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Respiration and Microbial Dynamics in Two Subarctic Ecosystems during Winter and Spring Thaw: Effects of Increased Snow Depth

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Abstract

Recent evidence suggests that biogeochemical processes in the Arctic during late winter and spring-thaw strongly affect the annual cycling of carbon and nutrients, indicating high susceptibility to climate change. We therefore examined the carbon and nutrient dynamics in a sub-arctic heath and a birch forest with high temporal resolution from March until snowmelt at both ambient and experimentally increased snow depths.

Ecosystem respiration (ER) from mid-March to snowmelt at ambient snow was high, reaching 99 ± 19 (birch) and 67 ± 1.4 g C m^{-2} (heath). Enhanced snow depth by about 20–30 cm increased ER by 77–157% during late winter but had no effects during spring-thaw. ER rates at the birch site were poorly described by classic first-order exponential models (R^2 = 0.06–0.10) with temperature as a single variable, but model fit improved considerably by including the supply of dissolved organic carbon (DOC) or nitrogen (DON) in the model (R^2 = 0.40–0.47). At the heath, model fit with temperature as the single variable was better (R^2 = 0.38–0.52), yet it improved when the supply of DOC or DON was included (R^2 = 0.65–0.72).

Microbial carbon decreased by 43% within a few days after the first soil freeze-thaw event, while microbial nitrogen and phosphorus decreased more slowly. Because soil inorganic nitrogen and phosphorus concentrations were low, nutrients released from lysed microbial cells may have been sequestered by surviving microbes or by plants resuming growth. The fast change in microbial biomass and the dependence of ER on substrate availability stress the need for high temporal resolution in future research on ecosystem carbon and nutrient dynamics at snowmelt in order to make robust models of their turnover.

Introduction

Biological activity in plants and soil microbes of the Arctic was traditionally assumed to be very low during the cold season due to long periods with subzero air and soil temperatures. Appreciable CO_2 emissions have, however, been observed in field studies at soil temperatures at least down to −5°C (Brooks et al., 1997), and the thermal insulation of snow cover restricts winter soil temperature minima despite low air temperatures. Consequently, wintertime respiration constitutes 10–50% of the total annual respiration in a variety of artic/alpine ecosystems (Sommerfeld et al., 1993; Clein and Schimel, 1995; Zimov et al., 1996; Oechel et al., 1997; Alm et al., 1999; Elberling and Brandt, 2003; Grogan and Jonasson, 2005). At the same time, net mineralization of nutrients in arctic ecosystems often appears to be higher during the cold season than during summer (Hobbie and Chapin, 1996; Schimel et al., 2004), which evidently is related to major structural and functional changes in the microbial community (Schadt et al., 2003; Schimel et al., 2004; Lipson and Schmidt, 2004). These recent findings suggest that ecosystem functioning is fundamentally different during the winter and summer seasons, yet we are still far from understanding the dynamics of winter soil processes, such as organic matter turnover and nutrient cycling (Brooks et al., 1997; Schimel et al., 2004).

Except for low air temperatures, the distribution of snow may be the single most important factor controlling the cold season respiration in these ecosystems (Walker et al., 1999). Snow insulates the soil, reduces temperature fluctuations, and constrains minimum temperatures (Brooks et al., 1997; Groffman et al., 2001). General circulation models predict increasing precipitation at high latitudes during winter (Maxwell, 1992; Kattenberg et al., 1996; Giorgi and Francisco, 2000; Hulme et al., 2000), which will lead to increased snow cover in some regions, and decreased cover in others if precipitation falls as rain. In currently low-statured vegetation like arctic tundra, increased shrub growth due to climate warming (Chapin et al., 1996) may also act to increase snow depths by as much as 10–25% due to increased wind shelter (Sturm et al., 2001). Manipulating natural snow depths with snow fences, as has been done at Toolik Lake, Alaska, and Niwot Ridge, Colorado (Walker et al., 1999) may therefore provide important new insight in snow-ecosystem dynamics. In the Toolik Lake experiment, the fences typically create a drift with a depth of up to 3 m, compared to ambient snow depths of 20–40 cm, resulting in dramatically increased soil temperatures during winter, higher winter respiration, prolonged period of snow cover, and changes in nutrient cycling (Schimel et al., 2004; Wahren et al., 2005). Similar strong effects have been observed at Niwot Ridge where the fences typically enhance snow depths by about 80 cm from ambient levels of 30–80 cm (Williams et al., 1998).

In this study, we established a much more moderate increase in snow accumulation, comparable to current inter-annual variability, in order to mimic a realistic scenario of changed

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future snow depth in a sub-arctic dwarf shrub heath and a birch forest, the two dominant vegetation types of northern Scandinavia (Sjörs, 1971). We measured the late winter and spring-thaw ecosystem CO_2 efflux and the soil and microbial pools of carbon, nitrogen, and phosphorus with high temporal resolution. The purpose was to: (1) quantify the biogeochemical transformations at short time steps during the transition from winter to spring, which has been suggested to be a very dynamic period for soil microbial processes (Lipson and Schmidt, 2004); and (2) quantify the effects of moderately increased snow depth. We expected that relatively moderate increases in the snow depths would increase soil temperatures, CO_2 flux rates, soil and microbial nutrient pools, and enhance nutrient transformation rates, with most pronounced effects at the heath, where ambient snow cover normally is lowest.

