Increased plant productivity in Alaskan tundra as a result of experimental warming of soil and permafrost

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Summary

1. The response of northern tundra plant communities to warming temperatures is of critical concern because permafrost ecosystems play a key role in global carbon (C) storage, and climate-induced ecological shifts in the plant community will affect the transfer of carbon-dioxide between biological and atmospheric pools.

2. This study, which focuses on the response of tundra plant growth and phenology to experimental warming, was conducted at the Carbon in Permafrost Experimental Heating Research project, located in the northern foothills of the Alaska Range. 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 summer air temperatures (summer warming).

3. Winter warming increased wintertime soil temperature (5–40 cm) by 2.3 °C, resulting in a 10% increase in growing season thaw depth. Summer warming significantly increased growing season air temperature; peak temperature differences occurred near midday when summer warming plots were approximately 1.0 °C warmer than ambient plots.

4. Changes in the soil environment as a result of winter warming treatment resulted in a 20% increase in above-ground biomass and net primary productivity (ANPP), while there was no detected summer warming effect on ecosystem-level ANPP or biomass. Both summer and winter warming extended the growing season through earlier bud break and delayed senescence, despite equivalent snow-free days across treatments. As with ANPP, winter warming increased canopy N mass by 20%, while there was no summer warming effect on canopy N.

5. The warming-mediated increase in N availability, coupled with phenological shifts, may have driven higher rates of ANPP in the winter warming plots, and the lack of ecosystem-level N and ANPP response to summer warming suggest continued N limitation in the summer warming plots.

6. *Synthesis:* These results highlight the role of soil and permafrost dynamics in regulating plant response to climate change and provide evidence that warming may promote greater C accumulation in tundra plant biomass. While warming temperatures are expected to enhance microbial decomposition of the large pool of organic matter stored in tundra soils and permafrost, these respiratory losses may be offset, at least in part, by warming-mediated increases in plant growth.

Key-words: biomass, carbon, climate change, net primary productivity, open-top chamber, permafrost, phenology, plant–climate interactions, snow fence, tundra

Introduction

Tundra ecosystems play a key role in biological feedbacks to global carbon (C) cycling because of the large pool of thermally protected C stored in permafrost soils (Schuur *et al.* 2008; Tarnocai *et al.* 2009) and the strong potential for changes in C storage in a warmer climate (Schuur *et al.* 2008, 2009; Dorrepaal *et al.* 2009). The magnitude and direction of these C inventory changes will depend upon the effect of

increasing temperature on photosynthetic C uptake relative to respiratory losses (Shaver *et al.* 2000). On the one hand, warming may increase microbial decomposition rates and organic substrate availability as previously frozen soil organic matter warms and thaws (Aerts 2006; Davidson & Janssens 2006; Grogan & Jonasson 2006; Larsen *et al.* 2007; Natali *et al.* 2011). However, some respiratory losses may be offset by warming-mediated increases in plant biomass, as observed in tundra over the past few decades (Hudson & Henry 2009).

Upland moist acidic tundra is characterized by strong nitrogen (N) limitation, short growing season length and a shallow

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active layer (seasonally thawed ground layer above perennially frozen permafrost), all of which place limitations on plant productivity and growth. Ecosystem models predict that warming surface air temperatures will positively affect plant productivity in northern regions (Keyser *et al.* 2000), primarily as a result of warming effects on soil N availability (Nadelhoffer *et al.* 1991; Rastetter *et al.* 1991; Chapin *et al.* 1995). Fertilization experiments in Arctic tundra clearly demonstrate the importance of N as a regulator of plant growth and ecosystem C exchange (Chapin *et al.* 1995; Chapin & Shaver 1996; Shaver *et al.* 2001; Mack *et al.* 2004). Warming temperatures may also bring about phenological changes and shifts in the plant community (Wookey *et al.* 1993, 2009; Arft *et al.* 1999; Aerts *et al.* 2004; Aerts, Cornelissen & Dorrepaal 2006) that, combined with changes in ecosystem N, may further increase the potential for warming temperatures to alter ecosystem productivity.

Surprisingly, while there has been observational evidence of increased plant biomass in the Arctic over the past few decades (Hudson & Henry 2009), few experimental tundra warming studies have resulted in greater plant biomass or N pools at the ecosystem level, as would be expected if N limitation was attenuated by warming. Experimental warming in tundra has caused shifts in plant community structure (Hollister, Webber & Bay 2005; Jonsdottir *et al.* 2005; Wahren, Walker & Bret-Harte 2005; Walker *et al.* 2006) and species/functional group-specific changes in biomass and growth (Chapin *et al.* 1995; Chapin & Shaver 1996; Hobbie & Chapin 1998; Dorrepaal *et al.* 2004), but these individualistic species-level effects have often acted in opposite directions so that there was no change in total plant biomass at the ecosystem level (Chapin *et al.* 1995). However, many previous studies using greenhouses and open-top chambers (OTCs) rarely warmed deep soils or increased thaw depth (Marion *et al.* 1997) because of lateral transfer of heat energy from the relatively small treatment plots as opposed to vertical transfer of heat that will occur with climate warming. While snow addition studies have been successfully used to raise wintertime soil temperatures and degrade permafrost, the delayed snowmelt associated with the experimentally accumulated snowpack is not a likely climate scenario and may decrease plant productivity (Wipf & Rixen 2010).

This study examines the responses of plant productivity and biomass in a new type of air and soil warming experiment that increased summer thaw depth and degraded surface permafrost, without delaying snowmelt (Natali *et al.* 2011). We hypothesized that both air and soil warming would increase growing season length through changes in leaf phenology, but that soil warming alone would increase plant-available N. We expected that these warming-mediated changes in leaf phenology and nutrient availability would increase plant productivity and biomass at the ecosystem level. We tested these hypotheses at the Carbon in Permafrost Experimental Heating Research (CiPEHR) project, located in moist acidic tundra in Interior Alaska near Denali National Park. The CiPEHR project combines OTCs to increase summer air temperatures with snow fences, coupled with spring snow removal, to warm surface and deep-soil temperatures (Natali *et al.* 2011). This novel approach achieves the type of whole ecosystem warming and permafrost degradation that is expected as a consequence of climate change.

