

Foliar Nitrogen and Carbon Responses to Experimental Warming in the Low Arctic

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Arctic ecosystems are characterized by a short growing season, low nutrient availability, and permafrost soils—factors making them highly vulnerable to climate warming. This study investigates the effects of experimental warming on foliar carbon and nitrogen, variables that reflect water status, photosynthesis, and nutrient dynamics. We deployed open-top chambers and snow fences to simulate three future climate scenarios in interior Alaska: 1) elevated summer air temperatures, 2) elevated winter time soil temperatures, and 3) elevated summer air temperatures and winter time soil temperatures (i.e., annual warming). Leaves from the six dominant plant species in moist acidic tundra were analyzed for percent nitrogen (%N), percent carbon (%C), and isotopic composition ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$). Leaf mineral nutrition varied across species and functional groups, owing to differences in growth form, water needs, N source, N demand, and mycorrhizal status. Significant treatment effects were observed in four of six species. Highly significant annual warming effects were found in the deciduous shrub *B. nana*, with a decrease in foliar $\delta^{15}\text{N}$ and an increase in foliar $\delta^{13}\text{C}$. The high responsiveness of *B. nana* is consistent with global observations of shrub expansion into higher latitudes. Continued changes in N and C dynamics could feed back to the C balance and to plant community diversity, especially if they alter plant competitive ability.

INTRODUCTION

Detecting plant response to environmental change is critical to understanding arctic ecosystems. Recent models predict global temperature increases of between 1.0 to 3.5° C by the year 2100 (IPCC 2007), with the greatest changes predicted for high latitudes. Changes are already underway and include the loss of permafrost, an increased growing season length, and the advance of shrubs into higher latitudes (Sturm 2001, Walker et al. 2006, Tape et al. 2006), often at the expense of graminoids (Shaver 2001). The objective of this study was to evaluate short-term (two years) warming effects on leaf C and N, which can expose underlying soil and plant processes in a warmer world.

“Arctic greening” is driven by direct climate change impacts on temperature and water availability and indirect effects on nutrient dynamics. Increased soil temperatures stimulate microbial decomposition of soil organic matter and mineralization of organic nitrogen (N) (Chapin et al. 1995). Typically, this process leads to increased productivity during the growing season. However, productivity may be limited as warming increases transpiration, prompting plants to close their stomata to conserve water. Warming-mediated changes in plant C and N can feed back to plant community composition (Schuur et al. 2007), ultimately determining whether the landscape is net source or sink of C.

The Carbon in Permafrost Experimental Heating Research (CiPEHR) field site was established in 2008 near

Denali National Park in interior Alaska. The goal of this experiment is to assess ecosystem responses to experimental warming (Natali et al. 2011). During winter, snow fences trap an insulating layer of snow; during summer, open-top chambers behave as greenhouses. Combined, these treatments succeed in warming deep soil and surface air temperatures by 0.5–1.5°C. Previous warming experiments indicate positive effects on plant productivity in as little as two seasons of warming (Walker et al. 2006), and increased net soil N mineralization in as little as three seasons of experimental warming (Aerts et al. 2009). Overall, most studies agree on a positive correlation between temperature and biomass production for some species (Michelsen et al. 1996, Hudson & Henry 2009, Chapin et al. 1995, Lin et al. 2010).

Leaf percent C and N (%C and %N) are useful metrics for assessing ecosystem response to climate change because they represent soil nutrient levels, resource allocation, and resource use efficiency (Welker et al. 2005). These values vary greatly among plant species and functional groups, owing to differences in physiology, nutrient demand, and acquisition strategies (Cornelisen et al. 1997). Thus, the response of plants to changes in climate can range from positive, negative, to no response at all, and they are likely to be species-specific (Aerts et al. 2009, Chapin et al. 1995, Chapin et al. 1985). However, even small changes in leaf chemistry can affect processes at multiple trophic levels. For example, increased foliar %N is likely to lead to higher rates of soil N turnover rates

when leaves senesce and return to the soil as litter, and elevated C:N ratios can reduce herbivore forage quality (Klein et al. 2007, Walsh et al. 1997).

