

# Temperature and substrate controls on intra-annual variation in ecosystem respiration in two subarctic vegetation types

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## Abstract

Arctic ecosystems are important in the context of climate change because they are expected to undergo the most rapid temperature increases, and could provide a globally significant release of CO<sub>2</sub> to the atmosphere from their extensive bulk soil organic carbon reserves. Understanding the relative contributions of bulk soil organic matter and plant-associated carbon pools to ecosystem respiration is critical to predicting the response of arctic ecosystem net carbon balance to climate change. In this study, we determined the variation in ecosystem respiration rates from birch forest understory and heath tundra vegetation types in northern Sweden through a full annual cycle. We used a plant biomass removal treatment to differentiate bulk soil organic matter respiration from total ecosystem respiration in each vegetation type.

Plant-associated and bulk soil organic matter carbon pools each contributed significantly to ecosystem respiration during most phases of winter and summer in the two vegetation types. Ecosystem respiration rates through the year did not differ significantly between vegetation types despite substantial differences in biomass pools, soil depth and temperature regime. Most (76–92%) of the intra-annual variation in ecosystem respiration rates from these two common mesic subarctic ecosystems was explained using a first-order exponential equation relating respiration to substrate chemical quality and soil temperature. Removal of plants and their current year's litter significantly reduced the sensitivity of ecosystem respiration to intra-annual variations in soil temperature for both vegetation types, indicating that respiration derived from recent plant carbon fixation was more temperature sensitive than respiration from bulk soil organic matter carbon stores.

Accurate assessment of the potential for positive feedbacks from high-latitude ecosystems to CO<sub>2</sub>-induced climate change will require the development of ecosystem-level physiological models of net carbon exchange that differentiate the responses of major C pools, that account for effects of vegetation type, and that integrate over summer and winter seasons.

*Keywords:* arctic, birch, carbon, climate change, CO<sub>2</sub>, heath, respiration, soil, temperature, tundra, vegetation type, winter

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## Introduction

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<sub>2</sub> release to the atmosphere (Lashof, 1989). Over the long term, it is hypothesized that the increased nutrient availability associated with

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enhanced soil organic matter decomposition will stimulate plant growth and ultimately result in a negative feedback to atmospheric CO<sub>2</sub> concentrations (Shaver *et al.*, 1992). Field measurements indicating a warming trend in the Arctic over the last 30 years (Serreze *et al.*, 2000), net CO<sub>2</sub> release from tundra during the growing season in the 1980s (Oechel *et al.*, 1993), followed by a return to net C uptake more recently (Oechel *et al.*, 1998), are consistent with the hypothesized temporal dynamics of tundra net C balance responses to climate change. Modelling studies validated with summertime experimental field manipulation data concur (McKane *et al.*, 1997). Nevertheless, full evaluation of the temporal dynamics of arctic ecosystem carbon balance responses to climate change can only be achieved by including winter along with growing season activities in field and modelling studies (Hobbie *et al.*, 2000).

Ecosystem respiration (gross ecosystem CO<sub>2</sub> release), rather than gross primary production (gross CO<sub>2</sub> uptake), is often the most critical component determining large-scale spatial and temporal variation in annual net C balance. For example, ecosystem respiration is the driving component of regional differences in net C balance across latitudes in European forests (Valentini *et al.*, 2000). Similarly, inter-annual differences in growing season net CO<sub>2</sub> exchange from an arctic tussock tundra ecosystem were almost completely explained by interannual differences in ecosystem respiration (Vourlitis & Oechel, 1999). At a global scale, the response of soil respiration is critical to net CO<sub>2</sub> sink or source projections in models that couple carbon cycle feedbacks to the climate system (Cox *et al.*, 2000). Thus, our capacity to characterize spatial and temporal variabilities in ecosystem net C balance, and to develop models of how net C balance will respond to perturbations such as climate change strongly depends on understanding the controls and component source pools of ecosystem respiration.

Ecosystem respiration during winter is especially important in arctic ecosystems as General Circulation Models (GCMs) of global climate change predict that the most rapid increases in regional air temperature will occur at high latitudes during the cold season, and will be accompanied by increased snowfall (Giorgi *et al.*, 2001). Recent studies indicate that wintertime respiration typically ranges from 15% and 50% of total annual respiration in arctic and boreal ecosystems (Zimov *et al.*, 1996; Oechel *et al.*, 1997; Fahnestock *et al.*, 1998; Fahnestock *et al.*, 1999; Vourlitis & Oechel, 1999; Aurela *et al.*, 2002; Lafleur *et al.*, 2003). Differentiation of the source pools contributing to winter respiration is important because it is warming effects on the extensive bulk soil organic matter pool that make arctic ecosystems important in terms of the potential for

globally significant feedbacks to atmospheric CO<sub>2</sub> concentrations. Preliminary investigations attempting to differentiate bulk soil and more recent plant C pool contributions clearly demonstrate that respiration derived from both bulk soil and more recently fixed plant C pools are each active components of total ecosystem respiration during winter (Winston *et al.*, 1997; Grogan *et al.*, 2001). These initial studies suggest dominance by plant-associated pools in heath tundra in midwinter at least (Grogan *et al.*, 2001), and a substantial ongoing winter contribution from deep bulk soil organic matter in boreal forests (Winston *et al.*, 1997). In summary, it has only recently become clear that we must develop a mechanistic understanding of the *relative* responses of bulk soil and plant-associated C pools through *both* winter and summer seasons, if we are to be able to accurately predict the time course and direction of potential feedbacks from arctic ecosystems to global climate change.

