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Cold Season Respiration across a Low Arctic Landscape: the Influence of Vegetation Type, Snow Depth, and Interannual Climatic Variation

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Abstract

Cold season respiration may significantly affect arctic terrestrial ecosystem annual net carbon balances. Here, the influences of vegetation type, experimentally deepened snow, and interannual climatic variation on total cold season CO₂ efflux were investigated in a Canadian low arctic site containing dry heath, tall birch understory, birch hummock, and wet sedge ecosystems.

Total efflux ranged from 34 to 126 g CO₂-C m⁻² among the vegetation types, with the tall birch understory respiring at least twice that of the birch hummock and four times that of either the dry heath or wet sedge. This variation did not correlate with soil temperature differences alone, but instead was attributed to ecosystem-specific interactions between snow depth, vegetation canopy cover, soil temperature, and moisture, as well as differences in plant biomass and litter production. Respiration from the birch hummock site was twice as high in 2006/2007 (the year of relatively warm fall and late winter soil temperature phases) as compared to 2004/2005, and was enhanced by the snow fence treatment only in the latter year. Together, these data demonstrate that cold season CO₂ release differs substantially among tundra vegetation types, and strongly suggest that these effluxes can significantly offset growing season carbon gains, resulting in annual net carbon losses in some years.

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Introduction

The carbon (C) balance of the Arctic is important to understanding and predicting global climate change (ACIA, 2005; Solomon et al., 2007) because the northern circumpolar permafrost region contains twice as much C as is currently in the entire atmosphere (Schuur et al., 2008). Warming of the Earth's climate is occurring most rapidly in the arctic region (Hinzman et al., 2005), and is consistently predicted to be greatest during winter rather than summer over the course of this century (ACIA, 2005; Solomon et al., 2007). Permafrost thawing and enhanced microbial decomposition of high-latitude soil organic matter as a result of rising temperatures will lead to a substantial release of CO₂ to the atmosphere, further amplifying global warming if this release is not matched by enhanced uptake (Lashof et al., 1997; McGuire et al., 2010). Although the controls and vegetation feedbacks affecting growing season C balance in the Arctic have been intensively researched for several decades (e.g. Shaver et al., 1992; Oechel et al., 1993; Michelsen et al., 1996; Aurela et al., 1998; Soegaard and Nordstroem, 1999; Oechel et al., 2000; Chapin et al., 2005; Lafleur and Humphreys, 2008), only in the last ~15 years has it become clear that significant biological activity can continue through the long cold season (i.e. fall, winter, and early spring) at high latitudes (Oechel et al., 1997; Fahnestock et al., 1999; Rivkina et al., 2000; Mikan et al., 2002; Panikov et al., 2006; Larsen et al., 2007b). Accordingly, there is now an urgent need to quantify the magnitude of arctic tundra CO₂ efflux during the cold season, and its spatial and temporal variability at the plot, ecosystem, and landscape scales (Hobbie et al., 2000; Lafleur and Humphreys, 2008).

Variation in vegetation type is clearly an important control on summertime CO₂ exchange across arctic tundra landscapes (McFadden et al., 1998; Christensen et al., 2000; Nobrega and Grogan, 2008), and therefore it may also be an important control on cold season CO₂ effluxes. In one of the very few arctic studies specifically addressing this topic, instantaneous rates of CO₂ efflux on three sampling days between March and May varied significantly among a wide range of northern Alaskan tundra vegetation types (Fahnestock et al., 1998). To the best of my knowledge, all other investigations of winter respiration in the Arctic have been focused on single or at most two vegetation types (Oechel et al., 1997; Grogan et al., 2001; Grogan and Jonasson, 2005, 2006; Larsen et al., 2007a; Nobrega and Grogan, 2007; Sullivan et al., 2008; Morgner et al., 2010), and none have included interannual comparisons. Accordingly, this study is novel in that: (a) it compares full cold season CO₂ effluxes (i.e. cumulative release from early fall to spring) across a wide range of low arctic vegetation types; (b) it includes CO₂ efflux measurements from the understory of a tall shrub ecosystem—a vegetation type that is of particular interest because it seems to be expanding in cover across the low Arctic over the past few decades (Chapin et al., 1995; Bret-Harte et al., 2001; Stow et al., 2004; Tape et al., 2006; Walker et al., 2006), and its relatively high production of woody stems that decompose slowly is likely to enhance growing season net C uptake; and (c) it reports interannual variation in winter respiration from one of the vegetation types (a birch hummock site in which CO₂ effluxes were measured from ambient and experimentally deepened snow plots as part of an earlier study; Nobrega and Grogan, 2007).

Snow accumulation clearly influences rates of winter respiration (Brooks et al., 2011), but its relative importance compared to

vegetation type in determining landscape-level patterns of CO₂ efflux may depend on the extent of snow depth. In areas of deep snow (>1 m), and in most experimental snow-fence studies, soil (and subsurface snow) temperatures are often very close to 0 °C (Taras et al., 2002; Brooks et al., 2011), resulting in high respiration rates (Walker et al., 1999). In a study of sites under such conditions, total winter CO₂ production did not differ between heath and birch forest understory vegetation types (Grogan and Jonasson, 2006). By contrast, in shallow snow areas, temperatures are much colder and therefore respiration rates are relatively low, but in these circumstances, efflux may differ significantly between the same vegetation types (Grogan and Jonasson, 2006). These results suggest that under low to moderate snow depths (<1 m), vegetation type exerts a significant influence on landscape level patterns of cold season CO₂ efflux. The study reported here tests this hypothesis across a wide range of vegetation types.

