



Plant Performance and Soil Nitrogen Mineralization in Response to Simulated Climate Change in Subarctic Dwarf Shrub Heath

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To simulate a future, warmer climate, we subjected subarctic dwarf shrub heath to 5°C direct soil warming for five consecutive growing seasons (1993–1997). Supplemental air warming treatments were imposed on warmed soil by plastic tents in 1994 and open-top chambers in 1995. Plant responses to warming were assessed by changes in: 1) shrub phenology, 2) current-year aboveground biomass in the dominant shrubs (*Empetrum hermaphroditum*, *Vaccinium myrtillus*, *V. uliginosum* and *V. vitis-idaea*), and 3) vascular and nonvascular plant cover. We estimated warming effects on soil nitrogen (N) availability by *in situ* buried bag incubation of soils.

Soil warming stimulated soil N cycling and shrub growth and development in the short term (2–3 yr). In the second year, net N mineralization rates doubled in warmed soil ($4.3 \text{ kg N ha}^{-1} \text{ season}^{-1}$ in untreated soil vs $9.2 \text{ kg ha}^{-1} \text{ season}^{-1}$). Greater N availability likely contributed to the observed 62% increase in current-year growth of *V. myrtillus*, the dominant deciduous shrub. In the third year, soil and air warming increased shoot production by > 80% in the evergreen shrubs *V. vitis-idaea* and *E. hermaphroditum*. Soil warming had no detectable effects on plant growth or soil N cycling in the fifth year, suggesting that the long-term response may be less dramatic than short-term changes.

Past fertilization studies in arctic and subarctic tundra reported an increase in the abundance of graminoids. Despite enhanced soil N mineralization in the second year, we found that warming had little effect on plant community composition after five years. Even in an extreme climate warming scenario, it appears that subarctic soils mineralize an order of magnitude less N than was applied in fertilization experiments. High-dose fertilization studies provide insight into controls on plant communities, but do not accurately simulate increases in N availability predicted for a warmer climate.

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Global circulation models predict that a doubling of atmospheric CO₂ concentrations will raise the average annual global temperature 1.5–4.5°C by the year 2050 (Kattenberg et al. 1996). Model projections at sub-continental scales are less certain, but a number of projections indicate that warming will be more pronounced at high latitudes (Mitchell et al. 1990, Maxwell 1992, Cattle and Crossley 1996). Warmer temperatures are expected to bring about changes in soil nutrient cycling and plant species composition (Melillo et al. 1990);

however, long-term field manipulations are needed to predict these changes.

Arctic ecosystems have large soil organic carbon (C) and nitrogen (N) stores (Oechel and Billings 1992). Soil warming accelerates organic matter decomposition and thereby promotes nitrogen mineralization, as demonstrated in laboratory (Nadelhoffer et al. 1991, Hobbie 1996) and field studies (Van Cleve et al. 1990, Melillo 1996). Laboratory incubations of Alaskan tussock tundra soils mineralized two orders of magnitude more N

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Table 1. Climatic conditions during the soil warming experiment: a) mean monthly air temperature (°C) and b) total monthly precipitation (mm) from 1993–1997, relative to the 30-yr mean (Abisko Scientific Research Station, unpubl.).

	1993	1994	1995	1996	1997	1961–90 m
a) Mean air temperature (°C)						
June	6.1	7.4	8.3	7.5	9.6	8.4
July	12.4	11.0	8.7	11.0	13.2	11.0
August	9.7	10.4	9.8	12.1	11.5	9.7
Growing season	9.4	9.6	8.9	10.2	11.4	9.7
b) Total precipitation (mm)						
June	28	17	29	50	4	22
July	56	28	22	25	48	54
August	77	28	66	49	25	45
Growing season	161	73	117	124	77	121

at 10°C than at 4°C (Hobbie 1996). Greater N availability in arctic and subarctic soils has been associated with shifts in plant species composition in these typically N-limited ecosystems (Shaver et al. 1986, Jonasson 1992). Nitrogen is generally considered to be the nutrient that most limits plant growth in tundra and boreal forest ecosystems (Nadelhoffer et al. 1992, Chapin et al. 1993, Kielband 1994). If soil warming enhances net N mineralization, one would expect to see changes in the relative abundance of plant species and perhaps growth forms.

In a latitudinal transect of greenhouse warming experiments from high arctic through subarctic to temperate ecosystems (see review by Jonasson et al. 1996a), air warming enhanced subarctic plant growth and development (Parsons et al. 1994, Michelsen et al. 1996, Press et al. 1998), but had no effect on soil N mineralization or soil N pools (Jonasson et al. 1993, Robinson et al. 1995). The absence of a warming effect on soil microbial processes may be due to the low level of treatment (maximum 2°C) imposed in these experiments (Havström et al. 1993).

In this experiment, we applied a 5°C soil warming on dwarf shrub tundra in Abisko, Sweden during the 1993–1997 growing seasons using buried heating cables. This level of warming is at the upper end of the range in arctic growing-season temperatures projected for the year 2050 (Maxwell 1992), and is several degrees higher than previous climate change experiments in arctic and subarctic tundra. By warming the soil directly, we expected to observe a stronger microbial response than observed in previous climate change studies in the region. We hypothesized that direct soil warming would stimulate soil N cycling, promote shrub growth and development, and increase the relative abundance of graminoids, as suggested by fertilization studies in subarctic tundra (Jonasson 1992, Parsons et al. 1995).

Materials and methods

Study site

This study was carried out in northern Sweden near the Abisko Scientific Research Station on the southern shore of Lake Torneträsk (68°35' N 18°82' E, 380 m a.s.l.). Experimental plots were located in a dwarf shrub understory of an open birch woodland (*Betula pubescens* Ehrh. ssp. *tortuosa* Ledeb. Nyman) where the dominant plants are evergreen (*Empetrum hermaphroditum* Hagerup and *Vaccinium vitis-idaea* L.) and deciduous (*V. myrtillus* L. and *V. uliginosum* L.) dwarf shrubs (Sonesson and Lundberg 1974).

Climate

The Abisko climate is milder than other areas at the same latitude because of its proximity to the Atlantic Ocean. Its 30-yr mean July temperature (1961–1990) is 11.0°C, 1.0°C warmer than the 10°C isotherm used to define arctic zones (Andersson et al. 1996). Mean July air temperatures were higher than the 30-yr mean in 1996 and 1997 (Table 1a). Total growing season precipitation ranged from a high of 161 mm in 1993 to lows

Table 2. Experimental warming of subarctic dwarf shrub tundra in Abisko, Sweden, 1993 to 1997. Mean increase in soil and air temperatures in the three treatments: soil warming by buried cables (Cable), and on four of the cable-warmed plots, supplemental air warming by tents in 1994 (Cable+Tent) and open-top chambers in 1995 (Cable+OTC).

