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Ecosystem CO_2 production during winter in a Swedish subarctic region: the relative importance of climate and vegetation type

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Abstract

General circulation models consistently predict that regional warming will be most rapid in the Arctic, that this warming will be predominantly in the winter season, and that it will often be accompanied by increasing snowfall. Paradoxically, despite the strong cold season emphasis in these predictions, we know relatively little about the plot and landscape-level controls on tundra biogeochemical cycling in wintertime as compared to summertime.

We investigated the relative influence of vegetation type and climate on CO_2 production rates and total wintertime CO_2 release in the Scandinavian subarctic. Ecosystem respiration rates and a wide range of associated environmental and substrate pool size variables were measured in the two most common vegetation types of the region (birch understorey and heath tundra) at four paired sites along a 50 km transect through a strong snow depth gradient in northern Sweden.

Both climate and vegetation type were strong interactive controls on ecosystem CO_2 production rates during winter. Of all variables tested, soil temperature explained by far the largest amount of variation in respiration rates (41–75%). Our results indicate that vegetation type only exerted an influence on respiration when snow depth was below a certain threshold ($\sim$1 m). Thus, tall vegetation that enhanced snow accumulation within that threshold resulted in more effective thermal insulation from severe air temperatures, thereby significantly increasing respiratory activity. At the end of winter, within several days of snowmelt, gross ecosystem photosynthesis rates were of a similar magnitude to ecosystem respiration, resulting in significant net carbon gain in some instances. Finally, climate and vegetation type were also strong interactive controls on total wintertime respiration, suggesting that spatial variations in maximum snowdepth may be a primary determinant of regional patterns of wintertime CO_2 release. Together, our results have important implications for predictions of how the distribution of tundra vegetation types and the carbon balances of arctic ecosystems will respond to climate change during winter because they indicate a threshold ($\sim$1 m) above which there would be little effect of increased snow accumulation on wintertime biogeochemical cycling.

Key words: arctic, biomass, birch, carbon, climate change, heath, microbe, respiration, shrub, snow, soil, temperature, tundra

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Introduction

Most mid- and high-latitude and high-altitude terrestrial ecosystems experience prolonged seasonal snow cover. For a long time, it had generally been assumed that wintertime biological activity in these ecosystems was very limited (Coyne & Kelley, 1971), and of insufficient magnitude to substantially offset carbon gains during the summer growing season. Recent studies have now refuted this assumption, indicating appreciable respiration rates, and annually significant total wintertime CO_2 effluxes in tussock tundra, dry heath

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tundra, shrub tundra and nonacidic tundra in Alaska (Oechel *et al*., 1997, 2000; Fahnestock *et al*., 1998; Grogan & Chapin, 1999), in the forest tundra of Russia (Zimov *et al*., 1996), in subarctic birch forest understorey and heath tundra in Sweden (Grogan & Jonasson, 2005), in boreal peatlands (Alm *et al*., 1999; Lafleur *et al*., 2003), and boreal fens (Aurela *et al*., 2002), in alpine tundra (Brooks *et al*., 1997) and subalpine wetlands (Sommerfeld *et al*., 1996). Wintertime ecosystem CO_2 losses via respiration typically range from 15% to 50% of total annual respiration in arctic and boreal ecosystems (Zimov *et al*., 1996; Oechel *et al*., 1997; Fahnestock *et al*., 1998, 1999; Vourlitis & Oechel, 1999; Aurela *et al*., 2002; Lafleur *et al*., 2003) and, therefore, can often significantly offset summer net carbon gains. Thus, it is now clear that *wintertime* biogeochemical cycling can no longer be overlooked in our attempts to understand and model *annual* carbon fluxes and vegetation change in many mid- to high-latitude and high-altitude ecosystems.

The net carbon (C) balance of arctic and subarctic ecosystems is of particular importance in linking terrestrial C cycling and global climate change because tundra and boreal forest soils contain 27% of the Earth's soil C pool (Post *et al*., 1982). The sheer magnitude of their soil C pools implies that these ecosystems could provide a significant initial positive feedback to climate change if warming stimulates bulk soil organic matter decomposition and CO_2 release to the atmosphere (Lashof, 1989). For example, the carbon pool in just the top meter of arctic tundra soil is equivalent to $\sim$25% of the total global atmospheric pool (Post *et al*., 1982). This potential feedback is of immediate concern because general circulation models (GCMs) of global climate change predict that the most rapid increases in regional air temperature across the globe will occur at high latitudes during the cold season (Giorgi *et al*., 2001). Projected warming is greatest for late autumn and winter, largely due to the decrease in albedo associated with delayed onset of sea ice and snow cover (Serreze *et al*., 2000). Furthermore, these same factors are expected to result in increased snowfall on many arctic ecosystems (Giorgi *et al*., 2001). These climate predictions are supported by analyses of meteorological data over the past 50 years which indicate a particularly strong trend toward warmer winter air temperatures in many parts of the Arctic (Serreze *et al*., 2000; ACIA, 2004), and a series of record-breaking minima in arctic sea ice cover in recent years (Stroeve *et al*., 2005). Therefore, characterizing the controls on winter respiration in tundra ecosystems, and evaluating the impacts of warmer winter temperatures and deeper snow is now considered an urgent priority for predicting the responses and potential feedbacks of the Arctic to climate change (Hobbie *et al*., 2000; Callaghan *et al*., 2004).

As a first step to including winter biogeochemical processes in ecosystem models, regional Modellers have generally relied on basic first-order soil respiration relationships with temperature (e.g. McGuire *et al*., 2000; Oechel *et al*., 2000) that have been derived from summertime soil incubation and field experiments (e.g. Lloyd & Taylor, 1994; Katterer *et al*., 1998), and that assume close linkage between air and soil temperatures. Relatively little is known about the specific controls on the various components of *ecosystem* respiration (i.e. respiration derived from bulk soil organic matter, as compared with that derived from plants and their associated litter and exudates), especially in the winter season (Grogan *et al*., 2001). Recent evidence suggests that this distinction may be important because respiration from bulk soil and plant-associated carbon pools can differ significantly in their apparent sensitivity to temperature variations occuring through winter and summer (Grogan & Jonasson, 2005). Furthermore, regional models have tended to rely on a close relationship between air and soil temperature, but this relationship is likely to be far more complicated in winter than in summer because of the potential influence of snowcover as a thermal insulator (Taras *et al*., 2002). Recent experimental manipulations using fences that raised snowdepths to approximately six times ambient levels demonstrate that large increases in snow depth in arctic tundra can result in very substantial increases in soil temperature and rates of respiration and nitrogen cycling (Schimel *et al*., 2004). The key question now is what is the nature of the relationships between changes in air temperature, changes in snowdepth, and changes in rates of biogeochemical cycling? Would more moderate increases in snowdepth result in corresponding increases in biogeochemical cycling rates? Is there a threshold snow depth above which increases in snow accumulation are unlikely to have much impact in enhancing the thermal insulation of soils? At the regional scale, could patterns of total wintertime CO_2 release be accurately modelled on the basis of spatial and temporal patterns of snow accumulation?

Apart from snowcover effects on soil temperature, regional patterns of CO_2 production during winter may also be influenced by the spatial distribution of vegetation types. Regional patterns of summertime respiration from tundra are clearly influenced by vegetation type (Giblin *et al*., 1991; Oberbauer *et al*., 1991, 1992, 1996; Shaver *et al*., 1998; Grogan & Chapin, 1999; Johnson *et al*., 2000). Some studies suggest that ecosystem respiration during winter can vary substantially among vegetation types even at local scales (Fahnestock *et al*., 1998; Grogan & Jonasson, 2005), while others conclude that at least the belowground component of ecosystem respiration (i.e. from roots plus soil) does not vary significantly among vegetation types within a common climatic zone (Grogan & Chapin, 1999). Where differences in winter CO_2 effluxes have been observed, it is unclear whether these differences are due to variations in soil temperature alone, or whether biogeochemical differences among vegetation types in the size and lability of plant and soil pools available for respiration have a significant impact. Furthermore, with a view to modelling at the regional scale, we do not yet understand the relative importance of, and potential interactions between, variation in snowcover and differences in vegetation type on winter CO_2 production. For example, tall vegetation types that modify patterns of snow accumulation and redistribution by wind may interact with local winter climate to determine spatial heterogeneities in snow cover and therefore soil temperatures across a region. Do particular vegetation types modify snow accumulation patterns to the extent that they *significantly* influence soil temperatures and biogeochemical cycling rates across a region? Answers to these kinds of questions are likely to be fundamental to developing spatially explicit and accurate regional models of wintertime CO_2 release in seasonally snow-covered ecosystems.

