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Response of nitrogen cycling to simulated climate change: differential responses along a subalpine ecotone

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Abstract

***In situ* nitrogen (N) transformations and N availability were examined over a four-year period in two soil microclimates (xeric and mesic) under a climate-warming treatment in a subalpine meadow/sagebrush scrub ecotone. Experimental plots that spanned the two soil microclimates were exposed to an *in situ* infrared (IR) climate change manipulation at the Rocky Mountain Biological Laboratory, near Crested Butte, Colorado. Although the two microclimates did not differ significantly in their rates of N transformations in the absence of heating, they differed significantly in their response to increased IR. Under a simulated warming in the sagebrush-dominated xeric microclimate, gross N mineralization rates doubled and immobilization rates increased by up to 60% over the first 2 years of the study but declined to pre-disturbance rates by the fourth year. This temporal pattern of gross mineralization rates correlated with a decline in SOM. Concurrently, rates of net mineralization rates in the heated plots were 60% higher than the controls after the first year. There were no differences in gross or net nitrification rates with heating in the xeric soils. In contrast to the xeric microclimate, there were no significant effects of heating on any N transformation rates in the mesic microclimate. The differing responses in N cycling rates of the two microclimate to the increased IR is most certainly the result of differences in initial soil moisture conditions and vegetation type and cover.**

Keywords: climate change, mineralization, nitrogen cycling, sagebrush steppe, soil microclimate, subalpine

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Introduction

The anticipated doubling of atmospheric CO_2 concentration and climatic changes that will accompany this doubling are expected to disproportionately affect high-altitude and high-latitude ecosystems (IPCC 1995). The associated warming is expected to induce changes in growing-season precipitation, growing-season length, and soil moisture (Mitchell *et al*. 1990; Maxwell 1992). The potential effects of climatic changes on these ecosystems have been discussed by a number of authors (Field *et al*. 1992; Chapin *et al*. 1993; Schimel *et al*. 1994; Chapin *et al*. 1996; Burke *et al*. 1997; Chapin & Starfield 1997; McKane *et al*. 1997). Litter decomposition, N turnover rates and nutrient availability can be influenced greatly by even small changes in soil temperature and moisture (Addiscott 1983; Lee *et al*. 1983; Binkley *et al*. 1994; Robinson *et al*. 1995). Indeed, one of the important primary effects of climate change will be the modification of litter decomposition and nutrient mineralization rates that control the availability of nutrients in a system (Nadelhoffer *et al*. 1991; Jonasson *et al*. 1993; Chapin *et al*. 1995; Chapin *et al*. 1996; Nadelhoffer 1997).

Because nutrient availability, particularly nitrogen (N) availability, is the primary limiting factor for plant productivity in most high-altitude and high-latitude ecosystems (Shaver & Chapin 1980; Marion *et al*. 1989), changes in temperature, season length, moisture availability, and CO_2 concentration will have an impact on primary production and species composition via nutrient availability changes (Van Cleve *et al*. 1983; Pastor *et al*. 1984; Giblin *et al*. 1991; Leadley & Reynolds 1992; Melillo *et al*. 1993; Burke *et al*. 1997). The subalpine ecotone

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supports a diverse assemblage of plant communities, the distribution and production of which is determined by a combination of climatic, topographic and biotic factors (Walker *et al*. 1993; Walker *et al*. 1994). Because N limits production in the subalpine ecosystem and therefore mediates species composition, any changes in rates or timing of N turnover will be important in determining species composition and plant community structure.

Very few studies have investigated N dynamics in subalpine ecosystems (O'Lear & Seastedt 1994; Fisk & Schimdt 1996; Fisk & Schmidt 1995; Brooks *et al*. 1997). For this reason, the timing, magnitude and controls on N availability in subalpine ecosystems are not well understood, making the assessment of the potential effects of climate change on N cycling difficult. This study seeks to characterize the timing and rate of N availability in a subalpine ecosystem, and to explain how the increased infrared radiation (IR) associated with a doubling of atmospheric CO_2 may influence rates of N transformations directly and indirectly. In particular, the purpose of this study is to ascertain whether and how gross and net rates of N transformations in a subalpine ecosystem: (i) are influenced by spatial and temporal changes in soil microclimate; (ii) are directly or indirectly altered by the increased infrared heating that will occur in a doubled CO_2 climate; and (iii) will feedback to global climate change.

Materials and methods

Study site

The study site was a subalpine ecotone located at the Rocky Mountain Biological Laboratory, 10 km north of Crested Butte, Colorado in Gunnison County (latitude 38°53′ N, longitude 107°02′ W, elevation 2920 m). The subalpine ecotone site lies at the upper elevational boundary of the Great Basin sagebrush desert scrub and supports plant species from both the sagebrush desert scrub and the subalpine meadow ecosystems. This study meadow is characterized primarily by vegetation consisting of long-lived perennial herbaceous plants and two woody shrubs. The meadow plant community is diverse and supports 85 species of forbs. All vegetation in the meadow senesces completely in the winter, except the sagebrush which maintains evergreen, overwintering leaves.

The soil at the study site is a well-drained, deep and rocky, noncalcareous glacial till generally classified as a subalpine cryoboroll soil (Wilson 1969; Erickson & Smith 1985). These soils, like most subalpine soils, develop in regions of heavy snowfall with short growing-seasons and under grass–shrub cover (Erickson & Smith 1985). The average bulk density of the soil to a depth of 10 cm is $0.40\ g\ cm^{-3}$ and the average pH is 6.3. The mineral horizon of the soil is uniform in texture and colour to 50 cm. Organic content averages approximately 10% at 5 cm below the litter layer and drops to 6% at 50 cm (Harte *et al*. 1995). Annual precipitation at the study site averages 700–750 mm, of which 80% falls as snow. The snow normally melts entirely by mid-May or the beginning of June. Rain falls in the summer months primarily as late afternoon showers in August.

