. (2008). Regional climate change projections for the Northeast USA. *Mitigation and Adaptation Strategies for Global Change* 13, pp. 425–436.

Hedstrom, N. R. and Pomeroy, J. W. (1998). Measurements and modelling of snow interception in the boreal forest. *Hydrological Processes* 12 (10–11), pp. 1611–1625.

Henry, H. A. L. (2007). Soil freeze-thaw cycle experiments: trends, methodological weaknesses and suggested improvements. *Soil Biology & Biochemistry* 39, pp. 977–986.

Henry, H. A. L. (2008). Climate change and soil freezing dynamics: historical trends and projected changes. *Climatic Change* 87, pp. 421–434.

Hentschel, K., Borken, W. and Matzner, E. (2008). Leaching losses of nitrogen and dissolved organic matter following repeated freeze/thaw events in a forest soil *Journal of Plant Nutrition and Soil Science* 171, pp. 699–706.

Hentschel, K., et al. (2009). Effects of soil frost on nitrogen net mineralization, soil solution chemistry and seepage losses in a temperate forest soil. *Global Change Biology* 15, pp. 825–836.

Hobbie, S. E. and Chapin, F. S. (1996). Winter regulation of tundra litter carbon and nitrogen dynamics. *Biogeochemistry* 35, pp. 327–338.

Hobbie, S. E., Schimel, J. P., Trumbore, S. E. and Randerson, J. R. (2000). Controls over carbon storage and turnover in high-latitude soils. *Global Change Biology* 6 (S1), pp. 196–210.

Hong, B., Swaney, D. P., Woodbury, P. B. and Weinstein, D. A. (2005). Long-term nitrate export pattern from Hubbard Brook Watershed 6 driven by climatic variation. *Water, Air and Soil Pollution* 160, pp. 293–326.

Huntington, T. G., Richardson, A. D., McGuire, K. J. and Hayhoe, K. (2009). Climate and hydrological changes in the northeastern United States: recent trends and implications for forested and aquatic ecosystems. *Canadian Journal of Forest Research* 39, pp. 199–212.

IPCC (2007). *Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* [Core Writing Team, Pachauri, R.K and Reisinger, A. (eds.)]. Geneva, Switzerland: IPCC, 104 pp.

IPCC (2008). *Technical Paper of the Intergovernmental Panel on Climate Change Rep*. Bates, B. C., Kundzewicz, Z. W., Wu, S. and Palutokof, J. P. (eds.) Geneva: IPCC Secretariat, 210 pp.

Isard, S. A. and Schaetzl, R. J. (1998). Effects of winter weather conditions on soil freezing in southern Michigan. *Physical Geography* 19, pp. 71–94.

Ivarson, K. C. and Sowden, F. J. (1966). Effect of freezing on the free amino acids in soil. *Canadian Journal of Soil Science* 46, pp. 115–120.

Ivarson, K. C. and Sowden, F. J. (1970). Effect of frost action and storage of soil at freezing temperatures on the free amino acids, free sugars, and respiratory activity of soil. *Canadian Journal of Soil Science* 50, pp. 191–198.

Jackowicz-Korczynski, M., et al. (2010). Annual cycle of methane emission from a subarctic peatland. *Journal of Geophysical Research-Biogeosciences* 115, G02009, doi: 10.1029/2008jg000913.

Jandl, R. and Sollins, P. (1997). Water extractable soil carbon in relation to the belowground carbon cycle. *Biology and Fertility of Soils* 25 (2), pp. 196–201.

Jefferies, R. L., Walker, N. A., Edwards, K. A. and Dainty, J. (2010). Is the decline of soil microbial biomass in late winter coupled to changes in the physical state of cold soils? *Soil Biology & Biochemistry* 42, pp. 129–135.

Jobbagy, E. G. and Jackson, R. B. (2000). The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications* 10 (2), pp. 423–436.

Jones, H. G., et al. (1999). CO2 in Arctic snow cover: landscape form, in-pack gas concentration gradients, and the implications for the estimation of gaseous fluxes. *Hydrological Processes* 13 (18), pp. 2977–2989.

