Permafrost degradation stimulates carbon loss from experimentally warmed tundra

Susan M. Natali,[1,2,3] Edward A. G. Schuur,[2] Elizabeth E. Webb,[2] Caitlin E. Hicks Pries,[2] and Kathryn G. Crummer[2]

[1]*Woods Hole Research Center, 149 Woods Hole Road, Falmouth, Massachusetts 02540 USA*
[2]*Department of Biology, 220 Bartram Hall, University of Florida, Gainesville, Florida 32611 USA*

Abstract. A large pool of organic carbon (C) has been accumulating in the Arctic for thousands of years because cold and waterlogged conditions have protected soil organic material from microbial decomposition. As the climate warms this vast and frozen C pool is at risk of being thawed, decomposed, and released to the atmosphere as greenhouse gasses. At the same time, some C losses may be offset by warming-mediated increases in plant productivity. Plant and microbial responses to warming ultimately determine net C exchange from ecosystems, but the timing and magnitude of these responses remain uncertain. Here we show that experimental warming and permafrost (ground that remains below 0°C for two or more consecutive years) degradation led to a two-fold increase in net ecosystem C uptake during the growing season. However, warming also enhanced winter respiration, which entirely offset growing-season C gains. Winter C losses may be even higher in response to actual climate warming than to our experimental manipulations, and, in that scenario, could be expected to more than double overall net C losses from tundra to the atmosphere. Our results highlight the importance of winter processes in determining whether tundra acts as a C source or sink, and demonstrate the potential magnitude of C release from the permafrost zone that might be expected in a warmer climate.

Key words: Arctic tundra; carbon; climate change; Eight Mile Lake, Alaska, USA; net ecosystem exchange; permafrost.

Introduction

By the end of the 21st century, warming temperatures in the Arctic are projected to result in a 30–70% decline in surface permafrost extent, which will bring about profound changes in ecological communities and ecosystem C storage (Schaefer et al. 2011, Lawrence et al. 2012, Schuur et al. 2013). An increase in microbial decomposition as temperatures warm may place the large permafrost C pool at risk of being transferred to the atmosphere as greenhouse gasses, which will result in a significant positive feedback to global climate (Hobbie et al. 2000, Shaver et al. 2000, Dutta et al. 2006, Vogel et al. 2009). At the same time, warmer temperatures and nutrients released from decomposing organic material are expected to increase plant productivity and ecosystem C storage (Natali et al. 2012). Process models predict that tundra will act as a C sink in a warmer climate (McGuire et al. 2009), but these models are limited by a lack of observations and experiments that examine warming effects on both vegetation and permafrost C simultaneously.

Over the past decades there have been widespread shifts in tundra plant community composition (Sturm et al. 2001, Elmendorf et al. 2012) and increases in aboveground productivity and biomass (Goetz et al. 2005, Hudson and Henry 2009, Jia et al. 2009, Beck and Goetz 2011, Hill and Henry 2011), both of which have been attributed to climate warming. However, unlike these observed aboveground trends, regional observations of changes in whole-system C dynamics are lacking, and thus net change in terrestrial C storage has not been measured on a landscape scale. In parallel with observed greening trends, there has been a long history of tundra warming experiments that have caused similar shifts in vegetation (Walker et al. 2006, Elmendorf et al. 2012). However, many of these experiments utilized open-top greenhouses, which warmed air and sometimes surface soils but rarely thawed permafrost (Marion et al. 1997, Walker et al. 2006). Consequently, these experiments are unlikely to influence belowground processes and ecosystem C balance in the same way as is expected from climate warming and permafrost thaw. In one long-term study, where greenhouse warming did alter the belowground community, the highly heterogeneous nature of the soil C pool limited ability to significantly detect change in the size of the thawed C pool (Sistla et al. 2013). This knowledge gap hinders efforts to simulate carbon–climate feedbacks in the Arctic, where the permafrost

C pool is twice the global atmospheric pool (Tarnocai et al. 2009) and is potentially highly vulnerable to a changing climate (Schuur et al. 2008, 2009).

We examined warming effects on ecosystem carbon dioxide (CO_2) exchange at a whole ecosystem warming experiment, the Carbon in Permafrost Experimental Heating Research (CiPEHR) project, which is situated in moist acidic tussock tundra in Interior Alaska at a location underlain by permafrost (Appendix: Fig. A1). The CiPEHR project is the first warming experiment to degrade permafrost without delaying spring snow melt and to also document the effects on annual tundra C balance. Here we present results from three years of whole-ecosystem warming and the warming effects on annual ecosystem CO_2 exchange.