Interannual variability in growing season arctic tundra net ecosystem CO₂ exchange can vary substantially, and therefore may have a significant impact on annual net C balance (Vourlitis and Oechel, 1999; Lafleur and Humphreys, 2008). However, the latter authors point out that given the small magnitude of growing season C gains typically observed in low arctic tundra over successive years, even low rates of CO₂ efflux over the cold season have the potential to greatly influence whether a site is ultimately a net C sink, source, or neutral on an annual basis. Therefore, it is important to determine not only the magnitude of cold season CO₂ efflux, but also the extent to which that magnitude may vary interannually. Here, cold season CO₂ effluxes from the same vegetation type (using the same measurement technique and the same plots) over two climatically different winters are compared. Interannual variation in efflux is interpreted according to corresponding soil and air temperature and ambient snow depth data. Finally, although it is well established that experimentally deepened snow enhances winter respiration (e.g. Nobrega and Grogan, 2007; Walker et al., 1999), the potential interaction between interannual climatic variation and deepened snow effects on cold season respiration has not been explored. Here, the influence of experimentally deepened snow on CO₂ effluxes in these two winters is investigated (using the same snow-fence plots in the same vegetation type in both years) to determine the consistency of the effect, and the potential impact of climatic variation.

The following hypotheses were tested: (1) Total CO₂ efflux during the cold season differs significantly among the principal vegetation types of the low Arctic. (2) Vegetation type is more important than snow depth in determining cold season CO₂ efflux across tundra landscapes where snow accumulation is low to moderate (<1 m). (3) Cold season CO₂ efflux from birch hummock tundra vegetation is significantly larger in years with relatively warm fall and late winter/spring phases. (4) Experimentally deepened snow (increased from 0.3 to 1 m) does not enhance cold season CO₂ efflux from birch hummock tundra in years when the snow-fence moderating effect on soil temperature is confined to the mid-winter deep cold phase.

Methods

SITE DESCRIPTION

This study was conducted near the Tundra Ecological Research Station at Daring Lake, Northwest Territories, Canada

(64°52'N, 111°35'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. The region is characterized by numerous Canadian Shield outcrops and occasional eskers that were formed toward the end of the most recent glacial period (Rampton, 2000). 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 near Daring Lake (Nobrega and Grogan, 2008). Patches of tall birch vegetation are found scattered across the landscape in mesic and wet locations, but generally close to areas of obvious periodic surface water flow, or in areas protected from wind, and where snow preferentially accumulates (Obst, 2008). The soils underlying these vegetation types generally consist of an organic layer overlying sand and silt, and the whole region is underlain by continuous permafrost with a soil active layer ranging from 0.3 to 2 m (Nobrega and Grogan, 2008; Obst, 2008). The research site lies in the center of the summer range of the Bathurst caribou herd (*Rangifer tarandus groenlandicus*), whose population has been in severe decline since the mid-1980s (Adamczewski et al., 2009).

Local climate records indicate daily mean air temperatures ranging from as low as −40 °C in winter to as high as 22 °C in summer, with a mean annual rainfall of 152 mm (S.D. = 54; 1996–2010; Bob Reid, Department of Indian and Northern Affairs, Canada, unpublished data). Snow is present for ~200 days (mid-October to mid-June), with snow depth generally <10 cm until early November, by which time soil temperatures have dropped below 0 °C (Buckeridge and Grogan, 2008). Snow then accumulates toward maximum depths in late April and varies substantially among years (e.g. peak annual snow depth in exposed heath vegetation at the Daring Lake weather station ranged from 18 to 59 cm (mean 36 cm) over the period 1997–2010).

EXPERIMENTAL DESIGN

This experiment compared cumulative CO₂ effluxes among dry heath, tall birch understory, birch hummock, and wet sedge vegetation types over the cold season of 2006/2007. In addition, CO₂ effluxes from snow-fenced birch hummock plots that had previously been measured over the cold season of 2004/2005 (Nobrega and Grogan, 2007) were determined using the same measurement protocol (see below). These snow fences (1.2 m tall, 15 m long, and 30–60 m apart; *n* = 5) typically increase peak snow depth from ~0.3 to ~1 m and extend spring snow cover duration by ~10 days (Nobrega and Grogan, 2007; Buckeridge and Grogan, 2010). Properties of the vegetation types and their associated soils have been described elsewhere (Nobrega and Grogan, 2007, 2008; Buckeridge et al., 2010; Chu and Grogan, 2010). Briefly, dry heath vegetation is dominated by mosses and lichens with some mat-forming evergreen shrubs [*Rhododendron subarctica* (Harmaja) {formerly *Ledum decumbens* (Ait.)}, *Vaccinium vitis-idaea* (L.), *Empetrum nigrum* (L.), *Loiseleuria procumbens* (L.), and *Arctostaphylos alpina* (L.)], and occasional deciduous dwarf shrubs [*Betula glandulosa* (Michx.) and *Vaccinium uliginosum* (L.)] and graminoids (mostly *Carex* spp.). Mesic birch hummock ecosystems are characterized by hummocks 10–30 cm high and deciduous dwarf birch (*B. glandulosa*) shrubs (10–40 cm tall, and ~2 clusters of

ramets m^{-2}). The vegetation is dominated by mosses, lichens, and dwarf ericaceous shrubs [*V. vitis-idaea*, *V. uliginosum*, *L. decumbens*, *Andromeda polifolia* (L.)], with occasional sedges and herbs (*Rubus chamaemorus* L.). The tall birch ecosystem contains a dense cover of tall (50–150 cm high) *B. glandulosa* shrubs, with an understory of similar species composition as the birch hummock vegetation (above). Wet sedge vegetation consists of *Carex* and *Eriophorum* spp. above a thick layer of mainly *Sphagnum* spp. and algae, and occurs in low-lying flat areas that are generally inundated with surface water for a substantial part of the growing season.

Flux measurement sampling areas were randomly selected within single large patches of dry heath and wet sedge vegetation ($n = 8$ and 7 , respectively). At the tall birch site, sampling areas ($n = 9$) that were not in obvious ungulate pathways between the birch shrubs were selected in order to measure CO_2 efflux from the understory vegetation (i.e. the size of the tall birch shrubs precluded them from being included in the sampling chambers). In the birch hummock vegetation, each flux chamber sampling area within the control and snow-fence plots was centered on a single mature dwarf birch shrub and its surrounding evergreen and moss vegetation ($n = 9$ sampling areas in total for each treatment, 1–2 per plot). As in the 2004/2005 study (Nobrega and Grogan, 2007), sampling areas in the snow-fenced plots were located ~ 1.5 m perpendicular to the south-facing side of the fences and at least 2 m in from the ends of the fences.

