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Experimental Warming Alters Productivity and Isotopic Signatures of Tundra Mosses

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ABSTRACT

In the tundra, mosses play an important functional role regulating belowground and ecosystem processes, but there is still considerable uncertainty about how tundra moss communities will respond to climate change. We examined the effects of 5 years of *in situ* air and soil warming on net primary productivity (NPP), carbon (C) and nitrogen (N) isotope signatures (δ^{13}C and δ^{15}N), and C:N in dominant Alaskan tundra mosses. Air warming increased mean air temperatures by up to 0.5°C and resulted in an 80–90% reduction in NPP in the feather moss *Pleurozium* and the peat moss *Sphagnum*. Soil warming increased permafrost thaw depth by 12–18%, upper soil water content by 23–27%, and resulted in a threefold increase in *Sphagnum* NPP. δ^{13}C was positively correlated with moss NPP, and increased by 0.5–1‰ in all mosses under soil warming. C:N was reduced in *Sphagnum* and *Pleurozium*, due to increases in tissue %N in the soil warming treatment, suggesting that moss N availability could increase as temperatures increases. Higher N availability in warmer conditions, however, may be offset by unfavorable moisture conditions for moss growth. Similar to responses in tundra vascular plant communities, our results forecast interspecific differences in productivity among tundra mosses. Specifically, air warming may reduce productivity in *Sphagnum* and *Pleurozium*, but soil warming could offset this response in *Sphagnum*. Such responses may lead to changes in tundra moss community structure and function as temperatures increase that have the potential to alter tundra C and N cycling in a future climate.

Key words: global change; permafrost; bryophytes; *Sphagnum*; *Pleurozium*; *Dicranum*; NPP; δ^{13}C; δ^{15}N.

INTRODUCTION

Climate change is projected to be the greatest and most rapid in the high latitudes (Houghton and others 1996; IPCC 2013). Temperature increases in the tundra are projected to be twice that of the global mean (ACIA 2004), and tundra plant communities and ecosystems often display directional responses to warming (Epstein and others 2004;

Hudson and Henry 2009; Elmendorf and others 2012a). There is now substantial evidence from passive warming experiments in the tundra that vascular plant biomass and growth are affected by increased temperatures (Chapin and others 1995; Chapin and Shaver 1996; Hobbie and Chapin 1998; Borner and others 2008). In particular, warming is resulting in an increase in cover of graminoids and deciduous shrubs (Arft and others 1999; Brooker and van derWal 2003; Walker and others 2006; Elmendorf and others 2012b; Natali and others 2012), as well as woody shrub expansion into novel habitats (Tape and others 2006; Forbes and others 2010).

In the tundra, deep soils are frozen year-round as permafrost, and a shallow annual thaw (< 1 m) creates a seasonally variable active layer. Processes occurring just above the active layer at the soil surface exert strong regulatory control on feedbacks and exchange between tundra soils and the atmosphere. Soil surfaces in the tundra are nearly always covered by a thick and diverse photosynthetic layer dominated by mosses. This moss layer regulates soil temperature and moisture (Beringer and others 2001; Gornall and others 2007; Soudzilovskaia and others 2013), and in doing so controls water availability to plant and soil organisms as well as evaporative losses to the atmosphere. Mosses living in this layer also can dominate ecosystem carbon (C) inputs during spring and fall (Campioli and others 2009), when vascular plants are the least active, which influences ecosystem C balance (Beringer and others 2001; Gornall and others 2007; Rydin and Jeglum 2013; Lindo and others 2013; Street and others 2013). In addition to contributing to C cycling, mosses can alter nitrogen (N) cycling of tundra ecosystems. Two of the dominant functional types, feather mosses and peat mosses, commonly associate with N_2-fixing cyanobacteria, which represents a substantial N source of tundra ecosystems (Solheim and others 1996; DeLuca and others 2002, 2007; Markham 2009). Given their known importance as an intrinsic ecological component of high latitude ecosystems, changes in productivity and species composition of tundra mosses are likely have a profound impact on regional biogeochemistry and feedbacks to global climate.

In spite of their ecological role, it is still unclear how mosses in high latitude ecosystems will respond to projected change. Abundance of tundra peat mosses (for example, *Sphagnum*) and feather mosses (for example, *Pleurozium*) has been shown to increase as a function of temperature along natural gradients (Gunnarsson 2005; Hudson and Henry 2009; Lang and others 2012). But abundance and cover of these mosses remains unchanged, or, more commonly, decreases as a function of temperature in experimental warming studies (Press and others 1998; Wahren and others 2005; Walker and others 2006; Lang and others 2012). These contrasting results may arise because moss functioning is seldom directly addressed in most tundra warming experiments that are primarily designed to assess vascular plant or soil responses to increased temperatures.

Productivity in many mosses is governed by environmental water availability because tissue water content varies passively with the surrounding environment, and physiological performance and growth can be limited at both high and low ends of the spectrum (Dilks and Proctor 1979; Rice and Giles 1996; Williams and Flanagan 1996; Toet and others 2006; Coe and others 2012). Mosses also typically display the majority of their annual growth during the shoulder seasons (just before and just after the growing season), where they are often photosynthetically active under snowpack and can account for up to 25% of net aboveground carbon accumulation (Campioli and others 2009). Although long-term temperature manipulation experiments in the northern latitudes over the last 30 years have been ecologically extremely informative (van Wijk and others 2004; Elmendorf and others 2012b), most experimental warming in the tundra has taken place during the growing season only (for example, Chapin and Shaver 1985; Press and others 1998; Hobbie and others 1999). The few designs that have successfully increased winter temperatures do so using increased snow depth (for example, Wahren and others 2005), but the spring melt-out from the larger snowpack simultaneously delays the start of the growing season and increases ecosystem moisture inputs. Temperature increases are very likely to influence water availability to, and hence productivity of, tundra mosses, especially in areas undergoing permafrost thaw and subsidence (Camill and others 2001), but temperature manipulations confounded by unintended moisture alterations make it difficult to discern causation of plant responses.

Tundra mosses also have very different growth forms relative to their vascular neighbors: they grow as loose lateral mats, dense turfs, or deep hummocks, and most do not possess annual growth markers. Changes in moss biomass and productivity under warming conditions, therefore, may not be reflected in traditional sampling techniques for vascular plants (Henry and Molau 1997; van Wijk and others 2004; Elmendorf and others

2012b). Analyses of stable C and N isotopes in moss tissues have the potential to provide information on moss nutrient status and productivity, particularly if combined with moss-specific net primary productivity (NPP) measurements.

Because of the confounding influences of increased temperature and increased water availability in previous warming studies, and the limitations of traditional plant sampling techniques, it has thus far been extremely challenging to draw conclusions for moss response to warming in the tundra. Here, we examined the influence of warming temperatures on three dominant Alaskan tundra moss genera, *Sphagnum*, *Pleurozium*, and *Dicranum*, using a long-term field experiment that increased temperatures on an annual basis using soil warming (during the winter, via passive insulation with snow) combined with air warming (during the growing season) without manipulating ecosystem moisture inputs (see Natali and others 2011). We examined changes in moss NPP, C and N isotopic signatures, and C:N after 4 and 5 years of warming. Based on the relationship between tissue water content and productivity in mosses, we hypothesized that (1) air warming would result in reductions in moss productivity, because higher air temperatures that may increase potential evapotranspiration could function to reduce water availability to mosses; but (2) soil warming would result in increased moss productivity, because in the absence of air warming mosses would not be limited by temperature or water availability and might also benefit from increased soil N. Further, because *Sphagnum*, *Pleurozium*, and *Dicranum* differ in relative growth rates and tolerance to altered hydrologic environment, we predicted that the relative magnitude of responses to warming would differ across moss taxa and would be reflected in C and N isotopic signatures.