Ecosystem respiration is the sum of respiration derived from decomposition of accumulated 'bulk' organic matter in soils and respiration derived from C recently fixed by plants (i.e. respiration by shoots, roots, mycorrhizal and rhizosphere microbes, as well as that associated with microbial decomposition of fresh litter). An experimental manipulation study using previously-trenched plots to remove the influence of plants in a temperate mixed hardwood forest ecosystem concluded that the temperature sensitivity of respiration from 'recent' (root/rhizosphere) C pools exceeded that of 'old' (bulk soil) below-ground C pools during the growing season (Boone *et al.*, 1998). Here, for the first time, we have used a similar approach in two common high-latitude vegetation types to contrast relative contributions from bulk soil organic matter and plant-associated C pools to fall, winter, spring and summertime ecosystem respiration rates and to parameterize their first-order respiration equation coefficients for temperature sensitivity and substrate availability. We hypothesized that for intra-annual variation in ecosystem respiration in our heath tundra and birch forest understory subarctic vegetation types:

- I. Plant-associated and bulk soil organic matter C pools are both significant contributors to ecosystem respiration rates during all seasons.
- II. Differences in plant biomass, soil depth (i.e. substrate available for respiration) and soil temperature regime between vegetation types result in differences in ecosystem respiration rates through an annual cycle.
- III. The temperature sensitivity of respiration derived from recently fixed, plant-associated C pools exceeds that of bulk soil organic matter throughout the annual cycle.

## Materials and methods

### Experimental set-up

This study was conducted in adjacent birch forest and heath tundra vegetation types near Abisko (68°20'42"N, 18°50'18"E, elevation 415 m a.s.l.), in northern Sweden. The climate in this region is subarctic with mean summer and winter air temperatures of 10 and -9 °C, respectively, with snow cover usually lasting from mid-October to early May (Anonymous 2004). The vegetation in this region is broadly characterized into either birch (*Betula pubescens* ssp. *tortuosa* Ledeb.) forest containing an understory heath plant community, or heath tundra. The organic surface soils at both sites have similar bulk densities ( $\sim 0.06 \text{ g cm}^{-3}$ ), organic matter contents ( $\sim 84\%$  ash-free dry weight), but differ in depth ( $\sim 6 \text{ cm}$  at birch;  $\sim 17 \text{ cm}$  in heath). In June 1999, plant removal (treatment) plots were established by cutting trenches to the underlying bedrock around six areas ( $\sim 1.6 \times 2.2 \text{ m}^2$ ) of similar understory vegetation within the forest site in order to cut all penetrating birch roots (Grogan & Jonasson, 2003). Aluminum frames ( $1056 \text{ cm}^2$ ) were randomly placed within each trenched area. All enclosed rooted vegetation was guided up through each frame before cutting a slot in the soil around the outer edge, and pressing it down 2–8 cm into the soil organic layer. The above-ground vegetation (including mosses) was gently pulled out by hand, along with as much of the attached below-ground stem and root material from the surface soil as possible without causing excessive disturbance (Grogan & Jonasson, 2003). Senesced leaf litter of both the understory shrubs and overlying birch trees that had been trapped within the vegetation was separated from the removed vegetation and replaced on the soil surface. Control plot frames were randomly located outside the trenched areas. At the nearby heath tundra site, equivalent control and plant-removal treatment plot frames ( $n = 6$ ) were randomly located within areas of similar vegetation composition. In this case, the frames were pushed  $\sim 10 \text{ cm}$  down into the organic layer. Occasional regenerating shoots in treatment plots within both vegetation types were pulled out 1 week prior to the first flux measurement in October, and were extremely rare thereafter.

### CO<sub>2</sub> flux measurements

Ecosystem respiration was determined in early October, mid-January, early March, mid-May and mid-July of 1999/2000 using an infrared gas analyzer (LI-COR 6200, Lincoln NE, USA) attached to a cube-shaped chamber (35.5 L) which we constructed from perspex and fitted with a pair of small circulation fans. This chamber fitted

directly into a groove around the upper perimeter of each aluminum frame, and was covered with opaque sheeting prior to flux measurement. Sealing was achieved by slotting the chamber into the frame groove and filling the latter with water (during snow-free measurement periods – October, May and July), or packed snow (January, March). At each site visit during the snow-covered phase of winter, we located the plots and removed the overlying snow to expose the vegetated surface.

We assessed the disturbance effect of snow removal on CO<sub>2</sub> efflux in birch vegetation in January and March by making a time series of simultaneous measurements of ecosystem respiration and soil temperature (3–5 cm depth) on test areas from which snow had just been removed. As in similar previous tests on heath vegetation (Grogan *et al.*, 2001), initial flushes because of the release of accumulated soil CO<sub>2</sub> resulted in transient high efflux rates for up to 25 min after snow removal, and then steady rates for the next 60 min. Soil temperatures during the entire test period did not vary significantly because of the low differential between soil and air temperatures. On the basis of these tests, we measured CO<sub>2</sub> efflux from the plots 30–70 min after snow removal. Thus, our January and March data are estimates of ecosystem respiration rates beneath snow, rather than concurrent CO<sub>2</sub> release rates from the snow surface to the atmosphere which may be influenced by CO<sub>2</sub> storage within snow profiles.

