

RESEARCH ARTICLE

10.1002/2015JG003251

Key Points:

- Experimentally deepened snow is used to enhance winter soil temperatures
- Long-term deepened snow leads to significantly reduced summer carbon emissions
- The reduced carbon emissions are not driven by changes in microclimate

Supporting Information:

- Supporting Information S1

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Citation:

Semenchuk, P. R., C. T. Christiansen, P. Grogan, B. Elberling, and E. J. Cooper (2016), Long-term experimentally deepened snow decreases growing-season respiration in a low- and high-arctic tundra ecosystem, *J. Geophys. Res. Biogeosci.*, 121, doi:10.1002/2015JG003251.

Received 16 APR 2015

Accepted 17 APR 2016

Accepted article online 21 APR 2016

Long-term experimentally deepened snow decreases growing-season respiration in a low- and high-arctic tundra ecosystem

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Abstract Tundra soils store large amounts of carbon (C) that could be released through enhanced ecosystem respiration (ER) as the arctic warms. Over time, this may change the quantity and quality of available soil C pools, which in-turn may feedback and regulate ER responses to climate warming. Therefore, short-term increases in ER rates due to experimental warming may not be sustained over longer periods, as observed in other studies. One important aspect, which is often overlooked, is how climatic changes affecting ER in one season may carry-over and determine ER in following seasons. Using snow fences, we increased snow depth and thereby winter soil temperatures in a high-arctic site in Svalbard (78°N) and a low-arctic site in the Northwest Territories, Canada (64°N), for 5 and 9 years, respectively. Deepened snow enhanced winter ER while having negligible effect on growing-season soil temperatures and soil moisture. Growing-season ER at the high-arctic site was not affected by the snow treatment after 2 years. However, surprisingly, the deepened snow treatments significantly reduced growing-season ER rates after 5 years at the high-arctic site and after 8–9 years at the low-arctic site. We speculate that the reduction in ER rates, that became apparent only after several years of experimental manipulation, may, at least in part, be due to prolonged depletion of labile C substrate as a result of warmer soils over multiple cold seasons. Long-term changes in winter climate may therefore significantly influence annual net C balance not just because of increased wintertime C loss but also because of “legacy” effects on ER rates during the following growing seasons.

1. Introduction

The large amounts of carbon (C) currently stored as soil organic matter (SOM) in the arctic [Hugelius *et al.*, 2014] are a concern because climate warming could result in significant increases in global C-based greenhouse gas emissions [McGuire *et al.*, 2009]. Relatively old C from thawing permafrost soil layers [Schuur *et al.*, 2009], and younger C from more recently produced litter and SOM stored in the seasonally thawed active layer, is expected to be released through temperature-enhanced rates of ecosystem respiration (ER), potentially turning tundra ecosystems into considerable sources of C to the atmosphere [Davidson and Janssens, 2006; McGuire *et al.*, 2009]. This has been demonstrated in both growing-season [Melillo *et al.*, 2002; Rustad *et al.*, 2001] and cold-season (using snow fences [Morgner *et al.*, 2010; Nobrega and Grogan, 2007; Schimel *et al.*, 2004]) experimental warming studies. These temperature-induced changes in ER rates, however, appear to be transient and decline toward rates in unmanipulated control plots after a few years of air and/or surface soil warming in studies ranging from in situ growing-season warming [Oberbauer *et al.*, 2007; Welker *et al.*, 2004; Melillo *et al.*, 2002; Oechel *et al.*, 2000; Rustad *et al.*, 2001; Hobbie *et al.*, 1998], laboratory incubations [Craine *et al.*, 2013; Elberling *et al.*, 2013], and in modeling studies [Eliasson *et al.*, 2005; Kirschbaum, 2004] (but see Dorrepaal *et al.* [2009] and Natali *et al.* [2014] for special cases).

Temperature greatly restricts microbial decomposition rates during the arctic cold season. Considerable microbial activity has been found at freezing temperatures, however, with a steep drop in activity at temperatures below -5°C [Elberling and Brandt, 2003; Tilston *et al.*, 2010]. Given that the arctic cold season is much longer than the growing season, and that climate warming in these regions is most pronounced during the cold season [Sturm *et al.*, 2005; Hartmann *et al.*, 2013], warming experiments during the cold season are an important measure to assess the impact of climatic changes on annual arctic C balance.

Decomposition and respiration rates by heterotrophic soil microorganisms are, in addition to temperature controls, highly dependent on litter and SOM quantity and quality [Cornelissen *et al.*, 2007; Elberling, 2007]. Microbes utilize a broad range of C compounds falling within a quality gradient from labile to recalcitrant compounds [Berg, 2000; Davidson and Janssens, 2006]. Rapid depletion of the easily decomposable, labile SOM pool appears to be driving the decline in respiration rates observed in long-term warming experiments [Hartley *et al.*, 2007, 2008, 2009; but see Bradford *et al.*, 2008]. How decomposition rates respond to long-term temperature changes is, however, still one of the key uncertainties in our current knowledge of climate change impacts on arctic C budgets, and it continues to be a topic of ongoing debate (see recent reviews by Billings and Ballantyne [2013] and Conant *et al.* [2011]). Despite a rising focus on lag time and feedback effects of a changing cold-season climate on biogeochemical tundra ecosystem functioning [see, e.g., Bokhorst *et al.*, 2012], studies that include growing-season ER measurements after cold-season warming are rare and short-term (≤ 3 years) [Morgner *et al.*, 2010; Natali *et al.*, 2011, 2014; but see Dorrepaal *et al.*, 2009].

Although cold-season ER rates are lower than growing-season ER rates, the long duration of the cold season in arctic and sub-arctic regions results in a substantial cumulative net effect and can significantly affect the annual C balance [Oechel *et al.*, 2000]. For instance, experimentally deepened snow has been shown to enhance total cold-season CO₂ loss in arctic ecosystems by 60–160% [Larsen *et al.*, 2007; Morgner *et al.*, 2010; Natali *et al.*, 2011; Nobrega and Grogan, 2007; Schimel *et al.*, 2004], or by up to 22% of whole year CO₂ emissions [Morgner *et al.*, 2010]. Since labile plant inputs, e.g., root exudates, during the cold season are negligible, warmer soil temperatures may lead to a depletion in the labile soil C pool by late winter [Buckeridge and Grogan, 2008; Lipson *et al.*, 2000]. Thus, depending on the initial soil labile C pool size, and other ecosystem properties such as gross primary production and permafrost stability (see below), multiple consecutive warmed cold seasons could potentially increasingly deplete the labile C pool to a point where changes in SOM decomposition during the cold season could exceed replenishment of the labile C pool by plant inputs during the following growing-season with important consequences for biogeochemical processes during this time. In contrast, a recent study found increased growing-season ER rates following 2 and 3 years of experimentally deepened snow in Alaskan sedge tundra [Natali *et al.*, 2014], presumably due to a combination of legacy effects including warmer growing-season soil temperatures, lowering of the water table, and permafrost degradation in the deepened snow plots. This effect was not apparent after 1 year of treatment [Natali *et al.*, 2011], indicating that such legacy effects only develop following multiple years of experimental winter climate change.

In this study we investigate how growing-season ER rates in high- and low-arctic tundra sites (Adventdalen, Svalbard, and Daring Lake, Northwest Territories, Canada) are affected by long-term experimental snow fence treatments (5 and 9 years, respectively). The snow fences increased cold-season ER soon after experimental setup [Morgner *et al.*, 2010; Nobrega and Grogan, 2007] and had no effect on growing-season ER in Adventdalen after 2 years [Morgner *et al.*, 2010]. Based on these short-term ER observations, and because our study sites contain well-drained soils with no water table or evidence of permafrost degradation (in contrast to the studies by Natali *et al.* [2014] and Dorrepaal *et al.* [2009]), as well as the studies cited above indicating that warming-induced increases in soil CO₂ efflux may be transitory, we hypothesized that the cumulative effect of deepened snow over multiple years—2 to 3 times longer than most of the studies cited above—would ultimately reduce growing-season ER rates.