Materials and methods

SITE DESCRIPTION

The CiPEHR project, which was established in 2008, is located in the northern foothills of the Alaska Range (*c.* 700 m elevation) at the Eight Mile Lake (EML) study site, Alaska (63°52′59′ N, 149°13′32′ W; Schuur *et al.* 2009; Natali *et al.* 2011). The site is situated on moist acidic tundra 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 wind-blown loess. The active layer, which thaws annually during the growing season, is *c.* 50–60 cm thick and is situated above a perennially frozen permafrost layer. 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. 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*, *V. vitis idaea*, *Andromeda polifolia* and *Oxycoccus microcarpus*. Nonvascular plant cover is dominated by feather moss (primarily *Pleurozium schreberi*) and *Sphagnum* spp., as well as several lichen species (primarily *Cladonia* spp.; Schuur *et al.* 2007).

EXPERIMENTAL DESIGN

The soil warming treatment, hereafter called winter warming, was achieved using six replicate snow fences (1.5 m tall × 8 m long; $n = 6$) that trapped insulating layers of snow. To ensure that water input and timing of snowmelt were similar in warming and control plots, we removed the accumulated snow from winter warming plots prior to snowmelt in early spring. This is a key feature of this experiment that differs from traditional snow fence experiments and that allowed us to isolate the temperature effects of the snow fence treatment from moisture and snowmelt effects. Fences were removed at the time of snow removal to avoid shading of the plots during the growing season (May–September). All plots were snow free by 30 April in both 2009 and 2010. Each winter warming treatment and winter warming control area contained two summer warming plots and two summer warming control plots ($n = 24$). Summer warming was achieved using 0.36 m² × 0.5 m tall OTCs, which were set out during the snow-free period, between the first week in May and the last week of September. Treatment plots will hereafter be referred to as follows: Ambient (no warming), Winter (winter warming only), Summer (summer warming only) and Annual (both summer and winter warming). Further description of the site and experimental design can be found in the study by Natali *et al.* (2011).

ENVIRONMENTAL MONITORING

An Onset HOBO (Bourne, MA, USA) weather station was used to measure air temperature and rainfall. Growing season air temperatures in 2009 (9.7 °C) and 2010 (9.8 °C) were similar to the 7-year (2004–10) site average (10 °C). Growing season precipitation in 2009

(178 mm) was lower than the 7-year average (233 mm), while 2010 precipitation (250 mm) was slightly higher. Plot-level air temperatures were also measured at 15 cm from the ground surface using NTC thermistors and recorded to a Campbell Scientific CR1000 (Logan, UT, USA) data logger.

Soil profile temperatures (5, 10, 20, 40 cm) were recorded in each plot using constantan-copper thermocouples. Surface soil moisture was estimated using site-calibrated DC half-bridge resistance measurements (Natali *et al.* 2011). Volumetric water content (hereafter referred to as depth-integrated soil moisture) was measured from the soil surface to a depth of 20 cm using Campbell CS616 water content reflectometer probes (WCR). Soil moisture and temperature were measured half-hourly and recorded to a Campbell Scientific CR1000 data logger. Water-table depth was measured three times per week throughout the snow-free period from two water wells per winter warming and control plots. Thaw depth (thickness of unfrozen ground) was measured weekly at each plot using a thin (3 mm diameter) metal depth probe. We present here analyses of warming effects on micrometeorological variables for the second treatment year (September 2009–September 2010) and a summary of differences between the first and second years. Full analyses of 2008–09 environmental effects can be found in the study by Natali *et al.* (2011).

BIOMASS AND ANPP

Above-ground biomass and net primary productivity (ANPP) were determined in 2009 and 2010 with a nondestructive point-frame method using a 60×60 cm point frame with a grid size of 8×8 cm (Walker 1996). At each of the 49 intersecting grid points, a metal rod (1 mm diameter) was placed vertically through the plant canopy. We recorded species identity and tissue type (leaf, stem or fruit) for every plant that touched the rod ('hits'). We estimated above-ground live biomass for each vascular plant species, moss and lichen by applying allometric equations developed for this site to the average number of point-frame 'hits' per plot (Schuur *et al.* 2007). Vascular plant ANPP was estimated as the sum of the current year's apical growth (leaves, stems, flowers and fruits) and secondary growth. We based biomass values for plant tissue types on ratios of tissue type to total biomass determined from destructive harvest of a site adjacent to CiPEHR (Schuur *et al.* 2007). We estimated secondary growth using growth rates determined from tussock tundra at Toolik Lake, Alaska (Shaver *et al.* 2001). While our ANPP estimates do not account for potential warming effects on plant allometry, we have not observed any warming effects on the proportion of leaf to fruit/stem tissue (based on point-frame 'hits'), leaf length, or leaf mass per unit area (S. Natali, data not shown).

We estimated moss NPP by the cranked wire method, which measures vertical growth of moss using a stainless steel reference wire inserted at the moss surface (Clymo 1970; Schuur *et al.* 2007). We placed between three and five cranked wires in four moss types in each treatment at all fences and measured growth from mid-May to mid-September. The four dominant moss types measured were *S. fuscum*, hydrophilic *Sphagnum*. spp. (which included *S. girgenshonii*, *S. lenense*, *S. warnstorfii*, and *S. aongstroemii*), *Dicranum* spp., and feathermoss (primarily *P. schreberi*). With the exception of feather moss, vertical growth was converted to biomass increment using allometric equations developed for EML watershed (Schuur *et al.* 2007), and these point estimates of biomass increase were multiplied by per cent moss cover in each plot. Feathermoss NPP was estimated as

the product of linear growth per stem, stem density, biomass per unit stem growth (Benscoter & Vitt 2007) and per cent cover. Moss NPP was summed across groups for statistical analysis, but group-level results are presented in Supporting Information (Fig. S1).

PLANT AND SOIL ELEMENTAL ANALYSES

To assess warming effects on plant nutrient status, we collected leaves at peak biomass (mid July) and at the end of the growing season (late September) for total C, N and for stable isotope analyses (July only). Nitrogen isotopes provide information on N availability or sources to plants, and C isotopes provide information about plant water status. We collected fully formed green leaves from the current year's growth from six species found across plots. Leaves were dried at 60 °C, ground and analysed on a ThermoFinnigan (Waltham, MA, USA) continuous flow isotope ratio mass spectrometer coupled to a Costech (Valencia, CA, USA) elemental analyzer. Canopy N was determined as the product of leaf biomass and green leaf % N. We determined changes in N resorption efficiency $[(N_{green} - N_{senesce})/N_{green} \times 100]$ and proficiency (% N in senesced leaves), which are indicators of plant nutrient status. Leaf litter N mass was determined as the product of foliar biomass and senescent leaf % N.

