



Decade of experimental permafrost thaw reduces turnover of young carbon and increases losses of old carbon, without affecting the net carbon balance

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Funding information

Knut och Alice Wallenbergs Stiftelse, Grant/Award Number: KAW 2012.0152; Svenska Forskningsrådet Formas, Grant/Award Number: 214-2011-788; Swedish Research Council, Grant/Award Number: 621-2011-5444

Abstract

Thicker snowpacks and their insulation effects cause winter-warming and invoke thaw of permafrost ecosystems. Temperature-dependent decomposition of previously frozen carbon (C) is currently considered one of the strongest feedbacks between the Arctic and the climate system, but the direction and magnitude of the net C balance remains uncertain. This is because winter effects are rarely integrated with C fluxes during the snow-free season and because predicting the net C balance from both surface processes and thawing deep layers remains challenging. In this study, we quantified changes in the long-term net C balance (net ecosystem production) in a subarctic peat plateau subjected to 10 years of experimental winter-warming. By combining ²¹⁰Pb and ¹⁴C dating of peat cores with peat growth models, we investigated thawing effects on year-round primary production and C losses through respiration and leaching from both shallow and deep peat layers. Winter-warming and permafrost thaw had no effect on the net C balance, but strongly affected gross C fluxes. Carbon losses through decomposition from the upper peat were reduced as thawing of permafrost induced surface subsidence and subsequent waterlogging. However, primary production was also reduced likely due to a strong decline in bryophytes cover while losses from the old C pool almost tripled, caused by the deepened active layer. Our findings highlight the need to estimate long-term responses of whole-year production and decomposition processes to thawing, both in shallow and deep soil layers, as they may contrast and lead to unexpected net effects on permafrost C storage.

KEYWORDS

age-depth modelling, carbon accumulation, carbon cycle, climate change, decomposition, peat dating, permafrost thawing, production, snow addition, winter-warming

1 | INTRODUCTION

Ongoing climate change causes rapid thawing of permafrost (Biskaborn et al., 2019; Lemke et al., 2007) and deepening of

the seasonally thawing 'active layer' in high-latitude peatlands (Åkerman & Johansson, 2008; Johansson et al., 2013), which store c. 50% of the world's total soil carbon (C) and c. 26% of the permafrost soil C pool (Hugelius et al., 2014; Yu, 2012). There is a

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great concern that increased active layer thickness will facilitate the release of this large C store, causing a positive feedback to the climate system (Koven, Lawrence, & Riley, 2015; Koven, Schuur, et al., 2015; MacDougall, Avis, & Weaver, 2012; Schuur et al., 2015; Turetsky et al., 2020). However, the magnitude of the responses of the C pools and balance to thawing remains uncertain.

Quantifying the effects of thawing on the C pools and balance of permafrost peatlands is complex because of different interacting mechanisms that may respond differently, including C uptake versus losses, as well as depth-related C-age differences (Abbott et al., 2016; Hobbie, Schimel, Trumbore, & Randerson, 2000; Koven, Lawrence, et al., 2015; Koven, Schuur, et al., 2015). Higher soil temperatures and increased oxygen availability upon thawing (Lawrence, Koven, Swenson, Riley, & Slater, 2015; St Jacques & Sauchyn, 2009) may accelerate organic matter decomposition in deep soil layers and increase C losses to the atmosphere (Dorrepaal et al., 2009; Hick Pries, Schuur, & Crummer, 2013; Schuur et al., 2015). However, thawing-related changes in nutrient availability, plant biomass and moisture may increase C sequestration in surface layers by stimulating above-ground plant productivity, which may offset or even exceed increased C losses (Keuper et al., 2017; Natali, Schuur, & Rubin, 2012; Salmon et al., 2016). Estimating the net response of C in permafrost systems to, and its feedback on climate change remains a challenge (Abbott et al., 2016; McGuire et al., 2018), by lack of a detailed understanding of losses and inputs of the different C pools.

Responses of C inputs and losses in permafrost to climate change are generally estimated based on upscaling of laboratory incubation studies of permafrost soils (Elberling et al., 2013; Knoblauch, Beer, Sosnin, Wagner, & Pfeiffer, 2013; Koven, Lawrence, et al., 2015; Koven, Schuur, et al., 2015; Schädel et al., 2016), in situ flux measurements in ecosystem-scale permafrost thaw experiments (Hick Pries, Schuur, Schuur, Natali, & Crummer, 2015; Natali et al., 2011) or measurements made across naturally degrading permafrost gradients (Jones et al., 2017; Schuur, Grummer, Vogel, & Mack, 2007; Schuur et al., 2009; Trucco et al., 2012). Long-term effects pertinent to climate change are highly uncertain as current estimates are strongly biased towards short timescales, for example, weeks–months for soil incubations and thaw experiments (e.g. Li et al., 2016), or a limited number of years, with potentially considerable interannual variation, for field flux measurements (e.g. Schuur et al., 2009). Naturally degrading permafrost gradients may show longer term responses of the permafrost C balance, but suffer from high uncertainties due to the unknown spatial heterogeneity in initial soil conditions among sites. Furthermore, plot-scale measurements in experimental and gradient studies are often only carried out during the summer, thus ignoring C losses during the long cold season, which may significantly contribute to the annual soil C balance (Hobbie et al., 2000; Natali et al., 2019; Salmon et al., 2016; Schimel, Bilbrough, & Welker, 2004; Schuur et al., 2009; Zona et al., 2016). Robust estimates of the long-term effects of permafrost thaw on the net C balance, which integrate year-round C inputs and losses over annual and decadal timescales, are thus urgently required to predict the strength and direction of permafrost C cycle–climate feedbacks in a warming Arctic.

