Ecosystems (2007) 10: 419–431
DOI: 10.1007/s10021-007-9033-z

ECOSYSTEMS

Deeper Snow Enhances Winter Respiration from Both Plant-associated and Bulk Soil Carbon Pools in Birch Hummock Tundra

Sonia Nobrega, and Paul Grogan*

Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada

Abstract

It has only recently become apparent that biological activity during winter in seasonally snow-covered ecosystems may exert a significant influence on biogeochemical cycling and ecosystem function. One-seventh of the global soil carbon pool is stored in the bulk soil component of arctic ecosystems. Consistent climate change predictions of substantial increases in winter air temperatures and snow depths for the Arctic indicate that this region may become a significant net annual source of CO_2 to the atmosphere if its bulk soil carbon is decomposed. We used snow fences to investigate the influence of a moderate increase in snow depth from approximately 0.3 m (ambient) to approximately 1 m on winter carbon dioxide fluxes from mesic birch hummock tundra in northern Canada. We differentiated fluxes derived from the bulk soil and plant-associated carbon pools using an experimental 'weeding' manipulation. Increased snow depth enhanced the wintertime carbon flux from both pools, strongly suggesting that respiration from each was sensitive to warmer soil temperatures. Furthermore, deepened snow resulted in cooler and relatively stable soil temperatures during the spring-thaw period, as well as delayed and fewer freeze–thaw cycles. The snow fence treatment increased mean total winter efflux from 27 to 43 g CO_2-C m^{-2}. Because total 2004 growing season net ecosystem exchange for this site is estimated at 29–37 g CO_2-C m^{-2}, our results strongly suggest that a moderate increase in snow depth can enhance winter respiration sufficiently to switch the ecosystem annual net carbon exchange from a sink to source, resulting in net CO_2 release to the atmosphere.

Key words: climate change; winter; snow; soil; tundra; birch; arctic; respiration; carbon dioxide; temperature; Canada.

Introduction

Arctic ecosystems were once considered dormant during the long winter period, but recent studies have demonstrated that respiration of CO_2 is a significant portion of the annual carbon budget (Oechel and others 1997; Fahnestock and others 1998, 1999). These ecosystems contain 14% of the global soil carbon reserves (Post and others 1982) and the release of CO_2 from these systems in winter could contribute to a positive feedback to rising atmospheric CO_2 concentrations (Lashof 1989). The effects of climate change are impacting the

Received 3 March 2006; accepted 10 October 2006; published online 5 May 2007.
*Corresponding author; e-mail: groganp@biology.queensu.ca

entire planet, however, there is scientific consensus that warming is occurring earlier and more intensely in the Arctic (ACIA 2004). Winter in particular is being affected: mean air temperatures over arctic land areas have risen by 3–4°C during the last 50 years, and are expected to increase by a further 4–7°C by the 2090s (ACIA 2004). Furthermore, the amount of snowfall has increased in northern latitudes over the past century (Groisman and Easterling 1994; Vaganov and others 1999) and is predicted to increase further with anticipated climate change in this century (Giorgi and others 2001). An understanding of the effects of changes in winter climate on the physical and biological controls over carbon storage in arctic systems is essential to accurately model and predict potential feedbacks of terrestrial carbon fluxes in northern systems under future climatic changes.

Ecosystem respiration in the winter is the sum of respiration derived from carbon associated with recently fixed plant material (that is, shoots, roots, fresh plant litter, and mycorrhizal and rhizosphere-associated microbial respiration) and respiration derived from carbon in the bulk soil organic matter pool (that is, decomposition of older and presumably more recalcitrant organic pools). Because of its globally significant magnitude, the contribution and temperature sensitivity of the bulk soil carbon pool is particularly important in determining tundra CO_2 emissions and predicting the net annual carbon sink or source potential of arctic ecosystems. Analyzing the isotopic signature of respired CO_2 by arctic microbes, Biasi and others (2005) explored the temperature sensitivity of soil decomposition and demonstrated that relatively recalcitrant soil organic carbon (that is, bulk soil carbon pool) is preferentially respired at higher temperatures. However, others have concluded that respiration from labile and resistant soil organic matter pools respond similarly to changes in temperature (Fang and others 2005). Field manipulations have indicated that mid-winter ecosystem CO_2 production in heath tundra at least can be dominated by plant-associated carbon, rather than bulk soil organic matter (Grogan and others 2001). Longer term studies indicate that both pools can contribute substantially to total wintertime respiration and that the proportional contributions can vary amongst tundra ecosystem types (Grogan and Jonasson 2005). In contrast, CO_2 produced in a boreal forest during winter seems to originate mainly from the decomposition of old organic carbon stored at depth in the soil rather than from carbon fixed during the previous growing season (Winston and others 1997). Thus, there is currently considerable debate as to the relative magnitudes of bulk soil and recently fixed carbon contributions to ecosystem respiration, and to their relative temperature sensitivities (Davidson and others 2006).

The controls on microbial activity and their substrate use in frozen soils through the winter period are not well understood (Brooks and others 1997). Subnivean temperatures can be high enough that unfrozen water may exist, creating a favorable environment for soil microbial activity (Zimov and others 1993; Mikan and others 2002). Microbial metabolic activity has been detected at temperatures as low as −12 to −20°C (Carpenter and others 2000; Panikov and Dedysh 2000; Rivkina and others 2000). Arctic tundra snow manipulation experiments on ecosystem biogeochemistry are rare, the principal one being at Toolik Lake, Alaska where tall snow fences result in very large increases in snow depth that typically increase ambient snow accumulations of approximately 0.5 m by a factor of 6 (Schimel and others 2004). In that case, deeper snow results in warmer mean winter soil temperatures and reduced temperature fluctuations because of its thermal insulating properties, as well as enhanced respiration and soil nitrogen cycling activities (Walker and others 1999; Schimel and others 2004). Furthermore, deeper snow may alter the duration and dynamics of spring thaw thereby altering CO_2 production during the freeze–thaw cycle phase in late winter (Schimel and Clein 1996). In this study we simulated a moderate and therefore potentially more realistic climate change scenario for the low Arctic during winter by experimentally increasing snow depth from approximately 0.3 m (ambient) to approximately 1 m (snow fence). To our knowledge, this is the first arctic tundra study to investigate the effects of a moderate snow depth increase on total wintertime respiration and also the first winter trace gas study in the Canadian Arctic.

