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Snow distribution, soil temperature and late winter CO_2 efflux from soils near the Arctic treeline in northwest Alaska

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Abstract The Arctic treeline is advancing in many areas and changes in carbon (C) cycling are anticipated. Differences in CO_2 exchange between adjacent forest and tundra are not well known and contrasting conclusions have been drawn about the effects of forest advance on ecosystem C stocks. Measurements of CO_2 exchange in tundra and adjacent forest showed the forest was a greater C sink during the growing season in northern Canada. There is, however, reason to expect that forests lose more C than tundra during the wintertime, as forests may accumulate and retain more snow. Deeper snow insulates the soil and warmer soils should lead to greater rates of belowground respiration and CO_2 efflux. In this study, I tested the hypotheses that forests maintain a deeper snowpack, have warmer soils and lose more C during winter than adjacent tundra near the Arctic treeline in northwest Alaska. Measurements of snow depth, soil temperature and CO_2 efflux were made at five forest and two treeline sites in late winter of three consecutive years. Snow depth and soil temperature were greater in forest than treeline sites, particularly in years with higher snowfall. There was a close exponential correlation between soil temperature and CO_2 efflux across sites and years. The temperature-efflux model was driven using hourly soil temperatures from all the sites to provide a first approximation of the difference in winter C loss between treeline and forest sites. Results showed that greater wintertime C loss from forests could offset greater summertime C gain.

Keywords Arctic tundra · Boreal forest · Carbon cycle · Snow depth · Soil respiration · Soil temperature

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Introduction

Arctic and boreal ecosystems are of fundamental importance to the global climate system, as they cover vast areas of the Northern Hemisphere, hold large stocks of soil carbon (C) and reflect a substantial proportion of incident solar radiation back to space during the snow-covered season (e.g., Chapin et al. 2000a). Recent work has produced a wealth of evidence that belowground respiration continues beneath the snowpack for much of the winter in arctic tundra (Kelly et al. 1968; Zimov et al. 1993, 1996; Oechel et al. 1997; Fahnestock et al. 1998, 1999; Jones et al. 1999a; Grogan and Chapin 1999; Sullivan et al. 2008) and boreal forests (Winston et al. 1997; Wang et al. 2002; Vogel et al. 2005; Ilvesniemi et al. 2005; Kim et al. 2007;

Sullivan et al. 2008). Low rates of CO_2 efflux are thought to be sustained throughout much of the arctic and boreal winter months because the snowpack insulates the soil from extremely cold air temperatures. While winter air temperatures in arctic and boreal ecosystems frequently fall below −40°C, near surface soil temperatures lower than −20°C are rarely observed and annual minimum soil temperatures between −5 and −10°C are common (e.g., Olsson et al. 2003). Laboratory and field observational studies have generally found that belowground respiration declines to undetectable rates at soil temperatures between −16 and −10°C (Panikov and Dedysh 2000; Mikan et al. 2002; Schimel et al. 2006; Sullivan et al. 2008), although there is some evidence that respiration may continue at temperatures as low as −39°C (Panikov et al. 2006).

Recent warming in the Arctic has been associated with treeline advance in some areas (Lavoie and Payette 1996; MacDonald et al. 1998, 2008; Suarez et al. 1999; Lloyd et al. 2003). Changes in Arctic treeline positions will likely have important implications for ecosystem C stocks in high latitude landscapes, though few studies have examined CO_2 exchange at the Arctic treeline. Eddy covariance measurements have shown that a treeline forest assimilates more C during the growing season than an adjacent fen at the Arctic treeline near Churchill, Manitoba (LaFleur et al. 2001). To my knowledge, measurements of CO_2 exchange have not been made during the snow-covered season at the Arctic treeline. Given the importance of winter CO_2 efflux to the annual C budget of arctic ecosystems (Fahnestock et al. 1999), it remains unclear if treeline forests have a more positive C balance than adjacent tundra when the entire year is considered.

There is good reason to expect a difference in winter CO_2 efflux between the treeline forest and adjacent tundra. Sturm et al. (2001, 2005) have developed a conceptual model that describes interactions between tall shrubs and snow accumulation in arctic tundra. Briefly, snow depth and distribution in arctic tundra is determined as much by wind, as by spatial variation in winter precipitation. Shrub stems that extend above the snow surface behave like snowfences, in the sense that they reduce wind speeds and lead to both leeward snow deposition and reduced sublimation. As a result, large snow drifts are often found on the leeward side of tall shrubs. Not only is there more snow on the leeward side of tall shrubs, the stratigraphy of the snow differs strongly from that away from the shrubs. The presence of shrub stems promotes development of large faceted crystals, which develop under strong temperature gradients. Large faceted crystals are much better insulators than wind-blown snow which has not undergone metamorphosis. The combined effects of deeper snow and a better insulating snowpack lead to warmer soils in the area downwind of large shrubs. Warmer soils, in turn, promote greater rates of microbial respiration and greater rates of CO_2 efflux. The treeline forest should interact with snow in a manner similar to that of large shrubs in arctic tundra. When the treeline is downwind of the tundra, abrupt reductions in wind speed should lead to snow drifting near the forest limit (Greene et al. 1999; Hiemstra et al. 2002). Lower wind speeds at the snow surface in the forest should also reduce losses to sublimation. Lastly, the presence of tree stems should promote development of a snowpack that is a better insulator per unit thickness than the snow cover in adjacent tundra.

I set out to test the hypothesis that interactions between snow and the treeline forest lead to deeper snow, warmer soils and greater rates of late winter CO_2 efflux in the forest than in the adjacent tundra. The study was carried out near the Agashashok River in Noatak National Preserve, where recent work has shown advance of the white spruce (*Picea glauca*) treeline during the last 200 years (Suarez et al. 1999). Point measurements of CO_2 efflux were made at five forest and two treeline sites when soil temperatures were near their annual minimum in three consecutive winters. In the later two winters, measurements were made along transects from the treeline sites into the adjacent forests.