Foliar C and N isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) index warming-mediated changes in the soil environment, suggesting possible mechanisms behind plant community responses. Isotopic values imply discrimination at various stages of biochemical cycles, leading to a unique isotopic signature of source and product pools. As such, the resulting ratio of plant leaves can serve as a “fingerprint” of that resource or transitional form (Dawson et al. 2002). N isotopes are expressed as the ratio of $^{15}\text{N}/^{14}\text{N}$ and can be used to infer N sources and pathways (Dawson et al. 2002, Robinson 2011, Evans 2001). Prior studies also indicate a positive correlation between foliar $\delta^{15}\text{N}$ values and soil net mineralization rates (Kahmen et al. 2008) as well as inorganic N availability in soil (Garten 1993). Similarly, foliar $^{13}\text{C}/^{12}\text{C}$ is controlled by the C isotope ratio of the CO_2 source and isotope discrimination during plant C assimilation and can be used to integrate plant physiological responses to environmental changes (Michelsen et al. 1996, Dawson et al. 2002). For example, plants undergoing water stress will close their stomata in order to conserve water. This creates a high demand for CO_2 , with plants becoming less discriminating against $\delta^{13}\text{C}$ and an expected increase in $\delta^{13}\text{C}$.

Our aims for this experiment were to quantify the effects of ecosystem warming on foliar C, N, and isotopic composition ($\delta^{15}\text{N}$ & $\delta^{13}\text{C}$), variables that reveal changes in soil nutrient processes and plant functional response to warming. We expected increases in $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and %C in all warming treatments, with the most pronounced effects in annually warmed plots. We also expected %N to remain the same or to decrease slightly, due to a dilution of overall N through increased leaf biomass (Schuur et al. 2007). We expected the magnitude of response to warming to vary according to species, which was found in the first year of warming at CiPEHR (Natali et al. 2011). Finally, we anticipated “background” variation in leaf chemistry among species due to differences in physiological pathways, reproductive structures, and leaf morphology (Arft et al. 1999, Nadelhoffer et al. 1996).

METHODS

CiPEHR is located at Eight Mile Lake (63° 52' 59"N, 149° 13' 32"W elevation 700 m), just outside Denali National Park in the northern foothills of the Alaska Range. The vegetation is moist acidic tundra characterized by tussock-forming sedges, forbs, and shrubs and underlain by permafrost. The six most common vascular plant species at this site are *Betula nana* (deciduous shrub), *Vaccinium uliginosum* (deciduous shrub), *Eriophorum vaginatum* (sedge), *Carex bigelowii* (sedge), *Rubus chaemomorus* (forb), and *Rhododendron subarcticum* (evergreen shrub).

CiPEHR was initiated in 2008 with the goal of warming surface air and deep soil. During winter, six 1.5 m tall \times 8 m long snow fences trapped an insulating layer of snow over six winter warming plots; during the summer, twenty-four 0.36 m² \times 0.5 m tall open-top chambers increased surface air temperatures. The snowpack was removed from the experimental plots in spring to ensure equivalent melt-out dates between treatments. Chambers were placed on 12 cm tall bases inserted 5 cm into the soil to improve the seal, and control plots also contained chamber bases. Combined, this warming regime warmed air and deep soil temperatures by between 0.5°C and 1.5°C (Natali et al. 2011).

Fieldwork for this paper was completed between July 14 and August 18 of 2010. We surveyed vegetation using the point-intercept method in order to determine the six most abundant vascular plant species at the field site. Next, we harvested fully expanded leaves from the six dominant vascular plant species from both experimental and control plots. We collected a minimum of three leaves from two–three individuals in each plot in order to obtain a sample representative of the population.

Samples were dried at 60°C before transport to the University of Florida for processing at the Ecosystem Dynamics Lab. We re-dried samples at 60°C for at least 24 hours, weighed them, and finely chopped each sample with scissors. We weighed approximately 3 mg of homogenized material from each sample and rolled them in Costech 4x6 mm tins. Samples were analyzed for C and N using a Costech Instruments EC54010 elemental analyzer, and they were combusted in a ThermoFinnigan Delta-plus XL mass spectrometer at 1010 °C to determine $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures. Stable isotope abundances are reported as the ratio of $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$, expressed in relation to a reference standard (atmospheric N_2 and PeeDee belemnite C).

Means and standard errors were calculated in Microsoft Excel, and data were then analyzed using a two-way ANOVA using JMP 7 software by SAS. Species not fitting the assumptions of normality were transformed using a Box-Cox transformation. Post hoc tests (Tukey’s Honestly Significant Difference Test) were used to identify contributions to the interaction effect between summer and winter warming. Due to the high structural heterogeneity of CiPEHR, tests were analyzed at significance values of $P \leq 0.10$.