Methods

SITE DESCRIPTION AND EXPERIMENTAL DESIGN

The experiment took place near Abisko in northern Swedish Lapland at 68°20′N, 18°47′E (heath site) and 68°20′N, 18°50′E (birch site). The elevation is approximately 430 m a.s.l. Climate is sub-arctic/alpine and records (1970–2000) from a nearby climate station show a mean annual temperature of –0.5°C. The mean air temperatures in winter (December–February) and spring (March–May) are −9.9°C and −2.3°C, respectively. Annual precipitation is 315 mm, with 75 mm falling in the winter and 41 mm in the spring. The two sites have a nonsignificant difference in depth of the organic soil layer with means ± standard errors of 12.1 ± 0.7 cm and 10.7 ± 0.4 cm at the heath and birch site, respectively (*t*-test; $n = 72/140$, $P = 0.08$). The organic soil layer overlays stones and bedrock, and a mineral soil layer is often absent. Soil organic matter (SOM) content ranged from 69 to 95% and 88 to 95% of dry soil mass at the birch and heath sites, respectively, while soil water content of dry soil mass was 472–829% at the birch site and 324–721% at the heath.

Dominant species at the heath are the ericoid dwarf shrubs *Empetrum nigrum* ssp. *hermaphroditum*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea*, *Andromeda polifolia*, and *Rhododendron lapponicum*. Other common species are *Arctostaphylos alpinus*, *Cassiope tetragona*, *Tofieldia pusilla*, *Carex vaginata*, *Betula nana*, and various mosses. The species composition at the birch (*Betula pubescens* ssp. *czerepanovii*) site differs mainly by *Vaccinium myrtillus* as an additional dominant species. Plant biomasses were not determined, but in similar vegetation types within 100–1000 m from the sites in this study, plant biomasses were 1426 ± 96 g m^{-2} and 1792 ± 92 g m^{-2} in the birch understory and the heath vegetation, respectively, with approximately 30% above-ground and 70% below-ground in both ecosystems (Grogan and Jonasson, 2005).

On 11 January 2000, when the snow depths still were <5 cm, 12 plots of about 150 m^2 were selected at each site. At six of the plots per site, we installed 1.2-m-high snow fences made of semi-permeable plastic, while the other six plots served as controls. At the heath site, each fence was 6 m long and was erected perpendicular to the expected prevailing winds. A prevailing wind direction could not be predicted at the more sheltered birch site. We therefore erected 12-m-long fences with a 90° bend at the middle. One fence in the heath fell down after the first measurement, and this plot was thereafter excluded from the experiment. On 9 and 10 March, 12 temperature loggers (Gemini Tinytags) were placed in three fenced and three control plots at each site at 5 cm soil depth, and temperature was logged every 10 minutes from 10 March to 18 May 2000.

CHAMBER CO2 FLUX MEASUREMENTS

Closed chamber CO_2 flux measurements were done once during late winter (mid-March) and six and seven times during spring-thaw (April–May) in the birch and heath ecosystems, respectively. We used a LICOR 6200 Infrared Gas Analyzer attached to a 35.5 L Perspex chamber with a basal area of 1076 cm^2 and equipped with a fan to ensure proper air mixing. During measurements, the rate of evapotranspiration usually was below 0.01 mmol H_2O m^{-2} s^{-1}. We therefore set the air flow through the desiccant to zero and calculated the CO_2 fluxes using the original LI-COR equations (LI-COR, 1990; Hooper et al., 2002).

At each date of measurements, the gas fluxes were measured at new, random positions within the plots to make sure that they were always done in places where the snow had been undisturbed. Rather than measuring fluxes on the snow surface, which may be influenced by snow physical structure (e.g. ice layers) and CO_2 storage, we removed the snow prior to measurements in order to measure instant respiration instead of instant release. Previous test studies have shown a pulse of CO_2 from the soil after snow removal due to changes in the CO_2 level and diffusion rates at the soil-atmosphere interface, but with reduced and stable flux rates after a maximum time of 25 min (Grogan et al., 2001; Grogan and Jonasson, 2005). The snow was therefore always removed 45–90 min before measurements were done. We monitored the soil temperatures from the time of snow removal until measurements and did not observe soil temperature changes at any time.

Snow was packed tightly to the sides of the chambers to seal the chamber air from the atmosphere. Sunlight was excluded by covering the chambers with a double layer of black plastic, and the ecosystem respiration (ER) was measured as the CO_2 flux over six successive 20 s intervals and averaged (Alm et al., 1999; Grogan et al., 2001; Grogan and Jonasson, 2005). Further details on the methodology of the flux measurement are given by Grogan and Jonasson (2005).

SOIL COLLECTION AND ANALYSES

In four plots at each site on every measurement day, a 10 × 10 cm soil sample was sawed out of the frozen soil to a depth of 5 cm after the CO_2 measurements. The soil samples were enclosed in plastic bags, kept cool (2–5°C), and sorted within 48 h.

As many roots as possible were removed by hand sorting during a standardized time of 30 min, and the soil was divided into three subsamples. One subsample of 30 g was used for determination of water content by drying for 24 h at 90°C. A second subsample of 10 g was immediately extracted in 50 mL of 0.5 M K_2SO_4 to recover soil inorganic N and P and dissolved organic C (DOC) and N (DON). After the K_2SO_4 addition, the samples were shaken, filtered through a Whatman GF-D filter, and kept frozen at −18°C until analysis. The third subsample of 10 g was fumigated for 24 h in chloroform (CH_3Cl) vapor to release nutrients from the microbial biomass (Jenkinson and Powlson, 1976), after which the samples were extracted and handled in the same way as the unfumigated samples.

The extracts were analyzed on a Shimadzu TOC-5000A total organic C analyzer for DOC and extractable microbial C, estimated as the difference between the DOC content in fumigated and unfumigated samples.

The NH_4^+-N content was determined by the indophenol method, inorganic P by the molybdenum blue method, and NO_3^--N with the cadmium reduction method (Allen, 1989). Sample values for NO_3^--N were mostly below the detection limit of about

0.05 μg g^{-1} SOM, and the soil NO_3^--N content was therefore considered to be negligible.