Warming effects on soil nutrient availability were assessed using ion exchange resin bags (Giblin *et al.* 1994). Separate anion and cation exchange bags (Biorad 20–50 mesh; 3 g wet weight resin per bag) were placed in each plot at a depth of 10 cm during three seasonal intervals (25 May–16 September 2009; 16 September 2009–24 May 2010; 24 May–14 September 2010). Upon removal, resin bags were extracted for 1 h in 100 mL of 0.1 M HCl/2.0 M NaCl and analysed for NH_4^+ and NO_3^- on an Astoria Analyzer (Astoria-Pacific Int., Clackamas, OR, USA). We calculated total dissolved inorganic N (TDIN) as the sum of NH_4^+ and NO_3^-. While ion losses from resin exchange bags (due to microbial competition or ion substitution) are possible, ion exchange resins have been effectively used to provide a relative measure of soil N availability (Binkley 1984; Giblin *et al.* 1994). A summary of 2009 foliar elements and resin results can be found in the Supporting Information and in the study by Natali *et al.* (2011).

LEAF PHENOLOGY AND PLANT REPRODUCTIVE EFFORT

In 2010, we observed the timing of bud break from 11 to 29 May and senescence from August 21 to September 23. We recorded the date when bud break (*V. uliginosum*, *B. nana*) or green leaves (*C. bigelowii*) were first observed in each plot, and we recorded senescence as the date when no green leaves were present for these same species as well as for *R. chamaemorus*. Senescence in *E. vaginatum* was recorded as the percentage green leaves remaining per tussock at the last sampling date. Senescence was also detected using normalized difference vegetation index (NDVI) images taken 3 September 2009 and 23 September 2010 using an ADC multispectral digital camera (Tetracam, Chatsworth, CA, USA). To examine warming effects on reproductive effort, in 2010 we recorded number of flowers per unit area for *R. chamaemorus*, number inflorescence clusters for *E. vaginatum*, *B. nana*, *R. subarcticum* and number of flowering tillers for *C. bigelowii* (*c.* 1 male and 2 female spikes per tiller). Hereafter, we use the term flowers to mean flowers, inflorescence or flowering tillers. In late July in both 2009 and 2010, we recorded the number of berries produced by *R. chamaemorus*, *V. uliginosum* and *V. vaccinium idaea*. While variation in sex ratio of dioecious species (i.e. *R. chamaemorus*) can affect phenological, reproductive and

growth estimates, we do not expect this variation to be affected by or correlated with our experimental treatments; our measurements presented here represent species-level averages that include all individuals within each experimental plot.

STATISTICAL DESIGN AND ANALYSES

Data were analysed with a mixed linear model analysis of variance (ANOVA; SAS 9.0; SAS Inst., Cary, NC, USA) 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. Soil depth was included as a fixed factor (nested within plot) for analysis of treatment effects on soil temperature (5, 10, 20 40 cm depths), and functional group or species were included as additional fixed factors, also nested within plot, for tests of treatment effects on foliar elements, ANPP/biomass and phenology. We used repeated measures ANOVA to examine changes in environmental variables over the growing season and ANPP and biomass changes between years, with plot as the unit of replication for time effects. Family-wise error rates were controlled using the Hochberg method for planned contrasts or Tukey 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 WARMING

Winter warming increased wintertime soil temperatures across the soil depth profile. In 2010, WW increased soil temperature (5–40 cm depth) by 2.3 ± 0.4 °C from December to March, when average ambient soil temperature was -6.2 ± 0.1 °C. Differences were significant in December for 5 and 10 cm depths, and from January to March for all depths ($P < 0.05$ for all; Fig. S2). Surprisingly, warming effects continued into the growing season when deep-soil (40 cm) temperatures were higher with WW (2.9 ± 0.6 °C) than control (1.6 ± 0.2 °C) during the months of July and August ($P < 0.05$). As expected, soil temperatures differed among depths ($F = 210.0$, $P < 0.001$) and months ($F = 488.3$, $P < 0.001$). Winter warming effects on soil temperature resulted in a *c.* 10% (2.9 ± 0.9 cm) increase in growing season thaw depth ($F = 31.02$, $P < 0.001$; Fig. S3). In late September, 2010, maximum active layer depth was 58.2 ± 0.7 in control plots and 65.3 ± 1.7 in WW plots. There was no detected effect of SW on thaw depth ($F = 0.58$, $P = 0.464$) or soil temperature ($F = 0.17$, $P = 0.685$). Wintertime soil temperature was *c.* 3 °C lower in 2010 than in 2009, while growing season soil temperature and thaw depth were slightly higher in 2010 than in 2009; despite these differences, warming effects were similar across years (Table S1).

Average air temperature in the SW plots (12.4 ± 0.1 °C) was significantly warmer than control (11.9 ± 0.1 °C) during all months of the 2010 growing season ($F = 5.47$, $P = 0.020$). Temperature differences were greatest mid-day (11:00–15:00), when SW plots were 1.0 ± 0.1 °C warmer than control ($F = 18.26$, $P < 0.001$). Air temperatures in 2010 were

slightly higher than 2009, but the magnitude of the SW effect was similar across years (Table S1).

In addition to direct effects of warming on temperature and active layer depth, WW also altered soil moisture, which probably resulted from surface subsidence in the WW plots. Winter warming increased depth-integrated soil moisture from June to September of 2010 ($F = 5.54$, $P = 0.029$); there was also a significant SW × WW effect (SW × WW × month; $F = 3.46$, $P = 0.022$), with lowest moisture content in Ambient plots and highest in Annual plots. Surface moisture (2010) was also slightly, but not significantly, higher with warming (Fig. S4). Winter warming effects on soil moisture were reflected in water-table depths, which were closer to the ground surface (nonsignificant) in WW (16.7 ± 1.7 cm) than control plots (19.3 ± 1.1) throughout the 2010 growing season (Table S1, Fig. S4). In 2009, winter warming similarly affected soil moisture, resulting in significant differences in water-table depth (Table S1).