RESULTS

Nitrogen Responses

Warming-mediated changes in N dynamics were detected in three out of four functional groups present at CiPEHR. Graminoids and forbs responded as we expected, with increased $\delta^{15}\text{N}$ values. *R. chaemomorus* (forb) $\delta^{15}\text{N}$

increased with both summer warming ($P=0.04$, $F=3.04$) and winter warming ($P=0.09$, $F=5.03$) (Figure 1). $\delta^{15}\text{N}$ values increased in both graminoid species present at CiPEHR (*E. vaginatum* and *C. bigelowii*). A shift in *E. vaginatum* (a dominant tussock forming sedge) $\delta^{15}\text{N}$ was driven by an interaction between summer and winter

warming ($P=0.07$, $F=3.608$), and *C. bigelowii* $\delta^{15}\text{N}$ enrichment occurred in summer warming plots ($P=0.09$, $F=3.1$). The opposite was found for *B. nana*, a ubiquitous deciduous shrub at CiPEHR. *B. nana* $\delta^{15}\text{N}$ decreased in annual warming plots, which was driven by a summer x winter interaction ($P=0.02$, $F=6.88$) (Figure 1).

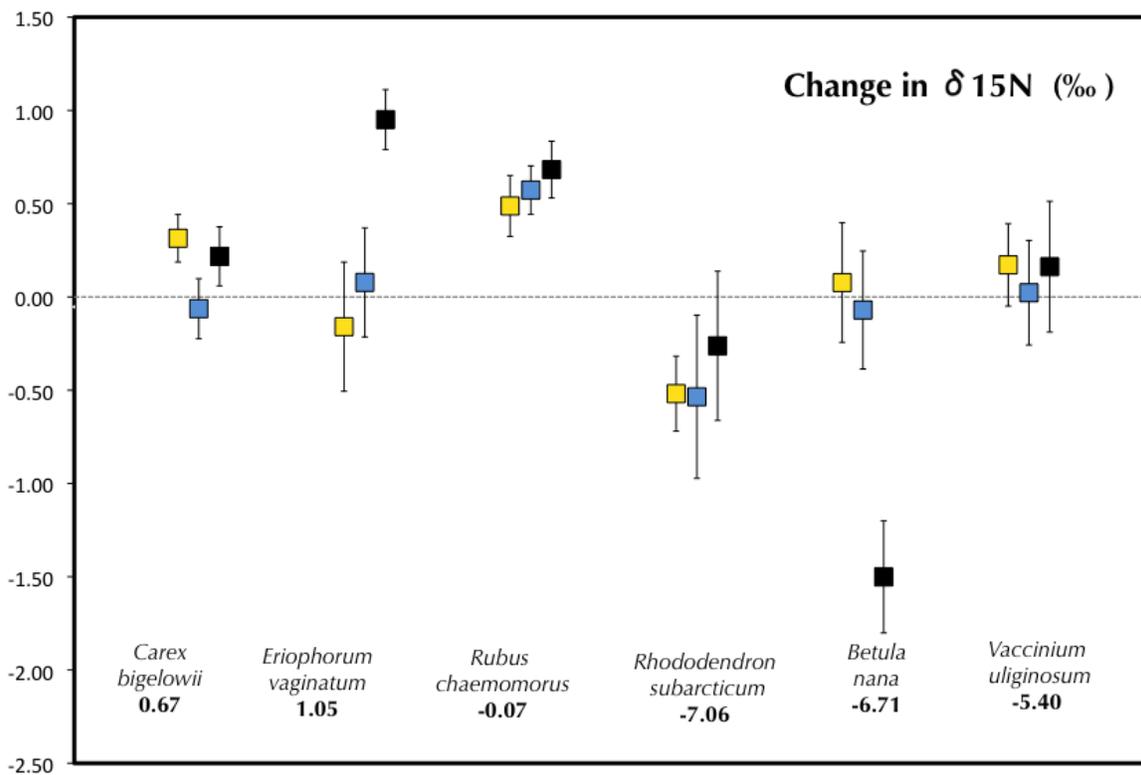


Figure 1. Change in $\delta^{15}\text{N}$ calculated as treatment-control. Yellow: summer warming; blue: winter warming; black: annual warming. Values under species label indicate %N of plants in ambient conditions.

Overall, leaf N content (%N) remained constant before and after warming in all species studied (Table 1). However, there was considerable variation in %N among

species under ambient conditions, which ranged from 1.57% (*R. subarcticum*) to 2.08% (*C. bigelowii*) (Figure 2).