METHODS

Site Description

The Carbon in Permafrost Experimental Heating Research (CiPEHR) project, established in 2008, is located at the Eight Mile Lake study site in the Northern foothills of the Alaska Range (63°52′59′N, 149°13′32′W, c. 700 m elevation). Mean monthly temperatures range from −16°C in December to +15°C in July, with a historic mean annual temperature (1976–2013) of −1.0°C and more recent (2004–2013) mean annual temperature of −2.7°C. The site is positioned on moist acidic tundra with Gelisol soils composed of a 0.45–0.64 m thick organic horizon above a cryoturbated mineral soil. The active layer (c. 50–60 cm thick) thaws annu-

ally during the growing season, and is situated above a perennially frozen layer of permafrost. For additional site details please refer to Schuur and others (2007, 2009) and Natali and others (2011).

Dominant vascular plants at the site are the tussock-forming sedge *Eriophorum vaginatum*, the deciduous shrubs *Betula nana* and *Vaccinium uliginosum*, and the evergreen groundcovers *V. vitis idaea* and *Rhododendron subarcticum*. Common lichen genera include *Cladonia*, *Cetraria*, *Flavocetraria*, and *Peltigera*. The three dominant mosses at the site are *Sphagnum fuscum*, *Pleurozium schreberi*, and *Dicranum* spp. Other common mosses include *Aulacomnium turgidum*, *A. pallustre*, *Hylocomium splendens*, *Polytrichum commune*, *P. strictum*, *S. squarrosum*, *S. magellanicum*, *S. girghonsonii*, *S. cuspidatum*, and *S. compactum*.

Experimental Design

Soil warming was achieved using snow fences (1.5 m tall × 8 m long, n = 6) placed perpendicular to the prevailing wind direction that trapped insulating layers of snow during the winter. To control water input during snowmelt in warming plots, and to enable us to isolate warming effects from moisture effects or delayed phenology, excess snowpack was removed from warming plots before spring thaw. All plots were snow-free by 1 May in 2009–2012 and by 1 June in 2013.

Each soil warming and control treatment area within a treatment pair (on either side of a snow fence) contained four plots: two air warming plots and two control plots (n = 24 each, across 6 fences). Air warming was applied during the growing season using plexiglass open top chambers (0.36 m² × 0.5 m tall) placed over plots from May through September. Treatments will be referred to in figures and analyses as follows: Control, air warming only (Air), soil warming only (Soil), and combined annual soil and air warming (Air + Soil). Additional information on the experimental design can be found in Natali and others (2011, 2012), although note in previous publications that treatments were referred to as follows: Ambient (Control), Summer Warming (Air), Winter Warming (Soil), and Annual Warming (Air + Soil).

Environmental Monitoring

Constantan-copper thermocouples were used to measure soil temperature at 5 and 10 cm depths, and in each plot, and air temperature 10 cm above the tundra surface was monitored with thermistors. Surface soil moisture (gravimetric water content)

was measured at 5-cm depth in each plot using DC-half-bridge resistance measurements. Depth-integrated (0–20 cm) soil moisture (volumetric water content) was measured using CS-616 water content reflectometer probes (Campbell Scientific Inc., Logan, Utah, USA). Air temperature, soil temperature, and soil moisture were measured half-hourly and recorded to a Campbell Scientific CS-1000 datalogger.

Percent Cover, Biomass, and NPP

Moss percent cover in each plot was measured using a 60 × 60 cm grid placed over each plot. The percent cover within each 8 × 8 cm grid square was recorded for each of three dominant moss types: *Pleurozium* spp. (primarily *P. schreberi*), *Dicranum* spp., and *Sphagnum spp.* (primarily *S. fuscum*, and also including *S. girgensohnii*, *S. magellanicum*, and *S. compactum*). Cumulative percent cover for each moss type and total moss percent cover was recorded for each plot.

Moss biomass was determined using a non-destructive 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 3-mm-diameter metal rod was inserted vertically through the tundra plant canopy. Species (or genus) identity and number of 'hits' were recorded for every moss shoot that touched the rod. If the bottom end of the rod became inserted into a dense tuft or mat of *Dicranum* spp. (the growth form this genus typically exhibits in this habitat), where it was difficult to count the number of touching shoots in the field, the number of *Dicranum* 'hits' was recorded as four. This was previously determined experimentally by removing a 20 × 20 cm section of *Dicranum* from the field, and manually counting the number of shoots touched by the rod inserted into the mat ($n = 50$, mean hits = 4 ± 0.2; data not shown). We determined moss biomass per plot using allometric relationships describing the relationship between moss 'hits' per point and biomass (g m^{-2}) from six 60 × 60 cm destructive harvest plots adjacent to the site (Table 1).

To estimate NPP for the acrocarpous *Sphagnum* spp. and *Dicranum* spp., we used the cranked wire method, which measures vertical growth of moss using a stainless steel reference wire inserted at the moss surface (Clymo 1970). We placed 3–5 cranked wires in each treatment at all fences and measured growth from May to September. Vertical growth for these two species was converted to biomass increment using allometric equations developed for an adjacent site (Schuur and others 2007), and point

estimates were multiplied by percent cover in each plot. To estimate NPP for the pleurocarpous *P. schreberi*, we used the product of linear growth per stem (measured using the change in distance from the shoot tip to the "branch" above a small reference wire twisted around a portion of the stem), stem density, biomass per unit stem growth, and percent cover (Benscoter and Vitt 2007).

Tissue Carbon and Nitrogen Analyses

In plants, $\delta^{15}N$ ($^{15}N{:}^{14}N$ compared to the atmospheric air standard) represents the relative tissue nitrogen composition from different sources (Evans 2001), and $\delta^{13}C$ [(($^{13}C{:}^{12}C_{sample}/^{13}C{:}^{12}C_{standard}$) − 1)*1000‰] represents discrimination against $^{13}CO_2$ during the processes of CO_2 diffusion into leaves and subsequent fixation by the enzyme Rubisco. In C3 vascular plants, $\delta^{13}C$ is directly linked to the ratio of partial pressures of CO_2 inside the leaf (c_i) compared to outside the leaf (c_a), and reflects the balance between net C assimilation and stomatal conductance, thus providing information about plant water status. Mosses are also C3 plants, and possess the same photosynthetic machinery (including the discriminating enzyme Rubisco) but do not possess stomata or other active means for regulating water status, and water content is controlled by that of the surrounding environment. Carbon uptake in mosses is impeded at very high water contents due to diffusion limitation of CO_2 through films of surface water, and at low water contents due to an overall decrease in metabolic processes. Net C assimilation in mosses therefore represents a balance between conductance and photosynthetic capacity (both of which relate to water content) and is typically maximized at intermediate water contents (Dilks and Proctor 1979; Rice and Giles 1996; Williams and Flanagan 1996; Coe and others 2012). Similar to C3 vascular plants, $\delta^{13}C$ in mosses reflects biochemical discrimination against the heavier isotope during photosynthesis, yet in contrast to vascular plants, $\delta^{13}C$ varies with water status imposed by the surrounding environment rather than active regulation via stomata. Overall, moss $\delta^{13}C$ provides information about photosynthetic performance and relative growth rates, integrates moss photosynthetic activity throughout a growth period, and typically increases as a function of water availability (Rice and Giles 1996; Rice 2000).

We collected moss shoots of *Sphagnum*, *Pleurozium*, and *Dicranum* in July 2012 and 2013 from all treatment replicates for tissue N and C content as well as $\delta^{15}N$ and $\delta^{13}C$ analyses. Samples from the

Table 1. Allometric Relationships Used to Calculate Moss Biomass (g m^{-2}) from Average Number of Contact Points per Pin Drop in Six 60 X 60 cm Destructive Harvest Plots Adjacent to the Field Warming Treatments (49 drops per plot using a point frame)

Moss genus	Equation coefficients		Model strength	
	Slope	Intercept	r^2	P
Dicranum	130.0	4.008	0.972	<0.0001
Pleurozium	42.62	−0.738	0.973	<0.0001
Sphagnum	132.6	−3.011	0.905	0.003
All mosses	122.8	−5.172	0.865	<0.0001

same treatments at each snow fence were pooled to ensure that sufficient sample material was collected while minimizing destructive harvesting. Shoots were dried at 60°C, ground, and analyzed on a Thermo Finnigan (Waltham, Massachusetts, USA) continuous flow isotope radio mass spectrometer coupled to a Costech (Valencia, California, USA) elemental analyzer. Isotope corrections for delta^{13}C were performed with a peach leaf standard reference material (NIST 1547) relative to VPDB, and δ^{15}N relative to air.