ABOVE-GROUND NET PRIMARY PRODUCTIVITY AND BIOMASS

The environmental effects caused by the WW treatment led to significant increases in plant growth. Winter warming increased both total above-ground biomass ($F = 5.53$, $P = 0.023$) and ANPP ($F = 2.87$, $P = 0.096$) after 2 years of warming (Fig. 1a,b). In the WW plots, above-ground biomass and ANPP were 20% and 40% higher, respectively, in 2010 compared to 2009 (biomass: $F = 46.14$, $P < 0.001$; ANPP: $F = 33.71$, $P < 0.001$), while there was no change between years in the control plots. In contrast to the strong effect of WW on plant growth, there was no observed SW effect on biomass ($F = 0.01$, $P = 0.92$) or ANPP ($F = 0.05$, $P = 0.82$).

The observed WW effects on ANPP were driven by enhanced graminoid growth in the WW plots after 2 years of warming ($F = 37.02$, $P < 0.01$; Fig. 1c–f), while there was no difference across years in control plots for this functional group. These changes were primarily due to increased *E. vaginatum* ANPP, which was almost 40% higher in WW plots compared to control in 2010 ($F = 18.78$, $P < 0.001$, Table 1). While there were no significant SW effects on species or functional group ANPP in our repeated measures analyses, we also ran individual ANOVAs on each species and functional group within each year to examine shifting trends in ANPP across the plant community. In 2009, *E. nigrum* ANPP declined with SW, while in 2010 evergreen ANPP, and *R. subarcticum* in particular, were significantly higher in the Annual plots relative to Ambient ($P < 0.05$; Table 1). Warming effects on above-ground biomass at the functional group and species level were similar to these ANPP results (Table S2). As expected, both ANPP and biomass were significantly different among species and functional groups ($P < 0.001$ for all).

LEAF AND SOIL C AND N

Consistent with warming effects on plant productivity, WW significantly increased the total mass of N in green foliage
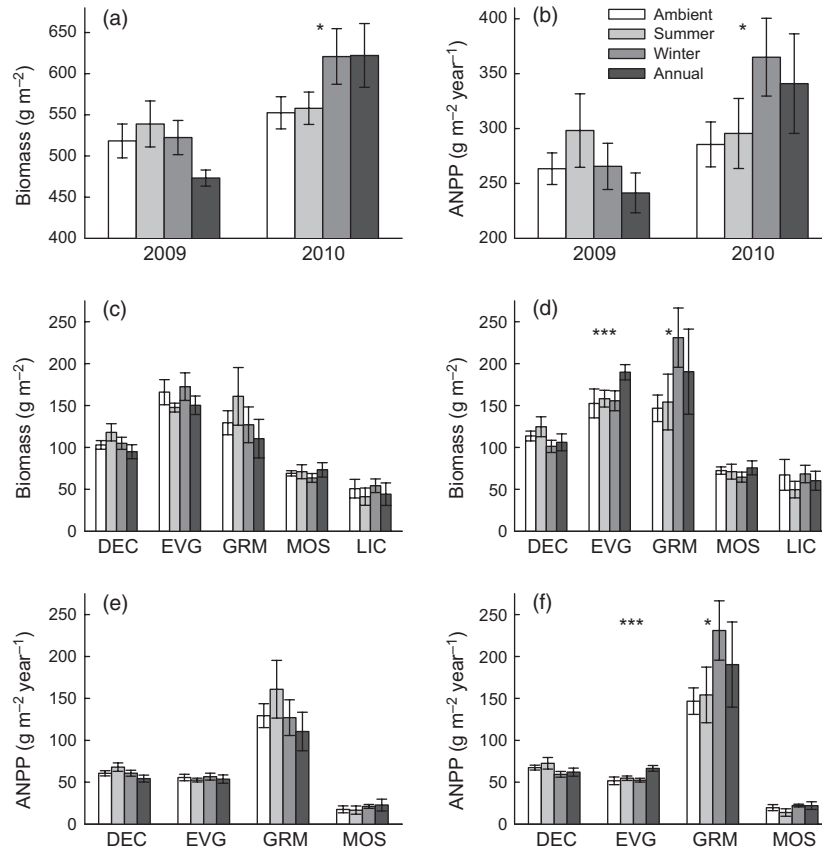
Fig. 1. Warming effects on (a) total above-ground biomass; (b) total ANPP; functional group biomass in (c) 2009 and (d) 2010; and functional group ANPP in (e) 2009 and (f) 2010. Abbreviations as follows: deciduous (DEC), evergreen (EVG), graminoids (GRM), moss (MOS), and lichen (LIC). Significant differences: *WW effect; **SW effect; ***WW × SW interaction effect.

Table 1. Above-ground net primary productivity (g biomass m^{-2} year^{-1} ± SE) for ambient and warmed plots at Carbon in Permafrost Experimental Heating Research in 2009 and 2010*