Tundra containing dwarf shrubs (such as the birch hummock tundra of this study, or the acidic tussock tundra common in N. Alaska) is one of the major vegetation types in the Arctic (23% of total land area), contains 22% of the Arctic's soil organic matter (Bliss and Matveyeva 1992) and has demonstrated modest carbon loss over the winter season (Fahnestock and others 1999). Dwarf shrubs typically extend vertically up to 0.4 m and therefore can influence snow accumulation. Climate modeling studies and experimental manipulation studies predict increased plant productivity of tundra communities and a resulting expansion in height and density of shrub communities (Chapin and others 1995; McKane and others 1997a, b;

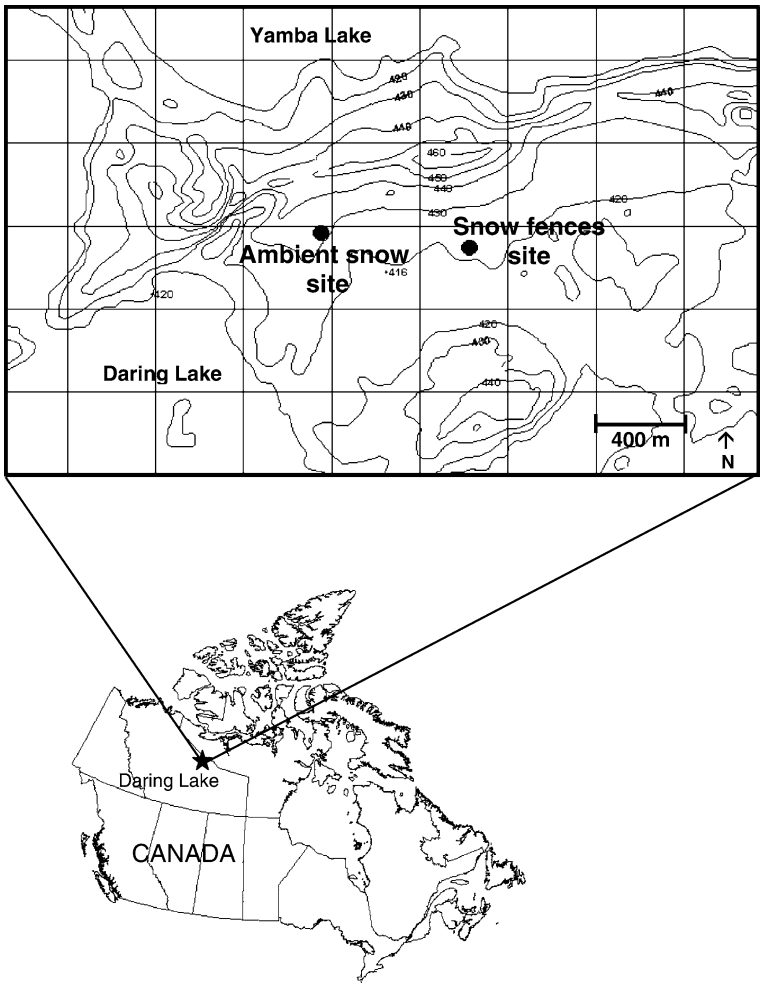

Figure 1. Study site location at Daring Lake, Northwest Territories, Canada in the sub-arctic ecozone.

Sturm and others 2005). Additionally, the snow-shrub interaction hypothesis predicts a positive feedback loop to winter CO_2 emissions as taller shrubs increase snow trapping resulting in warmer soil temperatures (Sturm and others 2001). Therefore understanding the interaction and effect of moderately enhanced snow depth on ecosystem respiration of dwarf shrub communities is necessary to predict the potential for changes in productivity and vegetation distribution as a result of future climate change.

In this study, we quantified the short-term effects of increased snow depth on winter respiration from a birch hummock type ecosystem that is widespread throughout northern Canada. In addition, we differentiated the relative contributions of recently fixed plant-associated and older bulk soil carbon sources to respiration. We tested the following hypotheses within a birch hummock tundra ecosystem:

1. Moderately enhanced snow cover increases total wintertime respiration.
2. The proportion of winter CO_2 effluxes originating from the bulk soil carbon pool is not affected by an increase in snow depth.
3. Freeze–thaw cycles in the spring period are delayed and less in number with increased snow depth due to more effective insulation of the snow cover from cold springtime air temperatures, and later snow melt.

Materials and Methods

Site Description

This study was conducted over the winter of 2004–2005 in a mesic birch hummock ecosystem at the Tundra Ecological Research Station (TERS) at Daring Lake, Northwest Territories, Canada (64°E 50′N, 111°E 38′W) which is located 300 km northeast of Yellowknife, close to the geographic center of the western continental Arctic within the Coppermine River drainage basin (Figure 1). This area is an important habitat for various wildlife species including the Bathurst Caribou herd

Table 1. Aboveground Biomass (n = 10), Rooting Biomass to ~6.4 cm depth (n = 6), Leaf Area Index (LAI), Moss and Lichen Cover (n = 6) for Birch Hummock Vegetation at Daring Lake, Northwest Territories

Aboveground biomass (g dry mass m^{-2})	
Vascular shoots	1237.5 (73.3)
Non-vascular shoots (mosses and lichens)	620.3 (26.5)
Total vascular plus nonvascular shoots	1857.8 (87.5)
Belowground biomass (g dry mass m^{-2})	
Fine Roots (≤ 1 mm diameter)	162.0 (24.6)
Coarse Roots (> 1 mm diameter)	86.1 (36.2)
Leaf Area Index (live leaf area per unit ground m^2/m^2)	0.89 (0.05)
Moss cover (%)	18.5 (8.3)
Lichen cover (%)	41.2 (13.5)

Parentheses indicate standard errors.

(*Rangifer tarandus*), which migrates through the local area in large numbers (~1000s) in the spring (May–June) and fall (August–September) of some years (including 2004/2005).

The region is underlain by continuous permafrost and is characterized by numerous eskers and Canadian shield outcrops. A hydrologically driven mosaic of vegetation types including dry heath tundra, dwarf birch tundra and inundated wet sedge tundra occurs within the lowlands and gentle slope depressions between the eskers and outcrops. This experiment was located at two sites of similar mesic dwarf birch (*Betula glandulosa (Michx.)*) hummock tundra vegetation that were approximately 700 m apart within the same lowland (Figure 1). Point frame data at randomly selected quadrats (0.25 m^2; n = 6; 100 sample points per quadrat) indicate that dwarf birch is frequent in this vegetation type in both hummocks dominated by *Eriophorum vaginatum (L.)* and in hollows alongside *Ledum decumbens (Ait.), Vaccinium vitis-idaea (L.), Vaccinium uliginosum (L.), Andromeda polifolia (L.)*, and *Carex* spp. *(L.)*. A well-developed moss layer composed largely of *Sphagnum* spp. and *Aulacomnium turgidum (Wahlenb.)* with lichen cover is found on the hummocks and hollows. Roots in this ecosystem are generally confined to the surface organic horizon (depth ~19 cm; Table 1). The total carbon, nitrogen and sulfur contents of the organic horizon are 39.98, 1.44 and 0.15% of total soil dry weight, respectively (n = 6).

Climate records from the Daring Lake weather station (1996–2005; Bob Reid, Indian and Northern Affairs Canada, unpublished data) indicate frequent mean diel air temperatures of up to 20°C in summer and of −35°C in winter. On average there are 123 days when the mean diel temperature is above 0°C (May-September). Mean total annual precipitation is 158 mm and the maximum mean monthly snow depth of 33 cm generally occurs in April and May. Summer thawing of the active layer extended to a mean maximum depth of 0.77 m in this vegetation type during the growing season of 2004.

