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THE RESPONSE OF TUNDRA PLANT BIOMASS, ABOVEGROUND PRODUCTION, NITROGEN, AND CO_2 FLUX TO EXPERIMENTAL WARMING

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Abstract. We manipulated air temperature in tussock tundra near Toolik Lake, Alaska, and determined the consequences for total plant biomass, aboveground net primary production (ANPP), ecosystem nitrogen (N) pools and N uptake, and ecosystem CO_2 flux. After 3.5 growing seasons, in situ plastic greenhouses that raised air temperature during the growing season had little effect on total biomass, N content, or growing-season N uptake of the major plant and soil pools. Similarly, vascular ANPP and net ecosystem CO_2 exchange did not change with warming, although net primary production of mosses decreased with warming. Such general lack of response supports the hypothesis that productivity in tundra is constrained by the indirect effects of cold temperatures (e.g., low nutrient availability or short growing-season length) rather than by cold growing-season temperatures per se.

Despite no effect on net ecosystem CO_2 flux, air warming stimulated early-season gross photosynthesis (GP) and ecosystem respiration (ER) throughout the growing season. This increased carbon turnover was probably associated with species-level responses to increased air temperature. Warming increased the aboveground biomass of the overstory shrub, dwarf birch (*Betula nana*), and caused a significant net redistribution of N from the understory evergreen shrub, *Vaccinium vitis-idaea*, to *B. nana*, despite no effects on soil temperature, total plant N, or N availability. Thus, although air warming had no effect on total ecosystem N pools, it did mediate N distribution within the plant community. The early-season stimulation of GP is consistent with warming effects on leaf expansion of dominant shrubs (including *B. nana*) observed in other studies in tussock tundra. The stimulation of ER probably resulted from maintenance and growth respiration associated with higher aboveground *B. nana* biomass production and higher root N uptake and/or turnover in the greenhouses. The species responses to warming are consistent with changes in plant species assemblages associated with past warming and suggest that future warming may increase the abundance of *B. nana* in tussock tundra. We conclude that a 4°C rise in air temperature alone will significantly stimulate carbon turnover in tundra but will have little effect on net carbon balance.

Key words: arctic; Betula nana; *carbon; CO_2; global warming; microbial biomass; nitrogen; photosynthesis; plant biomass; primary production; respiration; tussock tundra;* Vaccinium vitis-idaea.

INTRODUCTION

Studies of the temperature response of arctic plant physiological processes such as photosynthesis and nutrient uptake suggest that arctic plants (1) are well adapted to low temperature, having low physiological temperature optima, and (2) show little physiological response to changes in temperature over a broad range (Chapin 1983). These observations have led to the hypothesis that cold temperatures mainly limit plant growth indirectly, by reducing the length of the growing season and the rates of nutrient input from weathering and recycling by decomposition (Chapin 1983).

However, despite relatively small temperature effects on physiological processes involved in resource acquisition, temperature in some cases can strongly limit plant growth (Körner and Larcher 1988). Furthermore, in situ experimental warming can have large effects on shoot growth, phenology, and reproductive allocation of individual species (Havström et al. 1993, Wookey et al. 1993, 1994, Parsons et al. 1994, Chapin et al. 1995*b*, Chapin and Shaver 1996). To what extent these warming effects are a result of direct temperature limitation vs. temperature limitation operating indirectly through soil nutrient availability has never been determined.

In this study we manipulated in situ air temperature, but not nutrient availability, in Alaskan tussock tundra, and measured direct warming effects on plant biomass, production, nitrogen (N), and ecosystem CO_2 flux. We focus on N because it limits plant biomass accumulation in this system (Shaver and Chapin 1986), and may thus constrain how increased temperature affects the carbon balance of tundra ecosystems (Shaver et al.

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1992, McKane et al. 1997). Temperature was manipulated using plastic greenhouses similar to those used in other studies of arctic tundra (Havström et al. 1993, Wookey et al. 1993, 1994, Parsons et al. 1994, Chapin et al. 1995*a*, *b*).

This study differs from similar studies of Alaskan tussock tundra (Chapin and Shaver 1985, 1996, Chapin et al. 1995*b*) in four major ways. First, in addition to measuring biomass and N pools, we also used a stable-isotope ^{15}N tracer to measure the response of annual plant N uptake to temperature manipulation. Detecting a plant or system-level response to a 4-yr manipulation is potentially difficult in tundra because biomass and N pools are large relative to rates of change in those pools (Shaver and Chapin 1991). We hoped that using a ^{15}N tracer would be a more sensitive measure of system response. Second, this study is the first to measure the response of root biomass and N to an environmental manipulation in tundra. Third, our manipulation resulted primarily in increased air temperature, allowing us to isolate effects of increased air temperature from confounding effects of increased soil temperature. Finally, this is one of only two studies of environmental manipulations in tundra that directly relate plant biomass and N to whole-ecosystem CO_2 flux, and the first to do so in upland tussock tundra (Shaver et al. 1998).

Methods

We experimentally increased temperature in upland tussock tundra at the Long-Term Ecological Research (LTER) site in Toolik Lake, Alaska (68°38′ N, 149°34′ W, elevation 760 m). We established 1-m^2 plots in 10 blocks of 2 plots each in a 20 × 50 m uniform region of gently sloping tundra. One of the plots in each block was randomly selected for cover by a wooden frame supporting 0.15-mm (6-mil) polyethylene ''greenhouses'' that extended 20 cm beyond the plot boundaries during the growing seasons of 1990–1993. We installed greenhouses on the plots each spring following snow melt and removed them each year in mid-August. Because of uneven microtopography, the bottom of the frames rested on the ground but air circulated in and out of the greenhouses at the bases. During 1991–1993, we cut 200-cm^2 holes in the tops of the greenhouses to increase air circulation (Parsons et al. 1994). We left the other 10 plots uncovered as unmanipulated controls. These 10 replicate control and greenhouse-covered plots (referred to henceforth as ''final-sampling plots'') were kept undisturbed for measurements of ecosystem CO_2 flux until a final destructive harvest in 1993 to determine plant and microbial biomass and N. In 1991, we established additional control and greenhouse plots (n = 5 blocks) distributed around the perimeter of the original 10 blocks of the experiment. In these plots (referred to henceforth as ''periodic-sampling plots'') we measured various soil parameters and processes that required periodic disturbance throughout the experiment (e.g., destructive soil sampling).

Environmental effects of greenhouses

During the 1991–1993 growing seasons we measured air temperature 20 cm above the canopy (n = 5 blocks) and soil temperature at 10 cm below the moss surface (n = 5 blocks during 1991–1992, n = 8 in 1993) in moss mats in the final-sampling control and greenhouse plots using copper-constantan thermocouples attached to a datalogger (Campbell CR10, Campbell Scientific, Logan, Utah). The datalogger logged hourly and daily means of 1-min measurements throughout the growing season. Maximum and minimum hourly mean temperatures were also determined daily and averaged for each plot during each season. Throughout the 1993 growing season we also recorded hourly relative humidity (n = 1 block) in a control and greenhouse plot and increased the number of replicate air temperature measurements to six using thermistor/relative humidity probes (Campbell HMP35C). From concurrent measures of temperature and relative humidity we calculated vapor pressure deficits. In 1993 we recorded photosynthetically active radiation (PAR) above the canopy hourly (n = 3 blocks) using photodiodes (Hamamatsu G1118, resin-sealed, Hamamatsu, Bridgewater, New Jersey) calibrated against a quantum sensor (LI-COR 190SA, LI-COR Instruments, Lincoln, Nebraska) (Pearcy 1989) and attached to the datalogger.

We measured depth of thaw to permafrost in moss mats in the final-sampling plots at peak biomass (late July–early August) during 1991–1993 using a stainless steel probe, averaging three measurements per plot (n = 10 blocks). We measured moss moisture (0–5 cm depth below the moss surface) and soil moisture (5–10 cm depth below the moss surface) gravimetrically in early August 1991 and in early and late July 1992 in the periodic-sampling plots (n = 5 blocks). We also measured soil moisture in early August of 1993 in the final-sampling plots (n = 10 blocks). We made spot-measurements of CO_2 concentration in the final-sampling plots above the canopy on several occasions using an open leaf cuvette attached to a LI-COR 6200 infra-red gas analyzer (IRGA, LI-COR Instruments, Lincoln, Nebraska). In 1991, CO_2 concentrations were compared in early August (n = 5) under conditions of low light (40–150 $\mu mol \cdot m^{-2} \cdot s^{-1}$), medium light (250–550 $\mu mol \cdot m^{-2} \cdot s^{-1}$), and high light (700–1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$). In 1992, CO_2 concentrations were compared on sunny days (PAR > 900 $\mu mol \cdot m^{-2} \cdot s^{-1}$) twice during the growing season (early and late July, n = 10 at each date), i.e., under conditions when we expected photosynthetic drawdown of CO_2 in the greenhouses to be strongest.

Decomposition and nutrient availability

To further characterize treatment effects on the belowground environment, we measured decomposition in the periodic-sampling plots (n = 5 blocks) using 10

× 10 cm litter bags made of 1-mm nylon mesh containing ~5 g of weighed, air-dried *Betula papyrifera* leaf litter collected from the taiga forest in Fairbanks, Alaska. We used this litter rather than locally available tundra litter because we were interested mainly in comparing treatment effects on decomposition of a common substrate, and *B. papyrifera* litter was available in large quantities. On 22 June 1991, we placed five litter bags 5–10 cm below the moss surface in randomly located mats within each plot. We harvested one litter bag from each plot 51, 361, 404, 720, and 782 d after deployment. Spring harvests occurred as soon as soils thawed to the depth of the litter bags. After each harvest we dried (65°C) and weighed the litter to determine the percentage of the original mass remaining.

We used ion-exchange resins to assess nutrient availability in the plots (Giblin et al. 1994). We constructed 5 × 5 cm resin bags by placing 7 mL of acid-washed (10% HCl) anion or cation exchange resins (Dowex 50W-X8 20–50 mesh H^+ or 1-X8 20–50 mesh Cl^-, respectively) into acid-washed nylon stockings and sewing the ends shut. We placed anion and cation resin bags at 5–10 cm depth in moss mats in the periodic-sampling plots in mid-June 1992 ($n = 5$). At the end of July 1992, we replaced those resin bags with fresh resin bags that we harvested the following spring (mid-June 1993).

After each harvest, we froze the resins until extraction. We extracted resins by rinsing them in a sieve with deionized water, placing them in a pre-leached 30-mL syringe with Whatman GF/A filter paper in the bottom, and dripping 100 mL of 2 mol/L NaCl (in 0.1 mol/L HCl) over them (Giblin et al. 1994). Extracts were analyzed for NH_4^+, NO_3^-, and PO_4^- colorimetrically on the Lachat QuickChem Autoanalyzer.