	2009				2010			
	Ambient	Summer	Winter	Annual	Ambient	Summer	Winter	Annual
Graminoid	129.4 ± 14.3	160.9 ± 34.4	127.0 ± 21.3	110.5 ± 23.0	**146.7 ± 15.8^w**	154.2 ± 33.2	**231.0 ± 35.3**	**190.3 ± 50.9**
Eriophorum vaginatum	113.4 ± 11.9	139.9 ± 36.5	104.3 ± 21.2	86.9 ± 25.9	**130.8 ± 16.5^w**	130.8 ± 34.9	**203.2 ± 36.8**	**163.0 ± 54.4**
Carex bigelowii	16.0 ± 2.6	21.1 ± 3.8	22.7 ± 2.9	23.5 ± 3.8	15.9 ± 2.3	23.4 ± 4.3	27.8 ± 3.6	27.3 ± 3.8
Deciduous	60.6 ± 3.1	68.0 ± 5.0	60.7 ± 3.5	54.3 ± 4.2	67.4 ± 2.9	72.6 ± 6.9	59.4 ± 3.4	62.0 ± 4.9
Betula nana	9.6 ± 2.1	11.3 ± 2.8	11.8 ± 2.9	13.0 ± 3.5	10.5 ± 2.7	13.0 ± 2.7	9.01 ± 2.8	11.0 ± 2.8
Rubus chamaemorus	14.7 ± 1.4	13.7 ± 0.9	13.9 ± 1.0	12.8 ± 0.9	17.2 ± 3.8	16.8 ± 1.6	13.6 ± 0.4	14.7 ± 0.7
Vaccinium uliginosum	36.6 ± 2.8	43.0 ± 4.3	35.0 ± 2.1	28.6 ± 4.0	40.0 ± 5.2	42.8 ± 6.1	36.8 ± 3.1	36.3 ± 4.1
Evergreen	55.7 ± 3.9	52.5 ± 2.2	56.7 ± 4.2	53.7 ± 5.0	**51.7 ± 4.7$^{s × w}$**	54.8 ± 2.7	52.4 ± 2.2	**66.5 ± 3.5***
Andromeda polifolia	5.2 ± 0.7	5.1 ± 0.4	5.2 ± 0.3	4.5 ± 0.1	4.8 ± 0.4	5.1 ± 0.5	4.6 ± 0.2	4.7 ± 0.2
Empetrum nigrum	**12.1 ± 3.6^s**	**6.5 ± 1.5**	12.6 ± 5.1	**6.7 ± 1.5**	9.9 ± 3.3	8.4 ± 2.4	9.6 ± 4.0	8.7 ± 2.3
Rhododendron subarcticum	19.1 ± 3.8	19.6 ± 2.4	23.5 ± 4.1	20.2 ± 2.2	**19.3 ± 2.5$^{s × w}$**	21.8 ± 1.5	22.4 ± 1.8	**30.0 ± 2.5***
Vaccinium vitis idaea	14.7 ± 2.5	16.7 ± 2.9	11.7 ± 1.2	18.8 ± 4.0	13.6 ± 1.7	14.5 ± 2.6	12.7 ± 1.9	19.2 ± 2.6
Oxycoccus microcarpus	4.6 ± 0.9	4.6 ± 0.7	3.7 ± 0.6	3.5 ± 0.3	4.1 ± 0.6	5.0 ± 0.9	3.1 ± 0.1	3.9 ± 0.5
All Vascular	245.8 ± 14.1	281.5 ± 33.9	244.4 ± 21.7	218.6 ± 21.7	**265.8 ± 19.8^w**	281.6 ± 33.5	**342.8 ± 35.1**	**318.8 ± 47.6**
Mosses	17.6 ± 4.2	16.7 ± 4.9	21.2 ± 2.3	22.8 ± 7.0	19.7 ± 3.6	13.9 ± 4.4	22.2 ± 1.7	22.1 ± 4.5
Total†	263.4 ± 14.4	298.2 ± 33.5	265.6 ± 21.1	241.4 ± 18.1	**285.5 ± 20.4^w**	295.5 ± 31.9	**365.0 ± 35.5**	**340.9 ± 45.3**

*S, significant SW effect; W, significant WW effect; S × W, significant interaction effect. When interaction effect, warming treatment that differed from ambient. All significant effects (bold values) at *P* < 0.05.
†Lichen was not included in ANPP calculations. Biomass values for all species can be found in Table S1.
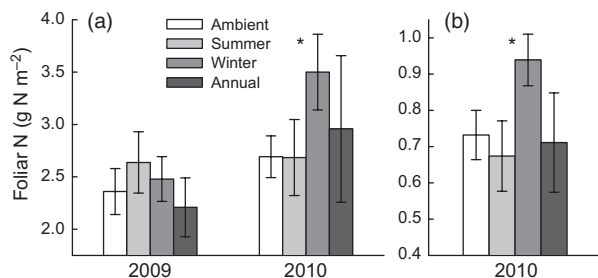
Fig. 2. Warming effects on (a) N mass in green foliage and (b) in senescent leaves. Green leaf N mass represents the sum of six main species found across plots: *Betula nana*, *Carex bigelowii*, *Eriophorum vaginatum*, *Rhododendron subarcticum*, *Rubus chamaemorus* and *Vaccinium uliginosum*. Senescent leaf N mass included these same species with the exception of *R. subarcticum*. Significance noted as in Fig. 1.

(Fig. 2). Foliar N mass in WW plots was significantly greater in 2010 compared to 2009 ($F = 11.09$, $P = 0.003$), while there was no change across years in the control plots ($F = 0.51$, $P = 0.484$). This increase in canopy N was primarily a result of higher biomass, and ANPP as green leaf % N was not significantly affected by WW treatment ($F = 0.04$, $P = 0.853$; Table S3). Changes in canopy N were driven by higher foliar N mass in the graminoids, where *E. vaginatum* canopy N was almost 70% greater in WW plots (2.33 ± 0.43 g Nm^{-2}) than control (1.38 ± 0.21 g Nm^{-2}; $F = 3.82$, $P = 0.053$), and *C. bigelowii* foliar mass was 40% greater in WW plots (0.40 ± 0.04 g Nm^{-2}) than control (0.28 ± 0.05 g Nm^{-2}; $F = 4.92$, $P = 0.028$). Litter N mass also increased in the WW plots in 2010 (Fig. 2), driven by a 50% increase in *E. vaginatum* litter N mass in the WW plots (0.48 ± 0.07 g Nm^{-2}) relative to control (0.32 ± 0.04 g Nm^{-2}; $F = 14.13$, $P < 0.001$). As with canopy N, the increase in litter N input was driven primarily by increased ANPP, as resorption proficiency (i.e. % N in senescence leaves) and efficiency did not change for most species, with the exception of *C. bigelowii*, which had higher % N in senescent leaves and lower resorption efficiency with WW ($P < 0.05$ for both; Table S4).

While changes in plant N uptake were dominated by the WW treatment, both SW and WW altered plant N dynamics, as reflected in foliar δ^{15}N (Table S3). There was a significant WW × SW interaction effect on foliar δ^{15}N for *B. nana* ($F = 8.93$, $P < 0.001$) and *E. vaginatum* in 2010 ($F = 2.79$, $P = 0.045$), driven by differences in the Annual plots where *B. nana* δ^{15}N decreased and *E. vaginatum* δ^{15}N increased relative to all other treatments ($P < 0.05$ for all comparisons). *C. bigelowii* δ^{15}N also increased in the SW plots ($F = 2.77$, $P = 0.099$), and both SW and WW increased δ^{15}N in *R. chamaemorus*. There was also a slight, but significant, increase in *B. nana* δ^{13}C ($F = 5.85$, $P = 0.017$) and a decrease in *R. subarcticum* δ^{13}C with SW ($F = 3.39$, $P = 0.068$). In 2009, there were no WW effects on green leaf elements and isotopes, but there were significant differences between SW and control plots (Tables S3). In both years, there were strong differences among species for all foliar variables measured ($P < 0.001$).