An alternative approach to study the long-term response of soil C balance to environmental changes is to use dated peat profiles (Heffernan, Estop-Aragonés, Knorr, Talbot, & Olefeldt, 2020; Hick Pries, Schuur, & Grace Crummer, 2012; Olid, Nilsson, Eriksson, & Klaminder, 2014). If the profiles encompass the whole stratum, age–depth relations of the C stocks can be used to calculate C accumulation rates over different depth intervals to evaluate how permafrost thaw affects both near surface (young) and deep (old) C stocks. Furthermore, developed peat growth models can be used to estimate the fluxes of organic matter added to the uppermost layer by plant primary production (i.e. C inputs) and lost by decomposition (i.e. C losses) over the continuum of young (decadal) and old (millennial) peat (Clymo, 1984). The imbalance between these fluxes can then provide mechanistic insights behind inferred net changes in long-term C accumulation rates. This approach has been used to evaluate the long-term C dynamics of peatlands at boreal and subarctic regions (e.g. Belyea & Malmer, 2004; Olid et al., 2014; Turunen, Tomppo, Tolonen, & Reinikainen, 2002). Studies in the permafrost region are limited and mostly focus on old C losses that occur deep in the profile (Heffernan et al., 2020; Hick Pries et al., 2012; Vardy, Warner, Turunen, & Aravena, 2000). While only few studies included young C fluxes' responses due to gradual thawing (Hick Pries et al., 2012), little is known about how the net C balance of the whole soil column responds to winter-warming. This knowledge gap is particularly pronounced in lowlands where permafrost thawing causes surface subsidence (thermokarst) and waterlogging, and thus, alter conditions for plants growing during the upcoming decades of climate change.

The aim of this study was to quantify how C fluxes (primary production and decomposition) in surface and deeper peat layers respond to thawing caused by a thicker insulating snowpack, and estimate the net effects on the C balance. To achieve this aim, we used a peat-age modelling approach to quantify surface C inputs and shallow and deep C losses from a subarctic ice-rich permafrost peatland subjected to 10 years of experimental snow addition (winter-warming). Unlike natural thaw gradient studies, this approach ensures homogeneous initial conditions for the studied profiles and enables attribution of changes in the C balance exclusively to thawing and directly associated changes. We hypothesize that winter-warming reduces the potential of permafrost peatlands to accumulate C (i.e. negative effect on the net C balance). Specifically, we expect this to be driven by greater increases in C losses from decomposing peat in both upper active layer and newly thawed permafrost, due to higher peat soil temperatures, than any positive effect on plant C sequestration, due to increases in nutrient availability. We further expect these responses to be regulated by moisture conditions and plant composition.

2 | METHODS

2.1 | Study site

The study was carried out in the subarctic Storflaket mire complex (68°20'48"N, 18°58'16"E; c. 900 m long, 400 m wide), located

approximately 6 km east of the Abisko Scientific Research Station (northernmost Sweden) within the zone of discontinuous/sporadic permafrost (Brown, Ferrians, Heginbottom, & Melnikov, 1997). The permafrost plateau at which the experiment was performed has a peat layer of 60–90 cm thick, underlain by a silty lacustrine sediment of glacial origin (Åkerman & Johansson, 2008; Klaminder, Yoo, Rydberg, & Giesler, 2008), and a water table depth around 30 cm in October 2013. The permafrost thickness was approximately 15 m in the 1980s (Åkerman & Johansson, 2008), but more recent measurements indicate that it may be thicker (Dobinski, 2010). Mean active layer thickness was around 60 cm for the period 1978–2012, and increased by 0.7 cm/year during the past three decades (Åkerman & Johansson, 2008; Johansson et al., 2013). Dominant vegetation consists of peat moss (*Sphagnum* spp.), *Eriophorum vaginatum* L., *Vaccinium vitis-idaea* L., *Andromeda polifolia* L., *Betula nana* L., *Empetrum nigrum* L. and *Rubus chamaemorus*.

Mean monthly temperatures in the area ranged from -10.6°C in January to $+12.4^{\circ}\text{C}$ in July, with a mean annual temperature of $+0.7^{\circ}\text{C}$ for the period of the experiment 2005–2016 (meteorological data from Abisko Scientific Research Station). Average annual precipitation increased from 304 to 327 mm between 1961–1990 and 2005–2016 period (Alexandersson, Karlström, & Larsson-McCann, 1991; Abisko Scientific Research Station), while mean snow depth increased about 5%–10% per decade (Kohler, Brandt, Johansson, & Callaghan, 2006). This has led to widespread degradation of permafrost and increasing thaw depths in the area (Åkerman & Johansson, 2008; Johansson et al., 2011), which will likely continue or even accelerate during the coming decades (Sælthun & Barkved, 2003; Swindles et al., 2015).

2.2 | Experimental setup

A long-term experiment to simulate ongoing permafrost thaw due to increased snow thickness was set up in Autumn 2005 and is described in detail elsewhere (Johansson et al., 2013). In brief, 12 random plots were established on the western part of the Storflaket peat plateau. Six of these were randomly chosen and, every winter (from September till late May/early June), snow fences (10 m long, 1 m tall) were erected perpendicular to the prevailing east-west wind. These plots are further on referred to as 'winter-warming'. The remaining six plots, with ambient snow accumulation, served as 'controls' or reference plots.

Snow fences increased mean winter snow accumulation 2.6-fold (by 16–24 cm) in the winter-warming plots, simulating predicted increase in winter precipitation in the Arctic (Biskaborn et al., 2019; IPCC, 2013). The enhanced snow accumulation in turn increased winter (October–May) soil temperatures by 1.8 and 1.3°C at 15 and 30 cm depth respectively. At 45 cm, soil temperatures in the winter-warming plots were 1.3°C lower than controls. In summer (June–September), soil temperatures were on average 1.8°C lower in the winter-warming plots for all depths (Blume-Werry, Milbau, Teuber, Johansson, & Dorrepaal, 2019; Figure S1), which is explained by the

fact that the snow disappeared quite early in the season (April–May). Three years after the onset of the experiment, enhanced snow depth and prolonged snow cover duration delayed the start of the growing season up to 22 days (Bosiö, Stiegler, Johansson, Mbufong, & Christensen, 2014).