Plant biomass, nitrogen, and ANPP

In early August 1993 (peak plant biomass before the onset of senescence), we destructively harvested two 400-cm^2 quadrats in all final-sampling plots ($n = 10$ blocks) to determine above- and belowground live biomass, aboveground vascular standing dead mass, and litter mass. We located the quadrats randomly within the plots, but avoided harvesting from a 20-cm wide margin around the plot edge because of possible effects of severed roots on plant biomass (a consequence of inserting CO_2-flux chamber bases). We clipped all vascular vegetation to the moss surface and sorted it by species and organ. We sorted aboveground biomass into standing dead, current year's production (apical stems, new leaves, and inflorescences or fruits), and old biomass (previous years' stems and evergreen leaves) by species. For the evergreen shrub *Cassiope tetragona* and the forbs *Pedicularis* spp. and *Polygonum bistorta*, we did not separate leaves from stems. We also collected litter that was present on the moss surface. We separated live moss (i.e., green moss or moss with structural integrity) from dead moss and sorted moss by species. We were able to separate the current year's production from that of previous years for the moss *Hylocomium splendens*, since this species produces recognizable annual growth increments (Callaghan et al. 1978). We did not sort lichens by species.

We sorted belowground stems (rhizomes) and roots by species in a subsample from 0 to 10 cm below the moss surface, saving a subsample of soil for further analysis (see *Nitrogen partitioning and uptake*). This is approximately equal to the O horizon since depth of the organic mat averages 12 cm in this system (S. E. Hobbie, *unpublished data*). We sorted all belowground stems and roots by species from 10 cm depth to permafrost, discarding the soil. After sorting, we dried all tissues at 65°C and weighed and ground them. We determined N concentration by combustion and mass spectrometry (Europa Scientific, Crewe, UK) on a subsample of all dried samples from each quadrat within a plot.

Shrub belowground stems were easily identified by comparing them to aboveground stems. Roots were easily identified to species when attached to belowground stems. We identified unattached roots to species mainly on the basis of size, color, texture, and mycorrhizal status. Sedge roots are light colored and relatively large, making them easily recognized. *Eriophorum vaginatum* roots differ from those of *Carex bigelowii* by being white colored, smooth, and unbranched. *Carex bigelowii* roots are tan colored, branched, and have a pubescent texture. Unattached *Betula nana* roots were recognized by the presence of ectomycorrhizal roots, since the only other species in the community that is ectomycorrhizal, *Salix pulchra*, was very uncommon at our site (see *Results*). *Rubus chamaemorus* roots have a distinctive color and texture (coarse, reddish-brown, smooth, and elastic). Roots of ericaceous species (*Vaccinium vitis-idaea, Ledum palustre, Cassiope tetragona, Andromeda polifolia, Arctostaphylos alpina, Empetrum nigrum, Vaccinium uliginosum*) were the most problematic roots to identify to species since all species resemble one another in having very fine, dark roots. Although ericaceous roots attached to belowground stems were recognizable based on stem characteristics, we assigned unattached roots only to *V. vitis-idaea* and *L. palustre*, by far the most common ericaceous species in the community (based on aboveground biomass, see *Results*). We assigned unattached roots to *V. vitis-idaea* and *L. palustre* based on color, assigning light-colored roots to *L. palustre* and dark-colored roots to *V. vitis-idaea*. Therefore, we potentially underestimated the root biomass of the less common ericaceous species, and the root biomass that we report for *V. vitis-idaea* and *L. palustre* represents our best estimate.

We calculated aboveground vascular apical production by adding together the mass of current year's growth for all species. This overestimates by ~50% the leaf production of one of the dominant sedge spe-

cies, *Eriophorum vaginatum,* which produces some evergreen leaves that overwinter (Shaver and Chapin 1991). We estimated moss production by assuming that all moss species have production : biomass ratios similar to that of *Hylocomium splendens,* using separate ratios for control and greenhouse-treated plots. Finally, we estimated stem secondary production using the method of Shaver (1986) and the regression equations from Shaver and Chapin (1991; G. R. Shaver, *personal communication*). Briefly, this method determines the annual percentage increase in stem mass of stems that are >1 yr old (secondary growth) by regressing mass per unit length of stem segments against stem age. We assumed that *Rubus chamaemorus* and *Andromeda polifolia* resemble *Vaccinium vitis-idaea* in having negligible secondary growth (Shaver 1986), and excluded those shrub species from our estimate. In addition, we excluded *Cassiope tetragona* from our estimate of secondary production since we did not separate stem and leaf biomass for this species. Its old stem biomass is <20% of total old stem biomass of those species that exhibit secondary growth (see *Results*).

We compared control and greenhouse treatments using independent *t* tests, after averaging the values from the two quadrats within any plot. When the assumption of homogeneity of variances was not met, we compared treatments using a Mann-Whitney *U* test. We did not statistically compare estimates of aboveground netprimary production (ANPP) that included stem secondary production or moss apical production.

Nitrogen partitioning and uptake

To determine the effects of the warming manipulation on N uptake over the growing season, we used a stable-isotope N tracer. On 19 June 1993, we applied 0.065 g/m^2 of $^{15}(NH_4)_2SO_4$ (99% atom percentage ^{15}N) to all of the 400-cm^2 quadrats designated for harvesting (see *Plant biomass, nitrogen, and ANPP,* above). We applied the ^{15}N tracer in solution by injecting 25 times in a grid over each quadrat. The solution was evenly distributed from 0 to 10 cm depth below the moss surface by inserting the needle to 10 cm depth and pulling it up as we dispensed 10 mL of the tracer solution per injection. The injection needle was sealed at the tip, and four holes drilled around the needle just behind the tip helped distribute the ^{15}N solution throughout the soil.

Concurrently with the plant biomass harvest, we homogenized and subsampled the soil from each quadrat to 10 cm below the moss surface. We determined soil moisture content gravimetrically on one subsample that we saved and used later for determination of total soil ^{15}N and N. Additional subsamples were used to determine microbial biomass N and ^{15}N using the chloroform-fumigation direct-extraction technique (Brookes et al. 1985). We extracted one 10-g (wet mass) subsample with 50 mL of 0.5 mol/L K_2SO_4 immediately and another subsample following fumigation with chloroform for 24 h. Frozen extracts were returned to Berkeley, where we digested them using Kjeldahl digestion and determined their N content colorimetrically on a Lachat QuickChem Autoanalyzer (Lachat Instruments, Milwaukee, Wisconsin). We determined the ^{15}N content of the digests by trapping the $^{15}NH_3$ generated by addition of concentrated NaOH to the digest on an acidified filter paper disk suspended above the digest (Brooks et al. 1989). We measured the atom percentage ^{15}N of the N trapped on the filter paper disk by mass spectrometry. The difference between the N and ^{15}N in the fumigated and nonfumigated samples was equal to chloroform-labile N and ^{15}N.

We determined atom percentage ^{15}N for all dried and milled plant and soil samples using mass spectrometry. We calculated recovery by adding up the plant and soil ^{15}N enrichment and dividing it by the amount of ^{15}N injected, using natural abundance values determined by Nadelhoffer et al. (1996) to determine enrichment. Our assumption was that the soluble soil N fraction equals the nonfumigated K_2SO_4-extractable N, that the soil microbial biomass N equals the chloroform-labile N pool multiplied by a conversion factor (K_N) of 0.54 (Brookes et al. 1985), and that the insoluble soil N fraction equals the total soil N minus (soluble soil N + microbial biomass N). We determined partitioning of the ^{15}N tracer at the ecosystem level by calculating the percentage of the injected label that ended up in various plant and soil N pools. In addition, ^{15}N uptake by the common plant species was calculated by multiplying plant N content on area basis by atom percentage ^{15}N above natural abundance (McKane et al. 1990).

CO_2 flux

We measured ecosystem CO_2 flux in five randomly selected blocks on four dates during the 1993 growing season: 17 June, 26 June, 15 July, and 28 July. These dates span the growing season, with 17 June being just after bud-break, and 28 July being just before the onset of senescence. In 1992 (1 yr prior to making measurements), we cut vertically into the soil around the perimeter of the plots with a keyhole saw to sever roots and allow temporary insertion of a chamber base. Approximately 0.5 h before making a measurement we inserted a 1 × 1 × 0.3 m stainless steel chamber base into the soil to 10–15 cm soil depth. The top of the chamber base averaged 16 cm above the moss surface, minimizing shading of the plot. Preliminary measurements indicated that this protocol prevented any detectable disturbance effects on CO_2 flux from inserting the chamber base.

We measured CO_2 flux using a passive closed system (Vourlitis et al. 1993) by removing the plastic greenhouse, if present, and fastening a 1 × 1 × 0.25 m Plexiglas chamber to the 2-cm lip of the base sealed with neoprene weather-stripping. A sensor head attached to the chamber wall sampled air from within

the chamber that was analyzed for CO_2 concentration by a LI-COR 6200 infra-red gas analyzer (IRGA, LI-COR Instruments, Lincoln, Nebraska). In addition, a thermocouple attached to the sensor head measured air temperature within the chamber and a quantum sensor (LI-COR 190SA) attached to the chamber top measured photosynthetically active radiation (PAR) concurrent with CO_2 flux measurements. Two fans attached to opposite corners of the chamber circulated air during measurements.

On each measurement date, we measured CO_2 flux in all plots every six hours, each time measuring first under ambient light conditions and then under dark conditions, achieved by covering the chamber with an opaque cloth. Measurements began as soon as the change in CO_2 concentration became constant. Each measurement consisted of three consecutive 20-s measurements that were later averaged for statistical analyses. The short measurement time minimized chamber heating, which rarely exceeded 1.5°C. In between the light and dark measurements the chamber was removed to return the plots to ambient CO_2 levels and temperatures. Plots were covered for at least 1 min before dark measurements were initiated. We refer to fluxes measured under ambient light as net ecosystem production (NEP) since they are the balance of gross photosynthesis, plant respiration, and soil microbial respiration. Dark measurements included both plant and soil microbial respiration, so we refer to them as measures of ecosystem respiration (ER). By adding the absolute value of ER to NEP for each plot, we estimated gross photosynthesis (GP). Because we removed the greenhouses to measure CO_2 flux, we necessarily measured ecosystem CO_2 flux in both the control and greenhouse plots at the same (ambient) air temperatures. Comparing fluxes in control and greenhouse plots measured at the same temperatures allowed us to determine the long-term (seasonal) treatment effect on flux resulting from biological changes in the treatment plots.