Experimental design

Five control and five heated plots ($3\ m \times 10\ m$), containing vegetation characteristic of the meadow, were positioned along a ridge and down the length of a slope. A slight arc in the ridge caused a N–S gradient, with the southern most plot facing 88°E and the northernmost plot orientated at 126°E. Each of the 10 plots spanned an E–W gradient of soil moisture and vegetation, from an upper, xeric zone to a lower, moister zone (Harte *et al*. 1995; Fig. 1). The xeric zone (at the top of the ridge) was dry and rocky and the predominant vegetation was *Artemisia tridentata* ssp. *vaseyana*, *Festuca thurberi* Vasey (Poaceae), and a variety of herbaceous perennials, including *Delphinium nuttallianum* Pritzel (Helleboraceae), *Erigeron speciosus* de Candolle (Asteraceae) and *Helianthella quinquenervis* Gray (Asteraceae). Midway down the ridge the vegetation was characteristic of a transition between the xeric and mesic zones and contained species from both. In the lower mesic zone, the slope was flat and moisture levels were high relative to the xeric zone. This zone was characterized by the presence of herbaceous perennials such as *Erythronium grandiflorum* Pursh (Liliaceae), *Pontentilla gracilis* Douglas (Rosaceae), *Rhodiola integrifolia* Rafinesque (Crassulaceae), *Veratrum californicum* (Melanthiaceae), and the shrub, *Pentaphylloides floribunda* Löve (Rosaceae, formerly *Potentilla fruticosa*).

In each plot, two 1.6-m electric heaters (Kalgo, Inc.) were suspended 2.5 m above the soil surface using steel cables. These heaters were positioned above the plots in the centre of the xeric and mesic zones. The five heated plots were continuously (24 h/day, 365 days/year) infrared-irradiated (IR) at an intensity of $15\ W\ m^{-2}$ starting on 1 January 1991. On 24 May 1993, we added an additional heater centred above the transition zone and raised the IR output of all heaters to $22\ W\ m^{-2}$ to achieve a 1.5–2 °C average soil temperature increase. The heaters gave off no visible radiation (400–700 nm), while in the far red (700–800 nm) spectrum the downward flux was estimated to be 10^{-6} of solar input. The $22\ W\ m^{-2}$ of IR simulated the net surface warming as a consequence of both the direct effect of a doubling of CO_2 and the contribution of the major feedbacks. The additional flux

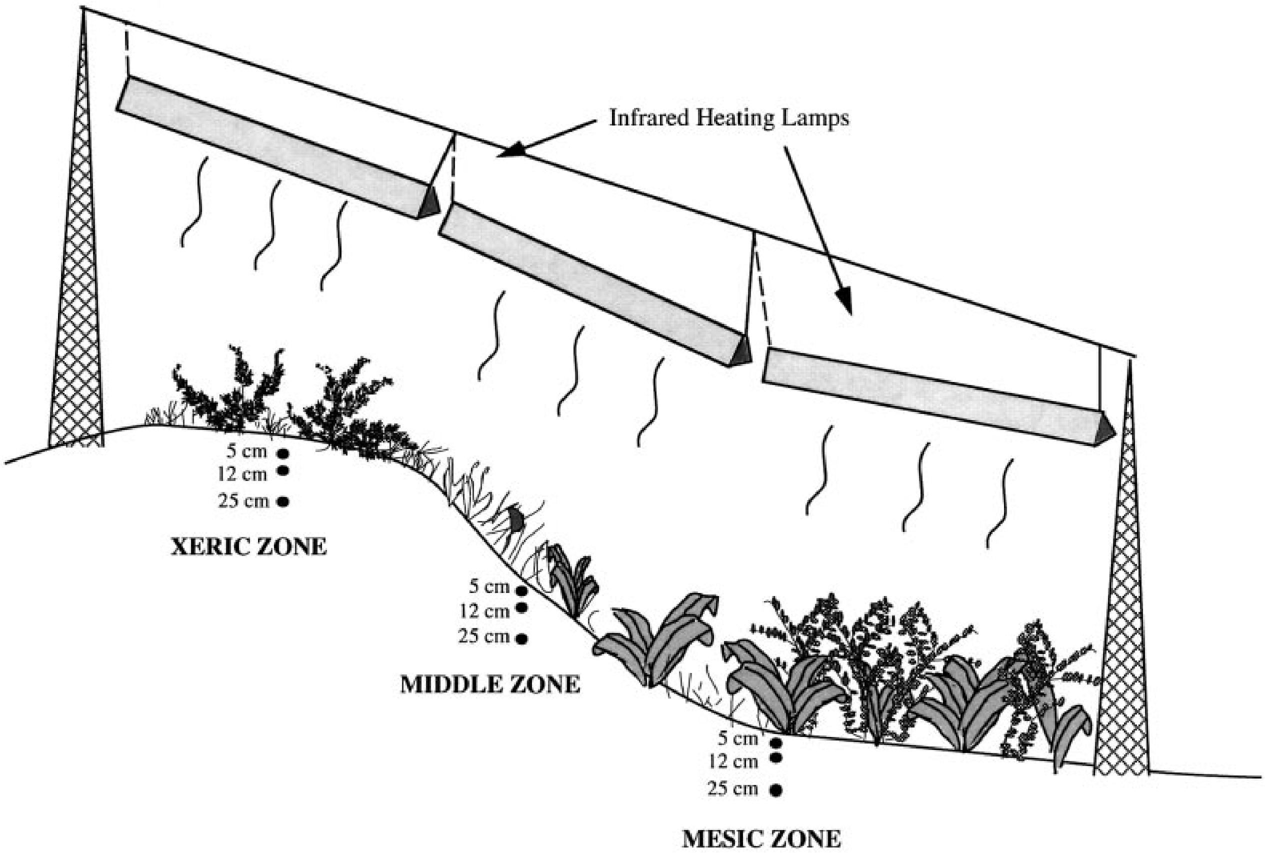

Fig. 1 Plot profile.

of $7\,W\,m^{-2}$ was intended to further compensate for the lack of convective warming.