Enhanced snow depth and higher winter soil temperatures in turn increased active layer thickness, which reached 98 ± 11 cm (mean \pm SD) in manipulated plots compared to 62 ± 3 cm in controls. Furthermore, the thawing of ice layers in the uppermost permafrost induced surface subsidence (average of 24 cm in 2012 compared to 2005, vs. 5 cm in control plots) and raised the water table level (up to 6–11 cm), with the formation of seasonal ponds (Johansson et al., 2013; Figure S2). As a consequence, soil moisture in the upper peat layers (above the ambient water table) increased during the (early) summer (Johansson et al., 2013). Winter-warming altered vegetation, with a decrease in bryophyte cover and an increase in the graminoid *Eriophorum vaginatum* in the manipulated plots (Blume-Werry et al., 2019; Johansson et al., 2013), which had more flowering tillers compared to the control plots (Johansson et al., 2013). Root depth distribution and growth were also affected, resulting in more roots and a greater total root length in deeper soil (Blume-Werry et al., 2019). Emissions of carbon dioxide (CO_2) increased with winter-warming compared to control conditions, while methane (CH_4) emissions were almost negligible within and outside the winter-warming plots (Njuabe, 2011).

Overall, the warming achieved at Storflaket together with responses in soil and above-ground vegetation are comparable to other snow fence, permafrost-thaw experiments (Aerts, Cornelissen, & Dorrepaal, 2006; Hinkel & Hurd, 2006; Wahren, Walker, & Bret-Harte, 2005), even those where the additional snow was removed before the end of the snow season (Natali et al., 2011, 2012; Salmon et al., 2016). These responses are also in line with changes that occurred in the area during the last decade (Åkerman & Johansson, 2008; Biskaborn et al., 2019; IPCC, 2013; Johansson et al., 2011; Sælthun & Barkved, 2003), which supports the validity of our experimental setup to realistically mimick near-future permafrost thaw conditions in northernmost Sweden.

2.3 | Peat sampling and analyses

One peat core per plot was collected between late June and late September 2015. In order not to compact the thawed upper peat, we collected the upper 20–30 cm by cutting rectangular blocks using a handsaw. The rest of the profile up to the thaw front was collected using a peat-corer (11 \times 11.4 cm, Eijkelkame Netherlands). For the (frozen) permafrost layer, we collected peat cores using a custom-made, gas powered, fluid-less concrete drill (10.2 cm diameter). Frozen peat segments were rinsed with sterilized deionized water, wrapped in plastic foil and stored in a cooler box until transport to the laboratory. The total length of the cores (unfrozen + frozen compartments) varied between 107 and 134 cm, as we stopped the drilling when the drill hit small rocks and/or we reached a mineral layer,

which happened at varying depths in the frozen soil. The upper, unfrozen compartments were stored in the fridge (4°C) while the frozen parts of the profiles were stored in the freezer (-20°C) until further processing.

The uppermost, unfrozen parts (i.e. on average 0–62 cm for control and 0–98 cm for winter-warming treatment) were sliced into 1 cm thick sections by hand. The lengths of all sides were measured to determine the volume of each slide. Samples were dried at 65°C to a constant mass and then weighed and ground. For the frozen compartments, samples were taken at intervals of ~5 cm using a hollow drill bit (3.7 cm diameter) perpendicular to the soil core. The length of each sampled cylinder was measured to determine its volume. Subsamples from cylinders collected at 40 and 70 cm depth were kept in the freezer for posterior radiocarbon dating analyses. Frozen samples were freeze-dried, weighed and ground.

Bulk density (g/cm^3) for each sample was determined by dividing the dry mass of each section by its volume. Linear interpolation between measured values was used to obtain the bulk densities along the whole profile for each core.

Carbon content (% = g C/g peat) was analysed for a subset of ground subsamples from the active layer (every 2 cm, from the surface) and for all collected permafrost samples (at intervals of 5 cm, from the thaw front) using an NCS 2500 elemental analyser (CE Instruments). Linear interpolation between analysed points was used to obtain the C content for the non-analysed sections. The organic/mineral boundary was determined based on a decrease in C content to values lower than 20% and all C stocks were calculated down to this boundary.

2.4 | Peat profile chronology

High-resolution dating for the past 100–150 years was applied to the upper 15–20 cm of the active layer of each core based on the distribution of the natural radionuclide ^{210}Pb . Thereto, we measured the emission of the ^{210}Po granddaughter, assumed in secular equilibrium with its parent nuclide ^{210}Pb . Briefly, ground subsamples (0.1–0.2 g) from each 1 cm section were acid digested after spiking with a known amount of ^{209}Po yield tracer (Sanchez-Cabeza, Masqué, & Ani-Ragolta, 1998). The material was plated onto silver discs and measured by alpha spectrometry using Ortec ULTRA-AS Ion-Implanted-Silicon Charged-Particle Detectors (Model U-020-450-AS). Activities of ^{210}Pb decreased exponentially with depth until reaching constant values around 15–20 cm (data not shown). The average deeper activity of ^{210}Pb was similar to ^{226}Ra activities at depth and considered thus as the supported fraction. Therefore, the supported ^{210}Pb activity was subtracted from the total ^{210}Pb activity to obtain the unsupported ^{210}Pb fraction used for dating. Total unsupported ^{210}Pb inventories (Bq/m^2) did not differ between treatments ($p = .681$), which indicates that the additional snow did not affect the accumulation of ^{210}Pb and thus, all cores were datable. The age of each depth interval was

estimated by applying the Initial Penetration – Constant Rate of Supply (IP-CRS) model (Olid, Diego, Garcia-Orellana, Cortizas, & Klaminder, 2016).

For six of the cores ($n = 3$ control and $n = 3$ winter-warming), the derived ^{210}Pb -chronologies were validated using the record of ^{137}Cs (Appleby, Shotyk, & Fankhauser, 1997). Dried and ground subsamples were sealed into PerkinElmer cylindrical polyethylene vials of 5.65 cm^3 and measured by gamma spectrometry, using a high-purity germanium well-detector (Canberra, GCW3523-type). The IP-CRS chronologies for one winter-warming and two control cores located the maxima of ^{137}Cs in 1957–1971 and 1984–1988 period, which is in good agreement with the maximum global fallout of artificial radionuclides (Appleby et al., 1997) and validates the ^{210}Pb -derived ages. Clear ^{137}Cs peaks were not identified for the rest of the cores likely due to the high mobility of ^{137}Cs in peat (MacKenzie, Farmer, & Sugden, 1997).