Experimental Treatment

In the summer of 2004, five snow fences (1.2 m tall and 15 m long) were arranged perpendicular to the prevailing winter wind direction (from the north east) to increase the depth and duration of snow cover within the birch hummock tundra vegetation. Because various other vegetation types occur within a mosaic on this landscape (see above), suitable replicate patches for the snow fences were located 30–60 m apart. The fence consisted of a double layer of diamond mesh (Quest Plastics DM 1004 X construction barrier fence, Mississauga, Ontario) secured by 2.1 m high steel T-posts spaced every 3 m. At each fence, we selected four experimental plots that contained at least one mature dwarf birch shrub and that were located approximately 1.5 m perpendicular to the south facing side of the fences and at least 2 m from the ends of the fences. Equivalent plots were established in an unfenced area of the same vegetation type approximately 700 m away within the same lowland (Figure 1). We recognize that this spatial separation between the snow fences site and the ambient snow depth site is not an ideal experimental design. The ambient site had been established early in the summer of 2004 for a growing season CO_2 exchange study using an infra-red gas analysis measurement approach (Nobrega and Grogan, unpublished). There was insufficient space within, or directly adjacent to the control site to accommodate the large snow fences and their potential drift areas. In selecting the snow fences site, we took great care to assure ourselves that the

Table 2. Active Layer Depth, Soil Horizon Depths and Bulk Densities at the Ambient and Snow Fence Birch Hummock Sites (22 July 2005)

		Ambient site		Snow fence site	
		Depth (cm)	Bulk Density (g dw cm^{-3})	Depth (cm)	Bulk Density (g dw cm^{-3})
Horizon	H1	4 (0.3)	0.09 (0.02)	4 (0.6)	0.11 (0.02)
	H2	6 (0.6)	0.24 (0.10)	8 (0.6)	0.15 (0.02)
	H3	6	0.28 (0.08)	6 (0.6)	0.22 (0.01)
	H4 (mineral)	14 (4.9)	0.88 (0.38)	15 (1.7)	1.38 (0.07)
	H5 (mineral)	12 (0.1)	0.93 (0.01)	N.D.	N.D.
Active layer depth (cm)		37 (4.0)		36 (1.5)	

Horizons were differentiated by soil color. Parentheses indicate standard errors (n = 2; bulk density data n = 4). None of the variables differed significantly between the two sites (t tests; P < 0.05) (N.D. = Not Determined).

fenced patches were truly comparable to the ambient control site. The vegetation composition, topography, elevation, soil horizon depths, soil bulk densities, and active layers were all very similar (Table 2).

In addition to the snow fence treatment, we established a plant removal treatment in July 2004 to differentiate bulk soil respiration from total ecosystem respiration during winter. We randomly selected two of the experimental plots in each of the snow fences and 10 of the 20 plots at the ambient snow site for the plant removal treatment (50 × 50 cm plots). All aboveground vegetation, including the green moss layer and as much of the coarse and attached fine roots as possible were carefully pulled out by hand, whilst minimizing disturbance to the underlying soil. The disturbance effect associated with this treatment generally results in elevated rates of respiration for several days later (Grogan and Chapin 2000), presumably as a result of enhanced aeration and labile C inputs arising from root mortality. Accordingly, we waited approximately 2 months after establishment of the treatment before beginning the CO_2 efflux measures, and assume that the disturbance effects had dissipated by that time. The effect of this 'weeding' treatment on plant biomass was measured in control and treated plots (n = 6) at the ambient site in July 2004.

Flux and Environmental Measurements

Ecosystem respiration during winter was measured using soda lime adsorption of CO_2 (Edwards 1982; Grogan 1998) released from an enclosed area (633 cm^2) into the headspace (18.9 l) of a sample chamber (inverted bucket, EMCO, Yellowknife, NWT). The chambers were in place from 13 September 2004 to 18 June 2005 (278 days) at the ambient snow depth plots and from 12 September to 23 June 2005 (284 days) at the snow fence plots. In preparation for the field experiment, the soda lime (Indicating type, 4–8 mesh, J.T. Baker, Phillipsburg, N.J.) was placed in weighed mason jars (1 l) and dried to constant weight in a large fan-assisted sealed oven for 66 h at 80°C at a laboratory in Kingston, Ontario. Immediately afterwards, the jars were tightly closed and initial soda lime weights recorded (~370 g). To ensure a good chamber seal, slots (~ 10 cm deep) were cut into the soil around the circumference of the sampling area several days prior to beginning the winter measurements to facilitate insertion of the bucket chambers. At the start of the measurement, the lid of one of the mason jar soda lime samples was opened and balanced on a platform of wooden skewers at the center of each plot approximately 10 cm above the soil surface. Water (~150 ml) was added to each soda lime sample to increase the CO_2 adsorption efficiency at freezing temperatures (Grogan and Chapin 1999). Immediately afterwards, an inverted bucket chamber was placed over the sampling area and pressed into the soil to approximately 10 cm depth so that a major part of the upper organic horizon soil volume was contained within the chamber. Thus, because of the concern that the enhanced diffusion gradient caused by soda lime may draw CO_2 from a soil volume wider than that contained by the cylindrical volume determined by the chamber sampling area (Grogan and Chapin 1999), we isolated the sampled soil volume (at least to 10 cm) to reduce the potential for overestimating the efflux rate due to this artifact.

Twelve of the jars were treated as blanks to correct for any weight changes associated with storage, transport, field exposure, and in particular CO_2 adsorption during final oven-drying (Grogan

1998). Blanks (n = 6) were placed in staked upright chamber buckets (24.6 l) which were than sealed with air tight lids and placed at each of the sites for the winter period. Soda lime samples were removed as soon as the soil at the two sites had thawed sufficiently to lift the buckets, and immediately sealed and shipped to the laboratory in Kingston. The samples were oven-dried to constant weight (at 80°C for 144 h followed by 31 h at 65°C). The mass of CO_2 released during the winter period was calculated as the change in soda lime weight corrected (×1.69) for water loss associated with adsorption (Grogan 1998). The winter efflux values were corrected for mean weight changes in the blanks (n = 6) for the ambient snow depth and snow fence sites (12.2 ± 0.6 and 13.6 ± 1.3 g CO_2-Cm^{-2}, respectively) and then divided by the exposed soil surface area.

Soil temperatures were measured continuously every 6 h in a hummock at depths of approximately 2 and approximately 7 cm (n = 2) at the ambient snow level site throughout the winter period and early spring using copper-constantan construction thermocouples (T type, OMEGA, Stamford, CT) and dataloggers (CR10 and CR10X, Campbell Scientific, Logan, UT). Comparison of soil temperature sensors located beneath and outside of the chambers in control and weeded plots at the ambient snow depth site indicated no significant effects of the plant removal treatment or the chambers on soil temperature through the winter measurement period. Mean diel temperatures recorded beneath the chambers were consistently lower than outside the chambers but within the ±0.5°C error of the sensors. Soil temperatures beneath the chambers at the snow fence site were marginally cooler than adjacent to the chamber (mean diel difference = −2.0°C, maximum mean diel difference = −3.3°C) during the thaw period at the end of May probably because the chambers protruded through the snow and were exposed to relatively cold air temperatures.