FLUX AND ENVIRONMENTAL MEASURES

Ecosystem respiration during the cold season was measured with the soda lime CO_2 adsorption technique (Edwards, 1982; Grogan, 1998; Keith and Wong, 2006) using a protocol very similar to our previous respiration study at this site (Nobrega and Grogan, 2007). Note that the soda lime technique estimates *cumulative production* of CO_2 from the enclosed vegetation and soil over the full cold season, including fall, as well as spring snowmelt. In the latter period in particular, substantial flushes of CO_2 that have built up over winter in the soil and within the snow can be rapidly vented to the atmosphere as the snow melts (Oechel et al., 1997; Elberling and Brandt, 2003; Morgner et al., 2010). Although it has several other methodological constraints (see below), the soda lime technique is in theory unaffected by this particular phenomenon since it is directly capturing the CO_2 produced from the soil and enclosed vegetation during the cold season. Subnivean CO_2 build-up beneath the developing snowpack is a consequence of higher rates of production relative to diffusion out through the snow. Assuming the ultimate goal is to measure the total CO_2 that is produced over the period from fall through to spring snowmelt, the soda lime method in theory circumvents this issue by capturing the CO_2 as it is produced.

Briefly, soda lime (Indicating type, 4–8 mesh, J.T. Baker, Phillipsburg, New Jersey) was used to estimate CO_2 released from an enclosed area (633 cm^2) of vegetation and underlying soil into the headspace (18.9 L) of a sample chamber (inverted 5 gallon bucket, EMCO, Yellowknife, Northwest Territories). The soda lime was first placed in weighed mason jars (1 L) and dried to constant mass in a large fan-assisted oven for 162 h at 80°C at a laboratory in Kingston, Ontario. Afterwards, the jars were closed tightly and weighed immediately to determine initial soda lime

mass ($\sim 370 \text{ g}$) prior to transport to the field site. Several days prior to beginning the cold season efflux measurements, a slot ($\sim 10 \text{ cm}$ deep) was cut into the soil around the circumference of each sampling area to facilitate insertion of the bucket chambers and ensure a good seal. At the beginning of each flux measurement, one of the mason jars containing soda lime was opened and balanced on a platform of wooden skewers ($\sim 10 \text{ cm}$ above the soil surface) close to the center of each sampling area. Water ($\sim 150 \text{ mL}$) was quickly added to increase the soda lime CO_2 adsorption efficiency at freezing temperatures (Grogan and Chapin, 1999), and then an inverted bucket chamber was placed over the sampling area and pressed into the soil slot to $\sim 10 \text{ cm}$ depth so that all of, or for the wet sedge a major part of, the organic horizon—which contains most of the root biomass (Churchland et al., 2010)—was enclosed within the chamber. CO_2 adsorption by the soda lime in the headspace enhances the CO_2 diffusion gradient, potentially drawing CO_2 from a larger soil volume than that contained by the cylindrical volume directly beneath the chamber sampling area (Grogan and Chapin, 1999), and resulting in an overestimate of efflux per unit ground area. We minimized this artifact by inserting the chamber lip down into the soil to 10 cm depth, thereby isolating the sampled soil volume to that depth at least. Blanks ($n = 9$ in total) to correct for any mass changes associated with storage, transport, field exposure, and in particular CO_2 adsorption during final oven drying (Grogan, 1998; Keith and Wong, 2006) were placed in all sites. Each mason jar sample assigned to the blank treatment was placed in a staked upright chamber bucket (24.6 L) which was then quickly sealed with an airtight lid and left *in situ* over the cold season.

On the first day in which the soil at the sites had thawed sufficiently to lift most of the buckets in the following spring (mid-June, details below), the mason jar soda lime samples were removed from the chambers and quickly sealed. In some cases, the chambers were still frozen in place, and had to be excavated with a mallet and chisel. Deciduous plant leaf-out had not yet begun at that time in either of the measurement years, and the ensuing data interpretation assumes that any photosynthesis by other plants was negligible. The effect of CO_2 adsorption by the soda lime on headspace concentrations was tested by drilling very small holes in the bucket wall and immediately taking syringe gas samples prior to chamber lifting. Syringe samples were analyzed within hours on a portable gas chromatograph (SRI 8610A, Wrennick Scientific Corporation, Ottawa, Ontario) fitted with a Porapak column (Alltech Canada, Guelph, Ontario) and a flame ionization detector. Mean headspace CO_2 concentrations in the birch hummock and tall birch chambers were 229 ppm ($n = 5$; SE = 13) and 563 ppm ($n = 4$; SE = 77), respectively, and 76 ppm ($n = 2$; SE = 7) in the blank chambers. These test results indicate that the soda lime was still very effective at drawing down headspace CO_2 concentrations in the birch hummock, and especially the blank chambers, even at the end of the study. However, the higher-than-ambient values in the tall birch understory chambers indicate that the soda lime's CO_2 adsorption capacity had been exceeded, and therefore that the flux values obtained underestimate the total cold season CO_2 efflux from that ecosystem.

The soda lime chambers were in place from 28 August 2006 until 18 June 2007 (294 days) in all plots (vegetation types and