In contrast to observed WW effects on canopy N, SW alone affected resin-available N (Fig. S5). In 2010, SW decreased resin NH$_4^+$ ($F = 4.24$, $P = 0.048$) and TDIN ($F = 4.73$, $P = 0.036$) by almost 40%, but there was no change in NO$_3^-$ ($F = 0.32$, $P = 0.577$). Warming effects on resin N in 2009 were similar to 2010 trends (Fig. S5).

LEAF PHENOLOGY AND REPRODUCTIVE EFFORT

Warming advanced bud break and delayed senescence in 2010 for all species measured, despite similar snowmelt dates across treatments. Bud break occurred earlier with WW in *C. bigelowii* ($F = 4.23$, $P < 0.042$), and both SW and WW advanced bud break in *B. nana* ($F = 10.48$, $P < 0.001$) and *V. uliginosum* ($F = 6.47$, $P < 0.001$, Fig. 3a). *B. nana* bud break occurred significantly earlier in all warming plots compared to Ambient, and *V. uliginosum* bud break was earlier in Winter and Annual plots compared to Ambient ($P < 0.05$ for all).

Both warming treatments also extended the end of the growing season by delaying senescence. Senescence occurred latest in the Annual plots in all species except *B. nana*, where there was no observed difference among treatments. Warming significantly delayed completion of senescence in *R. chamaemorus* (SW: $F = 7.40$, $P = 0.009$), *C. bigelowii* (SW: $F = 6.71$, $P = 0.014$; WW: $F = 4.41$, $P = 0.070$), *E. vaginatum* (SW: $F = 3.71$, $P = 0.058$; WW: $F = 23.86$, $P < 0.001$), and while not significant, similar trends were observed for *V. uliginosum* (Fig. 3b–c). These observed changes in senescence were supported by late-season NDVI values, which were significantly higher in WW plots compared to control ($F = 5.11$, $P = 0.037$; Fig. 3d). No NDVI differences were observed in 2009 ($P > 0.1$ for all), and while we did not record leaf phenology in 2009, no differences were observed in the field (S. Natali, pers. obs.).

In addition to increasing growing season length, warming also enhanced reproductive effort in most species. Both WW and SW increased flower production in *R. subarcticum* (WW: $F = 9.10$, $P = 0.030$; WW × SW; $F = 13.75$, $P < 0.001$). Winter warming also increased flower production in *C. bigelowii* ($F = 5.08$, $P = 0.030$) and *E. vaginatum* ($F = 5.17$, $P = 0.053$), but we detected no SW effect in these species (Fig. 4a). Warming effects on fruit production in 2010 were consistent with flowering results (Fig. 4c). Berry production increased in *V. uliginosum* ($F = 17.08$, $P = 0.002$) and *V. vitis idaea* ($F = 4.32$, $P = 0.071$) in response to WW, but there were no SW effects. As with flowering, warming did not alter *R. chamaemorus* berry production. Fruit production in 2009 did not differ among treatments (Fig. 4b).

Discussion

Changes in the soil environment brought about by winter warming treatment increased above-ground biomass and plant productivity by 20% compared to control plots in 2010, and this increase was associated with significantly higher canopy N. While moist acidic tundra are strongly N limited, nutrient limitation may be attenuated as warming temperatures
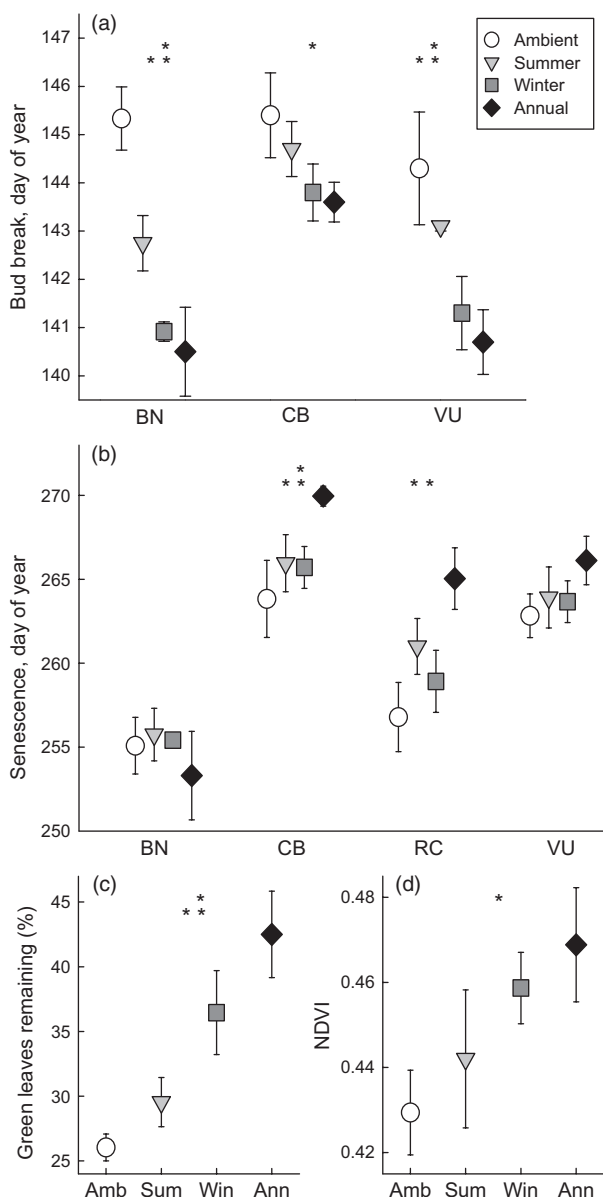
Fig. 3. Warming effects on date of plot-level (a) bud break; (b) complete senescence; (c) percentage green leaves remaining on *Eriophorum vaginatum* tussocks (23 September); and (d) NDVI values on 23 September 2010. Species abbreviations as follows: *Betula nana* (BN), *Carex bigelowii* (CB), *Vaccinium uliginosum* (VU) and *Rubus chamaemorus* (RC). Significance noted as in Fig. 1.

dicted to increase as the climate warms (Rustad *et al.* 2001). However, annual ecosystem respiration losses may be greater than photosynthetic gains (Grogan & Jonasson 2006; Larsen *et al.* 2007; Natali *et al.* 2011) so that plant C uptake may offset some, but not all, respiratory losses associated with climate warming.