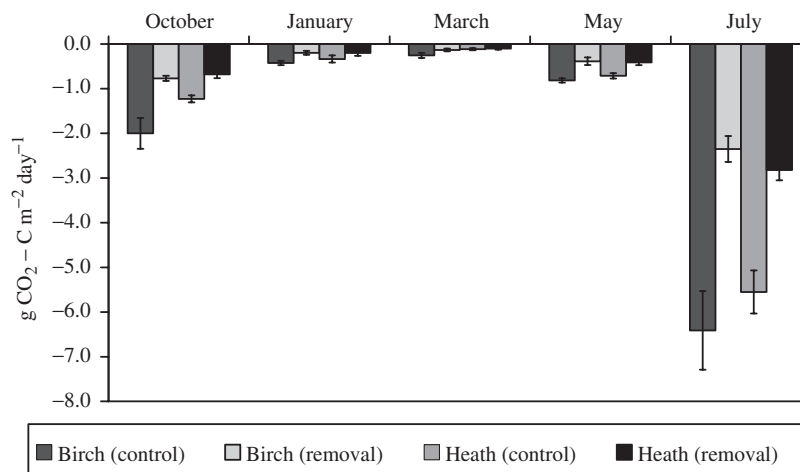
Ecosystem respiration rates in the heath site were measured repeatedly on the same plots through the annual cycle. In order to avoid long-term exposure and disturbance effects of snow removal at the birch site (where snow cover was sufficient to provide substantial thermal insulation), we established adjacent (<0.3 m) pairs of treatment plots and control plots during the experimental set-up so that we could use alternate plots for the January and March flux measures. Thus, fluxes in the birch site were measured on the same plots through all phases of the annual cycle except one of the midwinter periods, and in the statistical analysis, the latter was assumed to be a repeated measure. CO<sub>2</sub> fluxes for each period were measured over six successive 20 s intervals and averaged to calculate mean flux per sample area.

We tested the precision of our flux measurement protocol in March and May by repeating several plot flux measurements at the end of the sampling visit (i.e. 30–60 min after the initial measurements) to each site. Initial and repeat measures were closely correlated ( $r = 0.92$ ; Slope = 1.06) indicating close precision in the measurement protocol. To test the sensitivity of the equipment under winter field conditions, we placed the chamber on a plastic sheet, sealed the edges with packed snow and made successive blank measurements

**Table 1** Treatment effects on plant biomass and soil components ( $\text{g dry mass m}^{-2}$ ) and soil microbial biomass carbon ( $\text{g C m}^{-2}$ ) in each vegetation type in July 2000

Category	Birch understory (control)	Birch understory (removal)	Heath (control)	Heath (removal)
<i>Plant: above-ground</i>				
Vascular shoots				
Evergreen	155 <sup>a</sup> (33)	0	189 <sup>a</sup> (38)	0
Deciduous	122 <sup>a</sup> (24)	0	90 <sup>a</sup> (17)	0
Herbs	3.3 <sup>a</sup> (1.7)	0	40 <sup>b</sup> (10)	0
Non-vascular				
Mosses	110 <sup>a</sup> (42)	0	210 <sup>a</sup> (76)	0
Lichens	8.1 <sup>a</sup> (5.8)	0	49 <sup>b</sup> (11)	0
<i>Plant: below-ground</i>				
Coarse roots	796 <sup>a</sup> (72)	313 <sup>b</sup> (40)	694 <sup>a</sup> (74)	423 <sup>b</sup> (106)
Fine roots	231 <sup>a</sup> (26)	164 <sup>b</sup> (36)	522 <sup>c</sup> (41)	313 <sup>a</sup> (45)
Total plant biomass	1426 <sup>a</sup> (96)	477 <sup>c</sup> (47)	1792 <sup>b</sup> (79)	736 <sup>c</sup> (137)
Surface litter/standing dead	356 <sup>a</sup> (23)	nd	270 <sup>a</sup> (53)	nd
Soil	4684 <sup>a</sup> (618)	nd	5467 <sup>a</sup> (326)	nd
Soil microbial C	60 <sup>a</sup> (9)	48 <sup>a</sup> (4)	26 <sup>b</sup> (2)	22 <sup>b</sup> (3)

Mean sampled soil depth ranged from 7 to 9 cm, and did not differ statistically between vegetation types. Parentheses indicate standard errors ( $n = 6$ ). Differing superscript letters within a row indicate statistically significant differences ( $P < 0.05$ ) using a  $t$  test or two-way analysis of variance. Surface litter and soil total mass pools were not determined in the treatment plots (nd), but should not have been affected by our experimental protocol (see Materials and methods).

**Fig. 1** The effect of plant-removal treatment on ecosystem  $\text{CO}_2$  production rates during 1999–2000 in birch understory and heath vegetation types in northern Sweden. Bars indicate standard errors ( $n = 6$ ).

(mean =  $0.0034 \text{ g CO}_2\text{-C m}^{-2} \text{ day}^{-1}$ ; SD =  $0.0086$ ;  $n = 10$ ). These results suggest that the limit of detection for each plot efflux measurement was  $\pm 0.023 \text{ g CO}_2\text{-C m}^{-2} \text{ day}^{-1}$  (i.e. the minimum value significantly different from zero with 95% confidence).

#### Environmental and chemical measurements

Soil temperatures at 3–5 cm depth into the organic soil layer in each plot were recorded immediately after each

flux measurement using hand-held temperature probes ( $n = 3$ ). Preliminary checks of the midwinter soil temperature profile at 1 cm depth intervals down to 8 cm indicated no significant differences in temperature. Generally, soil temperatures (at 3–5 cm depth) ranged from  $-2$  to  $+2^\circ\text{C}$  (heath) and  $+5^\circ\text{C}$  (birch understory) above air temperatures on snow-covered flux measurement days, and 5 to  $6^\circ\text{C}$  lower than air temperature during snow-free periods. Gravimetric soil

moisture was measured when the sites were snow-free using a Theta probe (Delta-T Devices, Cambridge, U.K.) that provides an integrated reading for the top 4.5 cm of soil, and using a site-specific calibration. In mid-July 2000, the above- and below-ground biomass in the heath plots, and within adjacent treatment and control plots in the birch site, were sampled and sorted as described elsewhere (Grogan & Jonasson, 2003). Soil microbial biomass C was determined by chloroform fumigation (Brookes *et al.*, 1985) using a  $K_C$  of 0.35.