Table 1. Foliar C, N, C:N, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from Leaves Collected at Peak Growing Season at CiPEHR in 2010

Variable	Treatment	<i>B. nana</i>	<i>C. bigelowii</i>	<i>E. vaginatum</i>	<i>R. subarcticum</i>	<i>R. chaemomorus</i>	<i>V. uliginosum</i>
C (%)	Ambient	48.0 ± 0.2	44.5 ± 0.2	45.4 ± 0.1	50.7 ± 0.1 ^s	44.4 ± 0.2	47.6 ± 0.2
	Summer	47.9 ± 0.2	44.6 ± 0.2	44.9 ± 0.2	51.1 ± 0.1	44.9 ± 0.3	48.0 ± 0.2
	Winter	47.9 ± 0.2	44.3 ± 0.1	45.4 ± 0.2	50.9 ± 0.1	44.7 ± 0.3	48.1 ± 0.2
	Annual	48.0 ± 0.2	44.3 ± 0.1	45.4 ± 0.4	51.1 ± 0.2	45.0 ± 0.3	48.0 ± 0.2
N (%)	Ambient	2.0 ± 0.2	2.1 ± 0.1	1.9 ± 0.1	1.6 ± 0.1	2.2 ± 0.1	1.8 ± 0.1
	Summer	2.0 ± 0.1	1.9 ± 0.2	1.7 ± 0.1	1.6 ± 0.1	2.3 ± 0.1	1.8 ± 0.1
	Winter	2.1 ± 0.1	2.0 ± 0.1	1.9 ± 0.1	1.5 ± 0.0	2.1 ± 0.1	1.8 ± 0.1
	Annual	1.8 ± 0.1	2.1 ± 0.2	2.0 ± 0.2	1.6 ± 0.1	2.1 ± 0.1	1.8 ± 0.0
$\delta^{13}\text{C}$ (‰)	Ambient	-28.1 ± 0.2 ^{sxw}	-25.3 ± 0.3	-26.3 ± 0.1	-27.0 ± 0.2 ^s	-27.4 ± 0.4	-29.4 ± 0.1
	Summer	-28.0 ± 0.2	-25.2 ± 0.4	-25.8 ± 0.3	-27.5 ± 0.2	-27.2 ± 0.2	-29.3 ± 0.2
	Winter	-28.5 ± 0.2	-25.1 ± 0.2	-26.1 ± 0.1	-26.8 ± 0.1	-27.1 ± 0.3	-29.6 ± 0.1
	Annual	-27.4 ± 0.3	-25.0 ± 0.2	-26.0 ± 0.5	-27.1 ± 0.1	-27.0 ± 0.2	-29.3 ± 0.2
$\delta^{15}\text{N}$ (‰)	Ambient	-6.7 ± 0.2 ^{sxw}	0.7 ± 0.2 ^s	1.0 ± 0.2 ^{sxw}	-7.1 ± 0.3	-0.1 ± 0.2 ^{s,w}	-5.4 ± 0.2
	Summer	-6.6 ± 0.3	1.0 ± 0.1	0.9 ± 0.3	-7.6 ± 0.2	0.4 ± 0.2	-5.2 ± 0.2
	Winter	-6.8 ± 0.3	0.6 ± 0.2	1.1 ± 0.3	-7.6 ± 0.4	0.5 ± 0.1	-5.4 ± 0.3
	Annual	-8.2 ± 0.3 [*]	0.9 ± 0.2	2.0 ± 0.2	-7.3 ± 0.4	0.6 ± 0.2	-5.2 ± 0.4

Note. Treatments are categorized as follows: Ambient=full control; Summer=chambers only; Winter=snow fences only; Annual=chambers and snow fences. Statistical significance is expressed as follows: S = significant SW effect; W = significant WW effect; S×W = significant interaction effect. All significant effects at P ≤ 0.10.

