Global Change Biology

Global Change Biology (2011) **17**, 1394–1407, doi: 10.1111/j.1365-2486.2010.02303.x

Effects of experimental warming of air, soil and permafrost on carbon balance in Alaskan tundra

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Abstract

The carbon (C) storage capacity of northern latitude ecosystems may diminish as warming air temperatures increase permafrost thaw and stimulate decomposition of previously frozen soil organic C. However, warming may also enhance plant growth so that photosynthetic carbon dioxide (CO_2) uptake may, in part, offset respiratory losses. To determine the effects of air and soil warming on CO_2 exchange in tundra, we established an ecosystem warming experiment – the Carbon in Permafrost Experimental Heating Research (CiPEHR) project – in the northern foothills of the Alaska Range in Interior Alaska. We used snow fences coupled with spring snow removal to increase deep soil temperatures and thaw depth (winter warming) and open-top chambers to increase growing season air temperatures (summer warming). Winter warming increased soil temperature (integrated 5–40 cm depth) by 1.5 °C, which resulted in a 10% increase in growing season thaw depth. Surprisingly, the additional 2 kg of thawed soil C m^{-2} in the winter warming plots did not result in significant changes in cumulative growing season respiration, which may have been inhibited by soil saturation at the base of the active layer. In contrast to the limited effects on growing-season C dynamics, winter warming caused drastic changes in winter respiration and altered the annual C balance of this ecosystem by doubling the net loss of CO_2 to the atmosphere. While most changes to the abiotic environment at CiPEHR were driven by winter warming, summer warming effects on plant and soil processes resulted in 20% increases in both gross primary productivity and growing season ecosystem respiration and significantly altered the age and sources of CO_2 respired from this ecosystem. These results demonstrate the vulnerability of organic C stored in near surface permafrost to increasing temperatures and the strong potential for warming tundra to serve as a positive feedback to global climate change.

Keywords: climate change, NEE, permafrost, radiocarbon, snowfence, soil carbon, thermokarst, tundra, warming

Received 18 May 2010 and accepted 1 July 2010

Introduction

Northern latitude ecosystems are keystone contributors to global carbon (C) reservoirs. While northern permafrost soils comprise <20% of the global soil area, they store approximately 50% of the belowground global C pool (Schuur *et al*., 2008; Tarnocai *et al*., 2009). The estimated 1672 Pg of soil C stored in these regions (Schuur *et al*., 2008; Tarnocai *et al*., 2009) is more than twice the amount of C currently contained in the atmosphere (Post *et al*., 1982; Sabine *et al*., 2004; IPCC, 2007). The role of northern ecosystems in global C dynamics is particularly relevant in the context of feedbacks from ecosystems to global climate change. Global models predict future increases in surface air temperature to be greatest in northern latitudes, with late 21st century mean air temperature projected to increase up to 7–8 °C in some model scenarios, which is twice the projected global mean (ACIA, 2004). While northern soils have historically served as a C sink (Harden *et al*., 1992; Smith *et al*., 2004), both climate predictions (ACIA, 2004; Winton, 2006; IPCC, 2007) and recent climate trends (Serreze *et al*., 2000; Polyakov *et al*., 2002) portend a potential release of this large soil C stock as permafrost degrades (Oechel *et al*., 1993; Osterkamp & Romanovsky, 1999; Vogel *et al*., 2009) and ‘old’ C is increasingly lost to the atmosphere (Schuur *et al*., 2009). Because of the size and temperature sensitivity of this C pool, the release of old C from long-term soil pools in northern regions is one of the more likely positive feedbacks from terrestrial ecosystems to the atmosphere in a warmer world.

Latitudinal gradients of soil C storage (Post *et al*., 1982), field experiments (Van Cleve *et al*., 1990; Rustad *et al*., 2001) and laboratory incubations (Kirschbaum, 1995, 2000; Dutta *et al*., 2006) all show that soil C cycling in northern ecosystems is likely to be strongly influenced by the positive effect of temperature on soil

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organic matter (SOM) decomposition rates (Davidson & Janssens, 2006). However, warming-mediated changes in soil nutrient availability (Chapin *et al*., 1995; Hartley *et al*., 1999; Schimel *et al*., 2004; Biasi *et al*., 2008), plant biomass and community dynamics (Chapin *et al*., 1995; Chapin & Shaver, 1996; Hobbie & Chapin, 1998; Shaver & Jonasson, 1999; Wahren *et al*., 2005; Walker *et al*., 2006; Biasi *et al*., 2008; Euskirchen *et al*., 2009), plant nutrient status (Aerts *et al*., 2009), and plant phenology (Arft *et al*., 1999) may increase plant C uptake, partially offsetting C losses from increased decomposition. In addition to these temperature-mediated effects on plant and soil processes, warming temperatures in high latitude ecosystems may also bring about important landscape-level changes that can have profound effects on ecosystem C storage. Warming-mediated increases in active layer thickness, permafrost thaw, and thermokarst (subsidence driven by thawing ground ice) (Lachenbruch & Marshall, 1986; Osterkamp & Romanovsky, 1999) can dramatically alter soil C storage capacity (Chapin *et al*., 2000; Schuur *et al*., 2009; Vogel *et al*., 2009). These landscape-level processes can affect the amount and age of C released to the atmosphere through the thawing and decomposition of previously unavailable organic C (Schuur *et al*., 2009) and can also alter local hydrology and surface erosion, both of which affect the transfer of C from ecosystems to the atmosphere (Schuur *et al*., 2008). The balance between these biological and physical processes will determine whether these systems will act as a C source or sink under future climate change scenarios.

Ecosystem warming experiments have a long history of use as a means to understand potential effects of climate change in the Arctic on plant and soil processes. Early warming experiments starting in 1979 used polyethylene greenhouses to warm tundra during the growing season (Chapin & Shaver, 1985). Some of these experiments are still in progress and provide an unmatched record of experimental warming (Chapin *et al*., 1995; Shaver *et al*., 2000). More recently, in 1991, the International Tundra Experiment (ITEX) program initiated a coordinated warming experiment using open-top chambers (OTCs) at sites distributed across the circumpolar region (Henry & Molau, 1997; Arft *et al*., 1999; Walker *et al*., 2006). Both polyethylene greenhouses and OTCs are effective in warming the air as predicted in climate warming scenarios, but do not necessarily warm the soil very deeply (Marion *et al*., 1997; Hobbie & Chapin, 1998; Shaver *et al*., 2000). Other warming experiments that use radiant heaters (Harte & Shaw, 1995; Harte *et al*., 1995; Oberbauer *et al*., 1998) avoid the artifacts of an enclosure, but may induce drying at the soil surface (Shaver *et al*., 2000). Manipulations that warm plots from above have difficulty achieving realistic soil warming since the affected plot size is small and water movement can transfer heat laterally rather than warming soil in the plot. Soil heating cables or panels apply heat directly to the soil, but have artifacts such as soil drying that limit downward conduction of heat (Van Cleve *et al*., 1990; Oberbauer *et al*., 1998; Shaver *et al*., 2000) and often do not include air warming.

Here, we describe a new warming experiment, the Carbon in Permafrost Experimental Heating Research (CiPEHR) project, established in September 2008 at a moist acidic tundra site in Interior Alaska near Denali National Park. The goal of CiPEHR is to examine the effects of air, soil and surface permafrost warming on C dynamics in tundra ecosystems. We have combined ITEX-style OTCs to increase summer air and surface soil temperatures (Henry & Molau, 1997; Marion *et al*., 1997; Walker *et al*., 2006) with snow fences coupled with spring snow removal to warm surface and deep soil temperatures in winter. Long-term snow fences at Barrow and Toolik Lake, Alaska have significantly raised surface and deep soil temperatures in the wintertime (Jones *et al*., 1998; Walker *et al*., 1999; Schimel *et al*., 2004; Welker *et al*., 2005; Hinkel & Hurd, 2006), and in some cases caused local ground subsidence from permafrost thawing (Hinkel & Hurd, 2006). However, snow fences may also alter surface hydrology and have an offsetting temperature effect as the persistent snow pack delays summer warming (Scott & Rouse, 1995; Hinkel & Hurd, 2006; Nobrega & Grogan, 2007). To ensure that water input and timing of snowmelt were similar in warming and control plots, we removed the accumulated snow from the snow fences in early spring. Snow fences and snow removal have been applied separately in many different studies (e.g., Walker *et al*., 1993, 1999; Brooks *et al*., 1995; Galen & Stanton, 1995; Jones *et al*., 1998; Groffman *et al*., 2001; Decker *et al*., 2003; Mellander *et al*., 2004; Chimner & Welker, 2005; Aerts *et al*., 2006; Nobrega & Grogan, 2007), but CiPEHR combines these approaches to warm surface and deep soil and degrade permafrost without delaying spring thaw or increasing water inputs. This coupled approach offers an energy-efficient method to achieve the type of whole ecosystem warming that might be expected as a consequence of climate change.