2. Materials and Methods

2.1. Characterization of the Study Sites

This study focuses on two contrasting study sites (Figures S1 and S2 in the supporting information) situated 3500 km apart with markedly different vegetation, climate, and soil types. The high-arctic study site in Adventdalen is located 12 km east of Longyearbyen, Western Spitsbergen, Svalbard, Norway (78°10'N, 16°04'E) and spans a dry heath area of approximately 2 km² on the Southwest Advent river bank, dominated by the deciduous dwarf shrub *Salix polaris* Wahlenb. and the two evergreen dwarf shrubs *Dryas octopetala* L. and *Cassiope tetragona* (L.) D. Don [Morgner *et al.*, 2010].

The low-arctic study site is located close to the Terrestrial Ecosystem Research Station at Daring Lake, 300 km NE of Yellowknife, Northwest Territories, Canada (64°52'N, 111°33'W), and consists of lowland mesic birch hummock tundra, located in the middle of a broad valley between an esker and a bedrock outcrop. This vegetation-type is

Table 1. Climate Information for Comparison Between Sites^a

Month	Precipitation (mm)		Mean Air Temp (°C)		Min. Temp (°C)	
	Adventdalen	Daring Lake	Adventdalen	Daring Lake	Adventdalen	Daring Lake
Jan	18.8	-	-10.6	-28.4	-24.5	-36.5
Feb	10.6	-	-11.0	-26.7	-23.6	-35.8
Mar	16.0	-	-13.8	-23.5	-27.0	-35.4
Apr	9.3	1.6	-8.6	-13.2	-23.1	-24.9
May	5.7	6.6	-1.8	-3.6	-11.0	-13.5
Jun	6.7	21.3	3.7	7.7	-1.1	0.0
Jul	18.2	31.0	7.0	13.2	2.2	6.4
Aug	16.5	35.4	6.2	10.1	0.8	4.1
Sep	22.5	25.8	1.9	3.4	-5.5	-3.5
Oct	20.3	4.5	-3.5	-6.1	-13.6	-18.4
Nov	17.9	0.1	-6.6	-17.5	-17.4	-28.9
Dec	18.0	-	-8.5	-24.5	-21.4	-34.1
Sum/Mean	180.5	119.2	-3.8	-9.1	-13.8	-18.4

^aAverage values from 2000 to 2011 from Longyearbyen airport (eklima.no) and Daring Lake weather station. Precipitation values from Adventdalen during winter months represent water equivalents of solid precipitation. No winter precipitation data available from Daring Lake.

characterized by hummocks (10–30 cm in height), and the biomass is dominated by evergreens such as *Rhododendron subarcticum* (Harmaja) (formerly *Ledum decumbens* (Ait.)) and *Vaccinium vitis-idaea* L. and mosses and lichens [Nobrega and Grogan, 2008]. The deciduous shrub *Betula glandulosa* Michx. only totals ~7% of the total plant biomass due to its relatively low frequency (1–2 ramets per square meter) and stature (typically <30 cm) [Zamin *et al.*, 2014]. Table 1 summarizes climatological differences between the two study sites. While annual averages of air temperature (Adventdalen -3.8°C, Daring Lake -8.9°C) and precipitation (Adventdalen 180.8 mm, Daring Lake 140 mm) are relatively similar between sites, monthly fluctuations of average air temperatures illustrate the maritime climate of Svalbard as opposed to the continental climate of Daring Lake.

Soil characteristics of both sites are summarized in Table 2. The cryoturbated gellisols of Adventdalen have soil organic carbon (SOC) concentrations of 20–27% in the upper organic soil horizon, while the orthic dystric turbic cryosols of Daring Lake contain 40–44% SOC in the organic soil horizon.

2.2. Experimental Setup and Design

Snow fences were erected in Adventdalen (6 m long, 1.5 m high, *n* = 12) in autumn 2006 and Daring Lake (15 m long, 1.2 m high, *n* = 5) in summer 2004. The snow fences reduce wind speeds on their lee side, resulting in relatively deep snow patches. The following three snow treatments were used in this study:

Ambient: Unmanipulated snow cover, control plots (10–35 cm deep snow at both sites).

Moderately deepened: Experimentally increased snow depth approximately 60–100 cm deep, present at both sites, i.e., Adventdalen and Daring Lake.

Greatly deepened: Experimentally increased snow cover approximately 150 cm deep, only present in Adventdalen.

In Adventdalen, this study focuses on two of the existing plots (i.e., the areas containing a snow fence and associated control, each approximately 50 × 30 m). Per plot and treatment, six collars for ER measurements

Table 2. Specific Soil Characteristics for Comparison Between Sites^a

	Stone Content	ALT	Fine Earth Texture	SOM Concentration	U.S.-Soil Taxonomy
Adventdalen	0	~90 cm	25% < 0.063 mm 75% < 1 mm	O-horizon 27% ^b A-horizon 20% ^b B/C horizon 5% ^b	Cryoturbated Gellisol
Daring Lake	NA	~70 cm	NA	5 cm depth 44% 10 cm depth 40% 15 cm depth 3%	Orthic dystric turbic cryosol

^aIf not stated otherwise, from own observations directly from the study sites.

^bfrom Strebel *et al.* [2010].

were randomly placed among the three most representative land-cover types (36 collars in total); two collars were installed in patches dominated by *D. octopetala*, two in patches dominated by *C. tetragona*, and two in bare soil patches, i.e., without vascular vegetation. In one plot, *C. tetragona* was not present in all snow treatments and *Luzula arcuata* ssp. *confusa* Lindeb. was used as substitute.

At Daring Lake, two collars were installed randomly >1 m apart in each plot ($n = 5$ per treatment), and each plot flux average was used as a single datum in the subsequent statistical analyses. The vegetation inside the collars included all of the most abundant vascular plant species present in the area, but *B. glandulosa* (<7% of the aboveground biomass—see vegetation description above) was omitted due to its large stature.

Generally, snowmelt was delayed by 1–2 weeks behind the snow fences in Adventdalen [Semenchuk et al., 2013] and Daring Lake [Buckeridge and Grogan, 2010; Nobrega and Grogan, 2007].

2.3. Gas-Flux and Soil Microclimate Measurements

We inserted dark polypropylene collars (10 cm length and diameter in Adventdalen; 10 cm length and 30 cm diameter at Daring Lake) ~6–7 cm into the ground, using a serrated knife, as soon as the soil was sufficiently thawed in June 2010 and 2012 in Adventdalen and Daring Lake, respectively. The collars were left in place for the remainder of the study.

At both sites, ER was measured with a Li6400 portable photosynthesis system (LI-COR Biosciences, Lincoln, NE, USA). In Adventdalen, a Li6400-09 soil chamber (10 cm diameter, 1 L volume) was used, while a bigger, custom made dark chamber was used at Daring Lake (30 cm diameter, 20 L volume). The respective soil chambers fitted on the aboveground parts of the collars and served as an airtight seal forming a closed system above the soil surface, in which the change of CO₂ concentrations was monitored with an infrared gas analyzer and flux rates calculated accordingly (standard procedures previously described in detail in Morgner et al. [2010] and Nobrega and Grogan [2008]).

Winter measurements in Adventdalen followed the snow pit method [Björkman et al., 2010; Morgner et al., 2010]. CO₂ bursts are known to occur for a while after snow removal because the snow pits provide an escape route for respired CO₂ that has been accumulating at the base of the snowpack during winter [Grogan and Jonasson, 2006; Morgner et al., 2010]. It has been shown by Morgner et al. [2010] that the snowpack effect at the experimental site in Adventdalen lasts less than 120 min. Here we sequentially measured 3 times for 2 h and used the lowest, usually last ER measurement for analyses. In instances when this type of sequential measurements were not possible (e.g., expired batteries), we corrected the measurements taken immediately after snow removal with a collar specific correction factor based on previous sequential measurements. After ER measurements, the snow pits were gently re-filled with the previously removed snow to restore the original snow depth, and to a certain degree snow density, and minimize the likelihood of follow-on effects across our series of winter/spring flux measurements. No soil temperature changes were observed during the excavation period.