METHODS

Site description

The Carbon in Permafrost Experimental Heating Research (CiPEHR) project is located in the northern foothills of the Alaska Range (~670 m elevation) in the region of Eight Mile Lake (EML), Alaska, USA (63°52′ 59″ N, 149°13′ 32″ W; Appendix: Fig. A1) (Natali et al. 2011, 2012). The experiment is situated on moist acidic tundra on a relatively well-drained gentle northeast-facing slope. Soils are Gelisols, and are comprised of an organic horizon, 0.35–0.45 m thick, above cryoturbated mineral soil that is a mixture of glacial till and loess. Soil C pools to a depth of 1 m are ~50 kg C/m^2. The active layer, which thaws annually during the growing season, reaches a maximum depth of ~60 cm, below which is the permafrost layer. Air temperature (2004–2011) ranges from a monthly average of $-17.4° \pm 1.7°C$ in January to $13.5° \pm 0.6°C$ in July, with a mean annual temperature of $-2.3 \pm 0.5°C$. Average growing-season precipitation (2004–2011) is 235 ± 31 mm (mean $\pm$ SE). The experimental site is fully underlain by permafrost but lies within the area of discontinuous permafrost in a location where permafrost thaw and thermokarst have been occurring over the past several decades (Schuur et al. 2009, Vogel et al. 2009). Vegetation at the site is dominated by the tussock-forming sedge, *Eriophorum vaginatum*, and deciduous shrub, *Vaccinium uliginosum*, and is further described in Natali et al. (2012).

Experimental design

The CiPEHR project is composed of two warming treatments that passively warmed air, soil, and permafrost during the growing season and winter. The soil warming treatment, hereafter called "winter warming" (WW), was achieved using snow fences (1.5 m tall × 8 m long) that trapped an insulating layer of snow (Appendix: Table A1, Figs. A2a, A3), followed by spring snow removal that ensured similar melt-out dates between treatments and prevented excess moisture inputs to the experimental plots. There were six replicate snow fences arranged in three experimental blocks. Each block comprised two snow fences separated by 5 m, and

blocks were approximately 100 m apart (Appendix: Fig. A2c). Plots were snow free by ~1 May in all years. Fences were removed at the time of snow removal to avoid shading the plots.

The second warming treatment, referred to as "summer warming" (SW), was achieved using 0.36 m^2 × 0.5 m tall open-top chambers (OTC), constructed of 0.6 cm thick clear polycarbonate (Appendix: Fig. A2b). The OTCs were set out during the growing season (May–September). Each WW treatment and control area contained two SW plots and two SW control plots. Treatment plots will hereafter be referred to as follows: *Ambient* (no warming), *Winter* (WW only), *Summer* (SW only), and *Annual* (SW + WW). Further description of the site and experiment can be found in the Appendix and in Natali et al. (2011).

Environmental monitoring

An Onset HOBO weather station (Onset Computer Corporation, Bourne, Massachusetts, USA) (~100 m distance from plots; Appendix: Fig. A2c) measured air temperature, rainfall, photosynthetically active radiation (PAR), wind speed and direction, air pressure, and relative humidity. Plot-level air temperatures were measured at 15 cm from the ground surface using NTC thermistors. Soil profile temperatures (5, 10, 20, 40 cm) were measured continuously in each of the 48 experimental plots using constantan-copper thermocouples. Gravimetric water content (0–5 cm depth) was estimated using site-calibrated DC half-bridge resistance measurements (Natali et al. 2011). Volumetric water content was measured from the soil surface to 20 cm depth using site-calibrated Campbell CS616 water content reflectometer probes (Campbell Scientific, Logan, Utah, USA), standardized to 20°C. The water-table depth was measured three times per week from two water wells located in each WW and control plot. Thaw depth (TD; the thickness of unfrozen ground during the growing season) was measured weekly in three locations just outside each flux plot using a metal depth probe, and inside the SW chambers at two time points in middle and late growing season.

Plant biomass, N pool, and NDVI

Aboveground biomass and net primary productivity (NPP) were determined with a nondestructive point–intercept method, coupled with allometric equations developed for this site (Schuur et al. 2007, Natali et al. 2012). Aboveground NPP for vascular species was estimated as the sum of the current year's apical growth (new leaves, new stems, flowers, fruits) and secondary growth (difference between the current and previous years' stem biomass), which was estimated using growth rates from Toolik Lake (Alaska, USA) moist acidic tundra site (Shaver et al. 2001).

We used a stainless steel reference wire (Clymo 1970) or a marked location on the moss stem (for *Pleurozium schreberi*, tied string) to measure moss vertical growth.

