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The importance of winter in annual ecosystem respiration in the High Arctic: effects of snow depth in two vegetation types

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Abstract

Winter respiration in snow-covered ecosystems strongly influences annual carbon cycling, underlining the importance of processes related to the timing and quantity of snow. Fences were used to increase snow depth from 30 to 150 cm, and impacts on respiration were investigated in heath and mesic meadow, two common vegetation types in Svalbard. We manually measured ecosystem respiration from July 2007 to July 2008 at a temporal resolution greater than previously achieved in the High Arctic (campaigns: summer, eight; autumn, six; winter, 17; spring, nine). Moisture contents of unfrozen soil and soil temperatures throughout the year were also recorded. The increased snow depth resulted in significantly higher winter soil temperatures and increased ecosystem respiration. A temperature–efflux model explained most of the variation of observed effluxes: meadows, 94 (controls) and 93% (fences); heaths, 84 and 77%, respectively. Snow fences increased the total non-growing season efflux from 70 to 92 (heaths) and from 68 to 125 g CO_2-C m^{-2} (meadows). The non-growing season contributed to 56 (heaths) and 42% (meadows) of the total annual carbon respired. This proportion increased with deeper snow to 64% in both vegetation types. Summer respiration rates were unaffected by snow fences, but the total growing season respiration was lower behind fences because of the considerably delayed snowmelt. Meadows had higher summer respiration rates than heaths. In addition, non-steady state CO_2 effluxes were measured as bursts lasting several days during spring soil thawing, and when ice layers were broken to carry out winter efflux measurements.

Arctic ecosystems are no longer considered to be dormant during the winter period as several studies have demonstrated that winter respiration of CO_2 is a significant component of the annual carbon budget (e.g., Oechel et al. 1997; Fahnestock et al. 1998; Elberling & Brandt 2003), and that winter respiration could contribute to a positive feedback of rising atmospheric CO_2 concentrations in the case of increasing snowfall (Lashof 1989). The quantity of snowfall has increased in northern latitudes over the past century (Groisman & Easterling 1994), and is predicted to increase further with the anticipated climate change in this century (Giorgi et al. 2001). Snow fence experiments have been initiated to investigate the effects of changes in snow depth on subsurface carbon storage in Arctic systems, and to predict feedback in terrestrial carbon cycling and effluxes in northern systems under future climatic change. At Toolik Lake, Alaska, tall snow fences typically increased the ambient snow accumulations by a factor of six (Schimel et al. 2004), resulting in warmer mean winter soil temperatures and enhanced respiration and soil nitrogen cycling activities (Walker et al. 1999). More recently, Nobrega & Grogan (2007) simulated a moderate climate change scenario by using 1.2 m tall snow fences during winter at Daring Lake, Northwest Territories, Canada, to experimentally increase the snow depth from 0.3 to 1 m. The study, conducted over the winter of 2004/05 in a mesic birch hummock ecosystem, shows that increasing snow depth almost doubled wintertime carbon efflux, and that the CO_2 released was derived from both bulk soil and plant-associated carbon pools.

Studies using climate modelling and experimental manipulation predict increased plant productivity of tundra communities, and a resulting expansion in the height and density of shrub communities (Chapin et al. 1995; McKane et al. 1997a, b; Sturm et al. 2005). This may have a positive feedback loop to winter CO_2 emissions as taller shrubs increase snow trapping (Sturm et al. 2001). Therefore, to understand the interaction and effect of increasing snow on ecosystem respiration it is necessary to be able to predict the potential for changes in productivity and vegetation distribution as a result of future climate change.

In this study, we have quantified the short-term effects of moderately increased snow depth on annual CO_2 effluxes in *Cassiope* heath and mesic meadow, two common vegetation types in High-Arctic tundra. We hypothesized that ecosystem respiration is controlled by the depth of snow cover because of its effect on soil temperature and soil moisture, and that these effects will be vegetation specific and will lead to increased winter soil CO_2 effluxes, at least on a short-term basis.

Material and methods

Study site

The study was carried out in Adventdalen (78°10′N, 16°04′E), a major valley near Longyearbyen in the western part of Spitsbergen, Svalbard. Bedrock in the lower parts of the valley is dominated by Jurassic and Cretaceous sediments, with the former containing easily weathered calcareous shales (Hjelle 1993). Sedimentary rocks are overlain by aeolian and fluvial deposits (Tolgensbakk et al. 2000). The study area is part of the middle Arctic tundra zone with *Cassiope tetragona* heath and *Dryas octopetala–Tomentypnum nitens* meadow tundra (Elvebakk 2005). Both associations belong to the same alliance, *Caricion nardinae* Nordhagen 1935 (Rønning 1965), but differ in their ecological demands. Whereas the former can be found on neutral to acidic substrate, the latter typically develops on finer textured mesic calcareous substrate (Elvebakk 2005). *Cassiope tetragona* heath is found in more sheltered localities with a steady supply of moisture during the growing period and some snow cover in winter (Rønning 1965). In contrast, *Dryas octopetala*, the dominant prostrate shrub in *Dryas octopetala–Tomentypnum nitens* meadow, is considered to be a chionophobous species, but can be found in mesic meadows as well as commonly on windswept ridge habitats.

Two vegetation types were investigated: *Cassiope* heath and mesic meadow. The dominant vascular plant species in heath vegetation were *Cassiope tetragona*, *Dryas octopetala*, *Salix polaris*, *Saxifraga oppositifolia*, *Alopecurus borealis* and *Bistorta vivipara*. Heaths were situated at the foot of mountain slopes, and were therefore influenced by solifluction material. The meadows were dominated by *Salix polaris*, *Luzula arcuata* ssp. *confusa*, *Dryas octopetala* and *Bistorta vivipara*, and were situated on a river terrace.

The closest official meteorological station is situated about 15 km west of the study area at Svalbard Airport. According to monthly normal data from this station for the years 1969–1990, the mean annual precipitation for the region is 190 mm, of which the major part falls as snow in winter. In this period, the mean annual temperature was −6.7°C. February, the coldest month, had a mean of −16.2°C, and July, the warmest month, was 5.9°C (data available at http://www.eklima.no). This station also provided the precipitation data for the study period (2007–08). Another weather station run by the University Centre in Svalbard, Adventdalen, only 6 km west of the study area, provided the air temperature at 4 m above ground and the wind direction during the study period. The area is strongly influenced by underlying continuous permafrost, and the maximum thickness of the active layer recorded a few kilometres from our study location in a Circumpolar Active Layer Monitoring (CALM) site averaged 105 cm in the years 2000–07. The sun is continuously below the horizon during November–February, leaf senescence occurs in mid–late August, and ground frosts and long-lasting snow can be expected from 1 September.

Experimental design and measurements

Within each of the two vegetation types (heath and meadow), six snow fences were established with paired control areas (giving a total of 12 fences and 12 controls). These were grouped geographically into blocks of three fences, with their paired controls, to account for the inherent spatial variability. There were two blocks of each vegetation type. The fences and controls of each block were spread out in an area of 200 × 200 m and separated from the next block by at least 500 m. Fences (1.5 m tall and 6.2 m long) were established perpendicular to the prevailing winter wind direction (south-east) in autumn 2006. All of the measurements carried out in the fence treatments were in the area behind the fences that received the deepest and longest lasting snow, as observed from the snowmelt patterns in June 2007 and 2008: the same pattern occurred in both years. The study areas were therefore 3–12 m behind the fences, and all subsequent measurements (snow depth, soil temperature, moisture and respiration) were made in this area.

Soil temperature was recorded using thermistors connected to data loggers (Gemini Data Loggers; Tinytag, Chichester, West Sussex, UK). Thermistors were installed just below the soil surface, well-shielded from direct solar radiation, and at depth of 5 cm. From 5 September 2007 the data loggers registered soil temperature at hourly intervals with a resolution of ±0.1°C. Additional soil temperature data collected by the International Polar Year project Thermal State of Permafrost in Norway and Svalbard at the CALM sites in Adventdalen were used for the period July–September 2007.

Volumetric soil moisture content was measured with an accuracy of 5% with a handheld soil moisture sensor (Theta Probe ML2x; Delta-T Devices, Cambridge, UK) that responds to changes in the dielectric constant of the soil, which is mainly determined by its unfrozen water content. Five soil moisture readings were taken close to each collar (to account for heterogeneity of the soil in the study area). Measurements were performed shortly after the CO_2 efflux measurements to avoid any disturbance of the soil. Soil moisture could not be measured in frozen soil as it was impossible to insert the moisture probe.