Here, we used a gradient approach along a 50 km transect in northern Sweden to investigate the influence of regional variation in snow accumulation on winter CO_2 production from two common subarctic vegetation types, and to characterize the major controls on respiration rates. We tested the following hypotheses:

(I) *Vegetation-snow interaction threshold*: Vegetation type interacts with climate to determine regional patterns of ecosystem respiration rates only at sites where snow accumulation is insufficient to provide an effective thermal barrier against winter air temperatures.
(II) *Vegetation type pool sizes matter*: Respiration rates during winter within a common vegetation type across a region are determined not just by variations in soil temperature, but also by biomass differences in evergreen and deciduous plants, mosses, surface litter mass, and soil organic layer depths.
(III) *Max snowdepth rules*: Patterns of total wintertime CO_2 production across a region are determined primarily by spatial heterogeneities in maximum snow depth.

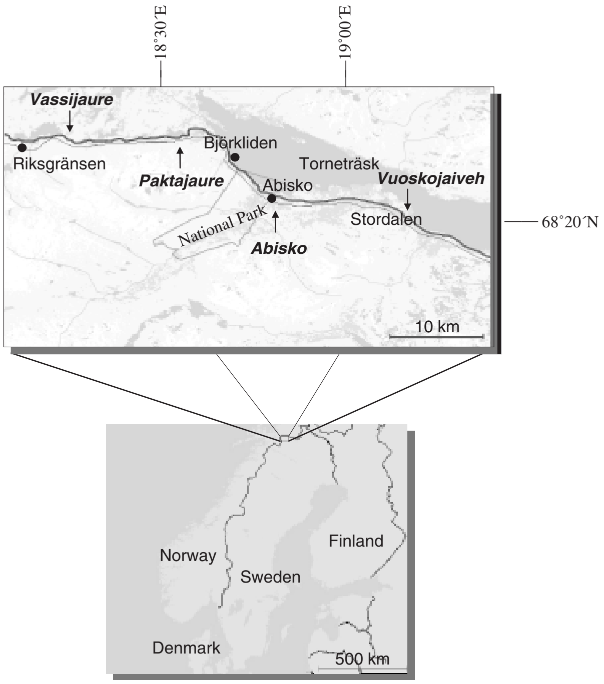

Fig. 1 Location of the four study sites along a decreasing snow depth transect from west to east in Northern Sweden.

Materials and methods

Site description

This study was conducted in two adjacent vegetation types at four sites along a 50 km east–west transect close to Lake Torneträsk in northern Sweden (Fig. 1). The climate in this region is subarctic with mean summer and winter air temperatures of 10 and −9 °C, respectively, and a snow-covered winter season usually lasting from early October to late May (www.ans.kiruna.se/ans.htm). Winter is characterized by prevailing westerly winds that transport moist air from the North Sea to the Norwegian coast and up over a steep mountain range to produce snow on both slopes. The transect in this study is located on the Swedish side of the slope, in the lee of the prevailing winds (Fig. 1). Total winter precipitation and snow accumulation generally decreases from west to east along the transect, presumably because of increasing distance from the oceanic source (Rosswall *et al*., 1975; Andersson *et al*., 1996). This general trend is modified by the sheltering effect of local mountains such as in the Abisko valley where annual precipitation rates are among the lowest in all Scandinavia (www.ans.kiruna.se/ans.htm). Hence, annual precipitation patterns among our transect sites are highest in the west (Vassijaure and Paktajaure), decrease to a minimum at Abisko, and then rise a little at the easternmost site (Vuoskojaiveh) (Rosswall *et al*., 1975; Andersson *et al*., 1996).

The vegetation in this region is broadly characterized into either birch forest with heath understorey communities or heath tundra containing species-rich dwarf shrub communities. Pairs of adjacent vegetation types

(<150 m apart) containing either birch or heath vegetation were identified at each site along the transect at the following locations: Vassijaure (68°26′ 03″N, 18°16′04″E, elevation 515 m a.s.l.); Paktajaure (68°25′ 52″N, 18°33′14″E, elevation 420 m a.s.l.); Abisko (68°20′ 42″N, 18°50′18″E, elevation 415 m a.s.l.), and Vuoskojaiveh (68°19′29″N,19°10′09″E, elevation 350 m a.s.l.). The birch trees (*Betula pubescens* ssp. *tortuosa* Ledeb.) tend to occur as polycormic (multistemmed) clones in this region (Bylund & Nordell, 2001). Zones were identified within birch forest that had similar tree density, flat topography and an understorey heath vegetation with substantial presence of the deciduous species *Vaccinium myrtillus* (L.), as well as the evergreen species *Empetrum hermaphroditum* (Hagerup.), and/or the deciduous species *Vaccinium uliginosum* (L.). In addition, considerable moss cover (predominantly *Hylocomium splendens* [Hedw.] Br. Eu.) was common along with occasional herbs (predominantly graminoids) and lichens. The adjacent paired heath tundra vegetation at each site along the transect was also chosen on the basis of similar flat topography. Each heath site was generally dominated by *Empetrum hermaphroditum* (Hagerup.), and had a similar overall plant community composition as in the understorey of the adjacent birch vegetation type.

CO_2 flux measurements

Ecosystem CO_2 production was determined using an infrared gas analyzer (LI-COR 6200, LICOR, Lincoln, NE, USA) attached to a cube-shaped perspex chamber (35.5 L, basal area 1076 cm^2) fitted with a pair of small circulation fans. At each site visit during the snow-covered phase of winter, we dug randomly located holes in the snow to expose the underlying vegetated surface for each replicate measurement of ecosystem CO_2 production ($n = 6$). Snow within the vegetation was gently brushed away, and then on the basis of initial tests of the CO_2 efflux measurement protocol (reported below), each plot was left undisturbed for 35–60 min before measurement. We assume that the CO_2 efflux rates we measured were indicative of ecosystem CO_2 production rates beneath snow.

We measured efflux four to five times during the 1999/2000 cold season at each site. Effluxes during the snow-covered phase were sampled on two to four occasions at each site, and additional measurements were made on one occasion in Autumn (pre-snowfall) and Spring (post-snowmelt) for most of the sites. Fluxes were measured on one day at each site over the following periods: early October (1st–4th); mid-October (16th–18th); mid-January (9th–11th); mid-March (2nd–4th); mid-May (11th–12th); and late May (24th–26th). At each plot, the junctions between the edges of the chamber and the vegetated surface were sealed with tightly packed snow before flux measurement. Where snow was not present, a strip of clear plastic sheeting (20 cm wide) was taped to the outside edges of the chamber and spread out onto the adjacent vegetation. Sealing at the heath sites was achieved by placing a heavy chain around the outside edge of the chamber to hold the plastic in place. This method did not work for the pre-snow October measures in the birch sites, and instead, we inserted aluminum frames (1056 cm^2) containing a 2 cm wide groove around the top perimeter into random locations at each site at least 1 week before flux measurement. All vegetation that was rooted within the frame was guided up through it, and having cut a slot in the soil around the outer edge, the frame was pressed down 2–8 cm into the soil organic layer (Grogan & Jonasson, 2005). Sealing in this case was achieved by slotting the chamber into the frame groove and then filling the latter with water (during snow-free measures), or snow (when available).

Fluxes were measured over six successive 20 s intervals and averaged to calculate mean flux per sample area. To test the sensitivity of the equipment under field conditions, we placed the chamber on a plastic sheet, sealed the edges with packed snow and made successive blank measurements (mean = 0.0034 g CO_2-C m^{-2} day^{-1}; SD = 0.0086; $n = 10$). These results suggest that the limit of detection for each plot efflux measurement was ± 0.023 g CO_2-C m^{-2} day^{-1} (i.e. the minimum value significantly different from zero with 95% confidence).