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The four moss groups measured were: *Sphagnum fuscum*, hydrophilic *Sphagnum*. spp. (which included *S. girgensohnii*, *S. lenense*, *S. warnstorfii*, *and S. aongstroemii*), *Dicranum* spp., and feathermoss (*P. schreberi*). Vertical growth was converted to biomass using allometric equations developed for Eight Mile Lake (EML) watershed (Alaska, USA) (Schuur et al. 2007) or from published studies (*P. schreberi*; Benscoter and Vitt 2007).

Seasonal variation in green-leaf biomass was detected using normalized-difference vegetation index (NDVI) images that were taken every two weeks throughout the 2011 growing season with an ADC multispectral digital camera (Tetracam, Chatsworth, California, USA). To assess warming effects on plant nutrient status, we collected fully formed green leaves from the current year's growth from six vascular plants found across plots (*Betula nana*, *Carex bigelowii*, *E. vaginatum*, *Rhododendron subarcticum*, *Rubus chamaemorus*, and *V. uliginosum*). Leaves were dried at 60°C, finely ground, and analyzed for total C and N on a Costech elemental analyzer (Costech Analytical Technologies, Valencia, California, USA). Canopy N (g N/m^2 ground area) was determined as the product of new leaf biomass and green-leaf percentage N.

CO_2 flux measurements

We measured ecosystem CO_2 balance using three automated systems, each of which measured CO_2 flux from eight experimental plots using an infrared gas analyzer (IRGA; LI-820, LICOR Corporation, Lincoln, Nebraska, USA). Automated measurements were collected from each flux chamber (Appendix: Fig. A2d) every 1.5 h, beginning the first week of May through the last week of September, from 2009 through 2011. Chambers were rotated weekly among plots so that all 48 plots were measured throughout the growing season. Winter respiration (October through April) was measured using an IRGA in a portable CO_2 flux system (Vogel et al. 2009, Natali et al. 2011). Winter respiration was measured in the fall of 2009 and 2011 (October through December) from 40 permanently installed sampling collars (0.06-m^2 area) placed adjacent to the CiPEHR project (further described in the Appendix) and directly from the plots in late winter of 2009 (Natali et al. 2011).

For all flux measurements (winter and growing season), air was circulated between the CO_2 flux chamber and IRGA at 1 L/min for 1.5 min. A total of ~125 000 growing-season fluxes and ~350 winter fluxes were used to parameterize CO_2 flux models for annual C-balance estimates. Additional information on flux measurements and the automated system can be found in Natali et al. (2011) and the Appendix.

CO_2-balance calculations

Carbon balance during the growing season was estimated for each plot by gap-filling flux measurements using response functions to environmental factors. Net ecosystem exchange (NEE; i.e., CO_2 exchange between the ecosystem and atmosphere) was modeled using a hyperbolic equation describing the relationship between NEE and PAR. For growing-season ecosystem respiration (R_{eco}), we used NEE measurements when PAR < 5 µmol·m^{-2}·s^{-1} to develop exponential relationships between R_{eco} and soil temperature (T_s, 10 cm depth). The winter respiration model was parameterized with flux and temperature data collected from the Eight Mile Lake (EML) watershed from 2005 to 2007 (Vogel et al. 2009) and from the permanently installed collars located adjacent to CiPEHR (in 2009, 2011). For the EML watershed data, we included only winter respiration fluxes from "Minimal Thaw" site, which is located ~1.5 km from the CiPEHR project and is similar in terms of plant composition and ground thaw. To test the model fit, we used respiration measured from CiPEHR experimental plots in March and April of 2009 (Natali et al. 2011), and we found that our model underestimated respiration from the WW plots by 28%. Thus, the model for the WW plots was adjusted proportionally to reflect basal respiration differences between measured data (winter 2008–2009) from control and WW plots (Natali et al. 2011). To examine effects of warming on an annual basis, we also modeled ecosystem respiration in autumn and early winter (October through December) based on a projected regional temperature increase of 4°C (Kattsov et al. 2005) because the experimental manipulation did not increase temperature during this period.

Statistical design and analyses

Data were analyzed with a mixed linear model analysis of variance (ANOVA; SAS Institute 2009) using a blocked split-plot design with WW as the main plot factor, SW as the within-plot factor, and fence (random and nested in block) as the experimental unit for WW. To examine changes across growing season or years, we used repeated-measures ANOVA, with plot as the unit of replication for time effects. Thaw depth, water table depth, and temperature were averaged within months for statistical analyses. We used a one-sample *t* test (compared against neutral = 0) to determine whether control plots were a net C sink or source. Family-wise error rates (α = 0.05) were controlled using the Hochberg method for planned contrasts. Data were transformed when necessary to meet ANOVA assumptions. Errors shown are one standard error of the mean.