Methods

Site descriptions

Measurements were made at five forest and two treeline sites near the Agashashok River (67°29′ N, 162°12′ W, 100 m asl) in Noatak National Preserve, northwest Alaska (Fig. 1). Climate of the region is predominantly continental, with air temperatures frequently below −40°C in the winter and approaching

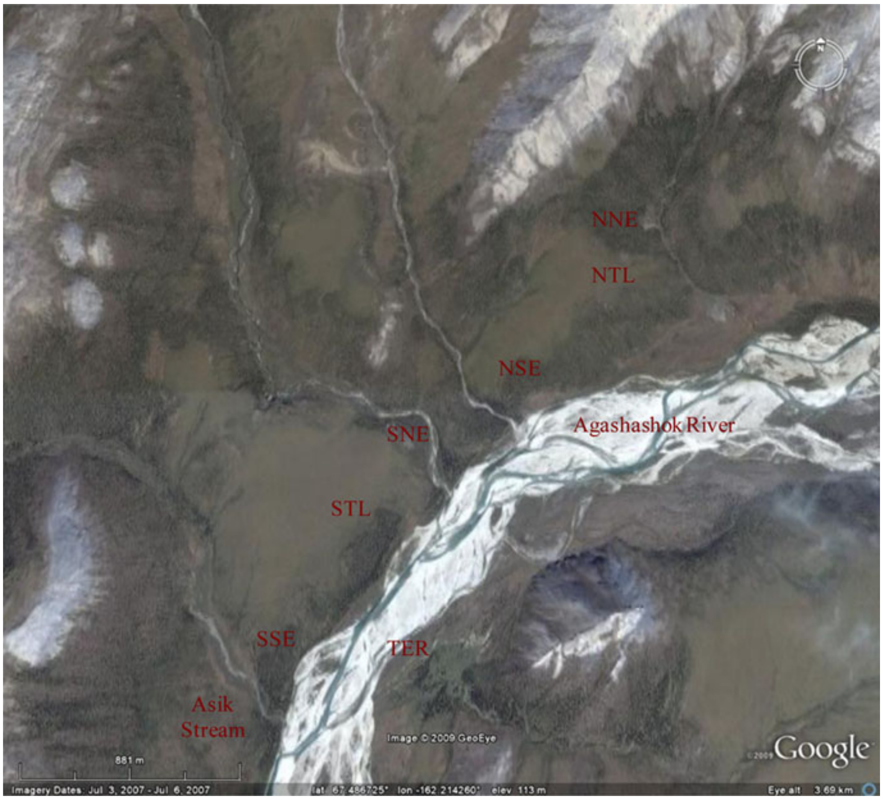

Fig. 1 Satellite image showing locations of the seven study sites in relation to the Agashashok River and the Asik Stream in Noatak National Preserve, northwest AK

30°C in mid-summer. Climate data collected at the mouth of the Asik watershed, within 3.0 km of the most distant study site, showed a close correlation with that of Bettles, AK (Stottlemyer 2001). The climate record for Bettles (1951–2007) shows an average annual air temperature of −5.4°C and average annual precipitation of 35.9 cm (Alaska Climate Research Center, Fairbanks, AK).

Six of the study sites were distributed across two knolls that rise to an elevation of approximately 150 m northwest of the Agashashok River. The seventh site, TER, is a low density white spruce stand on a riverside terrace southeast of the river. White spruce forests interface with tussock tundra at an elevation of approximately 125 m on the south knoll and 145 m on the north knoll. Forest sites were established on southeast and northeast aspects of both knolls, while treeline sites were identified on shallow (~5°) east-facing slopes. The treeline site on the south knoll has been the subject of previous research (Suarez et al. 1999). It is a low density white spruce stand that has advanced 80–100 m into the adjacent tundra during the last 200 years (Suarez et al. 1999). The site was named, Aggie, in the work of Suarez et al. (1999) and will be referred to as STL in the present study. The treeline site on the north knoll will be referred to as NTL. While much of the north knoll is dominated by tussock tundra, the site selected for investigation has slightly drier soils during the summer months and a greater abundance of Ericaceous shrubs. Forest sites on the northwest side of the river are named according to their knoll and their aspect. For instance, the forest site on the southeast aspect of the south knoll is referred to as SSE, while the forest site on the northeast aspect of the north knoll is referred to as NNE. The forest sites generally have larger trees and higher stand density than the treeline sites (Table 1). They have well-drained soils and three of the four forest sites on the northwest side of the river occur on moderate slopes (~20°). The one exception is NNE, which occurs on a shallow slope (~5°) above and below steeper adjacent slopes. Soils at the treeline sites are Ruptic-Histic Aquiturbels, while those in the forests on the northwest side of the river are Typic Historthels (Soil Survey Staff 1998). Soils at TER differ from those at the other

Table 1 White spruce stand structure and understory species composition at each of the seven study sites. Soil organic carbon (SOC) data are from the upper 15 cm of the soil profile

Site	Basal area (m^2/ha)	Stem density (#/ha)	Tree height (avg., m)	Tree diameter (avg., cm)	SOC (%)	SOC (kg/m^2)	Dominant understory species
SSE	68.6	2510	4.6	9.6	22.0 (2.5)	4.7 (0.4)	*Vaccinium uliginosum*, *Betula nana*, *Salix* spp., *Potentilla fruticosa*
SNE	24.9	4615	2.6	3.8	23.1 (4.1)	5.9 (0.5)	*Vaccinium uliginosum*, *Betula nana*, *Cassiope tetragona*, *Salix* spp.
NSE	34.1	2978	3.9	5.6	25.6 (0.7)	5.6 (0.3)	*Vaccinium uliginosum*, *Betula nana*, *Salix* spp., *Empetrum nigrum*
NNE	46.3	2867	4.0	6.6	24.0 (4.7)	6.4 (0.7)	*Salix* spp., *Equisetum arvense*, *Carex* spp., *Vaccinium uliginosum*
TER	10.9	1260	2.9	4.7	6.3 (0.4)	5.2 (0.3)	*Salix* spp., *Betula nana*, *Potentilla fruticosa*, *Dryas integrifolia*, *Shepherdia canadensis*
STL	2.6	1029	1.9	2.3	40.9 (1.8)	3.2 (0.3)	*Eriophorum vaginatum*, *Betula nana*, *Hylocomium splendens*, *Sphagnum* spp.
NTL	3.9	1193	2.2	2.9	33.0 (3.5)	5.7 (0.4)	*Vaccinium uliginosum*, *Betula nana*, *Rhododendron lapponica*, *Empetrum nigrum*

forest sites and are classified as Typic Cryorthents. Measurements were made at each of the study sites and along transects from the treeline sites, through the forest limit, into the adjacent east-facing forests. Transects were 150 m in length and measurements were made every 3 m for a total of 50 measurements per transect.