We measured CO_2 fluxes on each plot first under ambient light conditions and then under darkness (by covering with two layers of black plastic sheeting). For the light measurements, we waited ~30 s after placing the chamber in position, to allow equilibration before beginning to record CO_2 changes. After each light measurement, the chamber was lifted to equilibrate internal CO_2 concentrations and temperatures with ambient conditions. Dark measurements were initiated at least ~30 s after replacing the chamber and covering it with a double layer of black plastic sheeting. Preliminary measurements indicated that this was a sufficient period for acclimation to darkness. Fluxes under ambient light net ecosystem CO_2 exchange (NEE) are the balance between gross photosynthesis, respiration from plant-associated sources (i.e. shoots, roots, mycorrhizae, rhizosphere-associated microbes and microbes during decomposition of fresh surface litter) and respiration derived from the decomposition of soil organic matter. Flux measurements in the dark represent the sum of plant-associated and soil organic matter-derived respiration (ecosystem respiration (ER)), and are presented as negative values (to indicate ecosystem carbon loss). Gross ecosystem photosynthesis (GEP) was calculated by adding the absolute value of ER to the measured value of NEE for each plot.

All recommended precautions against problems associated with CO_2 boundary layer formation (Hooper *et al*., 2002) were included in the flux measurement protocol. No corrections for vapour pressure changes during flux measurement were made (Hooper *et al*., 2002), since the rate of change of water vapour pressure did not exceed 0.02 mb s^{-1}.

Flux interpolations

Winter length was defined as the continuous period during which mean diel soil temperature at ~3 cm was <0.5 °C. Applying this definition, and overlooking single deviations in soil temperature (to ~1 °C) in two of the sites for a 2-day period in October, there was a common start date for 'winter' at all sites (23 October 1999). Estimates of ecosystem total winter CO_2 production were calculated by linearly interpolating each of the six series of ER flux rates between the sampling intervals ($n = 6$ randomly selected plots per site at each sampling time). To complete the interpolations, we assumed that the flux rates at the beginning and end of 'winter' are equivalent to those measured on dates immediately before, and after this designated 'winter' period. ER and NEE measures did not differ significantly during the early and mid-winter periods (paired t tests; $P < 0.05$). There were, however, statistically significant differences between ER and NEE within some of the mid- and late-May measurements, indicating system potential for GEP when exposed to full light conditions. Where we made both mid- and late-May flux measures, and the latter were snow free and had statistically significantly different ER and NEE values, we used the NEE measures (rather than the ER measures) as the interpolation flux values. In cases where there was only one set of May measurements and the sites were snow free at that time (i.e. all heath sites except Vassijaure), we used the ER values for the interpolations on the basis that the associated overestimate of total winter efflux is likely to be substantially lower than the underestimate associated with using NEE values as the final interpolation point for the whole of the predominantly snow-covered period from March through May. Furthermore, the effect on total winter estimates of using ER rather than NEE values for the final interpolation point in these heath sites is limited because the overall estimates are strongly dominated by the efflux rates during the long period from October through March and onwards up to snowmelt.

We tested the precision of our measurement protocol at several different sites in January, March and May by repeating the flux measurement from the initial plot at the end of the sampling visit (30–60 min after the initial measurement). In most cases, the initial and repeat measures were closely correlated (repeat flux = 1.066 × [initial flux]–0.012; $r^2 = 0.88$; $n = 12$). At the Vassijaure birch site in May however, the repeat measure was >7 times lower than the initial value. After digging out the plots, substantial snowmelt waters were observed at the base of the snow column on this warm day (air temperature ~5 °C). We assume that the increasingly saturating soil moisture conditions may have inhibited biotic activity and CO_2 production between initial and subsequent repeat flux measures 80 min later and, therefore, that the initial value is more representative of subnivean respiration rates at that stage of winter.

The total 'winter' length was not determined for the Vassijaure birch site because the soil temperature loggers had to be removed on 19 June (for logistical reasons) which was before complete snow melt and associated soil temperature warming. As a result, the interpolated flux from this site is an underestimate. However, even if one assumed that soil temperatures did not rise for a further 3 weeks, the total estimated flux would be increased by <8%, indicating that the magnitude of this underestimation is small and, therefore, would have no impact on the study's overall conclusions concerning the statistical significances of vegetation type, transect site and their interaction on total wintertime CO_2 production. In summary, despite various constraints associated with the data, our strategy throughout the development of this interpolation procedure has been to provide the most robust *minimum* estimates of net ecosystem CO_2 production during 'winter' for these sites.

Soil temperature and moisture measurements

Soil temperatures at 3–5 cm depth into the organic soil layer (i.e. below the green moss horizon) in each plot were recorded immediately after each flux measurement using hand-held temperature probes ($n = 3$). Preliminary checks of the soil temperature profile at 1 cm depth intervals down to 8 cm indicated no significant differences in temperature during mid-winter. In addition, we used Tinytag Plus dataloggers and associated probes (Meaco, Surrey, UK) to record the soil temperature at ~3 cm depth and the temperature in the air or snowpack at 50 cm above the soil surface (as an indicator of the onset of substantial snowcover) every hour through the entire experiment at each of the birch sites. At the adjacent heath sites along the transect, Tinytalk II loggers were used to record hourly soil temperatures at ~ 3 cm soil depth from mid-May through to late-June 2000. Soil moisture was measured using a Theta probe (Delta-T Devices, Cambridge, UK) that provides an integrated reading for the top 4.5 cm of soil. We developed and applied a site-specific calibration curve to correct the probe output readings for the local soil type (soil moisture [$\mathrm{g\,H_2O\,g^{-1}}$ dry mass of soil] = [0.0045 × probe reading] −7.65; $P < 0.001$, $r^2 = 0.70$, $n = 24$). In many cases, no data were obtained because the probe could not be fully inserted into the soil either because of shallow soil organic depths, or because of soil hard freezing.

Plot biomass harvests

Small wooden flags were placed at the centre of each winter flux measurement plot so that they could be relocated in the following summer. In mid-July 2000, the aboveground biomass emanating from the central 20 cm × 20 cm area of each birch forest understorey plot and associated surface litter was harvested and sorted into the following categories: evergreen shrub; deciduous shrub plus herb; moss; standing dead plus surface litter. In addition, the full extent of the soil organic layer in each plot was determined using a knife to excavate down to the underlying mineral layer or rock substrate. Unfortunately, flag damage was extensive at the birch Vuoskojaiveh site (presumably because winter browsing by moose or reindeer), resulting in only six of the 24 flags remaining, and therefore a restricted biomass data set for this site. Similar harvests were conducted on the heath plots, but sorting was confined to the evergreen shrub, and deciduous shrub plus herb categories. All tissues were dried at 65 °C for 48 h before weighing.

Statistical analyses

Three-way factorial analyses of variances (ANOVAs) were used to test for effects of vegetation type, transect site and sampling month (categorical) on environmental variables measured through the winter (mid-October–initial-May sampling times). All of these factors and their interactions were significant in explaining patterns of air temperature, soil temperature and snow depth. In order to simplify the interpretation of these data in the context of our hypotheses, we confined our reporting of these results to discussing the broad patterns of these variables between transect sites and vegetation types. Two-way factorial ANOVAs were used to test for significant effects of vegetation type and site on pool size variables ($n = 6$–24). The relationships between individual plot efflux rates and each of the potential controlling environmental and pool size variables for the two vegetation types were tested using separate regressions. Two-way factorial ANOVAs were used to test for significant effects of vegetation type and site on the total ecosystem wintertime CO_2 production interpolations ($n = 6$). All significant ANOVA interactions ($P < 0.05$) are reported in the text. *Post hoc* multiple comparisons were analysed using Tukey's HSD tests.