Permanently placed thermocouples and calibrated gypsum blocks coupled to multiplexers and data loggers were installed in both control and heated plots to monitor changes in soil temperature and moisture every two hours throughout the year. Within each plot, each zone (xeric, transition and mesic) contained two probes (one soil and one moisture) at each of three depths (5 cm, 12 cm and 25 cm), for a total of nine moisture and nine temperature probes in each plot.

Nitrogen transformations

Gross rates of mineralization and nitrification and NH_4^+ and NO_3^- immobilization (Fig. 2) were measured using a 24-h incubation of an intact soil core as described by Davidson *et al*. 1991. We measured gross N transformation rates twice within the growing season (June and August) in three years (1991, 1992 and 1994) in two moisture zones (xeric and mesic). For each measurement, we placed four small carbon steel cylinders (4 cm diameter × 9 cm deep) inside four larger steel cylinders (8 cm diameter × 9 cm deep) and hammered each into the

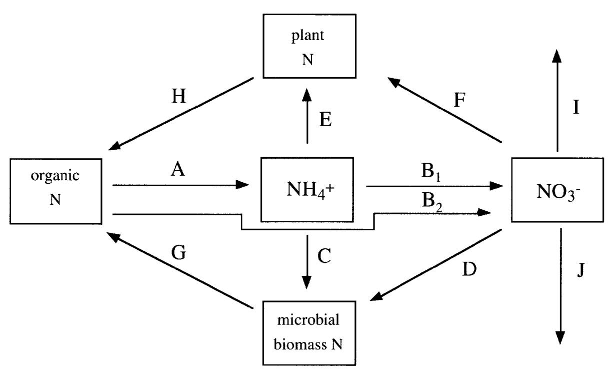

Fig. 2 Diagram of N cycle including relevant transformations, A = gross mineralization; B1 and B2 = gross nitrification with NH_4^+ and organic-N as the substrates, respectively; C and D = gross immobilization (microbial assimilation) of NH_4^+ and NO_3^-, respectively; E and F = plant uptake of NH_4^+ and NO_3^-, respectively; G and H = organic N inputs from microorganisms and plants, respectively; I = denitrification; J = NO_3^- leaching. *Indicates processes not measured in this study. Net N mineralization measured by ion-exchange resin cores = [(A + B1) – (C + D)]. Net nitrification measured by the same method = [(B1 + B2) – D)].

ground so that each pair formed concentric circles. To control for spatial heterogeneity in N transformation rates as a function of distance from shrub canopy (Burke *et al*. 1989; Halvorson *et al*. 1994; Smith *et al*. 1994), the cores were placed within 10 cm of a shrub's canopy. All four cores (8 cylinders) were removed immediately and the soil between the inner and outer cylinder of each core was mixed and immediately subsampled for extraction in 2 m KCl. These samples gave initial ambient ^{14}N concentrations and were the uninjected, T_0 sample. Twenty grams of the remaining between-core soil was analysed for gravimetric moisture determination by drying it at 105 °C for 24 h.

Six 1-mL injections were then made with an 18-gauge side-port needle into the remaining cylinders. We injected two out of the four cylinders with 0.67 mm $(^{15}NH_4)_2SO_4$ and two with 0.25 mm $K^{15}NO_3$ (30 mgN L^{-1} and 99% ^{15}N enrichment). Immediately after adding the^{15}N label, we retrieved one NH_4^+ cylinder and one NO_3^-cylinder, mixed the soils well and subsampled (approximately 20 g of field moist soil) for extraction in 100 mL of 2 m KCl, for estimation of initial ^{15}N concentrations. We then returned the remaining soil cores to their original orientation and position in the soil for a 24-h incubation. After 24 hours, we extracted the soil in the cylinders. These samples gave the postincubation $^{14+15}N$ samples. The KCl extracts of soil were shaken for one hour, filtered (Whatman no. 1) and analysed using a Lachat flow-injection autoanalyser (QuikChem 1986, 1987). Ammonium was determined by the indophenol blue method and nitrate by diazotization following cadmium reduction (Keeney & Nelson 1982).

N-15 diffusion procedures, modified from Brooks *et al.* (1989), were used to prepare samples for $^{15}NH_4^+$ and $^{15}NO_3^-$ analysis. The samples were allowed to diffuse for six days at room temperature and were stirred daily with the microstir bar. We analysed the acidified filters for total N and ^{15}N on the filters using an automated nitrogen and carbon isotope mass spectrometer (ANCA-IRMS, Europa Scientific Ltd, Crewe, England).