In Adventdalen, ER measurements were conducted monthly during the snow-covered period (mid-November 2010 to June 2011) and weekly during the growing season (June to early September 2011). We also present data obtained from the same study site and plots in 2007/2008, but using differently placed collars [Morgner et al., 2010]. At Daring Lake, weekly growing-season measurements were performed during mid-July to September in 2012, while for logistical reasons June and early July measurements were completed in 2013. All gas-flux measurements were calculated according to standard methods [Kutzbach et al., 2007; Pedersen et al., 2010].

2.4. Soil Microclimate

Soil microclimate data to be correlated with the ER measurements were collected in the following ways: In Adventdalen, soil temperature in each plot and treatment was logged hourly at 5 cm depth (Tiny Tag Plus with external thermistor probe, Gemini Data Loggers, Chichester, West Sussex, UK), while at Daring Lake hand-held thermometers were used (Spectrum Technologies, Aurora, IL, USA) 3–5 times at 5 cm depth around each collar after every ER measurement (only during the growing season) and averaged to a single datum for the statistical analyses. Additionally, in two of the plots at Daring Lake, soil temperatures were logged every 4 h (during all seasons) at 5 cm depth using thermocouple probes connected to CR10X data loggers (Campbell Scientific, Logan, Utah, USA).

Soil moisture, following soil thaw in spring, was recorded with hand held probes (Theta Probe ML2x at Adventdalen (Delta-T Devices, Cambridge, UK); Hydrosense Probe at Daring Lake (Campbell Scientific, Garbutt, Australia)) 4–5 times around each collar after every growing-season ER measurement.

2.5. Soil and Plant Sampling

At the end of the 2010/2011 campaign in Adventdalen, soil to 6–7 cm depth, including all aboveground biomass, within the collars was excavated and hand-sorted into the following fractions to determine their dry weight (oven dried for 24 h at 60°C) to be used as covariates in the statistical model: aboveground biomass, aboveground dead mass (litter including dead leaves still attached to stems, altogether referred to as litter), and root biomass (coarse roots as removed from the soil matrix by hand). Soil organic matter (SOM) content was determined as loss on ignition (LOI, here considered a proxy for SOC content) at 550°C.

In Adventdalen, no formal vegetation analysis data are available, but personal observations indicate no difference in vegetation composition or cover due to the snow fence treatments. At Daring Lake, vegetation cover inside all individual collars was determined by point framing [Jonasson, 1988] in August 2012, and a one-way ANOVA determined that there was no difference in collar plant cover across treatments.

2.6. Data Treatment and Statistical Analyses

The Adventdalen data sets from both the 2007/2008 and 2010/2011 campaigns were each divided into growing- (soil temperature > 0°C) and cold-season (soil temperature < 0°C) periods. Only growing-season data were available from Daring Lake.

Due to impurities in the optical pathway of the gas analyzer used in Adventdalen in 2010/2011, the absolute values obtained are overestimates with an unknown offset (Li-Cor, personal communication) and as such are not suitable for comparison between sites or studies. Accordingly, in order to focus on relative effects of the snow treatment, all statistical analyses have been performed on z-standardized values. This standardization allows us to make valid statistical comparisons between snow treatments, seasons, and sites based on differences in number of standard deviations from the overall ER mean and removes the bias of measurement method, instrumentation, calibration state of instruments, and other factors which can influence absolute values of field ER measurements [Björkman *et al.*, 2010]. Note that similar statistical analyses based on the absolute CO₂ data sets from both Adventdalen and Daring Lake indicate that the results, and therefore the main conclusions, were unchanged by the normalization procedure (Figure S5).

To test the effect of snow treatment on ER rates, we used linear mixed effects models (LMEs) of the lme4 and lmerTest packages in R v. 2.15.2 (R Development Core Team [Bates *et al.*, 2012]), where collars were specified as a random factor nested within plot, and sampling date was specified as an additional, separate random factor. The Adventdalen 2010/11 ER data were lognormal distributed, and therefore, we log-transformed all Adventdalen and Daring Lake data to achieve normality. The full LME models were different between sites and campaigns (i.e., Adventdalen 2007/2008 and Adventdalen 2010/2011 cold and growing seasons, and Daring Lake growing season), and a list of available predictor variables is presented in Table 3. Prior to model construction we tested whether the available predictor variables were autocorrelated by calculating their variance inflation factors (VIF) for each model separately (following procedure from Zuur *et al.* [2009]). This ensures that multicollinearity of predictor variables in each model is avoided. By stepwise removal of covariates with a VIF > 3, we removed only plant species from the Adventdalen 2010/2011 data set, which turned out to be correlated with LOI and litter mass (see Figure S8). These full models were then stepwise simplified using the Akaike information criterion (AIC; the simplified model was chosen when the AIC of the larger model containing more variables was larger than 2 times the amount of removed variables in the simplified model, see Arnold [2010]) and the respective minimal models used for interpretation and presentation of the data. As significance test of the individual variables retained in each of the minimal models, we used log likelihood comparisons between the minimal model containing the variable in question with a similar model where that specific variable was removed, and we provide the corresponding *p*-value of that test. We consider a *p*-value < 0.05 as significant.

In addition, we estimated the absolute CO₂-C emissions at Daring Lake for each snow treatment over the whole 2012 growing season from 24 May 2012 (first day of thawed soil) until 28 August 2012 (last day of data logger records). We used the minimal model, obtained as described above with log-transformed absolute ER rates, to estimate parameters to model daily CO₂ emissions based on average daily soil temperatures at 5 cm

Table 3. List of Predictor Variables and *P*-Values From the Different Statistical Minimal Models^a

	Adventdalen 2007/2008		Adventdalen 2010/2011				Daring Lake			
	Whole Year		Whole Year		Growing Season		Cold Season		Growing Season	
	Full Model	Minimal Model	Full Model	Minimal Model	Full Model	Minimal Model	Full Model	Minimal Model	Full Model	Minimal Model
Snow treatment	Yes		Yes	0.0009	Yes	0.0124	Yes		Yes	0.0107
Soil temp. 5 cm	Yes	1.2 ^c 10 ⁻⁹	Yes	5.4 ^c 10 ⁻¹⁰	Yes		Yes	0.0002	Yes	4.2 ^c 10 ⁻⁷
Soil temp x snow treatment	Yes		Yes	6.2 ^c 10 ⁻⁸	Yes		Yes		Yes	
Soil moisture ^b					Yes				Yes	0.087
Soil moist. x snow treatment					Yes				Yes	0.056
Plant species ^c			Yes ^c		Yes ^c		Yes ^c			
Above-ground biomass			Yes		Yes		Yes	0.499		
Root biomass			Yes		Yes	0.1	Yes	0.162		
Litter			Yes	1.2 ^c 10 ⁻⁵	Yes	0.0002	Yes	0.002		
Loss on ignition			Yes	0.005	Yes	0.011	Yes	0.0164		
Vegetation cover									Yes	

^a“Yes” in the full model columns denotes if the predictor variables were available for the respective model. *P* values are given for predictor variables retained in the minimal model, while removed variables have empty cells. Model selection was done by sequentially removing single terms from the full model and comparing the models’ AIC values (the simplified model was chosen when the AIC of the larger model containing more variables was larger than 2 times the amount of removed variables in the simplified model, see *Arnold* [2010]). Numbers denote *p*-values obtained by log likelihood tests of the minimal model containing the parameter in question with models without the parameter.

^bSoil moisture only in models treating growing-season data.

^cPlant species was not used in the full models due to its high VIF in combination with other covariates.

depth. We then back-transformed the data to g CO₂-C m⁻² d⁻¹ and summed these values to obtain the total seasonal amount of CO₂-C emissions for each snow treatment. Absolute ER flux rates at Daring Lake were similar to previously reported growing-season ER rates measured at a nearby mesic birch hummock patch [*Nobrega and Grogan, 2008*], indicating that our ER measurements were representative for this area. Furthermore, the snow fence treatment effect on absolute growing-season ER rates at Daring Lake was consistent between years (July to September 2012 and June to July 2013), suggesting that the observed reduction in CO₂ emissions was a consistently recurring effect of long-term deepened snow. See supporting information for further methodological details.