Snow depth was measured manually in the central study area by penetrating through the snowpack with an avalanche probe, and by digging snow pits. On 20 May 2008, before the onset of rapid snow melting, measurements of snow depth were taken in 16 positions behind each fence with an avalanche probe.

Ecosystem CO_2 efflux was measured using a LI-COR infrared gas analyser with a portable dark and closed-dynamic soil flux chamber, which includes CO_2 and water vapour analysers in the headspace (LI-COR 6400-09/6262 Soil CO_2 Flux Chamber; LI-COR Biosciences, Lincoln, NE, USA). This set-up provides the most direct way to measure soil respiration (Davidson et al. 2006). To minimize the disturbance of the soil and to reduce CO_2 leakage during measurements, the chamber was placed on top of permanently installed PVC collars (Luo & Zhou 2006). Collars of 10 cm in diameter and depth were installed in mid–late June 2007, soon after the snowmelt. Two collars were inserted behind each fence and the corresponding paired control. In addition, at two fences/controls from each vegetation type, a further four collars were installed (i.e., four fences/controls had six collars, and eight fences/controls had only two collars). It was envisaged from the outset that we would encounter many logistical difficulties in digging out the collars from deep snow in the winter, so we had an arrangement where we could get a greater spatial cover of measurements when the snow was shallow, and concentrate on fewer collars at the logistically most demanding time of the year. The height of the above-ground part of each collar was measured 10 times both at time of installation and after the spring thaw, and the heights were used to correct the volume used to calculate the CO_2 efflux. Measurements were taken following the approach of Welles et al. (2001). After placing the chamber on a collar, the CO_2 concentration inside the chamber was drawn down to a level of 10 ppm below the target concentration. Subsequently, increasing CO_2 concentrations in the chamber headspace were logged, and the CO_2 efflux was computed as the rate of CO_2 increase around ambient level. As the extent to which CO_2 concentration prior to measurements should be decreased depends on the anticipated magnitude of efflux (Norman et al. 1997), draw-down was changed to 5 ppm below the target concentration to keep the same total measuring time when effluxes were expected to be small. The start of measurements during the growing season was delayed for 30 s after the chamber was fitted onto a collar to reduce photosynthetic activity to negligible levels prior to measurements (Grogan & Chapin 2000).

During winter fieldwork the LI-COR system was kept in an insulated and heated container to maintain temperatures above freezing point. A similar set-up was successfully applied in previous studies (Elberling 2003, 2007), and the detection limit of this set-up was tested to be <0.01 μmol CO_2 m^{-2} s^{-1} (Elberling et al. unpubl. data). In order to measure ecosystem respiration rates beneath the snow rather than fluxes from the snow surface, which might be influenced by the physical properties of the snowpack and possible CO_2 storage within it (Larsen et al. 2007; Björkman et al. 2010 [this issue]), snow was removed with shovels prior to the measurements. Mostly, the removal of deep snow for such measurements was carried out after 1 February 2008. Previous studies have reported high rates of soil CO_2 release for up to 25 minutes after the removal of snow (Grogan et al. 2001; Grogan & Jonasson 2005), so our measurements were normally conducted at least 25 minutes after the removal of snow. However, on windy days holes were quickly refilled with snow, and measurements had to be made shortly after snow removal. Collars were excavated for each measurement and the holes were refilled with snow afterwards, but the snow density and stratigraphy may well have been altered by the process, thus affecting both the insulating properties of the snow and subsequent measurements. This may lead to lower flux rates than occur at sites with undisturbed snow, i.e., leading to an underestimation of fluxes. Removing the snow may have further implications on the subsurface temperatures and the CO_2 concentration gradient across the soil surface. Temperature effects resulting from snow removal were evaluated in a similar winter study in a nearby site

(Elberling 2007). No significant effects on near-surface soil temperatures were found at sites subject to snow removal at snow pits with a base area of about 200 cm^2 left open for less than 48 h (Elberling unpubl. data). If the temperature of the collars had been reduced by such exposure to the air, this would have resulted in a lower flux and thus an underestimation of flux rates. Snow removal also disrupts the CO_2 gradient between the soil surface and the atmosphere, making it steeper than with intact snow cover (McDowell et al. 2000); this effect may lead to an overestimation of soil CO_2 production.

Any ice lenses present were removed with an ice axe without destroying plant parts enclosed in the ice. Flux measurements were initiated 2 weeks after installation of the collars, and during the first summer and subsequent full winter after the snow fences were installed. In total, 40 measuring campaigns were made over one year with, on average, 35 efflux measurements per campaign (number of campaigns: summer, eight; autumn, six; winter, 17; spring, nine). Some campaigns made during the winter period resulted in incomplete data sets as a result of failing instruments and difficulties of finding collars buried in the snow. Table 1 outlines the dates of the sampling campaigns.

In order to quantify the effect on biomass, the top 10 cm of vegetation and soil from all collars from one block in each vegetation type (a total of 56 collars) was harvested at the end of July 2008. Material was divided into above- and below-ground biomass, and the above-ground fraction was further sorted into “heath” (alive and dead plant material of *Cassiope tetragona*), “meadow” (alive and dead plant material of *Dryas octopetala*) and “rest”, which included alive and dead plant material of all other vascular plants and the moss layer. The material was then immediately dried at 70°C for 7 days. Below-ground biomass samples were stored in a dark fridge at 4°C for 2 days before roots were washed out and dried at 70°C for 5 days. After drying, both above-ground and below-ground samples were stored at room temperature (20°C) for 19 days before they were dried once again for 2 h at 70°C and then left in a desiccator prior to weighing.

Table 1 Number of collars measured at fence and control areas for all CO_2 efflux measurement campaigns in Adventdalen, Svalbard. Measurements taken after breaking through an ice layer are not included.

Season	Date	Heath control	Heath fence	Meadow control	Meadow fence	Total
Summer	10 Jul 2007	14	14	14	14	56
	11 Jul 2007	6	6	6	6	24
Autumn	22 Aug 2007	20	20	20	20	80
	28 Aug 2007	20	19	20	20	79
	04 Sep 2007	20	20	20	20	80
	10 Sep 2007	20	19	20	20	79
	19 Sep 2007	14	14	14	14	56
	26 Sep 2007	14	14	20	20	68
Early winter	03 Oct 2007	14	14	6	10	44
	10 Oct 2007	14	6	0	0	20
	18 Oct 2007	0	0	14	14	28
	25 Oct 2007	14	14	0	0	28
	2 Nov 2007	0	0	5	0	5
	15 Nov 2007	0	0	12	12	24
	19 Nov 2007	6	6	0	0	12
	28 Nov 2007	8	12	0	0	20
	6 Dec 2007	0	0	13	14	27
Late winter	18 Jan 2008	1	6	0	0	7
	12 Feb 2008	0	0	0	5	5
	26 Mar 2008	0	0	4	3	7
	27 Mar 2008	0	0	6	6	12
	29 Mar 2008	0	0	5	6	11
	1 Apr 2008	0	0	5	5	10
	14 May 2008	0	0	6	6	12
	20 May 2008	12	0	12	0	24
Spring	30 May 2008	0	0	1	0	1
	4 Jun 2008	13	0	13	0	26
	6 Jun 2008	14	0	13	0	27
	7 Jun 2008	14	0	14	0	28
	9 Jun 2008	14	0	14	0	28
	11 Jun 2008	14	0	14	0	28
	12 Jun 2008	14	0	14	0	28
	15 Jun 2008	13	0	14	0	27
	19 Jun 2008	14	7	14	6	41
Summer	26 Jun 2008	14	14	14	14	56
	2 Jul 2008	14	14	14	14	56
	10 Jul 2008	14	14	14	14	56
	15 Jul 2008	20	19	20	20	79
	21 Jul 2008	14	14	14	14	56
	29 Jul 2008	14	14	14	14	56

Data and statistical analyses

To account for the seasonal character of this data, the complete data set (except biomass data) was separated into four different time periods—summer, autumn, winter and spring—and each time period was tested separately following Crawley (2005): summer, 23 June 2007–17 August 2007 (inclusive); autumn, 18 August 2007–1 October 2007 (inclusive); winter, 2 October 2007–29 May 2008 (inclusive); and spring, 30 May 2008–22 June 2008 (inclusive). Because of a winter warming event (Fig. 1), the winter season was subsequently divided into early winter (2 October 2007–31 December 2007) and late winter (1 January 2008–29 May 2008). It is important to note here that flux measurements in early winter were made during the time with rather little snow and no ice layers, and that therefore the measurements were easier and less problematic to make in contrast to those in late winter.