RESULTS

Winter warming (WW) increased soil temperature 2–3°C during the snow-covered months (Appendix: Fig. A4, Table A1) and increased growing-season ground thaw by 10% (*P* < 0.05, Fig. A5, Appendix: Table A1). Despite the removal of additional snow from the WW plots, WW treatment resulted in shallower water table
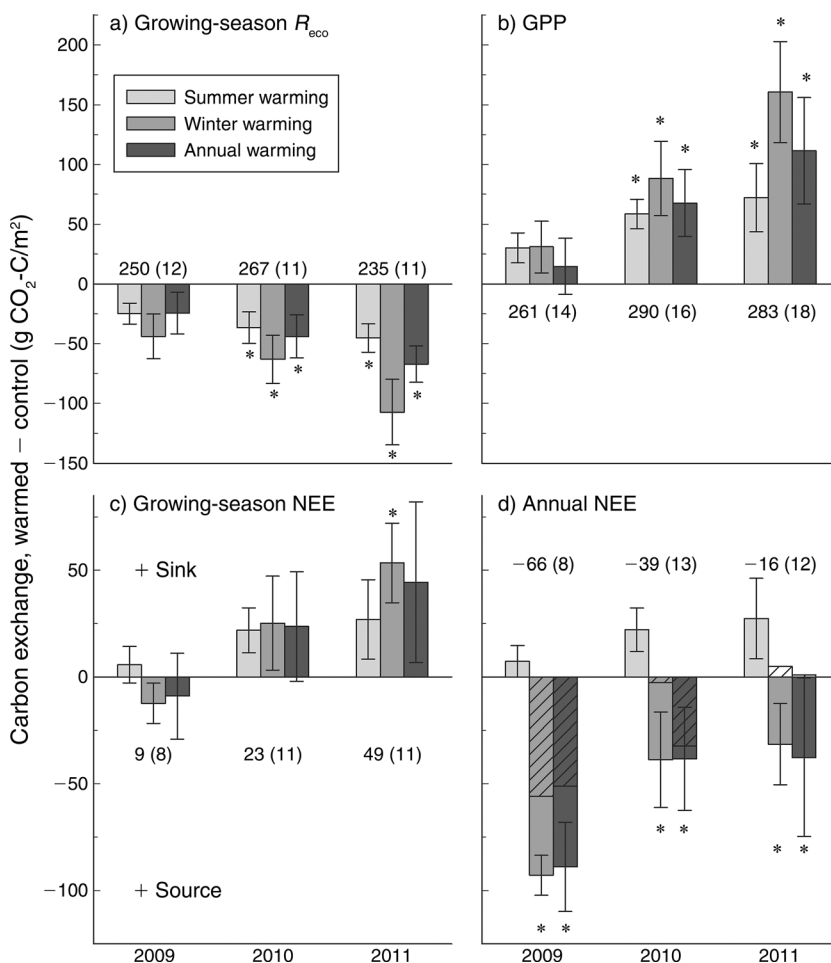
FIG. 1. Effects of soil warming and permafrost thaw (winter warming) and growing-season air warming (summer warming) on cumulative CO_2 exchange between a tundra ecosystem and the atmosphere. (a) Ecosystem respiration (R_{eco}), (b) gross primary productivity (GPP), (c) growing-season net ecosystem exchange (NEE), and (d) annual NEE were monitored for three years of experimental warming. Annual NEE estimates for winter and annual warming treatments include warming effects from field (January–September) and modeling (October–December) experiments. The hatched bars in panel (d) show annual NEE without autumn–early winter warming (i.e., experimental results only). Bars represent treatment effects on ecosystem CO_2 exchange: bars above the zero line represent increased ecosystem CO_2 uptake with warming ("+ Sink" in panel (c)) and below represent increased CO_2 loss to the atmosphere ("+ Source" in panel (c)). Numbers above/below the zero line are ambient CO_2 flux values (means with SE in parentheses; g CO_2-C/m²). Annual warming represents combined summer and winter warming. An asterisk denotes treatment differences from ambient (paired comparisons, $P < 0.05$).

and wetter soils throughout the growing season ($P < 0.05$; Appendix: Fig. A9, Table A1), likely due to localized surface subsidence brought about by permafrost thaw. Summer warming (SW) increased air temperature by ~1°C during the growing season (Appendix: Table A1) but did not warm soil or thaw permafrost ($P > 0.1$). A summary of treatment effects on all environmental variables measured can be found in Appendix: Table A1.