For older (deeper) parts of the profiles, we used ^{14}C -based dating. Because of the high cost associated with radiocarbon dating, we analysed millennial ages at two depths (40 and 70 cm) in the same cores where ^{137}Cs was measured ($n = 3$ control and $n = 3$ winter-warming). We used bulk peat subsamples (free of roots) without further pre-treatment for the analyses. Radiocarbon concentrations were analysed by acceleration mass spectrometer at Beta Analytic. Radiocarbon dates were converted to calibrated ages BP by IntCal1 ^{14}C age calibration curves (Reimer et al., 2013) and recalculated to calendar years.

Both ^{210}Pb and ^{14}C dates were used to obtain a continuous chronology along the whole profile using the age–depth model Plum (Aquino-López, Blaauw, Christen, & Sanderson, 2018). Unlike the traditional way of obtaining such chronologies, Plum calculates both chronology and uncertainties using Bayesian statistics.

2.5 | Carbon stocks and accumulation rates

Organic C stocks have been widely used as a proxy for organic C sequestration capacity. We estimated C stocks accumulated over three different depth compartments: (a) the ambient active layer depth (i.e. the upper 62 cm), (b) the intermediate layer that is seasonally thawed in the winter-warming plots but still frozen in controls (i.e. from 62 to 98 cm) and (c) the upper meter of accumulation. Standardizing C stocks to a certain depth may, however, give a misleading impression of the C sequestration capacity, due to differences in sedimentation rates. In contrast, data from C accumulation rates over time allows to normalize C stocks accumulated over a certain time period. We used bulk density and C content profiles (Figure S3) together with the derived age–depth relationships to quantify rates of organic C accumulation over time. Based on the peat chronology, we estimated C stocks for the past 10 (recent), 100 (decadal) and 7,000 (millennial) years of peat accumulation. The selected time-horizons corresponded to the period during which the winter-warming treatment was applied, and the oldest ages derived from ^{210}Pb and ^{14}C dating found in all the cores respectively.

2.6 | Modelling C inputs and decomposition rates

Carbon fluxes were estimated by fitting the cumulative C stocks versus derived-ages to the general equation provided by Clymo's model for peat growth (Clymo, 1984). This model assumes that the net change in the C storage in a peat deposit is given by the imbalance between annual C inputs (I) and decomposition losses (kC):

$$\frac{dC}{dt} = I - kC. \quad (1)$$

Other C losses (e.g. leaching or dissolved organic matter export) are considered negligible. When solved, the temporal variation in the cumulative C is given by:

$$C(t) = \frac{I}{k}(1 - e^{-kt}), \quad (2)$$

where C represents the cumulative C stock (g C/m^2) at a certain time t , I is the annual C input ($\text{g C m}^{-2} \text{ year}^{-1}$) at the surface and k is the first-order decomposition constant (year^{-1}).

We fitted Equation (2) to curves of cumulative C stocks versus decadal (past century; Figures S4 and S5) and old ages (up to 10,000 years; Figure S6) using the nls function in R (R Core Team, 2017). The best fitting determined C inputs (I) and decomposition constants (k) estimated for both decadal and millennial timescale. Estimated I and k at millennial timescales for cores without available ^{14}C dates were an average of the ^{14}C -dated parameters of peat cores.

2.7 | Ecosystem C balance: Net ecosystem production

We used the above estimates of C inputs and decomposition constants to calculate the annual ecosystem C balance (net ecosystem production [NEP]; Trumbore, Bubier, Harden, & Crill, 1999), and its response to 10 years winter-warming. We estimated NEP as the difference between decadal C inputs and C losses from both shallow (young) and deep (old) soil:

$$\text{NEP} = I_{\text{decadal}} - k_{\text{decadal}} \cdot C_{\text{decadal}} - k_{\text{millennial}} \cdot C_{\text{millennial}}, \quad (3)$$

where I_{decadal} and k_{decadal} correspond to the C inputs and decomposition constant derived from the decadal C accumulation model, $k_{\text{millennial}}$ is the decomposition constant from the millennial C accumulation model and C_{decadal} and $C_{\text{millennial}}$ are the cumulative C stocks in the shallow and the deep soil respectively. C_{decadal} was obtained by integrating all layers with measurable activities of ^{210}Pb (i.e. C accumulated over the past 100–150 years). $C_{\text{millennial}}$ corresponded to the amount of C accumulated from the end of the modelled decadal depths until the shallowest permafrost layer, where decomposition was assumed to be minimal due to frozen conditions. According to this notation, a positive/negative NEP indicates that the system is acting as a net sink/source.

2.8 | Statistical analyses

We tested the effects of winter-warming on our response variables (i.e. C stocks, C accumulation rates, C inputs, decomposition rates and NEP) using generalized linear mixed effects models (GLMMs). We ran the analyses with 'treatment' and 'depth/age' and their interaction as fixed factors. We added 'plot' as a random factor to account for non-independency between sampling depths within a profile. In case of interactions between depth/age and treatment, we further investigated the responses to winter-warming within each compartment using one-way ANOVAs. Treatment effects on the C stocks in the total active layer (i.e. total unfrozen compartment) were also analysed using one-way ANOVA.

All data were visually checked for normality and heteroscedasticity. Data were log-transformed if model assumptions were not met (Tables S1–S5). If no interactions were found, models were simplified and the interaction term was removed to increase statistical power. All statistical analyses were conducted in R (version 3.5.1: R Core Team, 2018) with additional packages (lme4 package, Bates, Mächler, Bolker, & Walker, 2015; for the GLMMs and ggplot2, Wickham, 2009) for graphical illustrations.