The criteria used to define the seasons were as follows: end of spring was defined as the first day when all collars were free of snow; end of summer was the first day when

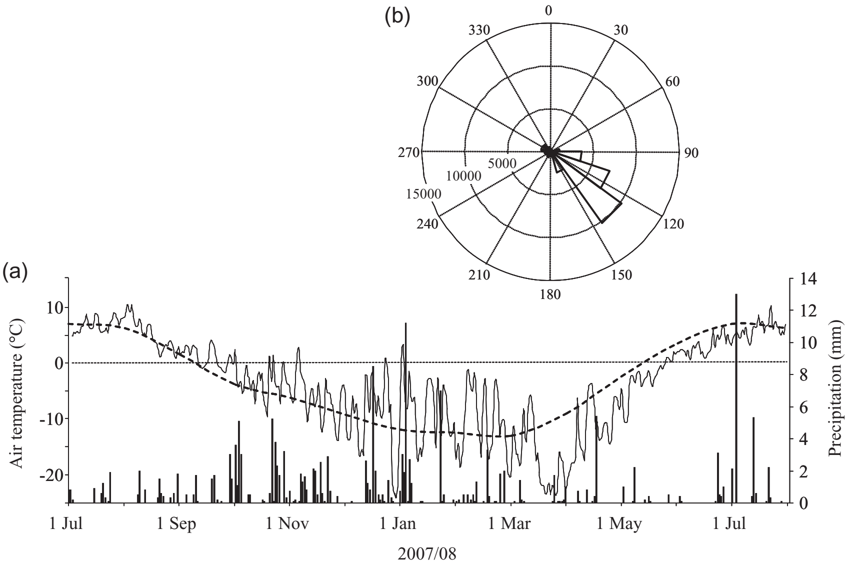

Fig. 1 (a) Air temperature and precipitation data and (b) wind directions during the winter season 2 October 2007–29 May 2008. (a) Mean monthly air temperatures for the years 1997–2007 are shown with a dashed line, and the observed air temperatures 2007/08 are indicated with a solid line. (b) The numbers of observations are given (n = 0–15 000).

Table 2 Dates when mean daily surface soil temperatures in the two different treatments in heath and meadow tundra fell below or rose above 0 or 5°C during the entire study period from 10 July 2007 to 29 July 2008. Dates in brackets indicate the days on which soil temperatures stayed in the relevant interval for at least 7 days. Soil temperatures during the winter warming event are not included.

Soil temperature at surface	Heath tundra		Meadow tundra	
	Control date	Fence date	Control date	Fence date
<5°C	18/8 (18/8)	17/8 (17/8)	17/8 (17/8)	17/8 (17/8)
<0°C	11/9 (8/10)	11/9 (21/9)	12/9 (2/10)	12/9 (2/10)
>0°C	31/5 (31/5)	13/6 (13/6)	30/5 (30/5)	1/6 (1/6)
>5°C	10/6 (2/7)	26/6 (2/7)	9/6 (2/7)	24/6 (2/7)

the mean daily soil surface temperatures of any logger dropped and stayed below 5°C for at least seven consecutive days; end of autumn was the first day with snow cover at all collars; and end of winter was the first day when the mean daily soil surface temperature of any logger increased and remained above 0°C for longer than 7 days. For details of some of the defining temperatures, see Table 2.

The start and end of the summer, autumn and winter seasons are periods when we are assured that all collars experienced the defined conditions, and therefore treatments can be compared during these periods. Spring starts at snowmelt, so the length of this season (and therefore the start of the growing season) varies across treatments, and so caution must be taken in comparing treatments in this period. The growing season was defined as summer plus the part of the spring season when the collars were free of snow, which was 16–17 days for the controls and none for the fence treatment.

Observed soil CO_2 effluxes were modelled in order to quantify seasonal and annual estimates. Soil CO_2 effluxes were related to near-surface soil temperatures by applying a commonly used first-order exponential equation of van't Hoff type 1 (Grogan & Jonasson 2005; Davidson et al. 2006):

$$Resp = \alpha e^{\beta T} \text{ (where } Q_{10} = e^{\beta 10}\text{)}, \tag{1}$$

where $Resp$ is respiration rate (measured as the soil CO_2 efflux), α and β are fitted parameters, T is the measured soil temperature and Q_{10} is the temperature sensitivity of respiration. The parameters α and β were calculated for each treatment and vegetation type by relating mean observed effluxes to recorded soil surface temperatures for each measurement. Finally, $Resp$ was calculated on an hourly basis using site-specific soil temperatures as the only unknown in Eqn. 1.

Statistical evaluations of significant ($P < 0.05$) variations between vegetation types and treatments were performed in the program R 2.7.1. Probability values between 0.1 and 0.5 were given, but were not considered as significant. Data were tested for normal distribution using the Shapiro–Wilk test, and a one-way ANOVA and Wilcoxon test was performed on normal distributed and non-normal distributed data, respectively. Student's *t*-tests were applied to evaluate significant differences between the two vegetation types and treatments. A restricted number of replicates in late winter were taken, so statistical analysis was carried out solely on data from early winter. Analysis was performed on data from the last days of early winter measurements, when the greatest treatment effects might be expected. CO_2 efflux values obtained during the "spring burst" were excluded from the statistical analysis.

Results

Climatic parameters

Air temperatures and precipitation from July 2007 to July 2008 are shown in Fig. 1. The mean air temperature was −4.0°C, July 2007 was the warmest month (6.7°C) and March 2008 was the coldest month (−17.1°C). Except for the period December–February, the mean monthly temperatures were below the normal mean monthly temperature for the years 1997–2007 (Fig. 1). The total precipitation for the study period of 181 mm was, on a monthly basis, below the mean monthly precipitation for the previous 10 years, except for October and December (data not shown). July, August and September 2007 were exceptionally dry months compared with the 10-years normal. In early winter the mean air temperature was −6.7°C and the total precipitation was 65.1 mm. In late winter the mean air temperature was −10.2°C and the total precipitation was 56.4 mm. The prevailing wind direction in the period 2 October 2007–30 May 2008 was south-east (Fig. 1).

The first snow occurred in early October 2007. Control areas in heaths accumulated more snow than in meadows (Figs. 2, 3), and significantly more in mid-November, 12 and 5.9 cm, respectively ($F_{1,24} = 11.617$, $P = 0.002$), and late-November, 12.7 and 4.7 cm, respectively ($W_{1,27} = 11.5$, $P < 0.001$). Fences had accumulated more snow than controls by 18 October 2007 in meadow ($W_{1,26} = 38$, $P < 0.006$), and by 25 October 2007 in heath ($F_{1,26} = 33.189$, $P < 0.001$). By 20 May, before the rapid onset of melt, snow depth was significantly greater behind the fences than in the controls, both in heath ($F_{1,61} = 396.3$, $P < 0.001$) and in meadow ($F_{1,63} = 346.13$, $P < 0.001$). Snow accumulation was increased to a distance of >20 m behind the fences, and the greatest depth and longest lasting snow occurred 2–14 m behind the fences.

Accumulated snow delayed the complete melt-out of collars in spring by 16–17 days; controls were snow-free on 6 June, whereas collars behind fences were snow-free on 22 June in meadows and on 23 June in heaths. The spring surface soil temperature was significantly lower behind fences than controls for both heath ($W = 7172$, $P < 0.001$) and meadow ($W = 12\,703$, $P < 0.001$). The mean surface soil temperature for controls in heath and meadow during the period 30 May 2008–22 June 2008 was 3.3 and 4.0°C, whereas behind fences mean temperatures were 0.3 (heath) and 0.5°C (meadow): meadow was significantly warmer than heath ($W = 6129$, $P < 0.05$), and this difference was most pronounced during the first 9 days in June 2008.

Soil water content

Volumetric soil moisture (Figs. 2, 3, Table 3) was very high immediately following snowmelt, e.g., on 19 June 2008 meadow soils had a moisture content of 53% in controls and 81% behind fences, and heath soils had 39 and 71%, respectively. In the following 2 weeks and throughout the summer, the soil moisture decreased markedly.