Both air and soil warming (SW and WW treatments, respectively) altered gross fluxes of CO_2 into and out of the ecosystem. There was a significant increase in growing-season respiration as a result of warming (Fig. 1a; $P < 0.05$ for all treatments), and this effect was amplified across the three years of the experiment.

Winter soil warming (WW) enhanced growing-season respiration by 18% in the first treatment year, which increased to 45% after three years, when an additional 107 ± 27 g C/m² were respired from the warmed and thawed plots (WW × year, $P < 0.01$). The effect of air warming (SW) on ecosystem respiration also increased over time, but the magnitude was less than with soil warming, and trends across time were nonsignificant (SW × year, SW × WW × year; $P > 0.05$).

Gross primary productivity (GPP) also significantly increased as a result of both warming treatments (Fig. 1b, $P < 0.05$ for all). As with respiration, treatment effects on GPP accumulated over the duration of this experiment, and the strongest effect occurred as a result of soil warming (WW), where GPP was 12% higher after
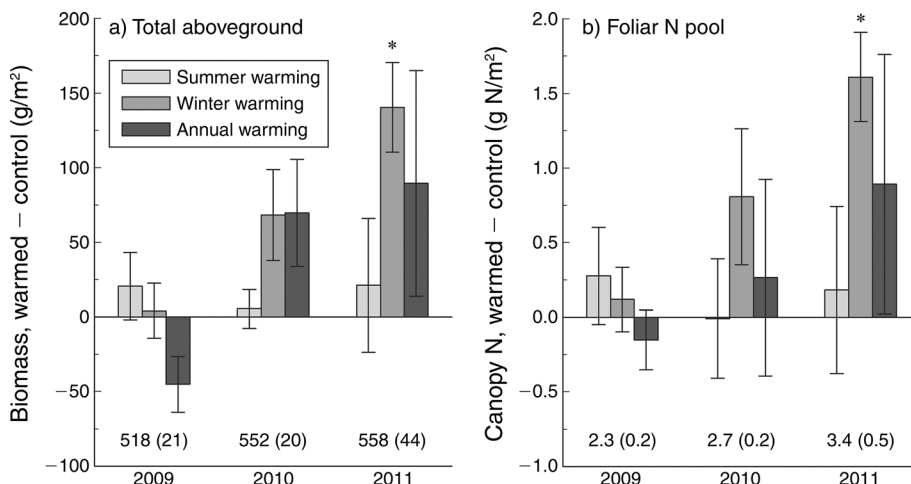
FIG. 2. Response of the plant community to three years of experimental soil warming and permafrost thaw (winter warming) and growing-season air warming (summer warming). Warming effects are on (a) total aboveground biomass and (b) foliar nitrogen (N) pool. Bars above the zero line represent an increase in ecosystem biomass or foliar N with warming and below represent a decrease. Numbers below the zero line are ambient values (means with SE in parentheses). Annual warming represents combined summer and winter warming. Green-leaf N mass represents the sum of six main species found across plots: *Betula nana*, *Carex bigelowii*, *Eriophorum vaginatum*, *Rhododendrum subarcticum*, *Rubus chamaemorus*, and *Vaccinium uliginosum*. Biomass includes all vascular and nonvascular plants (Appendix: Table A3). An asterisk denotes treatment differences from ambient paired comparisons.
      * $P < 0.05$.

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one year of warming and 57% higher after three years, when an additional 160 ± 42 g C/m^2 were taken up from the atmosphere. Air and combined air and soil warming effects also accumulated over time and increased GPP by 26% and 40%, respectively, after three years of warming.

The net effect of increasing plant uptake at a faster rate than ecosystem respiration was a twofold increase in cumulative growing-season C uptake in the second and third years of soil warming and permafrost thaw (Fig. 1c; Appendix: Fig. A6, Table A2; WW × year, $P = 0.02$). By the third treatment year, an additional 53 ± 19 g C/m^2 per growing season was sequestered by the ecosystem from the atmosphere in the soil-warmed plots (WW) compared to control. However, we did not detect a significant increase in net CO_2 uptake when air was warmed alone (SW; $P = 0.49$) or with combined air–soil warming (WW × SW, $P = 0.68$) because increased plant C uptake was matched by increased respiration losses.