birch hummock snow-fence treatment), and for 278 and 284 days (control and snow-fence birch hummock plots, respectively) over the period from 12 September–25 June in the winter 2004/2005 study (Nobrega and Grogan, 2007). After transport back to Kingston, the soda lime samples were oven-dried to constant mass (at 100 °C for 240 h followed by 24 h at 75 °C). The mass of CO₂ released during the cold season period was calculated as the increase in soda lime mass corrected ($\times 1.69$) for water loss associated with adsorption (Grogan, 1998). Afterwards, the cold season efflux values were corrected for mean CO₂ adsorption in the blanks ($n = 7$, because two were knocked over by wind or animals), and then divided by the exposed soil surface area to calculate flux per m². Mean CO₂ adsorption in the blanks in the current study were 0.03 g CO₂ (as compared to an overall mean of 16.1 g CO₂ for all samples), whereas it was 100 times higher in the 2004/2005 study (3.0 g CO₂ as compared to an overall mean of 11.1 g CO₂ for all samples from vegetated plots) (Nobrega and Grogan, 2007). Since the soda lime samples were dried at 100 °C in the current study (to comply with the latest soda lime measurement protocol (Keith and Wong, 2006) as compared to 80 °C in the previous study, I specifically tested the effect of this higher drying temperature on CO₂ adsorption during the oven drying stage. Fresh soda lime samples (~40 g) that had been moistened (20 mL) and exposed for 20 h in the lab gained $\sim 2\times$ more mass at the lower oven-drying temperature (corresponding to ~ 1.7 g mass increase for 400 g of soda lime if the proportional gain is constant). Finally, according to the ideal gas law, the minimum soda lime mass gain for the blanks should be the amount of CO₂ contained in the chamber volume (~ 0.018 g), which is very close to the 2006/2007 mean blank value. Together, these test and computation results support Keith and Wong's 2006 protocol, by strongly suggesting that most CO₂ adsorption by blanks occurs during the final oven-drying phase, and that this effect can be greatly reduced by rapid drying at high temperature (100 °C). Ultimately, this approach to estimating field respiration rates assumes that the drying rates for blank and exposed samples are similar. Note that the differences in soda lime blank correction values between the 2006/2007 and 2004/2005 studies should not affect our capacity to make inter-annual comparisons of CO₂ fluxes because the blank and exposed soda lime samples for each year were dried at the same oven temperature.

Soil temperatures at ~ 5 cm depth into the organic layer were measured throughout the cold season of 2006/2007 every 6 h in the tall birch, and once per day in the birch hummock control and snow-fence plots ($n = 4$, 4 and 3 probes, respectively, for each ecosystem) using copper-constantan thermocouples (T type, OMEGA, Stamford, Connecticut) and dataloggers (CR10 and CR10X, Campbell Scientific, Logan, Utah). Temperatures were measured adjacent to, but not within, the chambers so there was no test for biologically significant soil temperature differences as a result of the chambers being exposed to the atmosphere for periods while the surrounding vegetation was snow covered, nor for the magnitude of this effect for the different vegetation types. In theory, this effect would tend to underestimate the fluxes, especially for those vegetation types with generally shallow snow cover (dry heath and wet sedge). However, a previous test of this phenomenon (Grogan and Chapin, 1999) indicated that the decline in diel soil

temperature associated with this effect ranged from 0 to 0.7 °C, and that there were subsequent deep snow periods over winter when the chambers actually enhanced soil temperature relative to the adjacent, perhaps because of the insulating properties of the trapped air within the headspace. The 2004/2005 diel mean soil temperatures in the same birch hummock control plots were based on data at ~ 2 and ~ 6 cm depth ($n = 1$ probe each) (Nobrega and Grogan, 2007). Diel mean soil temperatures (5 cm depth) in nearby dry heath and wet sedge sites (1 probe per site) were provided by Bob Reid (Department of Indian and Northern Affairs, Canada, unpublished data) and Dr. Elyn Humphreys, respectively. Similar patterns of soil temperature differences among these vegetation types have been observed with multiple replicate probes in subsequent years. Data for air temperature and snow depth (SR50A ultrasonic acoustic distance sensor, Campbell Scientific, Logan, Utah) over 2004/2005 and 2006/2007 were provided by Bob Reid.

STATISTICAL ANALYSES

The influence of vegetation type on total cold season respiration was determined using a one-way analysis of variance (ANOVA). The impacts of the snow-fence treatment and year on total cold season respiration from the birch hummock ecosystem were tested using a two-way factorial ANOVA. All CO₂ efflux data were log transformed to pass Shapiro-Wilks normality tests prior to these analyses (JMP 8.0, SAS Institute, Cary, North Carolina).

Results

Total respiration over the cold season of 2006/2007 differed strongly among the vegetation types ($F_{3,26} = 38.39$, $P < 0.0001$; Fig. 1). CO₂ effluxes were lowest in the dry heath and wet sedge sites, $\sim 2\times$ higher in the birch hummock, and $\sim 4\times$ higher in the tall birch understory ecosystem. This pattern of variation among ecosystems was partly matched by differences in soil diel mean temperatures since the tall birch soil was clearly substantially

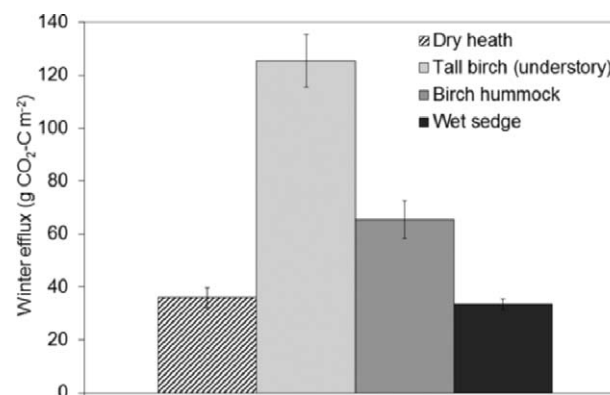


FIGURE 1. Mean CO₂ efflux over the 2006/2007 cold season in the four principal vegetation types near Daring Lake, Northwest Territories (NWT), Canada ($n = 7$ –9 plots, bars = standard errors). Note that the respiration measurement from the tall birch ecosystem included the shoots of understory plants and all underlying roots and soil, but not the shoots of the birch shrubs that dominate the vegetation of this ecosystem.