We compared seasonal mean fluxes as well as fluxes at each date and for each time using separate *t* tests. To gain insight into causes of variation in fluxes between treatments and among dates, we regressed fluxes against various measures of plant biomass and production. Since determining biomass throughout the season was impossible without destroying the plots, we have regressed peak-season biomass against fluxes made at each date. Although biomass obviously changes throughout the season, early- and late-season biomass should be correlated within any plot. Because of the low sample size ($n = 5$), treatments were combined for regressions. We regressed GP against leaf biomass of the dominant species and against total leaf biomass, current year's leaf biomass, and total moss biomass. We regressed ER against aboveground production and total biomass of the dominant species and against total ANPP, above- and belowground vascular plant biomass, moss biomass, and total plant biomass. We conducted all statistical analyses using SYSTAT (SYSTAT 1992).

Results

Environmental consequences of greenhouses

The greenhouse treatment primarily altered the aboveground environment, increasing mean air temperature by 4–5°C, increasing the vapor pressure deficit (VPD), and reducing PAR by 23% (Table 1). Daily mean, maximum, and minimum air temperatures were significantly higher in the greenhouses in all three years measured (repeated-measures ANOVA for each year separately: $F_{1,8} = 491.92$, $F_{1,8} = 650.77$, $F_{1,10} = 32.10$, $P < 0.001$, for mean air temperature in 1991, 1992, and 1993, respectively. $F_{1,8} = 514.70$, $F_{1,8} = 232.03$, $F_{1,10} = 38.63$, $P < 0.001$, for maximum air temperature in 1991, 1992, and 1993, respectively. $F_{1,8} = 60.96$, $P < 0.001$; $F_{1,8} = 14.41$, $P < 0.01$; $F_{1,10} = 17.13$, $P < 0.01$, for minimum air temperature in 1991, 1992, and 1993, respectively). Mean PAR over the growing season was significantly reduced by the greenhouse treatment (repeated-measures ANOVA: $F_{1,4} = 12.99$, $P = 0.02$). Mean and especially maximum VPD was also greater over the season. Although we did not have replicate relative humidity sensors, increased VPD occurred throughout the season and resulted primarily from increased saturation vapor pressure with higher temperatures, rather than from a change in ambient vapor pressure (data not shown). When measured, CO_2 concentrations never differed by >9 μL/L between controls and greenhouses. In 1991, CO_2 was higher by 5 μL/L in the greenhouses under low light ($t_8 = -2.39$, $P = 0.04$) and lower in the greenhouses under medium light (9 μL/L) and high light (5 μL/L) ($t_8 = 3.58$, $P = 0.007$; and $t_8 = 0.81$, $P = 0.44$, respectively). Similarly, in 1992 CO_2 was significantly lower in the greenhouses by 2–3 μL/L (repeated-measures ANOVA: $F_{1,18} = 5.92$, $P = 0.03$). Although we only made spot measurements of CO_2 concentrations, it is unlikely that differences between greenhouses and controls were ever very large, since the greenhouses were leaky around the bottom and through the hole in the top.

Although maximum, mean, and minimum air temperatures were all higher in the greenhouses than in controls, maximum temperatures were increased more than minimum temperatures. This resulted from greater warming by the greenhouses at midday than at night (Fig. 1). Similarly, the greenhouses caused air temperature to increase more on warm days than on cool days. PAR was also reduced more at midday and on sunny days, probably because of condensation on the greenhouse walls.

Compared to the aboveground environment, the greenhouse treatment had little effect on the belowground environment. Although mean soil temperatures at 10 cm depth were consistently warmer in the greenhouses by 0.5–1°C (Table 1, Fig. 1), this difference was

TABLE 1. Environmental parameters in control and greenhouse plots. Values are means ± 1 SE.

Parameter	1991		1992		1993	
	Control	Greenhouse	Control	Greenhouse	Control	Greenhouse
Mean air temperature (°C)	**10.0 ± 0.1**	**15.6 ± 0.2*****	**13.0 ± 0.1**	**17.1 ± 0.2*****	**13.1 ± 0.2**	**16.6 ± 0.6*****
Maximum air temperature (°C)	**18.4 ± 0.5**	**31.8 ± 0.3*****	**22.1 ± 0.4**	**31.9 ± 0.5*****	**22.5 ± 0.5**	**31.1 ± 1.3*****
Minimum air temperature (°C)	**2.6 ± 0.0**	**3.4 ± 0.1*****	**4.9 ± 0.1**	**5.3 ± 0.1****	**5.9 ± 0.1**	**6.4 ± 0.1****
Soil temperature (°C)	**2.9 ± 0.5**	**4.7 ± 0.7†**	5.4 ± 0.5	5.6 ± 0.8	7.6 ± 0.6	8.8 ± 0.6
Thaw depth (cm)	33.6 ± 2.3	35.6 ± 1.4	38.0 ± 1.7	38.3 ± 2.2	61.0 ± 1.7	59.8 ± 1.6
Moss moisture (% dry mass)						
Early season	···	···	282 ± 75	326 ± 103	···	···
Late season	332 ± 82	174 ± 90	662 ± 82	508 ± 64	···	···
Soil moisture (% dry mass)						
Early season	···	···	297 ± 64	448 ± 72	···	···
Late season	495 ± 61	467 ± 65	479 ± 92	469 ± 41	379 ± 47	360 ± 38
CO_2 (μL/L)						
Early season (high PAR)	···	···	**345.8 ± 0.2**	**343.9 ± 0.7***	···	···
Late season						
(high PAR)	341.9 ± 2.4	337.9 ± 4.3	**340.7 ± 0.2**	**337.9 ± 1.4***		
(medium PAR)	**343.5 ± 0.1**	**334.7 ± 2.4****				
(low PAR)	**344.6 ± 1.2**	349.4 ± 1.6*			···	···
PAR ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	···	···	···	···	**420.2 ± 26.8**	**323.2 ± 2.5***
Mean VPD (kPa)	···	···	···	···	0.69	1.49
Maximum VPD (kPa)	···	···	···	···	1.71	3.83
Minimum VPD (kPa)	···	···	···	···	0.02	0.08

Note: Boldface type indicates statistical significance at $P < 0.10$; ellipses indicate no data available.
† $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

not significant in any of the years measured (repeated-measures ANOVA: $F_{1,7} = 3.90$, $P = 0.09$; $F_{1,7} = 0.05$, $P = 0.84$; and $F_{1,14} = 2.25$, $P = 0.16$, for 1991, 1992, and 1993, respectively). Surface soil temperatures (0–5 cm) may have been warmed by the greenhouses but were not measured. Depth of thaw to permafrost, moss moisture, and soil moisture (1991–1992) did not differ between greenhouses and controls, despite the exclusion of precipitation within the greenhouses (repeated-measures ANOVA: $F_{1,18} = 0.09$, $P = 0.77$; $F_{1,8} = 1.24$, $P = 0.30$; and $F_{1,8} = 0.45$, $P = 0.52$, respectively), nor did soil moisture in 1993 ($t_{18} = 0.50$, $P = 0.63$). Interannual variation in soil temperature was probably related to variation in thaw depth, which in turn is controlled by season length and timing of snow melt.

Consistent with finding little or no change in soil temperature, we found no treatment effect on decomposition and nutrient availability, supporting our conclusion that the manipulation mainly altered the aboveground environment. Decomposition rates of a common litter did not differ between treatments ($t_8 = 0.72$, $P = 0.49$, comparing percentage initial mass remaining after the final harvest, Table 2). Treatments did not differ in the amount of NH_4^+ or NO_3^- that accumulated on ion-exchange resins during summer or winter (repeated-measures ANOVA: $F_{1,8} < 0.001$, $P = 0.98$; and $F_{1,8} = 0.07$, $P = 0.80$ for NH_4^+ and NO_3^-, respectively, Table 2). Ion-exchange resins accumulated more NH_4^+ than NO_3^-. More NO_3^- accumulated on resins during winter than summer (repeated-measures ANOVA: $F_{1,8} = 9.19$, $P = 0.02$), but NH_4^+ accumulation on resins did not differ significantly between seasons ($F_{1,8} = 1.44$, $P = 0.27$). Interactions between treatment and seasons were not significant ($F_{1,8} = 0.09$, $P = 0.77$; and $F_{1,8} = 0.01$, $P = 0.93$ for NH_4^+ and NO_3^-, respectively).

System-level properties and responses

Total biomass of the ecosystem was ~1900 g/m² (Table 3). Vascular and nonvascular plants made up nearly equal proportions of aboveground biomass. Over half of the total plant biomass was belowground in stems and roots. Including roots increases our measure of total biomass of tussock tundra by a factor of 1.5 over previous estimates that included belowground stems, but excluded roots (Shaver and Chapin 1991). Our measure of the ratio of aboveground vascular plant production to biomass is also similar to previous estimates (0.39; Shaver and Chapin 1991). However, including nonvascular plants decreases this ratio to 0.24, increasing the estimated turnover time of aboveground biomass in tussock tundra from 2.6 (Shaver and Chapin 1991) to 4.2 yr.

Soil N pools were large relative to plant N pools, and soils were an important sink for the added ^{15}N label (Fig. 2). The insoluble soil N pool was three times