Statistical Analyses

All data processing and analyses were performed using the *R* platform (R development core team 2015). Air temperature, soil temperature, soil moisture, thaw depth, δ^{13}C, δ^{15}N, and tissue C:N data were analyzed with a mixed linear model analysis of variance (ANOVA) using a blocked design with soil warming and air warming as fixed factors, and block and fence (nested in block) as random factors. Biomass and NPP data were analyzed using the framework above, only percent cover (PC) was added as a continuous predictor in models because these are area-based measures of productivity. Tukey's HSD post hoc comparisons were used to determine significant differences within groups. Data were transformed when necessary to meet ANOVA distribution requirements, and all errors presented represent one standard error of the mean.

RESULTS

When measurements were conducted, plots had been warmed continuously for either four (2012) or five (2013) years. Ambient conditions in 2013 were significantly drier than 2012, in terms of 0-20 cm depth-integrated moisture (VWC) ($P < 0.05$), 5 cm depth soil surface moisture (GWC) ($P < 0.05$), and total precipitation: 228 mm (2012), 138 mm (2013) (Table 2). Air temperatures were also 2–3°C warmer

in 2013 compared to 2012 ($P < 0.05$). The air warming treatment alone did not increase mean growing season air temperature in 2012, but increased it by 0.4°C in 2013 ($P < 0.01$). The air + soil warming treatment resulted in a 0.2°C increase in growing season air temperature in 2012, and a 0.6 increase in 2013 ($P < 0.05$). Soil warming increased average 10 cm soil temperatures by 0.10–0.25°C in 2012 and did not change 10 cm temperatures in 2013. Five centimeter soil temperatures were not altered by the warming treatments in 2012, and were slightly reduced by air warming in 2013 (Table 2). Air warming resulted in a 4.9% increase in GWC and no change in VWC in 2012, and no change in either GWC or VWC in 2013. Soil warming resulted in a 10% increase in GWC and an 11% increase in VWC in 2012, and a 17% increase in GWC and a 12% increase in VWC in 2013. Air + soil warming resulted in a 27% increase in GWC and an 22% increase in VWC in 2012, and a 23% increase in GWC and a 22% increase in VWC in 2013 (Table 2). Growing season permafrost thaw depth was also increased by warming in both years: in 2012 thaw depth was 13% deeper in the soil warming plots and 12% deeper in the air + soil warming plots, and in 2012 thaw depth was 18% deeper in the soil warming plots and 13% deeper in the air + soil warming plots ($P < 0.05$).

Total moss percent cover in plots ranged from 1.4 to 77%, and differed among the dominant moss genera ($P = 0.01$). The feather moss *Pleurozium* exhibited the greatest average percent cover (11.7 ± 2.26%), followed by *Dicranum* (6.48 ± 0.99%), and *Sphagnum* (4.28 ± 1.63%). Moss aboveground biomass ranged from 5 to 150 g m^{-2}, and *Dicranum* displayed the largest mean biomass among dominant mosses (Table 3). *Sphagnum* displayed the greatest range of biomass between plots, and included both the highest and lowest values observed. Percent cover and biomass were positively correlated in *Sphagnum* ($r^2 = 0.91$), *Pleurozium* ($r^2 = 0.64$), and *Dicranum* ($r^2 = 0.43$). Although there were species-specific trends towards increases (*Pleurozium*) and decreases

Table 2. Mean Air Temperature (°C ± SE), Soil Temperatures (°C ± SE) Measured at 5 and 10 cm, Mean (± SE) 0–20 cm Depth-integrated Soil Moisture (Volumetric Water Content; VWC), Mean (±SE) Surface Soil Moisture (Gravimetric Water Content; GWC), and Mean Maximum Growing Season Thaw Depth in Control Plots (Control) Compared to Air Warming (Air), Soil Warming (Soil), and Combined Air and Soil Warming (Air + Soil) Treatments

	Control		Air		Soil		Air + Soil	
	2012	2013	2012	2013	2012	2013	2012	2013
Air temperature (10 cm above soil)	$10.6^{ab} \pm 0.07$	$12.7^{c} \pm 0.13$	$10.8^{b} \pm 0.06$	$13.1^{d} \pm 0.11$	$10.3^{a} \pm 0.03$	$12.8^{cd} \pm 0.12$	$11.0^{b} \pm 0.05$	$13.2^{d} \pm 0.11$
Soil temperature (5-cm depth)	$7.50^{a} \pm 0.26$	$7.51^{a} \pm 0.25$	$7.34^{a} \pm 0.39$	$7.19^{a} \pm 0.43$	$7.36^{a} \pm 0.18$	$7.23^{a} \pm 0.17$	$7.25^{a} \pm 0.19$	$7.19^{a} \pm 0.25$
Soil temperature (10-cm depth)	$5.29^{a} \pm 0.27$	$5.24^{a} \pm 0.28$	$5.15^{a} \pm 0.25$	$5.01^{a} \pm 0.22$	$5.54^{a} \pm 0.18$	$5.34^{a} \pm 0.24$	$5.39^{a} \pm 0.23$	$5.12^{a} \pm 0.25$
Depth-integrated soil moisture (VWC)	$42.5^{ab} \pm 2.40$	$37.8^{a} \pm 3.40$	$42.9^{ab} \pm 1.80$	$38.5^{a} \pm 1.50$	$51.8^{ab} \pm 2.00$	$42.5^{ab} \pm 2.90$	$47.3^{b} \pm 2.50$	$46.1^{ab} \pm 2.10$
Surface soil moisture (GWC)	$8.1^{ab} \pm 1.5$	$6.5^{ab} \pm 0.8$	$8.5^{ab} \pm 0.2$	$5.9^{a} \pm 0.5$	$10.3^{b} \pm 1.2$	$8.0^{ab} \pm 1.1$	$8.9^{ab} \pm 0.8$	$7.6^{ab} \pm 0.7$
Thaw depth (cm)	$63.0^{a} \pm 0.5$	$67.0^{abc} \pm 1.7$	$62.6^{a} \pm 0.8$	$64.7^{ab} \pm 2.0$	$72.6^{cde} \pm 2.6$	$79.1^{e} \pm 2.8$	$70.4^{bcd} \pm 1.8$	$75.4^{de} \pm 2.8$

Growing season means (for air temperature) were determined by day of year (124–241 in 2012, 152–241 in 2013) and standard errors are based on fence replicates (n = 6). Treatment by year interactions that differ significantly (P < 0.05) are identified with different superscript letters. Sampling period for all environmental variables was day of year 121–273 except for air temperatures (121–264 in 2012, 154–264 in 2013).

(*Sphagnum*, *Dicranum*) in biomass with either experimental warming treatment, there were no significant treatment effects on these parameters.

Moss NPP ranged from 2 to 80 g m^{-2} y^{-1}, differed among dominant genera ($P < 0.05$), and was significantly lower in 2013 compared to 2012 ($P < 0.05$). NPP was largest in *Dicranum* in both 2012 and 2013, and did not differ across soil warming treatments (Figure 1). *Pleurozium* NPP was the smallest in both years (Figure 1), and was reduced by over 90% in the air warming treatment in 2012 ($P < 0.05$). In both years, *Sphagnum* NPP was reduced by the air warming treatment (by 80% in 2012 and 50% in 2013) and increased in the soil warming treatment (twofold in 2012, threefold in 2013) ($P < 0.05$). NPP was positively correlated with percent cover in both 2012 ($P < 0.001$; $r^2 = 0.16$) and 2013 ($P < 0.001$; $r^2 = 0.17$) (Figure 2).