Growing sea- sons	1993–97	1994 ¹	1995 ²
	(°C above am- bient)	Cable	Cable+Tent
Soil warming	5	4.3	5.4
Air warming	0	1.3	2.1

¹1994 temperatures recorded at 0.5-h intervals for 24 h in three soil+air-warmed (tented) and three soil-warmed plots on Julian days 227–237.

²1995 temperatures recorded in three OTCs at 0.5-h intervals for 24 h on Julian days 202–204.

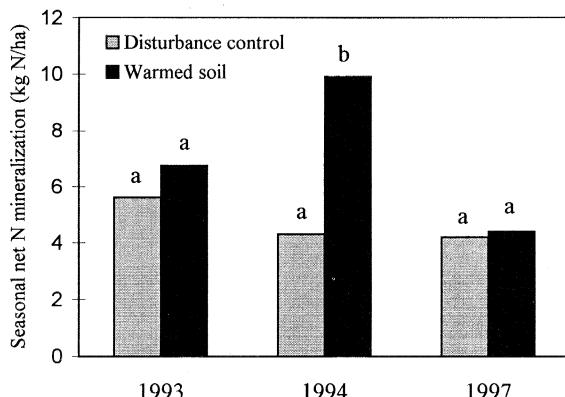


Fig. 1. Seasonal net N mineralization (kg N ha^{-1}) in soil-warmed vs disturbance-control plots. Treatment means were compared within year; different letters denote a statistically significant difference at $p \leq 0.05$.

of 73 and 77 mm in 1994 and 1997 (Table 1b). Mean annual precipitation in the Abisko valley is 300 mm.

Table 3. Effects of warming on dwarf shrub phenology in 1994, 1995 and 1997. Data represent the percentage of plants (mean per plot ± 1 SE; $n = 4$) that reached the specified stage of development by the given date. Statistical comparisons were made among treatments within a year.

a) <i>Empetrum hermaphroditum</i>				
	16 June 94	15 June 95	20 June 97	
Bud break				
Control	55 \pm 8 a	63 \pm 9 a	56 \pm 6 a	
Soil warming	75 \pm 10 a	83 \pm 10 ab	63 \pm 8 a	
Soil+air warming	92 \pm 3 a	96 \pm 4 b		
b) <i>Vaccinium myrtillus</i>				
	12 June 94	15 June 95	12 June 97	
Leaf emergence				
Control	51 \pm 12 a	63 \pm 7 a	93 \pm 4 a	
Soil warming	70 \pm 11 a	76 \pm 9 ab	95 \pm 3 a	
Soil+air warming	83 \pm 8 a	90 \pm 3 b		
Leaf maturation	30 June 94	26 June 95	12 June 97	20 June 97
Control	28 \pm 12 a	37 \pm 10 a	50 \pm 13 a	99 \pm 1 a
Soil warming	75 \pm 3 b	29 \pm 11 a	6 \pm 4 b	99 \pm 1 a
Soil+air warming	85 \pm 5 b	50 \pm 16 a		
c) <i>V. vitis-idaea</i>				
	16 June 94			
Bud break				
Control	51 \pm 12 a			
Soil warming	70 \pm 11 a			
Soil+air warming	83 \pm 8 a			
Leaf emergence	7 July 94	6 July 95	2 July 97	15 July 97
Control	44 \pm 13 a	32 \pm 6 a	39 \pm 10 a	31 \pm 10 a
Soil warming	43 \pm 6 a	67 \pm 10 b	42 \pm 5 a	75 \pm 13 b
Soil+air warming	93 \pm 4 b	78 \pm 10 b		
Leaf maturation	14 July 94	13 July 95	15 July 97	29 July 97
Control	12 \pm 5 a	5 \pm 3 a	45 \pm 10 a	58 \pm 8 a
Soil warming	15 \pm 10 a	16 \pm 7 a	43 \pm 10 a	56 \pm 5 a
Soil+air warming	67 \pm 16 b	35 \pm 4 b		
d) <i>V. uliginosum</i>				
	8 June 94		12 June 97	
Leaf emergence				
Control	52 \pm 13 a		100 \pm 0 a	
Soil warming	68 \pm 12 a		100 \pm 0 a	
Soil+air warming	85 \pm 9 b			
Leaf maturation	23 June 94	22 June 95	12 June 97	20 June 97
Control	60 \pm 10 a	52 \pm 8 a	88 \pm 8 a	100 \pm 0 a
Soil warming	62 \pm 12 a	42 \pm 11 a	74 \pm 14 a	100 \pm 0 a
Soil+air warming	68 \pm 12 a	67 \pm 17 a		

Experimental design

In 1992, one 4.8 by 6-m plot was installed using heating wires buried in the humic layer 5 cm below the soil surface, similar to that used in temperate forests (Peterjohn et al. 1993). Four sets of control plots were established at the corners of the cable-warmed plot; each set of control plots had a 1-m² untreated "Control" and a 1-m² "Disturbance Control" with unheated, buried cables. The warmed plot contained five thermistors which recorded soil temperatures every 2 h. The control and disturbance control plots had three thermistors. Wires in the warmed plot were heated when the temperature difference between heated and control plots at 5-cm soil depth dropped below 5°C. Soils were heated $5.0 \pm 0.5^\circ\text{C}$ from 17 June to 16 September, 1993, and the same treatment applied each year through 1997 from the time snow cover disappeared to the first frost.