Kane, D. L., et al. (2001). Non-conductive heat transfer associated with frozen soils. *Global and Planetary Change* 29 (3–4), pp. 275–292.

Karhu, K., et al. (2010). Temperature sensitivity of organic matter decomposition in two boreal forest soil profiles. *Soil Biology & Biochemistry* 42, pp. 72–82.

Kaste, O., Austnes, K., Vestgarden, L. S. and Wright, R. F. (2008). Manipulation of snow in small headwater catchments at Storgama, Norway: effects on leaching of inorganic nitrogen. *Ambio* 37, pp. 29–37.

Kielland, K., Olson, K., Ruess, R. W. and Boone, R. D. (2006). Contribution of winter processes to soil nitrogen flux in taiga forest ecosystems. *Biogeochemistry* 81, pp. 349–360.

Kreyling, J. (2010). Winter climate change: a critical factor for temperate vegetation performance. *Ecology* 91, pp. 1939–1948.

Kurganova, I., et al. (2003). Annual and seasonal CO_2 fluxes from Russian southern taiga soils. *Tellus Series B-Chemical and Physical Meteorology* 55 (2), pp. 338–344.

Lafleur, P. M., et al. (2003). Interannual variability in the peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog. *Global Biogeochemical Cycles* 17 (2), p. 1036, doi: 1010.1029/2002GB001983.

Leinonen, I. (1996). A simulation model for the annual frost hardiness and freeze damage of Scots pine. *Annals of Botany* 78, pp. 687–693.

Lewis, W. M. and Grant, M. C. (1980). Relationship between snow cover and winter losses of dissolved substances from a mountain watershed. *Arctic and Alpine Research* 12, pp. 11–17.

Link, T. E. and Marks, D. (1999a). Point simulation of seasonal snow cover dynamics beneath boreal forest canopies. *Journal of Geophysical Research-Atmospheres* 104, pp. 27841–27857.

Link, T. E. and Marks, D. (1999b). Distributed simulation of snowcover mass and energy-balance in the boreal forest. *Hydrological Processes* 13, pp. 2439–2452.

Lipson, D. A., Schadt, C. W. and Schmidt, S. K. (2002). Changes in soil microbial community structure and function in an alpine dry meadow following spring snow melt. *Microbial Ecology* 43, pp. 307–314.

Lipson, D. A., Schimdt, S. K. and Monson, R. K. (1999). Links between microbial population dynamics and nitrogen availability in an alpine ecosystem. *Ecology* 80, pp. 1623–1631.

Liptzin, D., et al. (2009). Process-level controls on CO_2 fluxes from a seasonally snow-covered subalpine meadow soil, Niwot Ridge, Colorado. *Biogeochemistry* 95 (1), pp. 151–166, doi: 10.1007/s10533-009-9303-2.

Lundquist, J. D., et al. (2008). Rain versus snow in the Sierra Nevada, California: comparing Doppler profiling radar and surface observations of melting level. *Journal of Hydrometeorology* 9 (2), pp. 194–211.

Maljanen, M., Alm, J., Martikainen, P. J. and Repo, T. (2010). Prolongation of soil frost resulting from reduced snow cover increases nitrous oxide emissions from boreal forest soil. *Boreal Environment Research* 15, pp. 34–42.

Mariko, S., et al. (2000). Winter CO2 flux from soil and snow surfaces in a cool-temperate deciduous forest, Japan. *Ecological Research* 15 (4), pp. 363–372.

Mast, M. A., Wickland, K. P., Striegl, R. T. and Clow, D. W. (1998). Winter fluxes of CO_2 and CH_4 from subalpine soils in Rocky Mountain National Park, Colorado. *Global Biogeochemical Cycles* 12 (4), pp. 607–620.

Matzner, E. and Borken, W. (2008). Do freeze-thaw events enhance C and N losses from soils of different ecosystems? A review. *European Journal of Soil Science* 59, pp. 274–284.

McDowell, N. G., Marshall, J. D., Hooker, T. D. and Musselman, R. (2000). Estimating CO_2 flux from snowpacks at three sites in the Rocky Mountains. *Tree Physiology* 20 (11), pp. 745–753.