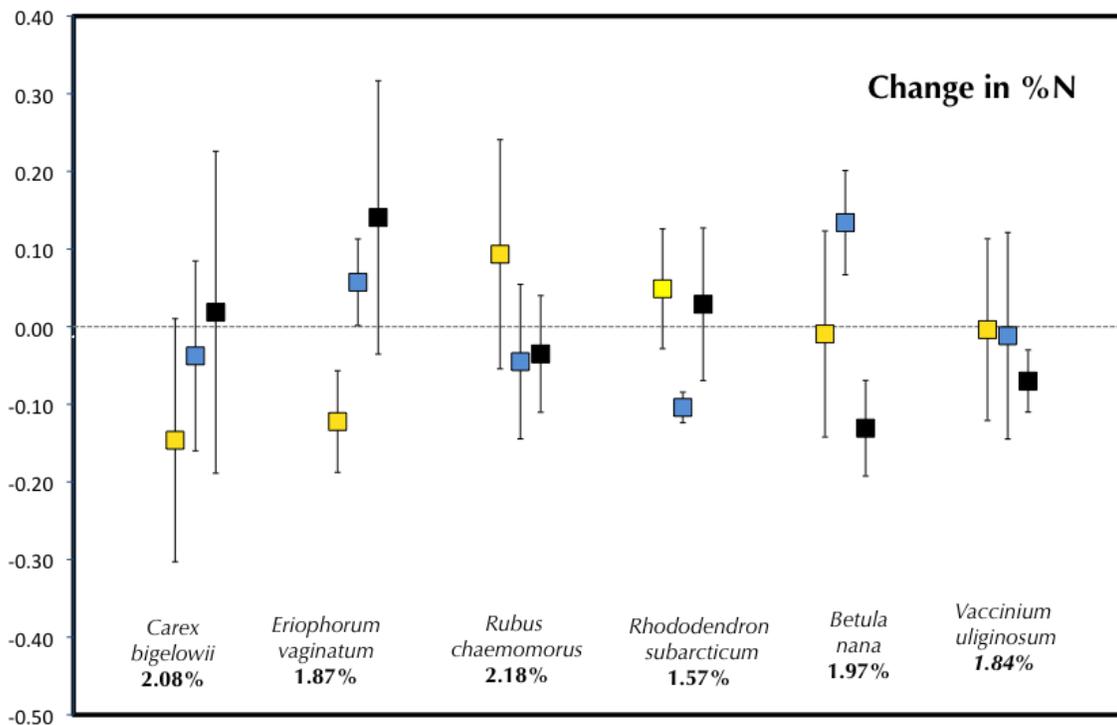


Figure 2. Change in %N with warming calculated as treatment-control. Note. Yellow; summer warming, blue; winter warming, black; annual warming. Values under species label indicate %N of plants in ambient conditions.

Carbon Responses

Summer and winter warming likely increased transpiration (i.e. water stress), as evidenced by the non-random pattern $\delta^{13}\text{C}$ enrichment for *C. bigelowii*, *E. vaginatum* and *R. chaemomorus* (Figure 3), although these changes were not statistically significant. Warming-induced changes in $\delta^{13}\text{C}$ were observed for *B. nana* and *R. subarcticum* (Table 1). *B. nana* $\delta^{13}\text{C}$ increased in annual warming plots, which was driven by a summer x winter

interaction ($P=0.04$, $F=4.71$) (Figure 4). On the other hand, *R. subarcticum* $\delta^{13}\text{C}$ decreased in summer warming plots ($P=0.03$, $F=5.27$) (Figure 4).

Summer warming also led to a significant increase in *R. subarcticum* %C ($P=0.03$, $F=5.48$) (Table 1). Species-level variation was found for $\delta^{13}\text{C}$, which ranged from -30.37‰ (*V. uliginosum*) to -26.26‰ (*C. bigelowii*) as well as for %C, which varied by as much as 5% among species (Figure 3).