For sampling, the central heated area was divided into 20 1-m² plots. Starting in 1993, we sampled soils from three of the 20 warmed plots, and from three untreated and three disturbance controls. Plant growth and cover were measured in a separate set of four 1-m²

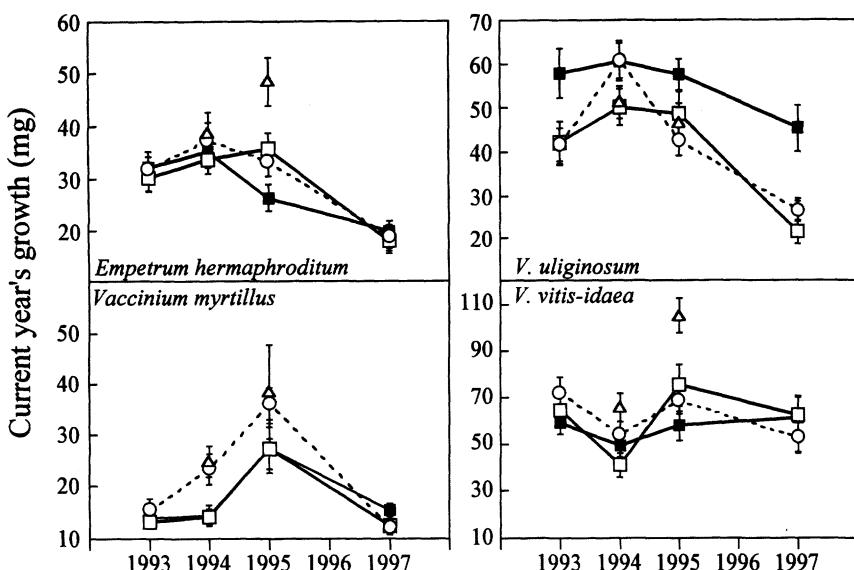


Fig. 2. Effects of disturbance (cable burial) and warming on current-year aboveground biomass production in four subarctic dwarf shrubs: *Empetrum hermaphroditum*, *Vaccinium myrtillus*, *V. uliginosum* and *V. vitis-idaea* in 1993–1995 and 1997 (mean \pm 1 SE; $n = 4$). (soil warming ○, soil and air warming △, control ■, disturbance control □).

warmed plots (not those used for soil sampling), plus the four untreated and four disturbance controls. Starting in 1994, shrub phenology was recorded in four warmed plots (not sampled previously), plus the four untreated and four disturbed controls. The heating cables were turned on in 1996, but no data were collected that year.

In 1994, small plastic tents were used to elevate air temperature above four of the 1-m² soil-warmed plots (Table 2). Tents were randomly assigned to four of the 20 plots in the cable-heated plot. The 0.75-m-tall vented tents were similar in design to those used in past air warming studies (Havström et al. 1993, Wookey et al. 1993). To decrease rain interception and increase air warming intensity, tents were replaced by International Tundra Experiment-style (ITEX) open-top chambers for the 1995 growing season (Marion et al. 1997). Shrub phenology, growth and plant cover were analyzed in the soil + air-warmed (tent) plots in 1994, and shrub phenology and growth were recorded in open-top chambers in 1995. Air warming treatments were not applied in 1993, 1996 or 1997.

Soil and vegetation analysis

We measured in situ net N mineralization and nitrification once during the growing season using the buried bag technique (Eno 1960) using season-long incubations in 1993, 1994 and 1997. We collected initial soil cores (5-cm diameter by 10-cm deep) from three disturbance control and three soil-warmed plots. Two paired soil cores were removed next to each initial core and were used for incubation. Coarse roots and rocks were culled from the second sample and the unsieved soil

was buried in polyethylene bags at 5-cm depth. In the lab, inorganic N was immediately extracted from a 10-g subsample of each initial core in 100 ml of 2 M KCl. These extracts were shaken vigorously for 1 h, then filtered after 24 h. The remainder of the sample was dried at 105°C for 48 h for gravimetric soil moisture determination. At the end of the growing season, the buried bags were removed, and final soil samples were processed as described above. Filtered extracts were frozen and transported to the Marine Biological Laboratory (Massachusetts, USA) for colorimetric analysis of NH₄⁺ and NO₃⁻ on an Alpkem RFA autoanalyzer. NH₄⁺ was measured by the phenol hypochlorite method and NO₃⁻ measured by cadmium reduction. Net N mineralization rates were calculated as the change in total inorganic N content during the growing season, and net nitrification was assumed to equal the change in NO₃⁻ contents.

The buried bag technique estimates net N mineralization or gross N mineralization minus microbial N uptake. This technique has some limitations. First, it captures soil moisture levels at one point in time – the beginning of the incubation period. In our study, soils were sampled, bagged and buried during snowmelt. The buried soils were moister than surrounding soils during field incubation, which means that net N mineralization could be overestimated. Secondly, this technique prohibits any study of root-mycorrhizal interactions with N mineralization. For example, if root-fungal interactions were to result in the production of protein-degrading enzymes, the effects of these enzymes would not show up in the buried bag measures. Likewise, the buried bag method does not provide information about the importance of organic N in plant nutrition. To

answer this latter question, analyses of the natural abundance of the nitrogen isotope, $\delta^{15}\text{N}$, have been used successfully (Michelsen et al. 1998).

We recorded the phenology of *E. hermaphroditum*, *V. myrtillus*, *V. vitis-idaea* and *V. uliginosum* on 10 individuals of each species in four plots of each treatment at 1–2-week intervals in 1994, 1995 and 1997. The phenological stages observed were bud break, leaf emergence and maturation. Leaf maturation was defined as the full expansion of *V. myrtillus* and *V. vitis-idaea* leaves.

To assess growth responses to warming with minimal damage, we measured current-year shoot biomass, rather than total biomass. Current-year growth was measured on individual shoots in 1993–1995 and in 1997. Six randomly selected shoots were harvested per plot per shrub species, then analyzed for stem length, stem dry mass, leaf dry mass, leaf number and leaf area (excluding *E. hermaphroditum* leaf number and leaf area). Leaf area was estimated using a Digital Image Analysis System (Delta-T Devices Ltd., England). The fraction of current-year growth in leaves (dry leaf mass/(dry stem + leaf mass) or leaf weight ratio; Chiariello et al. 1989) was used to assess changes in current-year biomass allocation. Live and senescent leaf tissue from the harvest was pooled for each species and within each plot. A subsample was analyzed for total nitrogen on a Perkin-Elmer 2400 elemental analyzer.

Plant cover and growth were measured at the approximate time of peak biomass (early August) in four plots of each treatment. We used a modified point intercept method to assess treatment effects on overall cover of dwarf shrubs (*E. hermaphroditum*, *V. myrtillus*, *V. uliginosum* and *V. vitis-idaea*), grasses (*Calamagrostis lapponica* and *Deschampsia flexuosa*), forbs (*Linnaea borealis* and *Rubus chamaemorus*), mosses and lichens in 1993, 1994 and 1997. We positioned the legs of a

0.5-m² frame into four permanently installed pipes in the center of each plot. The frame consisted of a two-tiered grid, with a total of 121 sampling points spaced at 5-cm intervals. Sighting down the cross hairs, we recorded the species observed. The number of total observations per species provided a relative estimate of plant cover.