Using this unique experimental approach, we seek to answer the following questions: (1) Does ecosystem warming cause a net release of C from the ecosystem to the atmosphere?, (2) Does the decomposition of old C that comprises the bulk of the soil C pool influence ecosystem C loss?, and (3) How do winter and summer warming alone, and in combination, affect ecosystem C exchange? We expected that plant C uptake would increase with warming, primarily as a result of increased soil nitrogen (N) availability as well as from a direct temperature effect; that warming would increase heterotrophic respiration more than photosynthetic C uptake by plants, resulting in a net release of C by the ecosystem to the atmosphere; and that there would be an increase in respiration from old C with deep-soil warming. Here, we show data from the first year of warming at CiPEHR that address these questions.

Materials and methods

Site description

The CiPEHR project is located in the northern foothills of the Alaska Range near Denali National Park and Preserve (63°52′59″N, 149°13′32″W) in the region of Eight Mile Lake (EML), Alaska (Schuur *et al*., 2007, 2009). The site is situated in moist acidic tundra at an elevation of 700 m on a relatively well-drained gentle northeast-facing slope. Soils are classified in the soil order Gelisol and are comprised of an organic horizon, 0.45–0.65 m thick, above a cryoturbated mineral soil that is a mixture of glacial till and windblown loess; active layer depth is ~50 cm. Mean monthly temperatures range from −16 °C in December to +15 °C in July, with a mean annual temperature (1976–2009) of −1.0 °C. Average annual precipitation is 378 mm. The experimental site lies within the area of discontinuous permafrost in a location where permafrost thaw and thermokarst have been occurring over the past several decades. In the EML region, permafrost temperatures have been monitored in a 30 m deep borehole since 1985 (Osterkamp & Romanovsky, 1999; Osterkamp *et al*., 2009), and ecosystem C fluxes and isotopes have been monitored since 2004 (Schuur *et al*., 2007, 2009; Vogel *et al*., 2009; Lee *et al*., 2010).

Vegetation at the site is dominated by the tussock-forming sedge, *Eriophorum vaginatum*, and deciduous shrub, *Vaccinium uliginosum*. Other common vascular plants include: *Carex bigelowii, Betula nana, Rubus chamaemorus, Empetrum nigrum, Rhododendron subarcticum, Vaccinium vitis-idaea, Andromeda polifolia* and *Oxycoccus microcarpus*. Nonvascular plant cover is dominated by feather moss (primarily *Pleurozium schreberi*) and *Sphagnum* species, as well as several lichen species (primarily *Cladonia* spp.). Species composition in this area has been observed to be shifting from graminoid- to shrub-dominated tundra with permafrost thaw and thermokarst (Schuur *et al*., 2007).

Experimental design

The CiPEHR project was designed to passively increase winter and summer temperatures, alone and in combination, to achieve air, soil and permafrost warming. Previous warming studies have shown that summer warming with OTCs would mainly heat the air and possibly the surface soil. We hypothesized that winter warming would warm the soil and permafrost surface, which more realistically simulates the effects of a warmer climate on permafrost ecosystems. The winter warming treatment was achieved by installing snow fences that captured an insulating layer of snow, coupled with spring removal of the excess snow. Six replicate snow fences were constructed and arranged in three blocks; fences within a block were separated by 5 m, and the blocks were approximately 100 m apart. The six 1.5 m tall × 8 m long snow fences were situated perpendicular to the dominant south-easterly winter winds so that snow carried by the wind was deposited on the leeward side of the fences (Fig. 1a, b). Winter warming plots were located in a footprint that extended 5 m back from the leeward side of the fence where the snowpack was of constant height; winter warming control plots were located 8–14 m upwind from the windward side of the fence to avoid the influence of the fences. Mean snow depth in March 2009 was 135 ± 1 cm in the winter warming plots and 38 ± 3 cm in the control plots (Fig. 1b). Snow was removed from the winter warming plots before snowmelt in early spring (March 8–15), which ensured comparable melt out dates across treatment plots; all plots were snow-free by April 30. Snow fences were

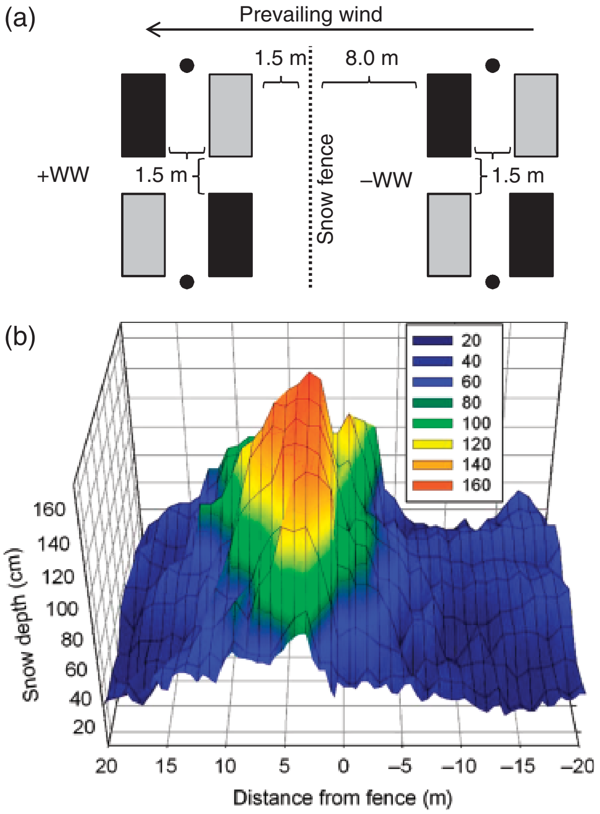

Fig. 1 Experimental design showing (a) treatment plots and (b) snow accumulation at one snow fence replicate ($n = 6$). (a) Two replicated summer warming (black-filled rectangles) and control plots (gray-filled rectangles) were located within each winter warming (+WW) and winter warming control (−WW) treatment. Black circles represent water well locations. (b) Snowpack on the leeward side of the fence (+WW) was 3.5 times deeper than control (−WW), causing a 50% increase in wintertime soil temperature.

taken down at the time of snow removal to avoid shading of the experimental plots during the growing season (May through September).

Summer warming was achieved using $0.36\,\mathrm{m}^2 \times 0.5\,\mathrm{m}$ tall OTCs, constructed of 0.6 cm thick clear polycarbonate and designed to interface with our automated CO_2 flux system. Chambers were mounted on 12 cm tall bases, which were inserted into the soil organic layer with 5 cm extending above the soil surface. Each winter warming treatment area contained two summer warming plots with OTCs and two control plots (Fig. 1a). Each plot consisted of three chamber bases; within each group of bases, one base was dedicated to CO_2 flux measurements, one to non-destructive sampling (resin bags, decomposition bags, ecosystem and soil $\Delta^{14}CO_2$), and one to destructive sampling. Summer warming chambers were set out during the snow-free period, which extended from May 2 through September 22, 2009. Warming treatment plots will hereafter be referred to as follows: Ambient (no warming), Winter (winter warming only), Summer (summer warming only), Annual (both summer and winter warming).

Environmental/climate monitoring

An Onset HOBO (Bourne, MA, USA) weather station, located approximately 100 m from the experimental plots, was used to measure air temperature, photosynthetically active radiation (PAR), relative humidity (RH), rainfall, air pressure, and wind speed and direction at 15 second intervals. Air temperature during the 2009 growing season (9.7 °C) was slightly lower than both 5- (10.6 °C) and 30-year means (12.3 °C). Precipitation during the 2009 growing season was 178.2 mm, which is less than half the long-term mean.