Significant differences between vegetation types were observed during both summers, with meadows having moister soil than heaths, both in controls (2007, $F_{1,38} = 38.806$, $P < 0.001$; 2008, $F_{1,59} = 7.1857$, $P < 0.001$) and in fence treatment areas (2007, $F_{1,38} = 10.075$, $P < 0.001$; 2008, $F_{1,82} = 15.202$, $P < 0.001$). Treatment effects were significant for meadow vegetation both summers (2007, $F_{1,38} = 18.901$, $P < 0.001$; 2008, $F_{1,71} = 34.533$, $P < 0.001$): soils behind fences were moister than controls. Heath soils only displayed a treatment effect in 2008 (2007, $F_{1,38} = 0.7069$, $P = 0.4057$; 2008, $F_{1,70} = 67.701$, $P < 0.001$). In autumn, soil moisture increased with time until early October 2007, when soil freezing started, and the unfrozen water content dropped below 8%. However, in autumn there were no significant treatment or vegetation type differences.

Soil temperature

In summer 2008 controls had significantly higher surface soil temperatures than fence areas in heaths ($F_{1,294} = 20.752$, $P < 0.001$), but not in meadows (Figs. 2, 3). In controls, mean temperatures at surface and 5 cm depth were significantly higher in heaths than in meadows ($F_{1,368} = 13.835$, $P < 0.001$), but the opposite was found for fence treatment areas ($F_{1,294} = 4.976$, $P = 0.026$). During autumn 2007 no difference between controls in meadow and heath areas could be observed, but meadow soils were significantly warmer in fence areas than heath soils ($W_{1,268} = 4014$, $P < 0.001$). However, in the heaths, controls were warmer than fence areas in this period ($W_{1,241} = 6928.5$, $P < 0.001$), and there was no difference between treatments in the meadows. At 5 cm depth the soil temperatures responded in the same way with similar significances.

In early October the strong diurnal variations in hourly surface soil temperatures started to disappear, and during the first month of the winter temperatures began to diverge between control and fence treatment areas in both vegetation types (Figs. 2, 3). From October 2007 to June 2008 soil surface mean temperatures at heaths were −7.2°C in controls and −2.8°C in fence areas, and at meadows were 9.0 (controls) and −3.6°C (fences). Mean soil temperatures at 5 cm depth deviated at most by 1.1°C from mean surface soil temperatures. Both early and late winter surface soil temperatures were higher in heath than meadow (controls, early winter, $W_{1,999} = 127\ 702.5$, $P < 0.001$; fences, early winter, $W_{1,908} = 74\ 192$, $P < 0.001$; controls, late winter, $W_{1,1648} = 340\ 729.5$, $P < 0.001$; fences, late winter, $W_{1,1498} = 192\ 202$, $P < 0.001$). Heaths were warmer than meadows: in early winter by 1.1°C in controls and by 1°C in fence areas, and in late winter by 2°C in controls and 0.5°C in fence areas.

There was a significant treatment effect on surface soil temperature throughout the winter, and fence areas were warmer than controls. In early winter there was a 2.8°C difference in heaths ($W_{1,817} = 31\ 370.5$, $P < 0.001$), which increased to 5.3°C in late winter ($W_{1,1348} = 48\ 443.5$, $P < 0.001$). In meadows the difference was 2.2°C in early winter ($W_{1,1090} = 44\ 294$, $P < 0.001$) and 6.8°C in late winter ($W_{1,1798} = 74\ 598$, $P < 0.001$). Maximum differences were 10.8°C on 3 February 2008 in heath and 17.2°C on 21 March 2008 in meadow. The minimum mean daily surface soil temperatures in meadow were −23.0°C in controls and −7.6°C in fence areas, and −16.9 and −7.0°C, respectively, in heath.

The mean daily air temperature increased above 0°C on 26 May 2008. Following elevated air temperatures, the mean daily soil surface temperature started to rise to above 0°C at controls on 30 May (meadow) and 31 May (heath). In fence areas this occurred on 1 June (meadow) and 13 June (heath). Following warming of the soil surface, there was a delay in the warming of the soil at 5 cm depth by 7 (heath) and 9 days (meadow) in controls, and by 9 (heath) and 22 days (meadow) in fence areas. Surface soil temperatures stayed between −0.5°C to +0.5°C for 5 (heath) and 4 days (meadow) in controls, and for 17 (heath) and 14 days (meadows) in fence areas.

Soil CO_2 effluxes

The highest mean effluxes were measured in summer 2007 (Figs. 2, 3, Table 4): effluxes from meadows were significantly higher than in heaths, both in summer 2007 (controls, $t = -5.3823$, $df = 36.154$, $P < 0.001$; fences, $W_{1,38} = 100$, $P = 0.006$) and 2008 (controls, $W_{1,178} = 67$, $P < 0.001$; fences, $W_{1,177} = 99$, $p < 0.01$). No significant treatment effect was observed in summertime. The effluxes decreased during autumn without significant treatment effects in either vegetation type. The lowest CO_2 effluxes were measured during winter. The mean measured efflux was higher in early winter than in late winter. Effluxes were higher behind fences ($P = 0.06$), but differences were not statistically significant. A comparison of mean efflux between fence areas and controls for the last day of measurement in early winter (heath, 28 November, and meadow 6 December, 2007), when the treatment effect was most pronounced, showed a clear trend towards higher effluxes in fence areas compared with controls, both from heaths, where respiration behind fences was 0.32 µmol C m^{-2} s^{-1}, and thus almost twice as high as in controls ($W_{1,18} = 23$, $P = 0.057$), and from meadows, where respiration was 0.29 µmol C m^{-2} s^{-1}, and almost three times as high as in fence areas ($W_{1,25} = 52$, $P = 0.061$). No significant difference in effluxes between the vegetation types was observed. In spring, meadows had greater fluxes than heaths, but there were no treatment effects.

Seasonal and annual CO_2 estimates

Several bursts of CO_2 were measured throughout this study, and are described in the next section, but these bursts are excluded in the following seasonal estimates. Temporal trends in observed ecosystem respiration rates could be explained reasonably well by near-surface temperatures alone (Fig. 4), with R^2 values of between 0.67 and 0.88 (Table 3). Based on these regressions, the temperature sensitivity of respiration (Q_{10} values) was estimated for a temperature range above and below 0°C for each vegetation type (Table 3). Values of Q_{10} differed between the vegetation types and were generally higher in meadow than in heath (Table 3). The only exception was a particularly high Q_{10} of 12.9 in heath fence treatment areas for subzero temperatures. Temperature sensitivity was between two- and seven-fold higher at temperatures below 0°C. Ecosystem respiration showed a stronger correlation with soil surface temperature in meadows than in heaths. Subzero Q_{10} values are higher than Q_{10} values above freezing (Fig. 4). This indicates that it is unlikely that the measured fluxes are overestimated, but we acknowledge that snow removal may influence the CO_2 gradient from soil to the atmosphere during non-steady state measurements. Modelled soil respiration rates fit well with the observed effluxes (Figs. 2, 3). Excluding spring burst data, the model explains 94 and