Statistical analysis

We analyzed the effects of disturbance and warming on plant phenology, growth and cover on individual species in each year using one-way analysis of variance (ANOVA). We analyzed the data year-by-year because different treatments were imposed in different years. Soil + air-warming treatments were added in 1994 and 1995. We used the Bonferroni post-hoc test to compare treatment means (Day and Quinn 1989). When necessary, data were transformed to meet the ANOVA assumptions of normality and homogeneity of variance. A nonparametric equivalent (Wilcoxon rank sum or Kruskal Wallis test) was used on data that failed to meet the ANOVA assumptions. All tests were performed at the $p \leq 0.05$ level. The Shapiro-Wilk *W* normality test, Bartlett's test for homogeneity of variance and nonparametric statistics were executed in JMP (SAS Institute Inc. 1996); all other analyses were performed in Data Desk (Data Description Inc. 1993).

The soil warming treatment was not replicated in this experiment. We installed cables into a single 4.8 by 6-m plot and sampled repeatedly over a 5-yr period to minimize disturbance. We treated a large area to avoid strong edge effects, while allowing enough interior space for destructive sampling (e.g. buried bag incubations).

Table 4. Treatment effects on shrub growth and allocation patterns in 1993 (mean per plot [1 SE]; $n = 4$). Treatments were compared within each species and year. Different letters denote statistically significant differences at $p \leq 0.05$. nd = not determined.

	Stem length (mm)	Leaf weight ratio	Leaf number	Leaf area (cm ²)
<i>E. hermaphroditum</i>				
Control	23.4 [3.0] a	0.74 [0.01] a	nd	nd
Disturbance control	25.0 [2.2] a	0.75 [0.01] a	nd	nd
Soil warming	24.9 [2.7] a	0.74 [0.01] a	nd	nd
<i>V. myrtillus</i>				
Control	17.2 [1.3] a	0.70 [0.02] a	4.5 [0.1] a	16.8 [1.2] a
Disturbance control	16.9 [1.5] a	0.70 [0.02] a	4.5 [0.2] a	15.7 [1.3] a
Soil warming	18.6 [1.9] a	0.66 [0.02] a	4.3 [0.1] a	16.5 [1.8] a
<i>V. uliginosum</i>				
Control	23.1 [2.8] a	0.81 [0.01] a	8.0 [0.4] a	57.7 [4.8] a
Disturbance control	14.6 [1.7] a	0.84 [0.01] a	6.5 [0.3] b	42.2 [4.5] b
Soil warming	18.3 [2.6] a	0.84 [0.02] a	7.2 [0.4] ab	45.1 [3.7] ab
<i>V. vitis-idaea</i>				
Control	26.4 [1.8] a	0.88 [0.01] a	8.4 [0.4] a	42.9 [3.1] a
Disturbance control	26.2 [2.2] a	0.89 [0.01] a	9.3 [0.3] ab	46.4 [4.9] a
Soil warming	29.8 [2.1] a	0.88 [0.01] a	9.7 [0.3] b	57.7 [4.7] a

Table 5. Treatment effects on shrub growth and allocation patterns in 1994 (mean per plot [1 SE]; $n = 4$). Treatments were compared within each species and year. Different letters denote statistically significant differences at $p \leq 0.05$. nd = not determined.

	Stem length (mm)	Leaf weight ratio	Leaf number	Leaf area (cm^2)
<i>E. hermaphroditum</i>				
Control	19.3 [1.9] a	0.80 [0.01] a	nd	nd
Disturbance control	19.0 [1.8] a	0.79 [0.01] a	nd	nd
Soil warming	21.8 [2.3] a	0.76 [0.01] a	nd	nd
Soil+air warming	21.9 [2.9] a	0.79 [0.01] a	nd	nd
<i>V. myrtillus</i>				
Control	14.6 [1.7] ab	0.75 [0.02] ab	4.3 [0.2] a	14.2 [1.3] a
Disturbance control	12.6 [1.1] ab	0.76 [0.01] ab	4.0 [0.2] a	14.3 [1.2] ab
Soil warming	22.9 [3.1] bc	0.68 [0.03] b	4.8 [0.2] a	20.7 [1.9] bc
Soil+air warming	24.5 [2.8] c	0.67 [0.02] b	4.8 [0.2] a	22.2 [2.2] c
<i>V. uliginosum</i>				
Control	20.0 [2.1] a	0.81 [0.01] a	8.2 [0.4] a	55.9 [3.3] a
Disturbance control	15.6 [2.1] a	0.84 [0.01] a	7.4 [0.4] a	48.2 [4.0] a
Soil warming	19.6 [1.6] a	0.84 [0.01] a	8.7 [0.3] a	60.3 [3.8] a
Soil+air warming	19.5 [1.7] a	0.82 [0.01] a	8.3 [0.3] a	48.0 [3.1] a
<i>V. vitis-idaea</i>				
Control	17.7 [1.0] a	0.91 [0.01] a	9.2 [0.4] a	34.6 [2.8] a
Disturbance control	16.2 [1.3] a	0.91 [0.01] a	8.1 [0.3] a	31.4 [3.1] a
Soil warming	18.9 [1.7] a	0.92 [0.01] a	9.1 [0.4] a	33.9 [3.3] a
Soil+air warming	20.0 [1.9] a	0.91 [0.01] a	9.2 [0.3] a	40.5 [3.2] a

Results

Effects of soil warming on soil N cycling

Seasonal net N mineralization was relatively constant in control soils across years (Fig. 1). Net N mineralization was marginally higher in warmed plots during the first season of warming, but not significantly so. After two years, net N mineralization in the warmed plots was more than double that in disturbance-control plots ($p \leq 0.05$). In 1997, net N mineralization was not significantly different in warmed vs disturbance-control plots. The inorganic soil N pool in both treatments was dominated by NH_4^+ . Nitrate concentrations at the end of the growing season were not significantly different from initial values in any year; therefore, seasonal net nitrification rates were zero. Soil moisture was significantly lower in cable-warmed soils vs disturbance controls (232% oven-dried weight vs 353%; 2-sample t -test: $p \leq 0.001$) in June 1997.

Effects of soil warming on plants

Shrub phenology

V. vitis-idaea leaves emerged earlier in warmed soil in 1995 and 1997 (Table 3). Soil warming caused *V. myrtillus* leaves to mature significantly earlier in 1994, but this treatment had the opposite effect in 1997. *V. uliginosum* and *E. hermaphroditum* showed no phenological response to soil warming in any year.