The additional growing-season C uptake in soil-warmed plots largely accumulated in plant biomass, where an additional 140 ± 30 g C/m^2 was stored aboveground after three years of soil warming (WW, $P = 0.01$; Fig. 2a; Appendix: Table A3). As with growing-season NEE, there was no detected change in biomass in the first year of warming, but 12% and 25% increases in the 2nd ($P = 0.08$) and 3rd years (WW, $P < 0.01$; Appendix: Fig. A7, Table A4). The foliar N pool also increased by 40% after three years of winter soil warming (WW, $P < 0.01$; Fig. 2b; Appendix: Table A4). This increase in canopy N in the soil-warmed plots was driven primarily by higher leaf biomass rather than

foliar percentage N, which remained relatively unaffected by the warming treatments (Natali et al. 2012). Additionally, plants in the soil-warmed plots leafed-out earlier, had delayed senescence, and had more green biomass throughout the growing season, as demonstrated by NDVI (normalized-difference vegetation index) measurements (Appendix: Fig. A8). There were no significant changes in plant biomass, canopy N, or NDVI as a result of summer air warming, nor were there SW × WW interactions ($P > 0.10$).

While winter soil warming and increased thaw (WW) doubled net C uptake during the growing season, additional respiratory C losses occurred during the snow-covered period. Winter warming increased average "winter" (October–April) respiration by 50%, and this additional loss completely offset growing-season C gains. However, this estimate does not account for soil warming during autumn and early winter, which is projected for the region (Kattsov et al. 2005) but was not altered by our experiment. When projected early winter soil warming (4°C) was included in our estimate, cumulative winter respiration was twofold higher in soil-warmed plots (WW, 142.9 ± 0.4 g C) compared to control (66.9 ± 0.9 g C) ($P < 0.01$; Appendix: Table A2). The additional early winter respiration resulted in significantly greater C losses from the ecosystem on an annual basis when soils were warmed and permafrost thawed compared to control plots ($P < 0.01$; Fig. 1d). In the first year of warming, annual C losses were greatest in the winter-warmed plots, where an additional 90–100 g $C·m^{-2}·yr^{-1}$ were lost from the ecosystem. In subsequent years, when growing-season C uptake increased,

additional C losses from soil warming and permafrost thaw were approximately 30–40 g $C \cdot m^{-2} \cdot yr^{-1}$. In contrast to the strong ecosystem response to soil warming (WW), summer air warming did not significantly change annual C balance ($P > 0.01$).

DISCUSSION

The experimental treatments were in line with century-scale warming projections (Kattsov et al. 2005) and caused a significant increase in ground thaw as is predicted for the region (Lawrence et al. 2012). As a result, 2 kg soil C/m^2 was moved from the thermally protected permafrost pool to the thawed active layer, resulting in a net loss of C from the ecosystem as a result of annual warming (experimental and modeled). While soil warming caused significant CO_2 losses, there was limited net effect of summer air warming. The observed differences in CO_2 flux responses to air and soil warming highlight the fundamental role of belowground dynamics in regulating net CO_2 exchange of permafrost ecosystems. These experimental results reconcile results from previous warming experiments that observed little or highly variable effects of air warming alone on net ecosystem C exchange and ecosystem productivity (Chapin et al. 1995, Hobbie and Chapin 1998, Oberbauer et al. 2007) with remote-sensing trends that observed widespread increases in "greenness" and NPP across northern tundra (Goetz et al. 2005, Sitch et al. 2007, Jia et al. 2009, Beck and Goetz 2011, Epstein et al. 2012). By focusing our observations on CO_2 fluxes, over a relatively short experimental timescale we were able to detect C cycling changes that may have been undetectable from the bulk soil C pool (e.g., Sistla et al. 2013). Our observations of warming impacts on C losses may be a conservative estimate as both methane emissions and hydrologic C losses are also expected to increase with permafrost thaw (Schuur et al. 2008). Estimates of dissolved C export for the Eight Mile Lake watershed (Alaska, USA) show that accounting for these losses could increase ecosystem C loss rates by an additional ~10–15% (Schuur et al. 2009).

The change in net ecosystem C exchange observed over the time course of this experiment was driven by the changing responses of plants and microbes to warming. That these processes respond on different scales emphasizes the importance of understanding both the timing and magnitude of these components of ecosystem CO_2 exchange as warming proceeds. These results highlight the dynamic responses of both plants and soil communities to warming and how their net response influences annual C balance. While C pools in soils are markedly higher than plant biomass pools, annual C uptake by the plant community offset more than half of respiratory C losses. It was not until plant productivity responded to warming in Years 2 and 3 that the magnitude of this C climate feedback could be accurately assessed (Natali et al. 2011).