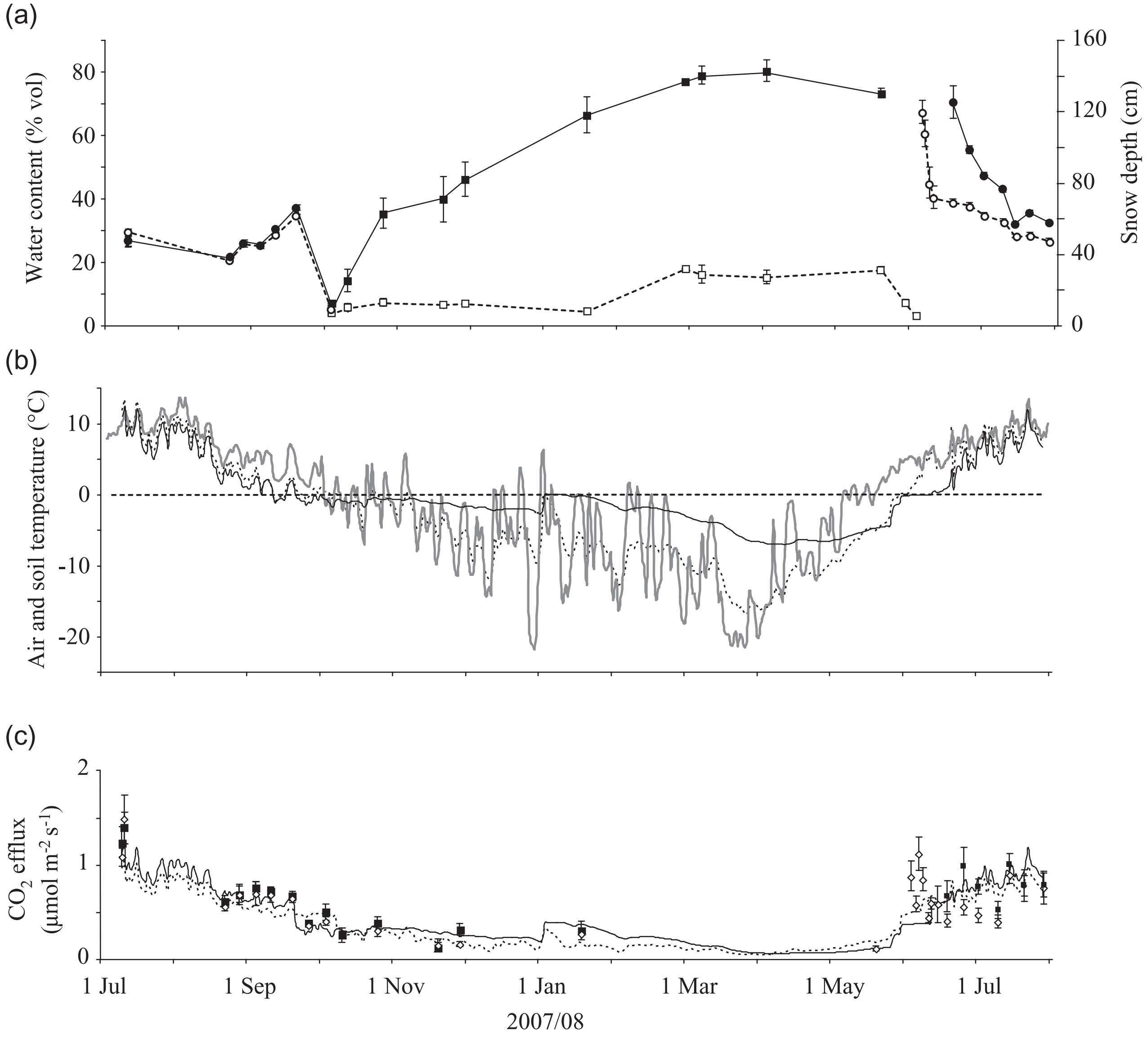

Fig. 2 Temporal trends in heath vegetation. Filled symbols and solid lines are data from fence treatment areas and open symbols and dashed lines are from controls. (a) Water content (squares) and snow thickness (circles): note the symbols overlap in early October. (b) Air temperature in grey and soil temperatures at 2 cm in black. (c) Observed soil CO_2 effluxes and modelled effluxes that are based on observed Q_{10} values (see Fig. 4) and soil temperatures. Standard errors are shown as bars.

93% of the temporal variation in meadow controls and fence areas, and 84 and 77% in heaths, which further highlights the importance of the soil temperature regime as the main environmental control on CO_2 production. Using these models, the annual ecosystem efflux was calculated based on observed soil temperatures in the field.

The annual ecosystem efflux was greater for meadows than for heaths, and higher for fence treatment areas than in controls. CO_2 effluxes during the growing season accounted for 44% of the annual efflux in heaths and 58% in meadows with ambient snow cover (Table 5). With deeper snow, as produced by fences, this decreased the proportion respired in summer to 36% in both vegetation types. Winter respiration contributed 24–33% to annual totals in controls, increasing to 38% under deeper snow. When considering the whole non-growing season, which includes autumn and part of the spring season as well as winter, a greater proportion of the annual total was respired in the fence treatment areas (64%) than in the controls (56% in heath and 42% in meadow).

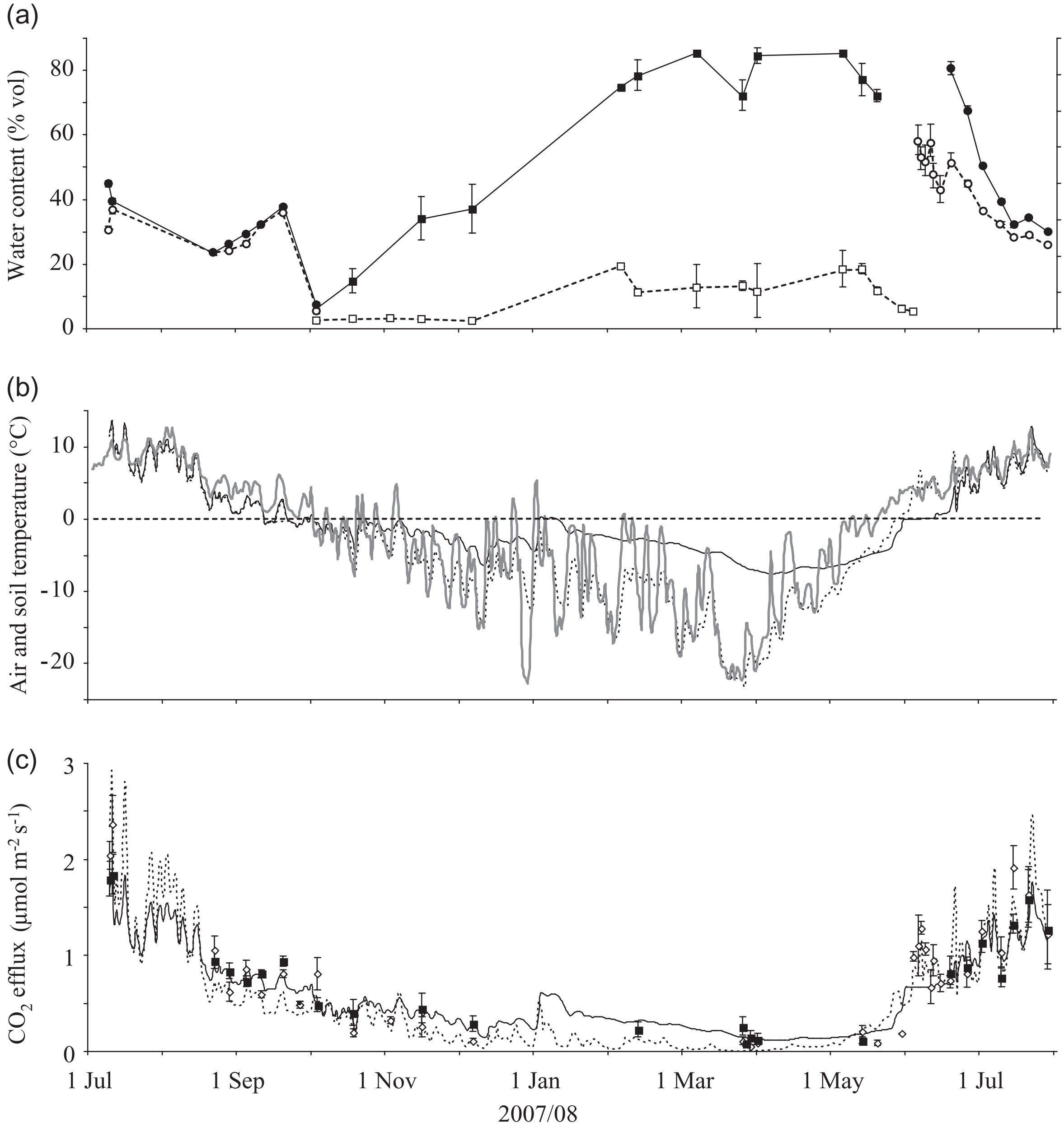

Fig. 3 Temporal trends in meadow vegetation. Filled symbols and solid lines are data from fence treatment areas and open symbols and dashed lines are from controls. (a) Water content (squares) and snow thickness (circles): note the symbols overlap in early October. (b) Air temperature in grey and soil temperatures at 2 cm in black. (c) Observed soil CO_2 effluxes and modelled effluxes that are based on observed Q_{10} values (see Fig. 4) and soil temperatures. Standard errors are shown as bars.