Ten mL subsamples of all extracts were used for estimates of extractable microbial N content. The extracts were digested for 4 h in 10 mL concentrated H_2SO_4 and selenous acid mixture with 1 mL of H_2O_2 added to reduce all N to NH_4^+-N. After digestion, the sample tubes were filled with distilled water to 100 mL, and the diluted extracts were analyzed using the indophenol method. Extractable microbial N was determined by subtracting the concentration in the nonfumigated, digested sample from the concentration in the fumigated, digested sample (Brookes et al., 1982, 1985a, 1985b; Vance et al., 1987). The extractable microbial P was determined by subtracting the P content of the unfumigated, undigested sample from the P content of the fumigated, undigested sample (Brookes et al., 1982; Jonasson and Michelsen, 1996).

STATISTICAL ANALYSES AND DATA PROCESSING

Statistical analyses were conducted using the GLM procedure (SAS Institute ver. 8.0). Since all CO_2 flux measurements and the soil samplings were done at new positions within plots at each date, repeated measurement ANOVA (analysis of variance) was not used. Instead, an overall three-way ANOVA was used with site (birch vs. heath), treatment (control vs. snow-fenced), and time as main effects and their interactions. Effect of site was always significant, and two-way ANOVA was therefore used to test the effects of time and treatment and their interactions at the individual sites. Since the study included one measurement during winter and the remaining measurements during spring-thaw, two-way ANOVA also was conducted to test for effects of site, treatment, and their interactions at individual measurement dates.

Some data were transformed to pass Brown and Forsythe's test for homogeneity of variance. When transformation failed to homogenize variances between groups, nonparametric one-way ANOVA (NOA) was used to test for differences on individual measurement dates. Data from the two sites were tested together to examine differences between sites, and separately to test for differences between fenced and control plots within each site. The *t*-test was used to test for selected differences when appropriate.

In order to investigate the major controls of ecosystem respiration, we related it to soil temperature and chemistry by fitting a classic first-order exponential equation (van't Hoff, 1898) in the form:

$$ER = A \exp^{(BT)} \quad (1)$$

to the data, where A (g C m^{-2} d^{-1}) is the respiration rate at 0°C representing an index of substrate availability, B ($°C^{-1}$) is a constant representing the temperature sensitivity of respiration, and T is temperature in °C (Grogan and Jonasson, 2005).

However, it has recently been suggested that robust models of ecosystem respiration need to incorporate also the effects of substrate supply and desiccation stress (Davidson et al., 2006). We therefore also tested models that incorporated simple, linear relationships between respiration and dissolved organic carbon (DOC, mg g^{-1} SOM) and nitrogen (DON, mg g^{-1} SOM), as indicators of substrate availability, and soil water content (SW, % of wet soil) in the form:

$$\text{Respiration rate} = (A + c \times DOC + d \times DON + e \times SW) \exp^{(BT)} \quad (2)$$

where c, d, and e are constants in flux units times the inverse of the units of the variable they are associated with. In this model, A integrates the respiration at 0°C with any offset (y-axis intercept different from zero) of the inferred linear relationships between respiration and DOC, DON, and SW. We ran the model with various combinations after removal of one or several of the variables in order to find the models with best fit. Similar models with microbial biomass C, N, or P were also tested, but did not produce good model fits and are therefore not presented.

Results

SNOW DEPTH AND SOIL TEMPERATURE

The snow fences caused a moderate increase of the snow cover by about 20–30 cm added to the depth of 74 ± 3 and 27 ± 3 cm at the time of maximum snow depth at the birch and heath sites, respectively. The increased depth was within the range of current interannual variation and, hence, simulated a realistic future snow depth within the limits of climate change projections (Giorgi and Francisco, 2000). However, the temporal patterns in the distribution of snow and the effects on soil temperatures varied between the two sites. On 9 March, both snow depths and soil temperatures were similar in controls and snow-fenced plots at the birch site (Figs. 1a and 1b). Until 24 April there was an increase in snow depth in the fenced plots resulting in 18–27 cm deeper snow than in the controls with the difference lasting throughout the remaining study period (Fig. 1a; $Treatment_{1,60}$, $F = 88.1$, $P < 0.0001$). At no time at the birch site did the differences in snow depth lead to differences in soil temperatures, which were just below 0°C and only increased slowly throughout the period (Fig. 1b). The temperature loggers recorded neither thaw nor freeze-thaw cycles during the study period (Table 1).

At the more wind-exposed heath site, the snow depth was significantly lower than at the birch site through the entire period (Figs. 1a and 1c; NOA, $P < 0.0001$ at all dates). Until snowmelt was completed, there was significantly deeper snow in fenced plots than in controls on all measurement days, ranging from a difference of 22 cm on 10 March to 31 cm on 25 April (Fig. 1c; $Treatment_{1,58}$, $F = 98.2$, $P < 0.0001$). In contrast to the birch site, where snow still remained on 18 May, snowmelt in the heath controls was completed already on 3 May. In the fenced plots, however, some snow remained on the last measurement day on 17 May, and completion of snowmelt was therefore delayed by more than 14 days.

On 10 March, the soil temperatures in the fenced plots at the heath were significantly higher than in controls (Fig. 1d; NOA, $P = 0.0042$). The temperature loggers in the fenced plots never recorded soil temperatures lower than −2°C, while soil temperatures sometimes decreased to below −4°C in the controls in both March and April (Table 1). The differences were significant in March (Table 1; *t*-test, $P = 0.0055$) and near significant in April ($P = 0.0585$). The temperature loggers recorded the first freeze-thaw cycle on 1 May and 5 May in control and fenced plots, respectively. In total, the 7.3 ± 4.1 and 5.7 ± 2.7 freeze-thaw cycles during the period from 1 to 19 May in the controls and fenced plots, respectively, were not significantly different (Table 1).