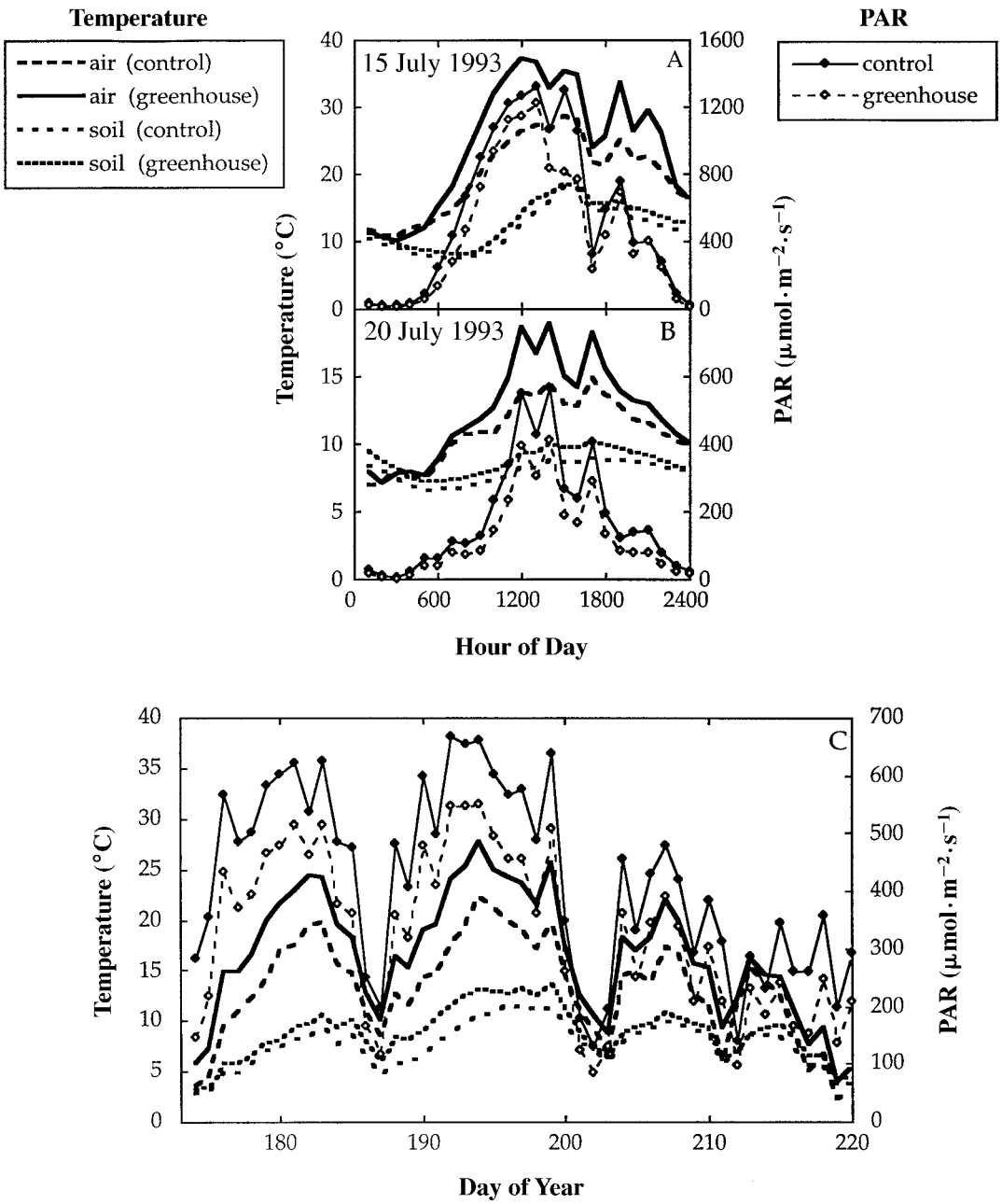

FIG. 1. Daily (A, B) and seasonal (C) patterns of air and soil temperature and PAR in the control and greenhouse-treated plots. Daily patterns are presented for (A) a sunny day and (B) a cloudy day in 1993. The seasonal pattern of daily means is presented for 1993 (C). Note different scales on the *y*-axes.

larger than total plant N. This pool is probably a mixture of humus, microbial cell wall and dead plant root material, and unrecovered live fine roots. Microbial biomass N was equivalent to total root N (Fig. 2) but exceeded soil solution N by an order of magnitude. The percentage of injected ^{15}N recovered in the microbial biomass was equal to that in the plant biomass, suggesting that microbial immobilization over the season may limit N availability to plants and/or that microbial N is turning over more rapidly than plant N. A high percentage of the injected ^{15}N ended up in the insoluble soil N pool (29%, Fig. 2), suggesting that this pool is actively exchanging with soil solution N and that adsorption of NH_4^+ to humus, microbial biomass turnover, and/or fine root turnover during the growing season is substantial.

Total biomass and aboveground vascular plant production showed little response to 3.5 yr of warming

TABLE 2. Accumulation of nutrients on ion-exchange resins (μmol/bag) and decomposition of *Betula papyrifera* (% initial litter mass remaining after 782 d) in control and greenhouse plots ($n = 5$). Values are means ± 1 SE.

	Control	Greenhouse
Ammonium		
Summer	3.50 ± 0.82	3.24 ± 0.58
Winter	10.26 ± 4.58	8.59 ± 1.26
Nitrate		
Summer	0.38 ± 0.07	0.27 ± 0.05
Winter	0.36 ± 0.09	0.35 ± 0.09
Phosphate		
Summer	0.24 ± 0.04	0.12 ± 0.02
Winter	0.89 ± 0.24	0.73 ± 0.28
Litter mass	61.80 ± 1.35	60.13 ± 1.88

(Table 3). However, we estimate that moss production was reduced by warming since the ratio of new biomass : total biomass of the moss *Hylocomium splendens* was significantly reduced by the greenhouse treatment (production : biomass ratio = 0.17 ± 0.02 and 0.10 ± 0.04 for control and greenhouse treatments, respectively [mean ± 1 SE]; $t_{18} = 3.75$, $P = 0.002$). Multiplying these two different ratios by total moss biomass in the control and greenhouse treatments, respectively, suggests that moss production was 17 $g \cdot m^{-2} \cdot yr^{-1}$ lower in the greenhouses than in the controls.

Treatments did not differ significantly in total soil or plant N pools, except that total root N was significantly greater in the greenhouses than in controls (Table 4 and Fig. 2). Soil ^{15}N pools also did not differ between treatments. However, total ^{15}N recovery was significantly higher in the greenhouse treatment (Mann-Whitney $U = 20.0$, $P = 0.02$; percentage of injected ^{15}N recovered = 45.1 ± 11.7% and 49.6 ± 3.4% in control and greenhouse treatments, respectively [mean ± 1 SE]) due to greater ^{15}N recovered in roots in the greenhouses (Table 4 and Fig. 2). The greenhouses also had significantly reduced ^{15}N in old leaves.

Species-level properties and responses

Graminoids, deciduous shrubs, evergreen shrubs, mosses, and lichens all made up substantial proportions of community biomass and N, while forbs were uncommon (Table 5). We focus our treatment comparisons on the most abundant species in the community and compare aboveground and belowground biomass separately for two reasons. First, because of sampling procedures, belowground biomass has a much larger variance associated with it than does aboveground biomass. Therefore, our power to detect treatment effects on aboveground biomass is greater. Second, if warming changes the ability of a species to acquire resources, we might expect the initial response to the treatment to be a change in allocation rather than a change in total biomass.

Few species differed significantly between control and greenhouse-treated plots in aboveground biomass, N, or ^{15}N uptake (Table 6 and Fig. 3). However, *Betula nana*, the overstory deciduous shrub, responded positively to the greenhouse treatment while *Vaccinium vitis-idaea*, the understory evergreen shrub, responded

TABLE 3. Total biomass, apical biomass production, and aboveground net primary production estimates and *t* statistics (df = 18) for comparisons between control and greenhouse treatments. Values are means (± 1 SE). Ellipses indicate that no statistical comparison was made.

Biomass or production component	Control	Greenhouse	*t*	*P*
Biomass (g/m^2)				
Aboveground vascular plant biomass	320.5 ± 22.5	326.6 ± 26.7	−0.18	0.86
New leaf biomass†	107.8 ± 18.7	109.5 ± 9.5	−0.08	0.94
New stem biomass	15.4 ± 2.3	19.6 ± 2.6	−1.22	0.24
Old leaf biomass	69.7 ± 7.5	61.8 ± 8.2	0.71	0.49
Old stem biomass	124.7 ± 16.0	132.4 ± 13.3	−0.37	0.72
Reproductive biomass	2.9 ± 0.7	3.3 ± 0.8	−0.40	0.75
Belowground vascular plant biomass	1116.9 ± 162.7	1214.0 ± 145.2	−0.45	0.66
Belowground leaf‡	103.7 ± 58.3	45.7 ± 19.6	0.94	0.36
Belowground stem biomass	710.4 ± 131.5	752.8 ± 94.9	−0.26	0.80
Root biomass	302.7 ± 37.0	415.5 ± 57.6	−1.65	0.12
Nonvascular plant biomass	408.5 ± 53.7	385.7 ± 41.4	0.34	0.74
Total plant biomass	1845.8 ± 162.1	1926.4 ± 138.4	−0.38	0.71
Production ($g \cdot m^{-2} \cdot yr^{-1}$)				
Moss apical production§	51.1	34.2	…	…
Apical aboveground vascular production	126.1 ± 19.9	132.5 ± 11.3	0.28	0.78
Total aboveground apical production	177.2	166.7	…	…
Stem secondary production§	10.3	13.6	…	…
Total aboveground net primary production‖	187.5	180.3	…	…

† *Cassiope tetragona* new and old leaf biomasses are included in new and old stem biomass totals, respectively; *Pedicularis* spp. and *Polygonum bistorta* new stem biomass is included in new leaf biomass total.
‡ Leaf bases of *Eriophorum vaginatum* and *Carex bigelowii.*
§ See *Methods: Plant biomass, nitrogen and ANPP* for explanation of methods.
‖ Excludes lichen production.

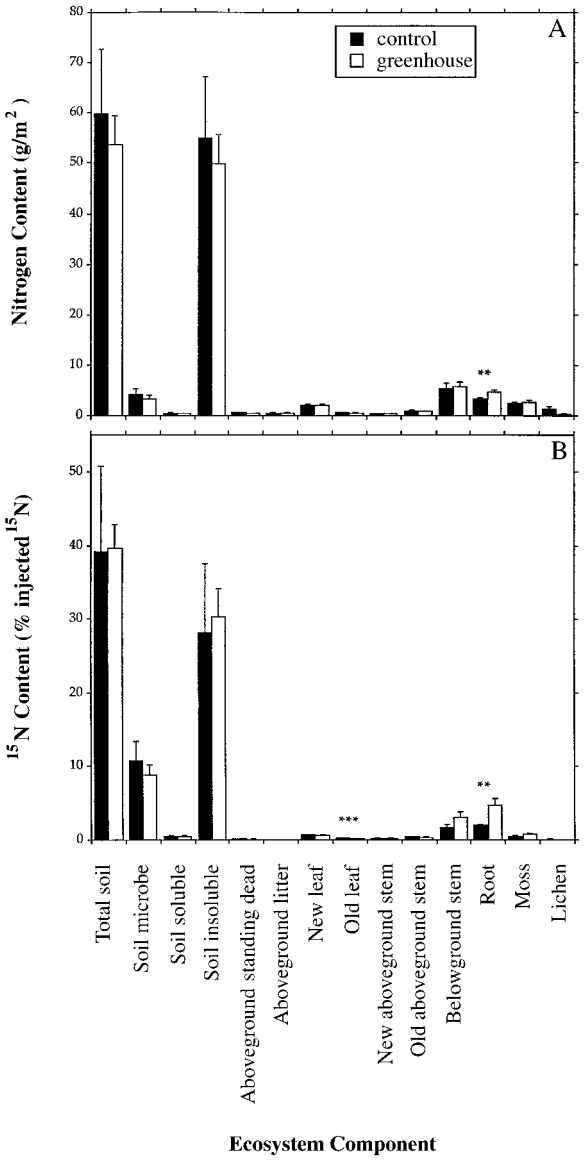

FIG. 2. Soil and plant N and ^{15}N content. Bars are means + 1 SE. Soil N pools refer to the top 10 cm of soil only. ** $P < 0.01$, *** $P < 0.001$.

negatively to the treatment. The aboveground biomass and N content of *B. nana* were two-fold greater in the greenhouse treatment; the most significant differences between the treatments were for current year's biomass (leaves and new stems). By contrast, *V. vitis-idaea* mainly responded in terms of old biomass, exhibiting reduced biomass of old leaves and stems. In particular, the N content and ^{15}N uptake of old leaves and stems were reduced by the greenhouse treatment. Other species showed large, but nonsignificant, responses to warming. *Carex bigelowii* and *Sphagnum* spp. had higher biomass, N content, and ^{15}N uptake with warming. *Eriophorum vaginatum*, *Dicranum* sp., and the lichens exhibited negative responses to warming. *Ledum palustre* mirrored *V. vitis-idaea* in having reduced ^{15}N uptake in old leaves and stems in response to warming.