Results

Seasonal temperature patterns across the transect region

The seasonal temperature trends in soil and air/snow at the birch sites across the 50 km long transect provide a broad overview of typical winter conditions in the region. Diel mean soil temperatures (Fig. 2, black lines) were typically warmer than −2 °C for all sites

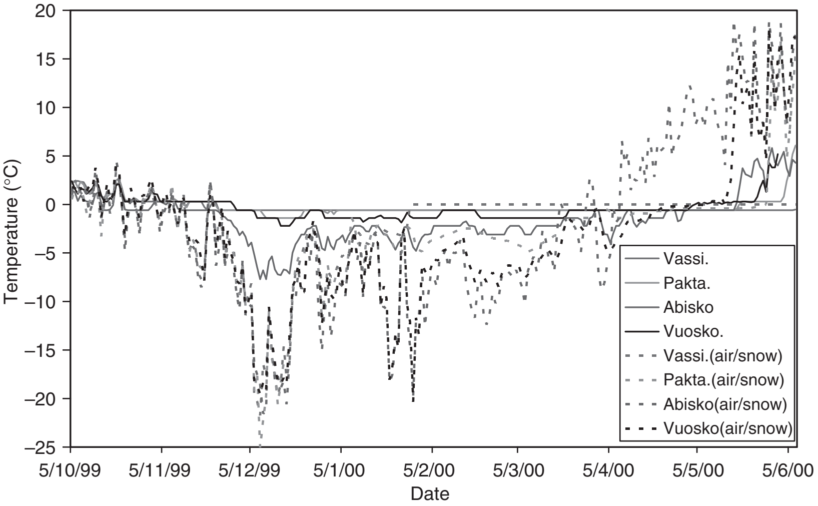

Fig. 2 Mean diel temperatures in the soil (~3 cm depth) and in the air/snow (i.e. 50 cm above the soil) at the birch sites along the transect during the study.

throughout the winter except for Abisko which was on average about 2° cooler, and where the temperature reached $-8\,^{\circ}\mathrm{C}$ on one occasion in December. Although we do not have continuous wintertime soil temperature data for the heath sites, we expect the broad seasonal temperature trends along the transect to have a very similar pattern to the adjacent birch sites, but with lower temperature means and minima (Grogan & Jonasson, 2005).

Air/snow temperatures (i.e. 50 cm above the soil surface) were almost identical at all sites up to 17 January (Fig. 2, grey lines). Together, these time series data which include some severe cold events, strongly suggest that although the transect sites extend over a 50 km distance and differ somewhat in elevation (see 'Materials and methods'), they generally experience similar air temperatures throughout the winter. It is noteworthy that in contrast to the other sites, the severe cold snap in December resulted in a correspondingly severe trough in soil temperature at the Abisko site in particular. After mid-January, the temperature measures at 50 cm above the soil surface remained similar for the Vuoskojaiveh and Abisko sites, and continued to fluctuate dynamically in the latter site in particular (Fig. 2). By contrast, the corresponding temperature measures at the more westerly Paktajaure and Vassijaure sites became much higher from this time onward, and were relatively smooth. Together, these data indicate that snow accumulation was deeper at the two westerly sites from mid-January and onwards (Table 1), and had reached sufficient depth to effectively insulate the 50 cm high probes from the air temperatures above the snow surface. In summary, although the winter air temperatures are not markedly different from typical conditions at mid- to high-latitude tundra sites, the winter soil temperature patterns in this region are relatively benign compared with other more arctic research sites (Oechel *et al*., 1997; Grogan & Chapin, 1999; Schimel *et al*., 2004) (P. Grogan, unpublished data from Daring Lake, N.W.T., Canada), part of which is likely due to relatively high snow accumulation. Of the four sites in our study, although the air temperatures were similar across the transect sites, soil temperatures were consistently cooler at the Abisko site right through the winter (Fig. 2), most probably due to thinner and less effective thermally insulating snowcover.

Environmental and pool size variables along the transect

The seasonal trend in winter air temperatures measured simultaneously with each set of flux measurements declined from October through to minimum values in March at all sites in both birch and heath vegetation types (Table 1). Seasonal trends in snow accumulation showed the opposite trend, peaking in March at all sites. Across the transect, snow accumulation rates and maximum snow depth values clearly decreased substantially from the westerly sites (Paktajaure and Vassijaure) to the more easterly sites (Vuoskojaiveh and Abisko) (Table 1). Furthermore, Abisko also had the shallowest recorded snow depths among all birch sites (Table 1), consistent with the pattern of relatively dynamic and low temperatures recorded at 50 cm above the soil (Fig. 2). Finally, snow accumulation rates and maximum snow depths were clearly larger in the birch sites as compared with the adjacent heath sites at all but the most westerly site along the transect (Table 1).

The pattern of soil temperatures measured simultaneously with the respiration fluxes was a result of the combined effects of seasonal changes in air temperatures, and rates and depths of snow accumulation. The seasonal trend in plot soil temperatures corresponded with that of air temperature, minima generally occurring in March except for the deepest snow site (Vassijaure) where minima were reached by January (Table 1). Across the transect, soil temperatures were substantially warmer in the more westerly sites, consistent with the mid-winter trends in snow accumulation. Furthermore, soil temperatures did not differ significantly between vegetation types at the Vassijaure site. By contrast, in Vuoskojaiveh, Abisko and Paktajaure where snow accumulation was relatively low, deeper snow accumulation in the birch vegetation type than in the adjacent heath resulted in warmer soil temperatures (Table 1). Finally, the sites differed in the total length of 'winter' defined as the continuous period during which mean diel soil temperature at ~ 3 cm was $< 0.5\,^{\circ}\mathrm{C}$ (Table 2). Total winter length was similar for the easterly sites and increased toward the western end of the transect, again consistent with the deeper (and therefore longer duration) snow cover at Paktajaure and Vassijaure (Tables 1 and 2). Shoot biomass of evergreen plants varied significantly between sites (Table 2; $\mathrm{Site}_{3,204}$ $F = 20.67$, $P < 0.001$) and was associated with a significant interaction (Site × $\mathrm{Vegetation}_{3,204}$ $F = 21.82$, $P < 0.001$), due to relatively low values in the Paktajaure birch site. Deciduous plus herb shoot biomass varied significantly between vegetation types ($\mathrm{Vegetation}_{1,212}$ $F = 26.52$, $P < 0.001$) and again was associated with a significant interaction (Site × $\mathrm{Vegetation}_{3,212}$ $F = 7.68$, $P < 0.001$), indicating significantly lower biomass in the Paktajaure and Vassijaure heath sites (Table 2). Soil organic layer depth was significantly different among sites (Table 2; $\mathrm{Site}_{3,215}$ $F = 95.02$, $P < 0.001$), was generally deeper in the heath vegetation type ($\mathrm{Vegetation}_{1,215}$ $F = 84.71$, $P < 0.001$), and again was associated with a significant interaction (Site × $\mathrm{Vegetation}_{3,215}$ $F = 17.19$, $P < 0.001$). At the birch site only, we measured moss biomass and surface plus

Table 1 Soil and weather conditions in the vegetation type sites along the transect at the time of each flux measurement

	Vuoskojaiveh					Abisko						Paktajaure				Vassijaure			
	October (mid)	January	March	May (mid)	May (late)	October (early)	October (mid)	January	March	May (mid)	May (late)	October (mid)	January	March	May (late)	October (mid)	January	March	May (late)
Birch																			
Air temperature (°C)	3.8	−1.0	−8.4	3.1	15.4	8.1	3.6	−0.2	−9.6	3.5	21.3	2.6	−4.0	−7.7	7.9	3.5	−1.7	−6.8	5.5
Snow depth (cm)	0	39	91	65	7	0	0	33	75	38	0	0	60	137	122	0	72	136	136
Soil temperature (°C)	1.5	−1.1	−1.8	−0.3	0.0	0.1	−0.2	−1.3	−3.9	−0.2	1.7	0.1	−0.3	−0.3	−0.1	0.5	−0.6	−0.5	−0.1
Soil water ($g\,H_2O\,g^{-1}$ dry mass soil)	2.7			2.1	3.4	0.7	0.7			2.0	3.0	2.7			nd	2.5*			5.0
Heath																			
Air temperature (°C)	2.5	0.1	−7.9	6.1		7.8	3.8	−0.6	−6.5	5.2		1.1	−5.1	−8.4	12.1	3.0	−2.5	−6.6	4.1
Snow depth (cm)	0	8	14	1		0	0	11	18	0		0	40	68	0	0	89	189	153
Soil temperature (°C)	0.7	−3.5	−8.6	−0.3		5.4	−0.6	−2.6	−8.5	0.2		−0.2	−1.1	−2.6	0.9	0.4	−0.4	−0.3	−0.1
Soil water ($g\,H_2O\,g^{-1}$ dry mass soil)	2.6			3.7		1.0	0.4			3.2		2.2			nd	3.9			nd

*Difficulties inserting the moisture probe fully into the relatively stoney soil in some of the plots at this site in October make this value a minimum estimate. No data (nd) are available for moisture measurements in May for the Paktajaure birch or heath sites or the Vassijaure heath site because the probe had broken.