The isotope dilution calculations of Kirkham & Bartholomew (1954) were followed for rate calculations:

$$m = \frac{M_0 - M_1}{t} \times \frac{\log (H_0M_1/H_1M_0)}{\log (M_0/M_1)} \quad (1)$$

$$c = \frac{M_0 - M_1}{t} \times \frac{\log (H_0/H_1)}{\log (M_0/M_1)} \quad (2)$$

where M_0 = initial $^{14+15}N$ pool (µg N g^{-1} dry soil), M_1 = postincubation $^{14+15}N$ pool (µg N g^{-1} dry soil), H_0 = initial ^{15}N pool (µg N g^{-1} dry soil), H_1 = postincubation ^{15}N pool (µg N g^{-1} dry soil), m = production rate (µg N g^{-1} soil day – 1), c = consumption rate (µg N g^{-1} soil day – 1) and t = time (1 day or 24 h)

Net nitrogen transformations

Net N transformation rates in the field were determined using the ion exchange resin core method with intact soil cores (Binkley & Matson 1983; Binkley 1984; DiStefano & Gholz 1986; Hart & Gunther 1989). Four soil cores (8 cm × 9 cm) were extracted with PVC pipe in each zone (xeric and mesic) in each plot. We subsampled one soil core from each zone for initial N concentrations. We placed 7.8 g oven-dry mixed-bed resins (J T Baker M-614) between two 20-mm mesh squares and flattened against the soil core on each end using plastic rims. Then the core was placed in its original hole and its overlying organic layer replaced on top. After one year, the cores were retrieved for analysis. We extracted the resins and 20 g of field moist soil samples from each core in 100 mL of 2 m KCl, prior to calculating net mineralization, net nitrification, net ammonification and N mobilization from the surface using the method described in DiStefano & Gholz 1986). All results were converted from an oven-dry soil weight to a hectare basis by multiplying the values by the mean bulk density to a depth of 10 cm (oven-dry mass of the < 4 mm soil fraction per core volume) of all the cores taken within the respective site.

All KCl extracts of soil and resin were shaken for one hour on a mechanical shaker, filtered (Whatman 1) and analysed using a Lachat flow-injection autoanalyser as described above. The filter paper was preleached with 50 mL of 2 m KCl to remove any NH_4^+ and NO_3^- initially present in the filter paper. Ammonium was determined using the indophenol blue method (Keeney & Nelson 1982; QuikChem 1986, 1987).

Mean residence time (MRT) was calculated for each incubation by dividing the total inorganic N pool by the gross N transformation rate.

Statistical analyses

The statistical analysis was designed to first characterize the site by testing whether broad-scale spatial and temporal changes in soil temperature and moisture (interzonally only the data from the control plots were utilized). For the first analysis, to determine the influence of variations in soil temperature and moisture on gross N transformation rates, a three-way analysis of covariance (ancova) was performed with year (1991, 1992 and 1994), zone (xeric and mesic) and season [early (June) and late (August)] as categorical variables and soil temperature and moisture as the independent covariates on all control data combined. the influence of variations in soil temperature and moisture on net N transformation rates were determined by performing a two-way analysis of covariance (ancova) with year (1991, 1992 and 1994) and zone (xeric and mesic) as categorical variables and soil temperature and moisture as the independent covariates on all control data combined.

The second part of the analysis was divided into three to determine how increased IR influenced the spatial and temporal patterns of N transformation rates: (1) an analysis combining years and zones; (2) an analysis by year within each zone; and (3) an analysis by season within each zone for each year. These analyses are described in detail in the following paragraphs:

1 Heating treatment across years and zones This analysis utilized a four-way analysis of covariance (ancova) with year (1991, 1992 and 1994), zone (xeric and mesic), season [early (June) and late (August)] and treatment (heated and control) as categorical variables and soil temperature and moisture as the independent covariates was performed on all data combined. In order to determine the influence of variations in soil temperature and moisture on net N transformation rates, a three-way analysis of covariance (ancova) with year (1991, 1992 and 1994), zone (xeric and mesic) and treatment (heated and control) as categorical variables and soil temperature and moisture as the independent covariates was performed on all data combined.

2 Heating treatment by year within each zone To further identify the factors important in influencing N transformation rates within a zone, a two-way ancova was performed for the gross N transformations with treatment and time of season (June and August) as the categorical variables and plot number as the independent covariate for each year separately. A one-way ancova was also performed for net transformations with treatment as the categorical variable and plot number as a covariate, again keeping zone and year separate. The plot-number covariate is used as an alternative to snowmelt date. The results are confounded by using snowmelt date as the covariate because snowmelt date has previously been found to be significantly dependent on treatment (Harte *et al*. 1995). The melt date is observed to progress from the higher number plots to the lower number plots within each treatment group as a result ofto the orientation of the plots. For this reason, plot number is used as a surrogate covariate for snowmelt date in the absence of heating.

3 Analysis of the heating treatment by season within each zone To determine how the treatment effect might have differed from season to season within a zone, a two-way ancova was performed for the both gross and net N transformations with treatment and year as the categorical variables and plot number as the independent covariate. Each season was analysed separately.

Regression analyses were performed for each N transformation rate across all years and zones to determine which variables provide the most explanatory power. Factors included in the analysis were year, zone, treatment, time of season, soil temperature and soil moisture, date of snowmelt, soil organic matter content, soil ammonium concentration and soil nitrate concentration.

All statistical analyses were performed using systat 5.2.1 (SYSTAT 1992).

Results

Soil chemical properties

The total N content was consistently higher in the xeric zone relative to the mesic zone in June and August in all three years, and the total N content in the soils increased from June to August across all years (Table 1). The soils in the heated plots generally had more total N than the controls across the growing season, years and zones.