McGuire, A. D., et al. (2000). Modeling the effects of snowpack on heterotrophic respiration across northern temperate and high latitude regions: comparison with measurements of atmospheric carbon dioxide in high latitudes. *Biogeochemistry* 48 (1), pp. 91–114.

Michalzik, B., et al. (2001). Fluxes and concentrations of dissolved organic carbon and nitrogen – a synthesis for temperate forests. *Biogeochemistry* 52, pp. 173–205.

Mikan, C. J., Schimel, J. P. and Doyle, A. P. (2002). Temperature controls of microbial respiration in arctic tundra soils above and below freezing. *Soil Biology & Biochemistry* 34, pp. 1785–1795.

Miller, A. E., et al. (2007). Mineralization responses at near-zero temperatures in three alpine soils. *Biogeochemistry* 84 (3), pp. 233–245, doi: 10.1007/s10533-007-9112-4.

Mitchell, M. J., et al. (1996). Climatic control of nitrate loss from forested watersheds in the northeast United States. *Environmental Science & Technology* 30 (8), pp. 2609–2612.

Molotch, N. P., et al. (2007). Estimating sublimation of intercepted and sub-canopy snow using eddy covariance systems. *Hydrological Processes* 21 (12), pp. 1567–1575.

Molotch, N. P., et al. (2009). Ecohydrological controls on snowmelt partitioning in mixed-conifer sub-alpine forests. *Ecohydrology* 2 (2), pp. 129–142, doi: 10.1002/eco.48.

Monson, R. K., et al. (2002). Carbon sequestration in a high-elevation, subalpine forest. *Global Change Biology* 8 (5), pp. 459–478.

Monson, R. K., et al. (2005). Climatic influences on net ecosystem CO_2 exchange during the transition from wintertime carbon source to springtime carbon sink in a high-elevation, subalpine forest. *Oecologia* 146 (1), pp. 130–147, doi: 10.1007/s00442-005-0169-2.

Monson, R. K., et al. (2006). The contribution of beneath-snow soil respiration to total ecosystem respiration in a high-elevation, subalpine forest. *Global Biogeochemical Cycles* 20, GB3030, doi: 10.1029/2005GB002684.

Mote, P. W., Hamlet, A. F., Clark, M. P. and Lettenmaier, D. P. (2005). Declining mountain snowpack in western north America. *Bulletin of the American Meteorological Society* 86 (1), pp. 39–49.

Musselman, K., Molotch, N. P. and Brooks, P. D. (2008). Effects of vegetation on snow accumulation and ablation in a mid-latitude sub-alpine forest. *Hydrological Processes* 22 (15), pp. 2767–2776.

Neilson, C. B., et al. (2001). Freezing effects on carbon and nitrogen cycling in northern hardwood forest soils. *Soil Science Society of America Journal* 65 (6), pp. 1723–1730.

Nilsson, M., et al. (2008). Contemporary carbon accumulation in a boreal oligotrophic minerogenic mire – a significant sink after accounting for all C-fluxes. *Global Change Biology* 14, pp. 1–16, doi: 10.1111/j.1365-2486.2008.01654.x.

Nobrega, S. and Grogan, P. (2007). Deeper snow enhances winter respiration from both plant-associated and bulk soil carbon pools in birch hummock tundra. *Ecosystems* 10, pp. 419–431.

Oechel, W. C., Vourlitis, G. and Hastings, S. J. (1997). Cold season CO_2 emission from arctic soils. *Global Biogeochemical Cycles* 11 (2), pp. 163–172.

Oechel, W. C., et al. (2000). Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming. *Nature* 406 (6799), pp. 978–981.

Olsson, P. Q., et al. (2007). Five stages of the Alaskan Arctic cold season with ecosystem implications. *Arctic, Antarctic, and Alpine Research* 35 (1), pp. 74–81, doi: 10.1657/1523-0430(2003)035[0074:FSOTAA]2.0.CO;2.