Data are means ($n = 6$). Shaded columns indicate conditions during those flux measurements that were made in the transition periods to and from 'winter' (defined as the continuous period during which mean diel soil temperature at ~3 cm was <0.5 °C). Frozen hard soil conditions prevented soil moisture measurements in January and March.

Table 2 Climatic and biogeochemical variables at the birch and heath sites along the transect. Parentheses indicate standard errors ($n = 6–24$)

	Vuoskojaiveh	Abisko	Paktajaure	Vassijaure
Birch understorey				
Winter length* (days)	215	209	224	240
Evergreen shoot biomass ($g\,m^{-2}$)	314^{a} (68)	189^{a} (22)	23^{d} (8)	150^{bc} (29)
Deciduous and herb shoot biomass ($g\,m^{-2}$)	148^{a} (13)	97^{a} (11)	138^{a} (12)	128^{a} (11)
Moss biomass ($g\,m^{-2}$)	76^{ab} (31)	172^{a} (25)	37^{b} (10)	133^{a} (24)
Surface litter plus standing dead mass ($g\,m^{-2}$)	523^{a} (65)	338^{b} (22)	355^{b} (14)	517^{a} (34)
Birch density (no. of clones per $100\,m^{-2}$)	8.6	8.2	13.2	8.6
Soil organic layer depth (cm)	4.1^{d} (1.1)	6.1^{d} (1.1)	14.1^{c} (1.1)	4.1^{d} (0.1)
Heath				
Winter length* (days)	208	207	219	233
Evergreen shoot biomass ($g\,m^{-2}$)	217^{ab} (24)	155^{bc} (16)	187^{ab} (18)	103^{c} (12)
Deciduous and herb shoot biomass ($g\,m^{-2}$)	111^{ab} (18)	111^{a} (11)	53^{b} (12)	56^{b} (8)
Soil organic layer depth (cm)	8.1^{d} (1.1)	17.1^{b} (1.1)	24.1^{a} (2.1)	5.1^{d} (0.1)

*Total winter length (as defined in Table 1) was underestimated for the Vassijaure birch site because the soil temperature loggers had to be removed on 19 June which was before complete snow melt and associated soil temperature warming.

Values for each variable that do not share superscript letters in common indicate significant differences (Tukey's HSD, $P < 0.05$) between sites and vegetation types.

standing dead litter, both of which differed significantly between sites ($\text{Site}_{3,97}$ $F = 12.05$, $P < 0.001$; $\text{Site}_{3,98}$ $F = 15.67$, $P < 0.001$, respectively).

Together, these results indicate that there was significant variation in almost all environmental and pool size variables measured among the transect sites and the two vegetation types. There were no consistent trends in the pool size variables from east to west along the transect among sites or between vegetation types, with the exception of the lower deciduous plus herb shoot biomass in the heath sites at Paktajaure and Vassijaure (Table 1). By contrast, there were consistent trends of deeper snow cover, warmer soil temperatures, and longer total winter lengths from east to west along the transect (Tables 1 and 2). Furthermore, the interacting effect of vegetation type on these variables differed consistently amongst sites along the transect. Vegetation type had little effect on soil temperature in the deep snow of the Vassijaure site at the western end of the transect (Table 1). By contrast, there were strong differences in soil temperature between adjacent vegetation types where snow accumulation was relatively shallow (sites at the eastern end of the transect). Together, these results strongly suggest that the overlying trees in the birch understorey vegetation type substantially enhanced snow accumulation at the eastern sites where snow cover was relatively shallow. This enhanced snow accumulation resulted in increased thermal insulation from the atmosphere, and therefore markedly warmer soils in the birch understorey compared with the adjacent paired heath vegetation in these transect sites (Table 1).

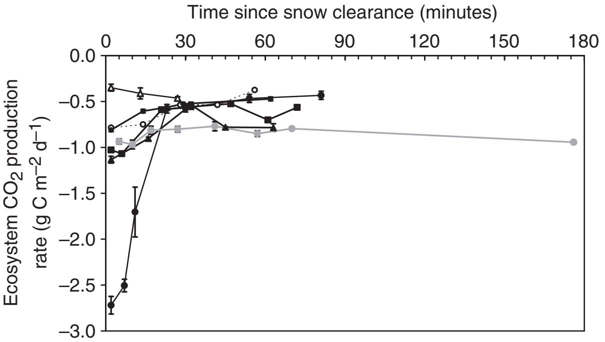

Fig. 3 The effect of snow removal on ecosystem CO_2 production rates over time for seven randomly located test plots within birch vegetation at several stages during winter. Plot soil temperature remained within 0.3 °C of initial conditions for all time series measurements. Error bars indicate standard errors of replicate 20 s measurements within each flux determination ($n = 6$). In many cases these error bars are not visible because of their low magnitude.

The effect of snow removal on CO_2 efflux rates

As a preliminary test of our measurement protocol for determining ecosystem CO_2 production rates, we assessed the disturbance effect of snow removal on CO_2 efflux by making a time series of respiration and soil temperature measurements on test areas from which snow had just been removed in a birch vegetation site. As in similar previous tests on heath vegetation (Grogan *et al.*, 2001), initial flushes due to the release of accumulated soil CO_2 resulted in *occasional* transient high efflux rates for up to 30 min after snow removal (Fig. 3). On the basis of these tests, we measured CO_2

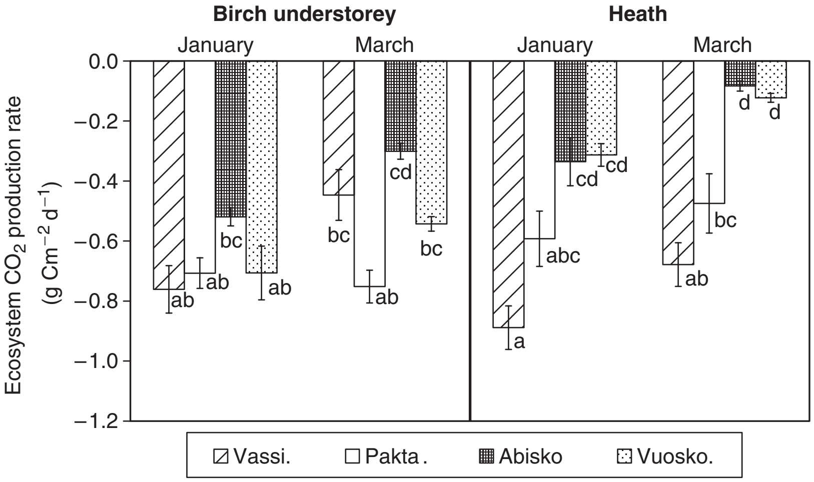

Fig. 4 Ecosystem CO_2 production rates on 2 days during the mid-winter months (January–March) in the birch understorey and heath vegetation types at four sites along a snow depth transect that decreases from left (Vassijaure) to right (Vuoskojaiveh). Columns that do not share superscript letters in common indicate significant differences (Tukey's HSD, $P<0.05$) between sites and vegetation types (bars = SEs; $n = 6$).

efflux from the exposed vegetated plots 35–60 min after snow removal, and report our data as ecosystem CO_2 production rates.

Mid-winter ecosystem CO_2 production rates

We measured appreciable ecosystem CO_2 production rates even in the coldest phase of winter (January–March), strongly suggesting that biological activity and therefore biogeochemical carbon cycling are active and significant in these ecosystems throughout winter. Ecosystem CO_2 production rates during this phase (i.e. mid-winter) differed significantly between transect sites (Fig. 4, $F_{3,80} = 31.00$, $P<0.001$), vegetation types ($F_{1,80} = 23.46$, $P<0.001$), and months ($F_{1,80} = 30.50$, $P<0.001$). The significant interaction (Site × Vegetation$_{3,80}$ $F = 14.40$, $P<0.001$) indicates that CO_2 effluxes were lower in heath relative to birch understorey vegetation but that this effect was confined to the two easterly sites along the transect. Thus, the sites with the shallowest snow, and coldest soil temperatures (heath at Vuoskojaiveh and Abisko – Table 1) had the lowest mid-winter CO_2 production rates (Fig. 4). Together, these results provide strong evidence to support Hypothesis I (that vegetation type only influences winter respiration rates when snowdepth is below a certain threshold).