Soil temperatures at approximately 2 and approximately 8 cm depths (n = 3) at the snow fence sites were measured in late winter and early spring using similar dataloggers. Temperatures at 20 and 40 cm above the soil surface at each site were measured by attaching thermocouples (unshielded) to wooden stakes. These data represent either ambient air temperatures or snow temperatures depending on whether the snow depth was sufficient to cover the sensor. Snow depths at the snow fence were measured on 17 April and 19 May 2005 along three transects perpendicular to the south side of each of the five snow fences. Snow depth measurements were collected at the ambient site along five south–north transects separated by 4 m on 19 May 2005.

Belowground root biomass was calculated by multiplying the dry weight of fine and coarse (diameter greater than 0.1 mm) roots by the soil sample bulk density and mean soil sample depth. Species of each living plant were identified down to the soil surface from each of the 100 sample points within each point frame quadrat (n = 6). The leaf area index (LAI) was calculated from the total sum of all vascular plant species live leaf hits, divided by 100, the number of points within the quadrat (Warren Wilson 1958, 1965).

Statistical Analysis

A two-way factorial analysis of variance (ANOVA) was used to test for significant effects of snow depth (n = 10), plant removal manipulation (n = 10) and their interactions on total winter ecosystem respiration measured during the winter of 2004–2005. Thus, despite an experimental design where the ambient and snow fences sites were separated, and where the plant removal and control plots occurred in pairs within each of the five snow fenced areas, we chose to apply a complete randomized block design based on our knowledge, and observations of the site. Specifically, our statistical analysis assumes that: (a) based on the data and observations reported above, there were no systematic differences between plots within the ambient snow site and the snow fence sites prior to the establishment of the treatment (b) because the two control and two plant-removal plots within each of the snow fence areas were located at least 2 m apart, and soil respiration is notoriously spatially variable even at intervals of less than 15 cm (Rochette and others 1991), the effect of each snow fence on respiration from each plot was independent of its effect on neighboring plots. Thus, although the plant removal and control plots were nested in pairs within each of the five snow fences, we have assumed that respiration from each plot responded independently to the treatments. The square root transformation was applied to the winter ecosystem respiration values to meet the assumption of variance homogeneity (J.M.P. 5.1; Cary, NC). Post hoc multiple comparisons were analyzed using the Tukey–Kramer HSD test to find significant differences between all possible combinations of pairs. To test for snow fence effects on the proportional increase in winter ecosystem respiration between plant removal and control plots, winter time respiration measurements from the plant removal

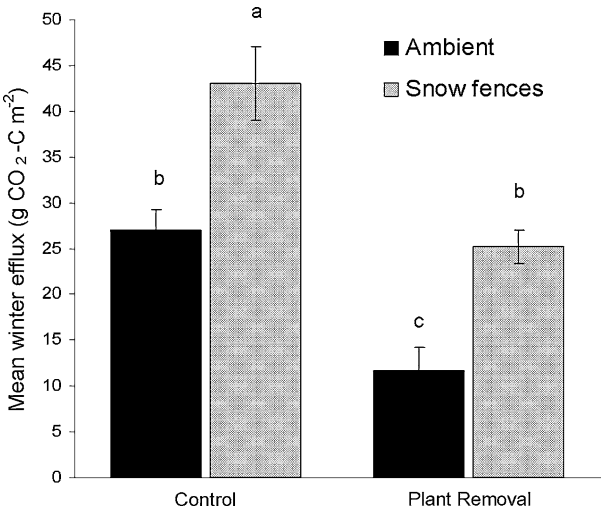

Figure 2. The effect of enhanced snow depth on wintertime ecosystem CO_2 production from control and plant removal treatment plots in birch hummock tundra. Bars indicate standard errors (n = 9–10). Columns not sharing the same letter are significantly different (Tukey HSD; $P < 0.01$).

plots were randomly paired with measurements from control plots within each snow depth regime. The calculated proportions were arcsine square-root transformed (Zar 1996) and a one-way ANOVA was used to test if the proportional contribution of the plant removal plots to total winter ecosystem respiration significantly differed between the ambient and snow fence sites.

Results

Snow Fence and Plant Removal Treatment Effects on CO_2 Flux

Total wintertime CO_2 production was significantly increased by the snow fence manipulation in both control and plant removal plots (Figure 2; $F_{3,34} = 27.8$, $P < 0.001$). By contrast, wintertime CO_2 release was significantly decreased by the removal of plants ($F_{3,34} = 34.9$, $P < 0.001$). There was no significant interaction between snow fence manipulation and plant removal treatments, indicating that these effects were independent of each other. Finally, the proportion of respiration from the plant removal plots relative to the total ecosystem respiration (from the control plots) was not significantly altered by the snow fence treatment, suggesting that CO_2 production from both the plant-associated and bulk soil carbon pools responded similarly to the enhanced snow cover ($F_{1,16} = 1.8$, $P = 0.2$).

Temperature Patterns in Early and Mid-Winter

Soils with ambient snow cover experienced an average diel mean temperature of −2.5°C during the first 3 months of the winter season (Figure 3). Following the first snowfall in September, there was a transition to the ''early cold'' stage (Olsson and others 2003), where air temperatures were consistently below 0°C and snow began to accumulate (Figure 3). This period of moderate soil temperatures (mean −2.2°C) was followed by a phase of continuous ''deep cold'' temperatures from the end of November to mid-February with typical mean daily air temperatures of −30°C. Soil temperatures reached lows of −20°C in this period, corresponding to air temperatures measured 40 cm above the soil surface of −43°C (Figure 3).

Our data indicate that the timing and depth of snow cover have a dynamic impact on the relationship between air and soil temperatures. Early in the winter, when there was little snow, the frequency of soil temperature fluctuations closely matched that of air temperatures (Figure 3). From mid-November to April, air temperatures at the ambient site (measured 20 cm above the soil surface) did not fluctuate as much, or reach lows as extreme as at 40 cm above the soil surface (Figure 3), indicating an insulating effect of snow cover to at least 20 cm above the soil surface during this period. At the beginning of the ''deep cold'' period in mid-November, air temperatures declined steeply as compared to the soil temperature profile. A switch occurred towards the end of March, when air temperatures rose rapidly and soil temperatures remained cool and relatively stable as a result of snow thermal insulation. Increasingly warmer air temperatures and the onset of snowmelt resulted in closely matched temperature records at the two heights above the soil surface from the end of April (Figure 3).

Air temperatures recorded at the weather station located less than 1 km away (data not shown) accurately corresponded to air temperatures recorded at 40 cm above the soil surface at the ambient site, providing further evidence that snow depths did not exceed approximately 40 cm at the ambient snow depth site. Air temperature values averaged from the winters of 1996 to 2004 portray a similar pattern to the 2004–2005 cold season (Figure 3).