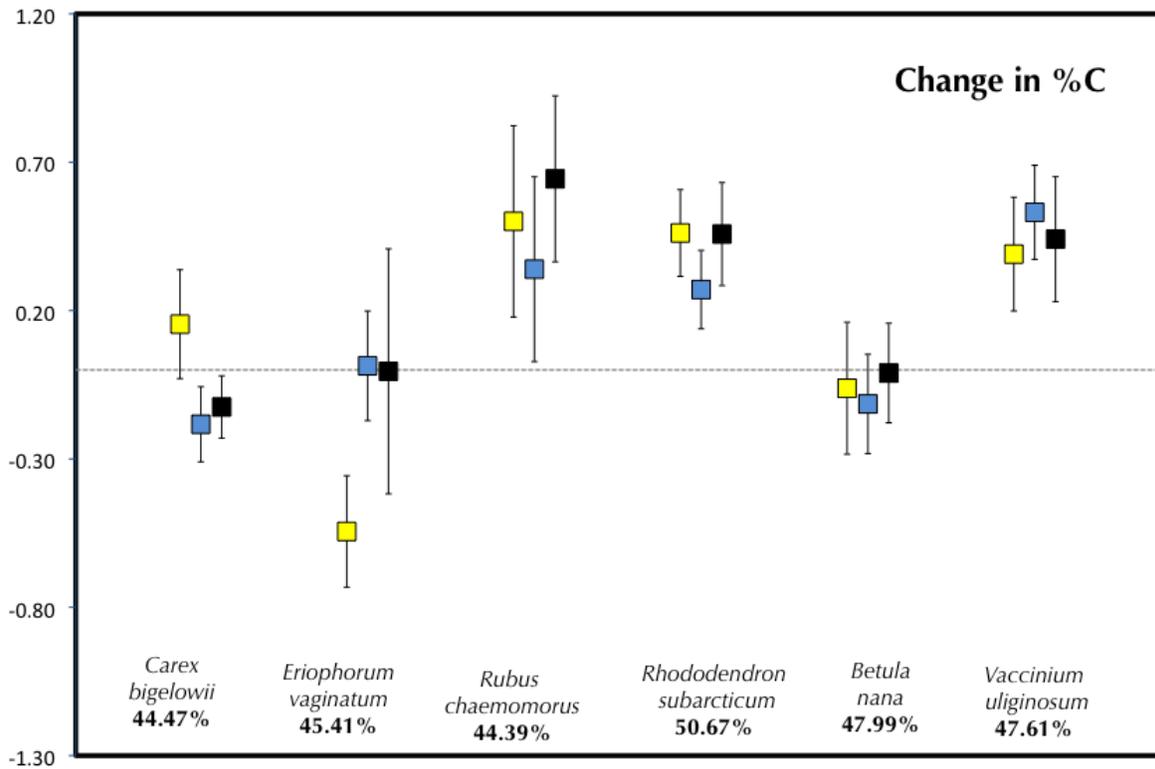


Figure 3. Change in %C calculated as treatment-control. Note. Yellow: summer warming; blue: winter warming; black: annual warming. Values under species label indicate %C of plants in ambient conditions.