Microclimate

Soil temperatures were monitored at the study sites on the northwest side of the river between October 1, 2007 and April 30, 2008. Sensors (S-TMB) were installed horizontally at a depth of 10 cm and read at hourly intervals by a Hobo Micro Station (Onset Computer Corp., Bourne, MA). The microclimate of TER has been monitored continuously since June 1, 2006 using three meteorological stations, evenly distributed along the terrace. Each station revolves around a CR1000 datalogger (Campbell Scientific, Logan, UT), which is programmed to read the sensors at 30 second intervals. In the present study, data are drawn from one air temperature sensor (2 m height, CS107, Campbell Scientific, Logan, UT), which was housed in a radiation shield, one wind speed sensor (2 m height, 014A, Met One Instruments, Grants Pass, OR) and 18 soil temperature sensors (10 cm depth, CS107, Campbell Scientific, Logan, UT). Wind direction data were not available for TER. Therefore, wind speed and direction data were drawn from a meteorological station at the mouth of the Asik watershed (Stottlemyer 2001). Wind data at the Asik site were collected at 10 m height, using an S-WCA wind speed and direction sensor and a Hobo H21 Weather Station (Onset Computer Corp., Bourne, MA). Wind speed and direction data were available from the Asik station for the entirety of the winter of 2007–2008. During the winter of 2008–2009, data were available until sensor failure in mid-December of 2008.

CO_2 efflux estimates

Measurements were made at each of the study sites during the periods of March 27–29, 2007, March 24–26, 2008 and April 3–5, 2009. At each site, 20 measurements of subnivean [CO_2] were made at 2 m intervals along a linear transect, perpendicular to the slope. Snow depth was measured following each measurement of subnivean [CO_2], using a folding fiberglass ruler ($n = 20$). Measurements of atmospheric [CO_2] were made above the snow surface at the beginning and end of the transect. Subnivean [CO_2] measurements were made using a hollow stainless steel probe, equipped with a perforated tip and plumbed with 3.2 mm ID polyethylene tubing (e.g., Fahnestock et al. 1998; Brooks et al. 1999; Hubbard et al. 2005; Sullivan et al. 2008). The tubing was attached to a LI-800 NDIR CO_2 analyzer (LI-COR Biosciences, Lincoln, NE), which was equipped with a micro-diaphragm pump (850 ml/min, KNF Neuberger Inc., Trenton, NJ) downstream of the 5 cm long optical bench. The LI-800 was allowed to warm-up for 1.5 hours and checked against two gases of known [CO_2] before taking measurements.

After completing the CO_2 measurements, one snow pit was excavated at each of the study sites. Measurements of snowpack density were made in continuous 10 cm increments along the vertical wall of the snow pit, using a stainless-steel RIP 1 density cutter (Elder et al. 1991) (Snowmetrics, Fort Collins, CO) and a 600 g capacity spring scale with 5 g resolution. Measurements of snow temperature were made at corresponding 10 cm intervals, using a dial stem thermometer. In each snow pit, a final measurement of the ground surface temperature was made beneath the wall of the pit. At TER, 45 measurements of subnivean [CO_2] and snow depth were made, while three snow pits were excavated to capture spatial variability.

During the 2008 and 2009 sampling campaigns, measurements of subnivean and atmospheric [CO_2] were made along transects down slope from the two treeline sites into the adjacent east-facing forests. The transects were 150 m in length and measurements of subnivean [CO_2] and snow depth were made at 3 m intervals. Three snow pits were excavated along the transects: one at each end and one in the middle. Measurements of snowpack density and temperature were interpolated using Proc Expand in SAS 9.2 (SAS Institute, Cary, NC) to provide continuous estimates along the transects. Transects were initiated in the treeline, rather than the tundra beyond the treeline, because snow depths were too shallow (<0.2 m) in the tundra for reliable estimates of CO_2 efflux by the diffusion gradient method.

Diffusion of CO_2 from the subnivean to the atmosphere was estimated following Musselman et al. (2005):

$$J_c = \theta\tau D\frac{P_o}{RT_o}\left(\frac{T}{T_o}\right)^{0.81}\frac{\Delta C}{z}, \qquad (1)$$

where J_c is CO_2 efflux (μmol m^{-2} s^{-1}), θ is snowpack porosity (unitless), τ is snowpack tortuosity (unitless), D is the diffusion coefficient for CO_2 in air (0.1381×10^{-4} m^{-2} s^{-1}), P_0/RT_0 is the molecular density of CO_2 at standard temperature and pressure (44.613 mol m^{-3}), T is snowpack temperature (K), ΔC is the difference in [CO_2] between the subnivean and the atmosphere (μmol/mol) and z is snow depth (m). Snowpack porosity (θ) was estimated using mean snowpack density (ρ):

$$\theta = 1 - \left(\frac{\rho}{973}\right), \qquad (2)$$

where 973 g/l is the density of ice. Snowpack tortuosity (τ) was also estimated as a function of density (Millington 1959):