Campbell Scientific (Logan, UT, USA) CR1000 data loggers recorded half-hourly soil temperature and moisture content since September 2008. Soil profile temperatures (5, 10, 20 and 40 cm) were measured using constantan-copper thermocouples. One 5 cm thermocouple was located in each CO_2 flux plot; the remainder were located outside the flux plots but within the winter warming and control footprints. Gravimetric water content (GWC; hereafter referred to as surface soil moisture) was estimated in each flux plot using site-calibrated DC half-bridge resistance measurements (Borken *et al*., 2003; Vogel *et al*., 2009). In May, we only examined winter warming effects on surface soil moisture because half-bridge sensors were located outside the flux plots but within the winter warming and control footprints; half-bridge sensors were moved inside the flux plots in June, at which point we examined both winter and summer warming effects. Volumetric water content (VWC; hereafter referred to as depth-integrated soil moisture) was measured from the soil surface to 15 cm depth using site-calibrated Campbell CS616 water content reflectometer probes (two per winter warming treatment).

Water table depth (WTD) in relation to the soil surface was measured three times per week throughout the snow-free period in water wells that were installed at each fence in May 2009 (two wells per winter warming treatment; Fig. 1a). Wells (10 cm ID) extended from the surface down to between 0.6 and 1.0 m into the soil profile and permafrost. Water table depth was manually measured as in Vogel *et al*. (2009). Thaw depth (TD; the thickness of unfrozen ground during the growing season) was measured weekly around the outside perimeter of each flux base using a metal depth probe. Monthly TD measurements were also taken inside the bases to determine potential summer warming effects on TD.

Ecosystem CO_2 balance

Net ecosystem exchange (NEE) and ecosystem respiration (R_{eco}) were measured using three automated CO_2 flux systems, each of which controlled eight flux chambers located within one experimental block (i.e., two snow fences). Automated flux chambers were rotated biweekly among replicate summer warming treatments at each fence. Autochamber measurements were supplemented with static chamber measurements in late spring (2–3 times per week), before the establishment of the automated system at all blocks. In late-March and April, CO_2 fluxes were measured weekly in snow pits dug to the soil surface, as in Vogel *et al*. (2009).

For all static and autochamber measurements, air was circulated between the chamber and an infrared gas analyzer (LI-820, LICOR Corp., Lincoln, NE, USA) at $1\,\mathrm{L\,min^{-1}}$ for 1.5 min, and the CO_2 concentration was measured at 2 s intervals. For the automated system, the LI-820 data were recorded to a Campbell Scientific CR1000 data logger. For the static measurements, CO_2 concentrations were recorded to a Palm (Sunnyvale, CA, USA) Tungsten C portable computing device using the software program Online (Conklin Systems, Eaton Rapids, MI, USA). Automated measurements were taken at each flux chamber every 1.6 h. In each flux chamber, two small fans mixed the chamber air, while chamber air temperature was monitored with a thermistor and chamber RH was monitored with a HOBO RH logger. An empirical correction factor (19% reduction) was developed for the weather station PAR measurements to account for the effect of reduced light transmission through the chamber walls and light interception by the chamber support structures. For the autochamber system, R_{eco} was determined only with night measurements ($\mathrm{PAR} < 5\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$); for the static chamber, R_{eco} was measured during the day by covering the flux chamber with an opaque cloth. Gross primary productivity (GPP) was estimated as the sum of NEE and R_{eco}.

Automated flux measurements were filtered to remove estimates that may have been biased by environmental conditions (Bubier *et al*., 1998). Measurements that occurred during rain events or when wind speeds exceeded $>7\,\mathrm{m\,s^{-1}}$ were removed because the fluxes were generally erratic. Data filtering removed approximately 5% of measurements.

C balance during the growing season was estimated by gap-filling flux measurements using response functions to environmental factors. NEE was modelled using a hyperbolic equation that described the relationship between NEE and PAR (Thornley & Johnson, 1990). For R_{eco}, we used the night-time autochamber measurements along with 'dark chamber' static measurements to develop exponential relationships between R_{eco} and soil temperature. Equations were developed for each flux chamber base on a monthly (NEE) or seasonal basis (R_{eco}).

A total of 31 323 individual NEE and R_{eco} measurements were used to estimate integrated growing season CO_2 flux. To model wintertime R_{eco}, we used an exponential R_{eco}-soil temperature equation developed from winter flux data collected within the EML watershed [R_{eco} ($< -2\,°C$) $= 0.23 \times \exp^{(0.1 \times \text{soil temp})}$, R_{eco} (-2 to $0.5\,°C$) $= 0.55\,\text{umol CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$; Vogel *et al.*, 2009]. During the months of March and April of 2009, when winter flux measurements were collected at CiPEHR, the model parameters were derived from CiPEHR measured values. Wintertime CO_2 fluxes were statistically analyzed for winter warming effects only, since the summer warming treatment did not begin until May 2009. While not compared statistically, yearlong CO_2 balance for Summer treatment was determined by applying Ambient wintertime flux estimates, and yearlong CO_2 balance for Annual treatment was determined by applying wintertime flux estimates for the winter warming treatment.

Soil and ecosystem respiration $\Delta^{14}CO_2$

The effect of warming on the age and sources of respired CO_2 was determined by $\Delta^{14}C$ analysis of soil profile and ecosystem respiration. Respiration $\Delta^{14}C$ values reflect contributions from decomposition of old C, which has negative $\Delta^{14}C$ values (i.e., before 1950's bomb testing), decomposition of decadal-aged C with $\Delta^{14}C$ values higher than atmospheric (i.e., postbomb C), and autotrophic respiration with $\Delta^{14}C$ values at, or slightly higher than atmospheric ($\sim$ 45‰ in 2009) due to respiration of recently fixed C.

Soil pore space $\Delta^{14}CO_2$ (hereafter referred to as soil profile $\Delta^{14}CO_2$), $\delta^{13}CO_2$, and CO_2 concentrations (five to six per treatment) were measured from gas samples collected during the last week of September 2009 from permanently installed soil gas wells located in each plot at 10 cm depth. The gas wells were made of stainless steel tubing (1/8″ ID), which was perforated and covered with mesh at the bottom and extended aboveground 10 cm to fittings with gas-tight stopcocks. Air was pumped from each gas well at $1.0\,\text{L min}^{-1}$ for 1.5 min through a 13X molecular sieve to quantitatively trap CO_2.

Ecosystem respiration $\Delta^{14}CO_2$ (three per treatment) was measured at permanently installed 25-cm-diameter PVC collars, which extended 8 cm into the soil profile. To collect samples, a 10 L chamber was fit to each collar, and atmospheric CO_2 was scrubbed from the chamber by pumping chamber air through soda lime for 45 min while maintaining pCO_2 at $\sim$380 ppm to maintain ambient concentrations. Chamber air was then pumped through a molecular sieve trap for 15 min.

In the laboratory, the molecular sieve traps were heated to 625 °C to desorb CO_2 (Bauer *et al.*, 1992). Carbon dioxide was then purified and analyzed for $\delta^{13}C$ and $\Delta^{14}C$. Graphitized samples were sent to UC Irvine W.M. Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory for $\Delta^{14}C$ analysis, and $\delta^{13}C$ was analyzed on a ThermoFinnigan continuous flow isotope ratio mass spectrometer at the University of Florida. The $^{13}C/^{12}C$ isotopic ratios measured on the traps were used to correct for atmospheric air in the gas wells and respiration chambers. Radiocarbon sampling only occurred under calm wind conditions to minimize atmospheric CO_2 intrusion.

Plant processes

To assess warming effects on plant nutrient status, leaves were collected during the last week of July 2009 for total C and N and stable isotope analysis. Nitrogen isotopes were measured to detect changes in N availability or sources to plants (Högberg, 1997), and C isotope abundance was measured to provide information about plant water status (Farquhar *et al.*, 1989). We collected fully formed green leaves from the current year's growth from six vascular plants that were found across plots (*B. nana, C. bigelowii, E. vaginatum, R. subarcticum, R. chamaemorus,* and *V. uliginosum).* We collected a minimum of three leaves from two to three individuals in each plot. Leaves were dried at 60 °C, finely ground, and analyzed on a ThermoFinnigan continuous flow isotope ratio mass spectrometer coupled to a Costech elemental analyzer. Stable isotope abundances are reported as: $\delta^{15}N$ or $\delta^{13}C = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$, where $R = {}^{15}N/{}^{14}N$ or $^{13}C/^{12}C$ of the sample and reference standard (atmospheric N_2 and PeeDee belemnite-C).