In order to evaluate the controls over mid-winter ecosystem CO_2 production rates, we used regressions to test for the influences of each of several potential controlling variables on plot respiration during the January and March measurement periods. Plot soil temperature was the best explanatory variable to characterize the spatial and temporal variation in winter CO_2 production rates for both vegetation types (Table 3). The van't Hoff first-order exponential relationship between respiration and soil temperature (Paul & Clark, 1996) explained 41% of the variation in efflux from the birch understorey vegetation and 75% of the variation in heath efflux rates (Table 3). Moss biomass was inversely related to winter efflux rates in the birch understorey, explaining 23% of the variation, and suggesting some plant community composition effect on respiration from this vegetation type. Nevertheless, in contrast to soil temperature, variation in the availability of carbon substrate for respiration in categories such as organic soil mass, ground surface litter mass, and shoot biomass of either evergreen or deciduous plants had relatively minor impacts on ecosystem respiration rates from these two vegetation types (Table 3). The results here refute Hypothesis II (that vegetation pool sizes matter as determinants of regional respiration patterns) and expand the conclusions of a more localized study of intraannual variation in respiration from these ecosystems (Grogan & Jonasson, 2005) by indicating that: (a) soil temperature is the primary control on winter respiration rates for these two vegetation types even at the regional scale; and (b) soil temperature explains a particularly large part of the variation in wintertime CO_2 release rates from heath vegetation.

Ecosystem CO_2 fluxes during the winter transition periods

Ecosystem gross carbon inputs via photosynthesis (GEP) were negligible in the early winter measurement

Table 3 Ecosystem CO$_2$ production rates in relation to potential controls for all plots during the mid-winter measurement days in January and March in each vegetation type (ns = regression not statistically significant at the 5% level)

	Birch understorey			Heath		
	P	r^2	n	P	r^2	n
Soil temperature (exponential)*	0.001	0.41	53	0.001	0.75	47
Air temperature (exponential)	0.019	0.08	53	ns	–	47
Snow depth	ns	–	53	0.001	0.34	47
Soil organic layer depth†	0.015	0.15	32	ns	–	46
Evergreen shoot biomass	ns	–	28	ns	–	46
Deciduous and herb shoot biomass‡	ns	–	32	0.012	0.11	46
Moss biomass§	0.003	0.23	31			
Surface litter plus standing dead mass	ns	–	32			

*The effects of soil temperatures on respiration rates were better characterized by the van't Hoff first-order exponential relationship (Paul & Clark, 1996) than by a linear relationship [birch understorey respiration rate = 0.708 $(\exp^{0.216T})$; heath respiration rate = 0.764$(\exp^{0.257T})$ where respiration rate = A $(\exp^{(BT)})$; A is a constant representing a chemical index of the mean amount of substrate readily available for respiration over the winter and is equivalent to the mean soil respiration rate at 0 °C (g CO$_2$-C m^{-2} day^{-1}), B is a constant representing the respiration response to variation in winter soil temperature (T^{-1} in °C), and T is the soil temperature (°C)].

†Organic layer depth should be an accurate representative indicator of organic soil mass because the soil bulk densities and carbon concentrations in the two vegetation types are similar (Grogan & Jonasson, 2005).

‡Heath plot respiration rate was inversely related to deciduous plus herb shoot biomass.

§Birch plot respiration rate was inversely related to moss biomass. Moss biomass and surface litter data were collected for the birch understorey plots only.

periods for all sites (data not shown), but were significant in late winter (Table 4). Within several days of snowmelt, in water-saturated soils close to 0 °C (Vuoskojaiveh and Abisko heath in mid-May, Abisko birch and Paktajaure heath in late May – Table 1), we measured substantial gross ecosystem photosynthetic rates that were of a similar magnitude to the carbon losses associated with ecosystem respiration (Table 4). Furthermore, where the flux measures were made at times before snowmelt, and therefore on plots from which the snow had first to be removed (Vuoskojaiveh and Abisko birch in mid-May, Vuoskojaiveh birch in late May – Table 1), we measured statistically significant and substantial levels of 'potential' GEP (i.e. GEP capacity when exposed to ambient daylight) within 35–60 min of exposure (Table 4). In the Vuoskojaiveh birch site in late May, the particularly high potential GEP rates are consistent with the relatively shallow snowcover at that time (Tables 1 and 4).

Ecosystem total wintertime CO$_2$ production

Our interpolated estimates of ecosystem total wintertime CO$_2$ production indicated carbon losses that are likely to be significant to the annual carbon balance of these ecosystems (Fig. 5). This interpolation method for total winter respiration yielded almost identical values to modelled outputs generated previously for the two vegetation types at the Abisko site (Grogan & Jonasson, 2005). In the transect study here, both vegetation type and site had strong effects on total ecosystem wintertime CO$_2$ production (Vegetation$_{1,40}$ $F = 28.73$, $P < 0.001$; Site$_{3,40}$ $F = 20.48$, $P < 0.001$). Furthermore, as in the analysis of mid-winter CO$_2$ efflux rates, the effect of vegetation type strongly depended on transect site (Site × Vegetation$_{3,40}$ $F = 3.10$, $P < 0.037$), indicating that heath ecosystem CO$_2$ production over the entire winter was substantially lower than that from the birch understorey (Fig. 5) at the easterly end of the transect (Vuoskojaiveh and Abisko) only. Note that our temperature-based definition of 'winter' matches the period of snowcover very well for the eastern sites (Tables 1 and 2) where snow depths are relatively low. By contrast, there is a mismatch in the western sites because soil temperatures generally reached the end of 'winter' well before snowmelt (Tables 1 and 2, Paktajaure birch; Vassijaure birch and heath). Thus, if we had applied a winter definition based on snowcover, our estimates of total winter CO$_2$ release would be substantially increased for each of the latter sites. As a result, the conclusions reached above on the relative importance of climate and vegetation type would be even more strongly supported by the data.

The above highly significant effects of transect site, vegetation type, and their interaction on total winter respiration were all entirely lost ($P > 0.27$) when

Table 4 Ecosystem component CO_2 fluxes during the May transition period from winter to summer ($g\,CO_2$-$C\,m^{-2}\,day^{-1}$) in the birch and heath sites along the transect

	Vuoskojaiveh	Abisko	Paktajaure	Vassijaure
Birch understorey				
Mid-May				
NEE	−0.87 (0.15)	−0.36 (0.10)		
ER	−1.32 (0.16)	−0.98 (0.13)		
GEP	***0.44*** *(0.04)*	***0.62*** *(0.12)*		
Late-May				
NEE	−0.26 (0.14)	−0.11 (0.08)	−0.88 (0.15)	−1.81 (0.18)
ER	−1.63 (0.34)	−2.30 (0.16)	−0.99 (0.11)	−2.31 (0.36)
GEP	***1.36*** *(0.31)*	**2.20** (0.12)	***0***	***0***
Heath				
Mid-May				
NEE	0.11 (0.12)	−0.34 (0.04)		
ER	−1.09 (0.08)	−0.72 (0.14)		
GEP	**1.20** (0.18)	**0.44** (0.07)		
Late-May				
NEE			0.37 (0.11)	−1.41 (0.20)
ER			−1.16 (0.06)	−1.93 (0.32)
GEP			**1.53** (0.15)	***0***

Gross ecosystem photosynthesis (GEP) rates indicated in bold text were computed on the basis of statistically significant differences (paired *t* tests; $P<0.05$) between net ecosystem CO_2 exchange (NEE) and ecosystem respiration (ER). Where these latter flux measurements were made at sites that were snow-covered, and therefore on plots from which the snow had first to be removed, the GEP values are italicized to indicate potential rather than actual rates of gross carbon gain.
Negative values indicate carbon dioxide fluxes out of the ecosystem to the atmosphere. Parentheses indicate standard errors ($n = 6$).