#### Data processing and statistical analyses

Treatment effects on plant root biomass components and soil microbial biomass carbon between vegetation types were tested using two-way analyses of variance (ANOVAS). Differences in plant biomass and soil components between vegetation types were tested using Student's *t* tests.

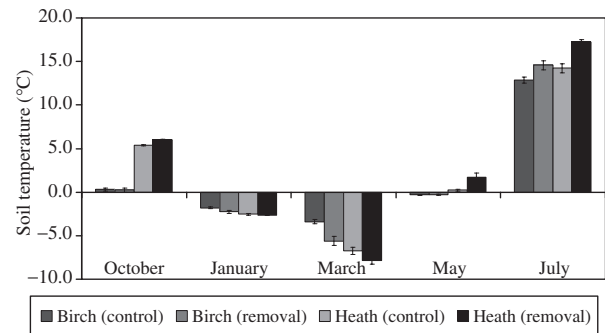
Nested three-way ANOVAS were used to test for significant effects of vegetation type, treatment and sampling month on ecosystem  $\text{CO}_2$  production rates, soil temperatures and soil moisture levels. Vegetation type, treatment and their interaction were tested within the main stratum (total  $df = 23$ ), while month and its interactions were tested within the substratum (total  $df = 96$ ). All statistically significant effects and interactions ( $P < 0.05$ ) are reported in the text.

Ecosystem respiration rates from each of the vegetation types and treatments were related to soil temperatures through the year using the classic first-order exponential relationship (Paul & Clark, 1996; van't Hoff, 1898):

$$\text{respiration rate} = A \exp^{(BT)},$$

where  $A$  is a constant ( $\text{g CO}_2\text{-C m}^{-2} \text{day}^{-1}$ ), representing an index that integrates both the chemical quality and the amount of substrate that is available for respiration over the annual cycle (equivalent to the mean soil respiration rate at  $0^\circ\text{C}$ ),  $B$  ( $\text{T}^{-1}$  in  $^\circ\text{C}$ ) is a constant representing the respiration response to intra-annual variation in soil temperature, and  $T$  ( $^\circ\text{C}$ ) is the soil temperature. We calculated first-order equation coefficients for the time series data for each of the replicate plots ( $n = 6$ ) in the vegetation types and treatments. We tested for significant effects of treatment and vegetation type on first-order exponential respiration equation coefficients using two-way ANOVAS (total  $df = 23$ ). The sensitivities of ecosystem respiration and bulk soil organic matter respiration to intra-annual variations in soil temperature were also calculated in the form of  $Q_{10}$  values ('Annual  $Q_{10}' = e^{10(B)}$ ).

Total wintertime  $\text{CO}_2$  production at the birch understory and heath tundra sites was estimated using the



**Fig. 2** The effect of plant-removal treatment on soil temperatures (5 cm depth) during 1999–2000 in birch understory and heath vegetation types in northern Sweden. Bars indicate standard errors ( $n = 6$ ).

mean values of the first-order exponential equation coefficients derived from this study and local mean diel soil temperature records for each vegetation type (Grogan *et al.*, 2001; Grogan & Jonasson, 2003). For this analysis, winter was defined as that period when mean diel soil temperatures  $< 0^\circ\text{C}$ . Local weather station records of soil temperatures at 5 cm depth between 1987 and 2001 (Anonymous, 2004) were used to generate estimates of interannual variability in total winter  $\text{CO}_2$  efflux for each vegetation type and treatment.