The carbon content of the soil did not differ significantly between heated and control plots in 1991 and 1992, but declined in heated plots relative to controls in 1994 (Table 1). The two zones were similar in total C content. Soil organic matter declined from June to August in each year of the study, and declined in the heated plots relative to the controls in 1994. Organic matter content was higher in the mesic zone compared to the xeric (anova, $F = 5.39$; $P = 0.022$).

Soil microclimate

The soil microclimate was influenced significantly by the heating treatment during the snowmelt and the growing-season. The snowmelt date (defined as the date after completion of the snow melt when the soil temperature at 5 cm reaches +1 °C) was advanced by heating by an average of 11 days in the xeric and mesic zones over the four-year period between 1991 and 1994 (Harte *et al*. 1995). The date of snowmelt has been shown to be significantly dependent on treatment (heated or control), as well as on zone (xeric or mesic) and on plot number (1–10) (Harte *et al*. 1995). Both soil moisture and temperature depended significantly on treatment during the period of snowmelt (Harte *et al*. 1995). The largest temperature difference between the control and heated plots occurred during the period of snowmelt. During this time, the average soil temperature of the heated treatment was 5 °C higher than that of the controls and daily averaged soil-temperature differences between adjacent control and treatment plots was as high as 12 °C (Harte *et al*. 1995). During snowmelt, moisture levels remained at field capacity (48% of dry soil mass)

Table 1 Chemical properties of the soil organic matter. Values are means of five replicates ± 1 SE. Soil samples were taken from the > 2 mm fraction for C, N, and C:N. The < 2 mm fraction used for percentage OM determinations. * Indicates samples not collected

Zone	Year	Month	Treatment	% C		% N		% OM		C:N	
Xeric	1991	June	control	5.737	(0.79)	0.476	(0.16)	*	*	12.105	(0.42)
			heated	6.153	(0.37)	0.530	(0.04)	*	*	12.229	(0.25)
		August	control	7.744	(1.97)	0.674	(0.16)	*	*	11.276	(0.21)
			heated	7.187	(1.00)	0.620	(0.08)	*	*	11.509	(0.16)
	1992	June	control	7.389	(1.22)	0.623	(0.09)	11.580	(1.02)	11.813	(0.11)
			heated	5.844	(0.81)	0.495	(0.07)	12.440	(1.42)	11.796	(0.30)
		August	control	7.870	(0.62)	0.693	(0.06)	14.180	(1.70)	11.359	(0.20)
			heated	5.931	(0.88)	0.516	(0.07)	13.625	(2.07)	11.504	(0.26)
	1994	June	control	6.158	(0.63)	0.481	(0.04)	11.518	(1.73)	12.802	(0.28)
			heated	4.321	(0.25)	0.527	(0.07)	7.272	(0.25)	8.199	(0.33)
		August	control	6.641	(0.26)	0.575	(0.04)	9.250	(1.87)	11.550	(0.17)
			heated	3.915	(0.84)	0.621	(0.03)	5.964	(0.31)	6.304	(0.34)
Mesic	1991	June	control	3.881	(1.02)	0.299	(0.07)	*	*	12.980	(0.54)
			heated	4.800	(0.81)	0.387	(0.06)	*	*	12.403	(0.31)
		August	control	5.845	(0.26)	0.544	(0.03)	*	*	10.744	(0.15)
			heated	6.826	(0.46)	0.616	(0.04)	*	*	11.081	(0.05)
	1992	June	control	4.719	(0.39)	0.430	(0.02)	12.500	(1.16)	10.974	(0.31)
			heated	5.217	(0.96)	0.477	(0.08)	12.260	(1.02)	10.937	(0.22)
		August	control	5.287	(0.34)	0.466	(0.02)	14.660	(3.22)	11.336	(0.36)
			heated	5.878	(0.28)	0.538	(0.02)	14.875	(4.15)	10.922	(0.14)
	1994	June	control	4.958	(0.25)	0.415	(0.04)	8.932	(0.82)	11.947	(0.38)
			heated	5.134	(0.44)	0.422	(0.06)	9.982	(0.91)	12.166	(0.19)
		August	control	5.285	(0.37)	0.461	(0.13)	8.284	(1.04)	11.464	(0.08)
			heated	5.661	(0.92)	0.474	(0.03)	8.008	(1.07)	11.943	(0.23)

Table 2 Extractable NH_4^+-N and NO_3^- -N in the soil 10 days after snowmelt. Values are means ± 1 SE, $n = 5$

		June				August			
		µgNH_4^--N g^{-1} day–1		µgNO_3^- -N/g^{-1} day–1		µgNH_4^+-N/g^{-1} day–1		µgNO_3^--N g^{-1} day–1	
Xeric Zone									
1991	control	10.20	(2.54)	0.16	(0.05)	9.313	(3.74)	0.45	(0.11)
	heated	14.36	(5.31)	0.08	(0.03)	7.797	(2.20)	1.32	(0.58)
1992	control	18.93	(3.46)	0.83	(0.36)	7.132	(1.95)	0.47	(0.11)
	heated	16.17	(2.52)	0.66	(0.18)	6.262	(1.44)	0.46	(0.12)
1994	control	5.02	(1.21)	6.62	(1.92)	9.874	(3.56)	2.34	(0.57)
	heated	3.82	(1.64)	4.87	(1.11)	8.034	(3.03)	0.97	(0.32)
Mesic Zone									
1991	control	8.81	(2.31)	0.37	(0.13)	4.760	(1.68)	0.38	(0.15)
	heated	9.78	(3.67)	0.46	(0.22)	12.770	(5.40)	0.37	(0.20)
1992	control	20.27	(3.87)	0.61	(0.32)	6.079	(0.69)	0.54	(0.13)
	heated	19.30	(2.76)	0.63	(0.22)	7.998	(3.26)	0.26	(0.04)
1994	control	9.06	(3.66)	3.67	(0.93)	5.213	(1.69)	2.78	(0.67)
	heated	12.57	(7.29)	4.65	(0.66)	7.954	(1.69)	1.42	(0.44)

until temperature increases caused substantial evaporative loss.