Öquist, M. G. and Laudon, H. (2008). Winter soil frost conditions in boreal forests control growing season soil CO_2 concentration and its atmospheric exchange. *Global Change Biology* 14, pp. 2839–2847.

Öquist, M. G., et al. (2004). Nitrous oxide production in a forest soil at low temperatures – processes and environmental controls. *FEMS Microbiology Ecology* 49, pp. 371–378.

Öquist, M. G., et al. (2009). Water availability controls microbial temperature responses in frozen soil CO_2 production. *Global Change Biology* 15, pp. 2715–2722.

Ostroumov, V. E. and Siegert, C. (1996). Exobiological aspects of mass transfer in microzones of permafrost deposits. *Advances in Space Research* 18, pp. 79–86.

Panikov, N. S., et al. (2006). Microbial activity in soils frozen to below −39°C. *Soil Biology & Biochemistry* 38, pp. 785–794.

Peters, N. E. and Leavesley, G. H. (1995). Biotic and abiotic processes controlling water chemistry during snowmelt at Rabbit-Ears-Pass, Rocky-Mountains, Colorado, USA. *Water Air and Soil Pollution* 79 (1–4), pp. 171–190.

Pomeroy, J. W., Parviainen, J., Hedstrom, N. R. and Gray, D. M. (1998a). Coupled modelling of forest snow interception and sublimation. *Hydrological Processes* 12 (15), pp. 2317–2337.

Pomeroy, J. W., et al. (1998b). An evaluation of snow accumulation and ablation processes for land surface modelling. *Hydrological Processes* 12 (15), pp. 2339–2367.

Post, W. M., Emanuel, W. R., Zinke, P. J. and Stangenberger, A. G. (1982). Soil carbon pools and world life zones. *Nature* 298 (5870), pp. 156–159.

Potter, C. S., Matson, P. A., Vitousek, P. M. and Davidson, E. A. (1996). Process modelling of controls on nitrogen trace gas emissions from soils worldwide. *Journal of Geophysical Research-Atmospheres* 101, pp. 1361–1377.

Räisänen, J., et al. (2004). European climate in the late twenty-first century: regional simulations with two driving global models and two forcing scenarios. *Climate Dynamics* 22 (1), pp. 13–31.

Rango, A. and Katwijk, V. F. (1990). Climate change effects on the snowmelt hydrology of western North America mountains basins. *IEEE Transactions on Geoscience and Remote Sensing* 28 (5), pp. 970–974.

Reetsma, T., Bredow, A. and Gehring, M. (1999). The nature and kinetics of organic matter release from soil by salt solutions. *European Journal of Soil Science* 50 (1999), 53–64.

Röver, M., Heinemeyer, O. and Kaiser, E. A. (1998). Microbial induced nitrous oxide emissions from an arable soil during winter. *Soil Biology & Biochemistry* 30, pp. 1859–1865.

Sagerfors, J., et al. (2008). Annual CO_2 exchange between a nutrient-poor, minerotrophic, boreal mire and the atmosphere. *Journal of Geophysical Research* 113, G01001, doi: 10.1029/2006JG000306.

Schadt, C. W., Martin, A. P., Lipson, D. A. and Schmidt, S. K. (2003). Seasonal dynamics of previously unknown fungal lineages in tundra soils. *Science* 301, pp. 1359–1361.

Schimel, D. S., et al. (2001). Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature* 414 (6860), pp. 169–172.

Schimel, J. P., Bilbrough, C. and Welker, J. A. (2004). Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biology & Biochemistry* 36 (2), pp. 217–227.

Schimel, J. P. and Clein, J. S. (1996). Microbial response to freeze-thaw cycles in tundra and taiga soils. *Soil Biology & Biochemistry* 28 (8), pp. 1061–1066.

Schimel, J. P. and Mikan, C. (2005). Changing microbial substrate use in Arctic tundra soils through a freeze-thaw cycle. *Soil Biology & Biochemistry* 37, pp. 1411–1418.

Schimel, J. P., Balser, T. C. and Wallenstein, M. (2007). Microbial stress-response physiology and its implications for ecosystem function. *Ecology* 88, pp. 1386–1394.