CO2 FLUXES

The ecosystem respiration (ER) rates (Fig. 2) were generally significantly higher at the birch site than at the heath ($Vegetation_{1,118}$, $F = 23.6$, $P < 0.0001$), and the temporal patterns were different at the two sites (Vegetation × $Time_{5,118}$, $F = 8.2$, $P < 0.0001$). On 9–10 March, there was a significant effect of the snow fences on ER rates ($Treatment_{1,20}$, $F = 7.4$, $P = 0.013$), which

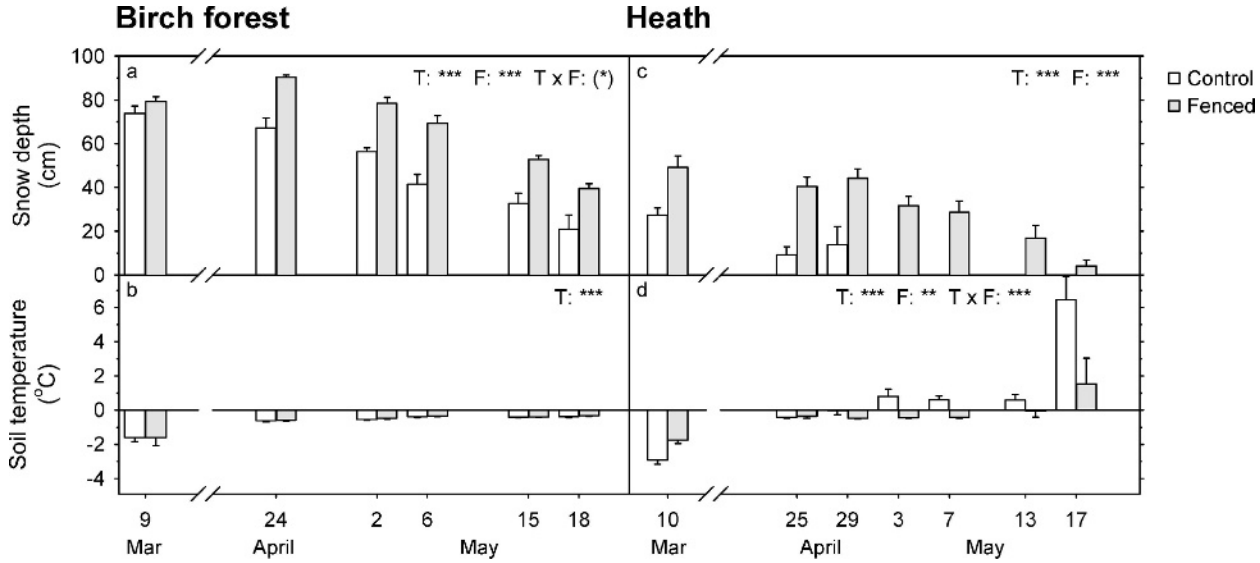

FIGURE 1. Snow depths (a, c) and soil temperature at 5 cm soil depth (b, d), in the birch and heath ecosystems (means + 1 SE of 6 replicated samples except for the heath in April/May with 5 samples). Differences at $P \leq 0.1$ from two-way ANOVA of effects of time (T) and snow fence (F) and their interactions (T × F) are shown in the upper right corner of each panel. Significance levels are: (*), $P \leq 0.1$; *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

were 77% and 157% higher in fenced plots than in the controls of the birch and heath sites, respectively. In the April–May period, there was no significant effect of different snow depths on ER in either vegetation type ($\text{Treatment}_{1,20}$, $F < 2.6$, and $P > 0.12$ on all dates).

The ER rates at the birch site was poorly described by the simple temperature-dependent exponential equation in both control and fenced plots (Table 2; model 1, $R^2 = 0.10$ and 0.06, respectively), as opposed to a better model fit at the heath site (Table 2; model 1, $R^2 = 0.52$ and 0.38, respectively). However, the model fit was significantly improved, especially at the birch site, when either DOC or DON were added to the equations as indicators of substrate availability (Table 2; models 4 and 5, $R^2 =$ 0.40 and 0.47 with DOC included and 0.65 and 0.72 with DON included at the birch and heath, respectively). The more complex models, which included more variables (Table 2; models 2 and 3), did not significantly improve the model fits further compared to models 4 and 5.

We were unable to estimate the respiratory carbon loss during the full study period at the birch site by using the various exponential equations, because of the poor model fit of the simple temperature-dependent exponential equation (model 1), and because temperature was the only parameter that was logged continuously. However, linear extrapolation over the measurements at the different dates estimated the respiration of the birch ecosystem to 99 ± 19 g C m^{-2} in the controls and to 112 ± 21 g C m^{-2} in plots with increased snow depths.

At the heath site, total respiratory carbon loss using model 1 was 67 ± 1.1 and 68 ± 1.3 g C m^{-2} in controls and fenced plots, respectively, indicating no overall significant effect of increased snow depth during the study period. However, during the 20 days in March, when soil temperatures were recorded, modeled respiratory losses were significantly different (*t*-test, $P = 0.02$), reaching 17.6 ± 0.4 g C m^{-2} in controls and 19.2 ± 0.2 g C m^{-2} in plots with increased snow depths.

SOIL AND MICROBIAL POOLS OF C, N, AND P

The microbial biomass carbon (MBC; Fig. 3) was significantly lower at the heath than at the birch site ($\text{Vegetation}_{1,78}$, $F = 28.5$, P

TABLE 1

Mean soil temperatures (°C) at 5 cm soil depth and recorded freeze-thaw cycles from 10 March to 19 May 2000. Temperature was logged with 10-minute intervals, and a freeze-thaw cycle was defined as thaw ≥3 hours followed by freezing ≥3 hours. SE are shown in parentheses, $n = 3$. Significant effects of snow fences on temperature tested by *t*-test are shown with the *P*-levels: (*), $P \leq 0.1$; *, $P \leq 0.05$; **, $P \leq 0.01$.