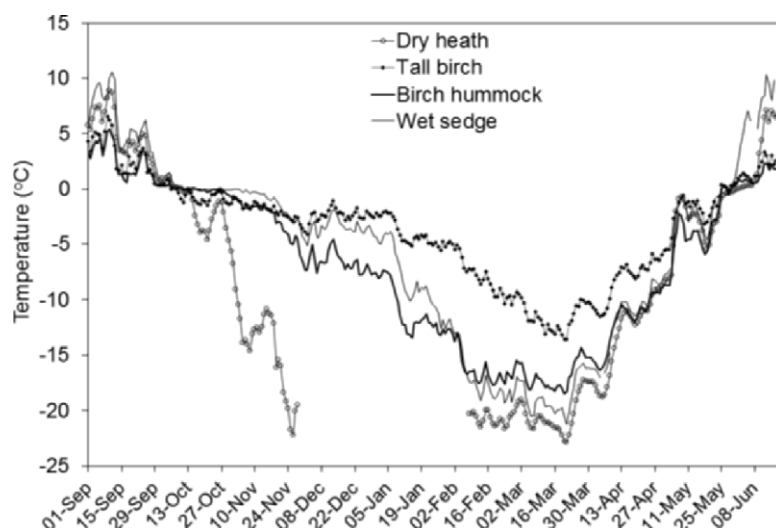


FIGURE 2. Diel mean soil temperatures at 5 cm depth during the 2006/2007 cold season in each of the four principal vegetation types near Daring Lake, NWT ($n = 4$ probes for the tall birch and birch hummock sites; $n = 1$ for the dry heath and wet sedge sites).

warmer than any of the other sites from December through April (Fig. 2). However, total respiration was lower in the wet sedge than in the birch hummock ecosystem even though soil temperatures in the former were warmer for much of the fall, and were similar for the remainder of the cold season (Fig. 2). Furthermore, CO_2 effluxes from the wet sedge and dry heath ecosystems were similar even though soil temperatures in the latter plummeted early in the fall, and were clearly substantially lower than in all of the other ecosystems throughout most of the remaining winter.

Total cold season respiration in the birch hummock vegetation was $\sim 2 \times$ higher in 2006/2007 compared to 2004/2005, while the deepened snow treatment significantly enhanced cold season respiration in 2004/2005 (by $\sim 50\%$), but had no effect in 2006/2007 (Year: $F_{1,31} = 32.11$, $P < 0.0001$, Snow fence: $F_{1,31} = 4.17$, $P < 0.05$; Year \times Snow fence: $F_{1,31} = 38.39$, $P < 0.06$; Fig. 3). Again, this pattern of CO_2 effluxes was at least partly matched by interannual differences in diel mean soil temperatures (Fig. 4). During 2006/2007, the control (unfenced) plot soils were generally $4\text{--}10^\circ\text{C}$ warmer from mid-September to mid-November, from early December to mid-February, and in May, than in the same periods in 2004/2005 (Fig. 4). However, in contrast, the snow fences did not enhance respiration in 2006/2007 even though the

soils there were substantially warmer than in the control plots (Figs. 3, 4). No snow-fence soil temperature data are available for 2004/2005 because of a datalogger malfunction.

Discussion

LANDSCAPE-SCALE VARIATION IN ECOSYSTEM RESPIRATION DURING THE COLD SEASON

Total cold season CO_2 efflux differed by at least a factor of four among the four principal vegetation types of low arctic tundra (Fig. 1), supporting Hypothesis 1. By contrast, an earlier study by this author reported no significant differences in wintertime soil CO_2 efflux from several Alaskan low arctic vegetation types (Grogan and Chapin, 1999), but the plots in that study had previously been clipped to remove aboveground plant tissues and diminish live root influences. Together, these results along with those of more recent studies (Grogan et al., 2001; Grogan and Jonasson, 2005; Nobrega and Grogan, 2007) are all consistent in suggesting that it is very likely that plants (both shoots and roots) are responsible for a significant proportion of total winter CO_2 production in many ecosystems, and that ecosystem differences in winter respiration are largely driven by variation in respiration of recently fixed plant carbon rather than respiration of bulk soil carbon.

The largest CO_2 efflux was from the tall birch site where the chambers measured respiration from the soil, all roots, and understory shoot vegetation. Since I have concluded above that plants are a significant component of winter respiration, total ecosystem CO_2 efflux at the tall birch site would undoubtedly have been even larger if our flux measurement chambers had been big enough to contain the shoots of the dominant birch shrubs. Furthermore, the headspace CO_2 concentrations in the tall birch chambers at the end of the study were $\sim 50\%$ higher than ambient (see Methods), indicating that the soda lime had become CO_2 saturated. Since neither of these constraints apply to our measurements in the other ecosystems, total cold season respiration from the complete tall birch ecosystem was underestimated in absolute magnitude, and relative to the others, and therefore undoubtedly differed by more than a factor of four among the vegetation types in this landscape.

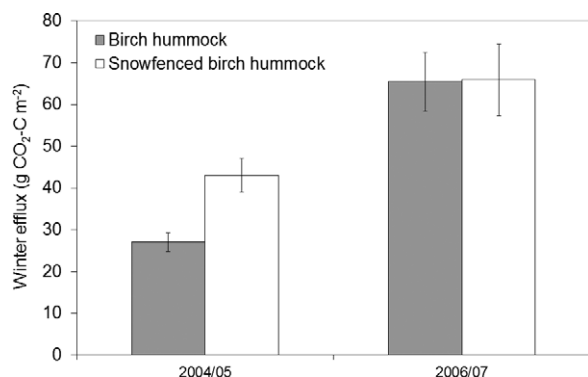


FIGURE 3. Mean CO_2 efflux during the cold seasons of 2004/2005 and 2006/2007 in control and snow-fenced birch hummock plots near Daring Lake, NWT ($n = 9\text{--}10$ plots, bars = standard errors).

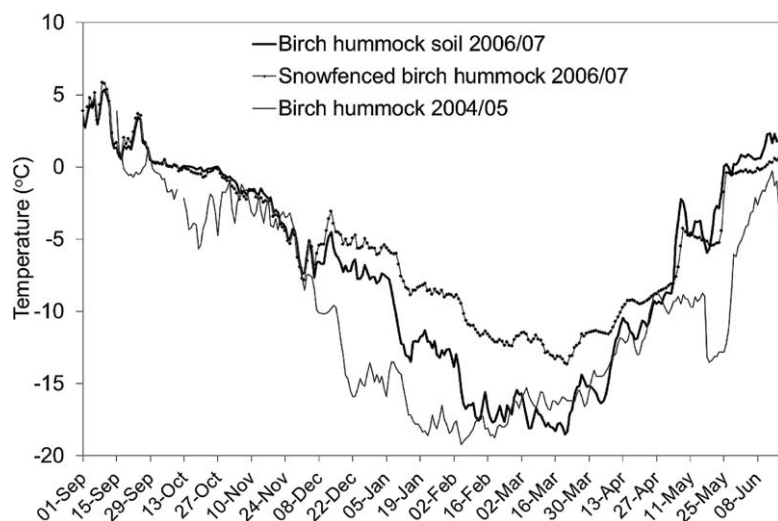


FIGURE 4. Diel mean soil temperatures at ~5 cm depth in control and snow-fenced birch hummock sites during the 2006/2007 cold season ($n = 4$ and 3 probes, respectively) and in the same control sites during the corresponding period in 2004/2005 ($n = 2$ probes).