Schmidt, S. K., et al. (2007). Biogeochemical consequences of rapid microbial turnover and seasonal succession in soil. *Ecology* 88 (6), pp. 1379–1385.

Scott, M. J., Jones, M. N., Woof, C. and Tipping, E. (1998). Concentrations and fluxes of dissolved organic carbon in drainage water from an upland peat system. *Environment International* 24 (5–6), pp. 537–546.

Scott-Denton, L. E., Rosenstiel, T. N. and Monson, R. K. (2006). Differential controls by climate and substrate over the heterotrophic and rhizosphere components of soil respiration. *Global Change Biology* 12, pp. 205–216.

Shurmann, A., Mohn, J. and Bachofen, R. (2002). N_2O emissions from snow covered soils in the Swiss Alps. *Tellus* 54B, pp. 134–142.

Sobczak, W. V., Findlay, S. and Dye, S. (2003). Relationships between DOC bioavailability and nitrate removal in an upland stream: an experimental approach. *Biogeochemistry* 62, pp. 309–327.

Sommerfeld, R. A., Mosier, A. R. and Musselman, R. C. (1993). CO_2, CH_4, and N_2O flux through a Wyoming snowpack., *Nature* 361 (6408), pp. 140–142.

Sperry, J. S., Nichols, K. L., Sullivan, J. E. M. and Eastlack, S. E. (1994). Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. *Ecology* 75, pp. 1736–1752.

Stähli, M. and Stadler, D. (1997). Measurement of water and solute dynamics in freezing soil columns with time domain reflectometry. *Journal of Hydrology* 165, pp. 352–369.

Starr, G. and Oberbauer, S. F. (2003). Photosynthesis of arctic evergreens under snow: implications for tundra ecosystem carbon balance. *Ecology* 84, pp. 1415–1420.

Steenberg Larsen, K., et al. (2007). Significance of cold-season respiration and photosynthesis in a subarctic heath ecosystem in Northern Sweden. *Global Change Biology* 13, pp. 1498–1508.

Steltzer, H. and Bowman, W. D. (2005). Litter N retention over winter for a low and a high phenolic species in the alpine tundra. *Plant and Soil* 275, pp. 361–370.

Storck, P., Lettenmaier, D. P. and Bolton, S. M. (2002). Measurement of snow interception and canopy effects on snow accumulation and melt in a mountainous maritime climate, Oregon, United States. *Water Resources Research* 38 (11), pp. 1223, doi: 10.1029/2002WR001281.

Stottlemyer, R. and Troendle, C. A. (2001). Effect of canopy removal on snowpack quantity and quality, Fraser experimental forest, Colorado. *Journal of Hydrology* 245 (1–4), pp. 165–176.

Sturm, M., et al. (2005). Winter biological processes could help convert arctic tundra to shrubland. *BioScience* 55 (1), pp. 17–26.

Sulkava, P. and Huhta, V. (2003). Effects of hard frost and freeze-thaw cycles on decomposer communities and N mineralisation in boreal forest soil. *Applied Soil Ecology* 22, pp. 225–239.

Sullivan, P. F., Arens, S. J. T., Sveinbjornsson, B. and Welker, J. M. (2010). Modeling the seasonality of belowground respiration along an elevation gradient in the western Chugach Mountains, Alaska. *Biogeochemistry* 101 (1–3), pp. 61–75, doi: 10.1007/s10533-010-9471-0.

Tarnocai, C., et al. (2009). Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycle*. 23, GB2023, doi: 10.1029/2008gb003327.

Teepe, R., Brumme, R. and Beese, F. (2000). Nitrous oxide from frozen soils under agriculture, fallow and forest. *Soil Biology & Biochemistry* 32, pp. 1807–1810.

Templer, P. H. and Socci, A. M. (2010). *Winter climate change and the effect of soil frost on nitrogen uptake by mature trees in a northern hardwood forest of the United States*. Paper presented at the 95th ESA Annual Meeting, Pittsburgh, PA, August.

Thomashow, M. F. (1999). Plant cold acclimation: freezing tolerance genes and regulatory mechanisms. *Annual Review of Plant Physiology and Plant Molecular Biology* 50, pp. 571–599.