Belowground biomass did not differ statistically between treatments for any species (Table 7 and Fig. 4). As with aboveground biomass, many species exhibited large but nonsignificant differences between treatment and controls. *Betula nana* and *C. bigelowii* showed large increases in belowground stems and roots, particularly in terms of ^{15}N uptake, probably explaining the significant increases in total root N and ^{15}N uptake (Table 3 and Fig. 2). *Eriophorum vaginatum* root biomass, N, and ^{15}N uptake all declined with warming.

CO_2 flux

The measurement dates for ecosystem CO_2 flux were alternately sunny (17 June and 15 July) and cloudy (26 June and 28 July) (Fig. 5). Three of the dates had approximately the same average air temperature, while 15 July was much warmer. Chamber heating on this date was slightly greater than on the cooler dates, with chamber temperatures exceeding ambient air temperatures by ~3°C (data not shown).

When measured under the same environmental conditions as the controls, the greenhouse treatment significantly increased early-season gross photosynthesis (GP) and ecosystem respiration (ER) throughout the season, but had little effect on late-season GP or net ecosystem production (NEP) (Figs. 5 and 6). That the greenhouses significantly changed CO_2 flux even when they were not in place suggests that plots subject to the greenhouse treatment had become different biologically from the controls. The magnitude, significance, and sometimes the direction of the effect depended on time of day and date. Greenhouses significantly increased GP in June and increased ER across the season, especially during the day. On average over the growing season, the greenhouse treatment significantly enhanced GP ($t_8 = -2.22$, $P = 0.06$) and ER ($t_8 = 2.63$, $P = 0.03$) so that NEP was unchanged ($t_8 = 0.65$, $P = 0.53$) when measured at ambient temperatures (Fig. 6).

Leaf biomass of several of the dominant species was significant in explaining variation in GP, but the significance of any one species changed throughout the growing season. GP was significantly related to leaf biomass of *B. nana* early in the season (17 June: $R^2 = 0.45$, $P = 0.03$), to leaf biomass of *E. vaginatum* in the middle of the season (15 July: $R^2 = 0.62$, $P = 0.01$), and to leaf biomass of *V. vitis-idaea* late in the season (28 July: $R^2 = 0.57$, $P = 0.01$). Total and current year's leaf biomass explained >80% of the variation in GP in the middle of the growing season (15 July: $R^2 = 0.83$, $P < 0.001$; and $R^2 = 0.87$, $P < 0.001$, respectively), but were only weakly related to GP at the beginning and end of the growing season ($P > 0.1$ on all other dates).

Total biomass and production of any given species explained little or none of the variation in ER except

TABLE 4. Statistics (t test; df = 8) for ecosystem N pools and ^{15}N partitioning (as % injected ^{15}N).

Ecosystem compartment	N content		^{15}N content	
	t	P	t	P
Soil and litter				
Total soil	47.00†	0.82	28.00†	0.10
Soil microbe	0.89	0.38	0.70	0.49
Soil soluble	0.11	0.91	0.16	0.87
Soil insoluble	48.00†	0.88	32.00†	0.17
Aboveground standing dead	61.00†	0.41	69.00†	0.15
Aboveground litter	0.18	0.86	1.69	0.11
Plant				
New leaf	0.15	0.88	0.34	0.74
Old leaf	1.36	0.19	4.82	<0.001
New aboveground stem	−0.20	0.84	0.03	0.98
Old aboveground stem	0.15	0.88	1.31	0.21
Belowground stem	−0.41	0.69	−1.67	0.11
Root	−2.82	0.01	10.00†	0.003
Moss	−0.86	0.40	−0.83	0.42
Lichen	68.00†	0.17	74.00	0.06

† Mann-Whitney U tests were done instead of t tests because of heterogeneous variances; Mann-Whitney U statistics are presented.

TABLE 5. Plant biomass and nitrogen content of all species in the community in control and greenhouse treatments. Values are means ± 1 SE (n = 10). Aboveground biomass includes biomass above the moss surface, and belowground biomass includes biomass from the moss surface down to permafrost.

Species	Component	Biomass (g/m²)		Nitrogen pool (g/m²)	
		Control	Greenhouse	Control	Greenhouse
Eriophorum vaginatum	aboveground	47.1 ± 18.4	30.3 ± 6.6	0.89 ± 0.34	0.55 ± 0.12
	belowground	218.8 ± 109.4	57.2 ± 22.5	2.84 ± 1.56	0.70 ± 0.22
Carex bigelowii	aboveground	5.0 ± 1.8	14.6 ± 5.1	0.10 ± 0.03	0.29 ± 0.10
	belowground	115.4 ± 42.5	271.7 ± 129.4	0.91 ± 0.34	2.03 ± 0.76
Betula nana	aboveground	52.8 ± 10.9	99.7 ± 18.2	0.61 ± 0.07	1.20 ± 0.22
	belowground	217.6 ± 97.5	333.4 ± 130.7	1.64 ± 0.69	3.13 ± 1.19
Salix pulchra	aboveground	0	0.6 ± 0.4	0	0.01 ± 0.00
	belowground	0	0	0	0
Rubus chamaemorus	aboveground	6.8 ± 3.2	5.0 ± 2.8	0.12 ± 0.05	0.09 ± 0.05
	belowground	21.0 ± 11.2	22.2 ± 10.8	0.20 ± 0.10	0.24 ± 0.12
Arctostaphylos alpina	aboveground	2.7 ± 2.6	0	0.04 ± 0.04	0
	belowground	0	0	0	0
Vaccinium uliginosum	aboveground	10.0 ± 5.4	3.8 ± 2.9	0.11 ± 0.06	0.04 ± 0.03
	belowground	0.4 ± 0.4	0	0.01 ± 0.01	0
Vaccinium vitis-idaea	aboveground	91.4 ± 11.3	65.7 ± 10.2	0.82 ± 0.09	0.52 ± 0.08
	belowground	174.7 ± 26.6	174.6 ± 30.8	1.50 ± 0.23	1.80 ± 0.35
Ledum palustre	aboveground	61.6 ± 11.7	73.6 ± 13.6	0.86 ± 0.14	0.92 ± 0.16
	belowground	299.4 ± 39.5	309.6 ± 75.8	2.26 ± 0.31	2.56 ± 0.56
Cassiope tetragona	aboveground	29.1 ± 12.8	18.3 ± 5.0	0.26 ± 0.12	0.17 ± 0.05
	belowground	45.6 ± 41.0	17.2 ± 7.5	0.38 ± 0.36	0.16 ± 0.07
Empetrum nigrum	aboveground	8.4 ± 5.2	10.0 ± 4.3	0.08 ± 0.05	0.07 ± 0.03
	belowground	0	3.9 ± 3.9	0	0.03 ± 0.03
Andromeda polifolia	aboveground	2.4 ± 2.2	1.0 ± 0.9	0.02 ± 0.02	0.01 ± 0.01
	belowground	0	0	0	0
Pedicularis spp.	aboveground	2.2 ± 1.0	1.6 ± 0.5	0.03 ± 0.02	0.02 ± 0.01
	belowground	2.9 ± 2.7	7.8 ± 4.0	0.05 ± 0.05	0.14 ± 0.08
Polygonum bistorta	aboveground	1.2 ± 0.4	2.4 ± 0.9	0.02 ± 0.01	0.05 ± 0.02
	belowground	8.9 ± 6.2	14.9 ± 8.6	0.12 ± 0.08	0.16 ± 0.09
Sphagnum spp.	total biomass	94.1 ± 39.3	148.9 ± 44.5	0.74 ± 0.31	1.18 ± 0.34
Aulocomnium turgidum	total biomass	60.2 ± 13.8	64.5 ± 9.9	0.49 ± 0.10	0.53 ± 0.08
Dicranum spp.	total biomass	101.1 ± 41.8	66.6 ± 19.0	0.78 ± 0.26	0.54 ± 0.16
Pleurozium shreberi	total biomass	4.1 ± 2.3	0.6 ± 0.4	0.03 ± 0.02	0.01 ± 0.00
Polytrichum spp.	total biomass	2.0 ± 1.0	7.5 ± 4.5	0.02 ± 0.01	0.06 ± 0.04
Tomenthypnum nitens	total biomass	2.1 ± 1.5	1.7 ± 1.1	0.02 ± 0.01	0.01 ± 0.01
Ptilium crista-castrensis	total biomass	1.4 ± 0.9	0.3 ± 0.3	0.01 ± 0.01	0
Lichen	total biomass	107.9 ± 40.5	43.5 ± 9.9	1.28 ± 0.51	0.29 ± 0.07

TABLE 6. Statistics (t test; df = 18) comparing belowground biomass, nitrogen content, and ^{15}N uptake between treatments.

Species	Part	Biomass		N pool		^{15}N uptake	
		t	P	t	P	t	P
Carex bigelowii	leaf	35.0†	0.26	32.0†	0.17	30.0†	0.13
Eriophorum vaginatum	leaf	46.0†	0.76	54.0†	0.76	−0.94	0.36
Betula nana	leaf	25.0†	0.06	23.0†	0.04	25.0†	0.06
	new stem	24.0†	0.05	25.0†	0.06	29.0†	0.11
	old stem	−1.73	0.10	−1.92	0.07	47.0†	0.82
	total apical	24.0†	0.05	24.0†	0.05	26.0†	0.07
	total aboveground	−2.22	0.04	25.0†	0.06	32.0†	0.17
Ledum palustre	new leaf	−0.84	0.41	−0.55	0.59	1.18	0.25
	new stem	−0.91	0.38	−0.52	0.61	−0.59	0.57
	old leaf	26.0†	0.07	44.0†	0.65	1.74	0.10
	old stem	0.08	0.94	53.0†	0.82	1.62	0.12
	total apical	−0.81	0.43	−0.57	0.58	0.66	0.52
	total aboveground	−0.67	0.51	−0.20	0.85	1.64	0.12
Vaccinium vitis-idaea	new leaf	0.75	0.46	1.12	0.28	1.63	0.12
	new stem	−1.11	0.28	−0.38	0.71	0.86	0.40
	old leaf	1.88	0.08	0.30	0.02	97.0†	<0.001
	old stem	2.13	0.05	0.29	0.009	3.34	0.004
	total apical	0.48	0.64	0.52	0.32	1.62	0.12
	total aboveground	1.69	0.11	0.68	0.03	3.50	0.003
Aulacomnium turgidum		−0.25	0.81	−0.33	0.75	48.0†	0.88
Dicranum sp.		−0.75	0.46	−0.79	0.44	0.68	0.50
Hylocomium splendens		0.62	0.54	0.61	0.55	−0.05	0.96
Sphagnum spp.		−0.92	0.37	−0.95	0.36	−1.54	0.14
Lichen		60.0†	0.45	68.0†	0.17	74.0†	0.06

† Mann-Whitney U tests were done instead of t tests because of heterogeneous variances; Mann-Whitney U statistics are presented.