During the growing season, the period from snowmelt to late August, the effect of the heating treatment on soil temperature and moisture was significant but less dramatic. The treatment- and depth-averaged temperatures were 1.2 °C higher in treatment plots relative to the controls in the xeric zone. In the mesic zone, no such

Table 3 Gross and net mineralization rates in treatment plots in two soil microclimates. Values are means of five replicates ± 1 SE for 1992 and 1994, $n = 3$ for 1991. Units are mg NH_4^+-N g^{-1} dry soil day–1. 'Days' refers to the number of days between the average snowmelt date for the treatment and the date of the gross N transformation incubation. Net/gross ratios are seasonally averaged (net min. divided the average of August and June gross rates)

					Gross rates					Net mineralization			
Zone	Year	Month	Treatment	days	Gross Miner.		NH_4^+ cons		Immob.	Net/gross min		Gross imm/ Gross min	
Xeric	1991	June	control	23	7.68	(1.25)	7.29	(2.59)	5.28	0.41	(0.09)	0.10	0.69
			heated	27	17.19	(6.47)	9.20	(5.11)	7.33	0.83	(0.17)	0.08	0.43
		August	control	86	0.63	(0.39)	3.79	(3.48)	3.51				5.62
			heated	90	2.97	(1.53)	0.78	(0.33)	0.15				0.05
	1992	June	control	38	7.55	(2.44)	11.24	(2.05)	10.05	0.69	(0.17)	0.12	1.33
			heated	44	15.80	(3.43)	17.46	(4.24)	16.14	1.16	(0.27)	0.12	1.02
		August	control	106	3.66	(1.64)	4.18	(1.67)	3.27				0.89
			heated	112	2.86	(0.45)	4.70	(1.12)	3.04				1.06
	1994	June	control	42	3.27	(1.04)	2.57	(0.48)	0.58	0.28	(0.04)	0.06	0.18
			heated	53	1.48	(0.43)	1.85	(0.43)	0.07	0.45	(0.04)	0.17	0.05
		August	control	96	6.54	(2.08)	5.15	(0.97)	4.27				0.65
			heated	107	3.75	(1.51)	2.96	(0.96)	1.63				0.43
Mesic	1991	June	control	16	7.08	(2.26)	5.27	(2.88)	3.90	0.60	(0.14)	0.15	0.55
			heated	26	9.06	(2.58)	9.01	(3.31)	5.78	0.58	(0.03)	0.11	0.64
		August	control	79	1.11	(0.57)	2.40	(1.82)	1.92				1.73
			heated	89	1.09	(0.39)	1.31	(0.47)	1.07				0.99
	1992	June	control	37	6.46	(3.42)	5.90	(3.13)	3.50	0.57	(0.21)	0.14	0.54
			heated	43	14.61	(2.34)	18.79	(1.98)	16.76	0.68	(0.21)	0.08	1.15
		August	control	105	1.84	(0.43)	3.50	(0.70)	2.78				1.51
			heated	111	2.06	(1.00)	2.92	(1.63)	2.39				1.16
	1994	June	control	38	5.68	(3.10)	9.85	(7.49)	7.00	0.47	(0.07)	0.12	1.23
			heated	45	3.75	(3.10)	5.02	(4.28)	2.49	0.35	(0.07)	0.13	0.66
		August	control	92	2.40	(0.46)	1.43	(0.53)	0.53				0.22
			heated	99	1.66	(0.44)	1.71	(0.57)	0.58				0.35

difference existed. The treatment- and depth-averaged moistures were 10 and 20% in treatment plots relative to the control in the xeric and mesic zones, respectively.

Nitrogen cycling in absence of heating treatment

Inorganic N pool sizes. There were no significant differences between the inorganic N concentrations in the xeric and mesic zones at any time (anova, $F = 0.02$, $P = 0.883$; Table 2). The NH_4^+-N concentration was greatest at snowmelt and declined thereafter with the exception of spikes associated with rain events during the growing season. The NO_3^--N concentration was always low and did not change dramatically through the growing season or with rain events (anova, $F = 5.74$, $P = 0.004$; Table 2).

There were significant changes in the pools of NH_4^+-N and NO_3^--N (anova, $F = 32.73$, $P < 0.001$) from year to year. In the xeric zone, early in the growing season, the NH_4^+-N pools were high in 1991 and 1992 but were significantly lower in 1994 (anova, $F = 7.28$, $P = 0.002$; Table 2). The opposite was true of the NO_3^--N pools in the xeric zones, which were dramatically higher in 1994 than in either earlier year (anova, $F = 17.11$, $P < 0.001$). Late in the growing season in the xeric zone, no such year-to-year variation existed for either ammonium or nitrate. The mesic zone NH_4^+-N pools were not significantly different across years (anova, $F = 1.15$, $P = 0.325$), but the NO_3^--N pools were higher in 1994 in both the late and early seasons ($F = 14.90$, $P < 0.001$; Table 2).

N transformation rates

Mineralization. Gross mineralization rates did not differ significantly across the spatial gradients or from year to year (Table 3). Gross mineralization rates did not differ seasonally; early growing-season rates were higher than late growing-season rates (Table 3).