#### Results

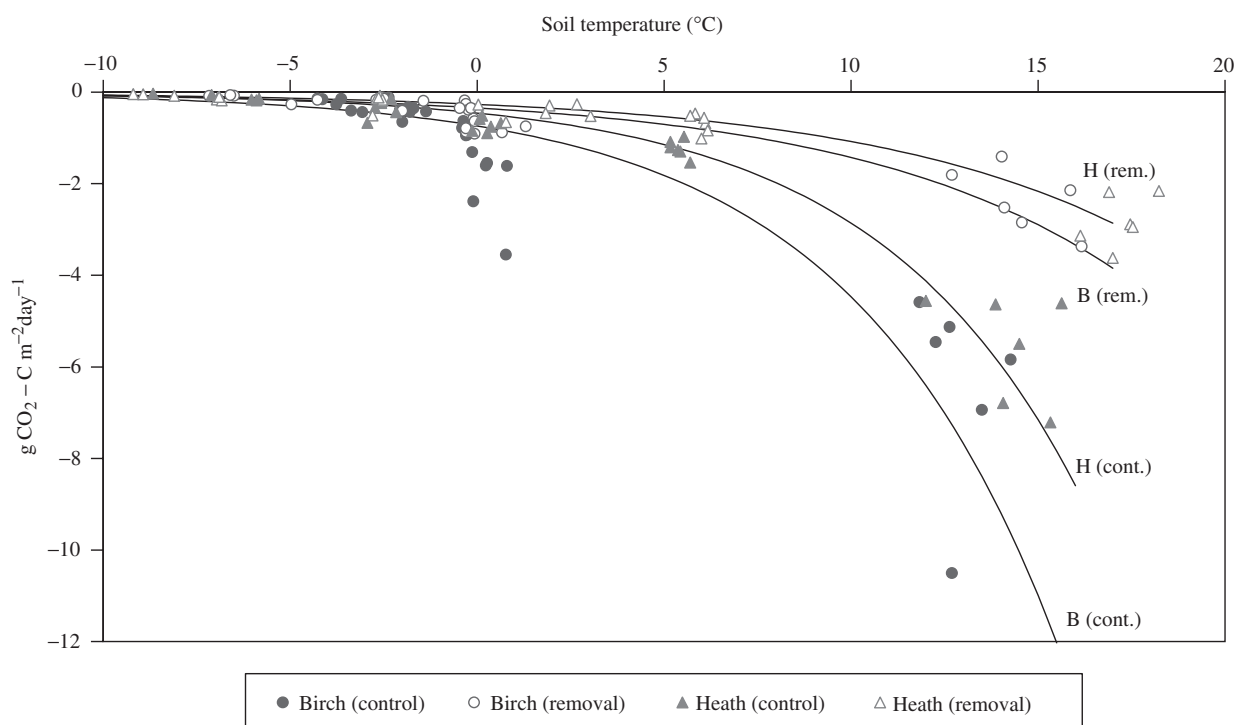
Our plant removal treatment in early June 1999 eliminated all shoots, as well as significantly reduced both coarse and fine root biomass within each of the vegetation types (Table 1). By contrast, soil microbial biomass C was not significantly affected by the treatment, but differed between vegetation types (Table 1). The reduction in root biomass, and the absence of a treatment effect on microbial biomass C, were observed during each of the winter flux measurements in the birch site (Grogan & Jonasson, 2003), indicating that the treatment had been effective from the onset of respiration measures in October 1999 through to their completion in July 2000.

Respiration rates were significantly lowered in the treatment plots of both vegetation types during the selected fall, winter, spring and summer months of 1999/2000 (Fig. 1;  $\text{Treatment}_{1,20}$ ,  $F = 48.4$ ,  $P < 0.001$ ). As expected, there were significant differences in ecosystem respiration rates between sampling months in both vegetation types (Fig. 1;  $\text{Month}_{4,80}$ ,  $F = 203.7$ ,  $P < 0.001$ ). This effect was associated with a significant interaction with treatment ( $\text{Treatment} \times \text{Month}_{4,80}$ ,  $F = 33.8$ ,  $P < 0.001$ ), indicating that plant removal had relatively little effect during the coldest sampling time (March soil temperature  $< -5^\circ\text{C}$ ) when fluxes were at their

**Table 2** Soil moisture levels and snow depths during each of the CO<sub>2</sub> flux sampling times for both vegetation types

Month	Birch understory (control)	Birch understory (removal)	Heath (control)	Heath (removal)
<i>Soil moisture (g H<sub>2</sub>O g DW<sup>-1</sup>)</i>				
October	0.76 <sup>a</sup> (0.07)	0.78 <sup>a</sup> (0.01)	0.99 <sup>a</sup> (0.03)	0.83 <sup>a</sup> (0.06)
January	nd	nd	nd	nd
March	nd	nd	nd	nd
May	2.58 <sup>a</sup> (0.26)	3.76 <sup>b</sup> (0.46)	4.03 <sup>b</sup> (0.21)	3.46 <sup>c</sup> (0.39)
July	2.10 <sup>a</sup> (0.12)	2.36 <sup>ab</sup> (0.15)	2.55 <sup>b</sup> (0.11)	2.14 <sup>a</sup> (0.33)
<i>Snow depth (cm)</i>				
January	35 (2)	33 (2)	11 (1)	10 (1)
March	71 (5)	70 (5)	31 (4)	27 (4)

Parentheses indicate standard errors ( $n = 6$ ). Differing superscript letters within a row indicate statistically significant soil moisture differences ( $P < 0.05$ ) using 2 way ANOVA and Fisher's Least Significant Difference for comparing effects of vegetation-type and treatment. Soil moisture was not determined (nd) during periods when soils were frozen (i.e. snow-covered).



**Fig. 3** First-order exponential relationships between plot CO<sub>2</sub> efflux and soil temperature during winter and summer for each vegetation type and treatment.

lowest (Figs 1 and 2). Together, these results support hypothesis I by demonstrating that both respiration derived from bulk soil organic matter decomposition and respiration derived from recently fixed plant C (i.e. control minus treatment plot effluxes) are each important components of total ecosystem respiration rates during most phases of the year.

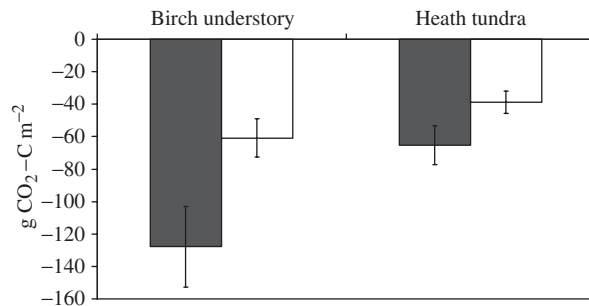
Soil temperatures differed significantly between vegetation types, treatments and sampling months, and was associated with significant interactions with all experimental factors (Fig. 2; statistical data not shown).