B. nana, whose production was weakly related to ER throughout the growing season. In contrast, total ANPP was significantly related to ER throughout the growing season, explaining between 40 and 60% of the variation in ER ($R^2 = 0.40$, $P = 0.05$; $R^2 = 0.50$, $P = 0.02$; $R^2 = 0.60$, $P = 0.01$; $R^2 = 0.48$, $P = 0.03$ on 17 June, 26 June, 15 July, and 28 July, respectively). Total aboveground biomass was also related to ER, but more strongly at the end of the growing season (15 July: $R^2 = 0.46$, $P = 0.03$; 28 July: $R^2 = 0.48$, $P = 0.03$). Total belowground biomass was only weakly related to ER ($P \leq 0.1$ on all dates).

DISCUSSION

Treatment effectiveness

Our intent was not to mimic all of the environmental changes likely to result from rising concentrations of greenhouse gases, but rather to manipulate one or two factors that are most likely to alter plant growth in tundra. Current climate projections predict that arctic regions will warm more than other regions of the globe, but that warming will be greater in winter than in summer and that winter precipitation will likely increase (Houghton et al. 1996). Increased winter precipitation and temperature will interact to control the timing of snow melt and the length of the growing season. Of these various expected climatic changes, our manipulation increased growing-season air temperature by a magnitude that will probably occur in the next century (Houghton et al. 1996).

The growing-season temperature increase achieved by our manipulation differs from warming that will accompany rising concentrations of greenhouse gases in several ways. Climate projections predict a reduction in diurnal temperature range (because of relatively greater warming at night; Houghton et al. 1996), while our manipulation increased diurnal temperature range. Our manipulation decreased PAR, which will decline if summer precipitation increases. Our manipulation also increased vapor pressure deficit, which may increase as warmer temperatures increase the saturation vapor pressure. Finally, our manipulation warmed air temperature with little or no increase in soil temperature (at depth), probably because of the small size of the greenhouses and the large thermal mass of the soil water and permafrost. Nevertheless, isolating the effects of air warming from soil warming or from changes in growing-season length increases our understanding of temperature limitation of tundra. Below, we interpret our results in light of the specific environmental changes caused by the greenhouses.

Although the environmental changes imposed by the greenhouses do not necessarily reflect all of the changes that will result with greenhouse-gas-induced climate change, they do resemble those imposed by similar studies of arctic tundra, facilitating comparisons of our results with those studies (Havström et al. 1993, Wookey et al. 1993, 1994, Parsons et al. 1994, Chapin et al. 1995*b*, Chapin and Shaver 1996, Michelson et al. 1996). The air temperature changes achieved by our manipulation resemble those achieved by plastic greenhouses used in tundra in Northern Sweden and on Sval-

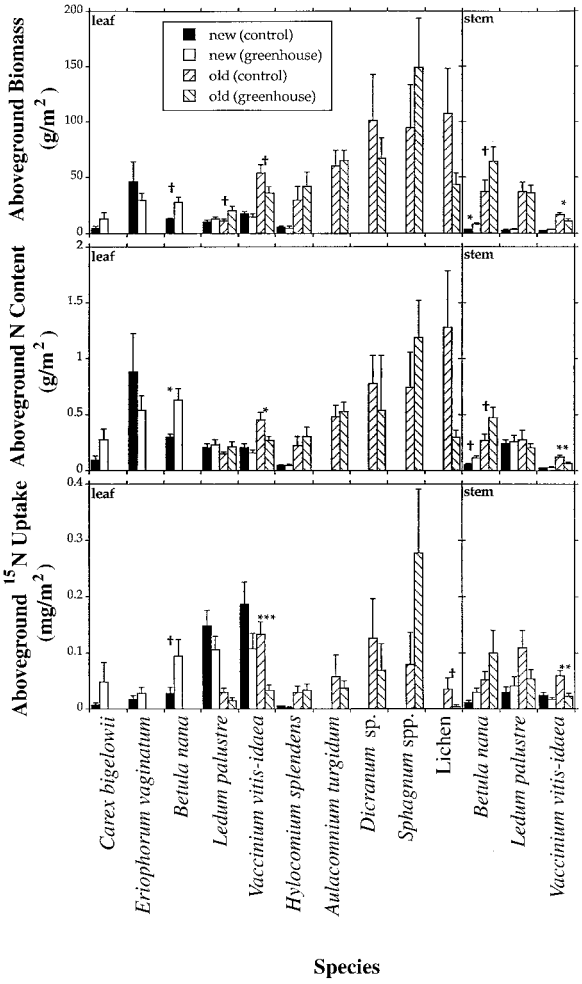

FIG. 3. Aboveground biomass, N, and ^{15}N uptake of the most abundant species in control and greenhouse-treated plots. For nonvascular species, ''old leaf'' includes both new and old tissue. Bars are means + 1 SE. † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

bard, although the reduction in PAR was greater in our study (Havström et al. 1993, Wookey et al. 1993, Michelson et al. 1996). The increase in soil temperature reported by Havström et al. (1993) was more significant, perhaps because they reported only daytime soil temperature at 5 cm depth. Alternatively, the lack of permafrost at these Swedish sites may promote soil warming. Both the air temperature increase and the PAR reduction resembled those of plastic greenhouses used in Alaskan tussock tundra near our sites (Chapin et al. 1995*b*), although the soil temperature increase was smaller in the our study, perhaps because of our smaller greenhouses.

System-level responses

In general, total biomass, total N pools, and ^{15}N uptake of the major plant and soil pools in tundra responded little to 3.5 yr of air warming. Similarly, ANPP of the vascular plants was unchanged with warming. Other studies that have experimentally warmed tundra have also found little or no effect on total aboveground biomass, despite significant effects on growth and reproduction of species within the community (Chapin and Shaver 1985, 1996, Havström et al. 1993, Wookey et al. 1993, 1994, Parsons et al. 1994, 1995, Chapin et al. 1995*b*, Harte and Shaw 1995, Michelson et al. 1996). Our study adds to the growing evidence supporting the idea that plant biomass accumulation in tundra is constrained by nutrient availability rather than by cold temperatures per se (Chapin 1983), and that biomass accumulation during the growing season will only increase with future climate warming if mineralization of soil organic nutrients is stimulated (Shaver et al. 1992, McKane et al. 1997). Alternatively, a depressing effect of reduced PAR in the greenhouses may have offset any stimulatory effect of increased temperature, causing us to underestimate the effect of

TABLE 7. Statistics (*t* test; df = 18) comparing belowground biomass, nitrogen content and ^{15}N uptake between treatments.

Species	Part	Biomass		N pool		^{15}N uptake	
		t	*P*	*t*	*P*	*t*	*P*
Carex bigelowii	stem	37.0†	0.64	37.0†	0.32	35.0†	0.23
	root	1.15	0.26	31.0†	0.15	30.0†	0.13
	total belowground	37.0†	0.33	32.0†	0.17	30.0†	0.13
Eriophorum vaginatum	stem	66.5†	0.21	62.0†	0.35	0.10	0.92
	root	73.0†	0.08	70.0†	0.13	67.0†	0.20
	total belowground	70.0†	0.13	70.0†	0.13	0.85	0.41
Betula nana	stem	0.47	0.65	0.66	0.52	36.5†	0.29
	root	1.39	0.18	1.65	0.12	27.0†	0.08
	total belowground	0.71	0.49	1.08	0.29	30.0†	0.13
Ledum palustre	stem	0.09	0.93	0.04	0.97	1.27	0.22
	root	0.86	0.40	1.15	0.26	1.52	0.15
	total belowground	0.12	0.91	0.46	0.65	1.67	0.11
Vaccinium vitis-idaea	stem	0.02	0.99	0.92	0.37	0.62	0.54
	root	0.04	0.97	0.27	0.79	52.0†	0.88
	total belowground	<0.01	1.00	0.71	0.49	0.87	0.39

† Mann-Whitney *U* tests were done instead of *t* tests because of heterogeneous variances; Mann-Whitney *U* statistics are presented.

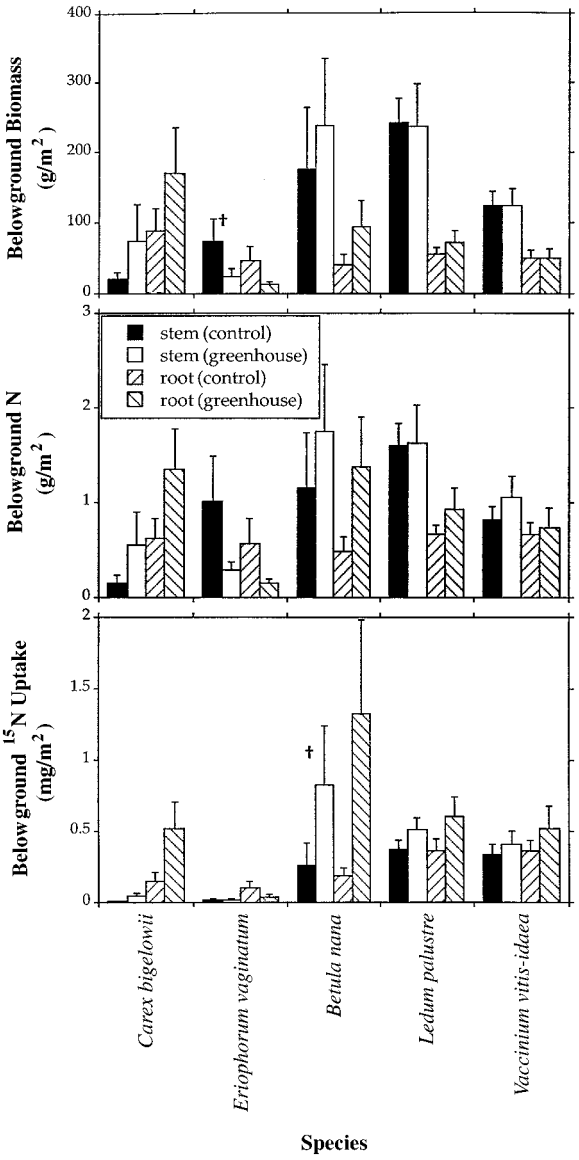

FIG. 4. Belowground biomass, N, and ^{15}N uptake of the most abundant species in control and greenhouse-treated plots. Bars are means + 1 SE. † $P < 0.1$.

warming on biomass and productivity (Chapin et al. 1995*b*, McKane et al. 1997).