Shrub growth

Cable burial had an insignificant effect on current-year shrub growth, with one exception. *V. uliginosum* growing in control plots produced more shoot biomass than any other treatment in 1997 ($p \leq 0.001$; Fig. 2). In this case, we used disturbance control values to assess the impact of warming on growth.

None of the shrub species exhibited a significant response to soil warming in 1993 (Fig. 2, Table 4). By the end of summer 1994, we found a significant treatment effect on current-year growth of *V. myrtillus* (Fig. 2). Soil warming enhanced mean shoot production by 62% ($p \leq 0.03$), leaf production by 44% ($p \leq 0.04$), and leaf area by 46% ($p \leq 0.04$) relative to controls (Table 5). *E. hermaphroditum* and *V. vitis-idaea* shoots tended to be heavier and longer in the warmed plots, but this effect was not significant. Soil warming had no effect on allocation of current-year biomass in any species relative to controls. *V. myrtillus* shoot production in soil warming plots was 32% higher than controls in 1995, although treatment effects were no longer significant (Fig. 2). These treatment effects were of the same order as interannual variability in *V. myrtillus* growth.

None of the species responded positively to soil warming in 1997 (Fig. 2, Table 6). *V. vitis-idaea* growing in heated soil had significantly higher leaf weight ratios and shorter stems than control plants (Table 6). Current-year growth in all species was significantly lower in 1997 than in any other year ($p \leq 0.0001$). During this 5-yr experiment, *V. uliginosum* was the only species that did not respond to soil warming.

Soil warming had no effect on foliar N concentrations in any year (Table 7).

Plant cover

Cable burial had no effect on vascular plant or cryptogam cover, with the exception of lichen cover in 1997 ($p \leq 0.05$; Fig. 3). Soil warming had no effect on vascular plant cover (Fig. 4); however, lichen cover was reduced during the 5-yr experiment. By 1997, lichen cover was significantly lower in the warmed plots, relative to disturbance controls ($p \leq 0.04$). Moss cover was significantly higher in the soil-warmed plots than in controls the first year ($p \leq 0.02$), but that trend was reversed in 1994 and 1997.

Effects of soil + air warming on plants

Shrub phenology

Soil + air warming advanced leaf development in *V. uliginosum*, *V. myrtillus* and *V. vitis-idaea* in 1994 (Table 3). In 1995, *E. hermaphroditum* bud break, and leaf development in *V. myrtillus* and *V. vitis-idaea* were accelerated significantly by soil + air warming.

Shrub growth

Soil + air warming stimulated *V. myrtillus* growth dramatically in 1994 (Fig. 2, Table 5). Plants produced 73% heavier shoots ($p \leq 0.01$), 120% more stem ($p \leq 0.02$) and 52% more leaf biomass ($p \leq 0.02$) with 57% greater leaf area ($p \leq 0.01$) than controls. A larger fraction of current-year growth was allocated to stems compared to controls, but this trend was not significant ($p \leq 0.06$).

V. myrtillus shoot production remained 40% higher in the soil + air warming treatments than in controls through 1995, but treatment effects was not significant after 1994 (Fig. 2, Table 8). After three seasons, *E. hermaphroditum* produced significantly more shoot

biomass in the soil + air-warmed plots than in controls with > 80% heavier ($p \leq 0.0001$) and 70% longer ($p \leq 0.004$) shoots. Similarly, *V. vitis-idaea* produced > 80% heavier ($p \leq 0.00003$) and 38% longer ($p \leq 0.003$) shoots. *V. vitis-idaea* produced 83% more leaf ($p \leq 0.00001$) and 70% more stem ($p \leq 0.003$) biomass, while *E. hermaphroditum* produced 73% more leaf ($p \leq 0.00003$) biomass with 122% heavier ($p \leq 0.0004$) and 70% longer ($p \leq 0.004$) stems than controls. Warming did not alter current-year allocation to leaves vs stem in *V. vitis-idaea* or *E. hermaphroditum*.

Air warming treatments were discontinued at the end of August 1995. There were no significant effects of treatment on foliar N concentrations except in 1995 when soil and air warming lowered foliar N in *V. myrtillus* by 0.4% ($p \leq 0.05$; Table 7).

Plant cover

Soil and air warming had no effect on dwarf shrub, moss, lichen or grass cover in 1994 (Figs 3, 4). No cover data were collected from open-top chambers in 1995.

Discussion

Effect of warming on soil N cycling

The results of this 5-yr study suggest that direct soil warming by 5°C stimulates soil N cycling, shrub growth and development, but does not alter plant community composition over the short term (3–5 yr). A 5°C warming appeared to be sufficient to stimulate N mineralizing microbes, in contrast to other field experiments that raised soil temperatures by only 1–2°C, but did not promote N mineralization (Robinson et al. 1995). We observed marginally higher net N mineralization in

Table 6. Treatment effects on shrub growth and allocation patterns in 1997 (mean per plot [1 SE]; $n = 4$). Treatments were compared within each species and year. Different letters denote statistically significant differences at $p \leq 0.05$. nd = not determined.

	Stem length (mm)	Leaf weight ratio	Leaf number	Leaf area (cm ²)
<i>E. hermaphroditum</i>				
Control	17.5 [1.9] a	0.82 [0.01] a	32.2 [1.5] a	nd
Disturbance control	14.1 [1.8] a	0.83 [0.01] a	28.5 [2.0] a	nd
Soil warming	14.7 [1.3] a	0.80 [0.01] a	30.1 [2.2] a	nd
<i>V. myrtillus</i>				
Control	21.5 [1.7] a	0.65 [0.02] a	5.0 [0.2] a	17.5 [1.1] a
Disturbance control	18.4 [2.0] a	0.64 [0.04] a	4.4 [0.2] a	13.7 [1.4] a
Soil warming	16.1 [1.6] a	0.70 [0.02] a	4.5 [0.2] a	13.4 [1.1] a
<i>V. uliginosum</i>				
Control	13.5 [3.2] a	0.72 [0.05] a	7.9 [0.4] a	30.5 [5.8] a
Disturbance control	10.2 [1.9] b	0.82 [0.02] ab	5.7 [0.4] b	24.8 [2.5] b
Soil warming	10.8 [1.9] b	0.84 [0.01] b	6.5 [0.3] b	29.6 [2.6] ab
<i>V. vitis-idaea</i>				
Control	31.9 [2.2] a	0.82 [0.02] a	9.3 [0.6] a	43.4 [6.1] a
Disturbance control	30.5 [2.7] a	0.84 [0.01] ab	9.6 [0.7] a	41.9 [4.6] a
Soil warming	21.2 [1.6] b	0.88 [0.01] b	8.8 [0.5] a	33.9 [3.6] a

Table 7. Treatment effects on foliar N in current year biomass (%N in dry leaf tissue; mean [1 SE]), 1993–1997. Treatments were compared within each species and year. nd = not determined.