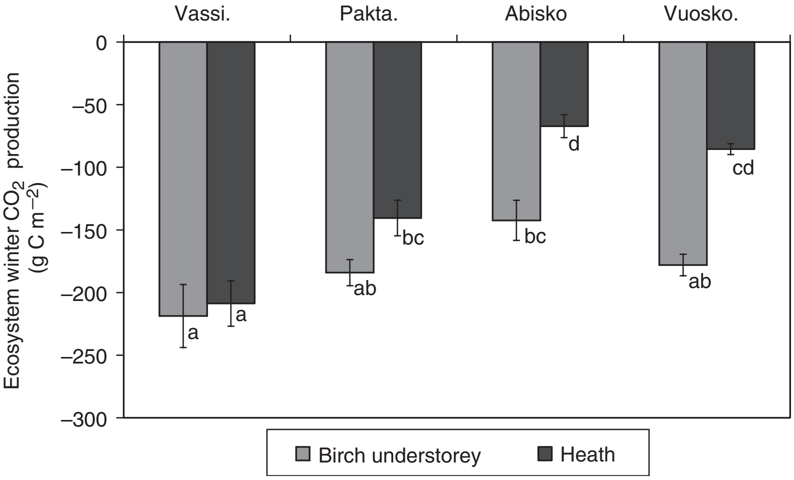

Fig. 5 Estimated total CO_2 production during winter 1999/2000 in the birch understorey and heath vegetation types at four sites along a snow depth transect that decreases from left to right. These estimates are based on interpolations of individual ecosystem respiration flux measurements from the vegetated surface at several sampling times (4–5) through the winter (bars = SEs; $n = 6$). Winter is defined as in Table 1 legend. Columns that do not share superscript letters in common indicate significant differences (Tukey's HSD, $P<0.05$) between sites and vegetation types.

maximum snow depth was included as a covariate (maximum snow $depth_{1,39}$ $F = 2.90$, $P<0.10$) in the statistical analysis. Together, these analyses strongly support Hypothesis III (that snowdepth maxima are a primary determinant of regional patterns of total wintertime CO_2 release).

Discussion

Climate and vegetation type as controls on winter respiration

Our study of winter respiration in adjacent vegetation types at several sites along a strong climatic snowdepth

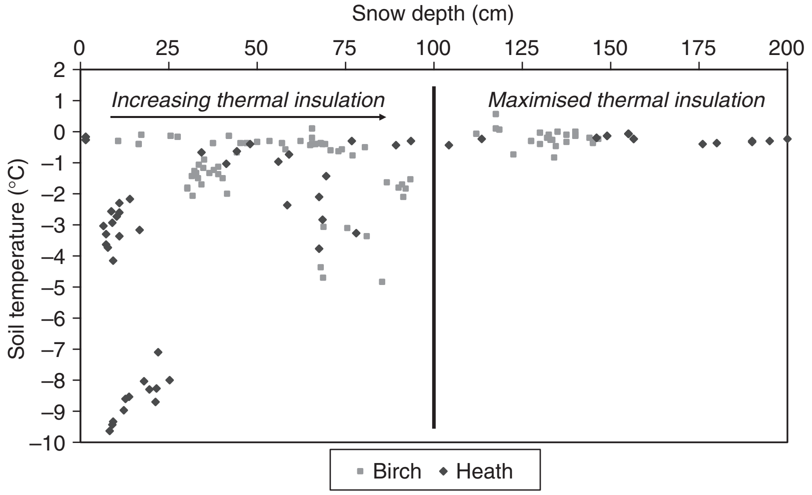

Fig. 6 Soil temperature (~ 3 cm depth) in relation to snow depth during each plot flux measurement over the entire snow-covered period at the birch and heath sites along the transect.

gradient clearly demonstrates that both winter climate and vegetation type can be important factors driving regional patterns of CO_2 release. The major climatic feature of the gradient was not air temperature but rather site differences in snow accumulation that resulted in corresponding differences in soil temperature. The influences of both climate and vegetation type were evident in the mid-winter efflux rates (Fig. 4) and in total winter CO_2 production (Fig. 5). Furthermore, the effect of vegetation depended on transect site in both analyses: heath efflux rates were significantly lower than birch only at sites where snow accumulation (and therefore soil temperature) was relatively low. In other words, CO_2 efflux from the birch sites was broadly similar across all transect sites, corresponding with the substantial snow cover at these sites. By contrast, heath efflux was substantially lower at the eastern side of the transect (Vuoskojaiveh and Abisko) compared with the western side (Figs 4 and 5). These low effluxes were due to more severe soil temperatures caused by limited snow accumulation that led to relatively ineffective thermal insulation against winter air temperatures.

The second part of our study attempted to determine the relative importance of environmental and pool size variables in explaining regional patterns of efflux from each of the two vegetation types. We found that soil temperature was a much more powerful explanatory predictor of mid-winter CO_2 efflux rates than substrate availability (i.e. plant, litter or soil carbon pool sizes).

Together these results explain the mechanisms by which vegetation can influence CO_2 release rates and total winter CO_2 production. If snowfall is relatively low, tall vegetation can influence the spatial pattern of deposition, and/or subsequent redistribution by wind resulting in preferential accumulation of snow within that vegetation. By contrast, adjacent vegetation of lower stature such as heath cannot influence accumulation patterns. This analysis leads to two conclusions. First, vegetation type is only likely to influence winter CO_2 efflux and biogeochemical cycling in areas of low-to-moderate snowfall. Our data suggest that if snow accumulation is greater than about 1 m, vegetation has negligible effect on regional patterns of efflux (Fig. 6). Second, vegetation influences efflux by physical effects (i.e. increasing snow accumulation by promoting localized deposition and preferential redistribution that restricts soil temperature declines) rather than by biogeochemical effects (such as vegetation type differences in carbon pool sizes). Our results, therefore, suggest that total winter respiration may be explained largely by differences in maximum snow depth accumulated during the season. Maximum snow depth may be an appropriate and representative index of overall total winter respiration in that it directly influences efflux rates during winter through its integrated effect on the time course of winter soil temperatures at a site. As deeper snowcover leads to a longer snow-covered period in the Spring, maximum snow depth also determines total winter length because it defines the temporal extent of winter at a site. Our results show that where vegetation type influences total winter release, that impact is manifested in the physical effect of vegetation (i.e. snow trapping, rather than biogeochemical differences) meaning that once again, this influence is incorporated within maximum snow depth. In conclusion, our results together strongly suggest that regional patterns of total winter CO_2 production could be reasonably estimated on the basis of variations in maximum snow depth.

Winter flux measurement protocol

This approach to winter CO_2 flux measurements has been used previously (Alm *et al*., 1999; Grogan *et al*., 2001; Grogan & Jonasson, 2005), but raises several methodological issues: (a) accumulation of CO_2 in snow-covered soils during winter can result in *occasional* initial CO_2 flushes following snow removal (Oechel *et al*., 1997) that are not representative of ambient CO_2 production rates (Fig. 3). The flux values reported here may over-estimate ambient ecosystem CO_2 production rates if the stored soil CO_2 pool was not fully released by the end of the 35 min 'wait' period. The test evidence from a birch site reported here (Fig. 3) and from a heath site in a previous study (Grogan *et al*., 2001; Grogan & Jonasson, 2005); however our regular repeatability tests (see 'Materials and methods') should alleviate this concern; (b) soil temperature and moisture can change during the 'wait' period following snow removal, resulting in altered respiration rates by the time of measurement. Typically, plot soil temperatures remained within 0.3 °C of initial conditions during this interval, presumably because there was not a large difference between air temperatures on the winter flux measurement days (ranging from 0 to −10 °C) and soil temperatures. Again, the time series tests and repeatability tests referenced above should alleviate this concern; (c) since some of the CO_2 respired by plants and soil organic matter during winter is accumulated within soil and the overlying snow column, our measures of ecosystem CO_2 production rates are not necessarily equivalent to simultaneous rates of ecosystem CO_2 release from the snow surface to the atmosphere; (d) removal of overlying snow enhances the CO_2 concentration gradient for diffusion from vegetation/soil to the atmosphere. However, *in situ* production of CO_2 by the soils and vegetation should not be directly influenced by this effect unless the subnivean CO_2 concentrations were high enough to inhibit respiratory activity. We are not aware of any evidence to suggest that typical subnivean CO_2 concentrations (<5000 ppm) can significantly inhibit soil microbial activity.