Snow Fence Effects on the Physical Environment During the Late Cold and Thaw Periods

The snow fences created leeward drifts approximately 9 m long beyond which there were no sig-

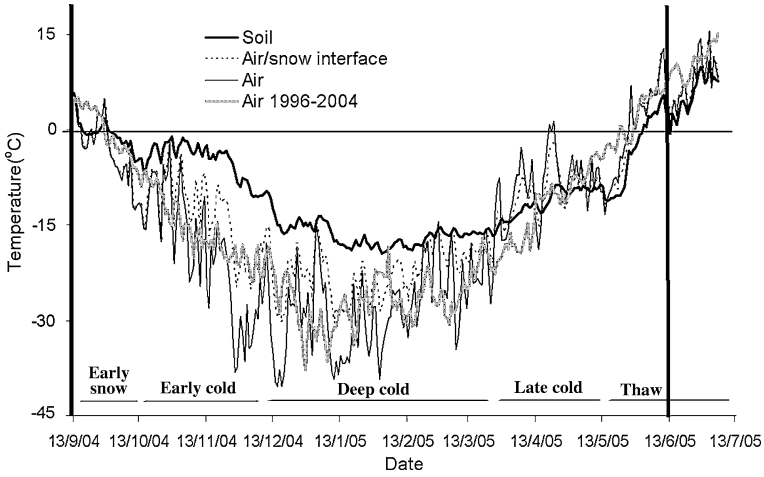

Figure 3. Daily mean temperatures in the soil (2 cm depth), air/snow interface (20 cm above soil) and air (40 cm above the soil surface) at the ambient snow depth site between mid-September 2004 to mid-July 2005 (n = 2). Mean daily air temperatures from a nearby weather station calculated for the same period from 1996 to 2004 are also indicated. The different stages of winter correspond to Olsson and others (2003). The *bold vertical lines* indicate the dates of installation and removal of the winter respiration measurement chambers at the ambient snow depth site.

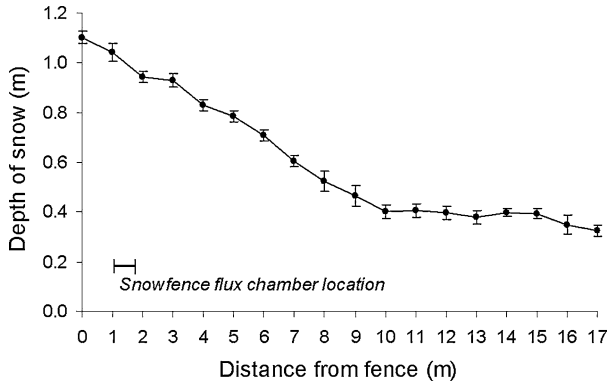

Figure 4. Spatial pattern of snow depth along southern transects from the snow fences on 19 May 2005. Values represent means (n = 15) and vertical lines are one standard error of the mean. Mean snow depth of the ambient snow site collected on the same day was 0.27 m (SE = 0.009; n = 15).

nificant differences in measured snow depths between the snow fence and ambient snow sites (Figure 4; paired t-test; $P < 0.05$). On 19 May snow depths at the snow fence site were approximately 1 m where the chambers were located, as compared to 0.28 m at the ambient snow site (Figure 4). Snow cover at the snow fence site persisted for 10 days after complete snowmelt at the ambient site.

In the late cold period, from 17 May onwards (Figure 5a), soil temperatures at the snow fence site were about 3°C warmer, and much more stable than at the ambient site, indicating enhanced thermal insulation as a result of increased snow depth. As demonstrated elsewhere (Walker and others 1999; Schimel and others 2004) we assume that this snow fence thermal effect resulted in warmer and more stable soil temperatures throughout most of the preceding winter period. Snow fence and control soil temperatures for this site over the winter subsequent to this study indicate that similar increases in snow depth raised the mean temperature during the ''deep cold'' phase from −13°C to −8°C (data not shown). Our data here indicate that soil temperatures at both sites increased within a short time period at the end of May (Figure 5). Following complete snow melt at the ambient site, soil temperatures were warmer and more dynamic than those measured at the snow fence site at the same time.

Snow depth at the snow fence site was less than 40 cm in early June, and was below 20 cm by 6 June as indicated by the air temperatures measured at the two heights (Figure 5b). During the late thaw period, freeze–thaw cycles in soil temperatures occurred at both sites. The deeper snow cover at the snow fence took longer to melt, however, resulting in a 1 week delay in the onset of freeze–thaw fluctuations and also in fewer freeze–thaw cycles in total (Figure 5a). Following complete snowmelt at the snow fence site in early June, the soil temperatures corresponded to the ambient site.

Discussion

Snow Fence Effects on Ecosystem Biogeochemistry

Our study demonstrates that moderate increases in snow depth can result in strong increases in wintertime biological activity in a tundra ecosystem. Total winter CO_2 release from this mesic birch hummock ecosystem that is common across Canada and is very similar to the acidic tussock tundra vegetation of Alaska was enhanced by 60% in plots where snow depth was raised from approximately 0.3 m up to approximately 1 m. Furthermore, the onset of soil freeze–thaw cycles in spring was de-

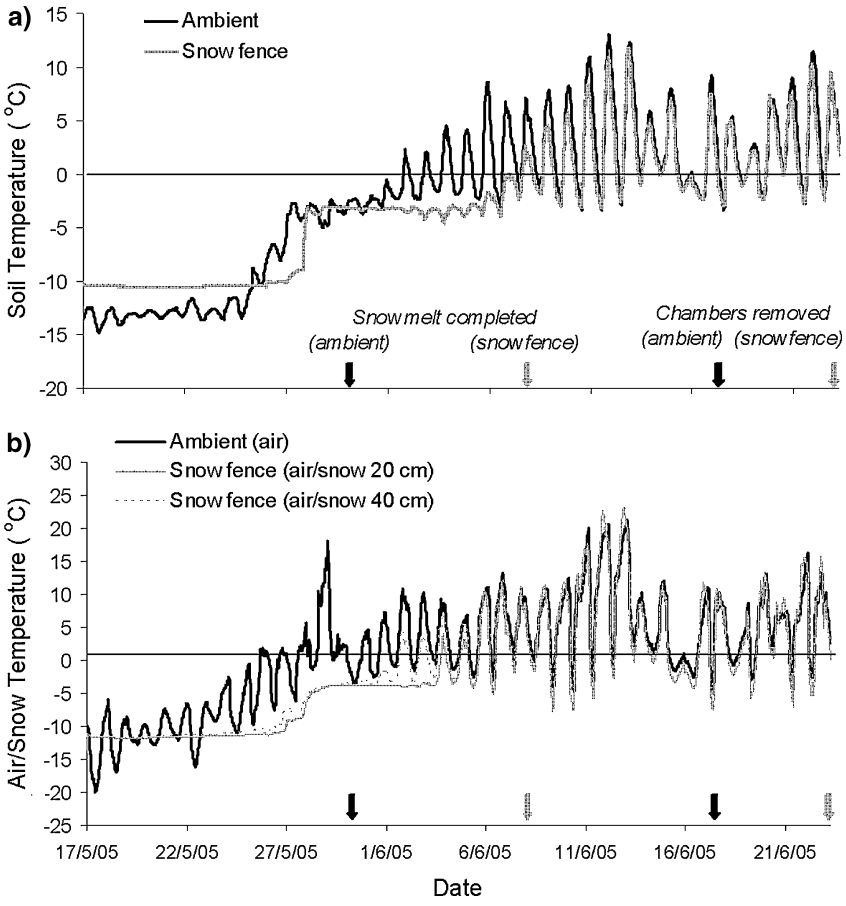

Figure 5. Mean soil temperature (2 cm depth) (**a**) and (**b**) air (20 cm above soil surface), air/snow (40 cm above soil surface) temperatures at the ambient snow and snow fence plots from mid-May to June 2005. Temperatures were recorded every 30 min (n = 3).