	Birch forest (control)	Birch forest (fenced)	Heath (control)	Heath (fenced)
Mean March	−1.15 (0.12)	−1.31 (0.20)	**−2.11 (0.20)**	**−0.99 (0.06) ****
Mean April	−0.64 (0.03)	−0.84 (0.16)	**−1.24 (0.19)**	**−0.71 (0.06) (*)**
Mean May	−0.60 (0.00)	−0.60 (0.00)	0.67 (0.68)	0.05 (0.29)
Max March	−0.60 (0.00)	−0.60 (0.00)	−0.60 (0.00)	−0.60 (0.00)
Max April	−0.60 (0.00)	−0.60 (0.00)	−0.60 (0.00)	−0.60 (0.00)
Max May	−0.60 (0.00)	−0.60 (0.00)	6.20 (2.96)	7.27 (1.97)
Min March	−1.93 (0.27)	−2.80 (0.60)	**−4.00 (0.52)**	**−1.93 (0.27) ***
Min April	−1.13 (0.27)	−1.13 (0.27)	−4.30 (1.31)	−1.40 (0.46)
Min May	−0.60 (0.00)	−0.60 (0.00)	−0.60 (0.00)	−0.60 (0.00)
First freeze-thaw	none	none	1 May	5 May
No. of freeze-thaw cycles	0.0 (0.0)	0.0 (0.0)	7.3 (4.1)	5.7 (2.7)

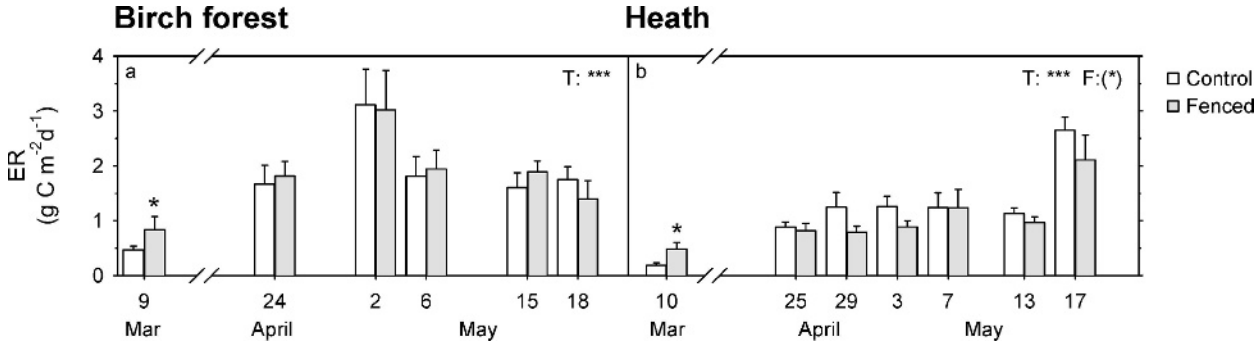

FIGURE 2. Ecosystem respiration (ER), in the birch (a) and heath (b) ecosystem (means + 1 SE). Sample sizes, effect abbreviations, and significance levels are denoted as in Figure 1. The asterisks on 9 and 10 March denote significant effect of snow fence tested by two-way ANOVA of effects of vegetation and snow fence on individual measurement dates.

< 0.0001), and the temporal patterns were different in the two vegetation types (Vegetation $\times$ $Time_{5,78}$, $F = 8.8$, $P < 0.0001$). This was mainly due to a 43% reduction between 25 April and 3 May (*t*-test, $P = 0.03$) in the control plots at the heath as they became snow-free, while MBC was constant or even tended to increase in both controls and fenced plots at the birch site. MBC stayed at a significantly lower level at the heath controls throughout the study period ($Treatment_{1,42}$, $F = 40.4$, $P < 0.0001$).

The contents of nitrogen and phosphorus in the microbial biomass (MBN and MBP; Table 3) also were significantly higher at the birch site than at the heath ($Vegetation_{1,78}$, $F > 25.7$, $P < 0.0001$ for both), and both decreased significantly with time at the heath ($Time_{1,42}$, $F = 3.77$, $P = 0.0043$ and $F = 6.45$, $P < 0.0001$, respectively). However, the decrease was much less pronounced than the decline of MBC in the controls, and there was no significant treatment effect.

The concentrations of soil NH_4^+-N (Table 3) were very low and at similar levels in both ecosystems, except for significantly higher NH_4^+-N content at the birch than at the heath site on 9–10 March (NOA, $P = 0.0109$). The inorganic P showed more pronounced differences (Table 3), with higher concentrations in the birch plots on all measurement days (NOA, $0.0001 < P < 0.0013$), except 13–15 May (NOA, $P = 0.1239$). No treatment effect was observed for any of the nutrients, but P concentrations decreased significantly with time at the birch site ($Time_{5,36}$, $F = 4.45$, $P = 0.003$).

TABLE 2

Mean coefficients (SE in parentheses), explained model variances (R^2), and sample sizes (*n*) for first-order exponential relationships between ecosystem respiration and soil temperature, dissolved organic carbon and nitrogen (DOC and DON, respectively), and soil water (SW) in various combinations. See text for explanations and units of model parameters.