In contrast to the strong effect of winter warming on productivity and ecosystem N pools, summer warming had no detected effect on above-ground biomass, ANPP or canopy N, similar to previous air-warming experiments. In these earlier studies, warming with greenhouses and OTCs caused shifts in species dominance, but individual species-level responses often offset one another so that effects at the ecosystem level were limited (Chapin *et al.* 1995). Furthermore, in studies that manipulated both air temperature and soil nutrients, ecosystem-level effects of warming were small in contrast to fertilization effects (Chapin *et al.* 1995; Dormann & Woodin 2002; van Wijk *et al.* 2004). These results highlight the unique experimental design of CiPEHR, which achieves whole ecosystem warming and surface permafrost degradation that more closely simulates future climate warming scenarios for this region.

Surprisingly, summer warming significantly decreased resin-available N, which was probably mediated by warming effects on plant processes since summer warming altered air but not soil temperatures. The negative effect of summer warming on resin-available N may have been driven by an increase in microbial competition for N or potential ion losses from the exchange resins during deployment (Giblin *et al.* 1994). The opposing responses of canopy and resin N call into question the ability of ion exchange resins to measure the plant-available N pool; our results suggest that resin-available N may not be capturing soil N dynamics from the full soil profile or tracking plant-available soil N.

Changes in total above-ground biomass and ANPP with winter warming at CiPEHR were dominated by enhanced graminoid growth. This result supports the hypothesis that warming temperatures in the Arctic will have the strongest effect on deciduous species, which, because of faster rates of leaf turnover than evergreen species, have a higher capacity to respond to biological and environmental changes (Aerts & Chapin 2000). Several other warming studies have found similarly strong growth responses from graminoids to both air (Arft *et al.* 1999) and soil warming (Brooker & van der Wal 2003). In contrast to our study, long-term snow additions at Toolik Lake, AK, negatively affected *E. vaginatum* growth and survival (Borner, Kielland & Walker 2008); however, the additional snow at the Toolik experiment was not removed from the experimental plots, which resulted in a 2-week delay in melt-out. Species with early season development, such as *E. vaginatum,* may be particularly sensitive to snowmelt date (Wipf 2010). While we did not measure below-ground production and growth, we expect that observed increases in graminoid biomass and ANPP at CiPEHR underestimated total plant response, since root allocation in tundra graminoids increases with higher air and soil temperatures (Kummerow & Ellis 1984). Future research efforts are needed to quantify
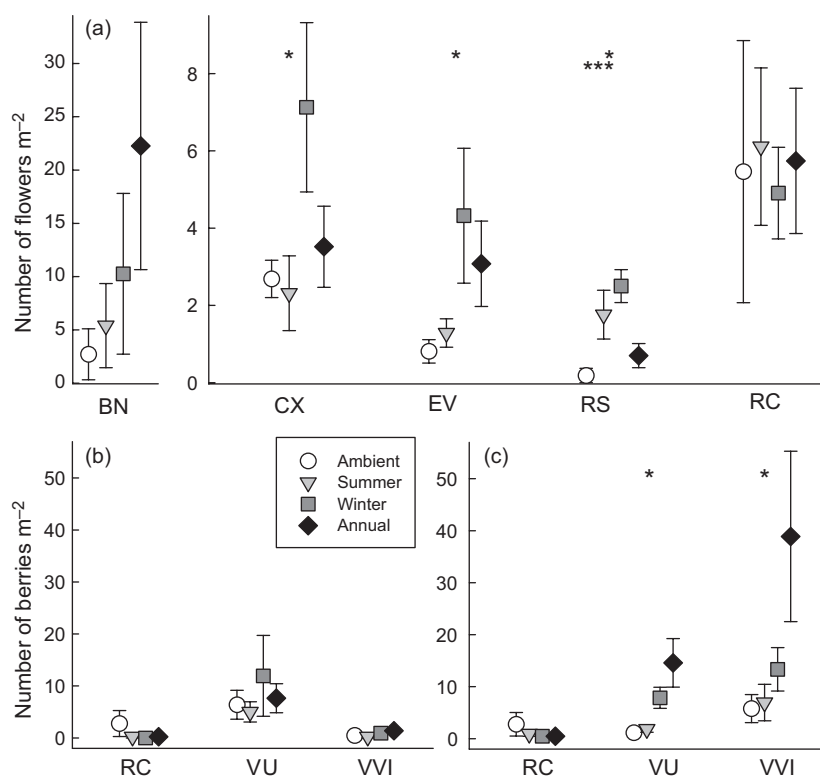
accelerate rates of organic matter decomposition and N mineralization (Rustad *et al.* 2001; Schimel, Bilbrough & Welker 2004; Aerts, Cornelissen & Dorrepaal 2006). Nitrogen cycling in tundra plants and soils is tightly integrated so that plant N uptake closely tracks soil N mineralization (Rastetter *et al.* 1991). While winter warming treatment did not increase resin-available N, the observed increase in canopy N suggests that winter warming increased soil N availability as a result of enhanced rates of N mineralization and/or an increase in the thawed soil N pool. The effects of winter warming on ecosystem productivity and N availability highlight the potential for plant C uptake to offset respiratory C losses, which are pre-

Fig. 4. Warming effects on (a) flower production in 2010 and berry production in (b) 2009 and (c) 2010. Mean flower or inflorescence production was analysed for the following species, followed by the day of year when flower production peaked: *Betula nana* (BN, 143), *Carex bigelowii* (CX, 162), *Eriophorum vaginatum* (EV, 131), *Rhododendron subarcticum* (RS, 162) and *Rubus chamaemorus* (RC, 155). Berry production was measured for *R. chamaemorus*, (RC), *Vaccinium uliginosum* (VU) and *V. vitis idaea* (VVI). Significance noted as in Fig. 1.

warming impacts on C allocation and root production because changes in below-ground plant biomass can have a profound effect on ecosystem C storage.

We did not detect a positive warming effect on deciduous shrub production, as has been found in long-term nutrient experiments (Chapin & Shaver 1996; Shaver *et al.* 2001); however, a warming-mediated decrease in *B. nana* foliar δ^{15}N indicates a shift in N dynamics, which may, over longer timescales, positively affect plant growth. The decrease in *B. nana* foliar δ^{15}N may have been driven by changes in the ectomycorrhizal fungal community (Deslippe *et al.* 2011) and a subsequent increase in the transfer of ^{15}N-depleted organic N through mycorrhizal networks (Hobbie & Hobbie 2008). In contrast, warming increased foliar δ^{15}N in several graminoid and forb species (*E. vaginatum*, *C. bigelowii* and *R. chamaemorus*). These changes in foliar δ^{15}N can result from an increase in inorganic N availability (Craine *et al.* 2009), change in rooting depth (Nadelhoffer *et al.* 1996), or changes in N sources to the plant community (Evans 2001; Robinson 2001). While further research is needed to discern the exact mechanism of the observed shifts in foliar δ^{15}N, these species and functional group-specific responses indicate resource shifts, which may drive changes in the plant community as the climate warms.