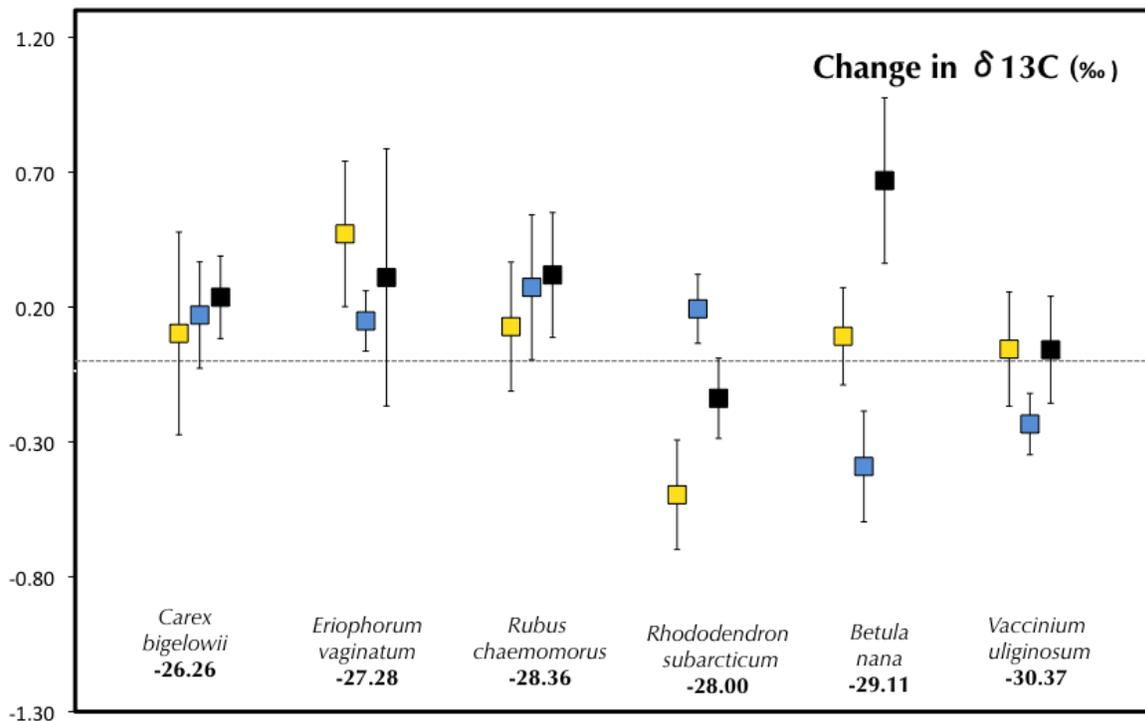


Figure 4. Change in $\delta^{13}\text{C}$ calculated as treatment-control. Note. Yellow; summer warming, blue; winter warming, black; annual warming. Values under species label indicate $\delta^{13}\text{C}$ of plants in ambient conditions.

DISCUSSION

This study examined species-level variation as well as warming effects on leaf chemistry. At CiPEHR, warming mediated shifts occurred in five out of six dominant species. As microbial respiration and photosynthesis are often accompanied by shifts in N availability, it is important to view changes in C and N together rather than in isolation. Changes in foliar C and N also feed back to larger processes, such as the role of tundra as a net source or net sink of C. Our results indicate a link between leaf chemistry and climate warming, suggesting that leaf responses may forecast structural changes to the arctic landscape.

Effects of Experimental Warming

Warming caused an increase in foliar $\delta^{15}\text{N}$ in *E. vaginatum* (sedge) and *R. chaemomorus* (forb). Changes in $\delta^{15}\text{N}$ values can reflect either a passive response of plants to increased N availability and N cycling rates (Kahmen et al. 2008, Craine et al. 2009) or to an active shift in the N source utilized (Robinson 2011, Evans 2001). N inputs result in $\delta^{15}\text{N}$ enrichment of soil N pools as the lighter $\delta^{14}\text{N}$ isotope is lost through leaching and denitrification (the production of gaseous N from nitrate by soil bacteria in the absence of O_2) (Dawson 2002). Interestingly, all three of

the species that had enriched $\delta^{15}\text{N}$ with warming are deciduous and have relatively high $\delta^{15}\text{N}$ values under ambient conditions (Figure 1). Since deciduous species lose and gain N faster than other functional groups (Aerts 1995), they may be more responsive to warming-mediated increases in soil N. Another possible scenario is that plants could be shifting their N sources (e.g., from nitrate to ammonium, which is less depleted in $\delta^{15}\text{N}$) (Miller & Bowman 2002).

While forb and graminoid $\delta^{15}\text{N}$ increased, the strongest responses were observed in the ubiquitous deciduous shrub at CiPEHR *B. nana*. Previous studies have also shown that *B. nana* was highly responsive in fertilization studies (Shaver & Chapin 1980, Sydonia Bret-Harte et al. 2004) and with experimental warming (Hobbie et al. 1999). One possible explanation for this decrease in $\delta^{15}\text{N}$ is heightened mycorrhizal fungi activity. Warming can lead to increased biomass and abundance of ectomycorrhizal fungi, which typically transfer $\delta^{15}\text{N}$ -depleted N to plant roots (Clemmensen et al. 2006). A long-term warming experiment at Toolik Lake found that warming alters the ectomycorrhizal community of *B. nana* in arctic tundra, suggesting that warming may facilitate the expansion of *B. nana* by forming larger mycorrhizal networks (Deslippe et al. 2011). This high responsiveness of *B. nana* (Figure 2) is important because woody species are indeed increasing in abundance across the arctic biome (Sturm et al. 2001,

Sturm et al. 2005, Chapin & Shaver 1995, Tape et al. 2006).

We did not find any warming-induced changes in %N, but this was not unexpected. Studies in Sweden (Aerts et al. 2009); Ellesmere Island, Canada (Tolvanen and Henry 2001); and Toolik Lake, AK (Hobbie and Chapin 2008) detected no change or minimal decreases in %N with experimental warming. However, the biomass of winter-warmed plots at CiPEHR in 2010 was 20% higher than in non-warmed plots (Natali, *unpublished data*). This indicates that plants were able to acquire enough N to accommodate increased C sequestration.