Carbon isotope discrimination differed among the three genera, with *Pleurozium* displaying the most negative $\delta^{13}C$ signatures in both years ($P < 0.05$; Figure 3). On average, $\delta^{13}C$ was lowest in mosses exposed to the air warming treatment, and highest in the soil warming treatment (Figure 3). There was an overall significant effect of soil warming on $\delta^{13}C$ for all mosses ($P < 0.05$), and a trend towards an effect of air warming ($P = 0.06$) in 2013. There was a significant air warming effect on *Sphagnum* and *Dicranum* $\delta^{13}C$ in 2012 ($P < 0.05$), and *Pleurozium* $\delta^{13}C$ in 2013 ($P < 0.05$). There was a significant soil warming effect on *Dicranum* $\delta^{13}C$ in 2013 and *Pleurozium* $\delta^{13}C$ in 2012 ($P < 0.05$). *Sphagnum* $\delta^{13}C$ in 2013 was significantly influenced by air warming, soil warming, and the interaction between them, and was highest under soil warming and lowest under air + soil warming ($P < 0.05$). There was also a significant, positive correlation between NPP and $\delta^{13}C$ in mosses collected both years: $\delta^{13}C = 0.64*Log(NPP + 1) - 30.6$ (2012) and $\delta^{13}C = 0.33*Log(NPP + 1) - 30.1$ (2013) (Figure 2). $\delta^{13}C$ explained 31% of the variability in NPP in 2012 ($P < 0.0001$) but only 10% in 2013 ($P < 0.05$).

Nitrogen isotopic signature, $\delta^{15}N$, differed among moss genera and was, on average highest in *Sphagnum* in both years (Figure 4; $P < 0.0001$). Moss $\delta^{15}N$ was not significantly altered by treatments in either year, although in 2013 $\delta^{15}N$ displayed higher variability across treatments compared to 2012. *Sphagnum* $\delta^{15}N$, in contrast to *Dicranum* and *Pleurozium,* differed substantially between the 2 years with values of 2.77 ± 0.34 in 2012 and −3.30 ± 0.26 in 2013.

Percent C in *Pleurozium* and *Sphagnum* was significantly reduced by the air warming treatment in

2012 ($P < 0.05$; Table 3), and percent N was significantly increased by the soil warming treatment (*Sphagnum*, 2013) and air + soil warming treatment (*Pleurozium*, 2012) ($P < 0.05$; Table 3). As a consequence, C:N was significantly reduced in *Sphagnum* in the soil warming treatment (2013, $P < 0.05$), and in *Pleurozium* in the air + soil warming treatment (2012, $P < 0.05$).

DISCUSSION

Air warming caused a reduction in NPP in the feather moss *Pleurozium* in 2012 and the peat moss *Sphagnum* in both 2012 and 2013, in support of our first hypothesis. Declines were most dramatic in 2012, where NPP in both of these mosses was reduced by over 80% on average. *Dicranum* NPP, on the other hand, was not influenced by treatments in either year, but did exhibit NPP rates on average twice that of *Pleurozium* and *Sphagnum*, with the greatest differences between the genera observed in 2013. Air warming also resulted in a consistent reduction in δ^{13}C in all three mosses, and we found that δ^{13}C was positively correlated with NPP in both years, as has been observed in other moss communities (Rice 2000). In contrast to vascular plants, where low δ^{13}C values typically result from greater growth rates due to high water use efficiency, low δ^{13}C values in mosses are most commonly observed when growth rates are low due to low tissue water content, when chloroplastic demand and diffusional resistance of CO_2 are both low (Rice and Giles 1996; Rice 2000). Collectively, the reduction in NPP and δ^{13}C in two of the three dominant mosses at our site points to the possibility of drier conditions that reduced moss growth as a result of air warming.

In partial support of our second hypothesis, soil warming resulted in an increase in NPP in *Sphagnum* in both 2012 and 2013, but did not result in changes in productivity in *Pleurozium* or *Dicranum*. *Sphagnum* δ^{13}C was also highest in soil warming treatments in both years, and together with higher NPP, suggests that soil warming (and the changes in soil and permafrost dynamics that accompany it) could alleviate negative effects of air warming on productivity. Indeed, *Sphagnum* NPP was no different from control in the air + soil warming treatment, suggesting that increased growth under warmed soils could offset reductions occurring as a result of increased air temperatures.

Table 3. Percent C, Percent N, C:N, and Biomass (g m^{-2}) for *Dicranum*, *Pleurozium*, and *Sphagnum* Following Four (2012) and Five (2013) Year Exposure to Air and Soil Warming Treatments
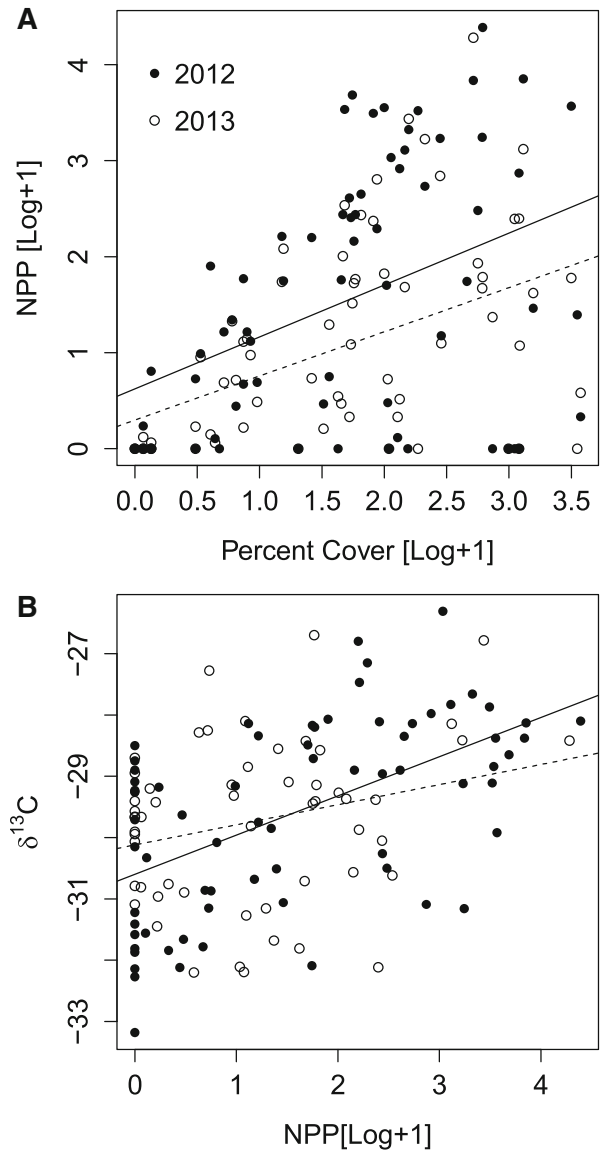
	Dicranum		*Pleurozium*		*Sphagnum*	
	2012	2013	2012	2013	2012	2013
%C						
Control	45.2 ± 0.20	44.3 ± 0.14	45.3 ± 0.11	44.4 ± 0.21	42.0 ± 0.23	42.7 ± 0.31
Air	44.8 ± 0.30	44.2 ± 0.40	**44.9 ± 0.23**	44.1 ± 0.34	**41.3 ± 0.20**	42.4 ± 0.23
Soil	45.2 ± 0.22[†]	44.3 ± 0.21	44.9 ± 0.11[†]	44.3 ± 0.21	41.9 ± 0.22	42.4 ± 0.21
Air + Soil	45.4 ± 0.12	44.0 ± 0.14	44.4 ± 0.22	44.4 ± NA	41.3 ± 0.33	42.3 ± 0.11
%N						
Control	0.83 ± 0.04	0.57 ± 0.09	0.98 ± 0.04	0.71 ± 0.05	1.49 ± 0.05	0.91 ± 0.03
Air	0.91 ± 0.06	0.55 ± 0.08	0.93 ± 0.04	0.72 ± 0.06	1.56 ± 0.05	0.77 ± 0.03
Soil	0.90 ± 0.05	0.57 ± 0.03	0.89 ± 0.02	0.81 ± 0.04	1.49 ± 0.06	**1.17 ± 0.14**
Air + Soil	0.86 ± 0.04	0.47 ± 0.02	**1.03 ± 0.04**	0.68 ± NA	1.46 ± 0.06	0.98 ± 0.09
C:N						
Control	55.5 ± 2.87	85.3 ± 10.7	46.8 ± 1.71	63.6 ± 3.99	28.3 ± 0.93	47.1 ± 1.94
Air	50.3 ± 3.71	85.9 ± 14.3	48.9 ± 2.10	61.5 ± 4.85	26.7 ± 0.88	55.1 ± 1.85
Soil	51.4 ± 3.73	79.3 ± 4.74	50.8 ± 1.22	55.4 ± 2.51	28.4 ± 1.15	**38.7 ± 4.41**
Air + Soil	54.2 ± 2.47	94.0 ± 3.10	**44.1 ± 1.94**	65.3 ± NA	28.6 ± 0.98	43.7 ± 3.85
Biomass (g m^{-2})						
Control	21.4 ± 9.27	23.1 ± 6.11	5.11 ± 2.17	8.52 ± 3.95	14.1 ± 12.3	16.4 ± 15.2
Air	19.4 ± 4.43	12.6 ± 3.26	7.80 ± 2.00[†]	6.93 ± 2.62[†]	8.25 ± 5.29	5.11 ± 3.41
Soil	23.2 ± 8.21	22.0 ± 5.23	5.92 ± 2.10	6.13 ± 2.07	4.61 ± 2.86	5.74 ± 2.85
Air + Soil	18.7 ± 5.28	19.5 ± 9.56	13.0 ± 3.90	9.02 ± 2.90	11.4 ± 9.44	8.30 ± 7.39