The large CO_2 efflux from the tall birch site was at least in part due to its relatively deep snow (Table 1) and tall vegetation canopy cover that together insulated the soil and understory vegetation from severe air temperatures. For example, the tall birch soils cooled very slowly in the fall/winter and remained above -5°C until the beginning of February (Fig. 2) even though mean air temperatures were already below -20°C two months earlier (Fig. 5). In addition, this ecosystem had the largest plant biomass (Table 1), and although shoots of the dominant birch shrubs were not included within the flux chambers, their abundant belowground stems and roots (Vankoughnett, 2009) must surely have contributed substantially to our measures of cold season respiration. Finally, this ecosystem has large senesced leaf litter inputs (~ 10 times larger than birch hummock tundra—Grogan, unpublished data) that help to insulate the soil as well as being an important substrate for microbial respiration (Buckeridge et al., 2010).

Total cold season respiration for the birch hummock ecosystem was about half as large as from the tall birch understory, but

twice as large as from the dry heath and wet sedge ecosystems (Fig. 1). Again, relatively deep snow, warmer soils, and larger plant biomass are likely to be the primary factors contributing to the high effluxes in the birch hummock compared to the latter two ecosystems. Finally, differences in water content were probably an important factor in explaining the similar magnitudes of CO_2 efflux between the wettest and driest sites. Both the wet sedge and the dry heath vegetation types tended to have low snow accumulation (Table 1), resulting in relatively cool vegetation and potentially very cold soils. However, the wet sedge ecosystem is inundated with water for most of the growing season (Table 1), and consequently its soil has a high specific heat capacity which, coupled with the very high latent heat of freezing associated with the water-ice phase transition, would have resulted in very slow rates of soil cooling in the fall (Fig. 2). Although plant biomass is particularly low in this ecosystem (Table 1), the relatively warm fall soil temperatures may have promoted microbial decomposition of its sedge litter inputs as well as older plant materials in its relatively deep

TABLE 1

Plant and soil characteristics in each of the major vegetation types near Daring Lake, Northwest Territories, Canada. Data were derived from two separate previous studies (Vankoughnett, 2009) (Tall birch and Birch hummock) and (Nobrega and Grogan, 2008) (Dry heath and Wet sedge).

	Dry heath	Tall birch	Birch hummock	Wet sedge
Snow depth at seasonal peak ^a (cm)	17	56	37	22
Vascular plant biomass ^b (g m^{-2})	564	2974	1038	175
Non-vascular plant biomass (g m^{-2})	997	220	369	258
Total plant biomass (g m^{-2})	1561	3194	1408	433
Soil organic layer depth (cm)	5	6	7	~ 45
Active layer depth (cm)	84	61	52	53
Soil organic layer bulk density (g cm^{-3})	0.29	0.29	0.17	0.09
Summer soil moisture range ^d (% volumetric water content)	20–34	17–25	26–33	85–95

^aMean snow depths ($n = 14$ –88) at the flux measurement sites on 12–13 May 2009. Similar values were recorded for the birch hummock and tall birch sites in the late winters of 2007 and 2008 (Vankoughnett, 2009).

^bVascular biomass includes above- plus belowground plant components.

^cActive layer depths ($n = 15$) were measured in late August (Tall birch) and mid-September.

^dSoil moisture data for tall birch and birch hummock sites are for the top 5 cm of soil during summer 2008 (Vankoughnett, 2009), and for the dry heath and wet sedge sites are for the top 10 cm of soil during the summer of 2004 (Nobrega and Grogan, 2008). Total summer rainfall was almost identical (~ 120 mm) in both years (Bob Reid, Department of Indian and Northern Affairs, Canada).

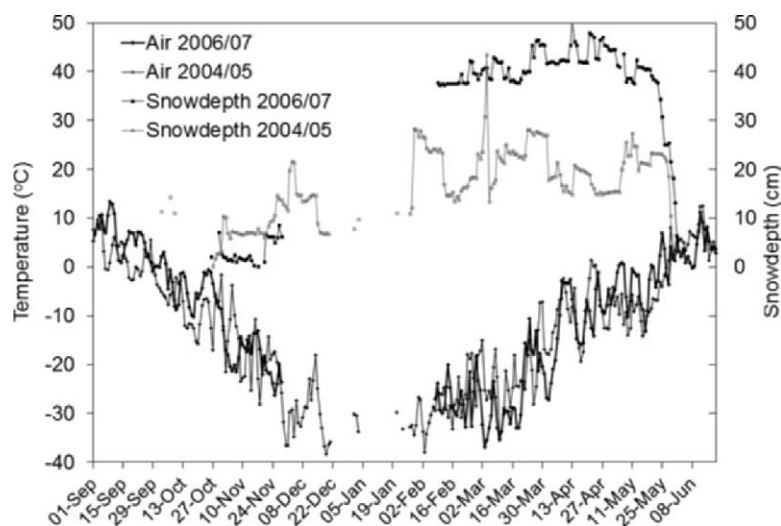


FIGURE 5. Diel mean air temperatures and snow depths in dry heath vegetation at the Daring Lake weather station during the cold seasons of 2004/2005 and 2006/2007 (data courtesy of Bob Reid, Department of Indian and Northern Affairs, Canada).

organic layer. By contrast, the similar total cold season efflux from the dry heath site may be the consequence of a much larger plant biomass, but particularly early and rapid cooling to severe temperatures in the well-drained soils of this ecosystem (Fig. 3). I conclude that the differences in cold season CO_2 efflux among low arctic ecosystems demonstrated here cannot be attributed to differences in soil (and subsurface snow around the shoot vegetation) temperatures alone, but rather are likely the result of its interactions with snow depth, canopy cover, and soil moisture, as well as differences in plant biomass and litter production.