Soil processes

The effect of warming on soil nutrient availability was assessed using ion exchange resin bags (Giblin *et al.*, 1994). Separate anion (Biorad, AG 1-X8, 20–50 mesh) and cation (Biorad, AG 50W-X8, 20–50 mesh) exchange bags (3 g wet weight of resin per bag) were deployed from May 25 through September 16, 2009. One cation and one anion bag were placed in each non-destructive sampling plot at 10 cm depth. Upon removal, resin bags were extracted for one hour in 100 mL of 0.1 M HCl/2.0 M NaCl solution and analyzed for NH_4^+ and NO_3^- on an Astoria Analyzer (Astoria-Pacific Int., Clackamas, OR, USA). Resin extracts are reported as g NO_3^--N or NH_4^+-N g wet-weight-resin^{-1} day^{-1}.

Warming effects on decomposition were estimated using cellulose decomposition bags, which were comprised of four 7.5×5.0 cm pieces of Whatman P8 cellulose filter paper (Whatman, Piscataway, NJ, USA) arranged two-by-two and sealed in 21.0×13.5 cm fiberglass mesh. In September 2008, bags were inserted into 0–20 cm soil depth in all winter warming and control plots. In mid-September 2009, decomposition bags were removed from the soil, and percent mass loss was determined on room-temperature dried cellulose paper. Annual decomposition rates were determined for winter warming treatments at 0–10 and 10–20 cm depth intervals; mass loss of cellulose pairs within a depth interval were averaged before statistical analyses.

Statistical analyses

Data were analyzed with a mixed linear model analysis of variance (ANOVA; SAS 9.0) using a blocked split-plot design with winter warming (WW) as the main plot factor, summer warming (SW) as the within plot factor, and fence (random and nested in block, also random) as the experimental unit for WW. For soil temperature and decomposition data, depth was included as an additional fixed within plot factor. A significant WW effect refers to an effect of WW across SW plots, and similarly, a significant SW effect refers to SW differences across WW plots. A warming effect in any single one of the four treatments (e.g., Summer only) would be detected by a SW × WW interaction. We use the treatment abbreviations, SW and WW, in reporting statistical results only.

To examine changes over the growing season, response variables were analyzed among months with repeated measures ANOVA using PROC MIXED. We also summed the monthly flux estimates and analyzed cumulative growing season fluxes. We refer to results of the repeated measures analysis as monthly flux estimates to differentiate from cumulative growing season fluxes. We used a one-sample *t*-test (compared against neutral = 0) to determine whether treatment plots were a net C sink or source during the growing season. Family-wise error rates ($\alpha = 0.05$) were controlled using the Hochberg method for planned contrasts or Tukey's method for all pair-wise comparisons. Data were transformed when necessary to meet assumptions of ANOVA. All errors presented are one standard error of the mean.

Results

Environmental effects of experimental warming

Winter warming increased soil temperatures at all depths ($F = 139.18$, $P < 0.01$), with significantly higher monthly temperatures from December 2008 through April 2009 (WW × month: $F = 16.28$, $P_{\mathrm{adj}} < 0.01$ for each month; Fig. 2a, b). Mean soil temperature in the warmed plots during the winter and early spring (December–April) was 1.6 ± 0.3 °C higher, with the greatest difference during the month of March (2.9 ± 0.4 °C). In the WW plots, soil temperatures never dropped lower than −10 °C, while in the control plots, temperatures at both 5 and 10 cm depths dropped to −18 °C and −12 °C, respectively. As expected, soil temperatures differed among depths ($F = 239.12$, $P < 0.01$) and months ($F = 185.73$, $P < 0.01$; Fig. 2a, b).

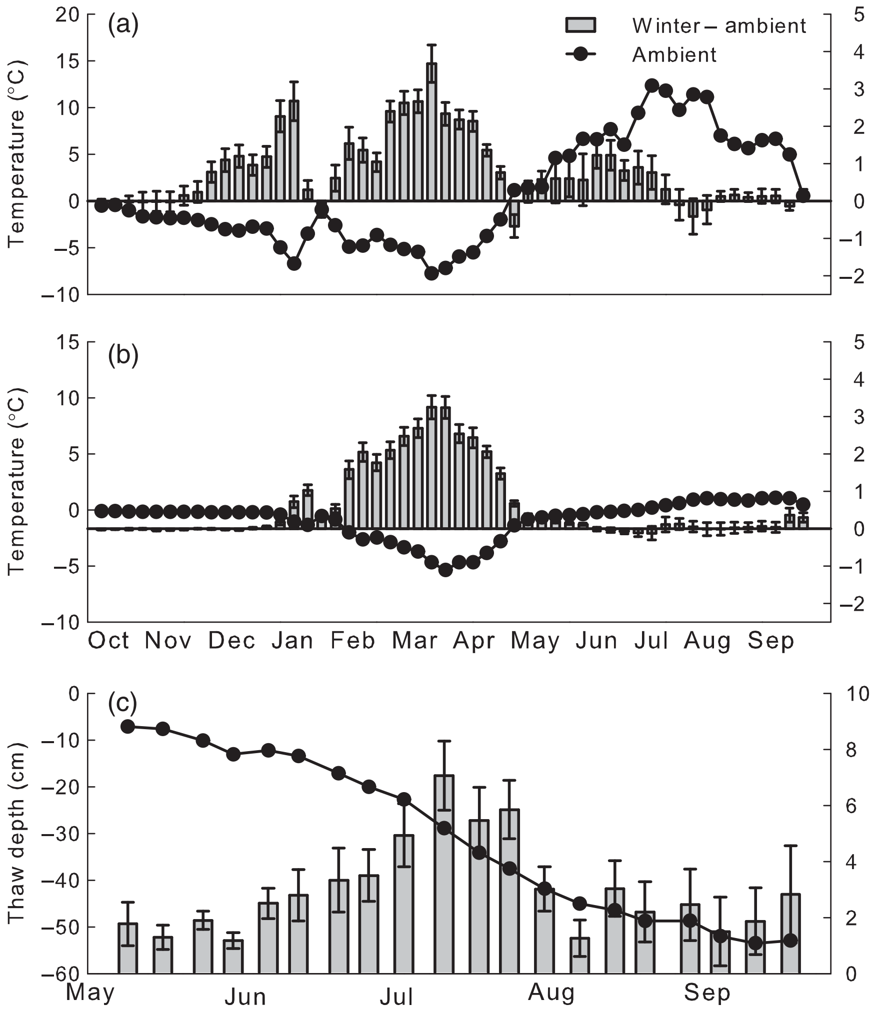

Fig. 2 Winter warming effects on soil temperatures at (a) 5 cm and (b) 40 cm depths, and (c) growing season thaw depths (TD). Black circles represent Ambient temperature and TD, and gray bars represent the difference in temperature or TD between Winter and Ambient plots (Winter–Ambient). Soil temperatures represent weekly means of half-hourly soil data.

While WW affected soil temperatures primarily in winter and early spring, TD, which is an integrated measure of soil heat content, increased with WW throughout the 2009 growing season ($F = 19.88$, $P < 0.01$; Fig. 2c). Mean monthly TD was significantly greater in the WW plots during all growing season months ($P_{\mathrm{adj}} < 0.05$ for all months except May when $P_{\mathrm{adj}} = 0.06$), with an average increased TD of 3.0 ± 0.9 cm in the WW plots. There was no detected SW effect on TD ($F = 1.77$, $P = 0.19$).

As expected, SW increased mean growing season air temperature (+ 0.3 °C; $F = 23.74$, $P < 0.01$), as well as average daily maximum (+ 0.4 °C; $F = 42.70$, $P < 0.01$) and minimum (+ 0.2 °C; $F = 4.21$, $P = 0.04$) air temperatures. There were no detected SW effects on daily mean, maximum or minimum relative air humidity ($P > 0.10$ for all) or growing season soil temperatures ($F = 1.12$, $P = 0.29$).