Snow treatment effects on the covariates litter mass, aboveground, and root biomass collected during the 2010/2011 campaign in Adventdalen were tested by simple linear models and reported in the text (data not shown).

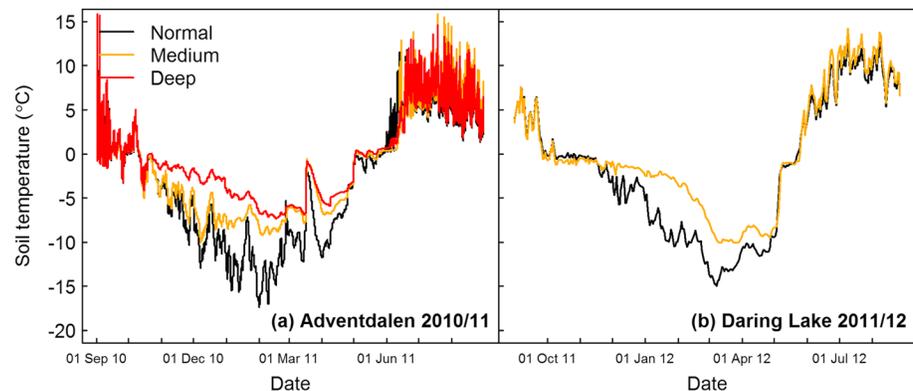


Figure 1. Daily means of soil temperature (°C) at 5 cm depth during the years of measurements in the different snow treatments (ambient, moderately deepened, and greatly deepened) at (a) Adventdalen, 2010/2011 (*n* = 2 per snow treatment) and (b) Daring Lake, 2011–2013 (*n* = 2–3 per snow treatment). Note the different x axis scaling between panels. In Adventdalen, unusually warm periods in February and early-March melted the snow in all snow treatments except the greatly deepened snow treatment, and another extreme warming period in late-March melted snow in all snow treatments.

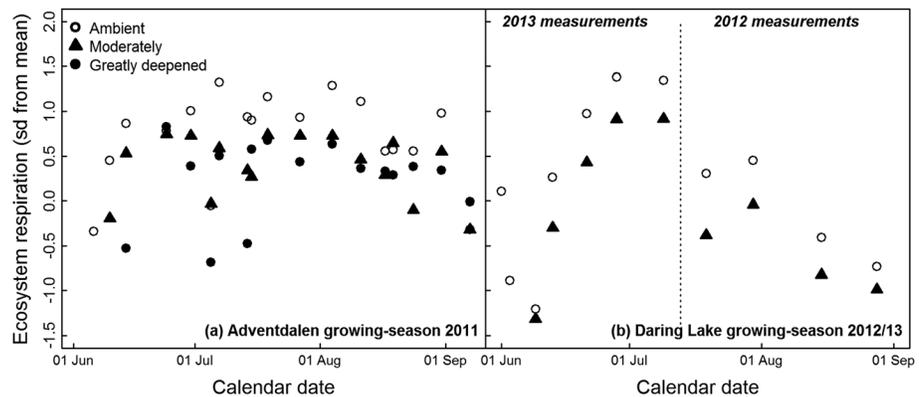


Figure 2. Standardized growing-season ER rates from (a) Adventdalen 2011 and (b) Daring Lake 2012/2013, expressed as number of standard deviations from the overall mean of logged values for each site. *ambient* and both deepened snow treatments were measured at Adventdalen, while *ambient* and *moderately deepened* snow treatments were measured at Daring Lake. Data are missing from the deepened snow treatments in early June as snow was still present in those plots at that time. Presented data are means over all measurements per treatment and calendar date (12 replicates per treatment in Adventdalen, 5 at Daring Lake).

3. Results

3.1. Snow Fence Effects on Microclimate

At both Adventdalen and Daring Lake, the deepened snow treatments enhanced and stabilized winter soil temperatures (Figure 1 and Table S1 in the supporting information) with deepened snow treatments being approximately 2–5° warmer on average throughout the cold season preceding the growing season where ER measurements were performed. The *moderately deepened* snow treatments at Adventdalen and Daring Lake generally enhanced soil temperatures similarly. Both *moderately deepened* snow treatments resembled their respective *ambient* snow treatments during the early cold season, lasting until mid-December/January, after which the enhanced snow accumulation in the experimentally deepened snow plots resulted in relatively warmer soil temperatures (Figure 1). At both sites, the observed temperature trend in ambient and deepened snow treatments were generally similar to observations in previous years [Buckeridge and Grogan, 2008; Grogan, 2012; Semenchuk *et al.*, 2013]. All experimentally deepened snow treatments appeared to slightly increase mean growing-season soil temperature by <1°C at both sites, but this effect was not statistically significant. Generally, initial growing-season soil moisture levels were enhanced in the two deepened snow treatments at Adventdalen. However, for the growing season as a whole, there were nonsignificant negligible differences in soil moisture content across treatments at Daring Lake ($p=0.94$) and Adventdalen (5.3% increase in *moderately deepened*, $p=0.02$, and 3.2 % increase in *greatly deepened*, $p=0.16$, relative to *ambient*; linear mixed effects models) (Figure S9).

3.2. Snow Fence Treatment Effects on Ecosystem Respiration

Mean growing-season ER rates were lower in the snow fence treatments than in *ambient* during the Adventdalen 2010/2011 campaign and at Daring Lake (Figures 2 and S3; see Table 3 and text below for details on the statistical models used). In contrast, there was no difference between treatments during the Adventdalen 2007/2008 growing-season campaign [Morgner *et al.*, 2010]. Mean cold-season ER rates were consistently higher in the snow fence treatments than in *ambient* during all Adventdalen campaigns (Figures 3 and S4; see Table 3 and text below for details on the statistical models used).

Predictor variables retained in all minimal models are summarized in Table 3. In the following text, we focus solely on the two predictor variables snow treatment and soil temperature. For other covariates retained in the minimal models, please refer to Table 3. For the growing-season Adventdalen 2010/2011 and Daring Lake campaigns, the predictor variable snow treatment was retained in the minimal models, while the variable temperature was removed for Adventdalen, indicating that the observed lower ER rates in the snow fence treatments were treatment specific and independent of temperature. The modeled 95% confidence intervals of effect sizes of *moderately deepened* relative to *ambient* were between –1.2 and –0.2 standard deviations for Adventdalen and between –1.4 and –0.3 for Daring Lake, respectively. Similarly, the modeled

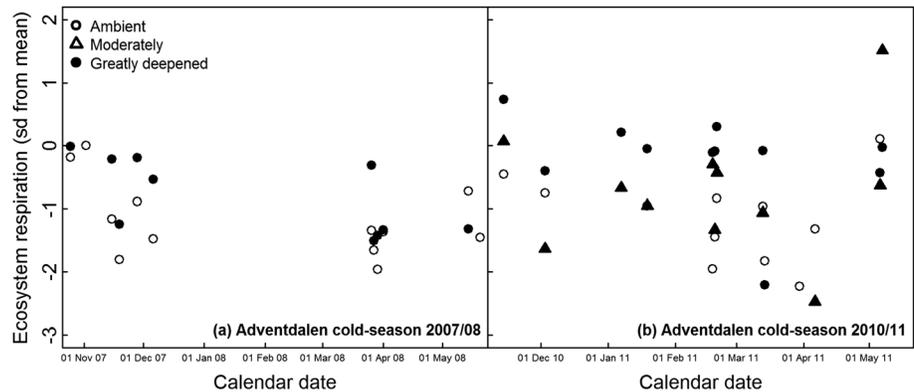


Figure 3. Standardized cold-season ER data from (a) Adventdalen 2007/2008 and (b) 2010/2011, expressed as number of standard deviations from the overall mean of logged values for each measurement campaign. Two snow treatments were measured in 2007/2008 (*ambient* and *greatly deepened*) while three snow treatments were measured in 2010/2011 (*ambient*, *moderately deepened*, and *greatly deepened*). The study site experienced unusually warm periods in early and late March 2011 (see Figure 1), resulting in short-term melting of snow in most snow treatments during March, and melting of snow in all snow treatments in late-March. The impact of these warming events can be seen in Figure 3b, where the effect of snow treatment on ER rates changes in April where the *ambient* snow treatment have higher ER rates, relative to deeper snow treatments.

confidence interval for effect size of *greatly deepened* relative to *ambient* in Adventdalen was between -1.3 and -0.3 standard deviations ($p = 0.012$ and 0.01 for Adventdalen and Daring Lake, respectively; see Figure 4 for the estimates and Table 3 for the statistical model results).