Values presented are means ± one standard error. NAs indicate instances where only one sample was available for the treatment × genus × year combination, thus standard error could not be calculated. Bold face indicates treatment differences from control where P < 0.05; †P < 0.10.
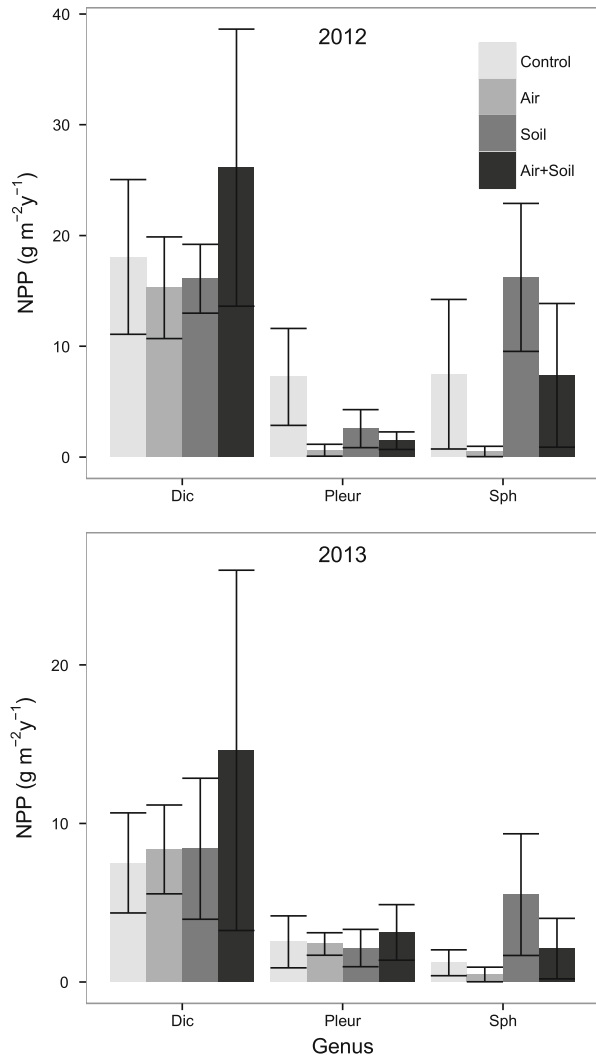
Figure 1. Mean net primary productivity (g m^{-2} y^{-1}) ± standard error for *Dicranum*, *Pleurozium*, and *Sphagnum* in control, air warming (Air), soil warming (Soil), and combined air and soil warming (Air + Soil) treatments measured in 2012 and 2013. Mixed model effects: Air (*Pleurozium*, 2012), Air and Soil (*Sphagnum*, 2012 and 2013). Note the difference in *y*-axis scales in 2012 and 2013.

Figure 2. A The relationship between percent cover and net primary productivity (NPP, g m^{-2} y^{-1}) measured in 2012 (*closed symbols and solid line*; $r^2 = 0.16$, $P < 0.001$) and 2013 (*open symbols and dashed line*; $r^2 = 0.17$, $P < 0.001$). **B** The relationship between NPP (g m^{-2} y^{-1}) and $\delta^{13}C$ (‰) in all mosses combined in 2012 (*closed symbols and solid line*; $r^2 = 0.31$, $P < 0.0001$) and 2013 (*open symbols and dashed line*; $r^2 = 0.10$, $P < 0.05$).

Water availability plays a central role in moss productivity, and changes in soil moisture that accompanied warming are likely to have strongly influenced the productivity and $\delta^{13}C$ of mosses. As mosses inhabit the region at the soil-atmosphere interface, their growth is limited by the interactive effects of water availability at the soil surface and rates of passive water loss from tissues to the surrounding air. The relationship between warmer and drier conditions and moss productivity was most apparent between the sampling years: 2013 was 2–3°C warmer than 2012 on average, and total

precipitation was 40% lower in 2013 compared to 2012. These conditions likely caused the low moss NPP in 2013 compared to 2012, and the suppressed moss C assimilation apparent in the shallower NPP versus $\delta^{13}C$ relationship in 2013.

The field warming treatments similarly affected soil moisture, which is likely to have altered moss water availability and performance. Soil warming increased surface moisture by 10–17%,
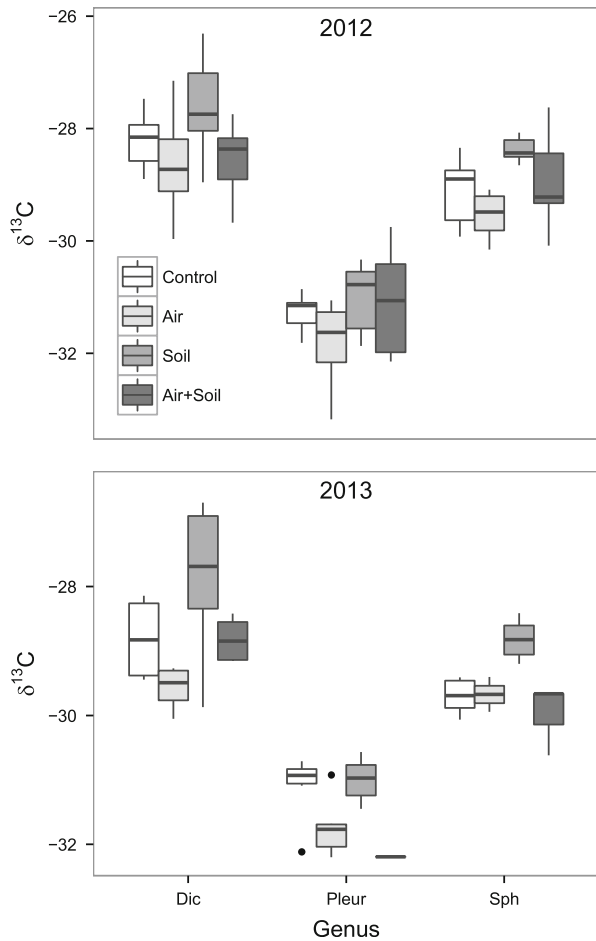
Figure 3. Carbon isotopic signatures ($\delta^{13}C$; ‰) for *Dicranum*, *Pleurozium*, and *Sphagnum* in control, air warming (Air), soil warming (Soil), and combined air and soil warming (Air + Soil) treatments measured in 2012 and 2013. *Bold horizontal lines* in *box interiors* represent median values, and *upper and lower edges of boxes* represent interquartile ranges. Mixed model effects: Soil (all genera combined, 2012 and 2013), Air (*Sphagnum* and *Dicranum* in 2012, *Pleurozium* and *Sphagnum* in 2013), Soil (*Dicranum* and *Sphagnum* in 2013, *Pleurozium* in 2012), Air + Soil (*Sphagnum* 2013).