Surface soil moisture increased with WW ($F = 14.72$, $P < 0.01$), but there also was a significant WW × SW effect ($F = 6.69$, $P = 0.01$). In the Winter plots, surface water content (13.5 ± 1.4 g water g soil dry weight^{-1}) was significantly greater than in Ambient ($7.1 \pm 1.0\,\mathrm{g\,g^{-1}}$), Summer ($7.0 \pm 0.7\,\mathrm{g\,g^{-1}}$), and surprisingly, the Annual plots ($8.3 \pm 1.0\,\mathrm{g\,g^{-1}}$; $P_{\mathrm{adj}} < 0.01$ for all comparisons). There was no detected difference in surface moisture ($F = 0.36$, $P = 0.564$) in the month of May between WW ($7.8 \pm 0.7\,\mathrm{g\,g^{-1}}$) and control plots ($7.2 \pm 0.7\,\mathrm{g\,g^{-1}}$; Fig. 3a). Growing season depth-integrated soil moisture (0–15 cm) was also slightly higher with WW ($41.4 \pm 0.6\%$) compared with control plots ($39.0 \pm 0.6\%$; $F = 3.26$, $P = 0.08$); there was a significant WW × month interaction ($F = 2.83$, $P = 0.03$), with marginally significant higher moisture at the end of the growing season in September ($F = 6.12$, $P_{\mathrm{adj}} = 0.08$; Fig. 3b). We also found unexpected differences in WTD in the latter part of the growing season (WW × month, $F = 8.37$, $P < 0.01$; Fig. 3c). In August and September, water table in the WW plots was 3.5 cm closer to surface compared with control (26.3 ± 1.8 cm), with marginally significant monthly WTD differences during the month of August ($F = 3.02$, $P = 0.09$).

There were no significant pretreatment differences (measured in September 2008) in soil temperature, TD, or soil moisture across the study area ($P > 0.10$ for all).

Ecosystem CO_2 balance

Ecosystem CO_2 fluxes responded significantly to the altered environmental conditions in the warming treatments. Summer warming significantly increased GPP ($F = 41.44$, $P < 0.01$), with an average monthly increase

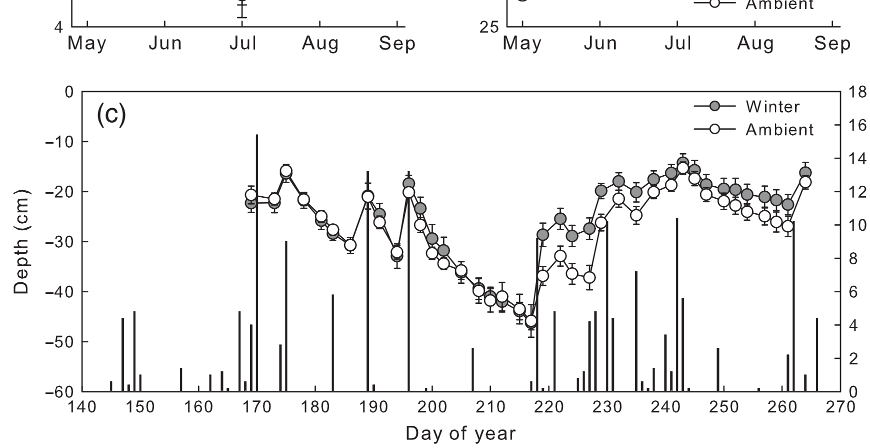

Fig. 3 Growing season variation and experimental warming effects on (a) monthly surface water content (GWC; 0–5 cm), (b) depth-integrated water content (VWC; 0–15 cm) and (c) daily precipitation (bars) and water table depth (circles) at CiPEHR in 2009.

of 20% relative to SW control plots during the growing season. Despite this observed increase in gross CO_2 uptake, there was no detected effect of SW on NEE ($F = 1.02$, $P = 0.32$) because R_{eco} also increased with SW ($F = 36.59$, $P < 0.01$), offsetting the additional CO_2 fixed through photosynthetic activity (Fig. 4). Unlike these SW effects, WW did not affect GPP ($F = 0.20$, $P = 0.66$), but did in fact cause a slight increase in growing season R_{eco} across months ($F = 4.34$, $P = 0.04$), resulting in significantly lower monthly NEE during the growing season ($F = 4.44$, $P = 0.04$; Fig. 4). All growing season CO_2 flux estimates were significantly different among months (month effect, $P < 0.01$ for all), and there were no significant warming treatment interactions ($P > 0.10$ for all).

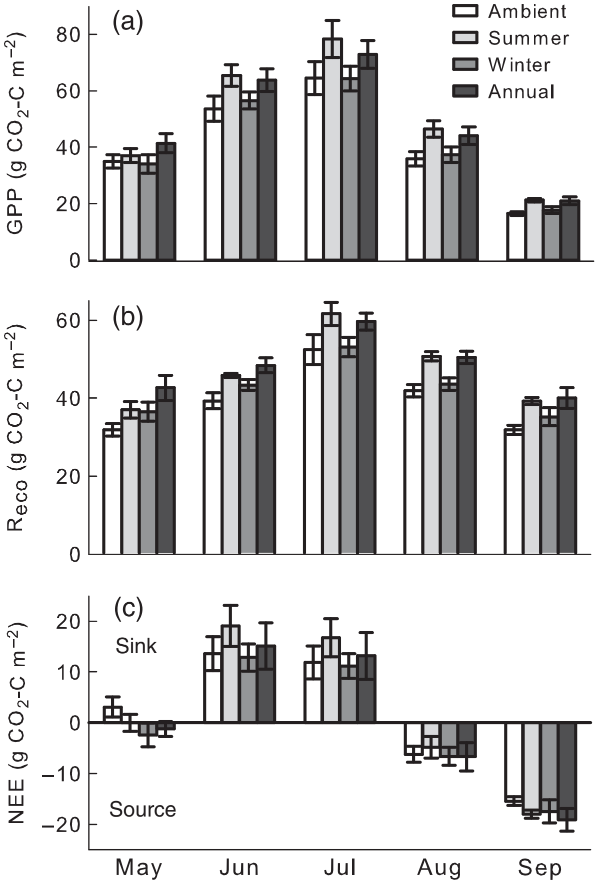

Fig. 4 Warming effects on mean monthly (a) GPP, (b) R_{eco}, and (c) NEE during the 2009 growing season.

As with the monthly flux estimates, SW significantly increased cumulative growing season GPP ($F = 11.72$, $P < 0.01$) and R_{eco} ($F = 11.09$, $P < 0.01$), but there was no SW effect on cumulative NEE ($F = 0.65$, $P = 0.42$; Fig. 5). While WW had a significant effect on monthly CO_2 fluxes (repeated measured ANOVA), there were no detected effect on cumulative growing season GPP, R_{eco}, or NEE ($P > 0.10$ for all; Fig. 5), and there was no detected SW × WW interaction effect. Cumulative growing season CO_2 uptake was greatest in Summer plots (12.9 g CO_2-C m^{-2}), followed by Ambient (6.9 g CO_2-C m^{-2}) and Annual (2.4 g CO_2-C m^{-2}) plots. In Winter plots, there was a net loss of CO_2 from the ecosystem to the atmosphere during the 2009 growing season (−2.5 g CO_2-C m^{-2}). However, none of the growing season NEE estimates were significantly different than zero ($P > 0.10$ for all).