$$\tau = \theta^{1/3}. \qquad (3)$$

Studies that have compared this approach with chamber-based methods of estimating CO_2 efflux from snow-covered soils have consistently concluded that the diffusion gradient approach provides more accurate estimates of the flux (Mast et al. 1998; McDowell et al. 2000; Schindlbacher et al. 2007). Use of the diffusion gradient approach to estimate CO_2 efflux assumes that [CO_2] increases in a linear manner with depth in the snowpack from the atmosphere to the subnivean. Two scenarios can disrupt the linear gradient. High wind speeds may reduce [CO_2] near the snow surface through advection (Massman et al. 1995, 1997; Massman 2006; Massman and Frank 2006; Bowling et al. 2009; Seok et al. 2009). In some cases, marked reductions in subnivean [CO_2] have been observed during and following high wind events (Massman and Frank 2006; Bowling et al. 2009; Seok et al. 2009). In the present study, measurements were made during periods with light winds. The strongest hourly average and maximum wind speeds observed during the three measurement campaigns were 3.4 and 5.1 m/s, respectively. This period of moderate wind speeds occurred on March 24, 2008, when measurements were made at TER. The presence of an impermeable layer in the snowpack, such as laterally-continuous ice layer may also disrupt the linear [CO_2] gradient, leading to a build-up of [CO_2] beneath the layer that may extend to the subnivean (Mast et al. 1998; Jones et al. 1999b). Schindlbacher et al. (2007) compared CO_2 efflux estimates made using CO_2 profiles and the two-point concentration gradient method employed in the present study. They found the two methods provided very similar estimates, with the exception of one sampling date, when an ice layer within the snowpack partially disrupted diffusion. Snow pits excavated at each site on each sampling date in the present study showed no evidence of a laterally continuous ice layer, despite brief periods with air temperatures above 0°C in each of the three winters.

Data processing and statistical analyses

Differences in snow depth and CO_2 efflux estimates across sites and years were examined using Analysis of Variance (ANOVA) in the General Linear Model Procedure of SAS 9.2. Data were $\log_{10}$-transformed to meet assumptions of normality and constant variance. Comparisons of interest were made using Tukey's Honest Significant Difference (HSD). The relationship between snow depth and soil temperature across sites and years was fit with a three parameter exponential model, while the relationship between soil surface temperature and CO_2 efflux across sites and years was fit with a 2 parameter exponential model using the Nonlinear Regression Procedure in SAS 9.2.

Point measurements of soil surface temperature were made at each site during each measurement campaign, while hourly measurements of soil temperature at 10 cm depth were made between November 1, 2007 and April 30, 2008. Because measurements of CO_2 efflux were related to soil surface temperatures, hourly soil surface temperatures were estimated between November 1, 2007 and April 30, 2008 using a linear regression of soil surface temperature on soil temperature at 10 cm depth measured across sites in late March of 2008 ($n = 7$, $r^2 = 0.90$, $P < 0.01$). Hourly estimates of CO_2 efflux were made using the aforementioned exponential model and hourly estimates of soil surface temperatures. Hourly estimates of C efflux were then summed to provide estimates of total C loss at each site between November 1, 2007 and April 30, 2008. The use of a temperature response model developed across sites in late winter to estimate hourly C efflux throughout the winter necessitates two somewhat tenuous assumptions. First, this approach assumes the temperature response of belowground respiration is the same across sites. It is not possible to test this assumption at present, as only three measurements are available for each site. Second, use of a temperature-response model developed in late winter assumes the temperature response of microbial respiration remains constant throughout the winter. There is evidence that microbes become limited by labile C availability during late winter beneath the snow in subalpine ecosystems of the Rocky Mountains (Brooks et al. 2004; Liptzin et al. 2009), but it remains unknown if arctic and boreal microbes similarly deplete their labile C supply.

Results

Microclimate

The winter of 2006/2007 was characterized by shallow snow cover and cold soils. Comparison of the air and soil temperature records at TER shows a relatively tight coupling throughout the winter, with soil temperatures reaching a minimum of −7.4°C in the final week of March (Fig. 2). During the winter of 2007/2008, shallow snow cover apparently persisted through the first half of the winter and soil temperatures briefly reached a minimum of −8.0°C in the second week of January. The soil temperature record for the later-half of the winter points to the development of a relatively deep snowpack, as large swings in air temperature were only weakly evident in the soil temperature record. The winter of 2008/2009 was similar to that of 2007/2008 in the sense that the strength of the coupling of air and soil temperatures declined over the course of the winter as the snowpack deepened. Soil temperatures reached a minimum of −6.4°C in mid-January and fell to similarly low levels again in mid-February of 2009.

Wind direction data were available for the entire winter of 2007/2008 and the early part of 2008/2009. Despite the short record for 2008/2009, the data show a similar pattern in both winters (Fig. 3). Strong winds were generally observed from one of two directions: north and east. The treelines examined in