THE INFLUENCE OF SNOW DEPTH ON COLD SEASON CO_2 EFFLUX

Total cold season respiration correlated with peak snow depth for the four vegetation types (Table 1, Fig. 1), suggesting that variation in snow accumulation across the landscape may be a primary determinant of CO_2 efflux. However, peak snow depth in the snow fences was typically 1 m—almost twice as high as in the tall birch ecosystem (Table 1), and yet CO_2 efflux in the former was about half that of the latter (Fig. 1). Furthermore, although the snow fences increased peak snow depth to levels $\sim 3\times$ ambient, this treatment did not significantly increase cold season respiration from the birch hummock ecosystem in 2006/2007 (Fig. 3). Even in 2004/2005, the snow fence treatment only enhanced cold season CO_2 efflux by ~ 0.5 . By contrast, the variation in efflux among ecosystems was at least a factor of four (Fig. 1). These results indicate that landscape-scale variation in cold season CO_2 efflux was influenced more by differences in microclimatic and biogeochemical characteristics associated with the vegetation types than by snow depth, supporting Hypothesis 2. Note that this conclusion applies to tundra vegetation types where snow accumulation is low to moderate (<1 m) and therefore winter soil temperatures are generally well below freezing. An earlier study based on just two vegetation types reached a similar conclusion (Grogan and Jonasson, 2006). However, where snow can accumulate above the ~ 1 m threshold, soil (and subsurface snow around the shoot vegetation) temperatures were the primary determinant of efflux, and variation in efflux between the two vegetation types tested was negligible (Grogan and Jonasson, 2006). These latter results suggest that where snow accumulation is substantial (i.e. >1 m), landscape-

scale variation in cold season respiration is determined more by variation in snow depth than by variation in vegetation type (Grogan and Jonasson, 2006).

INTERANNUAL VARIATION IN COLD SEASON RESPIRATION FROM BIRCH HUMMOCK TUNDRA

Total cold season CO_2 efflux from the birch hummock tundra ecosystem was almost twice as high in 2006/2007 than in 2004/2005 (Fig. 3). The Daring Lake weather station data indicate that air temperatures were much colder in 2004/2005 than in 2006/2007 during three separate periods: mid-fall (mid-September to end of October), the deep cold phase (mid- to late November, after which the sensors malfunctioned), and late winter/early spring (end of April to mid-June) (Fig. 5). For example, the overall mean air temperature from 16 September to 4 November was -6.1°C in 2004/2005 and -2.5°C in 2006/2007 (Fig. 5), resulting in corresponding mean soil temperatures (5 cm depth) in the birch hummock site of -1.8 and $+0.4^\circ\text{C}$, respectively (Fig. 4). Mean soil temperatures from 3 December to 12 February were -15.0°C in 2004/2005 and -10.1°C in 2006/2007 (Fig. 4). Finally, the overall mean air temperature from 29 April to 17 June was -2.4°C in 2004/2005 and -0.4°C in 2006/2007, resulting in corresponding mean soil temperatures of -7.5 and -2.2°C , respectively. Together, these data clearly demonstrate that air and soil temperatures were substantially cooler over several different phases during the cold season of 2004/2005 as compared to 2006/2007. By implication, temperatures in the subsurface snow surrounding the plant shoots must also have followed a similar pattern. Since soil, plant, and whole ecosystem respiration are exponentially related to temperature (Lloyd and Taylor, 1994; Grogan and Jonasson, 2005; Davidson and Janssens, 2006), I conclude that the much larger CO_2 efflux in 2006/2007 is primarily the result of the relatively warm mid-fall and late winter/spring phases in that year, supporting Hypothesis 3.

INTERANNUAL VARIATION IN THE INFLUENCE OF DEEPEMED SNOW ON COLD SEASON RESPIRATION FROM BIRCH HUMMOCK TUNDRA

The snow-fence results were surprising in that the treatment enhanced cold season respiration in 2004/2005—consistent with

all other comparable arctic tundra studies of which I am aware (Walker et al., 1999; Schimel et al., 2004; Larsen et al., 2007a; Morgner et al., 2010) —but had no effect in 2006/2007 (Fig. 3). This novel result should be very robust in the sense that it is based on a *relative* comparison (rather than absolute accuracy) using the same rigorous application of a measurement technique that was applied to the same plots in both years. The absence of a snow-fence stimulatory effect on cold season respiration in the latter year may be attributed to at least two potentially interacting factors: temperature (air, snow, and soil) and snow (timing and depth).

First, the snow-fence treatment restricted soil temperature declines only during the deep cold phase (mid-December to end of April) of 2006/2007, when soils were generally well below -5°C (Fig. 4). Since respiration rates decrease at exponential or even greater rates as temperature declines over sub-zero temperatures (Mikan et al., 2002), the contribution of the deep cold phase to total cold season CO_2 efflux may be small compared to the ‘shoulder’ phases, resulting in a negligible snow-fence effect in 2006/2007. Unfortunately, the snow-fence soil temperatures for 2004/2005 are not available (because the datalogger failed), but the consistent pattern of warmer and more stable temperature profiles in these snow fences in all subsequent years (Buckeridge and Grogan, 2008; Vankoughnett, 2009) strongly suggests a similar effect in that year. Nevertheless, soil temperatures in the control plots were obviously much cooler during both fall and late winter shoulder phases of 2004/2005 than in 2006/2007 (Fig. 4), implying a greater *potential* for snow-fence effects in the former year.