and depth-integrated moisture by 11–12%. This occurred because soil warming induced permafrost degradation and surface subsidence, leading to a 13–18% increase in thaw depth and saturated soils. Under soil warming, mosses were therefore unlikely limited by water availability, leading to increases in NPP and $\delta^{13}C$. Air warming, on the other hand, did not alter soil moisture, but did increase mean air temperatures above the soil by up to 0.5°C and maximum daily temperatures by up to 1.5°C, which may have increased potential evapotranspiration at the soil surface where the mosses were growing. Mosses were often visibly desiccated and brittle in the air warming plots,
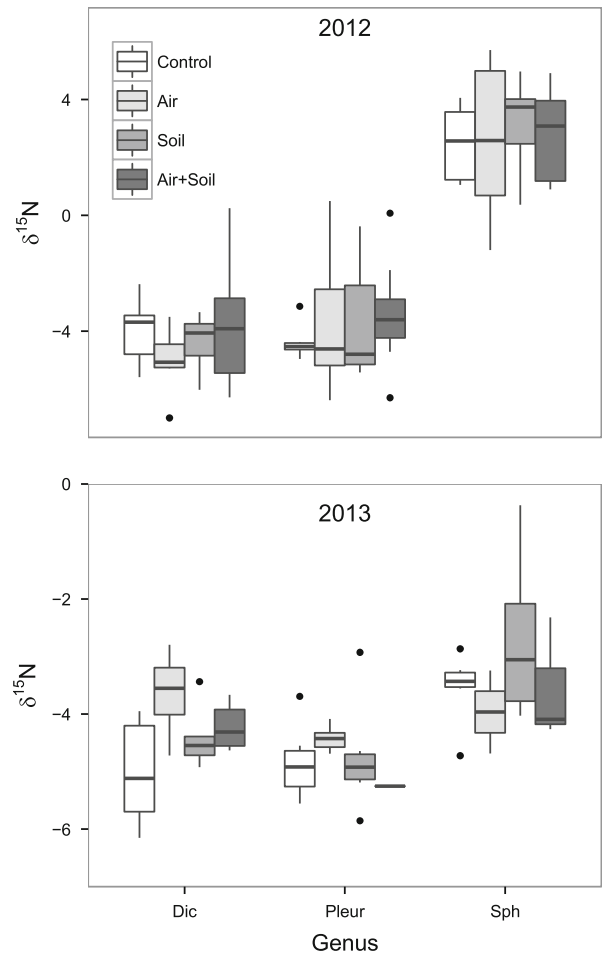
Figure 4. Nitrogen isotopic signatures ($\delta^{15}N$; ‰) for *Dicranum*, *Pleurozium*, and *Sphagnum* in control, air warming (Air), soil warming (Soil), and combined air and soil warming (Air + Soil) treatments measured in 2012 and 2013. *Bold horizontal lines* in *box interiors* represent median values, *upper and lower edges of boxes* represent interquartile ranges, and *dots* represent outliers. Note the difference in *y*-axis scales in 2012 and 2013.

which, along with reduced NPP and $\delta^{13}C$, reveal that moss performance and growth at or above the soil surface may be adversely affected by increased air temperatures. As soil moisture at 5 cm depth was not influenced by air warming, but moss growth was still sensitive to this treatment, these data also suggest that moss performance could become decoupled from soil hydrology under increased air temperatures.

Changes in water availability to mosses as a result of increased air temperatures may have negatively impacted growth and C assimilation of *Sphagnum* and *Pleurozium* because of their sensitivity to desiccation. Most tundra *Sphagnum* species are extremely hydrophilic, existing as dense, moist hummocks, or mats at or below the soil surface,

commonly growing submerged in water. On average, tundra *Sphagnum* species display a low degree of desiccation tolerance, and shoots will cease to grow under conditions of low water availability (Schipperges and Rydin 1998; McNeil and Waddington 2003). Reductions in biomass have been previously observed in *Sphagnum* under air warming conditions in the field (Jonasson and others 1999; Gunnarsson and others 2004), with causes attributable to an overall drier growth environment, revealing the sensitivity of *Sphagnum* to desiccation imposed by increased air temperatures. In contrast to the thick *Sphagnum* mats, the feather moss *Pleurozium* grows in a loose weft above the soil surface, and although more tolerant of drying and rewetting than *Sphagnum*, ceases photosynthetic activity when dry (Williams and Flanagan 1996). Feather mosses like *Pleurozium* rely on capillary action to move water from lower to upper portions of the shoot, and if water availability is low at the soil surface, entire shoots and colonies can desiccate rapidly (Skre and others 1983). It is interesting to note that, in contrast to *Sphagnum* and *Pleurozium* (both of which might have been living closer to their physiological limits under air warming), *Dicranum* did not display reduced productivity in the air warming treatment. This could arise from differences in temperature tolerance due to plasticity in the genus (*Dicranum* is diverse with a global distribution; Bellolio-Trucco and Ireland 1990; Hedenäs and Bisang 2004), or increased tolerance for fluctuations in water availability due to its dense, colonial growth form.

In addition to genus-specific productivity responses, we also observed differences in δ^{15}N across species and some changes in C:N in response to warming treatments. Moss δ^{15}N depended primarily on genus, where it was highest in *Sphagnum*, and sampling year, where reductions of up to 5‰ were observed in *Sphagnum* between 2012 and 2013. This dramatic difference in δ^{15}N observed in *Sphagnum* may be related to altered N supply pathways that accompany environmental changes in hydrology (Handley and others 1999). *Sphagnum* tissue δ^{15}N in 2012, the cooler and wetter year, was consistent with substrate (organic and mineral soil) δ^{15}N signatures (Houle and others 2006; Pries and others 2012), whereas δ^{15}N signatures from 2013, the warmer and drier year, were consistent with what has been recorded in mosses receiving nutrients exclusively from atmospheric deposition (Bragazza and others 2005). This is potentially evidence for a shift from a terrestrial to an atmospheric source of N in *Sphagnum* when water availability at the soil surface is low and mosses

must rely more heavily on precipitation for hydration. As this 5‰ change in δ^{15}N was not observed in the other genera at our site that do not have shoots that extend deep into the soil profile, these results also reveal that changes in N availability that accompany changes in local hydrology could have a disproportionate effect on mosses like *Sphagnum* with significant belowground biomass. It is also possible that δ^{15}N shifts in *Sphagnum* were due to changing soil sources due to microbial processing or other mechanisms that exhibited inter-annual variability. Differences between years and among mosses were far greater than any treatment effects, suggesting tundra moss δ^{15}N is largely determined by inter-annual environmental changes that result in differences in N source composition, or the physiological ecology and N metabolism of individual taxa.

Macronutrient tissue composition among tundra mosses reflected changes in productivity and N availability that accompanied warming. C:N exhibited modest declines in both *Pleurozium* (2012) as a result of air + soil warming, and *Sphagnum* (2013) as a result of soil warming. For both of these mosses, declines in C:N resulted from a combination of increased %N in the soil warming treatment and reduced %C in the air warming treatments. This suggests that N availability to mosses may be higher in warmer soils, as appears to be the case for vascular plants in regions undergoing permafrost thaw (Schuur and others 2007; Natali and others 2012). Yet, air warming that reduces overall NPP appears to manifest as reductions in tissue %C in some taxa. For mosses, ecosystem warming may therefore increase N availability under certain conditions, but also may create a less favorable moisture environment for growth and C assimilation.