	1993	1994	1995	1997
<i>E. hermaphroditum</i>				
Control	1.6 ± 0.04 a	1.2 ± 0.03 a	1.2 ± 0.1 a	1.3 ± 0.03 a
Soil warming	1.6 ± 0.04 a	1.2 ± 0.01 a	1.3 ± 0.1 a	1.2 ± 0.1 a
Soil+air warming	nd	1.2 ± 0.04 a	1.1 ± 0.1 a	1.2 ± 0.1 a
<i>V. myrtillus</i>				
Control	1.8 ± 0.04 a	1.6 ± 0.06 a	1.9 ± 0.1 a	1.7 ± 0.03 a
Soil warming	1.7 ± 0.04 a	1.7 ± 0.07 a	1.6 ± 0.1 ab	1.4 ± 0.1 a
Soil+air warming	nd	1.7 ± 0.08 a	1.5 ± 0.1 b	1.4 ± 0.1 a
<i>V. uliginosum</i>				
Control	2.0 ± 0.04 a	1.7 ± 0.08 a	1.8 ± 0.1 a	1.7 ± 0.04 a
Soil warming	2.2 ± 0.04 a	1.8 ± 0.08 a	1.9 ± 0.1 a	1.5 ± 0.1 a
Soil+air warming	nd	1.6 ± 0.09 a	1.6 ± 0.1 a	1.6 ± 0.1 a
<i>V. vitis-idaea</i>				
Control	1.2 ± 0.04 a	1.4 ± 0.08 a	1.2 ± 0.1 a	0.9 ± 0.03 a
Soil warming	1.2 ± 0.04 a	1.2 ± 0.05 a	1.1 ± 0.1 a	0.9 ± 0.02 a
Soil+air warming	nd	1.0 ± 0.04 a	1.0 ± 0.1 a	0.9 ± 0.03 a

5°C-warmed soils the first growing season, and rates doubled with warming the second year. Jonasson et al. (1993) observed a flush of N mineralization in high-elevation fellfield soils after they were transplanted into dwarf shrub tundra and incubated in an approximately 4°C warmer environment. Our study offers further evidence that *in situ* soil warming of 4–5°C will enhance microbial activity in subarctic soils.

Net N mineralization did not remain elevated in warmed plots for the entire 5-yr study and appeared to decline in the last year. Lack of a significant warming effect in the final year may have several explanations. One possibility is that microbial populations grew faster in warmed soils, increasing microbial demand and uptake of N. Microbes compete effectively with plants for nutrients in arctic (Jonasson et al. 1996b) and temperate soils (Schimel et al. 1989, Harte and Kinzig 1993, Jonasson et al. 1996c). In subarctic dwarf shrub tundra soils, approximately 6% of total soil N is stored in microbial biomass, compared to only 0.1% in inorganic forms (Jonasson et al. 1996b). After four years of treatment, microbial population growth may have increased the demand for N, potentially explaining the lack of a warming effect on net N mineralization in the final year.

Another possible explanation is that despite large organic C stores in tundra soils, microbial growth is limited by the availability of labile C (Marion et al. 1982, Jonasson et al. 1996b, c). Depletion of readily respirable C in the first several years of warming would effectively reduce the C:N ratio of remaining soil organic matter, lowering substrate quality and reducing N mineralized. Changes in plant litter C:N or shifts in plant community composition toward species with lower litter qualities (higher C:N) can alter that ratio as well, but the fact that C:N ratios for the dominant

shrub species did not change even after five years and the absence of observable shifts in plant species composition make it unlikely that the chemical composition of soil organic matter was altered by plant inputs.

We cannot rule out the influence of abiotic factors on microbial responses to warming. Soil moisture may have become depleted in 1997 during an unusually hot, dry summer (Table 1). Soils were saturated by snowmelt (353% oven-dried weight) in early June 1997, but moisture availability declined as the summer progressed. We do not have the soil moisture data that would allow us to correlate N mineralization to soil moisture over the course of the experiment. Soil moisture may not be limiting, however, because net N mineralization rates doubled during a similarly dry growing season (1994).

Our data suggest that net N mineralization rates significantly enhanced N availability in warmed soil, and thereby promoted plant growth. We found no increase in leaf N concentrations, as reported in fertilization studies (Chapin et al. 1995, Michelsen et al. 1996). However, foliar N concentrations did not decline with soil warming. This is consistent with the findings of Jonasson and others (in press a, b) that total N storage in subarctic vegetation is likely to increase in a warmer climate, driven by an increase in plant biomass. We found no evidence of nitrification in these subarctic soils, as in arctic wet sedge and dry heath ecosystems (Giblin et al. 1991); therefore losses of mineralized N in soil solution or in gaseous form should be negligible.

Warming-induced increases in net N mineralization may be sustained for a longer period in soils with larger reservoirs of organic N. Organic soils in this experiment have a total N content of 100 g N m⁻² (Melillo et al. unpubl.), comparable to a subarctic *Cassiope* heath (105 g N m⁻²; Jonasson et al. in press a, b) and to a

dry heath in the Alaskan Arctic (112 g m^{-2} ; Nadelhoffer et al. 1997). Total soil N stores are much higher in wet arctic tundra soils (moist tussock, $359\text{--}883 \text{ g m}^{-2}$; wet sedge, $419\text{--}874 \text{ g m}^{-2}$; Nadelhoffer et al. 1997). Wet arctic soils may have greater potential for increased soil N mineralization than subarctic soils in a warmer climate; however, the rate of soil N turnover will depend on other factors such as the chemical composition of litter inputs and soil organic matter.