layed, and there were fewer cycles in total compared to ambient snow plots. Previous arctic tundra snow fence studies in Alaska that enhanced snow depth to approximately six times ambient raised the average ''deep cold'' phase soil temperature from approximately −20°C to approximately −4°C, resulting in substantial increases in soil respiration and nitrogen pools (Walker and others 1999; Schimel and others 2004). Similar results have been obtained in shallow (~0.5 m) and snow fence plots (~1.7 m) in alpine tundra (Brooks and others 1997; Brooks and others 1998). Our data place the results from these snow fence biogeochemistry studies into the context of current climate change projections. Interannual variation in maximum snow depth at an exposed ridge close to our site ranges from 0.15 to 0.60 m (1996–2005; Bob Reid, Indian and Northern Affairs Canada, unpublished data). General Circulation Model projections for the mean wintertime precipitation increase across the Arctic by the end of the century vary from approximately 5% to approximately 50% (Maxwell 1992; Giorgi and others 2001; Kattsov and Kallen 2004). Here, for the first time as far as we know, we have demonstrated that moderately enhanced snow accumulation that is within the range of climate change scenarios can substantially increase wintertime respiration.

Respiration From Plant-Associated and Bulk Soil Carbon Pools

Discerning the sources of winter respiration in arctic ecosystems is important to evaluating the potential for significant feedbacks to atmospheric CO_2 concentrations. It is the substantial bulk soil organic matter pool in these systems that make arctic ecosystem carbon balance responses to climate change potentially important at the global scale. Plant-associated respiration (that is, derived from recently fixed plant carbon such as living shoots and roots as well as rhizosphere exudates) and respiration derived from bulk soil organic matter carbon pools can both be substantial components of boreal and arctic ecosystem respiration in winter (Winston and others 1997; Grogan and Jonasson 2005). Winter CO_2 fluxes have been measured in a range of arctic ecosystems (Fahnestock and others 1998), but the differences in the relative sensitivities of the bulk soil organic matter

and plant-associated carbon pools to enhanced snow depth is unknown.

The plant removal treatment lowered total wintertime CO_2 efflux to approximately 50% of control plot values (Figure 2), suggesting that respiration from plant-associated and bulk soil C sources were both significant contributors to wintertime CO_2 release. Our plant removal treatment took away the above-ground sources of plant respiration (that is, shoots, but not surface litter). A separate plant removal experiment during the previous growing season resulted in a strong trend toward decreased fine root biomass (37% reduction, $n = 6$, $P = 0.09$) but no significant effects on coarse roots (data not shown) indicating that the total plant-associated carbon pool was substantially diminished rather than completely eliminated. Thus, our data may have underestimated ecosystem CO_2 losses from the plant-associated pool. That issue notwithstanding, our results indicate that the *proportion* of total respired C derived from plant removal plots relative to controls in this vegetation type was not significantly affected by the snow fence treatment, suggesting that respiration from both bulk soil and more recently fixed plant-associated C pools respond similarly to deeper snow. Nevertheless, since any loss in the long term store of C in the bulk soil pool is of concern because of the enormous size of this pool across the Arctic, our results are important because they indicate that the stability of this pool is sensitive to changes in winter climate.

The Magnitude of Wintertime CO_2 Emissions

This study supports the conclusion that winter CO_2 emission to the atmosphere is a substantial contribution to the total annual carbon budgets of arctic ecosystems (Zimov and others 1993; Oechel and others 1997; Fahnestock and others 1999; Welker and others 1999; Lafleur and others 2001; Grogan and Jonasson 2005). Our estimate of wintertime CO_2 efflux (27 CO_2-C m^{-2}) exceeds those by Fahnestock and others (1998) who used a snow CO_2 concentration gradient approach on various arctic communities including tussock tundra (1.3 to 10.9 g CO_2-C m^{-2}). By contrast, our estimate was much lower than that of Oechel and others (1997) for tussock tundra (70 g CO_2-C m^{-2}) based on an interpolation from infrared gas analysis chamber measures. It is well established in the literature that when respiration rates are low to moderate, the soda lime technique tends to overestimate CO_2 effluxes compared to infra-red gas analysis methods because of an enhancement in the diffusion gradient of CO_2 from the soil to the chamber headspace due its adsorption (Nay and others 1994). Although there are some field data directly relating soda lime and infra-red gas analysis (IRGA) based measures of soil CO_2 efflux (Ewel and others 1987; Grogan 1998), we did not apply any ''correction factor'' to our data because the latter studies did not include flux rates that were as low as those measured here, and therefore the calibration may be unreliable. Furthermore, previous data suggest that this overestimation effect is of greatest impact during measurement periods of 1–24 h (as in the above studies) where the effect of the enhanced diffusion gradient in drawing out CO_2 from ''storage'' pools within the soil profile can be substantial in magnitude relative to the efflux rate (Grogan and Chapin 1999). Finally, in contrast to almost all previous soda lime studies, and to address our concern that CO_2 can be drawn from a much larger volume than that contained directly below the chamber sampling area (Grogan and Chapin 1999), we isolated a large part of the sampled soil volume by inserting the chambers to approximately 10 cm soil depth (see ''Methods'').

A very recent methodological study on the soda lime technique strongly suggests that past disparities with flow-through IRGA approaches for moderate to high efflux rates (2–6 g C m^{-2} day^{-1}) were due in part to inaccuracies associated with insufficient moisture addition to the exposed soda lime, and inadequate measurement of blanks (Keith and Wong 2006). These authors conclude that the use of soda lime in a rigorously applied measurement protocol on finely textured soils of high diffusion resistance will result in quantitatively similar and unbiased measures as compared to those determined by the flow-through IRGA technique. Although our efflux rates were much lower than those tested above (Keith and Wong 2006), we note, however, that our soda lime procedure was compliant with all of the relevant recommendations contained within that protocol. In any event, with the exception of relating winter to summertime fluxes, the main conclusions of this study are based on relative comparisons between treatments and therefore should not be affected by these methodological concerns.

Effect of Enhanced Snow Depth on the Soil Environment

The enhanced snow depth treatment resulted in fewer freeze–thaw cycles in soil temperature during the spring-thaw (Figure 5). Soil freeze–thaw cycles that involve severe temperature minima can result

in initial pulses of relatively high CO_2 production (Burton and Beauchamp 1994; Schimel and Clein 1996) that are thought to be associated with the death and lysis of soil microbes releasing organic substrate and nutrients into the soil (Schimel and Clein 1996). Other soil freeze–thaw incubation studies at relatively benign temperature minima (such as experienced at our site during spring thaw; Figure 5a) indicate little effect on respiration. Thus, although the snow fences reduced the number of spring freeze–thaw events, we suggest that persistently warmer soil temperatures through the majority of the winter period were the primary explanation for the treatment effects on total CO_2 efflux. Previous studies have also found changes in soil nutrient and microbial dynamics as a result of freeze–thaw events (DeLuca and others 1992; Schimel and Clein 1996; Brooks and others 1998; Lipson and others 2000; Grogan and others 2004). Plant primary production and vegetation composition in arctic tundra ecosystems is generally strongly controlled by nutrient availability (Chapin 1995; Press and others 1998; Jonasson and others 1999) and freeze–thaw cycles at spring-thaw seem to be critical in the annual cycle of nutrient mobilization (Schimel and Clein 1996; Lipson and Monson 1998; Grogan and others 2004). If the number of freeze–thaw cycles is important to the processes of nutrient release and transfer, our results suggest that deeper snow will not just enhance wintertime biogeochemical activity but may also have substantial follow-on effects on primary production and vegetation composition during the growing season.