Winter warming, ice and spring CO_2 effluxes

A sudden winter warming event occurred over New Year 2007/08, with rapidly increasing air temperatures from −12.7 to 2.8°C, accompanied by precipitation (Fig. 1). A few days later temperatures dropped to −6.9°C. The maximum hourly surface soil temperatures recorded during the warm event in controls were 0.4°C in heath and 0.1°C in meadow, and surface soil temperatures in fence areas were 0.1 and 0.3°C, respectively. Surface soil temperatures in heath stayed above −1°C for 3 days in controls, and for 25 days in fence areas. Controls in meadow experienced soil surface temperatures above −1°C for less than 24 h, whereas temperatures in fence areas stayed above −1°C for 10 days.

Table 3 Summary of vegetation- and treatment-specific results. Numbers in brackets present the standard errors of the means.

Vegetation	Heath	Heath	Meadow	Meadow
treatment	Control	Fence	Control	Fence
Biomass (g m^{-2}) (±SE)				
Above-ground	2306 (±254)	2052 (±227)	3297 (±386)	2308 (±389)
Below-ground	2335 (±319)	3183 (±396)	2576 (±361)	2903 (±401)
Total biomass	4641 (±413)	5235 (±416)	5872 (±517)	5211 (±591)
Water content (% by vol) (±SE)				
Summer 2007	27 (±0.9)	28 (±1.3)	33 (±1.2)	43 (±1.0)
Autumn 2007	27 (±0.7)	27 (±0.8)	28 (±0.5)	29 (±0.5)
Spring 2008	38 (±3.4)	53 (±5.1)	45 (±4.3)	61 (±3.0)
Summer 2008	29 (±0.5)	34 (±0.7)	29 (±1.1)	33 (±0.8)
Mean snow depth (±SE) 20 May 2008				
Mean	32 (±14)	130 (±25)	21 (±11)	129 (±24)
Q_{10} values (followed by R^2 values from regression lines)				
Q_{10}	2.7 (0.78)	3 (0.67)	4.3 (0.84)	3.9 (0.88)
$Q_{10} < 0°C$	3 (0.54)	12.9 (0.09)	8.7 (0.62)	8.3 (0.73)
$Q_{10} > 0°C$	1.8 (0.39)	1.8 (0.55)	4.4 (0.75)	2.1 (0.79)

Table 4 Mean measured ecosystem CO$_2$ efflux (µmol C m^{-2} s^{-1}) (±SE).

Vegetation type	Heath	Heath	Meadow	Meadow
Treatment	Control	Fence	Control	Fence
Snow depth	Shallow	Deep	Shallow	Deep
Summer 2007	1.29 (±0.17)	1.33 (±0.16)	2.21 (±0.21)	1.82 (±0.38)
Autumn 2007	0.63 (±0.06)	0.66 (±0.06)	0.74 (±0.07)	0.80 (±0.06)
Early winter 2007	0.26 (±0.05)	0.33 (±0.06)	0.34 (±0.07)	0.41 (±0.11)
Late winter 2008	0.19 (±0.03)	0.31 (±0.98)	0.11 (±0.03)	0.16 (±0.06)
Spring 2008	0.68 (±0.11)	0.68 (±0.16)	0.86 (±0.12)	0.82 (±0.16)
Summer 2008	0.65 (±0.10)	0.81 (±0.13)	1.31 (±0.20)	1.17 (±0.18)

As a result of this warming event, an ice layer was formed on the soil surface in controls, and persisted throughout the rest of the winter. Thickness of the soil surface ice layer (so-called basal ice) was 6 cm in heath controls on 18 January 2008, and 8.5 cm in meadow controls on 12 February 2008. Behind fences, ice lenses formed in the deep snow pack instead of a basal ice layer at all fences, with one exception. Behind one fence in one row consisting of three collars where snow depth did not exceed 26 cm prior to the warming event, an ice layer on the soil surface was formed. This ice layer had a mean thickness of 18 cm on 26 March 2008. Above all three collars in the second row behind this fence the snow depth ranged from 94 to 130 cm prior to the warming event, and these collars stayed ice-free.

The necessity for breaking through the ice layer before CO$_2$ efflux could be assessed led to difficulties in measuring soil respiration for those ice-covered collars. A major decrease in CO$_2$ effluxes with time after breaking through the ice layer was studied in one collar on 12 February 2008, in two collars on 26 March 2008 and in a further collar on 14 May 2008 (Fig. 5). These non-steady state bursts were directly caused by breaking through the ice in the field. CO$_2$ effluxes were measured immediately after breaking through the ice, and were higher than summer efflux rates. The highest efflux measured directly after breaking through the ice was 5.78 µmol C m^{-2} s^{-1} on 14 May 2008, 132 days after the formation of the ice layer. Efflux measured directly after breaking through the ice on 12 February 2008, 40 days after the formation of the ice layer, was 3.91 µmol C m^{-2} s^{-1}. The CO$_2$ efflux decreased with time, and stabilized at levels of 0.25 µmol C m^{-2} s^{-1} around 230 minutes after breaking through the ice layer on 12 February 2008. Efflux measured 20 h after breaking through the ice layer of two collars on 26 March 2008 was 0.08 and 0.12 µmol C m^{-2} s^{-1}. Because of these apparent CO$_2$ bursts, efflux values obtained on collars that were broken free from ice less than one day before measurement were excluded from further analysis.

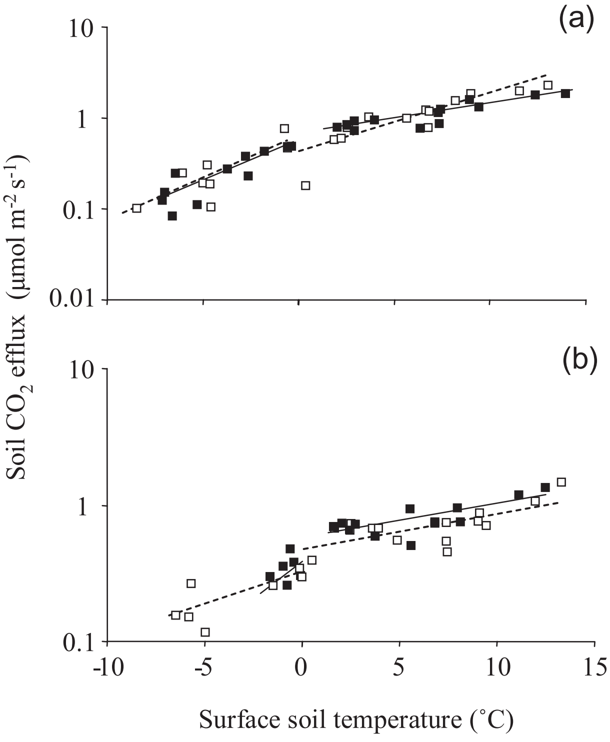

Fig. 4 Observed CO_2 efflux versus surface soil temperature in control and fence treatment areas in (a) meadow and (b) heath. Note the log scale on the *y*-axis. Filled symbols and solid lines represent data from fenced treatment areas and open symbols and dashed lines are controls. Effluxes measured at end of March 2008 in meadow controls at soil temperatures below –10°C are not included. Exponential regression fits are shown as lines for temperatures above and below 0°C. Q_{10} values and R^2 values are reported in Table 3.

Biomass

Total biomass (above- and below-ground) showed no treatment or vegetation type effects. Although non-significant, below-ground biomass was 36 (heath) and 13% (meadow) greater behind fences than in controls, and the proportion of the total biomass below-ground was greater in the fence treatment areas (Table 3). The above-ground biomass in heath controls was significantly lower than in meadow controls ($F_{1,23} = 5.2372$, $P = 0.032$). When separating above-ground biomass into the woody plants *Cassiope tetragona* (from heath) or *Dryas octopetala* (from meadow) and the "rest", including all other vascular plants and mosses, it became clear that there was a vegetation-type specific difference between the fraction of woody plants and the "rest" in relation to the quantity of total above-ground biomass. Whereas *Cassiope tetragona* contributed 21.4% to the total above-ground biomass in heath controls, *Dryas octopetala* accounted for only 5.2% of the total above-ground biomass in meadow controls. The biomass of other vascular plants and mosses was significantly higher in controls of meadow than in those of heath ($F_{1,23} = 9.5877$, $P = 0.005$). Data further indicate that the above-ground biomass in meadow was significantly lower in fence areas than in controls ($W_{1,18} = 80$, $P = 0.002$). Whereas there was no treatment effect on *Dryas octopetala* in terms of biomass, a significant decrease in the mass of other vascular plants and mosses was found ($F_{1,18} = 4.9516$, $P = 0.032$).