3 | RESULTS

3.1 | Carbon stocks and accumulation rates

Carbon stocks for compartments of equal depth for both treatments (i.e. ambient active layer, intermediate layer and upper meter) did not differ between treatments ($F = 0.264$, $p = .616$; Figure 1; Table S1). In contrast, winter-warming increased C stocks accumulated in the current total active layer (i.e. 36 cm thicker in winter-warming plots) by up to 81% ($F = 9.284$, $p = .012$; Figure 1). Because C content was not affected by the treatment ($F = 1.448$, $p = .256$; Table S2), increased C stocks in the current total active layer are due to the 36 cm thicker active layer in the winter-warming plots.

When C stocks were calculated as a function of peat age, overall lower C stocks were observed in the winter-warming plots compared to control conditions ($F = 8.20$, $p = .014$; Figure 2; Table S3). The response varied with age (treatment \times age interactions $F = 8.87$, $p = .002$; Table S3), with the strongest and only significant reduction (–35%) for the recent (past 10 years) C stocks ($F = 5.18$, $p = .0461$).

Similarly, winter-warming overall reduced C accumulation rates across recent, decadal and millennial timescales ($F = 6.53$, $p = .025$; Figure 3; Table S4), with responses that varied depending on the covered temporal scale (treatment \times age interaction $F = 5.325$, $p = .0058$; Table S4). The strongest and only significant response (–33%) was found for the recent (<10 years) C accumulation rates ($F = 6.16$, $p = .0324$).

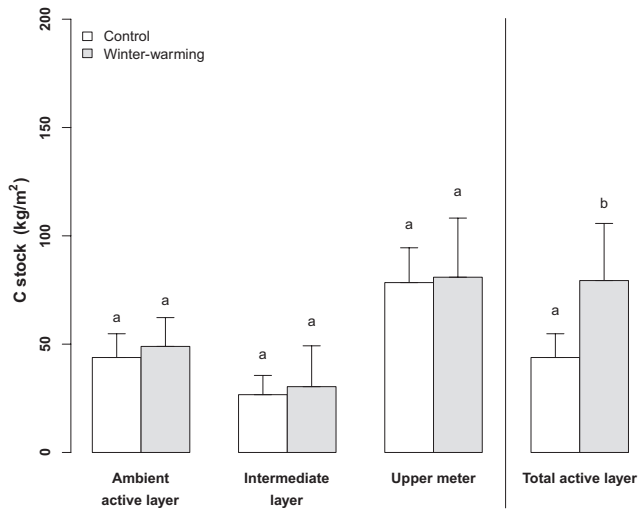


FIGURE 1 Carbon (C) stocks (mean ± SD) at different depth compartments in a subarctic permafrost peat plateau subjected to long-term winter-warming (grey; $n = 6$) or ambient (white) conditions ($n = 6$). Different lower-case letters indicate differences between treatments within the same compartment. Notice that differences in the current total active layer were evaluated with an individual test

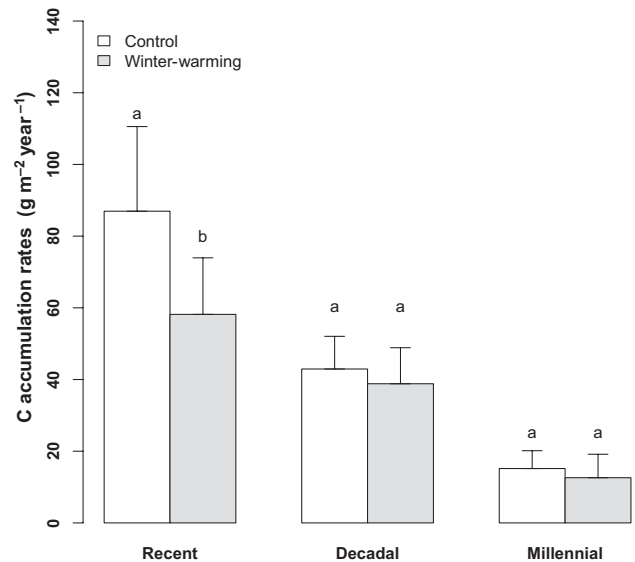


FIGURE 3 Carbon (C) accumulation rates (mean ± SD) at recent (past 10 years), decadal (past 100 years) and millennial (past 7,000 years) timescales in a subarctic permafrost peat plateau subjected to long-term winter-warming (grey; $n = 6$ for recent and decadal values, $n = 3$ for millennial values) or ambient (white) conditions ($n = 6$ for recent and decadal values, $n = 3$ for millennial values). Different lower-case letters indicate differences between treatments within the same temporal compartment

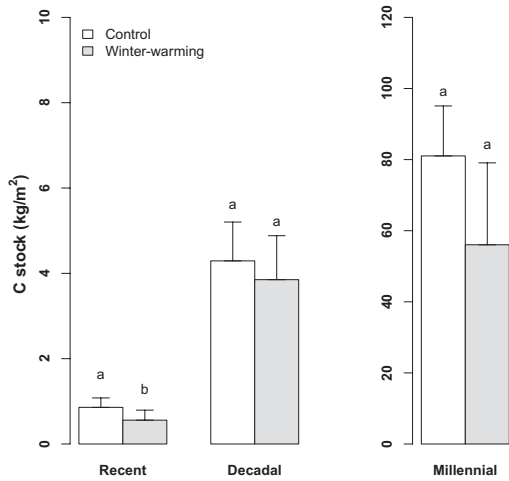


FIGURE 2 Carbon (C) stocks (mean ± SD) at recent (past 10 years), decadal (past 100 years) and millennial (past 7,000 years) timescales in a subarctic permafrost peat plateau subjected to long-term winter-warming (grey; $n = 6$) or ambient (white) conditions ($n = 6$). Different lower-case letters indicate differences between treatments within the same temporal compartment

3.2 | Modelled C inputs and decomposition rates

In contrast to what we expected, winter-warming decreased (decadal) C inputs at the uppermost peat layers, with a reduction of 31% of the total amount of C being incorporated to the palsa surface ($F = 5.257, p = .0448$; Figure 4). Decadal decomposition constants were one order of magnitude higher than those inferred over a millennial timescale ($F = 333, p < .001$; Figure 4; Table S5). Also here,