Springtime gross ecosystem photosynthesis

Together, our gross ecosystem photosynthesis data demonstrate that plant communities in both vegetation types develop the physiological capacity for photosynthesis well before snowmelt at the end of winter, and may even be photosynthesizing under a shallow snowpack. A recent physiological study of Alaskan tussock tundra species reached a similar conclusion (Starr & Oberbauer, 2003). Furthermore, our data indicate that significant *gross* ecosystem carbon gain can be initiated very rapidly after snowmelt in these vegetation types, occasionally resulting in overall ecosystem *net* carbon gain (Table 4 – heath at Vuoskojaiveh in mid-May, and Paktajaure in late May) at this very early stage in the growing season. Steenberg Larsen *et al*. (submitted) have reached a similar conclusion based on an independent study of the same two vegetation types in a different year.

Overall, these results indicate substantially different carbon dynamics between the two vegetation types. We found no significant GEP carbon inputs in either vegetation type in October at the onset of winter. Wintertime respiratory carbon losses were relatively low in heath as compared with birch understorey at the eastern side of the transect (Figs 4 and 5), where soil temperatures were lower (Table 1) and the snow-covered period was shorter (Tables 1 and 2). Heath vegetation at these sites also experienced earlier net carbon gain (Table 4) and, therefore, potentially a longer growing season compared with the adjacent birch understorey. These patterns suggest that, in areas of low-to-moderate snowfall, heath ecosystems have longer effective growing seasons and therefore larger annual net carbon gains than at least the understorey vegetation of neighbouring birch sites. Larger carbon accumulation rates by heath vegetation may explain the two to three times deeper organic soil layers in heath as compared with adjacent birch sites at all but the most western end of the transect (Table 2). Nevertheless, the influence of the overlying trees in the birch sites on net annual soil carbon accumulation remains to be determined.

Implications of this study

Overall, the results of this study lead to three major insights. First, they provide a basis for modelling regional patterns of winter respiration rates and total CO_2 release in terms of its primary controls: climate and vegetation type. Specifically, the overall conclusions concerning the primary impact of snow cover as a thermal insulator provides the basis for estimating regional patterns of total CO_2 release during winter using maximum snow depth derived from remote sensing data (Derksen *et al*., 2005). Success with this approach would depend on resolving the scalar differences in spatial resolution between maximum snowdepth across the landscape and passive microwave data.

Second, arctic regions are widely and consistently predicted to undergo both rapid increases in winter temperature and increases in snowfall (Giorgi *et al*., 2001). Our results provide a basis for interpreting the potential impacts of these changes on wintertime biogeochemical cycling for a variety of vegetation types (Fig. 7). Predicted air temperature increases of up to 12 °C in the winter months by the end of the century

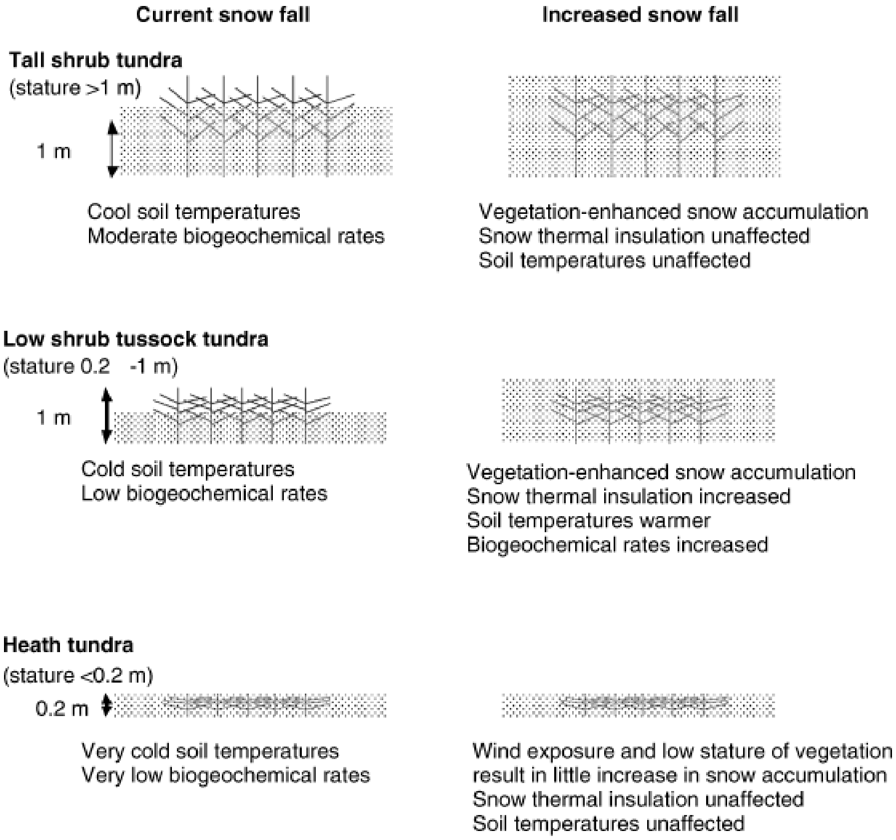

Fig. 7 Predicted impacts of increased snowfall associated with arctic climate change on snow accumulation, soil temperature and wintertime biogeochemical rates in three tundra vegetation types of differing stature. These predictions apply to the many regions of the Arctic and sub-Arctic that currently experience snow accumulation to depths ranging from 0 to 1 m (Taras *et al*., 2002; Grogan & Jonasson, 2003; Derksen *et al*., 2005; www.ans.kiruna.se/ans.htm).

(ACIA, 2004) will have little impact on winter respiration in landscape patches where snow accumulation is already >1 m, such as typically occurs in the tall shrub tundra of riparian and floodplain localities or in most birch forest tundra. By contrast, increases in air temperature and/or snow accumulation in areas where current snow cover is generally <1 m deep are likely to result in substantial increases in rates of biogeochemical activities. This threshold concept is supported by empirical and modelling studies of the relationship between air and snow-ground interface temperatures in Alaska that suggest the two become decoupled at snowdepths >0.8 m (Taras *et al*., 2002). Our results strongly suggest that biogeochemical cycling would be most enhanced by increased snowfall in vegetation types of moderate stature such as low shrub tussock tundra where the vegetation is typically 0.2–1 m above the surface (Aleksandrova, 1980; Bliss & Matveyeva, 1992), current snowdepth is generally below the threshold, and deeper snow accumulation is likely as a result of vegetation 'snow trapping' (Fig. 7). Finally, our transect study shows that the potential for enhanced snow accumulation as a result of increased snowfall on heath vegetation is clearly variable, and will depend primarily on the potential for snow trapping by local topography rather than the vegetation itself (which is typically <0.2 m high). In general, heath tundra vegetation most commonly occurs on topographic prominences where severe wind exposure constrains the potential for snow accumulation (Bliss & Matveyeva, 1992), resulting in current snowdepths of 0–0.2 m. Therefore, we expect that winter respiration from most heath vegetation is unlikely to be sensitive to enhanced snowfall (Fig. 7).

Third, there is now a growing body of evidence indicating increasing density and spatial cover of shrubs such as alder, birch, and willow in Alaska and elsewhere (Sturm *et al*., 2001b, 2005). Sturm *et al*. (2001a) have hypothesized that shrubs may facilitate their own growth and advance by accumulating snow during winter, thereby restricting soil temperature declines and promoting wintertime biogeochemical cycling of nutrients from which the shrubs benefit in the following growing season. Photographic and remote sensing data indicate that there may have been substantial increases in shrub cover (particularly alder) over the past 50 years not just in Alaska but across much of the arctic region (Sturm *et al.*, 2005). Modelling studies indicate that increased shrub dominance may lead to profound changes in snow, energy and moisture fluxes within tundra ecosystems (Liston *et al.*, 2002). Our results provide fundamental insights into the potential mechanism underlying the series of interconnected hypotheses that have been proposed to explain the increasing proliferation of shrubs (Sturm *et al.*, 2001b). We have demonstrated that ecosystem respiration is sensitive to increases in snow accumulation within the snowdepth range up to 1 m. Typically, birch, willow and alder shrubs on the large flat tracts of tundra between riparian and slope streamflow areas extend 0.2–1 m above the soil surface (Aleksandrova, 1980). Our results here indicate that it is enhanced snow accumulation by shrubs within this particular height range that is most likely to lead to biologically significant increases in winter soil temperature. Furthermore, our flux measurement data strongly support Sturm *et al.*'s hypothesis (2001a) that the advance and increasing density of shrubs under future climate would also enhance subnivean respiration, presumably increasing wintertime biogeochemical activities and the availability of soil nutrients that limit plant primary production in the subsequent growing season.

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