While cumulative growing season fluxes did not vary significantly across warming treatments, significant warming effects on winter-season R_{eco} (Ambient = 76 g CO_2-C m^{-2}, WW = 119 g CO_2-C m^{-2}; $F = 96.97$, $P < 0.01$) resulted in a two-fold increase in the annual CO_2 loss to

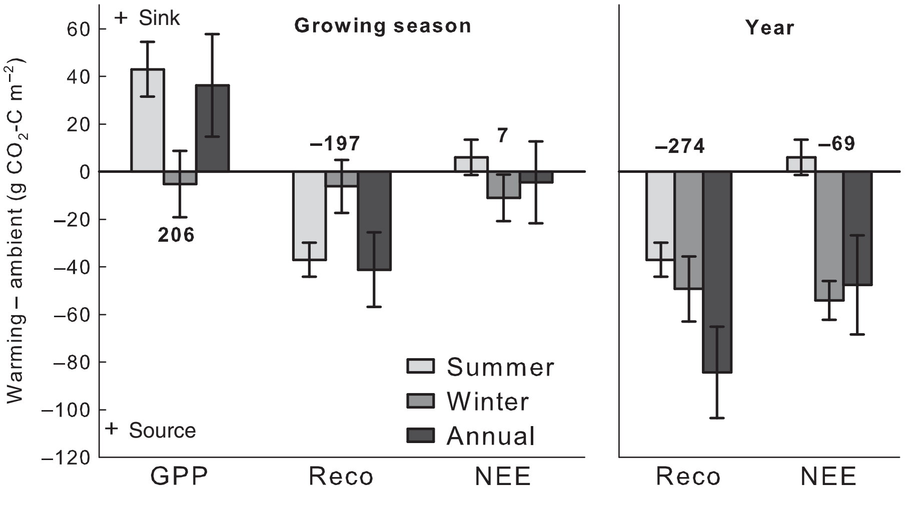

Fig. 5 Warming effects on cumulative growing season and yearlong CO_2 fluxes. Bars represent flux differences between warming and Ambient plots; bars above the zero line represent increased CO_2 uptake with warming and below represent increased CO_2 loss. Numbers above/below the zero-line are Ambient CO_2 flux values (g CO_2-C m^{-2}); negative values represent net CO_2 loss from the ecosystem.

the atmosphere (NEE: Ambient = 69 g CO_2-C m^{-2} yr^{-1}, WW = 123 g CO_2-C m^{-2} yr^{-1}; $F = 29.47$, $P < 0.01$; Fig. 5). The relative contribution of wintertime R_{eco} to annual R_{eco} (Ambient R_{eco} = 274 g CO_2-C m^{-2} yr^{-1}; WW R_{eco} = 323 g CO_2-C m^{-2} yr^{-1}) increased from 28% in Ambient plots to 37% in the WW plots. While these wintertime estimates are modelled from observed differences in soil temperature, the magnitude of the warming effect on winter-season R_{eco} was similar to direct flux-rate treatment differences measured in March and April, when mean R_{eco} was more than double in the WW plots (0.72 ± 0.11 μmol CO_2 m^{-2} s^{-1}) relative to control (0.30 ± 0.11 μmol CO_2 m^{-2} s^{-1}; $F = 8.54$, $P = 0.03$).

Soil and ecosystem respiration $\Delta^{14}CO_2$

The relative contributions of plant and soil sources to R_{eco}, as measured with $\Delta^{14}C$, were consistent with observed changes in CO_2 fluxes. Soil profile $\Delta^{14}CO_2$ values in all treatment plots were below atmospheric, reflecting respiration of old C pools (i.e., before 1950's bomb testing). The $\Delta^{14}CO_2$ values from the soil profile was approximately 13‰ lower with summer warming (6.5 ± 2.7‰) compared with control (20.0 ± 2.13‰; $F = 39.84$, $P < 0.01$). There was no detected WW or SW × WW interaction effect on soil profile $\Delta^{14}CO_2$ ($P > 0.10$; Fig. 6). Across treatments, total ecosystem respiration $\Delta^{14}CO_2$ values generally increased from late June to September, which was opposite our expectation. One exception was the Annual plots, which had similar $\Delta^{14}CO_2$ values in both months (WW × SW × month: $F = 21.90$, $P = 0.01$; Fig. 6). In June, Summer R_{eco} $\Delta^{14}C$ was lower than in all other treatments and significantly different than both Annual and Control plots; while in September, Annual R_{eco} $\Delta^{14}C$ was lower than all plots, with a significant difference between Annual and Winter plots ($P < 0.05$ for all).

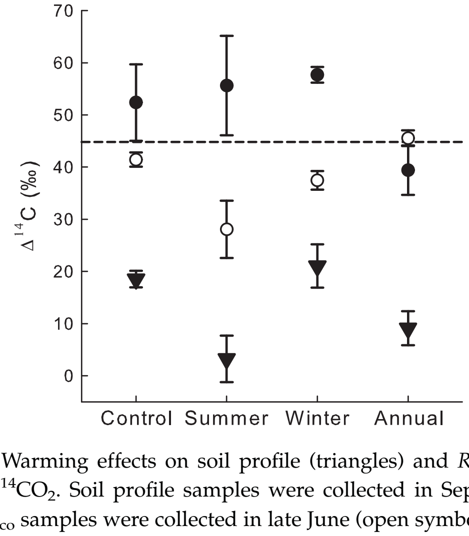

Fig. 6 Warming effects on soil profile (triangles) and R_{eco} (circles) $\Delta^{14}CO_2$. Soil profile samples were collected in September and R_{eco} samples were collected in late June (open symbols) and September (filled symbols). Dotted line represents atmospheric $\Delta^{14}CO_2$.

Plant processes

As expected, foliar N, C, C:N, $\delta^{13}C$ and $\delta^{15}N$ were all significantly different among species ($P < 0.01$ for all variables), reflecting differences in growth form and mycorrhizal status. As with growing season fluxes, plant nutrient status was also affected by summer warming treatment. There were no detected warming effects on foliar C or N concentrations alone; however, there was a significant SW effect on foliar C:N ($F = 3.77$, $P = 0.05$). There was a general trend of increased C:N with SW in most species, with a significant difference detected in *B. nana* and a marginally significant difference in *R. subarcticum* (Table 1). There was a significant SW × species interaction effect on foliar $\delta^{13}C$ ($F = 2.77$, $P = 0.02$), with a slight but significant increase in *B. nana* $\delta^{13}C$ in the SW plots (Table 1). There was also a significant SW × species effects on $\delta^{15}N$ ($F = 2.24$, $P = 0.05$); *R. subarcticum* $\delta^{15}N$ was significantly lower, and *V. uliginosum* $\delta^{15}N$ showed a marginally significant increase with SW (Table 1).

Soil processes

Warming-mediated changes in soils were consistent with other observations of ecosystem dynamics at CiPEHR. Changes in soil N availability may have contributed to the observed changes in foliar element and isotope values. While there was no detected warming effect on total inorganic N (sum of NO_3^- and NH_4^+; $P > 0.10$), there was a significant increase in NO_3^- (control: 11.5 ± 2.0; SW: 19.3 ± 4.1; $P = 0.04$) and decrease in NH_4^+ (control: 35.6 ± 8.8, SW: 21.2 ± 4.1; $P = 0.09$) with SW. As with foliar chemistry, there was no detected effect of WW on inorganic soil N availability. In contrast to soil N, decomposition of a common substrate reflected changes in soil temperature with the WW treatment. Decomposition tended to be higher with WW (18.4 ± 3.5% mass loss) than control (13.5 ± 3.5% mass loss), although differences were not significant ($F = 7.34$, $P = 0.27$). This lack of significance, however, is not surprising since decomposition rates in tundra are low and this result reflects decomposition during a single year. As expected, decomposition was greater at 0–10 cm depth (18.6 ± 3.8% mass loss) than 10–20 cm (13.1 ± 2.9%; $F = 3.10$, $P = 0.09$) due to generally cooler conditions at depth.