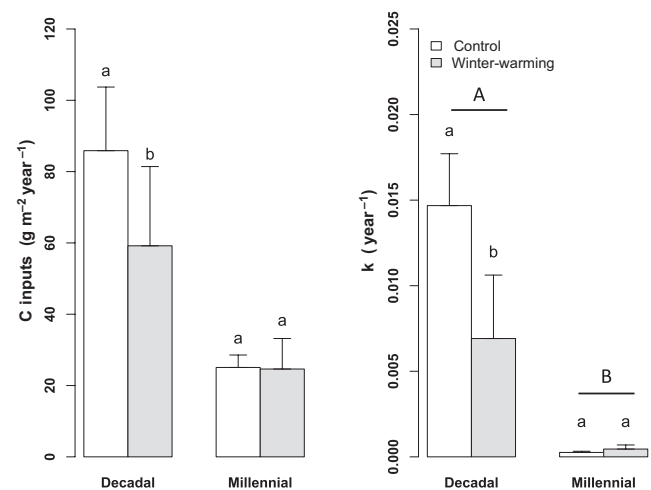


FIGURE 4 Carbon (C) inputs (I) at the surface and decomposition constants (k) at both decadal (^{210}Pb) and millennial (^{14}C) timescales in a subarctic permafrost peat plateau subjected to long-term winter-warming (grey) or ambient (white) conditions ($n = 6$ for each treatment for decadal values, $n = 3$ for each treatment for millennial values). Different upper-case letters indicate differences between compartments while different lower-case letters indicate differences between treatments within the same temporal compartment

the effect of winter-warming on decomposition constants differed between temporal compartments (treatment × age interaction $F = 13.6, p = .00167$; Table S5). While winter-warming strongly decreased (−53%) decomposition constants in the uppermost (young)

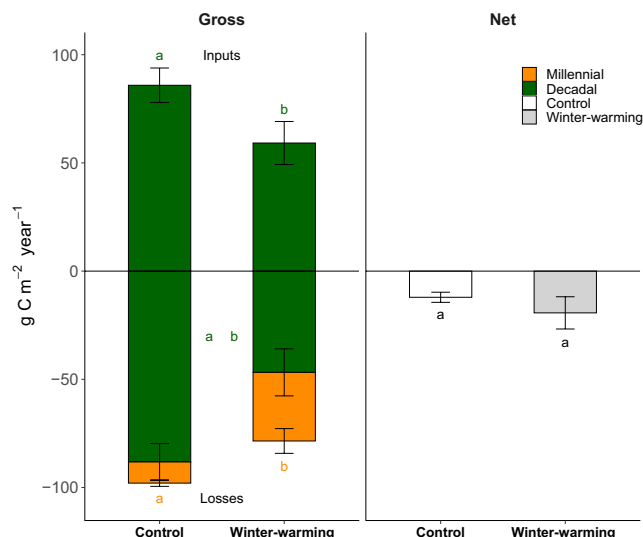


FIGURE 5 Gross C inputs as well as loss rates (mean \pm SD) at decadal ($n = 6$) and millennial ($n = 6$) timescales (left panel) and resulting net ecosystem production (right panel) in a subarctic permafrost peat plateau subjected to long-term winter compared or ambient conditions. Different lower-case letters indicate differences between treatments between the gross C fluxes

peat ($F = 15.79$, $p = .00263$), no effect was observed for layers accumulated over the past millennia ($F = 1.81$, $p = .242$). The reduced decadal decomposition constants led to 47% lower young C loss rates from the upper 20 cm of the active layer in the winter-warming plots than controls ($F = 10.80$, $p = .0082$; Figure 5). Although millennial decomposition constants did not vary with the treatment, winter-warming effects on active layer thickness ($F = 8.625$, $p = .0149$) resulted in a threefold increase in old C losses ($F = 16.50$, $p = .00228$; Figure 5).

3.3 | Net ecosystem production

Estimates of NEP averaged -10 ± 9 g C m⁻² year⁻¹, with no statistically significant differences between winter-warming (-19 ± 17 g C m⁻² year⁻¹) and control (-12 ± 5 g C m⁻² year⁻¹) conditions, whether based on all fully dated cores only ($n = 6$, $F = 0.3851$, $p = .568$) or including all cores based on interpolated millennial ages (see Section 2, $n = 12$, $F = 1.020$, $p = .3362$; Figure 5).

4 | DISCUSSION

A decade of experimental snow addition and active layer deepening of a peat plateau induced contrasting effects on the shallow and deep processes that drive the C balance of permafrost ecosystems. In the uppermost active layer, both C inputs by plants and losses of young C by decomposition were reduced by winter-warming and associated permafrost thaw effects. At depth, in contrast, decomposition constants of old C were unaffected by winter-warming, but

the higher amount of thawed C in the active layer available for decomposition dramatically increased old C losses. Despite the clear deceleration in short-term turnover of young C and acceleration in turnover of old C, the long-term net C balance (NEP) was not affected. Several indirect effects associated to permafrost thaw were likely driving the contrasting responses of C fluxes and are discussed below.

4.1 | Winter-warming effects on C losses

In contrast to our hypothesis, we found that winter-warming decreased decadal C losses, while millennial C losses increased as expected. The unexpected strong decrease in decadal C losses was partially caused by the smaller size of the C stocks accumulated during the 10 years of experimental manipulation, but was primarily due to a lower decadal decomposition constant. This contrasts with field and laboratory incubations studies where enhanced decomposition of organic matter was found with warming (Dutta, Schuur, Neff, & Zimov, 2006; Kirschbaum, 1995; Rustad et al., 2001). The negative response may, in part, be due to indirect effects of the extra snow and thawing of permafrost on soil conditions. Firstly, soil temperatures in our snow fence plots increased overall, but the effects strongly differed in different parts of the year. In winter (October–May), thicker snow cover increased shallow peat temperatures by 1.8°C (Blume-Werry et al., 2019; Johansson et al., 2013). Although such increase might enhance winter respiration (Natali, Schuur, Webb, Pries, & Crummer, 2014; Nobrega & Grogan, 2007; Walker et al., 1999), the absolute increase in winter respiration may have only caused a marginal increase in young C losses, because temperatures in winter-warming plots were only at or below 0°C during winter (Figure S1). In line with this, Grogan (2012) found negligible snow-fence effects on soil respiration when higher soil temperatures were restricted to the deep cold phase of winter. Instead, lower shallow soil temperatures during the warm growing season (Figure S1; Blume-Werry et al., 2019; Johansson et al., 2013) may have strongly reduced absolute microbial activity during the most active season, which may explain part of the lower decomposition constant of shallow/young C in the winter-warming plots.