While the Arctic has been a net C sink during the Holocene (Pries et al. 2012), our results show that this site was a net C source during the time frame of this experiment (~40 g $C \cdot m^{-2} \cdot yr^{-1}$ in control plots; $P < 0.05$), consistent with changes across the region (Pries et al. 2012) that are likely a result of regional climate change. The C source strength is expected to increase with additional soil warming and permafrost degradation as demonstrated both by our warming experiment as well as by trends observed across a natural permafrost thaw gradient (Schuur et al. 2009, Vogel et al. 2009). Warming has the potential to almost double current rates of loss, pushing annual net C losses from tundra into the range of 60–70 g·m^{-2}·yr^{-1} (based on experimental and modeled warming in Years 2 and 3 of this experiment). While this estimate includes fall and early winter warming not achieved in our experiment, our results show C losses that resulted from experimental soil warming and thaw (winter warming [WW]) completely offset C gained during the growing season. At the same time, additional C offsets by plant community shifts that cannot be observed in a three-year experiment may be reasonably expected over longer timescales (van Wijk et al. 2004). Given the size of the soil C pool relative to potential C stores in biomass of future plant communities, it is unlikely that net soil C losses can be fully offset. However, both the magnitude and timing of C losses and gains will determine the short- and long-term feedbacks from permafrost thaw to global climate. These observations highlight the importance of permafrost thaw in determining the trajectory of ecosystem C balance, the dynamic responses of plant and microbial communities to warming, as well as the potential for significant global C emissions if rates calculated here become typical for permafrost ecosystems in a warmer world.

LITERATURE CITED

Beck, P. S. A., and S. J. Goetz. 2011. Satellite observations of high northern latitude vegetation productivity changes between 1982 and 2008: ecological variability and regional differences. Environmental Research Letters 6:045501.

Benscoter, B. W., and D. H. Vitt. 2007. Evaluating feathermoss growth: a challenge to traditional methods and implications for the boreal carbon budget. Journal of Ecology 95:151–158.

Chapin, F. S., III, G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer, and J. A. Laundre. 1995. Responses of arctic tundra to experimental and observed changes in climate. Ecology 76:694–711.

Clymo, R. S. 1970. Growth of *Sphagnum*: methods of measurement. Journal of Ecology 58:13–49.

Dutta, K., E. A. G. Schuur, J. C. Neff, and S. A. Zimov. 2006. Potential carbon release from permafrost soils of Northeastern Siberia. Global Change Biology 12:2336–2351.

Reports

Elmendorf, S. C., et al. 2012. Plot-scale evidence of tundra vegetation change and links to recent summer warming. Nature Climate Change 2:453–457.

Epstein, H. E., M. K. Raynolds, D. A. Walker, U. S. Bhatt, C. J. Tucker, and J. E. Pinzon. 2012. Dynamics of aboveground phytomass of the circumpolar Arctic tundra during the past three decades. Environmental Research Letters 7:015506.

Goetz, S. J., A. G. Bunn, G. J. Fiske, and R. A. Houghton. 2005. Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. Proceedings of the National Academy of Sciences USA 102: 13521–13525.

Hill, G. B., and G. H. R. Henry. 2011. Responses of High Arctic wet sedge tundra to climate warming since 1980. Global Change Biology 17:276–287.

Hobbie, S. E., and F. S. Chapin, III. 1998. Response of tundra plant biomass, aboveground production, nitrogen, and CO_2 flux to experimental warming. Ecology 79:1526–1544.

Hobbie, S. E., J. P. Schimel, S. E. Trumbore, and J. R. Randerson. 2000. Controls over carbon storage and turnover in high-latitude soils. Global Change Biology 6:196–210.

Hudson, J. M. G., and G. H. R. Henry. 2009. Increased plant biomass in a High Arctic heath community from 1981 to 2008. Ecology 90:2657–2663.

Jia, G. J., H. E. Epstein, and D. A. Walker. 2009. Vegetation greening in the Canadian Arctic related to decadal warming. Journal of Environmental Monitoring 11:2231–2238.

Kattsov, V. M., et al. 2005. Future climate change: modeling and scenarios for the Arctic. Pages 100–150 in Arctic Climate Impact Assessment. Cambridge University Press, Cambridge, UK.

Lawrence, D. M., A. G. Slater, and S. C. Swenson. 2012. Simulation of Present-Day and Future Permafrost and Seasonally Frozen Ground Conditions in CCSM4. Journal of Climate 25:2207–2225.

Marion, G. M., et al. 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems. Global Change Biology 3:20–32.