Observed changes in plant N dynamics at CiPEHR may be further accelerated by warming-mediated changes in litter biomass and composition (Hobbie & Chapin 1998). Despite the lack of warming effects on foliar N concentrations, variation

in foliar N across species and functional groups, coupled with shifts in species abundance, may significantly impact the distribution and cycling of N in this system. With the exception of *C. bigelowii*, we detected no change in litter N concentrations, yet warming-mediated changes in litter biomass and composition significantly increased N mass returned to soils in leaf litter. The predominant increase in graminoid litter in the winter warming treatment may further alter N cycling because graminoid litter decomposes faster than other functional groups (Hobbie 1996).

In combination with observed changes in ecosystem N dynamics, plant growth at CiPEHR may also have been stimulated by warming-mediated shifts in leaf phenology. In the winter warming plots, where higher soil temperatures are expected to enhance wintertime N mineralization (Schimel, Bilbrough & Welker 2004), earlier leaf-out and growth may have increased plant access to early-growing-season N pools. However, while phenological shifts can contribute to higher plant productivity by extending the time period when plants can assimilate C, earlier bud break and delayed senescence will not necessarily translate into greater plant productivity if N limitation persists. In the case of our summer warming treatment, in which phenological shifts were not accompanied by an increase in canopy N, the short-term benefit of advanced leaf-out may have limited plant growth later in the season. An increase in plant N pools in the winter warming treatment, combined with phenological shifts,

together supported higher plant growth throughout the growing season. While the delay in senescence observed at CiPEHR in the second year of warming would not have affected biomass accumulation to date, these late-season dynamics may be important for plant C stores in subsequent growing seasons.

The observed warming effects on leaf phenology at CiPEHR lend insight into processes governing bud break and senescence in northern latitude ecosystems. Accelerated bud break and early season plant growth, which have been observed across the Arctic over the past few decades, have been attributed to earlier snowmelt and warmer air temperatures (Myneni *et al.* 1997; Arft *et al.* 1999; Walker, Billings & De Molenaar 2001; Wipf 2010). An observational study in an alpine ecosystem suggested a relationship between phenology and soil temperature (Holway & Ward 1965); however, in that study, higher soil temperature co-occurred with snowpack retreat, confounding the effect of these two variables on phenology. Results from CiPEHR, where soil temperature and active layer increased but snowmelt date was held constant, demonstrate direct effects of warmer soil temperature or advanced soil thawing on early-season leaf phenology in northern latitude tundra. Furthermore, while previous studies found that warming of air and surface soils had limited effect on late-season leaf phenology (Arft *et al.* 1999), our results show that warming significantly delayed senescence, with the strongest effect in the combined summer and winter warming treatment (i.e. Annual warming). This result is in agreement with that by Marchand *et al.* (2004), who found that air and soil warming significantly delayed the loss of green cover in high Arctic tundra. While photoperiod plays a role in initiating senescence, our results demonstrate that temperature and soil resources play a key role in controlling the duration of plant senescence in this ecosystem.

The effects of winter warming treatment on reproductive effort also point to an alleviation of N limitation with warmer soils and degrading permafrost; increased reproductive effort requires a higher nutrient investment, and without a concomitant increase in N availability, higher reproductive investment should occur at the cost of vegetative growth (Bazzaz *et al.* 1987; Aerts & Chapin 2000). Winter warming may have also enhanced reproductive effort through protection of overwintering reproductive buds by the insulating layer of the snowpack (Bokhorst *et al.* 2008). However, we observed no change in flower (S. Natali, pers. obs.) or berry production after the first year of warming, which suggests that warming effects on reproductive investment resulted from increased production rather than decreased loss of reproductive buds. The 1-year time-lag of warming effects on reproductive effort is not surprising because several tundra plant species form flowering buds in the year prior to flowering (Mark & Chapin 1989). In a meta-analysis of ITEX experiments, Arft *et al.* (1999) found that reproductive and vegetative responses of plants to warming varied across climatic zone and suggest that in the low Arctic, where seedling establishment opportunities are lower because of a closed plant canopy, allocation to vegetative growth should be favoured. However, at CiPEHR, where canopy cover is complete, we found that winter warming increased both reproductive and vegetative growth, which were probably supported by increased N availability. These results highlight the importance of changes in the soil environment, including nutrient availability, in determining tundra plant responses to a changing climate.

Conclusions

This study examined the responses of plant productivity and biomass to experimental warming of air, soil and permafrost in moist acidic tundra. The CiPEHR project is the first warming experiment to degrade permafrost without additional water inputs or delayed snow melt. We hypothesized that warming would increase ecosystem-level plant productivity, but only if nutrient availability also increased with warming. Changes in the soil environment brought about by the winter warming treatment increased plant-available N, extended the period between bud break and senescence, and led to an increase in above-ground C accumulation. While summer warming also caused phenological shifts and altered species-level ANPP, we detected no ecosystem-level increases in plant productivity with summer warming, which we attribute to continued N limitation in the summer warming plots. These results highlight the role of soil and permafrost dynamics in regulating plant response to climate change and suggest that phenological shifts coupled with increased nutrient availability may promote greater C accumulation in tundra plant biomass. Climate-induced changes in tundra plant communities is of critical concern because permafrost systems play a key role in global C storage, and as demonstrated from this study, increased plant C uptake has a strong potential to offset some respiratory losses expected as the climate warms.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Warming effects on environmental variables measured at CiPEHR in 2009 and 2010.

Table S2. Warming effects on aboveground biomass.

Table S3. Foliar C and N concentrations and isotopes in peak growing season leaves.

Table S4. Nitrogen concentration and mass in senescent leaves.

Figure S1. Warming effects on moss net primary productivity.

Figure S2. Winter warming effects on soil temperatures.

Figure S3. Winter warming effects on thaw depth.

Figure S4. Growing season trends and warming effects on soil moisture and water table depth.

Figure S5. Resin-available inorganic N in warming and control plots at CiPEHR.

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