Net mineralization rates in the controls were generally higher in the mesic zone relative to the xeric zone, although the difference was not significant ($F = 2.96$, $P = 0.10$). Year and soil moisture were statistically significant factors for rates of net mineralization (Table 3, $P = 0.05$), but not for gross mineralization. Net rates were much higher in 1991 and 1992 than in 1994

Table 4 Coefficients of correlation (r) among pool sizes and rates. Plot means for each variable were calculated for each date and a correlation matrix was generated. Bonferroni probabilities: *Significant at $P < 0.05$; **significant at $P < 0.01$

	NO_3^-	Net min	Net nit	Gross min	Gross nit	Gross imm	Melt date	SOC
NH_4^+	−0.25	0.18	0.38*	0.39*	0.07	0.44*	−0.26	−0.08
NO_3^-		−0.38*	−0.31	−0.15	0.06	−0.25	0.23	−0.21
Net mineralization			0.85**	0.33*	−0.20	0.43*	−0.62**	−0.06
Net nitrification				0.32	−0.10	0.39*	−0.50**	0.16
Gross mineralization					−0.01	0.91**	−0.29	0.13
Gross nitrification						−0.25	0.28	−0.02
Gross immobilization							−0.45**	−0.02
Melt date								0.37**

Table 5 Gross and net nitrification rates in treatment plots in two soil microclimates. Values are means of five replicates ± 1 se for 1992 and 1994, $n = 3$ for 1991. Units are mg NO_3^--N g^{-1} dry soil day^{-1}. 'Days' refers to the number of days between the average snowmelt date for the treatment and the date of the gross N transformation incubation. Net/gross ratios are seasonally averaged (net min. divided the average of August and June gross rates)

					Gross rates								
Zone	Year	Month	Treatment	days	Gross nitr.		NO_3^- cons		Net Nitrification		Net/gross nitr.	Gross nitr./ Gross min.	Net nitr./ Net min
Xeric	1991	June	control	23	2.01	(0.21)	1.75	(0.03)	1.35	(0.22)	1.18	0.26	13.85
			heated	27	1.88	(0.03)	1.88	(0.08)	1.82	(0.41)	1.45	0.11	22.05
		August	control	86	0.28	(0.04)	0.22	(0.10)				0.45	
			heated	90	0.64	(0.27)	1.92	(0.94)				0.21	
	1992	June	control	38	1.19	(0.43)	1.40	(0.27)	2.07	(0.28)	1.97	0.16	16.81
			heated	44	1.32	(0.46)	1.31	(0.57)	2.11	(0.42)	1.41	0.08	16.99
		August	control	106	0.91	(0.26)	0.84	(0.27)				0.25	
			heated	112	1.66	(0.65)	2.44	(0.74)				0.58	
	1994	June	control	42	2.00	(0.38)	3.20	(0.96)	0.93	(0.23)	0.65	0.61	16.46
			heated	53	1.78	(0.87)	3.63	(1.57)	0.52	(0.10)	0.34	1.20	3.03
		August	control	96	0.88	(0.44)	0.70	(0.51)				0.13	
			heated	107	1.34	(0.57)	1.97	(0.05)				0.36	
Mesic	1991	June	control	16	1.38	(0.58)	4.02	(1.70)	1.31	(0.41)	1.42	0.19	8.90
			heated	26	3.24	(2.81)	4.58	(4.16)	1.14	(0.07)	0.66	0.36	9.93
		August	control	79	0.48	(0.22)	1.01	(0.16)				0.43	
			heated	89	0.23	(0.18)	0.53	(0.13)				0.21	
	1992	June	control	37	2.41	(0.61)	2.58	(0.52)	1.41	(0.37)	0.90	0.37	10.34
			heated	43	2.03	(1.24)	3.14	(2.18)	1.43	(0.38)	1.12	0.14	17.58
		August	control	105	0.72	(0.26)	1.13	(0.37)				0.39	
			heated	111	0.53	(0.30)	2.47	(1.26)				0.26	
	1994	June	control	38	2.85	(1.30)	4.78	(2.75)	1.07	(0.16)	0.57	0.50	9.25
			heated	45	2.52	(0.72)	3.90	(9.26)	0.93	(0.25)	0.51	0.67	7.14
		August	control	92	0.90	(0.34)	1.91	(0.52)				0.37	
			heated	99	1.13	(0.45)	1.21	(0.79)				0.68	

(mean = 0.75, 0.89, and 0.18 μg N-NH_4^+ g^{-1} dry soil day^{-1}, respectively) and were accompanied by higher soil temperatures overall, independent of heating treatment.

Net and gross rates of N mineralization were weakly correlated (Table 4, $r = 0.36$, $P = 0.06$). The seasonally averaged ratio of net to gross mineralization rates was lower in the xeric zone than the mesic zone (Table 3). In the xeric zone, this ratio declined in the 1994 relative to 1991 and 1992 (Table 3).

The NH_4^+-N pool size was weakly correlated with gross mineralization (Table 4, Pearson correlation, $r = 0.39$, $P < 0.05$). The NO_3^--N pool was weakly correlated with net mineralization (Table 4, Pearson correlation, $r = 0.38$, $P < 0.05$).