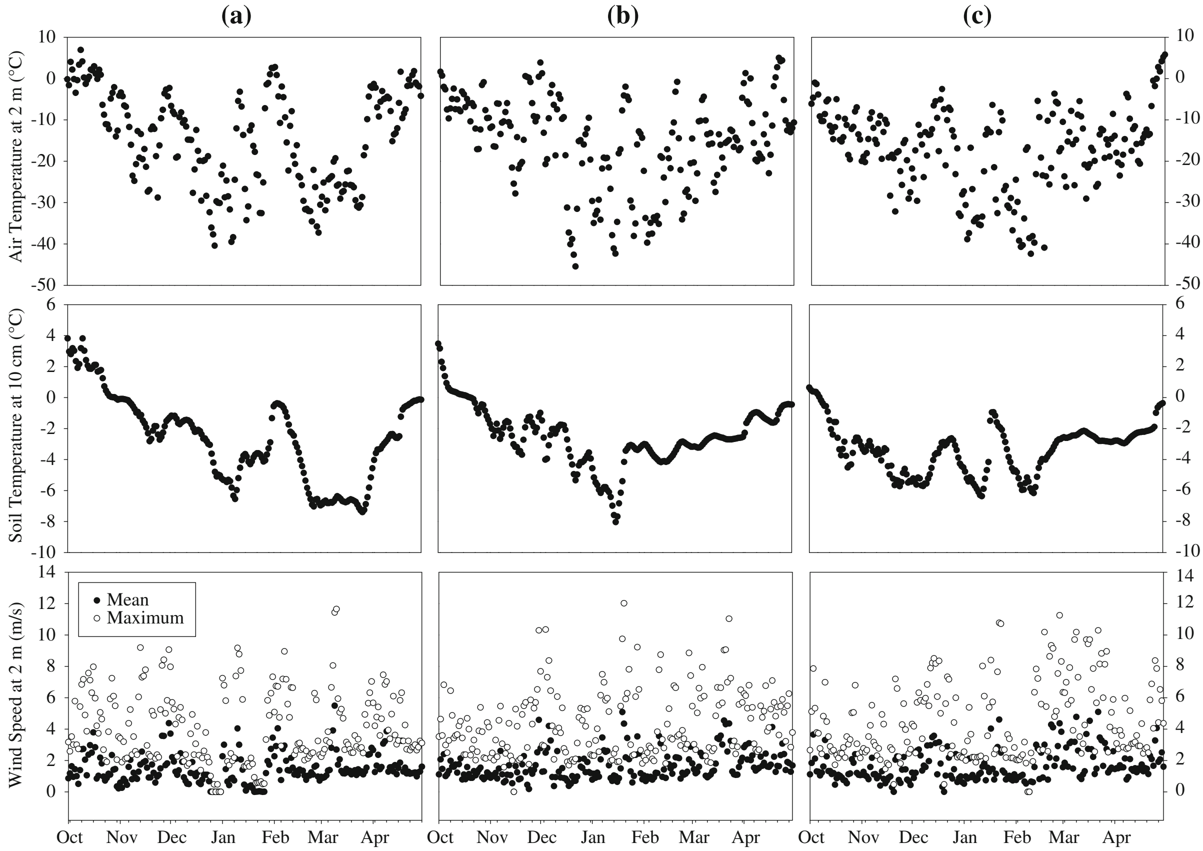

Fig. 2 Daily mean air and soil temperatures and daily mean and maximum wind speeds measured at TER between October 1 and April 30 in the winters of 2006/2007 (**a**), 2007/2008 (**b**) and 2008/2009 (**c**). Soil temperature data are the mean of 18 sensors

this study run from the southwest to the northeast and face the northwest. Strong winds from the north strike the treeline at an oblique angle with a short fetch of upwind tundra. A strong wind from the north should, therefore, lead to modest drifting at the treeline. Strong north winds should also lead to snow drifting at TER, which has a relatively long fetch of open floodplain to the north and northeast, and at NNE, which has vast areas of alpine tundra to the north. The majority of strong winds observed during the winter of 2007/2008 were east winds. Observations of snow drift patterns in late winter of 2008/2009 also point to the importance of east winds. Strong east winds are not expected to lead to snow drifting at the treeline, nor are they expected to accumulate snow at TER. East winds may, however, lead to snow deposition in several of the forest sites. SNE and NSE, in particular, have a long fetch of open floodplain to the east-northeast. In contrast with SNE and NSE, which may accumulate snow, observations of E-W trending erosional features at the snow surface suggest that SSE loses snow under strong east winds.

Snow depth and distribution

Averaging across sites, there was significant variation in snow depth across the three years ($F = 160.3$, $P < 0.01$) (Fig. 4). Snow depths were lowest in 2007 (0.47 m), intermediate in 2008 (0.69 m) and deepest in 2009 (0.79 m). All pair-wise comparisons were significant at $P < 0.01$. Snow depth also depended strongly upon site, when averaging across years ($F = 255.1$, $P < 0.01$). The deepest snow was observed at TER (0.88 m) and NNE (0.86 m), while the shallowest snow was found at the treeline sites: STL (0.33 m) and NTL (0.28 m). The remaining forest sites were intermediate, but all forest sites had

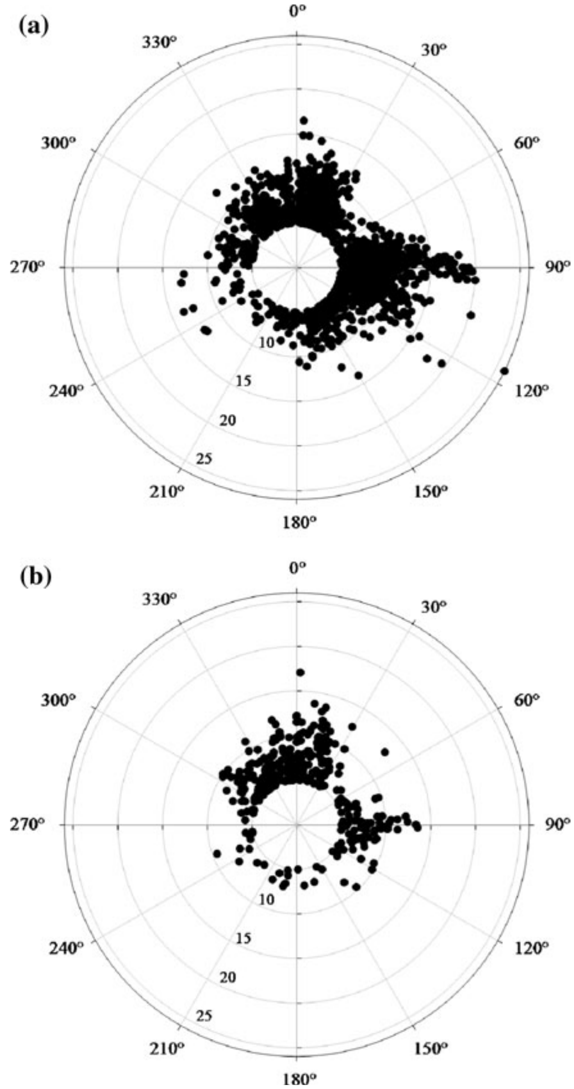

Fig. 3 Wind speed (m/s) and direction (°) of hourly gusts greater than 5 m/s measured at 10 m height near the mouth of Asik stream between October 1 and April 30 in the winters of 2007/2008 (**a**) and 2008/2009 (**b**). Sensor failure in December of 2008 limited the length of the record for 2008/2009. Inner rings indicate gust speed in increments of 5 m/s