Effect of warming on plants

Our manipulations of soil temperature stimulated shrub growth and development by the second year of this study. Consistent with greenhouse studies that reported a delayed response to air warming (Shaver et al. 1986, Parsons et al. 1994), we attribute these responses to the

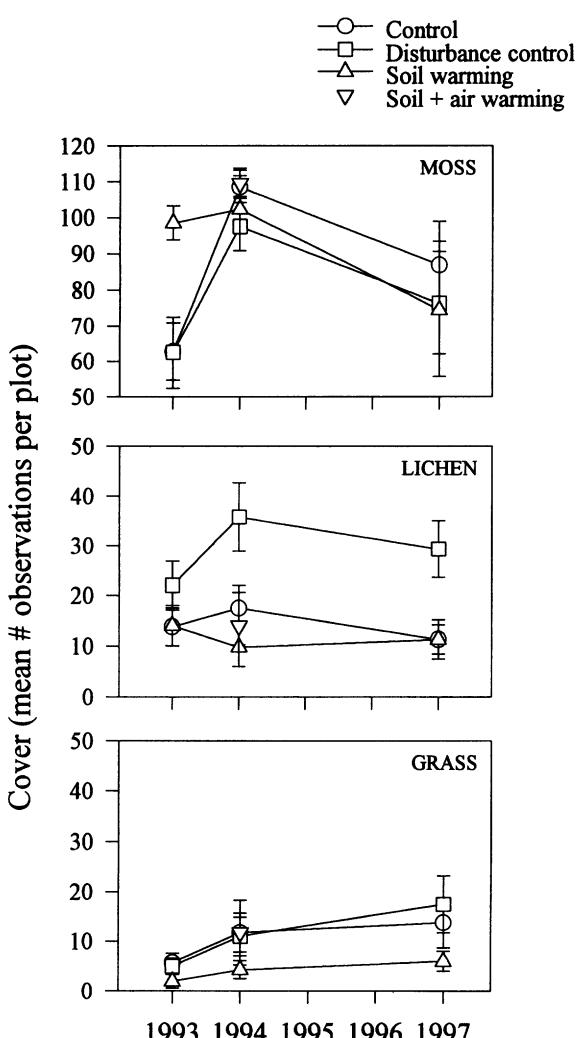


Fig. 3. Effects of warming on moss, lichen and grass cover, estimated by the point intercept method (mean number of hits per plot $\pm 1 \text{ SE}$) in 1993, 1994 and 1997.

growth habits of slow-growing, clonal plants that store C and nutrients in rhizomes and stems and remobilize them in years when resources are suboptimal (Berendse and Jonasson 1992). This strategy implies that microbial and plant responses to warming are not always tightly coupled in any one growing season.

Soil warming accelerated growth and development of the deciduous shrub, *V. myrtillus*, in the second year of treatment. Deciduous plants have higher rates of leaf turnover, and presumably have higher nutrient requirements than evergreens (Shaver and Chapin 1980 and references therein). Because of their presumably higher demands for N, we hypothesized that deciduous shrubs would respond more strongly to warming than evergreen shrubs. Press et al. (1998) reported that five years of greenhouse warming increased aboveground biomass of *V. uliginosum* by 125%, but affected no other species. In our study, *V. uliginosum* was unaffected by soil warming (Fig. 2). There appears to be a substantial variation in the response of species of the same growth form to an altered climate.

In the third year (1995), soil + air warming stimulated growth of *V. myrtillus* as well as the two evergreen shrubs, *V. vitis-idaea* and *E. hermaphroditum*. The evergreen species also produced significantly more shoot biomass after two years of greenhouse warming (Parsons et al. 1994). This strong evergreen response was unexpected, given that this growth form is considered to be adapted to low-nutrient environments (Eckstein and Karlsson 1997). Other evidence also suggests that evergreen shrubs may exploit added N more successfully than deciduous shrubs (Karlsson 1985, Parsons et al. 1994).

After five years, soil warming no longer promoted plant growth. Two explanations are possible. Shrub growth was lower in 1997 than any other year. This was possibly due to the early-season drought (Table 1). Vegetative growth is largely completed by the end of July; therefore, an early-season drought with above-average midsummer temperatures could have inhibited shrub growth. It is also possible that plant C or nutrient stores may be depleted after five years of warming. Following shrub growth in future years that included above-average precipitation could determine which hypothesis is most likely.

During this 5-yr experiment, interannual variability in shrub growth was greater than that imposed by experimental treatments, with the exception of *V. vitis-idaea* exposed to soil + air warming in 1995. It appears that year-to-year climatic variability affects aboveground dwarf shrub growth more than 5°C soil warming.

We detected no changes in shrub cover after 5 yr, despite higher aboveground biomass production in the second and third years of this study. We expected moss and lichen cover to decline with soil warming. Greenhouse warming lowered production of nonvascular

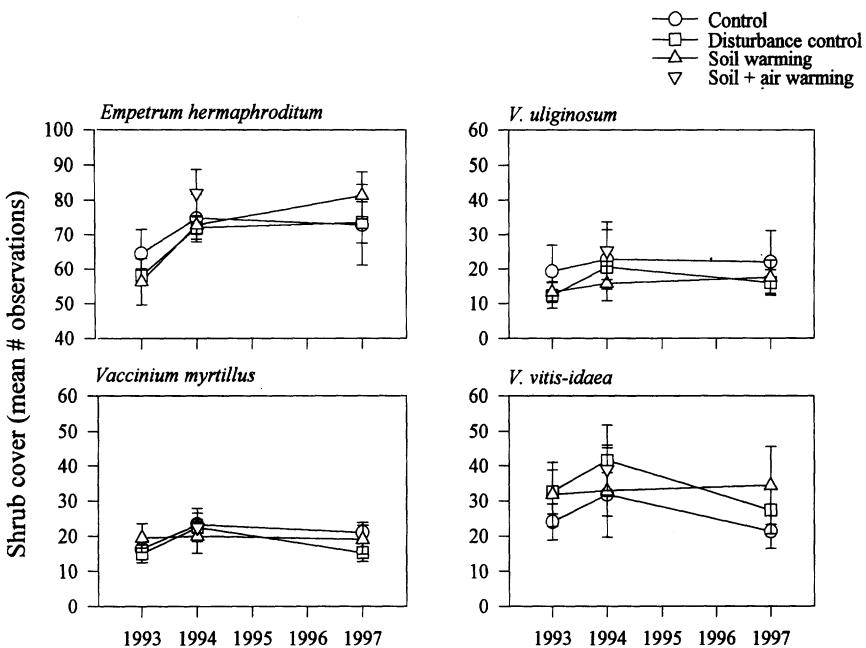


Fig. 4. Effects of warming on subarctic dwarf shrub cover, estimated by the point intercept method (mean number of hits per plot \pm 1 SE) of *Empetrum hermaphroditum*, *Vaccinium myrtillus*, *V. uliginosum* and *V. vitis-idaea* in 1993, 1994 and 1997.

plants in the Alaskan tussock tundra (Chapin et al. 1995) and reduced lichen biomass production by half in the Swedish dwarf shrub tundra after five years (Press et al. 1998). We cannot draw conclusions about the effect of warming on moss cover. The lack of pretreatment data makes it difficult to distinguish treatment effects from initial differences in moss cover. Lichen cover remained constant in warmed soil over the 5-year study, but was significantly lower than controls in 1997 (Fig. 3).