McGuire, A. D., L. G. Anderson, T. R. Christensen, S. Dallimore, L. D. Guo, D. J. Hayes, M. Heimann, T. D. Lorenson, R. W. Macdonald, and N. Roulet. 2009. Sensitivity of the carbon cycle in the Arctic to climate change. Ecological Monographs 79:523–555.

Natali, S. M., E. A. G. Schuur, and R. L. Rubin. 2012. Increased plant productivity in Alaskan tundra as a result of experimental warming of soil and permafrost. Journal of Ecology 100:488–498.

Natali, S. M., E. A. G. Schuur, C. Trucco, C. E. H. Pries, K. G. Crummer, and A. F. Baron Lopez. 2011. Effects of experimental warming of air, soil and permafrost on carbon balance in Alaskan tundra. Global Change Biology 17:1394–1407.

Oberbauer, S. F., et al. 2007. Tundra CO_2 fluxes in response to experimental warming across latitudinal and moisture gradients. Ecological Monographs 77:221–238.

Pries, C. E. H., E. A. G. Schuur, and K. G. Crummer. 2012. Holocene carbon stocks and carbon accumulation rates altered in soils undergoing permafrost thaw. Ecosystems 15: 162–173.

SAS Inistitute. 2009. SAS software, version 9.0. SAS Institute, Cary, North Carolina, USA.

Schaefer, K., T. Zhang, L. Bruhwiler, and A. P. Barrett. 2011. Amount and timing of permafrost carbon release in response to climate warming. Tellus Series B—Chemical and Physical Meteorology 63:165–180.

Schuur, E. A. G., et al. 2013. Expert assessment of vulnerability of permafrost carbon to climate change. Climatic Change 119:359–374.

Schuur, E. A. G., et al. 2008. Vulnerability of permafrost carbon to climate change: implications for the global carbon cycle. BioScience 58:701–714.

Schuur, E. A. G., K. G. Crummer, J. G. Vogel, and M. C. Mack. 2007. Plant species composition and productivity following permafrost thaw and thermokarst in Alaskan tundra. Ecosystems 10:280–292.

Schuur, E. A. G., J. G. Vogel, K. G. Crummer, H. Lee, J. O. Sickman, and T. E. Osterkamp. 2009. The effect of permafrost thaw on old carbon release and net carbon exchange from tundra. Nature 459:556–559.

Shaver, G. R., M. S. Bret-Harte, M. H. Jones, J. Johnstone, L. Gough, J. Laundre, and F. S. Chapin, III. 2001. Species composition interacts with fertilizer to control long-term change in tundra productivity. Ecology 82:3163–3181.

Shaver, G. R., et al. 2000. Global warming and terrestrial ecosystems: a conceptual framework for analysis. BioScience 50:871–882.

Sistla, S. A., J. C. Moore., R. T. Simpson, L. Gough, G. R. Shaver, and J. P. Schimel. 2013. Long-term warming restructures Arctic tundra without changing net soil carbon storage. Nature 497:615–618.

Sitch, S., A. D. McGuire, J. Kimball, N. Gedney, J. Gamon, R. Engstrom, A. Wolf, Q. Zhuang, J. Clein, and K. C. McDonald. 2007. Assessing the carbon balance of circumpolar Arctic tundra using remote sensing and process modeling. Ecological Applications 17:213–234.

Sturm, M., C. Racine, and K. Tape. 2001. Climate change: increasing shrub abundance in the Arctic. Nature 411:546–547.

Tarnocai, C., J. G. Canadell, E. A. G. Schuur, P. Kuhry, G. Mazhitova, and S. Zimov. 2009. Soil organic carbon pools in the northern circumpolar permafrost region. Global Biogeochemical Cycles 23.

van Wijk, M. T., et al. 2004. Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. Global Change Biology 10:105–123.

Vogel, J., E. A. G. Schuur, C. Trucco, and H. Lee. 2009. Response of CO_2 exchange in a tussock tundra ecosystem to permafrost thaw and thermokarst development. Journal of Geophysical Research: Biogeosciences 114(G4).

Walker, M. D., et al. 2006. Plant community responses to experimental warming across the tundra biome. Proceedings of the National Academy of Sciences USA 103:1342–1346.

SUPPLEMENTAL MATERIAL

Appendix

Annual and growing-season weather data and expanded description of methods for flux measurements, chamber volume estimation, and CO_2-balance calculations. The Appendix also contains nine supplementary figures (pictures and a map of the field site, soil temperature, thaw depth, monthly fluxes, ANPP, NDVI, water table depth) and five tables (statistical results and summaries of warming effects on environmental variables, monthly fluxes, biomass/ANPP/canopy N, and model parameters) (*Ecological Archives* E095-053-A1).

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