Model		Birch forest (control)	Birch forest (fenced)	Heath (control)	Heath (fenced)
(1)	A	2.40 (0.49)	2.22 (0.36)	1.05 (0.10)	1.05 (0.09)
	B	0.53 (0.35)	0.35 (0.28)	0.12 (0.02)	0.16 (0.02)
$ER = A \exp^{(BT)}$	R^2	0.10	0.06	0.52	0.38
	n	36	36	36	36
(2)	A	−1.33 (2.39)	−3.42 (3.31)	3.80 (2.37)	11.11 (4.97)
	B	0.86 (0.43)	0.12 (0.25)	0.07 (0.03)	1.10 (0.24)
$ER = (A + c \times DOC + d \times DON + e \times SW) \exp^{(BT)}$	c	0.59 (0.47)	0.64 (0.25)	−0.09 (0.09)	0.17 (0.16)
	d	2.20 (1.20)	1.07 (1.06)	0.87 (1.10)	0.34 (0.74)
	e	3.13 (2.84)	4.74 (3.83)	−3.23 (2.92)	−11.46 (5.92)
	R^2	0.48	0.51	0.72	0.68
	n	23	24	20	21
(3)	A	1.16 (0.67)	0.69 (0.48)	1.19 (0.17)	1.52 (0.34)
	B	0.73 (0.38)	0.17 (0.25)	0.09 (0.03)	1.36 (0.26)
$ER = (A + c \times DOC + d \times DON) \exp^{(BT)}$	c	0.55 (0.43)	0.56 (0.25)	−0.09 (0.08)	0.06 (0.02)
	d	2.28 (1.13)	1.56 (1.04)	0.46 (0.80)	0.34 (0.86)
	R^2	0.47	0.5	0.71	0.64
	n	23	24	20	21
(4)	A	0.87 (0.70)	0.54 (0.47)	0.98 (0.12)	1.50 (0.24)
	B	0.87 (0.41)	0.18 (0.25)	0.13 (0.02)	1.47 (0.17)
$ER = (A + c \times DOC) \exp^{(BT)}$	c	1.03 (0.47)	0.82 (0.20)	−0.02 (0.05)	0.11 (0.14)
	R^2	0.40	0.47	0.72	0.65
	n	24	24	28	28
(5)	A	1.93 (0.43)	1.56 (0.38)	1.04 (0.11)	1.61 (0.23)
	B	0.59 (0.34)	0.26 (0.27)	0.12 (0.02)	1.33 (0.24)
$ER = (A + d \times DON) \exp^{(BT)}$	d	2.88 (1.05)	3.17 (0.91)	−0.01 (0.4)	0.37 (0.82)
	R^2	0.44	0.41	0.71	0.66
	n	23	24	20	21

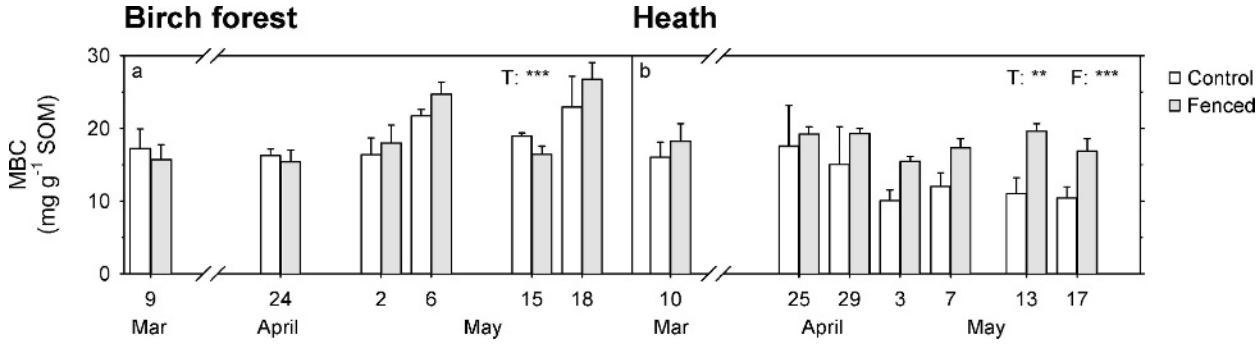

FIGURE 3. Extractable microbial biomass carbon (MBC) in the birch (a) and heath (b) ecosystems (means + 1 SE; $n = 4$). Effect abbreviations and significance levels are denoted as in Figure 1.

Discussion

ECOSYSTEM RESPIRATION DURING WINTER AND SPRING-THAW

It is well documented that soil respiration rates in late winter depend on the timing of snow accumulation in late fall and early winter, because the snow constrains both temperature fluctuations and soil cooling, providing improved conditions for microbial decomposition (Brooks et al., 1998; Brooks and Williams, 1999; Olsson et al., 2003; Schimel et al., 2004). Snow buildup later in the season is usually thought to be less important. In our study, however, despite a long and cold period of bare ground in early and mid-winter, lasting until mid-January, the increased snow depth in fenced plots yet increased the respiration rate in March

TABLE 3

Mean concentrations of soil microbial biomass N (MBN) and P (MBP), dissolved organic C (DOC) and N (DON) and of soil NH_4^+ and inorganic P in control and fenced plots at all measurement days. Data are means with SE in parentheses, $n = 6$ except for at the heath in April/May with $n = 5$. b.d. = below detection limit.

	MBN (mg g^{-1} SOM)		MBP (mg g^{-1} SOM)		NH_4^+-N (µg g^{-1} SOM)	
	control	fenced	control	fenced	control	fenced
Birch forest						
9 Mar	0.85 (0.10)	0.75 (0.09)	0.44 (0.08)	0.36 (0.06)	3.6 (0.3)	4.6 (2.5)
24 Apr	0.75 (0.06)	0.71 (0.03)	0.37 (0.02)	0.27 (0.05)	5.3 (1.7)	2.0 (0.7)
2 May	0.48 (0.06)	0.68 (0.19)	0.38 (0.04)	0.31 (0.04)	10.0 (4.4)	11.6 (6.8)
6 May	0.46 (0.07)	0.91 (0.12)	0.29 (0.03)	0.39 (0.01)	b.d.	9.9 (6.3)
15 May	0.68 (0.06)	0.55 (0.09)	0.37 (0.03)	0.35 (0.07)	b.d.	b.d.
18 May	0.67 (0.24)	0.56 (0.13)	0.28 (0.05)	0.38 (0.09)	10.3 (5.4)	3.8 (2.8)
Heath						
10 Mar	0.51 (0.10)	0.53 (0.05)	0.25 (0.02)	0.27 (0.04)	b.d.	b.d.
25 Apr	0.67 (0.12)	0.51 (0.06)	0.36 (0.04)	0.34 (0.05)	12.2 (7.2)	3.2 (1.1)
29 Apr	0.41 (0.06)	0.53 (0.03)	0.26 (0.02)	0.29 (0.02)	2.5 (1.6)	4.3 (2.8)
3 May	0.50 (0.09)	0.64 (0.05)	0.28 (0.02)	0.31 (0.01)	14.5 (7.8)	10.0 (6.6)
7 May	0.37 (0.03)	0.30 (0.10)	0.23 (0.02)	0.21 (0.03)	b.d.	b.d.
13 May	0.39 (0.04)	0.51 (0.05)	0.23 (0.01)	0.27 (0.02)	3.9 (1.6)	b.d.
17 May	0.27 (0.07)	0.45 (0.08)	0.18 (0.02)	0.21 (0.03)	b.d.	5.3 (5.6)