Table 8. Treatment effects on shrub growth and allocation patterns in 1995 (mean per plot [1 SE]; $n = 4$). Treatments were compared within each species and year. Different letters denote statistically significant differences at $p \leq 0.05$. nd = not determined.

	Stem length (mm)	Leaf weight ratio	Leaf number	Leaf area (cm^2)
<i>E. hermaphroditum</i>				
Control	18.1 [2.1] a	0.80 [0.01] a	nd	nd
Disturbance control	22.6 [2.4] ab	0.78 [0.01] a	nd	nd
Soil warming	23.0 [2.2] ab	0.76 [0.01] a	nd	nd
Soil + air warming	30.8 [3.1] b	0.76 [0.01] a	nd	nd
<i>V. myrtillus</i>				
Control	27.6 [4.1] a	0.63 [0.03] a	4.7 [0.3] ab	23.7 [3.4] a
Disturbance control	27.2 [3.4] a	0.62 [0.02] a	4.5 [0.2] ab	24.7 [3.2] a
Soil warming	37.3 [2.4] a	0.56 [0.02] a	5.7 [0.2] b	31.6 [2.0] a
Soil + air warming	37.8 [5.6] a	0.57 [0.02] a	5.5 [0.3] ab	30.6 [5.0] a
<i>V. uliginosum</i>				
Control	27.3 [1.9] a	0.79 [0.01] a	7.7 [0.2] a	57.4 [2.6] a
Disturbance control	22.1 [2.1] ab	0.81 [0.01] ab	7.3 [0.4] a	49.5 [4.0] ab
Soil warming	21.2 [1.4] b	0.85 [0.01] b	7.6 [0.2] a	50.9 [2.8] b
Soil + air warming	21.0 [1.7] ab	0.81 [0.01] ab	7.3 [0.3] a	47.2 [4.3] ab
<i>V. vitis-idaea</i>				
Control	21.8 [2.2] a	0.89 [0.01] a	8.8 [0.3] a	44.7 [4.2] a
Disturbance control	23.0 [2.0] a	0.88 [0.02] a	9.3 [0.3] a	47.2 [3.9] a
Soil warming	23.8 [1.4] ab	0.90 [0.01] a	9.2 [0.2] a	49.5 [3.3] a
Soil + air warming	30.2 [2.0] b	0.90 [0.01] a	11.6 [0.3] b	68.1 [4.4] b

Table 9. Organic C stores in high-latitude tundra ecosystems (kg C m^{-2}).

	Subarctic		Arctic	
	Dry dwarf shrub tundra ¹	Moist dwarf birch-willow ¹	Moist tussock tundra ^{2,3}	Wet sedge tundra ^{2,4}
Plant biomass	0.9	1.5	3.3	1.5
Soil organic matter	2.4	6.0	15.7	34.0
Total	3.3	7.5	19.0	35.5

¹Jonasson (1992).²plant biomass estimate from Shaver and Chapin (1991).³soil organic C estimate from McKane et al. (1997).⁴soil organic C estimate from Gersper et al. (1980).

net N mineralization rates in our study averaged from 4 to 6 kg N ha^{-1} , comparable to other estimates from subarctic ecosystems (Jonasson et al. 1993, Robinson et al. 1995). The absence of community change in our study suggests that high-dose fertilization studies, while shedding some insight into controls on plant communities over broad ranges of resource availability, are poor predictors of responses to even large climate changes. Even the most extreme climate predictions will not mineralize the N equivalent to that applied in these fertilization studies. Dramatic changes in community composition are more likely to occur where there are additional atmospheric N inputs (Werkman et al. 1996), but increased N mineralization rates alone will not increase N availability sufficiently to produce this response in subarctic tundra, at least in the short term. Atmospheric inputs to these remote ecosystems remain low (Kindbom et al. 1998).

Future changes in ecosystem C storage will be determined by the effect of warming on soil nutrient cycling, which controls plant growth and C accumulation (Shaver et al. 1992). Climate warming could alter C balances of arctic ecosystems (Oechel and Billings 1992). If warming stimulates soil respiratory losses of CO_2 more than net photosynthetic uptake, then arctic ecosystems may become a net source of atmospheric CO_2 (Billings et al. 1983, 1984, Grulke et al. 1990). Subarctic tundra soils store less organic C than other tundra ecosystems (Table 9), and thus represent a smaller potential source of CO_2 . In our study, short-term increases in soil nitrogen mineralization and plant growth indicate that increases in C storage are possible. Several years of greenhouse warming increased plant C and N storage in the subarctic dwarf shrub tundra (Jonasson et al. in press a, b). The absence of a shift in plant community composition toward more productive species (McKane et al. 1997) suggests that in the long term, subarctic ecosystems do not represent a large potential sink for atmospheric CO_2 .

To understand the response of this subarctic ecosystem to warming, we need to investigate the role of the

overstory trees (*Betula pubescens* ssp. *tortuosa*). The N economy of birch seedlings has been studied intensively (Weih 1998), but we do not know how successfully mature trees compete with the understory species for nutrients. If trees outcompete the dwarf shrubs for nutrients, there is a greater potential for C storage in vegetation in the long run because woody tissue has a higher C to N ratio than non-woody tissue (Rastetter et al. 1997).

Conclusions

Our results are consistent with past studies which show that warming accelerates plant growth and development and soil N cycling in subarctic heath (Jonasson et al. 1993, Wookey et al. 1993, Parsons et al. 1994). We observed 2–3-yr increases in aboveground biomass production and net N mineralization; however, longer-term studies are needed to detect the impact of experimental warming on these ecosystem processes, given the interannual variability in climate. Five years of 5°C soil warming treatment did not enhance N mineralization sufficiently to alter plant community composition, as suggested by fertilization studies (Jonasson 1992, Parsons et al. 1995), but species shifts may occur over a longer time scale.

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