A second explanation for the reduced decadal decomposition constant likely stems from changes in moisture/waterlogging conditions and associated anoxia, both indirect effects of increases in snow depth and associated permafrost thaw. Thawing of both the excess snow as well as the segregated ice layers in the uppermost permafrost followed by surface subsidence increased water content at the surface of the mire in our study system. Ground surface subsidence and increasing soil water content are typical characteristics of thermokarst systems (Osterkamp et al., 2009) and have been observed in other snow manipulation experiments (Blanc-Betes, Welker, Sturchio, Chanton, & Gonzalez-Meler, 2016; Hinkel & Hurd, 2006; Natali et al., 2011, 2014), even when the excess of snow was removed in spring (Natali et al., 2011, 2014). Low oxygen availability

in water saturated soils inhibit microbial activity and thereby reduce decomposition and C losses below the water table (Schädel et al., 2016; Treat et al., 2014; Voigt et al., 2019). Both decreased summer soil temperatures and increased waterlogging likely explain the reduced decomposition rates of young C in the shallow part of the active layer. Our findings suggests that reduced decomposition rates of young C may occur in lowland permafrost sites in northern Scandinavia and Eurasia, where permafrost monitoring revealed an ongoing shift towards wetter conditions (Christensen, 2004; Johansson, Christensen, Akerman, & Callaghan, 2006; Jorgenson, Racine, Walters, & Osterkamp, 2001). A projected increase in winter snow depth during the latter part of the 21st century seems likely to amplify this trend further (Callaghan et al., 2011). However, other regions may see contrasting trends as peat plateaus and better-drain thermokarst bogs in the North American Arctic may experience a drop on the water table position upon thawing, which is likely to lead to higher decomposition losses of C from shallow layers (Hick Pries et al., 2013; Schuur et al., 2015). Note that peatlands within the sporadic and discontinuous permafrost zones are disproportionately likely to be inundated and affected by anoxic conditions following permafrost thaw (Koven, Lawrence, et al., 2015; Koven, Schuur, et al., 2015; Schuur et al., 2015). Our results clearly highlight the importance of recognizing these region-specific responses in surface peat hydrology when predicting the fate of young C accumulated in arctic mires underlain by permafrost.

The threefold higher old C losses, as observed here, are in line with our hypothesis and previous observations in arctic and sub-arctic ecosystems (Dorrepaal et al., 2009; Schuur et al., 2009). This effect was primarily due to the deepened active layer, while the winter-warming treatment did not (significantly) increase the decomposition constant of the old C. In contrast to the shallow active layer, deeper layers of the studied peat plateau were permanently water saturated for both control and manipulated plots during the whole experiment. Furthermore, the additional snow increased peat soil temperatures in winter by 1.3°C at 30 cm compared to controls (primarily during short, severe cold spells), but caused no clear difference between treatments at greater depths during the summer (Figure S1; Blume-Werry et al., 2019; Johansson et al., 2013). The similar deep soil temperatures in all plots for an important part of the year may thus partly explain the absence of difference in decomposition constants for the old C pool. In addition, a rapid consumption of the pool of labile C substrates, initially available following thawing, may have left only the more recalcitrant C fraction in the long term (Monteux et al., 2018; Semenchuk et al., 2019), thus potentially rendering the millennial decomposition constants insensitive to thawing. Our results therefore suggest that previously observed increases in old C losses with permafrost thaw (Dorrepaal et al., 2009; Hick Pries et al., 2013) are likely primarily caused by the increased thickness of the active layer, rather than a high thermal sensitivity of old C decomposition. In addition, the marked differences in the response and driving mechanisms of decomposition rates of deep (old) versus shallow (young) peat underscores the need of recognizing and understanding specific factors (e.g. soil temperature, moisture,

active layer depth) at different depths (shallow/deep) and at different temporal scales (seasonal, decadal, millennial) when evaluating the fate of permafrost C.

4.2 | Winter-warming effects on C inputs

We hypothesized that winter-warming would increase incorporation of C at the surface of permafrost peatlands due to enhanced plant production. Instead, we found a strong decrease in decadal C inputs (i.e. net primary production [NPP], Trumbore et al., 1999), which suggests that gross primary production (GPP) was reduced and/or plant respiration enhanced. Reduced GPP upon thawing contrasts to previous studies on interactions between thaw and vegetation from experiments in tussock tundra in Alaska (Natali et al., 2012, 2014; Wahren et al., 2005). The discrepancy may arise from differences in plant community composition and the relative contribution of different plant types to total primary production, combined with hydrological responses. The vegetation in the Storflaket peat plateau is characterized by low vascular plant cover and dominated by peat mosses, especially *Sphagnum fuscum* (Wielgolaski, 1972). Bryophytes such as *S. fuscum* are the main peatformers in ombrotrophic peatlands (Malmer & Wallen, 1999; Rosswall & Granhall, 1980), and can account for up to 45% of the total above-ground NPP (Chapin, Shaver, Giblin, Nadelhoffer, & Laundre, 1995; Svensson & Rosswall, 1980). Soil subsidence and the formation of seasonal ponds during spring and early summer in our winter-warming plots tended to increase alkalinity in the active layer (Monteux et al., 2018), which can limit growth rate and photosynthesis of the hummock-adapted *S. fuscum* (Udd, Sundberg, & Rydin, 2015; Williams & Flanagan, 1996, 1998). The high loss of bryophyte cover (~75%) observed in our experiment (Blume-Werry et al., 2019), and a likely lower relative production of peat moss in the winter-warming plots, may thus explain the lower input of newly fixed C in response to snow addition and permafrost thaw.