significantly deeper snow packs than the treeline sites ($P < 0.01$). The distribution of snow among sites varied across years (site × year, $F = 22.1, P < 0.01$). Four of the sites (TER, NNE, NSE and SNE) showed strong increases in snow depth from 2007 to 2008 and, to a lesser degree, from 2008 to 2009. Three of the sites (SSE, STL and NTL), including the two treeline sites, showed no evidence of a difference in snow depth across years.

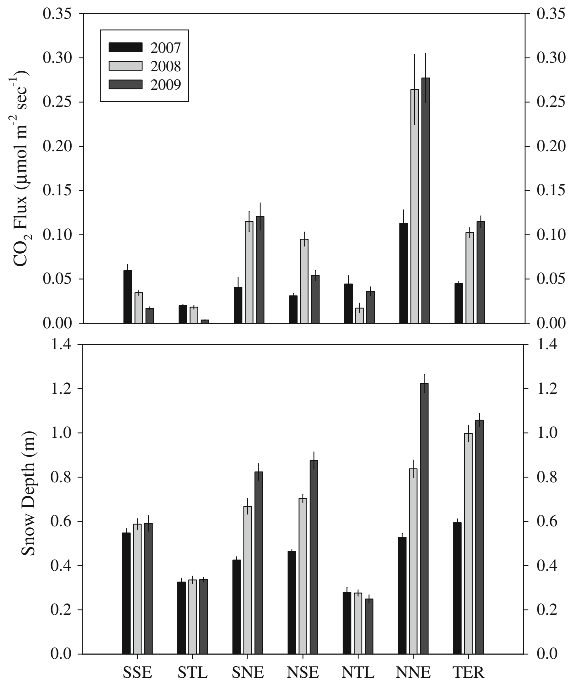

Fig. 4 Estimates of CO_2 efflux and measurements of snow depth across the seven sites and three years of measurement. CO_2 efflux and snow depth are the mean of 20 replicates per site and year, except at TER where $n = 45$. Bars are 1.0 S.E

CO_2 efflux

There were strong correlations across sites and years between snow depth and soil surface temperature ($r^2 = 0.73$, $P < 0.01$) and between soil surface temperature and estimates of CO_2 efflux ($r^2 = 0.77$, $P < 0.01$) (Figs. 4 and 5). As a result, patterns of CO_2 efflux across sites and years were similar to patterns of snow depth. Averaging across sites, there was a significant effect of year ($F = 29.6$, $P < 0.01$). The lowest rates of CO_2 efflux were observed in 2007 (0.05 μmol m^{-2} s^{-1}), while similar rates of CO_2 efflux were observed in 2008 and 2009 (0.09 μmol m^{-2} s^{-1}). There was also a significant effect of site, when averaging across years ($F = 102.7$, $P < 0.01$). By far, the greatest rates of CO_2 efflux were observed at NNE (0.22 μmol m^{-2} s^{-1}). Intermediate rates of CO_2 efflux were observed at SNE, TER and NSE, while the lowest rates of CO_2 efflux were found at SSE (0.04 μmol m^{-2} s^{-1}) and the two treeline sites: STL (0.01 μmol m^{-2} s^{-1}) and NTL (0.03 μmol m^{-2} s^{-1}). The pattern of CO_2 efflux across sites also depended upon year ($F = 12.1, P < 0.01$). Four of the

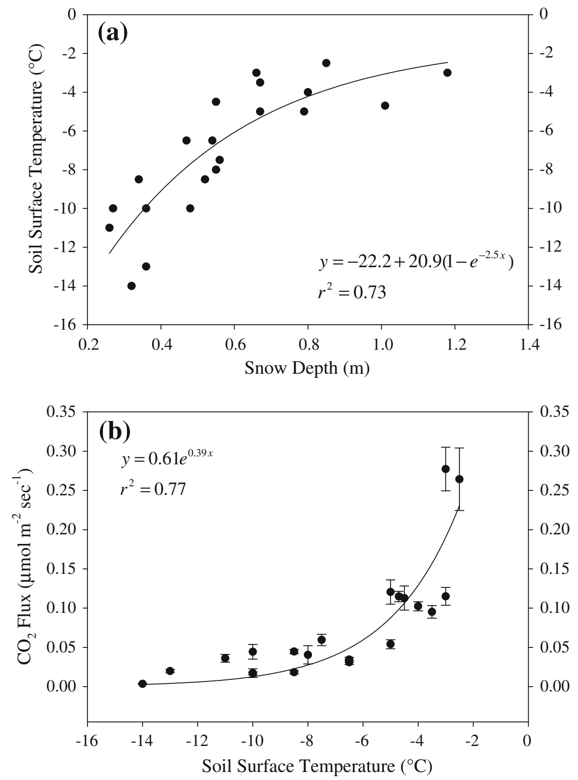

Fig. 5 Relationships between snow depth and soil surface temperature (**a**) and between soil surface temperature and estimates of CO_2 efflux (**b**) across the seven sites and three years of observation. Bars on the CO_2 efflux estimates are 1.0 S.E

sites (TER, NNE, NSE and SNE) showed increases in CO_2 efflux from 2007 to 2008 and 2009, when CO_2 efflux was generally similar. Meanwhile, three of the sites (SSE, STL and NTL), including the two treeline sites, showed only subtle differences in CO_2 efflux across years.