Table 1 Foliar C, N, C:N, δ^{13}C and δ^{15}N from leaves collected at peak growing season in warming and control plots at CiPEHR

	CB	EV	BN	RS	RC	VU
C (%)						
Ambient	45.0 ± 0.3	45.7 ± 0.4	49.2 ± 0.3	52.7 ± 0.1	45.6 ± 0.5	49.1 ± 0.2
Summer	45.1 ± 0.3	45.7 ± 0.2	49.4 ± 0.4	52.4 ± 0.3	45.8 ± 0.4	49.2 ± 0.3
Winter	45.1 ± 0.3	45.5 ± 0.4	49.5 ± 0.2	51.9 ± 0.4	45.6 ± 0.3	49.2 ± 0.2
Annual	45.6 ± 0.2	45.3 ± 0.4	48.9 ± 0.3	51.8 ± 0.7	46.0 ± 0.3	49.3 ± 0.3
N (%)						
Ambient	2.1 ± 0.2	1.7 ± 0.1	2.2 ± 0.2	1.6 ± 0.1	2.4 ± 0.1	1.8 ± 0.1
Summer	2.2 ± 0.1	1.7 ± 0.1	2.1 ± 0.1	1.6 ± 0.2	2.3 ± 0.1	1.7 ± 0.1
Winter	2.1 ± 0.1	1.8 ± 0.1	2.3 ± 0.1	1.7 ± 0.1	2.2 ± 0.1	1.9 ± 0.1
Annual	2.1 ± 0.2	1.8 ± 0.1	1.8 ± 0.1	1.5 ± 0.2	2.4 ± 0.1	1.8 ± 0.1
C:N						
Ambient	21.5 ± 1.5	27.3 ± 2.3	23.3 ± 1.7**	34.2 ± 1.8*	19.4 ± 0.6	27.3 ± 1.6
Summer	20.4 ± 1.3	28.0 ± 1.9	24.4 ± 1.6	35.4 ± 3.7	20.4 ± 1.0	29.1 ± 2.0
Winter	21.3 ± 1.0	24.7 ± 0.4	22.0 ± 1.6	31.1 ± 1.4	21.0 ± 0.6	26.6 ± 1.3
Annual	22.6 ± 2.1	25.1 ± 1.5	27.5 ± 1.4	35.4 ± 3.6	19.5 ± 0.7	27.9 ± 1.4
δ^{13}C (‰)						
Ambient	−24.7 ± 0.3	−25.5 ± 0.4	−28.0 ± 0.4**	−26.5 ± 0.1	−27.0 ± 0.2	−29.3 ± 0.3
Summer	−25.1 ± 0.4	−25.4 ± 0.2	−27.5 ± 0.6	−26.6 ± 0.4	−26.8 ± 0.1	−29.6 ± 0.3
Winter	−25.1 ± 0.3	−25.9 ± 0.2	−28.4 ± 0.1	−26.2 ± 0.4	−27.1 ± 0.2	−29.7 ± 0.4
Annual	−24.3 ± 0.2	−25.4 ± 0.5	−26.8 ± 0.4	−27.3 ± 0.2	−27.1 ± 0.2	−29.4 ± 0.2
δ^{15}N (‰)						
Ambient	0.9 ± 0.3	1.3 ± 0.2	−7.6 ± 0.6	−7.3 ± 0.4**	−0.2 ± 0.2	−5.9 ± 0.2*
Summer	1.1 ± 0.3	1.2 ± 0.2	−7.3 ± 0.3	−8.3 ± 0.4	0.2 ± 0.1	−5.3 ± 0.2
Winter	0.9 ± 0.2	1.7 ± 0.2	−7.3 ± 0.6	−7.8 ± 0.3	0.5 ± 0.1	−5.8 ± 0.3
Annual	0.9 ± 0.2	1.4 ± 0.2	−8.3 ± 0.5	−8.2 ± 0.2	0.4 ± 0.2	−5.2 ± 0.2

There was no significant effect of winter warming; significant summer warming effects are denoted as *$P<0.10$, **$P<0.05$.
Species abbreviations are as follows: CB: *C. bigelowii;* EV: *E. vaginatum;* BN: *B. nana*; RS: *R. subarcticum;* RC: *R. chamaemorus*; VU: *V. uliginosum*

Discussion

Effectiveness of warming treatments

The warming achieved at CiPEHR simulates some future climate scenarios and is in line with changes that are already occurring in Alaska and across the Arctic region (Polyakov *et al*., 2002; Karl *et al*., 2009). By combining snow fences with spring snow removal, CiPEHR increased wintertime soil temperatures by 50% without delaying spring thaw or cooling soils in the early growing season (Fig. 2a, b), as has occurred at other snow addition experiments (Scott & Rouse, 1995; Walker *et al*., 1999; Hinkel & Hurd, 2006; Nobrega & Grogan, 2007). In addition to increasing surface and deep soil temperatures, winter warming resulted in a 10% increase in growing season TD, suggesting that we have initiated surface permafrost degradation (Fig. 2c). This increase in active layer depth may have transferred an additional $\sim$2 kg of C m^{-2} from surface permafrost to biologically available pools (based on 55–69 kg C m^{-2} to 1 m depth; C. Hicks, unpublished data).

One unexpected effect of warming was altered surface hydrology. Winter warming increased soil moisture and decreased WTD (i.e., raised the water table surface; Fig. 3) even though snow removal ensured similar snow-water equivalents across treatments. Soil moisture and WTD differences were not detected in the early growing season, which supports the idea that snowmelt inputs were comparable across treatments and that other warming-mediated effects (e.g., changes in the partitioning of the soil energy balance or local surface subsidence) may have indirectly caused these soil moisture trends. This surprising change in surface hydrology as a function of increased winter warming highlights the cascading effects of permafrost thaw on both temperature and moisture availability (Hinzman & Kane, 1992; Waelbroeck, 1993; Schuur *et al*., 2008).

While most of the changes in the abiotic environment at CiPEHR were driven by winter warming, increased air temperature in the summer warming plots had the strongest effects on individual plant and soil processes (Fig. 7). Given the absence of a summer warming effect

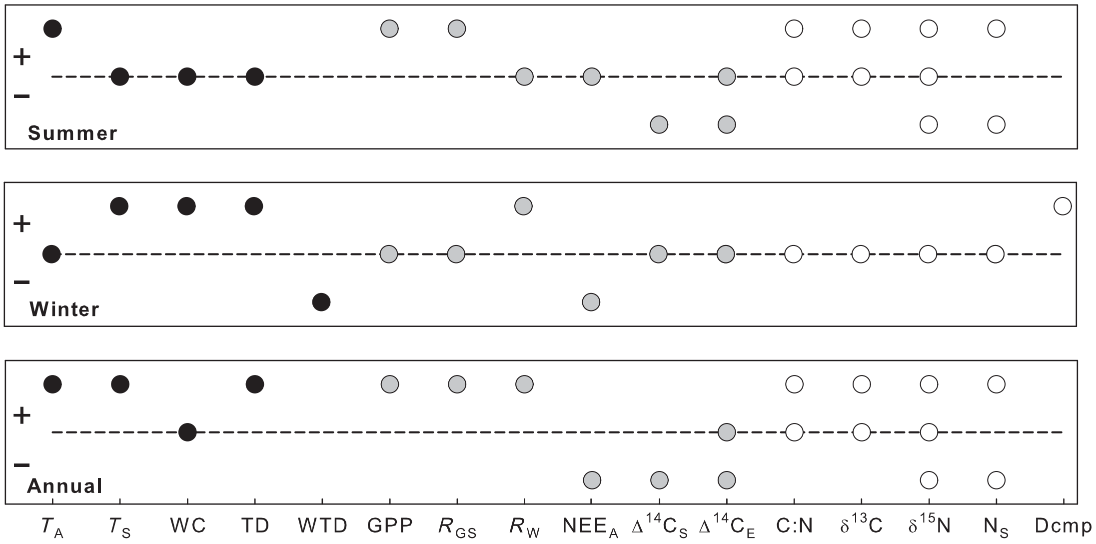

Fig. 7 Warming effects on environmental variables (black fill), CO_2 flux and $\Delta^{14}CO_2$ (gray fill), and plant and soil variables (white fill). Symbols above the dashed line represent an increase relative to Ambient, below a decrease; multiple symbols within a variable are presented when effects varied across plant species, sampling date or N-form. Missing symbols denote a variable that was not measured in one of the treatments. Variable abbreviations are as follows: air temperature (T_A), soil temperature (T_S), soil water content (WC), thaw depth (TD), water table depth (WTD), cumulative GPP (GPP), cumulative growing season R_{eco} (R_{GS}), wintertime R_{eco} (R_W), annual NEE (NEE_A), soil profile $\Delta^{14}CO_2$ ($\Delta^{14}C_S$), ecosystem $\Delta^{14}CO_2$ ($\Delta^{14}C_E$), foliar C:N (C:N), foliar $\delta^{13}C$ ($\delta^{13}C$), foliar $\delta^{15}N$ ($\delta^{15}N$), inorganic soil N (N_S), and decomposition (Dcmp).

on soil temperature, the observed changes in soil processes with summer warming (e.g., soil profile $\Delta^{14}C$ and soil N) may have been mediated by warming effects on plant dynamics; however, further research is needed to discern the mechanism of these effects. Both summer and winter warming contributed significantly to changes in ecosystem C dynamics, which are controlled by the net response of plants and the soil environment. The combined summer and winter warming effects (i.e., Annual) were often additive, but in some cases (e.g., R_{eco} $\Delta^{14}C$) Annual warming elicited a unique and surprising response that could not be predicted from the response of either summer or winter warming treatment alone.