Based on the response of *Hylocomium splendens* to warming, we estimate that nonvascular production declined with warming by 33%. Moss production was also negatively correlated with temperature across sites in the Alaskan boreal forest, whose understory is dominated by many of the same moss species reported here (Skre and Oechel 1979). However, moss moisture content also declined as temperature warmed across those sites. In contrast, we measured no difference in moss moisture between controls and greenhouse-treated plots. Therefore, the decline in moss production with warming reported here may directly result from the low temperature optimum for photosynthesis of many moss species (~15°C, Oechel and Sveinbjörnsson 1978, Tenhunen et al. 1992).

In contrast to the general lack of vascular plant response to air warming aboveground, greenhouses did increase total root N and ^{15}N uptake and decrease ^{15}N uptake by old leaves. Root ^{15}N uptake increased even more than root N with warming, suggesting that the greenhouses stimulated root turnover. The significant increase in total root N and ^{15}N uptake with warming probably resulted from the combined responses of several species, including *C. bigelowii*, *B. nana*, *L. palustre*, and *V. vitis-idaea* (for ^{15}N). The reduction in old-leaf ^{15}N uptake probably resulted from a reduction in ^{15}N uptake by old leaves of *V. vitis-idaea.* These species-level responses are discussed below (see *Species-level responses*).

Approximately equal proportions of labeled N ended up in microbial and plant biomass, supporting the hypothesis that microbial immobilization of N during the growing season is at least partially responsible, along with slow decomposition, for N limitation of net primary production in this ecosystem (Shaver and Chapin 1986, Chapin et al. 1995*b*). Sequestration of NH_4^+ by soil organic matter is also a potentially important mechanism by which N becomes unavailable to plants in tundra, since a substantial amount of the labeled ^{15}N ended up in the insoluble N pool. Studies in tundra and in other systems have also demonstrated a large capacity for soil organic matter to acquire added ^{15}N (Marion et al. 1982; reviewed by Hart et al. 1993). This may occur through microbial and fine-root turnover as well as by direct chemical fixation by organic matter (Davidson et al. 1991, Hart et al. 1993).

The low total ^{15}N recovery that we achieved probably occurred because we injected ^{15}N into quadrats of tundra that were not physically isolated from adjacent tundra. Thus, ^{15}N that was not taken up by plants or microbes may have leached downward or laterally. Additionally, ^{15}N that was taken up by plants may have been transported laterally outside of the harvested quadrats. In the latter case, we may have underestimated N uptake, although our analysis of ^{15}N distribution among plant species should be accurate.

Species-level responses

An unfortunate trade-off exists when assessing treatment effects on biomass for a number of species. Comparing a number of response variables increases the probability of obtaining a significant treatment effect by chance alone, while adjusting α (the probability of Type I error) for individual comparisons to hold the experiment-wise error constant decreases the power to detect real differences (e.g., Winer et al. 1991). Thus, the questions arise as to whether the species responses that we measured were real and whether we were unable to detect other species responses to the treatment. We focus our discussion on treatment differences sig-

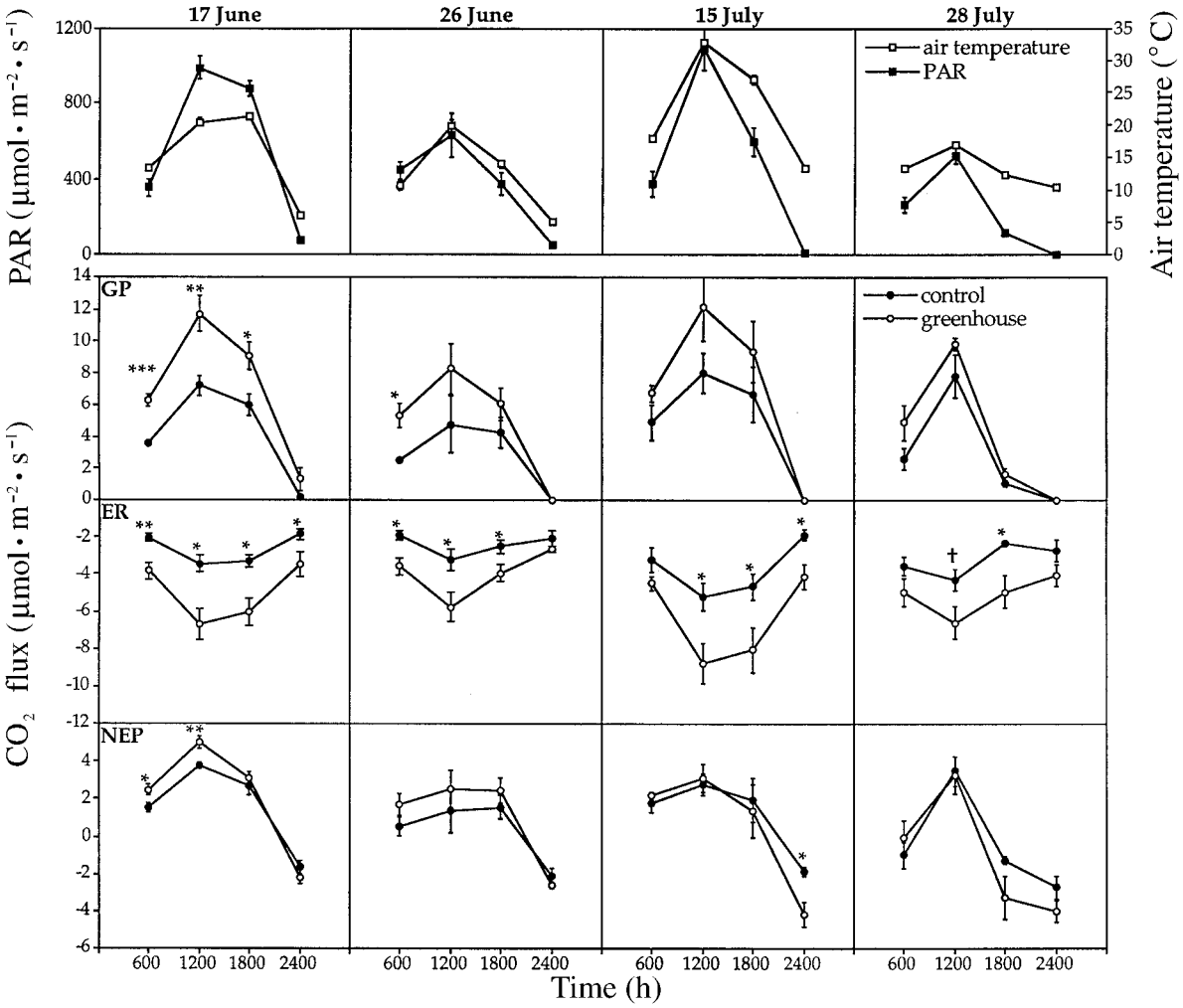

FIG. 5. Mean (±1 SE) diurnal CO_2 flux and ambient PAR (photosynthetically active radiation) and air temperature measured on four dates during the growing season in the control and greenhouse treatments (n = 5 at each time); GP = gross photosynthesis, ER = ecosystem respiration, and NEP=net ecosystem production. Positive values indicate net CO_2 flux to the ecosystem; negative values indicate net CO_2 flux to the atmosphere. Statistical significance refers to individual t tests done at each time; † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

nificant at $\alpha = 0.05$, an intermediate level of conservatism. We feel this is warranted by the relatively small sample size ($n = 10$) and large variance associated with biomass measures that afford little power to detect true differences between treatments (Scheiner 1993).

Despite the lack of warming effects on total ecosystem biomass and N pools, increased air temperature significantly affected two of the dominant shrubs in the community. Specifically, *B. nana* biomass and N content increased, while *V. vitis-idaea* N content and ^{15}N uptake decreased. Since our manipulation did not alter the belowground environment, the response by *B. nana* contradicts the prevalent idea among tundra ecologists that low temperature is not a strong direct limitation to plant growth in these systems, but limits plant growth mainly by impeding decomposition and thus reducing nutrient availability (Chapin 1983). Other studies that simultaneously increased both air and soil temperature in situ concluded that temperature affected plant growth mainly by changing nutrient availability (Chapin et al. 1995*b*). Our results suggest that air temperature influences how available N is distributed among species within the community even when N availability and total plant N pools do not change.

One explanation for the coincident increase in *B. nana* biomass and N and decline in *V. vitis-idaea* N and ^{15}N uptake is that air temperature mediated competition for N between these two species. Although *V. vitis-idaea* biomass did not significantly decline in the greenhouse treatment, this species relied more on N translocated from old leaves and stems than on current N uptake to support new growth in the greenhouse treatment. Continued translocation of N from old biomass should eventually increase mortality of old

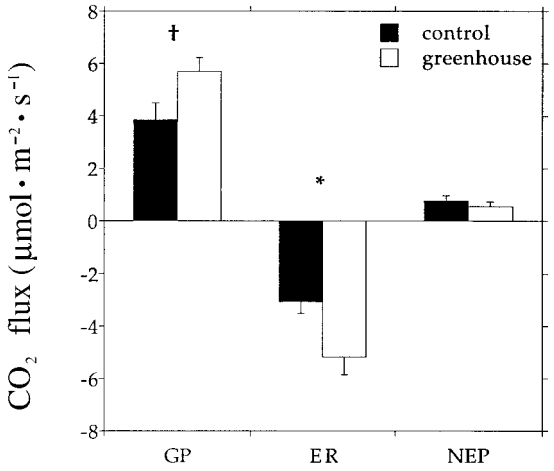

FIG. 6. Seasonal mean (+1 SE) CO_2 flux measured at ambient air temperature ($n = 5$ blocks; daily means from each plot were averaged across dates); GP = gross photosynthesis, ER = ecosystem respiration, and NEP = net ecosystem production. Positive values indicate net CO_2 flux to the ecosystem; negative values indicate net CO_2 flux to the atmosphere. † $P < 0.1$, * $P < 0.05$.

shoots, decreasing biomass. Warming causes earlier leaf expansion in *B. nana* leaves (Chapin and Shaver 1996; S. E. Hobbie, *personal observation*) but has no effect on timing of leaf expansion of *V. vitis-idaea* (Chapin and Shaver 1996). Tundra evergreen shrub roots begin growth and old leaves re-green earlier in the growing season than deciduous shrub leaves and roots begin growth (Kummerow et al. 1983). The later root growth of deciduous shrubs may limit their ability to take advantage of the early flush of N mineralization that occurs with soil thaw, forcing them to rely more on stored N than do evergreen species. Earlier *B. nana* leaf expansion may have increased N demand or allowed earlier root growth, increasing *B. nana*'s ability to compete with *V. vitis-idaea* during the short time (early spring during soil thaw) when net nutrient mineralization occurs (Kielland 1990, Nadelhoffer et al. 1992).