The transects, conducted in 2008 and 2009, showed strong increases in snow depth and CO_2 efflux from the treeline sites into the adjacent east-facing forests (Fig. 6). On the south knoll, snow depth and CO_2 efflux increased in a nearly linear manner, although there was a zone of high CO_2 efflux near the forest limit in 2008. The snow depth and CO_2 efflux pattern was not as clean at the north knoll, although both variables were much higher in the forest, on average. On the north knoll, there was a more abrupt transition in snow depth and CO_2 efflux from the treeline to the forest and there was an extended region of relatively deep snow and high CO_2 efflux near the forest limit. Both variables declined below the forest limit in an area of low stand density and increased again near the end of the transect where stand density recovered. Soil surface temperatures increased strongly from the treeline sites, to the mid-way points, to the ends of the transects in the closed canopy forests. Averaging across transects and years, soil surface temperatures were −10.9°C at the treeline, −6.1°C at the mid-way point and −4.0°C at the end of the transect in the forest.

Discussion

The three winters of study differed strongly in terms of snow depth, snow distribution across sites, soil temperatures and CO_2 efflux. The winter of 2006/2007 was generally characterized by shallow snow, while the winters of 2007/2008 and 2008/2009 had deeper snowpacks. The forest sites always had deeper snowpacks than the treeline sites and this difference was particularly large in 2007/2008 and 2008/2009. There was little difference in late winter snow depth across years at the treeline sites, while four of the five forest sites showed large increases in snow depth from the winter of 2006/2007 to those of 2007/2008 and 2008/2009. The forest sites that showed large inter-annual variation in snow depth are those that have a long fetch of floodplain or extensive alpine tundra upwind of one of the two prevailing winter wind directions (north and east). The stability of late winter snow depth across years at the treeline, despite substantial inter-annual variation in snowfall, suggests the combination of exposure and ecosystem structure prevents sustained retention of a snowpack deeper than approximately 0.4 m.

Across sites and years, there was a close correlation between snow depth and soil surface temperature. Consequently, soils were generally warmer when measurements were made in 2008 and 2009, particularly at the forest sites. The observation that deeper snow is associated with warmer soils is consistent with results of experimental snow additions (Brooks et al. 1997; Welker et al. 2000; Schimel et al. 2004) and comparisons across ecosystem types (Fahnestock et al. 1998, 1999). The non-linear, saturating form of the relationship between snow depth and soil temperature identified in the present study could be attributed to one of two mechanisms:

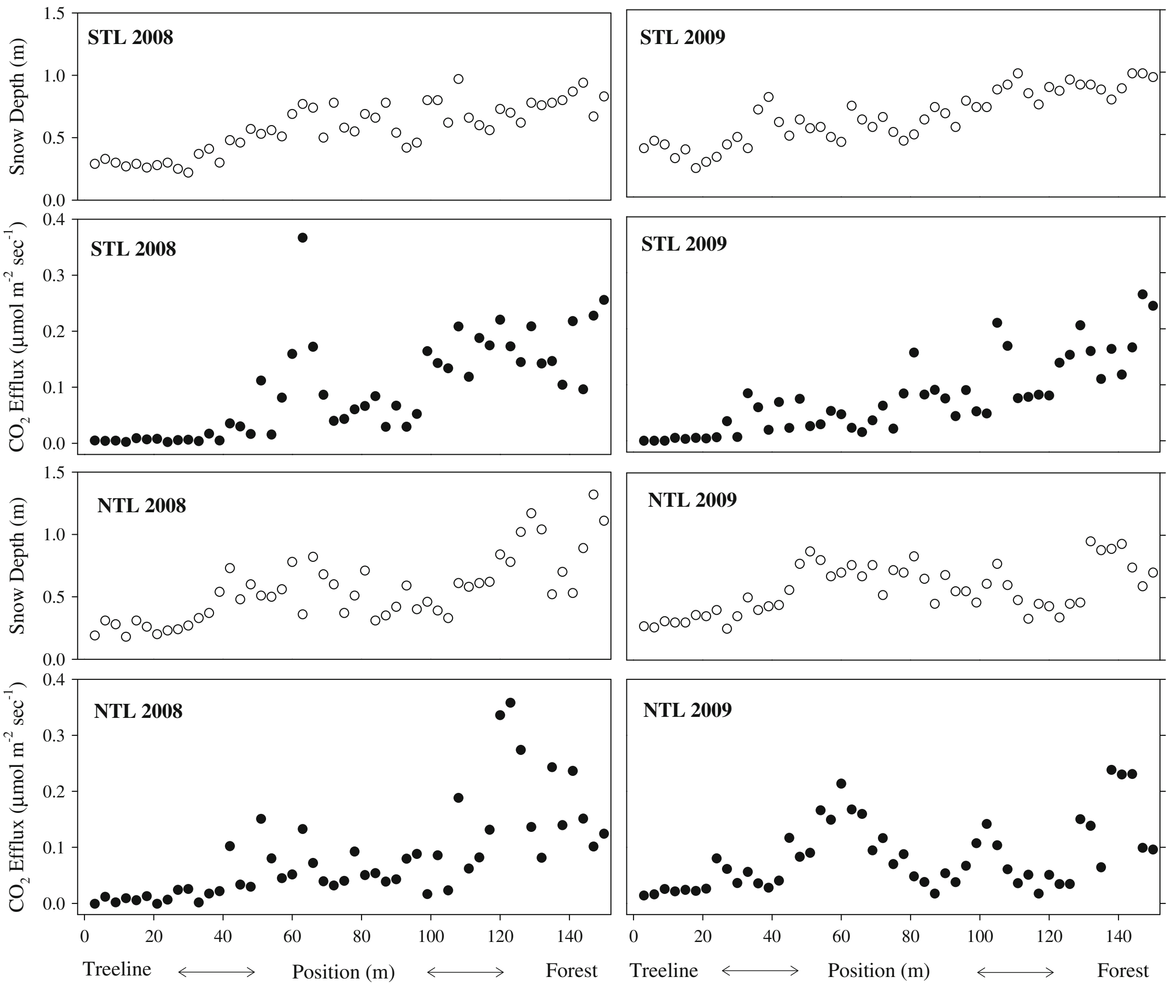

Fig. 6 Measurements of snow depth and estimates of CO_2 efflux along transects from the two treeline sites into the adjacent east-facing forests. Measurements of snow depth and subnivean [CO_2] were made every 3 m along the 150 m transects in late winter of 2008 and 2009

snow depths greater than 0.8 m may provide limited additional insulation or sites with late winter snow depths greater than 0.8 m accumulated much of their snow cover late in winter, after soils had cooled considerably. TER is likely a site that receives much of its snow cover late in the winter, as the site showed an unusual pattern of relatively cold soils and a deep snowpack, when measured in late winter.