Discussion

Winter CO_2 production and emissions

Estimated annual CO_2 effluxes in this study were 125 g C m^{-2} yr^{-1} from heath and 162 g C m^{-2} yr^{-1} from meadow, which are in line with the annual efflux estimations of 103–152 g C m^{-2} yr^{-1} for similar vegetation types in Endalen, a valley near Adventdalen (Elberling 2007). The total winter ecosystem CO_2 effluxes in Adventdalen (241 days) were 40 g C m^{-2} yr^{-1} from meadows and 42 g C m^{-2} yr^{-1} from heaths, which equates to a contribution of 24 and 33% to the annual ecosystem respiration. This substantial winter contribution to the annual respiration is reported from several Arctic ecosystems (Zimov et al. 1996; Fahnestock et al. 1999; Elberling & Brandt 2003), ranging between 20 and 40% of the annual effluxes. Furthermore, the non-growing season respiration is of the order of 68–71 g C m^{-2} yr^{-1}, a contribution of 42 and 56% of the annual total. The actual mass of carbon produced during winter in our study is within the range of published values. Oechel et al. (1997) reported 70 g CO_2-C m^{-2} for tussock tundra, based on an interpolation from infrared gas analysis chamber measurements, whereas Fahnestock et al. (1998) reported a lower total winter respiration based on snow CO_2 concentration gradients of 1–11 g CO_2-C m^{-2} from various Arctic communities, including tussock tundra.

Ecosystem CO_2 effluxes in this study were higher in early winter (0.26–0.34 g μmol C m^{-2} s^{-1}) than in late winter (0.11–0.19 μmol C m^{-2} s^{-1}). Our values lie within the range observed in northern Alaska (0.19–0.51 and 0.06–0.19 μmol C m^{-2} s^{-1} in early and late winter, respectively; Jones et al. 1999). Our mean winter effluxes of 0.15 (meadows) and 0.16 μmol C m^{-2} s^{-1} (heaths) are higher than that estimated for Endalen, Svalbard (0.11 μmol C m^{-2} s^{-1}; Elberling 2007), but are within the range measured in tussock tundra (0.12–0.29 μmol C m^{-2} s^{-1}; Oechel et al. 1997; Fahnestock et al. 1999; Sullivan et al. 2008) and dry heath tundra (0.17 μmol C m^{-2} s^{-1}) at Toolik Lake, Alaska (Fahnestock et al. 1999). They are also consistent with the mean winter efflux reported for north-eastern Siberia of

Table 5 Ecosystem CO_2 efflux (g C m^{-2}) and percentage of total annual efflux (shown in brackets), calculated using model based on Q_{10} and measured soil temperatures.

Vegetation type Treatment Snow depth	Heath Control Shallow	Heath Fence Deep	Meadow Control Shallow	Meadow Fence Deep
Spring				
30 May–22 June (24 days)	14 (11%)	12 (8%)	20 (13%)	17 (9%)
Summer				
23 June–17 Aug (56 days)	45 (36%)	52 (36%)	78 (48%)	71 (36%)
Autumn				
18 Aug–1 Oct (45 days)	24 (19%)	26 (18%)	24 (15%)	34 (18%)
Winter				
2 Oct–29 May (241 days)	42 (33%)	54 (38%)	40 (24%)	74 (38%)
Annual	**125**	**144**	**162**	**196**
Growing season	56 (44%)	52 (36%)	94 (58%)	71 (36%)
Non-growing season	**70 (56%)**	**92 (64%)**	**68 (42%)**	**125 (64%)**

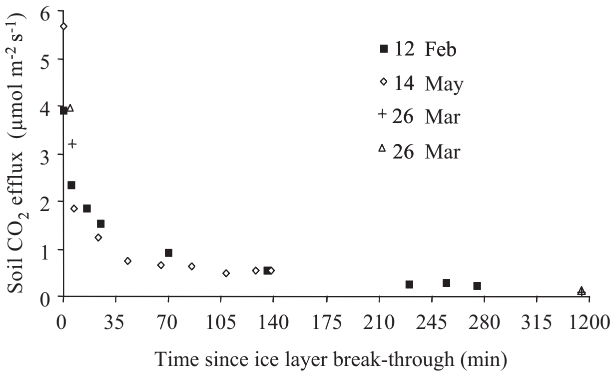

Fig. 5 Non-steady state CO_2 efflux observed through time after breaking through the ice layer of collars in 2008. The efflux from one collar was measured on 12 February, it was measured from two collars on 26 March, and from an additional collar on 14 May. Note the two overlapping data points at 1200 min.

0.14 µmol C m^{-2} s^{-1} (Zimov et al. 1993). Contrary to these estimates, Nobrega & Grogan (2007) report a much lower winter CO_2 production of 27 g C m^{-2} over a period of 278 days (mean production rate of 0.1 µmol C m^{-2} s^{-1}) for birch hummock tundra in northern Canada, as measured with soda lime traps. A non-growing season production of 57 g C from mesic meadow and 30 g C from wet moss tundra in Adventdalen (calculated from data presented by Sjögersten et al. 2008, using a 249-day period), also using soda lime traps, is within the range found in our mesic vegetation. Studies applying this technique have yielded efflux estimates both far below (Welker et al. 2000; Welker et al. 2004) and above (Grogan & Chapin 1999) our values based on measurements with flux chambers. In addition, Welker et al. (2004) also demonstrated that wetter and warmer soils had a higher winter CO_2 flux, a finding which our data support.

We have demonstrated that the proportion of non-growing season carbon lost as a result of ecosystem respiration compared with the annual respiration is 42% in meadows and 56% in heaths. These values are markedly higher than previously assumed, and are also higher than estimated using a different methodology (e.g., fluxes through snowpacks 1–18%; Björkman et al. 2010). This highlights the importance of taking manual measurements on a regular basis throughout the winter, and also calls attention to the wintertime contribution to the annual carbon cycle.

Even though winter soil CO_2 effluxes and emission rates reported here are within the range observed from a variety of Arctic sites, winter emissions are considered biased, as non-steady state emissions are not included. That means that the high proportion of non-growing season fluxes are considered to be minimum values. Observations in Adventdalen (Figs. 2, 3, 5) indicate that CO_2 produced during the winter is partly trapped in the frozen soil and underneath ice layers in the snowpack, and that trapped CO_2 was released as bursts that occurred artificially when ice layers in the ice pack were broken to access collars (Fig. 5), and trapped CO_2 was released over several hours, as well as naturally when ice and soil layers thawed and unexpectedly high CO_2 effluxes were noted for several days. The latter case is best seen at the heath site (Fig. 2).

Van Bochove et al. (2001) showed that an ice layer of 10 cm can act as an impermeable barrier to gas diffusion. Our measurements of CO_2 bursts reported here after breaking through the ice layer are consistent with that. Therefore, the observed CO_2 flux of 0.19 g C m^{-2} related to a burst presents a minimum estimate of winter respiration of at least 0.005 g C m^{-2} day^{-1} during 40 days in January and February, below the ice layer. As some CO_2 was probably released during ice break-through, a greater volume of gas might have been trapped under the ice than was measured. We conclude that CO_2 can be trapped beneath an ice layer, and that trapping must be considered when winter efflux is estimated, either by observing CO_2 concentration gradients in the snowpack or by measurements of CO_2 efflux from the snow surface, as both techniques lead to an underestimation of ecosystem respiration if a thick ice layer persists for a long time period. There is an upper limit for the build-up of CO_2 under ice layers, as the diffusion barrier also limits oxygen availability below the ice, and will therefore limit aerobic soil respiration.

Gas trapping in soil was discussed by Stoneström & Rubin (1989), who reported significant air trapping at water contents as low as 12% for unfrozen sand, and a regular, monotonically increasing trapping effect with increasing water content. CO_2 trapping in frozen soil was shown by Oechel et al. (1997), who measured an initial efflux of up to 82 g C m^{-2} day^{-1} after drilling through the soil surface, or more than 300-fold higher effluxes compared with undrilled controls. High effluxes during the initial soil thawing are considered to be a net effect of microbial growth kinetics controlled by the release of high-quality dissolved organic carbon from microbes killed by freezing temperatures (Skogland et al. 1988), and trapped CO_2 produced during winter and released upon soil thawing (Elberling & Brandt 2003). It is beyond the scope of this study to differentiate between microbial and physical processes in controlling these high spring effluxes.