By contrast, the cold-season Adventdalen 2010/2011 minimal model retained only soil temperature, indicating that snow treatment had no effect on ER rates other than changing soil temperature alone. For the whole-year Adventdalen 2007/2008 campaign (cold and growing seasons together), only soil temperature was retained in the minimal model, i.e., the observed differences in ER during the cold season were solely caused by temperature differences between the snow treatments and not by the treatments themselves. In contrast, for the whole-year Adventdalen 2010/2011 campaign, snow treatment plus soil temperature and their interaction remained in the minimal model, indicating different temperature responses of ER between treatments. For other covariates retained in the models, see Table 3 and Figures S7 and S8.

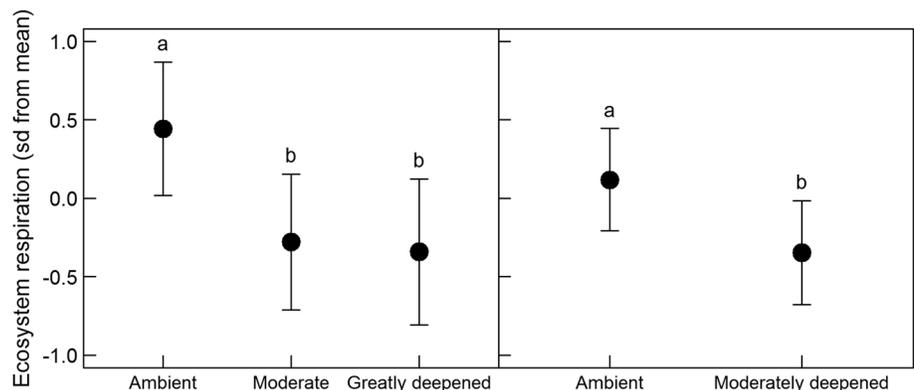


Figure 4. Predicted average growing-season (soil temperature $> 0^{\circ}\text{C}$) standardized ecosystem respiration rates (expressed as number of standard deviations from the overall mean of logged values for each site) in contrasting snow depth treatments (a) at Adventdalen 2011 and (b) at Daring Lake 2012/2013. The error bars show the 95% confidence intervals. Predictions are from linear mixed effects models run for each site separately and show differences in respiration rates which are not due to treatment differences in temperature, soil moisture, and additionally for Adventdalen: soil loss on ignition, litter mass, aboveground biomass, and root mass. At both sites, respiration rates in the deepened snow treatments were lower than in their respective ambient snow treatments, and this decrease was independent of the covariates listed above. Letters above model estimates denote statistically significant difference of snow treatments to the reference Ambient level at $p < 0.02$ (likelihood ratio test of models). See also Table 3.

Modeled daily CO₂ effluxes at Daring Lake during the growing season 2012 were consistently lower in *moderately deepened* than in *ambient* (Figure S6). Total estimated growing-season CO₂-C respired (24 May to 28 August 2012) was ~312 and ~363 g C m⁻² in the *moderately deepened* and *ambient* snow treatments, respectively, with the difference of 51 g corresponding to a 14% decrease in C efflux in the deepened snow treatment.

3.3. Snow Fence Treatment Effects on Litter and Biomass

Root biomass was significantly greater in both snow fence treatments relative to *ambient* during the Adventdalen 2010/2011 campaign ($p=0.0036$ and 0.0074 for *moderately deepened* and *greatly deepened*, respectively; data not shown). Aboveground biomass was significantly lower in *greatly deepened* compared to *ambient*, but not in *moderately deepened* ($p=0.024$ and 0.71 , respectively; data not shown). Litter mass was not significantly different across treatments ($p=0.226$ and 0.176 for *moderately deepened* and *greatly deepened*, respectively; data not shown).

4. Discussion

4.1. Effects of Long-Term Deepened Snow on Growing-Season CO₂ Emissions

We demonstrate that experimentally enhanced snow depth over multiple winters can significantly reduce growing-season ecosystem respiration (ER). On average, growing-season ER rates were reduced by ~20% in the *moderately deepened* snow treatment at Daring Lake (linear mixed effects model on nonstandardized ER data, corresponding to about 0.4 standard deviations), and ~0.7 standard deviations in Adventdalen (Figures 4 and Table 3), supporting our initial hypothesis. The results contrast with measurements of growing-season ER rates in Adventdalen [Morgner *et al.*, 2010] and Alaska [Natali *et al.*, 2011] after only 1–2 years of cold-season warming, and Abisko, Sweden, after 4–8 years of cold-season warming with open top chambers (OTCs) [Dorrepaal *et al.*, 2009]. All three studies reported no significant impact of their respective snow depth increase treatments on growing-season CO₂ loss, likely because of short treatment durations at the time of measurements [Natali *et al.*, 2011; Morgner *et al.*, 2010]. However, increased growing-season ER rates were observed after 2 and 3 years of experimentally deepened snow treatment in the Alaskan site [Natali *et al.*, 2014], contrasting with our longer-term results. Natali *et al.* [2014] reported both warmer growing-season soils, a lowered water table, as well as permafrost degradation as legacy effects of their experimentally deepened snow treatment—all of which are known to promote SOC mineralization and thus CO₂ release (see also Dorrepaal *et al.* [2009] for similar abiotic effects following simultaneous long-term winter, spring, and summer warming). In contrast, we only observed minor and/or nonsignificant differences in growing-season soil temperatures and moisture across treatments in our sites. Furthermore, the soils in Adventdalen and at Daring Lake are well drained, and therefore contain no water table during the growing season, and there were no signs of permafrost degradation occurring at the time of this study (*pers. obs.*). Together, this suggests that microclimatic differences were not causing the observed decline in growing-season ER due to snow enhancement and cold-season warming.

Deeper snow is generally associated with late snowmelt, which can lead to delayed plant phenology and reduced plant growth [Cooper *et al.*, 2011; Wipf and Rixen, 2010]. This could potentially lead to lower plant respiration and reduced root exudation of labile C compounds, which could help explain the observed reductions in growing-season ER rates in the snow fence treatments in this study. However, delayed snowmelt of 1–2 weeks does not necessarily reduce growth of all plant species [Rumpf *et al.*, 2014; Wipf and Rixen, 2010]. In fact, deeper snow increases soil nitrogen mineralization during the cold season [Schimel *et al.*, 2004] and availability during the growing season [DeMarco *et al.*, 2011; Semenchuk *et al.*, 2015] and thereby enhances canopy leaf area index and photosynthetic rates of, at least some, tundra plant species [Semenchuk *et al.*, 2015; Wahren *et al.*, 2005; Walsh *et al.*, 1997; Welker *et al.*, 2005]. Aboveground biomass in Adventdalen was reduced in the *greatly deepened* snow treatment but not in the *moderately deepened* treatment, and while this could potentially have an effect on ER, we do not see this differentiation between treatments in their ER responses. Root biomass was, in contrast, increased in both snow treatments in Adventdalen; however, we did not see an associated increase in ER caused by potentially increased root respiration or exudation of labile compounds. Therefore, while altered plant biomass in the experimentally deepened snow treatments could potentially modify the observed reductions in growing-season ER, to a certain extent, it seems unlikely that they are the key driver of these findings.