Experimental warming at our site forecasts potential changes in the tundra moss community in a future climate. In particular, these results lend clarity to a previously incomplete picture for *Sphagnum* in tundra ecosystems. Although most earlier work has shown declines in *Sphagnum* abundance and cover in response to air temperature manipulation (Jonasson and others 1999; Gunnarsson and others 2004; Walker and others 2006; Lang and others 2012), we reveal how air warming and soil warming can interact to create positive conditions for *Sphagnum* growth. In tundra ecosystems, soil warming can lead to positive feedbacks involving permafrost thaw and ground subsidence (Nelson and others 2001; Schuur and others 2009) therefore it is possible that *Sphagnum* may have an advantage in warming temperatures

based on its tolerance of saturation. This conclusion is supported by evidence from Northern peatlands suggesting *Sphagnum fuscum* will benefit from warming scenarios that do not reduce water availability (Dorrepaal and others 2004). *Pleurozium*, on the other hand, displayed high overall sensitivity temperature increases, particularly air warming, suggesting a potential reduction in dominance in the long-term. Although *Dicranum* displayed reduced NPP and treatment effects on $\delta^{13}C$ in the warmer and drier sampling year (2013), in general *Dicranum* was the one genus that did not appear to be as responsive to warming, and therefore may remain a feature in tundra moss communities in the future.

The moss responses observed here also have the potential to influence C and N cycling in the tundra. Because of their extensive groundcover and activity beyond the typical constraints of the vascular plant growing season, mosses can contribute substantially to carbon inputs in northern ecosystems. As *Pleurozium* accounted for the largest percent cover of all three genera at our site, reductions in *Pleurozium* NPP may influence ecosystem C inputs during times of year when vascular plants are less active. *Pleurozium* was also the most sensitive genus to annual warming overall, suggesting the possibility of changes in productivity on relatively rapid time scales. Through associations with N_2-fixing cyanobacteria, *Pleurozium* also accounts for substantial N inputs to Northern latitude systems (Solheim and others 1996; DeLuca and others 2002; DeLuca and others 2007; Markham 2009). *Pleurozium* productivity declines accompanying increased temperatures which therefore could result in reductions in ecosystem N inputs from N fixation. In spite of the potentially large ramifications of *Pleurozium* declines in this ecosystem, it is important to note that the genus with the largest biomass and greatest overall productivity at our site, *Dicranum*, and the genus comprising the majority of biomass in Northern latitude peatlands, *Sphagnum*, did not display the same responses, and may buffer altered C inputs from *Pleurozium* declines that accompany soil warming.

Because of their unique physiology and slow growth rates, detection of moss responses to environmental change in the field is often challenging. Our results reveal that although treatment level changes may not have been apparent from measurements of biomass on this timescale, tissue elemental analyses, and moss-specific measures of productivity do suggest that mosses are sensitive to warming. The fact that we could capture moss NPP and $\delta^{13}C$ responses in response to ecosystem warming, and observe pronounced inter-annual differences, makes the present results especially striking from a plant community standpoint. Examining vegetation responses across 2 years with strikingly different abiotic conditions also revealed the interactive effects of temperature manipulation and local hydrology, and future work examining how projected changes in precipitation interact with other climate factors would strengthen our knowledge of northern latitude response to global change.

As a consequence of increased temperatures, tundra plant communities are undergoing dramatic shifts in diversity, species composition, biomass, nutrient status, and NPP (Arft and others 1999; Walker and others 2006; Natali and others 2012). To understand how warming will impact future ecological relationships and ecosystem processes in the tundra, a holistic view combining information on non-vascular plant responses with the wealth of research on vascular plant responses is essential. As we have shown here, some responses may differ between non-vascular and vascular plants, that is, responses to altered hydrology that accompany warming and permafrost thaw, but others may be similar, that is, increased plant-available N. From a moss community standpoint, our results suggest that annual temperature increases may result in a shift away from a feather moss-dominated community towards a peat moss-dominated community, a result with consequences for species composition and diversity, ecosystem N inputs, and C balance in the tundra. Moreover, these conclusions could not have been reached without the year-round warming experiment employed here: changing air temperatures are also likely to manifest as changing soil temperatures, soil moisture, and permafrost dynamics (Osterkamp and Romanovsky 1999), and this work presents strong evidence that air warming and soil warming treatments in combination can offer a more complete picture of tundra plant communities under global change.

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REFERENCES

ACIA. 2004. Impacts of a warming Arctic. Cambridge: Cambridge University Press.

Arft AM, Walker MD, Gurevitch JEA, Alatalo JM, Bret-Harte MS, Dale M, Wookey PA. 1999. Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. Ecol Monogr 69(4):491–511.

Bellolio-Trucco G, Ireland RR. 1990. A taxonomic study of the moss genus *Dicranum* (Dicranaceae) in Ontario and Quebec. Can J Bot 68(4):867–909.

Benscoter BW, Vitt DH. 2007. Evaluating feathermoss growth: a challenge to traditional methods and implications for the boreal carbon budget. J Ecol 95:151–8.

Beringer J, Lynch AH, Chapin FS, Mack M, Bonan GB. 2001. The representation of Arctic soils in the land surface model: the importance of mosses. J Clim 14(15):3324–35.

Borner AP, Kielland K, Walker MD. 2008. Effects of simulated climate change on plant phenology and nitrogen mineralization in Alaskan Arctic tundra. Arct Antarct Alp Res 40:27–38.

Bragazza L, Limpens J, Gerdol R, Grosvernier P, Hajek M, Hájek T, Tahvanainen T. 2005. Nitrogen concentration and δ15N signature of ombrotrophic *Sphagnum* mosses at different N deposition levels in Europe. Glob Change Biol 11(1):106–14.

Brooker R, van derWal R. 2003. Can soil temperature direct the composition of high Arctic plant communities? J Veg Sci 14:535–42.

Camill P, Lynch JA, Clark JS, Adams JB, Jordan B. 2001. Changes in biomass, aboveground net primary production, and peat accumulation following permafrost thaw in the boreal peatlands of Manitoba, Canada. Ecosystems 4(5):461–78.

Campioli M, Samson R, Michelsen A, Jonasson S, Baxter R, Lemeur R. 2009. Nonvascular contribution to ecosystem NPP in a subarctic heath during early and late growing season. Plant Ecol 202(1):41–53.

Chapin FS, Shaver GR. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. Ecology 66(2):564–76.

Chapin FS, Shaver GR. 1996. Physiological and growth responses of Arctic plants to a field experiment simulating climatic change. Ecology 77:822–40.

Chapin FS, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA. 1995. Responses of Arctic tundra to experimental and observed changes in climate. Ecology 76:694–711.

Coe KK, Belnap J, Sparks JP. 2012. Precipitation-driven carbon balance controls survivorship of desert biocrust mosses. Ecology 93(7):1626–36.

Clymo RS. 1970. Growth of *Sphagnum*: methods of measurement. J Ecol 58:13–49.

DeLuca TH, Zackrisson O, Nilsson MC, Sellstedt A. 2002. Quantifying nitrogen-fixation in feather moss carpets of boreal forests. Nature 419(6910):917–20.

DeLuca TH, Zackrisson O, Gentili F, Sellstedt A, Nilsson MC. 2007. Ecosystem controls on nitrogen fixation in boreal feather moss communities. Oecologia 152(1):121–30.

Dilks TJK, Proctor MCF. 1979. Photosynthesis, respiration and water content in bryophytes. New Phytol 82(1):97–114.

Dorrepaal E, Aerts R, Cornelissen JH, Callaghan TV, Van Logtestijn RS. 2004. Summer warming and increased winter snow cover affect *Sphagnum* fuscum growth, structure and production in a sub-arctic bog. Glob Change Biol 10(1):93–104.

Elmendorf SC, Henry GH, Hollister RD, Björk RG, Boulanger-Lapointe N, Cooper EJ, Wipf S. 2012a. Plot-scale evidence of tundra vegetation change and links to recent summer warming. Nature Climate Change 2(6):453–7.