Tierney, G. L., et al. (2001). Soil freezing alters fine root dynamics in a northern hardwood forest. *Biogeochemistry* 56 (2), pp. 175–190.

Tilston, E., Sparrman, T. and Oquist, M. (2010). Unfrozen water content moderates temperature dependence of sub-zero microbial respiration. *Soil Biology and Biochemistry* 42 (9), pp. 1396–1407, doi: 10.1016/j.soilbio.2010.04.018.

Tipping, E., et al. (1999). Climatic influences on the leaching of dissolved organic matter from upland UK Moorland soils, investigated by a field manipulation experiment. *Environment International* 25 (1), pp. 83–95.

Veatch, W., Brooks, P. D., Gustafson, J. R. and Molotch, N. P. (2009). Quantifying the effects of forest canopy cover on net snow accumulation at a continental, mid-latitude site. *Ecohydrology* 2 (2), pp. 115–128, doi: 10.1002/eco.45.

Venäläinen, A., et al. (2001). Impact of climate change on soil frost under snow cover in a forested landscape. *Climate Research* 17, pp. 63–72.

Vestgarden, L. S. and Austnes, K. (2009). Effects of freeze-thaw on C and N release from soils below different vegetation in a montane system: a laboratory experiment. *Global Change Biology* 15, pp. 876–887.

Walker, D. A., Halfpenny, J. C., Walker, M. D. and Wessman, C. A. (1993). Long-term studies of snow-vegetation interactions. *BioScience* 43, pp. 287–301.

Walker, M. D., et al. (1999). Long-term experimental manipulations of winter snow regime and summer temperature. *Hydrological Processes* 13, pp. 2315–2330.

Walker, V. K., Palmer, G. R. and Voordouw, G. (2006). Freeze-thaw tolerance and clues to the winter survival of a soil community. *Applied and Environmental Microbiology* 72, pp. 1784–1792.

Wang, F. L. and Bettany, J. R. (1993). Influence of freeze-thaw and flooding on the loss of soluble organic carbon and carbon dioxide from soil. *Journal of Environmental Quality* 22, pp. 709–714.

Wang, W., Peng, S. S., Wang, T. and Fang, J. Y. (2010). Winter soil CO_2 efflux and its contribution to annual soil respiration in different ecosystems of a forest-steppe ecotone, north China. *Soil Biology & Biochemistry* 42 (3), pp. 451–458, doi: 10.1016/j.soilbio.2009.11.028.

Weintraub, M. N. and Schimel, J. P. (2003). Interactions between carbon and nitrogen mineralization and soil organic matter chemistry in arctic tundra soils. *Ecosystems* 6 (2), pp. 129–143, doi: 10.1007/s10021-002-0124-6.

Wickland, K. P., Striegl, R. G., Mast, M. A. and Clow, D. W. (2001). Carbon gas exchange at a southern Rocky Mountain wetland, 1996–1998. *Global Biogeochemical Cycles* 15 (2), pp. 321–335.

Wigmosta, M. S., Vail, L. W. and Lettenmaier, D. P. (1994). A distributed hydrology-vegetation model for complex terrain. *Water Resources Research* 30 (6), pp. 1665–1679.

Yamazaki, T. and Kondo, J. (1992). The snowmelt and heat-balance in snow-covered forested areas. *Journal of Applied Meteorology* 31 (11), pp. 1322–1327.

Zhang, T., Barry, R. G. and Armstrong, R. L. (2004). Application of satellite remote sensing techniques to frozen ground studies. *Polar Geography* 28, 163–196.

Zhu, X. B., Cox, R. M. and Arp, P. A. (2000). Effects of xylem caviation and freezing injury on dieback of yellow birch (*Betula alleghaniensis*) in relation to a simulated winter thaw. *Tree Physiology* 20, pp. 541–547.

Zimov, S. A., et al. (1996). Siberian CO_2 efflux in winter as a CO_2 source and cause of seasonality in atmospheric CO_2. *Climatic Change* 33 (1), pp. 111–120.