	DOC (mg g^{-1} SOM)		DON (µg g^{-1} SOM)		Inorganic P (µg g^{-1} SOM)	
	control	fenced	control	fenced	control	fenced
Birch forest						
9 Mar	1.953 (0.37)	1.435 (0.27)	78.5 (16.9)	69.9 (23.6)	53.5 (13.1)	51.0 (9.9)
24 Apr	2.658 (0.50)	1.946 (0.29)	146.7 (26.3)	96.0 (8.7)	66.8 (7.7)	41.8 (12.3)
2 May	2.101 (0.30)	2.692 (0.90)	604.9 (143)	472.9 (229)	67.5 (15.6)	55.8 (8.2)
6 May	1.484 (0.39)	2.502 (0.46)	40.8 (21.2)	175.0 (67.2)	39.3 (9.2)	40.2 (8.5)
15 May	1.528 (0.34)	1.147 (0.23)	73.0 (34.7)	49.4 (28.6)	16.9 (10.0)	20.2 (9.4)
18 May	2.021 (0.34)	2.004 (0.44)	188.5 (91.1)	415.3 (61.9)	21.3 (13.5)	33.1 (3.4)
Heath						
10 Mar	1.832 (0.58)	1.431 (0.32)	22.5 (22.5)	9.4 (6.0)	17.5 (9.6)	9.1 (2.4)
25 Apr	3.341 (1.62)	2.306 (0.37)	179.1 (86.7)	88.9 (24.3)	18.0 (5.5)	10.5 (1.9)
29 Apr	1.203 (0.25)	1.959 (0.40)	29.2 (20.1)	44.0 (34.4)	7.3 (1.1)	10.4 (1.5)
3 May	1.341 (0.32)	1.548 (0.21)	40.2 (28.7)	28.6 (17.5)	10.3 (2.5)	10.9 (0.7)
7 May	1.176 (0.26)	1.552 (0.19)	67.6 (22.2)	207.1(148.6)	7.6 (1.1)	9.3 (0.7)
13 May	1.626 (0.63)	1.837 (0.48)	43.3 (26.6)	26.7 (15.4)	7.5 (1.5)	8.6 (0.8)
17 May	0.866 (0.15)	1.396 (0.30)	224.5 (92.6)	275.6 (47.3)	b.d.	b.d.

by more than 70% in the birch forest and by more than 150% in the heath. In contrast, there were no effects of increased snow depths on respiration during snowmelt in April/May.

Soil temperatures in March were significantly increased by increased snow depths from 30 to 50 cm at the heath, while there was no temperature difference between heath soil with 50 cm snow depth and the birch soil with about 80-cm-deep snow. Our results, therefore, suggest that 40–50 cm of snow resulted in uncoupling of soil and air temperatures, which is slightly higher than the approximately 30 cm inferred from other studies (Brooks et al., 1997; Monson et al., 2006). The lack of effect of increased snow on soil temperatures during spring-thaw probably was due to higher air temperature during this period, which reduces the importance of snow as insulator and protector against extremely low temperatures. Indeed, the soil temperatures were just below 0°C in both the birch and heath sites despite a wide range of different snow depths. In contrast to the minimal effect of increased snow on soil temperatures and ER during spring-thaw, an important side effect of the increased snow cover at the heath site was the delayed completion of snowmelt, because the length of the snow-free period strongly affects the ecosystem C balance during the growing season (Tieszen, 1978; Soegaard and Nordstroem, 1999; Soegaard et al., 2000; Christensen et al., 2001; Monson et al., 2006).

The soil temperatures were above the empirical threshold of about −5°C for appreciable microbial activity (Brooks et al., 1997) throughout the entire study period in both controls and plots with increased snow. Indeed, the total respiration during the 66 days from 10 March to 17 May in the heath controls of 67 ± 1.4 g C m^{-2} is high compared with estimated growing season C sequestration in the net primary production of 125 g C m^{-2} at a similar heath nearby (Jonasson et al., 1999a). This demonstrates the importance of ecosystem respiration in late winter and during spring-thaw for the annual carbon budget.

Grogan and Jonasson (2005) estimated wintertime (late October to late May) respiration at 128 ± 25 g C m^{-2} in a birch understory and 65 ± 12 g C m^{-2} in a nearby heath ecosystem similar to ours by using first-order exponential models of annual ecosystem respiration and soil temperature. The explained variances in the models were high, ranging from 0.76 to 0.92. If applying their equations to our data, the estimated carbon loss at our heath would be only 29 ± 1 g C m^{-2} (57% reduction compared to model 1 estimate). The annual model, therefore, may underestimate ecosystem respiration during late winter and spring-thaw, in spite of high R^2 values. Higher than expected ecosystem respiration during spring-thaw may be partly due to the thawing of ice layers in the soil and release of trapped CO_2 produced earlier in the winter. However, classic exponential equations, which only include temperature as a variable and substrate availability as a constant are unfit for modeling respiration when substrate availability and free soil water are likely to fluctuate strongly because of freezing and thawing of soil water (Davidson et al., 2006). Indeed, at soil temperatures around 0°C, we observed a striking variability in respiration rates in both ecosystems. The equations, which included a measure of substrate availability, greatly improved model fits particularly at the birch site and, therefore, indicate that ecosystem respiration was substrate limited.