In particular, the heath site was substantially warmer during the October and July flux measurement phases, and significantly colder in March (Fig. 2). Plant removal resulted in a mean drop of 1.7 °C in soil temperature during March, and a mean rise of 2.3 °C in July. Soil moisture varied significantly between sampling months (Table 2; Month<sub>4,80</sub>,  $F = 344.6$ ,  $P < 0.001$ ), and responded differently to treatment depending on vegetation type (Treatment × Vegetation<sub>1,20</sub>,  $F = 6.7$ ,  $P = 0.018$ ). Substantial impacts of the plant-removal treatment were largely confined to May, when it tended to raise soil

**Table 3** Treatment effects on mean coefficients for the first-order exponential relationship (respiration rate =  $A \exp^{(BT)}$ ) applied to the time series data from each plot ( $n = 6$ ) in the vegetation types

	Birch understory (control)	Birch understory (removal)	Heath (control)	Heath (removal)
$A$ ( $\text{g CO}_2\text{-C m}^{-2} \text{ day}^{-1}$ )	0.75 <sup>a</sup> (0.05)	0.35 <sup>b</sup> (0.03)	0.47 <sup>c</sup> (0.03)	0.27 <sup>b</sup> (0.02)
$B$ ( $\text{T}^{-1}$ in $^{\circ}\text{C}$ )	0.18 <sup>a</sup> (0.01)	0.14 <sup>b</sup> (0.01)	0.18 <sup>a</sup> (0.01)	0.14 <sup>b</sup> (0.01)
Annual $Q_{10}$	6.3	4.2	6.3	4.1
$R^2$ (overall)	0.76	0.78	0.92	0.90

Parentheses indicate standard errors. All of the individual regression equations within the treatment groups were statistically significant ( $P < 0.05$ ,  $R^2 > 0.73$ ). Differing superscript letters within a row indicate statistically significant differences ( $P < 0.05$ ) using a 2 way ANOVA and Fisher's Least Significant Difference for comparing effects of vegetation type and treatment.



**Fig. 4** Calculated total wintertime ecosystem  $\text{CO}_2$  production for each vegetation type and treatment (dark columns = control; light columns = plant removal). Bars indicate estimates of standard errors based on interannual variability in winter soil temperatures for the locality between 1987 and 2001 (Anonymous).

moisture in the birch site and lower it in the heath site (Table 2). Overall, these results indicate that treatment effects on the soil physical environment were either of small magnitude relative to intra-annual variation (Fig. 2, Table 2), or opposing influence between vegetation types, strongly suggesting that the main effect of the plant-removal treatment on respiration rates was directly as a result of the diminished plant-associated C pool.

The birch understory and heath tundra vegetation types did not differ significantly in ecosystem respiration rates through the full annual cycle (Fig. 1). Although the birch site had a significantly smaller total plant biomass (Table 1), organic soils that are  $\sim 1/3$  as deep (see Materials and methods), and substantially cooler October and July soil temperatures (Fig. 2), these differences did not result in lower overall ecosystem respiration rates compared with the heath site. Thus, hypothesis II was not supported.

Respiration rates from each of the vegetation types and treatments were related to soil temperatures through the year (Fig. 3), using a first-order exponential

relationship (Paul & Clark, 1996) (respiration rate =  $A \exp^{(BT)}$ ; where  $A$  is a constant representing an index of the substrate readily available for respiration over the annual cycle,  $B$  is a constant representing the respiration response to intra-annual variation in temperature, and  $T$  is the soil temperature). We calculated first-order equation coefficients for the time series data for each replicate plot ( $n = 6$ ) within the control and treatment groups of each vegetation type. Every one of these individual exponential relationships was statistically significant ( $P < 0.05$ ;  $R^2 > 0.73$ ). Overall, the high  $R^2$  values associated with the mean values of the exponential relationship coefficients (Table 3) indicate that most (76–92%) of the intra-annual variation in ecosystem respiration rates for these two common mesic subarctic vegetation types was explained using the first-order relationship.

Statistical analyses of the replicate coefficients indicated that the mean value for the substrate chemical quality index  $A$  was substantially higher in birch understory than in heath (Table 3; vegetation type<sub>1,20</sub>,  $F = 27.84$ ,  $P < 0.001$ ), further supporting the preconditions for hypothesis II. As expected, the removal of plant tissues as well as the disruption of the annual inputs of plant-associated substrates (i.e. litter and exudates) reduced  $A$  (Treatment<sub>1,20</sub>,  $F = 71.97$ ,  $P < 0.001$ ). This effect was markedly stronger in the birch understory than in the heath tundra plots (Table 3; Vegetation  $\times$  Treatment<sub>1,20</sub>,  $F = 8.46$ ,  $P = 0.009$ ). Thus, vegetation types differed in the amount of substrate available for respiration, and the plant-removal treatment had the expected effect. By contrast, the mean temperature coefficient  $B$  did not differ significantly between vegetation types, but was reduced by the plant-removal treatment (Table 3; Treatment<sub>1,20</sub>,  $F = 31.25$ ,  $P < 0.001$ ). This latter result indicates that respiration derived from bulk soil organic matter had a significantly lower temperature sensitivity than that of total ecosystem respiration (i.e. derived from plant-associated plus bulk soil carbon pools). Therefore,

hypothesis III is supported in that the temperature sensitivity for plant-associated respiration must have exceeded that of bulk soil respiration through the annual cycle in each of these vegetation types. In conclusion, this analysis (Table 3) suggests that differences in vegetation type across the landscape have little impact on annual patterns of bulk soil organic matter decomposition, but exert relatively strong control (along with soil temperature) on respiration of recently fixed C in these ecosystems.