4.2. Effects of Long-Term Deepened Snow on Cold-Season CO₂ Emissions

At both our study sites, cold-season ER was initially (<2 years of snow manipulation) enhanced under deepened snow, while no change was observed during the growing season [Morgner *et al.*, 2010; Nobrega and Grogan, 2007]. After 5 years of deepened snow, cold-season ER was still higher in the deepened snow treatments in Adventdalen, relative to ambient snow conditions. Cold-season soil temperature was the only covariate directly affected by the snow manipulation, and once plot soil temperature differences were accounted for in the statistical models, cold-season ER rates were similar across all snow treatments. This suggests that the higher winter ER rates in the deepened snow treatments were due to a warmer winter soil microclimate.

During the cold season, soil microbes are responsible for the majority of the CO₂ being respired [Grogan *et al.*, 2001]. Soil microbial activity is inherently related to temperature and when soils are frozen even small temperature rises may greatly enhance unfrozen, liquid water availability and therefore promote microbial activity [Öquist *et al.*, 2009]. This enhances respiratory CO₂ loss, especially when soil temperatures are between 0 and –5°C, below which there is a steep dropoff in microbial activity [Elberling and Brandt, 2003]. At both our study sites, ambient mid-winter (January to May) soil temperatures were between –5 and –10°C (or lower), whereas the *moderately deepened* and *greatly deepened* snow treatments generally experienced soil temperatures closer to –5°C (or warmer), regardless of site (Figure 1 and Table S1). Temperature dominates over substrate quality in determining soil CO₂ production at 0 to –10°C [Mikan *et al.*, 2002], which further supports that the difference in winter soil temperature was indeed the primary environmental driver of cold-season ER rates across contrasting snow treatments.

4.3. Ecological Significance of a Changing Winter Climate

Future climatic changes in the arctic are expected to be most pronounced during the cold season [Collins *et al.*, 2013], where warmer air temperatures in conjunction with enhanced snowfall can lead to warmer cold-season soils. This may on a short-term basis increase cold-season respiration rates, and even growing-season ER rates [Natali *et al.*, 2014], resulting in increased C loss on an annual basis [Morgner *et al.*, 2010; Nobrega and Grogan, 2007; Schimel *et al.*, 2004]. Our results, however, indicate that this change in whole year ecosystem C balance due to deepened snow may be transient because the enhanced cold-season C loss is partly offset by reduced growing-season C release over the longer term. Our interpolated estimates of cumulative growing-season ER at Daring Lake suggest that 51 g less C m^{–2} was emitted due to the deepened snow treatment. Previous studies at this same site suggest that most of the additional winter C loss due to the deepened snow treatment range from 0 to 16 g CO₂-C m^{–2} [Grogan, 2012; Nobrega and Grogan, 2007]. Even though there are methodological and interannual differences that may affect this comparison [Björkman *et al.*, 2010], it is clear that the reduced growing-season ER reported here can be of sufficient magnitude to potentially reverse the effect of deepened snow on annual net ecosystem respiratory C loss.

To our knowledge, the results provided here are the strongest documentation so far that longer-term (5 and 8–9 years) changes in winter temperatures can reduce growing-season CO₂ emission rates and could ultimately influence annual net C release. Also, we have shown that despite differences in overall climate, vegetation, and soil C storage, our two study sites responded similarly when subjected to similar long-term changes in winter microclimate. The mechanism for this long-term effect remains unknown, but we suspect that due to warmer soil temperatures under deepened snow, roots and microbes are able to maintain higher ER rates during winter, relative to ambient conditions, even if the microbes are forced to metabolize on inferior quality SOM. In contrast, during summer, when microclimates are similar across snow treatments, a less-reduced labile C pool and longer growing season (potentially increasing fresh plant-soil C inputs; provided that the snow fence treatments do not enhance plant productivity, see discussion above) facilitate greater ER rates under ambient conditions, with the difference in CO₂ efflux between snow treatments being reduced as plants senesce during autumn. This response is similar to decreased respiration rates following long-term growing-season warming, which can be attributable to thermal acclimation of root respiration [Cooper, 2004] but not of soil microbial respiration [Hartley *et al.*, 2007; Hartley and Ineson, 2008]. A similar reduction in autumn soil respiration (SR) rates was observed in response to long-term (14 years) increased growing-season soil water supply that otherwise consistently enhanced summertime SR rates [Christiansen *et al.*, 2012]. We therefore speculate that fast depletion of the young, labile soil C-pool may be a common phenomenon following long-term climatic changes in temperature and precipitation treatments. This long-term response may, however, not apply to ecosystems with more organic rich soils, where labile C reserves are likely much greater than in mesic organic/mineral soils.

For example, long-term (8 years) spring and summer warming in a subarctic peatland continuously enhanced CO₂ release with extensive deep soil C contribution [Dorrepaal *et al.*, 2009]. Thus, warming-induced soil drying and lowering of the water table may explain how inundated peatlands, and other tundra ecosystems underlain by a water table during the growing season [Natali *et al.*, 2014] sustain elevated CO₂ efflux in response to long-term warming. Nevertheless, future changes in winter climate may have critical long-term implications for mesic tundra C balance, as observed in our study sites.

This study demonstrates that long-term ecosystem responses to climate change may be very different from short-term responses. Changes in one season may significantly impact the following seasons, highlighting the need for conducting seasonal and multiyear investigations. If we are to accurately understand and predict climate change impacts on overall ecosystem C balance, we need to be much more mindful of incorporating follow-on effects in our experimental designs. Our results imply that increasing cold-season temperatures might not turn arctic tundra into a long-term C source as previously thought and suggested by relatively short-term measurements, but that rather a limited amount of C is transferred into the atmosphere before other, so far unconfirmed constraints, potentially labile soil C depletion, overlay the temperature response and compensate for C loss.

Acknowledgments

We are grateful for field assistance from Jillian Lemmen, Karen Lone, Erica Näslund, Kristen Peck, and Megan Rueckwald. We appreciate advice on statistical analyses by Johanna Hovinen. This work was financed by UiT The Arctic University of Norway, University Centre in Svalbard, the Danish National Research Foundation (CENPERM DNR100), and NSERC (Frontiers program - ADAPT). Fieldwork at Svalbard was financed by the Arctic Field Grant provided by the Norwegian Polar Institute to Philipp Semenchuk. Fieldwork at Daring Lake was supported by NSERC and the Government of the Northwest Territories. Casper Christiansen was financed by an Ontario Trillium scholarship from the Ontario Ministry of Training, Colleges, and Universities. The principal data reported in this paper will be available for download from the Polar Data Catalogue <https://www.polardata.ca/>.