Elmendorf SC, Henry GH, Hollister RD, Björk RG, Bjorkman AD, Callaghan TV, Wookey PA. 2012b. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. Ecol Lett 15(2):164–75.

Epstein HE, Calef MP, Walker MD, Chapin FS, Starfield AM. 2004. Detecting changes in Arctic tundra plant communities in response to warming over decadal time scales. Glob Change Biol 10(8):1325–34.

Forbes BC, Fauria M, Zetterberg P. 2010. Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. Glob Change Biol 16(5):1542–54.

Gornall JL, Jónsdóttir IS, Woodin SJ, Van der Wal R. 2007. Arctic mosses govern below-ground environment and ecosystem processes. Oecologia 153(4):931–41.

Gunnarsson U, Granberg G, Nilsson M. 2004. Growth, production and interspecific competition in *Sphagnum*: effects of temperature, nitrogen and sulphur treatments on a boreal mire. New Phytol 163(2):349–59.

Gunnarsson U. 2005. Global patterns of *Sphagnum* productivity. Journal of Bryology 27(3):269–79.

Handley LL, Austin AT, Stewart GR, Robinson D, Scrimgeour CM, Raven JA, Schmidt S. 1999. The 15N natural abundance ($\cdot$15N) of ecosystem samples reflects measures of water availability. Funct Plant Biol 26(2):185–99.

Hedenäs LARS, Bisang IRENE. 2004. Key to European *Dicranum* species. Herzogia 17:179–97.

Henry GHR, Molau U. 1997. Tundra plants and climate change: the International Tundra Experiment (ITEX). Glob Change Biol 3(S1):1–9.

Hobbie SE, Chapin FS. 1998. Response of tundra plant biomass, aboveground production, nitrogen, and CO_2 flux to experimental warming. Ecology 79:1526–44.

Hobbie SE, Shevtsova A, Chapin FS. 1999. Plant responses to species removal and experimental warming in Alaskan tussock tundra. Oikos 84:417–34.

Houghton JT, Filho LGM, Callander BA, Harris N, Kattenberg A, Maskell K, Eds. 1996. Climate change 1995: the science of climate change. Cambridge: Cambridge University Press.

Houle D, Bilodeau Gauthier S, Paquet S, Planas D, Warren A. 2006. Identification of two genera of N_2-fixing cyanobacteria growing on three feather moss species in boreal forests of Quebec, Canada. Botany 84(6):1025–9.

Hudson JMG, Henry GHR. 2009. Increased plant biomass in a high Arctic heath community from 1981 to 2008. Ecology 90:2657–63.

IPCC. 2013. Climate change 2013: the physical science basis. Cambridge: Cambridge University Press.

Jonasson S, Michelsen A, Schmidt IK, Nielsen EV. 1999. Responses in microbes and plants to changed temperature, nutrient, and light regimes in the Arctic. Ecology 80(6):1828–43.

Lang SI, Cornelissen JH, Shaver GR, Ahrens M, Callaghan TV, Molau U, Aerts R. 2012. Arctic warming on two continents has consistent negative effects on lichen diversity and mixed effects on bryophyte diversity. Glob Change Biol 18(3):1096–107.

Lindo Z, Nilsson MC, Gundale MJ. 2013. Bryophyte-cyanobacteria associations as regulators of the northern latitude carbon balance in response to global change. Glob Change Biol 19(7):2022–35.

Markham JH. 2009. Variation in moss-associated nitrogen fixation in boreal forest stands. Oecologia 161(2):353–9.

McNeil P, Waddington JM. 2003. Moisture controls on *Sphagnum* growth and CO_2 exchange on a cutover bog. J Appl Ecol 40(2):354–67.

Natali SM, Schuur EAG, Trucco C, Hicks Preis CE, Crummer KG, Baron Lopez AF. 2011. Effects of experimental warming of air, soil and permafrost on carbon balance in Alaskan tundra. Glob Change Biol 17(3):1394–407.

Natali SM, Schuur EAG, Rubin RL. 2012. Increased plant productivity in Alaskan tundra as a result of experimental warming of soil and permafrost. J Ecol 100(2):488–98.

Nelson FE, Anisimov OA, Shiklomanov NI. 2001. Subsidence risk from thawing permafrost. Nature 410(6831):889–90.

Osterkamp TE, Romanovsky VE. 1999. Evidence for warming and thawing of discontinuous permafrost in Alaska. Permafrost Periglac Process 10:17–37.

Press MC, Potter JA, Burke MJW, Callaghan TV, Lee JA. 1998. Responses of a subarctic dwarf shrub heath community to simulated environmental change. J Ecol 86:315–27.

Pries CEH, Schuur EAG, Crummer KG. 2012. Holocene carbon stocks and carbon accumulation rates altered in soils undergoing permafrost thaw. Ecosystems 15(1):162–73.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Rice SK, Giles L. 1996. The influence of water content and leaf anatomy on carbon isotope discrimination and photosynthesis in *Sphagnum*. Plant Cell Environ 19(1):118–24.

Rice SK. 2000. Variation in carbon isotope discrimination within and among *Sphagnum* species in a temperate wetland. Oecologia 123(1):1–8.

Rydin H, Jeglum JK. 2013. The biology of peatlands, 2e. Oxford: Oxford University Press.

Schipperges B, Rydin H. 1998. Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation. New Phytol 140:677–84.

Schuur EAG, Crummer KG, Vogel JG, Mack MC. 2007. Plant species composition and productivity following permafrost thaw and thermokarst in Alaskan tundra. Ecosystems 10:280–92.

Schuur EAG, Vogel JG, Crummer KG, Lee H, Sickman JO, Osterkamp TE. 2009. The effect of permafrost thaw on old carbon release and net carbon exchange from tundra. Nature 459:556–9.

Skre O, Oechel WC, Miller PM. 1983. Moss leaf water content and solar radiation at the moss surface in a mature black spruce forest in central Alaska. Can J Res 13(5):860–8.

Solheim B, Endal A, Vigstad H. 1996. Nitrogen fixation in Arctic vegetation and soils from Svalbard, Norway. Polar Biol 16(1):35–40.

Soudzilovskaia NA, Bodegom PM, Cornelissen JH. 2013. Dominant bryophyte control over high-latitude soil temperature fluctuations predicted by heat transfer traits, field moisture regime and laws of thermal insulation. Funct Ecol 27(6):1442–54.

Street LE, Subke JA, Sommerkorn M, Sloan V, Ducrotoy H, Phoenix GK, Williams M. 2013. The role of mosses in carbon uptake and partitioning in Arctic vegetation. New Phytol 199(1):163–75.

Tape KEN, Sturm M, Racine C. 2006. The evidence for shrub expansion in northern Alaska and the Pan-Arctic. Glob Change Biol 12(4):686–702.

Toet S, Cornelissen JH, Aerts R, van Logtestijn RS, de Beus M, Stoevelaar R. 2006. Moss responses to elevated CO_2 and variation in hydrology in a temperate lowland peatland. Plant Ecol 182(1–2):27–40.

van Wijk MT, Clemmensen KE, Shaver GR, Williams M, Callaghan TV, Chapin FS. 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. Glob Change Biol 10:105–23.

Williams TG, Flanagan LB. 1996. Effect of changes in water content on photosynthesis, transpiration and discrimination against $^{13}CO_2$ and C18O16O in *Pleurozium* and *Sphagnum*. Oecologia 108(1):38–46.

Wahren CH, Walker MD, Bret-Harte MS. 2005. Vegetation responses in Alaskan Arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. Glob Change Biol 11(4):537–52.

Walker MD. 1996. Community baseline measurements for ITEX studies. In: Molau U, Mølgaard P, Eds. International tundra experiment (ITEX) manual. Copenhagen: Danish Polar Center. p 39–41.

Walker MD, Wahren CH, Hollister RD, Henry GH, Ahlquist LE, Alatalo JM, Wookey PA. 2006. Plant community responses to experimental warming across the tundra biome. Proc Natl Acad Sci USA 103(5):1342–6.