Second, significant snow accumulation in the exposed heath tundra vegetation directly beneath the Daring Lake weather station began in late November of 2006/2007—a month later than in 2004/2005 (Fig. 5)—restricting the likelihood of a snow-fence effect on respiration during the fall phase of 2006/2007 as compared to the earlier year. The post-fall patterns of snow accumulation in the control and snow-fence plots and their effects in ameliorating air temperatures in the two years are more complex. Although the weather station data indicate substantially deeper snow from early February onwards in 2006/2007 than in 2004/2005 (Fig. 5), our on-site measures in late winter indicated very similar mean snow depths in both years in the birch hummock (28 and 30 cm on 17 April and 18 May 2005, and 29 and 31 cm on 8 April and 10 May 2007) and snow-fenced birch hummock plots (100 cm on both 17 April and 18 May 2005, and 87 and 101 cm on 8 April and 10 May 2007). Clearly, temporal and spatial heterogeneities in snow accumulation due to re-dispersal across the landscape necessitate caution in interpreting the weather station snow data in the context of the snow-fence treatment on the birch hummock plots (0.5–1 km away). Nevertheless, since soil temperature is almost entirely insulated from air temperature at snow depths exceeding 0.8–1 m (Taras et al., 2002; Grogan and Jonasson, 2006), and these levels were reached in the snow-fenced plots in late winter in *both* years, but the control plot soils were $>5^{\circ}\text{C}$ cooler in 2004/2005 than in 2006/2007 from late April onwards (Fig. 4), the magnitude of any deepened snow effect on respiration during the late winter shoulder phase is likely to have been greater in the former year. In summary, the results support Hypothesis 4 by demonstrating that the effect of increased snow depth on cold season CO_2 efflux varies significantly between years, and suggest that snow-fence effects are negligible

in years where they only restrict soil temperature declines during the mid-winter deep cold phase.

THE SIGNIFICANCE OF VARIATION IN COLD SEASON RESPIRATION AMONG VEGETATION TYPES ON ANNUAL C BALANCE

Our estimates of total cold season respiration ($34\text{--}126\text{ g CO}_2\text{-C m}^{-2}$) fall well within the range of many previous studies in analogous low arctic and alpine tundra ecosystems (Sommerfeld et al., 1993; Brooks et al., 1997; Oechel et al., 1997; Mast et al., 1998; Fahnestock et al., 1999; Grogan and Jonasson, 2005; Schimel et al., 2006; Sullivan et al., 2008). Strong differences in late winter instantaneous efflux rates among a wide range of northern Alaskan tundra vegetation types have previously been reported (Fahnestock et al., 1998). However, the magnitude of the effluxes measured using the snowpack CO_2 diffusion technique were extremely low ($1\text{--}12\text{ g CO}_2\text{-C m}^{-2}$, assuming a 235 day winter) compared to most other studies included in a recent review (Bjorkman et al., 2010). Furthermore, differences among vegetation types were not consistent across the three measurement days, and the study’s time span confines the conclusions to the mid–late winter period, when respiration might be expected to be relatively low because of generally severe soil temperatures compared to fall and early winter. Unfortunately, the severe technical challenges of gathering continuous eddy covariance measurements through the harsh arctic winter have not yet been overcome, although subarctic locations with commercial electricity supply have been successfully measured (Aurela et al., 2002). Nevertheless, a very recent eddy covariance study from northern Alaska based on 85% complete data over 2 years reported total cold season respiration effluxes of $98\text{--}113\text{ g CO}_2\text{-C m}^{-2}$ for dry heath tundra and $132\text{--}137\text{ g CO}_2\text{-C m}^{-2}$ for wet sedge (Euskirchen et al., 2012). It is interesting that these two vegetation types had similar effluxes—just as reported here—but the absolute magnitudes of release were $\sim 3\times$ larger. As the technical challenges associated with running eddy covariance towers through winter are overcome during the next decade and multiple sites are measured over multiple years, we can anticipate better accuracy in the quantification of cold season effluxes and a much improved understanding of the temporal dynamics of instantaneous CO_2 release rates from the snow surface through the cold season.

Of the other techniques for measuring ecosystem respiration during winter (e.g. soda lime, chamber infrared gas analysis, and diffusion gradient approach), each has its limitations (Bjorkman et al., 2010) but at least soda lime has one distinct advantage in that it should incorporate *all* CO_2 released over the full cold season, thereby including the short, often large flushes that can occur as accumulated CO_2 beneath the snow is released during spring melt (Elberling and Brandt, 2003; Morgner et al., 2010). In contrast to its early use in this context (e.g. Grogan and Chapin, 1999), the soda lime technique has now been substantially improved by the development of a rigorous protocol (Keith and Wong, 2006), but it still undoubtedly has certain inherent methodological constraints (Nobrega and Grogan, 2007), some of which I have specifically tried to address in its use here (see Methods). Thus, while its use to test hypotheses that depend on *relative* comparisons among vegetation types or years (i.e. the focus of this paper, and points 1 and 2 below) should not be affected by these constraints, the absolute accuracy of the fluxes should be treated with caution.

Our data can be used to make several points relating to annual net C balances of these ecosystems. First, comparison of the cold season effluxes from dry heath, birch hummock, and wet sedge vegetation types (36, 65, and 34 g CO₂-C m⁻², respectively) with our previous infrared gas analysis static chamber estimates of growing season net C gain for 2004 (−1, 37, and 88 g CO₂-C m⁻², respectively) (Nobrega and Grogan, 2008) indicates very strong differences in the proportion of summer net C gains relative to cold season losses among the vegetation types. In the latter study, we concluded that growing season net C gain was largest in the wet sedge ecosystem because the inundated conditions there resulted in the lowest rates of soil (and ecosystem) respiration. The data here indicate that cold season respiration rates from wet sedge ecosystems are also relatively low. I conclude that, at the landscape scale, soil C accumulation is greatest in wet sedge ecosystems across the low Arctic because both summer and cold season decomposition processes are relatively restricted. At the regional scale, this conclusion is consistent with the fact that sedge-dominated wetlands contain the largest soil organic C contents (to 1 m depth) among all arctic vegetation types (Tarnocai et al., 2009). Second, growing season eddy covariance measurements of net ecosystem CO₂ exchange in a footprint dominated by heath and birch hummock tundra at Daring Lake varied by a factor of 2 (ranging from 32 to 61 g CO₂-C m⁻²) over the years 2004–2006 (Lafleur and Humphreys, 2008). Our data indicate that interannual variability in cold season net CO₂ fluxes may be just as large. Third, the data presented here—even if the method used overestimated efflux by a factor of two—suggest that cold season respiratory C losses can significantly offset growing season C gains, resulting in strong effects on annual C balance, and even net losses in some years.

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