Increased plant respiration may have further contributed to the observed reduction in C inputs, although likely to a lesser extent. Higher ecosystem respiration rates were measured in our winter-warming plots compared to controls after 6 years of treatment (Njuabe, 2011), which could have partly resulted from higher plant respiration. Indeed, in nearby ombrotrophic *Sphagnum* peatlands in Abisko, experimental warming increased respiration by living plants more than heterotrophic respiration (Dorrepaal et al., 2009; Hick Pries, van Logtestijn, et al., 2015). Overall, the net reduction in the incorporation of new C in the upper active layer with thawing observed in our permafrost mire likely results from the combination of an increase in autotrophic respiration and a stronger decrease in bryophyte production than an increase in vascular plant biomass.

4.3 | Warming effects on NEP

In contrast to our expectations, 10 years of winter-warming and thawing permafrost did not significantly affect the net C balance of

the studied peat mire. This is surprising, given the observed strong deceleration of the short-term turnover of young C (lower C input and C losses at decadal timescale) and acceleration in turnover of old C (higher C losses at millennial timescale). Winter-warming thus strongly reduced the C sink capacity of the ecosystem but that was entirely compensated by a similar decrease in young C losses from the upper 15–20 cm of the active layer. Unaffected C stocks and net C balance with permafrost thawing were also observed in warming experiments (Sistla et al., 2013) and natural thawing gradients (Heffernan et al., 2020; Schuur et al., 2009). Unlike what we observed, in these cases the higher release of old C was offset by increased plant C uptake during the growing season. The discrepancy in the response of surface C inputs is due to large differences in surface hydrologic conditions between sites. While winter-warming and associated permafrost thawing resulted in water ponding in Storflaket (Johansson et al., 2013; Keuper et al., 2012), well-drained tundra uplands experienced a deepening of the water table and became drier, likely stimulating primary production when soils became warmer (Keuper et al., 2017; Natali et al., 2012; Salmon et al., 2016). Therefore, our results highlight not only the fundamentally different role of the upper active layer and the permafrost C below in regulating net C exchange of peat plateau ecosystems, but also how the functioning of different processes in these ecosystems can respond differently depending on topographic and vegetation characteristics and reflect changes in environmental conditions without necessarily altering their overall, long-term C balance.

Predicting the overall winter-warming effects on greenhouse gas forcing is difficult as our method does not distinguish between the different forms of C emissions (e.g. CO₂, CH₄, dissolved organic C, volatile organic C), which strongly differ in greenhouse potential (Knoblauch, Beer, Liebner, Grigoriev, & Pfeiffer, 2018; Schädel et al., 2016). However, CH₄ production and emission were almost negligible during the first years of the experiment (Njuabe, 2011) and it seems reasonable to assume that most gaseous losses occurred as CO₂. The reduced decadal C losses observed here together with the lower potential of respiration rates measured in the active layer (Monteux et al., 2018), suggest lower losses of CO₂ from younger C pools upon thawing. The higher CO₂ respiration rates observed in the first years of the experiment (Njuabe, 2011), was thus likely a short-term response driven by the initial loss of labile C pool (Monteux et al., 2018; Semenchuk et al., 2019). The latter study identified a lower potential respiration from the deeper parts of the active layer for the winter-warming plots (Monteux et al., 2018). Low losses of CO₂ from the old, previously frozen C stocks following thawing is in line with mesocosm experiments and field observations that showed limited contribution of permafrost C to surface CO₂ (Estop-Aragonés, Cooper, et al., 2018; Estop-Aragonés, Czimczik, et al., 2018). Considering that our model captures the long-term effects and the highly sensitive response of short-term C release (Voigt et al., 2019), we suggest that previous studies likely reflect seasonal CO₂ emissions rather than the long-term permafrost C-feedback. However, we

do not rule out the possibility of higher CH₄ emission rates mostly from the uppermost layers when the system becomes wetter and sedge-dominated (Cooper et al., 2017). Integrated long-term measurements of CO₂ and CH₄ fluxes together with ¹⁴C dates of the released C would be necessary to accurately projecting future climate feedbacks of winter-warming and permafrost thaw.

Overall, experimental winter-warming in a permafrost peat plateau in the subarctic Sweden affected processes controlling accumulation and release of C from the shallow active layer and the deeper newly thawed permafrost. These results clearly demonstrate that determining the trajectory of ecosystem C balance cannot be based on short-term process studies but requires quantification of all integrating effects (short- and long-term) on young and old C stocks. Surprisingly, peat soil temperatures during the growing season had only a minor effect on the annual balance, emphasizing the necessity of year-round measurements integrating whole seasons. Finally, our age modelling approach revealed that the overall magnitude of the current permafrost C imbalance depends largely on near-surface hydrologic conditions and plant cover. Integrating whole-year C fluxes and the effects of (experimental) winter-warming and permafrost thaw along the whole peat continuum (i.e. active layer and newly thawed permafrost), as done here, will help to better constrain the long-term net C balance and climate change feedbacks between the permafrost C pool and the global climate system.

ACKNOWLEDGEMENTS

This study was funded by a Wallenberg Academy Fellowship (KAW 2012.0152), Swedish Research Council (Dnr 621-2011-5444), and Formas (Dnr 214-2011-788) grants all attributed to ED. The authors are grateful to Tuukka Mäkiranta and Pia Bartels for their help during fieldwork. Special thanks are also due to Gesche Blume-Werry for stimulating discussions. We thank the Laboratori de Radioactivitat Ambiental in Barcelona for their help with ¹³⁷Cs measurements and the Abisko Scientific Research Station for practical support.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Olid C, Klaminder J, Monteux S, Johansson M, Dorrepaal E. Decade of experimental permafrost thaw reduces turnover of young carbon and increases losses of old carbon, without affecting the net carbon balance. *Glob Change Biol.* 2020;26:5886–5898. <https://doi.org/10.1111/gcb.15283>