References

- Arnold, T. W. (2010), Uninformative parameters and model selection using Akaike's information criterion, *J. Wildl. Manage.*, *74*(6), 1175–1178.
- Bates, D., M. Maechler, and B. Bolker (2012), lme4: Linear mixed-effects models using Eigen and Eigenfaces, R package version 0.999999-0. [Available at <http://CRAN.R-project.org/package=lme4>.]
- Berg, B. (2000), Litter decomposition and organic matter turnover in northern forest soils, *For. Ecol. Manage.*, *133*(1–2), 13–22, doi:10.1016/S0378-1127(99)00294-7.
- Billings, S. A., and F. Ballantyne (2013), How interactions between microbial resource demands, soil organic matter stoichiometry, and substrate reactivity determine the direction and magnitude of soil respiratory responses to warming, *Global Change Biol.*, *19*(1), 90–102, doi:10.1111/Gcb.12029.
- Björkman, M. P., E. Morgner, E. J. Cooper, B. Elberling, L. Klemmedtsson, and R. G. Bjork (2010), Winter carbon dioxide effluxes from Arctic ecosystems: An overview and comparison of methodologies, *Global Biogeochem. Cycles*, *24*, GB3010, doi:10.1029/2009GB003667.
- Bokhorst, S., J. W. Bjerke, H. Tommervik, C. Preece, and G. K. Phoenix (2012), Rcosystem response to climatic change: The importance of the cold season, *Ambio*, *41*, 246–255, doi:10.1007/s13280-012-0310-5.
- Bradford, M. A., C. A. Davies, S. D. Frey, T. R. Maddox, J. M. Melillo, J. E. Mohan, J. F. Reynolds, K. K. Treseder, and M. D. Wallenstein (2008), Thermal adaptation of soil microbial respiration to elevated temperature, *Ecol. Lett.*, *11*(12), 1316–1327, doi:10.1111/j.1461-0248.2008.01251.x.
- Buckeridge, K. M., and P. Grogan (2008), Deepened snow alters soil microbial nutrient limitations in arctic birch hummock tundra, *Appl. Soil Ecol.*, *39*(2), 210–222, doi:10.1016/j.apsoil.2007.12.010.
- Buckeridge, K. M., and P. Grogan (2010), Deepened snow increases late thaw biogeochemical pulses in mesic low arctic tundra, *Biogeochemistry*, *101*(1–3), 105–121, doi:10.1007/s10533-010-9426-5.
- Christiansen, C. T., S. H. Svendsen, N. M. Schmidt, and A. Michelsen (2012), High arctic heath soil respiration and biogeochemical dynamics during summer and autumn freeze-in – Effects of long-term enhanced water and nutrient supply, *Global Change Biol.*, *18*(10), 3224–3236, doi:10.1111/j.1365-2486.2012.02770.x.
- Collins, M., et al. (2013), Long-term climate change: projections, commitments and irreversibility, in *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by T. F. Stocker et al., pp. 1029–1136, Cambridge Univ. Press, Cambridge, U. K., and New York, doi:10.1017/CBO9781107415324.024.
- Conant, R. T., et al. (2011), Temperature and soil organic matter decomposition rates - Synthesis of current knowledge and a way forward, *Global Change Biol.*, *17*(11), 3392–3404, doi:10.1111/j.1365-2486.2011.02496.x.
- Cooper, E. J. (2004), Thermal acclimation of root respiration in Arctic *Ranunculus*, *Arct. Antarct. Alp. Res.*, *36*(3), 308–313.
- Cooper, E. J., S. Dullinger, and P. Semenchuk (2011), Late snowmelt delays plant development and results in lower reproductive success in the High Arctic, *Plant Sci.*, *180*(1), 157–167, doi:10.1016/j.plantsci.2010.09.005.
- Cornelissen, J. H. C., et al. (2007), Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes, *Ecol. Lett.*, *10*(7), 619–627.
- Craine, J. M., N. Fierer, K. K. McLauchlan, and A. J. Elmore (2013), Reduction of the temperature sensitivity of soil organic matter decomposition with sustained temperature increase, *Biogeochemistry*, *113*(1–3), 359–368, doi:10.1007/s10533-012-9762-8.
- Davidson, E. A., and I. A. Janssens (2006), Temperature sensitivity of soil carbon decomposition and feedbacks to climate change, *Nature*, *440*(7081), 165–173, doi:10.1038/Nature04514.
- DeMarco, J., M. C. Mack, and M. S. Bret-Harte (2011), The effects of snow, soil microenvironment, and soil organic matter quality on N availability in three Alaskan Arctic plant communities, *Ecosystems*, *14*(5), 804–817, doi:10.1007/s10021-011-9447-5.
- Dorrepaal, E., S. Toet, R. S. P. van Logtestijn, E. Swart, M. J. van de Weg, T. V. Callaghan, and R. Aerts (2009), Carbon respiration from subsurface peat accelerated by climate warming in the subarctic, *Nature*, *460*(7255), 616–679, doi:10.1038/Nature08216.
- Elberling, B. (2007), Annual soil CO₂ effluxes in the high Arctic: The role of snow thickness and vegetation type, *Soil Biol. Biochem.*, *39*(2), 646–654.
- Elberling, B., and K. K. Brandt (2003), Uncoupling of microbial CO₂ production and release in frozen soil and its implications for field studies of arctic C cycling, *Soil Biol. Biochem.*, *35*(2), 263–272.
- Elberling, B., A. Michelsen, C. Schadel, E. A. G. Schuur, H. H. Christiansen, L. Berg, M. P. Tamstorf, and C. Sigsgaard (2013), Long-term CO₂ production following permafrost thaw, *Nat. Clim. Change*, *3*(10), 890–894, doi:10.1038/nclimate1955.
- Eliasson, P. E., R. E. McMurtrie, D. A. Pepper, M. Stromgren, S. Linder, and G. I. Agren (2005), The response of heterotrophic CO₂ flux to soil warming, *Global Change Biol.*, *11*(1), 167–181, doi:10.1111/j.1365-2486.2004.00878.x.