For both CO_2 trapped below ice layers and in the soil, CO_2 is released as non-steady state bursts of CO_2 that are not included in the annual estimates presented in this study. Results regarding CO_2 production and release during winter, however, emphasize the importance of differentiating between rates of winter CO_2 emissions, which are difficult to predict, but are measurable, and rates of winter soil CO_2 production, which seem easier to predict, but are difficult to measure in the field. Both processes are important, as knowledge of ecosystem CO_2 production is critical for evaluating ecosystem carbon cycling, whereas CO_2 release is a key parameter for modelling temporal and spatial trends of fluctuating atmospheric CO_2 concentration. Future snow fence experiments should aim to combine different approaches to evaluate both subsurface respiration rates (as in this study) and also evaluate the actual release of CO_2 to the atmosphere.

Uncertainties in predicting winter CO_2 effluxes are partly because ecosystems with low mean annual temperatures have high interseasonal Q_{10} variability (Davidson et al. 2006), and because both root and soil microbes contribute to soil respiration (Hanson et al. 2000). These two aspects may very well be coupled, as Q_{10} values for root and soil microbial contributions may not be the same, and at least the ratio of root : microbial respiration will decrease during winter compared with summer. Q_{10} values of respiration tend to decrease with increasing temperature (Kirschbaum 1995; Fang & Moncrieff 2001). An abrupt increase in Q_{10} with freezing has previously been reported, and the reasons behind this are still being debated. Mikan et al. (2002) suggested that a shift in temperature dependence with freezing reflects a shift in the dominant process controlling microbial respiration below 0°C, such as extracellular barriers to diffusion and/or intracellular desiccation. In contrast, Elberling & Brandt (2003) argued that at least part of the abrupt increase in Q_{10} results from trapping some of the CO_2 produced in frozen soil. In a laboratory experiment, Elberling & Brandt (2003) increased the proportion of CO_2 trapped (and thereby the Q_{10} shift at 0°C) by increasing the water content in soil samples, and eliminated the shift in Q_{10} in samples manipulated by salt amendments, thereby avoiding freezing and physical trapping, at temperatures below 0°C. The model used in this study aims to predict daily effluxes and is therefore based on separate sets of α and β for temperatures above and below 0°C. The limitation of that is that the model may be less suitable for predicting actual subsurface soil respiration. Sensitivity analyses on the influence of Q_{10} on the predicted annual CO_2 production rates indicated that using an average Q_{10} value (Table 3) for each vegetation type and treatment instead of two Q_{10} values at soil temperatures above and below 0°C increased predicted annual effluxes by up to 9%.

Snow fence effects on ecosystem carbon cycling

Winter CO_2 efflux from controls in both vegetation types was about 40 g CO_2-C m^{-2}, and was 54–74 g CO_2-C m^{-2} at fence areas. Non-growing season efflux from controls with both vegetation types was about 70 g CO_2-C m^{-2}, and was 92–125 g CO_2-C m^{-2} at snow fence areas, i.e., deep snow enhanced respiration by 30% in heath and 79% in meadow. This demonstrates clearly that increases in snow depth can substantially increase cold season respiration in tundra ecosystems. Snow fence studies from sub-Arctic and alpine areas also reported considerable increases in winter soil respiration (Brooks et al. 1997; Brooks et al. 1998; Walker et al. 1999; Schimel et al. 2004; Nobrega & Grogan 2007).

The fact that fence treatment areas became snow-free more than 2 weeks later than control areas is an additional effect of increasing snow, not only on the total winter activity but also on growing season length, and potential growing season respiration and carbon uptake.

However, warmer summer temperatures and changes in hydrology, root respiration and growth rates of vegetation (Hanson et al. 2000) add to the complexity of predicting growing season respiration as a function of increasing snow.

Because this study did not quantify carbon uptake during the growing season, a discussion about shifts in ecosystem carbon balance as a result of increasing winter activity must rely on published net growing season carbon uptake. Reported estimates of growing season carbon uptake estimates vary from site to site; net growing season carbon uptake of 29–37 g C m^{-2} for birch hummock tundra (Nobrega & Grogan 2007) and 36 g C m^{-2} for wet moss tundra in Adventdalen (calculated from data reported by Sjögersten et al. 2008, using a 60-day summer period) are in the same range as the winter respiration reported in this study. Increased snow depth in High-Arctic Svalbard may thus enhance dark and cold season respiration enough to push the ecosystem annual net carbon exchange from being a sink to a being source of carbon.

Study limitation and implications

Any study of winter activity, and the influence of snow on winter activity, faces problems in actually quantifying the absolute and relative effect of increasing snow. Problems include the fact that instrumentation has to cope with extremely low air temperatures and be used in the dark, and emissions are small and close to the detection limit of the equipment. The accuracy of winter measurements is therefore not as good as during the growing season, and often a reduced number of replicates are made. However, a comparison of mean efflux between fence areas and controls during the period 28 November–6 December 2007 clearly indicated that effluxes were two to three times higher behind fences than at controls. With the almost significant effect ($P = 0.057$ and 0.061) of fence treatment on ecosystem respiration, we conclude that future moderate increases in snow in the High Arctic will have a marked effect on winter ecosystem respiration rates, and also that additional measurements are needed to provide more robust data on both subsurface soil respiration production and the controls on physical trapping and release of CO_2 from the soil and snowpack.

Most snow fence experiments, as the experiment reported here, report short-term ecosystem effects as a result of increasing snow thickness. However, longer term effects may be as important as the short-term effects. Previous studies have reported changes in soil nutrient and microbial dynamics as a result of freeze–thaw events (DeLuca et al. 1992; Schimel & Clein 1996; Brooks et al. 1998; Lipson et al. 2000; Grogan et al. 2001). Plant primary production and vegetation composition in Arctic tundra ecosystems are generally strongly controlled by nutrient availability (Press et al. 1998; Jonasson et al. 1999), and freeze–thaw cycles at spring thaw seem to be critical in the annual cycle of nutrient mobilization (Schimel & Clein 1996). If the number of freeze–thaw cycles is important to the processes of nutrient release and transfer, this study suggests that increasing snow will enhance winter activity and also influence primary production, vegetation composition and subsurface carbon balance during the growing season. Increasing snow will lead to moister conditions during the growing season, a shorter growing season and possibly colder soil. Aboveground environmental conditions such as warmer air temperatures, increasing atmospheric CO_2 concentrations and higher evaporation rates will moderate the effects from increased snow. Furthermore, plants have been shown to respond to environmental conditions, such as manipulations of snow depth, for example, by moderating their epicuticular leaf waxes (Rieley et al. 1995). This study suggests that increasing snow levels led to reduced growth in non-shrub vegetation in the meadow site, and that plants allocated a greater proportion of biomass below the ground. The latter is in line with other studies of plants in cold soils (e.g., Cooper 2004). In the present study the shrub vegetation was not separated into present and previous year's growth. Consequently, changes in growth rates as a result of increasing snow for *Cassiope* and *Dryas* remain an open question. However, another study within the same experimental set-up (Wdowiak 2008) demonstrated a significant reduction in *Cassiope* growth in the snow fence plots, which suggests a vegetative impact from the snow, probably because of a shorter growing season, leading to delayed phenology, together with a cooler summer soil compared with control plots. The net effect of these factors on the growing season with a longer perspective is yet to be explored.

Conclusions

Our study reports one of the first estimates of total cold season CO_2 effluxes in ambient and snow fence plots in a High-Arctic ecosystem. Total winter effluxes in two dominant tundra vegetation types were increased by enhanced snow depth. The total carbon loss resulting from ecosystem respiration outside the growing season is on the same order of magnitude as reported ecosystem carbon gains through photosynthesis during the growing season. Our data therefore suggest that with a moderate increase in snow depth, Arctic tundra systems could become a net annual source (rather than a sink) of carbon to the atmosphere, even without alterations in growing season length or plant community composition. If deeper snow delays snowmelt, as in our experiment, thereby reducing growing season length and thus total carbon uptake, the net annual source estimate may be even larger. Over a longer timeframe, new plant species may be introduced with faster biomass accumulation, which would offset the increased carbon loss during winter. Our findings provide a basis for regional models to incorporate the interactions between predicted increases in snow depth and the biogeochemical processes and source carbon pools that control the wintertime carbon cycle in tundra ecosystems. In addition, they further highlight the importance of longer term snow fence experiments in the High Arctic.

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