Effect of Enhanced Snow Depth on Annual Net Carbon Balance

Our study reports one of the first estimates of total wintertime CO_2 flux in ambient and deepened snow plots within a Canadian arctic system. Our estimates of the total winter efflux in a mesic birch hummock system (27 g CO_2-C m^{-2}) were significantly increased by enhanced snow depth (43 g CO_2-C m^{-2}). Net ecosystem production was estimated at our site in the previous growing season by interpolation of frequent chamber net ecosystem exchange measures in birch hummock tundra (Nobrega and Grogan, unpublished). Our interpolated net ecosystem exchange data indicate that over the 88-day growing season leading up to the installation of the soda lime chambers, this birch hummock ecosystem had a net carbon gain of approximately 37 g CO_2-C m^2. Eddy correlation data from the same year for a footprint that includes the control site as well as substantial areas of other vegetation types suggest an overall growing season net carbon gain of 29 g CO_2-C m^2 (Lafleur and Humphreys, unpublished). We conclude that, if the soda lime data are accurate, and if methane and leachate C losses are negligible, then winter respiration would have resulted in an overall net *annual* C gain of approximately 10 g CO_2-C m^2 (June 2004 to June 2005) for the birch hummock ecosystem. By contrast, our data suggest that a moderate increase in snow depth could switch this system to being a net annual source of carbon to the atmosphere (6 g CO_2-C m^{-2}). The above conclusion assumes that deeper snow would not alter the summer growing season length. If deeper snow delays snowmelt, as our data suggest, thereby reducing growing season C uptake (photosynthesis), the net annual source estimate may be even larger.

Conclusions

Overall, the results of this study lead us to several insights: (a) a moderate increase in snow depth that is realistic within the context of climate change scenarios can result in a marked increase in CO_2 loss over the winter season, and has the potential to modify the annual carbon sink-source relationship; (b) the proportion of total winter carbon efflux from the bulk soil carbon pool relative to that of the recently fixed C in the plant-associated pool may not be affected by deeper snow; and (c) freeze–thaw cycles during the spring-thaw period are delayed and reduced in total number by deeper snow packs. These conclusions provide a basis for regional models to incorporate the interactions between predicted increases in snow depth and the biogeochemical processes and source carbon pools that control the wintertime carbon cycle in tundra ecosystems.

Acknowledgements

We thank Brian Reid, Liesha Mayo-Bruinsma, Mike English, Mike Treberg, Elyn Humphreys, Christopher Murray and Robbie A. Hember for help in the field. Many thanks to Peter Lafleur and Greg Henry for scientific assistance and advice, and especially to Steve Matthews and Karin Clark for logistical assistance. We are very appreciative of the review comments by Paddy Sullivan and an anonymous reviewer, as well as those from Ian McHugh. This research would not have been possible without the facilities and support provided at the Tundra Ecosystem Research Station (TERS) at

Daring Lake by the Wildlife Division for Environment and Natural Resources, Government of Northwest Territories. The research was funded by the Canadian Foundation for Climate and Atmospheric Sciences, NSERC and the Northern Scientific Training Program.

REFERENCES

ACIA. 2004. Impacts of a warming arctic: arctic climate impact assessment. Cambridge: Cambridge University Press.

Biasi C, Rusalimova O, Meyer H, Kaiser C, Wanek W, Barsukov P, Junger H, Richter A. 2005. Temperature-dependent shift from labile to recalcitrant carbon sources of arctic heterotrophs. Rapid Commun Mass Spectrom 19:1401–8.

Bliss LC, Matveyeva NV. 1992. Circumpolar arctic vegetation. In: Svoboda J, Ed. Arctic ecosystems in a changing climate: an ecophysiological perspective. San Diego: Academic. pp 59–89.

Brooks PD, Schmidt SK, Williams MW. 1997. Winter production of CO_2 and N_2O from Alpine tundra: environmental controls and relationship to inter-system C and N fluxes. Oecologia 110:403–13.

Brooks PD, Williams MW, Schmidt SK. 1998. Inorganic nitrogen and microbial biomass dynamics before and during spring snowmelt. Biogeochemistry 43:1–15.

Burton DL, Beauchamp EG. 1994. Profile nitrous oxide and carbon dioxide concentrations in a soil subject to freezing. Soil Sci Soc Am Jo 58:115–22.

Carpenter EJ, Lin SJ, Capone DG. 2000. Bacterial activity in South Pole snow. Appl Environ Microbiol 66:4514–7.

Chapin FS III. 1995. Ecology - new cog in the nitrogen-cycle. Nature 377:199–200.

Chapin FS III, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA. 1995. Responses of Arctic Tundra to experimental and observed changes in climate. Ecology 76:694–711.

Davidson EA, Janssens IA, Luo YQ. 2006. On the variability of respiration in terrestrial ecosystems: moving beyond Q(10). Global Change Biol 12:154–64.

DeLuca TH, Keeney DR, McCarty GW. 1992. Effect of freeze–thaw events on mineralization of soil nitrogen. Biol Fertility Soils 14:116–120.

Edwards NT. 1982. The use of soda-lime for measuring respiration rates in terrestrial systems. Pedobiologia 23:321–30.

Ewel KC, Cropper WP, Gholz HL. 1987. Soil CO_2 evolution in Florida slash pine plantations .2. Importance of root respiration. Can J Forest Rese- 17:330–333.

Fahnestock JT, Jones MH, Brooks PD, Walker DA, Welker JM. 1998. Winter and early spring CO_2 efflux from tundra communities of northern Alaska. J Geophys Res—Atmos 103:29023–29027.

Fahnestock JT, Jones MH, Welker JM. 1999. Wintertime CO_2 efflux from arctic soils: Implications for annual carbon budgets. Global Biogeochem Cycles 13:775–9.

Fang CM, Smith P, Moncrieff JB, Smith JU. 2005. Similar response of labile and resistant soil organic matter pools to changes in temperature. Nature 433:57–9.

Giorgi F, Hewitson B, Christensen J, Hulme M, Von Storch H, Whetton P, Jones R, Mearns L, FC. 2001. Regional climate information—evaluation and projections. In: Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA, Eds. Climate change 2001: the scientific basis. contribution of the working Group I to the third assessment report of the Intergovernmental Panel on Cimate Change. Cambridge University Press, Cambridge, pp 583–638.