Warming effects on CO_2 balance

Annual estimates of NEE at CiPEHR show that this upland tundra ecosystem was a significant net source of CO_2 to the atmosphere in this measurement year, and warming of soil and thawing the surface permafrost more than doubled CO_2 loss (Fig. 5). Warming effects on annual NEE were driven, in large part, by contributions from wintertime respiration. In contrast to the slight effect of winter warming on growing-season fluxes, winter warming increased CO_2 fluxes during the snow-covered period by more than 50%. Ambient wintertime fluxes at CiPEHR (76 g CO_2-C m^{-2}) fell within the range of reported values for tussock tundra (20–105 g CO_2-C m^{-2}; Oechel *et al.*, 1997; Fahnestock *et al.*, 1998, 1999; Oechel *et al.*, 2000; Welker *et al.*, 2000; Sullivan *et al.*, 2008; Vogel *et al.*, 2009), as did the relative warming effect on wintertime R_{eco} (Larsen *et al.*, 2007; Nobrega & Grogan, 2007). The magnitude of warming effects on wintertime R_{eco} were also supported by trends from our common substrate decomposition results, which showed an approximately 40% increase in mass loss during the first year of warming.

During the growing season, summer warming had the strongest treatment effect on CO_2 fluxes, with approximately 20% increases in both cumulative GPP and R_{eco} (Figs 5 and 6). Similar to previous warming studies, however, there was no detected summer warming effect on net growing season CO_2 flux (Hobbie & Chapin, 1998; Marchand *et al.*, 2004) as increases in both processes offset one another. We expected that GPP would increase with warming as a result of direct temperature effects or indirect effects of temperature on soil N availability (Chapin *et al.*, 1995). A direct temperature effect might be expected in the first treatment year, whereas soil N-cycle feedbacks may manifest more strongly after some time lag. The observed increase in foliar C:N (Table 1), coupled with the limited effect of warming on total inorganic soil N, may suggest that increased GPP was driven by direct effects of warming on plant growth. However, warming-mediated changes in *R. subarcticum* and *V. uliginosum* foliar δ^{15}N (Table 1) and changes in the relative availability of soil NO_3^- and NH_4^+ indicate shifts in soil N sources to plants have already begun, which in turn, may be contributing to changes in CO_2 uptake.

Species-level ecophysiological responses to summer warming, as detected by foliar δ^{13}C, also contributed to changes in CO_2 fluxes. Increased foliar δ^{13}C with summer warming, as observed in *B. nana*, indicates an increase in the rate of photosynthetic C fixation relative to CO_2 diffusion through stomata (Farquhar *et al.*, 1982, 1989). The lack of summer warming effects on RH and soil moisture (Fig. 3) and observed ecosystem-level increase in GPP (Figs 4 and 5) suggest the increase in *B. nana* δ^{13}C may have been driven by increased photosynthetic rates more so than decreased stomatal conductance. Increased *B. nana* foliar δ^{13}C, along with higher foliar C:N, suggests a positive effect of summer warming on C assimilation in this deciduous shrub, which agrees with other studies that have found an increase in *B. nana* biomass and abundance (Hobbie & Chapin, 1998) and earlier leaf expansion (Chapin & Shaver, 1996) with summer warming. These results also support area- (Schuur *et al.*, 2007) and region-wide (Sturm *et al.*, 2005) observations of increased shrub abundance associated with warming surface air temperatures across arctic Alaska.

In contrast to the strong summer warming effect on growing season fluxes, winter warming had no detected effect on cumulative growing season GPP or R_{eco} (Figs 4 and 5). These counterintuitive results suggest that the additional $\sim$2 kg thawed C m^{-2} at the bottom of the active layer in the winter warmed plots did not contribute significantly to growing season fluxes. While increased depth of thaw has been associated with the release of old C at both an adjacent natural permafrost thaw gradient (Schuur *et al.*, 2009) and at a snow accumulation study (Nowinski *et al.*, 2010), the higher water table in the CiPEHR winter warming treatment (Fig. 3c) may have reduced decomposition of the additional thawed deep soil C due to oxygen limitation at the base of the active layer. The potential importance of soil saturation (oxygen limitation) on SOM decomposition is supported by the positive correlation between R_{eco} and WTD (more respiration when water table is lower) at CiPEHR throughout the growing season ($R^2 = 0.33$, $P < 0.01$; data not shown). The influence of anaerobic conditions deep in the soil profile is also substantiated by nearby measurements of soil profile CO_2 (Lee *et al.*, 2010) and by above-ambient measurements of soil profile methane concentrations in an adjacent permafrost thaw gradient (C. Trucco, unpublished data), even though net methane emissions to the atmosphere at the soil surface are rare at that site (Schuur *et al.*, 2009). As observed at CiPEHR and across the Arctic region (Oberbauer *et al.*, 1991, 1992, 1998, 2007; Sommerkorn, 2008), both soil moisture and temperature are key regulators of soil CO_2 efflux from tundra ecosystems. Together, these results suggest that thawing of saturated soils may not cause an increase in growing season heterotrophic respiration because of anoxic conditions, but if soils are warmer *and* dryer there can be a significant transfer of C to the atmosphere.

Seasonal patterns of R_{eco} Δ^{14}C (Fig. 6) also suggest that oxygen limitation may have precluded decomposition of thawed C in the lower active layer. We expected R_{eco} Δ^{14}C to decline from peak biomass in late June to the end of the growing season in September due to reduced proportional contribution of plant respiration (which has Δ^{14}C values near atmospheric) to R_{eco}. We expected increased respiration of old soil C (which has negative Δ^{14}C values) as TD increased through the growing season; however, the unexpected increase in September R_{eco} Δ^{14}C suggests that waterlogged soils at the end of the growing season (Fig. 3b, c) may have inhibited respiration of old C across treatments. Surprisingly, among treatments, the oldest CO_2 was not respired from winter warmed plots with the deepest TD, but rather, it was summer warming that caused a significant decline in soil profile and June R_{eco} Δ^{14}C. This decrease in Δ^{14}C with summer warming may have been driven by a decline in decomposition of decadal-aged SOM (i.e., post-bomb C, which has Δ^{14}C higher than atmospheric) or an increase in decomposition of old C, as was found in a northern peatland in Sweden, where spring and summer warming caused a 50% increase in growing season R_{eco}, 70% of which was derived from deep active layer C (Dorrepaal *et al.*, 2009). Interestingly, Annual warming effects on R_{eco} Δ^{14}C were unique to this combined seasonal warming treatment (Fig. 6), highlighting potential interactions among abiotic and biological components of the ecosystem in response to seasonal temperature changes. While further research on respiration source partitioning is needed to fully discern which sources are driving changes in $\Delta^{14}CO_2$, it is clear that warming temperatures have altered the sources and age of CO_2 respired from this ecosystem.

These results demonstrate that plant and soil microbial communities were immediately responsive to the experimentally imposed increase in both air and soil temperatures, and that these changes had significant consequences for ecosystem C balance. Summer warming effects on biological processes increased growing season GPP and R_{eco}, while winter warming effects on the soil environment resulted in drastic changes in winter respiration and altered the overall annual C balance of this upland tundra ecosystem. Although northern tundra soils have been accumulating C in soils and permafrost throughout the Holocene (Marion & Oechel, 1993), there has been a recent shift in some tundra systems from C sinks to sources (Oechel *et al.*, 1993, 1995, 2000), as was found at CiPEHR. Warming of the surface and deep soil doubled the source strength of this ecosystem, demonstrating the strong potential for a significant loss of C from warming upland tundra ecosystems.

Acknowledgements

This work was made possible by assistance from D. DeRaps, J. Vogel, and the researchers and technicians of the Bonanza Creek LTER and of the Keck Carbon Cycle AMS Facility at University of California, Irvine. This work was funded by the NSF CAREER Program, NSF Bonanza Creek LTER Program, and the Department of Energy NICCR program.

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