The higher substrate limitation at the birch site than at the heath was unexpected, however, because the substrate quality of birch litter apparently is higher than that of the litter from mainly evergreen shrubs (Grogan and Jonasson, 2005). It could be that the deeper snow at the birch site, creating higher and more stable soil temperatures, led to higher microbial activity and growth, as also indicated by the higher microbial nitrogen and phosphorus concentrations there, which depleted the available substrate. Substrate limited respiration during late winter may therefore in itself be an indication of high microbial activity during the winter.

MICROBIAL BIOMASS DYNAMICS

The contents of microbial carbon and phosphorus, but not the nitrogen content, were appreciably higher in both ecosystems during the snow-covered period than summer estimates in other similar heaths nearby (Jonasson et al., 1999b). However, contrary to our expectation, we found no effects of increased snow depth on the microbial and soil nutrient pools. Nor did we find any correlation between the size of the microbial biomass pools and ER, demonstrating that the microbial biomass is a poor indicator of microbial activity (Wardle, 1992; Michelsen et al., 2004).

The high microbial C in the control plots of the heath measured from mid-March to late April rapidly decreased toward the earlier reported levels once the soil became snow-free. At the same time, microbial N and P also decreased, although at a less pronounced rate. This pattern of changes corresponds well with observations in alpine ecosystems of the Rocky Mountains (Lipson et al., 1999) and suggests that microbial populations may increase through the winter, if an insulating snowpack ensures stable temperature and if free water is available (Brooks et al., 1998).

Later, during spring-thaw, when the sampling was done with higher temporal resolution, we found pronounced variability in microbial biomass over short time intervals in both ecosystems. It appears, therefore, that the size of the microbial biomass, being high in winter, can vary strongly and decline significantly within a few days at the time of snowmelt. The fluctuations suggest large and rapid cycles of mobilization and immobilization of microbial nutrients, which are overlooked if sampling is done with larger time intervals. Indeed, it is possible that earlier reported high net nutrient mineralization rates in arctic soils during winter, measured as differences between autumn and spring content of soil inorganic N and P (Giblin et al., 1991; Nadelhoffer et al., 1992; Jonasson et al., 1993; Hobbie and Chapin, 1996; Schmidt et al., 1999) may reflect a high rate of mineralization in early spring rather than throughout the winter.

Brooks et al. (1998) suggested that freeze-thaw cycles were the main cause of decreased microbial biomass during snowmelt, and other studies have shown microbial diebacks when soils are exposed to freeze-thaw cycles (Schimel and Clein, 1996; Larsen et al., 2002), but initiated grazing by the soil fauna may also affect the microbial community (Ruess et al., 1999). The decline of C in the microbial biomass in the controls at the heath coincided with the first freeze-thaw cycle (Fig. 3b, Table 1), and the microbial C stayed low thereafter. It appears, therefore, that the first thaw had the most important effect on the microbial C content. Microbial N and P, however, decreased less and more slowly, indicating uptake of released nutrients by surviving microbes and causing decreased C-to-N and C-to-P ratios of the microbial biomass. The latter suggests structural changes in the microbial community when the food sources, such as plant labile carbon, increased as the vegetation resumed root growth. Indeed, substantial differences between winter and summer microbial communities have been shown for both fungi (Schadt et al., 2003) and bacteria (Lipson and Schmidt, 2004) in alpine soils of the Rocky Mountains, with fungi being most dominant during winter. If structural changes in the microbial community were the main reason for the changes, they apparently take place over a relatively short interval of time.

The decline in content of microbial nutrients was not accompanied by corresponding increases in soil concentrations of DON or inorganic N and P. Although some nitrogen can be lost by leaching and denitrification (Grogan et al., 2004), it is possible that plants, when they started nutrient uptake in spring, were strong sinks for the released nutrients (Brooks et al., 1998). Recent observations of subnivean photosynthesis (Starr and Oberbauer, 2003) indeed give support for possible plant sequestration of N and P earlier in the season than usually believed. Although further research is needed to establish the significance of subnivean photosynthesis, it may, therefore, partly cancel out the significant respiratory carbon losses during late winter and spring-thaw.

From our study, it seems most likely that most nutrients released from the microbial biomass at snowmelt are retained in the ecosystem by surviving microbes and by plants resuming growth and nutrient uptake at this period, when the availability of free water and light levels increase. High plant demand for nutrients would, indeed, minimize nutrient losses from the ecosystems, and the timing of the release of microbial nutrients may contribute to optimize plant growth and ecosystem production.

CONCLUSION

Our study provides several important insights. First, although the snow buildup in late fall and early winter is a key determinant of late winter soil temperatures and respiration rates in arctic ecosystems, delayed snow accumulation until mid–late winter may still affect late winter soil respiration and the timing of completion of snowmelt. Second, adding a simple, linear relationship between respiration and the supply of DOC or DON to classic first-order exponential equations with only temperature as a variable significantly improved ecosystem respiration models. Third, the microbial community may change rapidly within a few days indicating high nutrient turnover and high net mineralization rates just around completion of snowmelt. The high microbial turnover, contrasting with much smaller changes in organic and inorganic soil nutrient concentrations, indicate that released nutrients are immobilized rapidly and may even provide an important nutrient source for plants resuming their growth earlier than previously thought.

Our observations of fast changes in microbial biomass and the dependence of ER on substrate availability stress the need for high temporal resolution in future research on ecosystem carbon and nutrient dynamics at snowmelt in order to make robust models of their turnover.

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