There was a strong correlation across sites and years between soil surface temperature and estimates of CO_2 efflux, much like observations made within arctic and boreal ecosystems over time (Sullivan et al. 2008). Numerous investigators have noted that the change in CO_2 efflux per unit change in temperature is much higher in frozen soils than typically observed for thawed soils (Mikan et al. 2002; Schimel et al. 2006; Sullivan et al. 2008). The rapid decline in microbial respiration as soils cool below freezing is thought to reflect a transition from simple kinetic effects of temperature on respiration to a case where indirect effects of temperature on respiration, such as extracellular barriers to diffusion and intracellular desiccation, become increasingly important (Mikan et al. 2002). The high Q_{10} values of frozen soils mean that small changes in soil temperature between −10 and 0°C are expected to have large impacts on microbial respiration and CO_2 efflux.

CO_2 efflux was greater in the forest than at the treeline, in accordance with snow depth and soil temperature patterns. Eddy covariance measurements

Table 2 Maximum, minimum and average hourly soil temperatures (10 cm depth, °C), along with estimates of C efflux (g C m^{-2}) between November 1, 2007 and April 30, 2008 at the seven study sites

Site	Max. soil temperature (°C)	Min. soil temperature (°C)	Avg. soil temperature (°C)	Total C efflux (g C m^{-2} 182 d^{-1})
SSE	−0.17	−6.07	−2.74	26.5
SNE	−0.26	−4.14	−1.83	33.8
NSE	−0.20	−3.24	−1.32	42.1
NNE	0.08	−1.67	−0.50	61.1
TER	−0.41	−8.12	−2.97	21.9
STL	−0.23	−8.40	−3.57	23.6
NTL	−0.65	−6.74	−3.14	21.9

showed that a forest assimilated more C than an adjacent fen during the growing season near Churchill, Manitoba (Lafleur et al. 2001). My measurements, made over five forests and three winters, show that forest soils lose more C during late winter than soils at the treeline. Lafleur et al. (2001) reported the forest was a greater C sink than the tundra by 7, 30 and 120 g C m^{-2} over 65 days in three years of observation. Application of an exponential soil temperature- CO_2 efflux model, which was fit across sites and years, to hourly measurements of soil temperature, made at all of the study sites during the winter of 2007/2008, shows the difference in C efflux between the forest and treeline sites (14.3 g C m^{-2}, Table 2) is large enough to offset the aforementioned differences in growing season net ecosystem exchange (NEE) during some years. In other words, incorporating CO_2 efflux through the winter snowpack could offset growing season differences in the annual C budgets of forests and tundra at the Arctic treeline. The implication of this finding is that we cannot assume treeline advance will lead to greater C storage and serve as a negative feedback to climate warming.

I feel this conclusion represents a first approximation, but a conservative one. My estimates of total wintertime C loss from the seven study sites assume the temperature response of belowground respiration is the same across sites and does not vary throughout the winter. Furthermore, I have compared my estimates of total wintertime C losses with growing season NEE from sites in Canada, which differ from my sites at least in terms of hydrology. There are also several reasons why I think my conclusion is conservative. First, measurements were not made in the tundra, beyond the treeline, because snow depths were too shallow (<0.2 m). Given the close relationships between snow depth and soil temperature and between soil temperature and CO_2 efflux, it is likely that CO_2 efflux in the tundra is even lower than observed at the treeline. Second, the treeline and forest sites examined were not downwind of the tundra and there was limited evidence of snow transport from the tundra into the forest, which should manifest as drifting near the forest limit. Third, only CO_2 efflux from the soil was considered. While this captures most of the wintertime C losses from treeline and tundra sites, it does not consider additional C losses through stem and foliar respiration in the forests. Fourth, the simple exponential model used to estimate total wintertime C efflux systematically underestimated fluxes when soil temperatures were between −4 and 0°C, and soil temperatures at the forest sites were within this window more frequently than soil temperatures at the treeline sites. Until we have year-round measurements of CO_2 exchange from numerous paired forest and tundra sites, our estimates of the change in C storage that can be expected with arctic treeline advance will remain qualitative at best.

Treeline advance is expected to feedback to regional and global climates through changes in surface energy exchange and carbon cycling. Feedbacks associated with surface energy exchange are fairly well understood and treeline advance is expected to lead to greater sensible heating and enhanced warming at local to regional scales (Chapin et al. 2000b; Beringer et al. 2005). Carbon cycle feedbacks are less well understood. Inferences drawn through different approaches have drawn contrasting conclusions, with some studies suggesting that treeline advance will lead to greater C storage and serve as a negative feedback to climate warming (Lafleur et al.

2001; Rouse et al. 2002; Steltzer 2004), while another study has concluded that treeline advance will lead to C loss from the ecosystem (Wilmking et al. 2006). My study shows that forests hold a deeper snowpack, have warmer soils and lose more C during the winter months than adjacent arctic tundra. Furthermore, the difference in wintertime C efflux between the forest and the tundra may be sufficient to offset greater net C gain by the forest during the summer months. This finding raises doubt that treeline advance will lead to greater ecosystem C storage and feedback to slow the rate of climate warming. In order to predict the direction and magnitude of the C cycle feedback to climate change with treeline advance, future studies of C exchange at the treeline will need to consider C losses during the winter months.

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