Estimates of total wintertime CO<sub>2</sub> production (i.e. those periods when mean diel soil temperatures <0 °C) using the mean coefficient values for each vegetation type in the first-order relationship and our own records of local winter soil temperature records for each site (Grogan *et al.*, 2001; Grogan & Jonasson, 2003) suggest that the plant-associated and soil organic matter pools may each contribute about half of the total wintertime CO<sub>2</sub> production in these vegetation types (Fig. 4).

## Discussion

Our study is important because it indicates that ecosystem respiration rates can only be fully characterized and accurately modelled by distinguishing the bulk soil and plant-associated C pools in each vegetation type and parameterizing them separately. Comparison between control and plant-removal plots indicated that plant-associated and bulk soil organic matter carbon pools each contributed significantly to ecosystem respiration during most phases of winter and summer in the two vegetation types (Fig. 1). To our knowledge, this is the first study to demonstrate that bulk soil organic matter is respired in substantial amounts alongside 'recently fixed' C associated with plants and their current year's litter, throughout winter as well as summer the Arctic.

Comparison between vegetation types indicated no overall significant difference in ecosystem respiration rates through the annual cycle (Fig. 1). This result was surprising given the lower total plant biomass pools (Table 1), substantially shallower organic soils (see Materials and methods), and periodically cooler soil temperatures (Fig. 2) in the birch understory compared with the heath tundra. The first-order exponential equation analysis indicated a significantly higher substrate availability index (*A*) in the control plots of the birch understory compared with the heath tundra, strongly suggesting that they contained more labile or larger amounts of available substrate for respiration. The much larger soil microbial biomass pool associated with the birch site (Table 1) is also consistent with higher levels of readily available labile C substrate. In conclusion, the data suggest that significantly larger

amounts of more readily decomposable substrate were associated with the birch understory, and that this effect may have counteracted the impacts of smaller total plant and soil organic pools, and periodically lower temperatures, resulting in no overall differences in ecosystem respiration rates between the vegetation types through the year.

The higher substrate availability index (*A*) in the birch understory was probably at least partly because of the ongoing input of readily decomposable fresh birch leaf litter from the overstory canopy. This effect was most marked between control plots of the two vegetation types (Table 3), but also tended to occur between the treatment plots ( $P < 0.10$ ). The highly significant interaction between vegetation type and plant removal treatment on the substrate availability index suggests a positive interaction at the birch site between the presence of the understory plants and the bioavailability of the birch leaf litter substrate. More generally, this statistical interaction and the pattern of variation in substrate availability indices (Table 3) indicates that differences in vegetation type had relatively little influence over annual patterns of bulk soil organic matter respiration, but must have exerted relatively strong control (along with soil temperature) on respiration of recently fixed plant-associated C in these ecosystems.

The basic first-order exponential approach adopted here explained 76–92% of the intra-annual variation in ecosystem respiration (Table 3) in these two common tundra ecosystems of northern Sweden. These ecosystems are relatively mesic (moderately dry) compared with most tussock tundra and wet sedge ecosystems, partly because the combination of sloping topography, lack of permafrost, and bedrock structure provides superior drainage. In our study at least, the very high proportion of total intra-annual variation in ecosystem respiration explained on the basis of soil temperature (especially in heath tundra) indicates that variations in soil moisture variation were relatively unimportant to respiration from these vegetation types at this temporal scale. Considerable further research will be required to integrate winter and summer respiration patterns with gross ecosystem photosynthesis to develop more accurate predictions of the overall effects of warming, and soil moisture, on annual net C balance for these and other arctic vegetation types (Hobbie *et al.*, 2000).

Our treatment removed shoot sources of respiration from above-ground, and significantly reduced coarse and fine root biomass, resulting in a total plant biomass reduction of 59–66% (Table 1). The substantial root biomass remaining after the removal treatment implies that fluxes from these plots represent an altered balance between recent plant C and bulk soil organic matter contributions to ecosystem respiration in which the



plant-associated component had been diminished, rather than eliminated. In addition, enhanced labile C inputs arising from increased root mortality and exudation following treatment in June 1999 may have influenced plot efflux. We expect that most of these extra-labile C inputs due to the treatment would have been respired during the remainder of the growing season. In any event, even if there were increased labile C inputs in the treatment plots at the onset of winter, these should have stimulated (rather than inhibited) respiration, making it less likely that significant treatment effects on respiration rates (Fig. 1) or first-order equation substrate availability indices  $A$  (Table 3) would have been observed.

The  $Q_{10}$  values derived from our exponential temperature coefficients (Table 3) are approximately twofold higher than many previously reported values for total respiration from roots plus soil within the surface soil temperature range 0–35 °C (Lloyd & Taylor, 1994). The 'annual  $Q_{10}$ ' values reported here represent integrated measures of the response of ecosystem respiration (i.e. both plant and soil pools) to intra-annual fluctuations in soil temperature. Plant phenological changes during the growing season probably contributed to the treatment differences in CO<sub>2</sub> efflux rates for July, and are an inherent component of 'annual  $Q_{10}$ ' because they are probably driven by seasonal temperature changes.