The combined nonsignificant increases in root N and ^{15}N uptake by several species with warming (particularly *C. bigelowii* and *B. nana*) probably contributed to the highly significant increase in total root N and ^{15}N. Because the greenhouses primarily warmed the air, these responses represent indirect effects of air warming rather than direct effects of soil warming on root growth and nutrient uptake. Several explanations exist for the increased root N and ^{15}N uptake. As mentioned above, earlier leaf expansion by some species in the greenhouses may have allowed earlier root initiation and greater N acquisition. Alternatively, stimulation of aboveground growth may have increased nutrient demand, increasing allocation to roots.

The increased abundance of *B. nana* that we observed after 3.5 yr of warming may indicate how plant community structure will respond to increased air temperature in the future, since recruitment from seed is rare in this ecosystem, and most reproduction is asexual (McGraw and Fetcher 1992). Furthermore, the increased biomass of *B. nana* in the greenhouse treatment is consistent with a rise in *Betula* pollen in the fossil record in northern Alaska ~9000 yr BP, when summer temperatures were warmer than they are today (Brubaker et al. 1995). Increased *B. nana* abundance with warming could have ecosystem-level consequences, promoting carbon storage because of its recalcitrant litter resulting from relatively high allocation to stem production (Hobbie 1996).

Species responses to the greenhouses cannot easily be explained by reduced PAR or increased VPD, and thus probably represent responses to warming. Light attenuation has little effect on nutrient accumulation, production, or biomass in *B. nana* (Chapin and Shaver 1996). Reduced PAR in the greenhouses should, if anything, have caused us to underestimate treatment effects on evergreen shrubs. Light attenuation increases nutrient accumulation while reducing production and biomass of the evergreen shrubs *L. palustre* and *V. vitis-idaea* (Chapin and Shaver 1996). Mosses and lichens were probably affected most by greater VPD, since these species have low resistance to evaporative water loss and have less access to soil water than vascular species. Vascular species are unlikely to be water limited in moist tussock tundra (Oberbauer and Dawson 1992). The nonsignificant reductions in biomass and N content of *Dicranum* and lichen species could have resulted from greater VPD in the greenhouses. However, we measured no significant reduction in the moisture content of mosses in the greenhouses. Also, many moss species show sharp declines in photosynthesis at temperatures above 15°C (Oechel and Sveinbjörnsson 1978, Tenhunen et al. 1992), so these responses could have resulted directly from warmer temperature.

CO_2 flux

Our measurements of ecosystem CO_2 flux generally support our conclusions based on biomass and N. The small and nonsignificant effect of warming on net ecosystem production (NEP) supports the hypothesis that increased air temperature alone will have little effect on future NEP (i.e., net C storage) during the growing season. Whether air warming will change NEP during the portion of the season not measured in this study is unclear. The growing season may extend later in the fall because high-latitude warming is expected to be large in late autumn and in winter (Kattenberg et al. 1996). However, whether the growing season begins earlier or later will depend on the balance between increases in temperature and precipitation during winter.

Despite no effect on NEP, warming stimulated both C gain and loss, suggesting that air warming increases C turnover in tundra without changing C storage. The

higher gross photosynthesis (GP) that we observed in the greenhouse treatment cannot be explained by treatment effects on total leaf biomass, which did not differ between treatments; however, it is consistent with the species-level responses to warming. The restriction of the greenhouse stimulation of GP to the early growing season suggests that warmed plots differed from controls phenologically. Since much of the variation in GP early in the growing season was explained by variation in *B. nana* leaf biomass, the early-season stimulation of GP could have resulted from the significantly greater *B. nana* leaf biomass and N content in the greenhouses. This difference would have been exaggerated by earlier leaf expansion by *B. nana* in the greenhouses.

Earlier leaf expansion by *B. nana* is sufficient to explain the magnitude of the treatment effect on GP early in the season. For example, we can estimate the potential early-season treatment–control difference in GP by multiplying *B. nana*'s leaf biomass by its gross photosynthetic rate. Mean leaf biomass in the greenhouses was 27.5 g/m^2 (Fig. 3). Published values of maximum photosynthetic rates for *B. nana* vary considerably (Oberbauer and Oechel 1989), differing by as much as one order of magnitude (compare Johnson and Tieszen 1976, Chapin and Shaver 1996). Here we assume a photosynthetic capacity of 163.7 nmol $CO_2 \cdot (g\ leaf)^{-1} \cdot s^{-1}$ for *B. nana*, measured at a nearby site using infra-red gas analysis (Oberbauer and Oechel 1989). Assuming that *B. nana* was operating at half of its photosynthetic capacity on average, the greenhouse treatment could have stimulated GP by up to 2.3 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ above control plots if *B. nana* leaf expansion in the greenhouses exceeded that in the controls. This is probably an underestimate, since Oberbauer and Oechel (1989) measured net rather than gross photosynthesis. Nevertheless, the difference is close to the real treatment–control difference of 2.9 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ on 17 June. The treatment–control differences could also have partially resulted from stimulation of photosynthesis by the greenhouse treatment, as observed in other studies (Chapin and Shaver 1996).

The decline in the treatment–control difference in GP over the season may have resulted from leaf expansion in the controls ''catching up'' to that in the greenhouses. It probably also resulted from an increase over the growing season in the contribution to GP by species whose phenology does not respond to warming or whose biomass did not differ (or was reduced) between treatment and controls (e.g., *E. vaginatum* and *V. vitis-idaea*). This interpretation is consistent with the significant relationships between GP and leaf biomass of *E. vaginatum* and *V. vitis-idaea* in the mid- and late growing seasons, respectively.

Although aboveground biomass and ANPP explained significant amounts of variation in ecosystem respiration (ER), total aboveground biomass was not higher in the greenhouses, and thus cannot explain treatment effects on ER. However, the greater ER in the greenhouse-treated plots could have resulted from greater *B. nana* ANPP and possibly aboveground biomass. *B. nana* ANPP (which doubled with warming) was weakly correlated with ER across the season. The respiration required to produce and maintain this extra *B. nana* ANPP (24.4 g/m^2 greater ANPP in the greenhouses) is ~0.5 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$, assuming maintenance and growth coefficients of 0.04 and 0.25 g carbohydrate $\cdot g^{-1} \cdot d^{-1}$, respectively (Penning de Vries et al. 1974, Semikhatova et al. 1992) and a 60-d growing season. The respiration required to maintain the greater old *B. nana* biomass (22.5 g/m^2 greater old biomass in the greenhouses) is ~0.4 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$. While ignoring seasonal variation in both maintenance and growth respiration, these estimates nonetheless suggest that changes in aboveground production and biomass of *B. nana* could account for about half (0.9 μmol $\cdot m^{-2} \cdot s^{-1}$) of the increased respiration observed in the greenhouse treatment (2.11 μmol $\cdot m^{-2} \cdot s^{-1}$, Fig. 2).

The remaining treatment effect on respiration remains unexplained. One possible explanation is that belowground processes increased respiration in the greenhouses. The nonsignificant increases in belowground biomass may have contributed to greater respiration, especially since belowground biomass was weakly related to ER. More notable, however, were the significant increases in both root N and ^{15}N uptake with warming. Higher root N requires greater maintenance respiration, since up to half of root respiration is associated with protein turnover (van der Werf et al. 1992). Root ^{15}N uptake increased even more than did root N, a pattern that could only result from (1) greater current-year's nutrient uptake in the greenhouses or (2) greater root turnover in the greenhouses. Greater uptake would require higher maintenance respiration (Amthor 1994), while greater turnover would require higher growth respiration and contribute to greater microbial respiration.

Use of ^{15}N

By measuring ^{15}N uptake, we hoped to increase our ability to detect responses by the ecosystem to environmental perturbation. Indeed, some of the responses in ^{15}N uptake were greater in magnitude and significance than were responses in biomass or N content. Although 3.5 yr is a fairly long time for an ecological manipulation, it is short relative to the life span of the plants in tundra. Our assumption was that short-term responses in the uptake of a limiting nutrient are good indicators of longer term responses in other measures of plant performance such as biomass. Although such an assumption seems reasonable, it deserves explicit testing in the future.

Use of a ^{15}N tracer also allowed us to examine general differences among species in the relative importance of uptake vs. stored N in supporting new growth (above we focus on treatment differences). Evergreen species (*L. palustre* and *V. vitis-idaea*) supported more

of their new growth with uptake than did *B. nana* or the sedges (*C. bigelowii* and *E. vaginatum*), probably because their roots are initiated during the pulse of N mineralization that occurs with thaw (Kielland 1990, Nadelhoffer et al. 1992) (Fig. 4). The differences between evergreen and deciduous species in their nutrient use resemble differences previously documented in their carbon use. Because evergreens have old leaves present, they depend less on carbon storage than on current photosynthesis to support new growth (Kummerow et al. 1983). Deciduous species, whose leaves must expand before photosynthesis can occur, have later root initiation and support more of their growth with stored carbon (Kummerow et al. 1983). Other studies have also inferred (based on changes in total N pools) that graminoids depend heavily on belowground stores to support new growth (Shaver et al. 1986).

Conclusions

Our results support the hypothesis that increased air temperature will have little direct effect on biomass or production in tundra, but instead will act indirectly by increasing soil temperature and mineralization of organic nutrients. Two of the dominant shrubs in the community responded significantly to warming. In the dominant overstory deciduous shrub, *B. nana*, the aboveground biomass and N content of new growth doubled with warming. In the understory evergreen shrub, *V. vitis-idaea*, the N content and ^{15}N uptake of old leaves and stems declined with warming. Thus, although air temperature did not change total ecosystem N pools, it did influence N distribution within the plant community. These species-level changes were associated with increased carbon turnover at the ecosystem level. In particular, the increase in *B. nana* growth and N caused higher gross photosynthesis early in the growing season. Greater ecosystem respiration probably resulted from higher maintenance and growth respiration of aboveground *B. nana* biomass production and root N uptake and/or turnover in the greenhouses. The increased abundance of *B. nana* with warming may indicate how community structure will change with future climate warming and is consistent with increased *Betula* abundance during past warming in the Alaskan Arctic.

We suggest that the major effects of climatic warming will occur through increased soil temperature (not manipulated in this study) and consequent effects on soil processes (e.g., decomposition and nutrient mineralization, Shaver et al. 1992). Whether the increased C turnover resulting from air warming will interact with the ecosystem response to belowground warming remains to be tested.

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