Grogan P. 1998. CO_2 flux measurement using soda lime: Correction for water formed during CO_2 adsorption. Ecology 79:1467–8.

Grogan P, Chapin FS III. 1999. Arctic soil respiration: Effects of climate and vegetation depend on season. Ecosystems 2:451–9.

Grogan P, Chapin FS III. 2000. Initial effects of experimental warming on above- and belowground components of net ecosystem CO_2 exchange in arctic tundra. Oecologia 125:512–20.

Grogan P, Jonasson S. 2005. Temperature and substrate controls on intra-annual variation in ecosystem respiration in two subarctic vegetation types. Global Change Biology 11:465–75.

Grogan P, Illeris L, Michelsen A, Jonasson S. 2001. Respiration of recently-fixed plant carbon dominates mid-winter ecosystem CO_2 production in sub-arctic heath tundra. Climatic Change 50:129–42.

Grogan P, Michelsen A, Ambus P, Jonasson S. 2004. Freeze–thaw regime effects on carbon and nitrogen dynamics in subarctic heath tundra mesocosms. Soil Biology & Biochemistry 36:641–54.

Groisman PY, Easterling DR. 1994. Variability and trends of total precipitation and snowfall over the United-States and Canada. J Climate 7:184–205.

Jonasson S, Michelsen A, Schmidt IK, Nielsen EV. 1999. Responses in microbes and plants to changed temperature, nutrient, and light regimes in the arctic. Ecology 80:1828–43.

Kattsov VM, Kallen E. 2004. Chapter 4. Future climate change: modeling and scenarios for the Arctic. Cambridge: Cambridge University Press.

Keith H, Wong SC. 2006. Measurement of soil CO_2 efflux using soda lime absorption: both quantitative and reliable. Soil Biol Biochem 38:1121–31.

Lafleur PM, Roulet NT, Admiral SW. 2001. Annual cycle of CO2 exchange at a bog peatland. J Geophys Res—Atmos 106:3071–81.

Lashof DA. 1989. The dynamic greenhouse - feedback processes that may influence future concentrations of atmospheric trace gases and climatic-change. Climatic change 14:213–42.

Lipson DA, Monson RK. 1998. Plant-microbe competition for soil amino acids in the alpine tundra: effects of freeze–thaw and dry-rewet events. Oecologia 113:406–14.

Lipson DA, Schmidt SK, Monson RK. 2000. Carbon availability and temperature control the post-snowmelt decline in alpine soil microbial biomass. Soil Biol Biochem 32:441–48.

Maxwell B. 1992. Arctic climate: potential for change under global warming. In: Chapin FS III, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J, Eds. Arctic ecosystems in a changing climate: an ecophysiological perspective. San Diego: Academic. pp 11–34.

McKane RB, Rastetter EB, Shaver GR, Nadelhoffer KJ, Giblin AE, Laundre JA, Chapin FS III. 1997a. Climatic effects on tundra carbon storage inferred from experimental data and a model. Ecology 78:1170–87.

McKane RB, Rastetter EB, Shaver GR, Nadelhoffer KJ, Giblin AE, Laundre JA, Chapin FS III. 1997b. Reconstruction and analysis of historical changes in carbon storage in arctic tundra. Ecology 78:1188–98.

Mikan CJ, Schimel JP, Doyle AP. 2002. Temperature controls of microbial respiration in arctic tundra soils above and below freezing. Soil Biol Biochem 34:1785–95.

Nay SM, Mattson KG, Bormann BT. 1994. Biases of chamber methods for measuring soil CO_2 efflux demonstrated with a laboratory apparatus. Ecology 75:2460–63.

Oechel WC, Vourlitis G, Hastings SJ. 1997. Cold season CO_2 emission from arctic soils. Global Biogeochem Cycles 11:163–72.

Olsson PQ, Sturm M, Racine CH, Romanovsky V, Liston GE. 2003. Five stages of the Alaskan Arctic cold season with ecosystem implications. Arctic Antarctic Alpine Res 35:74–81.

Panikov NS, Dedysh SN. 2000. Cold season CH_4 and CO_2 emission from boreal peat bogs (West Siberia): winter fluxes and thaw activation dynamics. Global Biogeochem Cycles 14:1071–80.

Post WM, Emanuel WR, Zinke PJ, Stangenberger AG. 1982. Soil carbon pools and world life zones. Nature 298:156–59.

Press MC, Potter JA, Burke MJW, Callaghan TV, Lee JA. 1998. Responses of a subarctic dwarf shrub heath community to simulated environmental change. J Ecol 86:315–27.

Rivkina EM, Friedmann EI, McKay CP, Gilichinsky DA. 2000. Metabolic activity of permafrost bacteria below the freezing point. App Environ Microbiol 66:3230–33.

Rochette P, Desjardins RL, Pattey E. 1991. Spatial and temporal variability of soil respiration in agricultural fields. Canadian J Soil Sci 71:189–96.

Schimel JP, Bilbrough C, Welker JA. 2004. Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. Soil Biol Biochem 36:217–27.

Schimel JP, Clein JS. 1996. Microbial response to freeze–thaw cycles in tundra and taiga soils. Soil Biol Biochem 28:1061–66.

Sturm M, McFadden JP, Liston GE, Chapin FS, Racine CH, Holmgren J. 2001. Snow-shrub interactions in Arctic tundra: a hypothesis with climatic implications. J Climate 14:336–44.

Sturm M, Schimel J, Michaelson G, Welker JM, Oberbauer SF, Liston GE, Fahnestock J, Romanovsky VE. 2005. Winter biological processes could help convert arctic tundra to shrubland. Bioscience 55:17–26.

Vaganov EA, Hughes MK, Kirdyanov AV, Schweingruber FH, Silkin PP. 1999. Influence of snowfall and melt timing on tree growth in subarctic Eurasia. Nature 400:149–51.

Walker MD, Walker DA, Welker JM, Arft AM, Bardsley T, Brooks PD, Fahnestock JT, Jones MH, Losleben M, Parsons AN, Seastedt TR, Turner PL. 1999. Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. Hydrol Proc 13:2315–30.

Warren Wilson J. 1958. Analysis of the spatial distribution of foliage by two-dimensional point quadrats. New Phytol 59:92–101.

Warren Wilson J. 1965. Stand structure and light penetration. I. Analysis by point quadrats. J App Ecol 2:383–90.

Welker JM, Brown KB, Fahnestock JT. 1999. CO_2 flux in Arctic and alpine dry tundra: comparative field responses under ambient and experimentally warmed conditions. Arctic Antarctic Alpine Res 31:272–77.

Winston GC, Sundquist ET, Stephens BB, Trumbore SE. 1997. Winter CO2 fluxes in a boreal forest. J Geophys Res—Atmos 102:28795–804.

Zar JH. 1996. Biostatistical analysis. New Jersey: Prentice-Hall.

Zimov SA, Zimova GM, Daviodov SP, Daviodova AI, Voropaev YV, Voropaeva ZV, Prosiannikov SF, Prosiannikova OV, Semiletova IV, Semiletov IP. 1993. Winter biotic activity and production of CO_2 in siberian soils—a factor in the greenhouse-effect. J Geophys Res—Atmos 98:5017–23.