- Grogan, P. (2012), Cold season respiration across a low Arctic landscape: The influence of vegetation type, snow depth, and interannual climatic variation, *Arct. Antarct. Alp. Res.*, *44*(4), 446–456, doi:10.1657/1938-4246-44.4.446.
- Grogan, P., and S. Jonasson (2006), Ecosystem CO₂ production during winter in a Swedish subarctic region: The relative importance of climate and vegetation type, *Global Change Biol.*, *12*(8), 1479–1495.
- Grogan, P., L. Illeris, A. Michelsen, and S. Jonasson (2001), Respiration of recently-fixed plant carbon dominates mid-winter ecosystem CO₂ production in sub-arctic heath tundra, *Clim. Change*, *50*(1–2), 129–142.
- Hartley, I. P., and P. Ineson (2008), Substrate quality and the temperature sensitivity of soil organic matter decomposition, *Soil Biol. Biochem.*, *40*(7), 1567–1574, doi:10.1016/j.soilbio.2008.01.007.
- Hartley, I. P., A. Heinemeyer, and P. Ineson (2007), Effects of three years of soil warming and shading on the rate of soil respiration: Substrate availability and not thermal acclimation mediates observed response, *Global Change Biol.*, *13*(8), 1761–1770, doi:10.1111/j.1365-2486.2007.01373.x.
- Hartley, I. P., D. W. Hopkins, M. H. Garnett, M. Sommerkorn, and P. A. Wookey (2008), Soil microbial respiration in arctic soil does not acclimate to temperature, *Ecol. Lett.*, *11*(10), 1092–1100.
- Hartley, I. P., D. W. Hopkins, M. H. Garnett, M. Sommerkorn, and P. A. Wookey (2009), No evidence for compensatory thermal adaptation of soil microbial respiration in the study of Bradford et al. (2008), *Ecol. Lett.*, *12*(7), E12–E14, doi:10.1111/j.1461-0248.2009.01300.x.
- Hartmann, D. L., et al. (2013), Observations: Atmosphere and Surface, in *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by T. F. Stocker et al., pp. 159–254, Cambridge Univ. Press, Cambridge, U. K.
- Hobbie, S. E., and F. S. Chapin III (1998), The response of tundra plant biomass, aboveground production, nitrogen, and CO₂ flux to experimental warming, *Ecology*, *79*(5), 1526–1544.
- Hugelius, G., et al. (2014), Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps, *Biogeosciences*, *11*(23), 6573–6593, doi:10.5194/bg-11-6573-2014.
- Jonasson, S. (1988), Evaluation of the point intercept method for the estimation of plant biomass, *Oikos*, *52*(1), 101–106, doi:10.2307/3565988.
- Kirschbaum, M. U. F. (2004), Soil respiration under prolonged soil warming: Are rate reductions caused by acclimation or substrate loss? *Global Change Biol.*, *10*(11), 1870–1877, doi:10.1111/j.1365-2486.2004.00852.x.
- Kutzbach, L., J. Schneider, T. Sachs, M. Giebels, H. Nykanen, N. J. Shurpali, P. J. Martikainen, J. Alm, and M. Wilmking (2007), CO₂ flux determination by closed-chamber methods can be seriously biased by inappropriate application of linear regression, *Biogeosciences*, *4*(6), 1005–1025.
- Larsen, K. S., P. Grogan, S. Jonasson, and A. Michelsen (2007), Respiration and microbial dynamics in two subarctic ecosystems during winter and spring thaw: Effects of increased snow depth, *Arct. Antarct. Alp. Res.*, *39*(2), 268–276.
- Lipson, D. A., S. K. Schmidt, and R. K. Monson (2000), Carbon availability and temperature control the post-snowmelt decline in alpine soil microbial biomass, *Soil Biol. Biochem.*, *32*(4), 441–448.
- McGuire, A. D., L. G. Anderson, T. R. Christensen, S. Dallimore, L. D. Guo, D. J. Hayes, M. Heimann, T. D. Lorenson, R. W. Macdonald, and N. Roulet (2009), Sensitivity of the carbon cycle in the Arctic to climate change, *Ecol. Monogr.*, *79*(4), 523–555, doi:10.1890/08-2025.1.
- Melillo, J. M., P. A. Steudler, J. D. Aber, K. Newkirk, H. Lux, F. P. Bowles, C. Catricala, A. Magill, T. Ahrens, and S. Morrisseau (2002), Soil warming and carbon-cycle feedbacks to the climate system, *Science*, *298*(5601), 2173–2176.
- Mikan, C. J., J. P. Schimel, and A. P. Doyle (2002), Temperature controls of microbial respiration in arctic tundra soils above and below freezing, *Soil Biol. Biochem.*, *34*(11), 1785–1795.
- Morgner, E., B. Elberling, D. Strebel, and E. J. Cooper (2010), The importance of winter in annual ecosystem respiration in the high Arctic: Effects of snow depth in two vegetation types, *Polar Res.*, *29*(1), 58–74.
- Natali, S. M., E. A. G. Schuur, C. Trucco, C. E. H. Pries, K. G. Crummer, and A. F. B. Lopez (2011), Effects of experimental warming of air, soil and permafrost on carbon balance in Alaskan tundra, *Global Change Biol.*, *17*(3), 1394–1407, doi:10.1111/j.1365-2486.2010.02303.x.
- Natali, S. M., E. A. Schuur, E. E. Webb, C. E. H. Pries, and K. G. Crummer (2014), Permafrost degradation stimulates carbon loss from experimentally warmed tundra, *Ecology*, *95*(3), 602–608.
- Nobrega, S., and P. Grogan (2007), Deeper snow enhances winter respiration from both plant-associated and bulk soil carbon pools in birch hummock tundra, *Ecosystems*, *10*(3), 419–431, doi:10.1007/s10021-007-9033-z.
- Nobrega, S., and P. Grogan (2008), Landscape and ecosystem-level controls on net carbon dioxide exchange along a natural moisture gradient in Canadian low arctic tundra, *Ecosystems*, *11*(3), 377–396.
- Oberbauer, S. F., et al. (2007), Tundra CO₂ fluxes in response to experimental warming across latitudinal and moisture gradients, *Ecol. Monogr.*, *77*(2), 221–238.
- Oechel, W. C., G. L. Vourlitis, S. J. Hastings, R. C. Zulueta, L. Hinzman, and D. Kane (2000), Acclimation of ecosystem CO₂ exchange in the Alaskan Arctic in response to decadal climate warming, *Nature*, *406*(6799), 978–981.
- Öquist, M. G., T. Sparman, L. Klemetsson, S. H. Drotz, H. Grip, J. Schleucher, and M. Nilsson (2009), Water availability controls microbial temperature responses in frozen soil CO₂ production, *Global Change Biol.*, *15*(11), 2715–2722, doi:10.1111/j.1365-2486.2009.01898.x.
- Pedersen, A. R., S. O. Petersen, and K. Schelde (2010), A comprehensive approach to soil-atmosphere trace-gas flux estimation with static chambers, *Eur. J. Soil Sci.*, *61*(6), 888–902, doi:10.1111/j.1365-2389.2010.01291.x.
- Rumpf, S. B., P. R. Semenchuk, S. Dullinger, and E. J. Cooper (2014), Idiosyncratic responses of high Arctic plants to changing snow treatments, *PLoS One*, *9*(2), e86281, doi:10.1371/journal.pone.0086281.
- Rustad, L. E., J. L. Campbell, G. M. Marion, R. J. Norby, M. J. Mitchell, A. E. Hartley, J. H. C. Cornelissen, J. Gurevitch, and Gcte-News (2001), A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming, *Oecologia*, *126*(4), 543–562.
- Schimel, J. P., C. Bilbrough, and J. A. Welker (2004), Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities, *Soil Biol. Biochem.*, *36*(2), 217–227.
- Schuur, E. A. G., J. G. Vogel, K. G. Crummer, H. Lee, J. O. Sickman, and T. E. Osterkamp (2009), The effect of permafrost thaw on old carbon release and net carbon exchange from tundra, *Nature*, *459*(7246), 556–559, doi:10.1038/Nature08031.
- Semenchuk, P. R., B. Elberling, and E. J. Cooper (2013), Snow cover and extreme winter warming events control flower abundance of some, but not all species in high arctic Svalbard, *Ecol. Evol.*, *3*(8), 2586–2599, doi:10.1002/Eec3.648.
- Semenchuk, P. R., B. Elberling, C. Amtorp, J. Winkler, S. Rumpf, A. Michelsen, and E. J. Cooper (2015), Deeper snow alters soil nutrient availability and leaf nutrient status in high Arctic tundra, *Biogeochemistry*, *124*, 81–94, doi:10.1007/s10533-015-0082-7.
- Strebel, D., B. Elberling, E. Morgner, H. E. Knicker, and E. J. Cooper (2010), Cold-season soil respiration in response to grazing and warming in High-Arctic Svalbard, *Polar Res.*, *29*(1), 46–57.
- Sturm, M., J. Schimel, G. Michaelson, J. M. Welker, S. F. Oberbauer, G. E. Liston, J. Fahnestock, and V. E. Romanovsky (2005), Winter biological processes could help convert arctic tundra to shrubland, *BioScience*, *55*(1), 17–26, doi:10.1641/0006-3568(2005)055[0017:wbpchc]2.0.co;2.

- Tilston, E. L., T. Sparrman, and M. G. Oquist (2010), Unfrozen water content moderates temperature dependence of sub-zero microbial respiration, *Soil Biol. Biochem.*, *42*(9), 1396–1407.
- Wahren, C. H. A., M. D. Walker, and M. S. Bret-Harte (2005), Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment, *Global Change Biol.*, *11*(4), 537–552, doi:10.1111/j.1365-2486.2005.00927.x.
- Walsh, N. E., T. R. McCabe, J. M. Welker, and A. N. Parsons (1997), Experimental manipulations of snow-depth: Effects on nutrient content of caribou forage, *Global Change Biol.*, *3*, 158–164, doi:10.1111/j.1365-2486.1997.gcb142.x.
- Welker, J. M., J. T. Fahnestock, G. H. Henry, K. W. O'Dea, and R. A. Chimner (2004), CO₂ exchange in three Canadian High Arctic ecosystems: Response to long-term experimental warming, *Global Change Biol.*, *10*(12), 1981–1995.
- Welker, J. M., J. T. Fahnestock, P. F. Sullivan, and R. A. Chimner (2005), Leaf mineral nutrition of Arctic plants in response to warming and deeper snow in northern Alaska, *Oikos*, *109*(1), 167–177, doi:10.1111/j.0030-1299.2005.13264.x.
- Wipf, S., and C. Rixen (2010), A review of snow manipulation experiments in Arctic and alpine tundra ecosystems, *Polar Res.*, *29*(1), 95–109, doi:10.1111/j.1751-8369.2010.00153.x.
- Zamin, T. J., M. S. Bret-Harte, and P. Grogan, (2014), Evergreen shrubs dominate responses to experimental summer warming and fertilization in Canadian mesic low arctic tundra, *J. Ecol.*, *102*(3), 749–766.
- Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith (2009), *Mixed Effects Models and Extensions in Ecology with R*, Springer, New York.