Summer warming elicited a water-stressed response from several species, with a positive relationship between temperature and $\delta^{13}\text{C}$ values. Overall, it appears that summer warming lowered $\delta^{13}\text{C}$ discrimination (increased $\delta^{13}\text{C}$ values), as evidenced by the non-random pattern of $\delta^{13}\text{C}$ enrichment for *C. bigelowii*, *E. vaginatum* and *R. chaemomorus* (Figure 4), although these results were not statistically significant. *R. subarcticum* (forb) $\delta^{13}\text{C}$ decreased in summer-warmed plots, indicating a decrease in the rate of photosynthetic C fixation relative to diffusion through stomata (Farquhar et al. 1989). Perhaps *R. subarcticum* is more resilient to the effects of drying tundra. Surprisingly, *B. nana* was the only species in which $\delta^{13}\text{C}$ increased significantly during summer warming, indicating that *B. nana* may have been undergoing water stress. So, while *B. nana* can be facilitated through increased mycorrhizal networks, its growth may be constrained by water stress, a side effect of increased temperature.

Species Differences

Species vary naturally in %C, %N, $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ under ambient conditions. Changes in the soil environment can favor species that can exploit the most abundant N source (McKane et al. 2002) and have the greatest C storage potential (Schoor et al. 2007).

In N-limited tundra, plants coexist by partitioning N sources: nitrate, ammonium, and free amino acids (Nadelhoffer et al. 1996, McKane et al. 2002, Miller & Bowman 2001). Thus, the unique $\delta^{15}\text{N}$ signature among plant species is shaped by a variety of processes, including forms of N taken up, rooting depth, and mycorrhizal associations. For example, shallow-rooted species such as *B. nana* have relatively low $\delta^{15}\text{N}$ values because they are more likely to acquire N from sources near the soil surface (e.g., precipitation, runoff, and fresh leaf litter). Deep-rooted species such as *E. vaginatum*, on the other hand, compete more effectively for N deeper in soil profiles (Nadelhoffer et al. 1996). Furthermore, $\delta^{15}\text{N}$ depletion in woody species may also be explained by preferential use of nitrate over ammonium or by the transfer of $\delta^{15}\text{N}$ -depleted N by mycorrhizae (Miller and Bowman 2002). Warming-mediated changes in soil N status could favor certain

species that have improved access to their preferred N source.

Under ambient conditions, leaf carbon varied by as much as 5%. This variation may be driven by differences in leaf physiology, growth form, and phenology. For example, shrubs tend to have a higher percent cellulose, lignin, and silica than other plant groups (Klein 2007), and species vary in the amount of C they allocate below ground to roots (Hudson et al. 2011). If plant communities shift to shrub dominated, this could affect the amount of C stored above ground. Furthermore, differences in leaf chemistry among species can affect litter decomposition rates. For example, graminoid litter has been shown to decompose faster than shrubs (Hobbie 1996), leading to increased rates of C and N cycling. Also, $\delta^{13}\text{C}$ values differed among species and growth forms with values ranging from -30.37‰ (*V. uliginosum*) to -26.26‰ (*C. bigelowii*), indicating variation in C isotope discrimination, growth rate, and diffusive C uptake.

Future Directions

Short-term winter and summer warming (two years) resulted in leaf chemistry shifts in five out of six species at CiPEHR. Future study should address whether long-term warming will elicit a stronger response or a subdued response as plants acclimate to warmer conditions. Chapin et al. (1995) found that plant response to short-term (three years or less) changes in temperature were mostly a surge in vegetative growth, whereas long-term (nine years) warming more accurately represented changes in resource availability.

The effects of warming on plant nutrient dynamics may depend on site characteristics, such as the initial community structure (Jagerbrand et al. 2009, Walker et al. 2006). In Northern Alaska (Welker et al. 2005), moist tundra vegetation was much more responsive to experimental warming than dry tundra with up to a 25% increase in leaf N. Furthermore, these results vary globally, with $\delta^{13}\text{C}$ values increasing in *C. lapponica* and *D. integrifolia* with 16 years of warming on Ellesmere Island (Hudson et al. 2011) and $\delta^{13}\text{C}$ decreasing in *C. lapponica* with nine years of summer warming in Northern Sweden (Aerts et al. 2009). Continued sampling across a variety of tundra types may allow a better understanding of plant responses to warming across arctic and subarctic regions.

Lastly, more emphasis should be placed on the role of mycorrhizal fungi in attenuating N limitation in arctic tundra. Fungal symbioses can supply 61–86% of the nitrogen found in plants by providing access to inorganic and organic N pools (Hobbie & Hobbie 2006). Depending on the plant species, mycorrhizae may balance N levels in plants by giving N as a function of need. Or, in the case of *B. nana*, mycorrhizae may facilitate shrub expansion across the arctic landscape.

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