Our results indicating a higher temperature sensitivity of respiration from plant-associated C pools relative to bulk soil C in tundra suggest a mechanism to explain the temporal response of ecosystem CO<sub>2</sub> exchange in Alaskan ecosystems to decadal warming (Oechel *et al.*, 2000). The net CO<sub>2</sub> source activity observed with the onset of relatively warm and dry conditions in the 1980s may have been due predominantly to enhanced respiration from plant-associated C pools. Acclimation toward reduced ecosystem CO<sub>2</sub> source activity in the mid-1990s may have been as a result of the depletion of some of those pools, especially recent accumulations of root and shoot litter. Similar 'short-lived' flushes of net CO<sub>2</sub> release have been observed in a mid-latitude forest that was subjected to experimental soil warming (Melillo *et al.*, 2002). In that case, the initial flush response lasted 5–8 years and was assumed to have then been curtailed by the limited size of the labile soil C pool associated with recent C inputs from plants. Our study results suggest that the initial increase in net CO<sub>2</sub> release with warming of Alaskan tundra may have been primarily because of temperature effects on the plant-associated, rather than bulk soil C pools. Thus, although the latter pool would most likely have been affected (with consequent implications for globally significant atmospheric CO<sub>2</sub> feedbacks), the major effect

of initial warming may have been to stimulate respiration from 'recent' plant-associated C pools.

The first-order equation coefficients and continuous winter soil temperature records provide a method to estimate total wintertime CO<sub>2</sub> efflux from the two vegetation types (Fig. 4). Our results fall well within the range of previous estimates of total winter CO<sub>2</sub>-C release in seasonally snow-covered ecosystems. Previous estimates have been made using a variety of measurement techniques and calculation methods and include: 89 g C m<sup>-2</sup> yr<sup>-1</sup> for forest tundra (Zimov *et al.*, 1996); 2–69 g C m<sup>-2</sup> yr<sup>-1</sup> for tussock tundra (Oechel *et al.*, 1997; Fahnestock *et al.*, 1998); 110–190 g C m<sup>-2</sup> yr<sup>-1</sup> for a range of Alaskan tundra vegetation types (Grogan & Chapin, 1999); 29 g C m<sup>-2</sup> yr<sup>-1</sup> in a subarctic fen (Aurela *et al.*, 2002); 89–132 g C m<sup>-2</sup> yr<sup>-1</sup> for a southern boreal peatland; 41–68 g C m<sup>-2</sup> yr<sup>-1</sup> for a northern boreal peatland (Alm *et al.*, 1999); 12–36 g C m<sup>-2</sup> yr<sup>-1</sup> for subalpine wetlands (Sommerfeld *et al.*, 1993; Mast *et al.*, 1998); and 0.3–26 g C m<sup>-2</sup> yr<sup>-1</sup> for high alpine tundra (Brooks *et al.*, 1997). Despite concerns about quantitative accuracy with some of the diverse measurement techniques and calculation methods used in these studies, together they clearly demonstrate that winter respiration is an ongoing process in most seasonally snow-covered ecosystems.

The substantially higher total winter CO<sub>2</sub>-C efflux estimated for the vegetated plots in the birch understory compared with the heath ecosystem is clearly not a result of major differences in instantaneous efflux rates at the various sampling times (Fig. 1), or to differences in temperature sensitivity of respiration (Table 3). Instead, differences in temperature regime (mean winter soil temperature in the heath was 2.7 °C cooler than birch understory overall) and in the substrate availability indices (Table 3) were important. To our surprise, we estimated that the latter factor accounted for ~ 60% of the difference in total winter CO<sub>2</sub>-C efflux between the control plots of the two vegetation types. Thus, vegetation-type differences in the amount or chemical quality of substrate available for respiration were just as important as soil temperature differences in determining landscape-level variation in total winter CO<sub>2</sub>-C efflux. Furthermore, just as in the interpretation of the effect of vegetation type on instantaneous respiration rates through the full annual cycle above, here again the total winter efflux results suggest that the effect of vegetation type was primarily on the plant-associated component of respiration, rather than the bulk soil carbon pool.

The results lead to three major insights. First, plant-associated and bulk soil organic matter C pools are each substantial components of arctic ecosystem respiration in winter, as well as in summer. Thus, the strong winter

emphasis in GCM predictions for arctic climate warming indicate that potentially enhanced wintertime bulk soil C losses would need to be offset by disproportionately larger increases in growing season gross primary production relative to total annual plant respiration for overall net C balance to be maintained. Second, although the ecosystem respiration rates did not differ between vegetation types over the annual cycle, the first-order exponential equation coefficients for substrate availability differed substantially between vegetation types, especially in the plots containing plants. Specifically, our results suggest that the recently observed changes in vegetation distribution such as the increasing abundance of shrubs in northern heath and tussock tundra (Chapin *et al.*, 1995; Sturm *et al.*, 2001) may not alter overall ecosystem respiration rates, but nevertheless may result in significant changes in the relative proportion of respired C derived from plant-associated and bulk soil organic matter pools. Third, these ecosystems are important to global climate change because enhanced decomposition of their extensive bulk soil C reserves could provide a substantial positive feedback to atmospheric CO<sub>2</sub> concentrations, leading to enhanced global warming. Rising temperatures in the Arctic are predicted to enhance soil organic matter decomposition resulting in an initial net CO<sub>2</sub> release, but as the overall C to nitrogen (N) ratio in soils is greater than that of plants, and plant production is strongly N limited (Chapin *et al.*, 1995), the increase in N mineralization associated with decomposition should ultimately stimulate net C gains by tundra ecosystems (Shaver *et al.*, 1992). This latter hypothesis assumes a common temperature sensitivity for respiration derived from both bulk soil and plant-associated C pools. Our results indicating higher temperature sensitivity in the latter, but similar flux rates from both pools (Fig. 1), suggest that the hypothesized C gains associated with increased N availability under a warmer climate may be offset by proportionally larger C releases from the plant-associated pool relative to the bulk soil pool. For these mesic ecosystems at least, this conclusion constrains the potential for substantial tundra C gains due to enhanced N mobilization as warming proceeds in the Arctic.

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