Table 6 Factors affecting net N transformation rates including the influence of the heating treatment. F-statistics$_{df}$ from three-way ancova with year, zone and treatment as categorical variables and soil temperature and moisture as the independent covariates. Interaction term not shown unless significant ($P < 0.05$)

	Net mineralization			Net nitrification		
	F ratio d.f.)	P	R^2	F ratio (d.f.)	P	R^2
Year	$6.02_{2,38}$	**0.01**	0.45	$5.48_{2,38}$	**0.01**	0.51
Zone	$0.30_{1,38}$	0.58		$0.46_{1,38}$	0.50	
Treatment	$1.01_{1,38}$	0.32		$0.04_{1,38}$	0.84	
Temperature	$0.03_{1,38}$	0.87		$3.04_{1,38}$	0.09	
Moisture	$3.88_{1,38}$	**0.05**		$3.68_{1,38}$	**0.06**	

Nitrification. Gross nitrification rates were not significantly different between zones, seasons, or years (Table 5). Like gross mineralization, early growing-season nitrification rates were generally higher than the late season rates, but the difference was not statistically significant ($F = 2.70$, $P = 0.111$; Table 5).

The rates of net nitrification were statistically different among years but not among seasons or zones. Rates were higher in 1991 and 1992 than in 1994 (1.65, 1.87, and 0.61 μg N-NO_3^- g^{-1} dry soil day–1, respectively) although the differences were not significant (Tables 3 and 6).

Gross nitrification rates were not correlated with any of the other measured rates (Table 4). In contrast to what others have found, ammonium concentrations were not correlated with net nitrification rates ($r = 0.20$, $P = 0.33$). The seasonally averaged ratio of net to gross nitrification rates in the absence of heating declined in both zones from 1991 to 1994 (Table 5). In 1991 and 1992, the ratio was near or above one (Table 5).

Table 7 Factors affecting gross N transformation rates by zone and year. F-statisticsdf from two-way ancova with treatment (heated or control) and time of season (June or August) as categorical variables and plot number as the independent covariate. Plot number is used as a surrogate for snowmelt date and/or length of growing season. See Methods for complete explanation. Significant values ($P < 0.05$) shown in bold

			Gross mineralization			Gross nitrification			Gross immobilization			NO_{3}- consumption		
Zone	Year	Source	F d.f.	P	R^2	F d.f.	P	R^2	F d.f.	P	R^2	F d.f.	P	R^2
Xeric	1991	Treatment	$1.89_{1,7}$	0.21	0.77	$1.3_{1,8}$	0.29	0.60	$0.93_{1,6}$	0.41	0.93	$0.08_{1,4}$	0.80	0.55
		Time of season	$13.60_{1,7}$	**0.01**		$7.08_{1,8}$	**0.03**		$19.71_{1,6}$	**0.02**		$0.01_{1,4}$	0.95	
		Treatment*time of season	$1.54_{1,7}$	0.25		$0.25_{1,8}$	0.63		$6.89_{1,6}$	0.08		$0.25_{1,4}$	0.67	
		Plot number	$4.04_{1,7}$	0.08		$9.45_{1,8}$	**0.02**		$3.46_{1,6}$	0.16		$0.57_{1,4}$	0.53	
	1992	Treatment	$7.67_{1,15}$	**0.01**	0.68	$0.47_{1,13}$	0.51	0.11	$8.10_{1,13}$	**0.01**	0.71	$1.73_{1,12}$	0.21	0.27
		Time of season	$14.80_{1,15}$	**< 0.01**		$<0.01_{1,13}$	0.94		$15.57_{1,13}$	**<0.01**		$0.27_{1,12}$	0.62	
		Treatment*time of season	$9.79_{1,15}$	**0.01**		$0.25_{1,13}$	0.63		$5.11_{1,13}$	**0.04**		$2.31_{1,12}$	0.15	
		Plot number	$0.30_{1,15}$	0.59		$0.57_{1,13}$	0.47		$0.62_{1,13}$	0.44		$0.01_{1,12}$	0.94	
	1994	Treatment	$0.48_{1,14}$	0.50	0.17	$0.55_{1,11}$	0.47	0.25	$0.52_{1,9}$	0.49	0.06	$0.56_{1,9}$	0.48	0.33
		Time of season	$1.15_{1,14}$	0.30		$2.47_{1,11}$	0.14		$0.08_{1,9}$	0.79		$2.69_{1,9}$	0.14	
		Treatment*time of season	$0.98_{1,14}$	0.34		$0.45_{1,11}$	0.52		$0.01_{1,9}$	0.92		$0.12_{1,9}$	0.73	
		Plot number	$0.29_{1,14}$	0.60		$1.94_{1,11}$	0.19		$0.17_{1,9}$	0.69		$0.03_{1,9}$	0.88	
Mesic	1991	Treatment	$0.45_{1,6}$	0.53	0.67	$1.44_{1,6}$	0.27	0.47	$0.05_{1,4}$	0.84	0.28	$0.06_{1,4}$	0.81	0.23
		Time of season	$10.34_{1,6}$	**0.02**		$1.12_{1,6}$	0.33		$1.47_{1,4}$	0.29		$0.97_{1,4}$	0.38	
		Treatment*time of season	$0.15_{1,6}$	0.71		$0.20_{1,6}$	0.67		$0.10_{1,4}$	0.77		$<0.01_{1,4}$	0.97	
		Plot number	$0.32_{1,6}$	0.59		$2.66_{1,6}$	0.15		$0.12_{1,4}$	0.75		$0.32_{1,4}$	0.60	
	1992	Treatment	$5.29_{1,15}$	**0.04**	0.65	$3.63_{1,13}$	0.99	0.24	$10.42_{1,12}$	**0.01**	0.77	$2.21_{1,9}$	0.17	0.36
		Time of season	$16.66_{1,15}$	**< 0.01**		$0.13_{1,13}$	0.08		$14.87_{1,12}$	**<0.01**		$0.01_{1,9}$	0.94	
		Treatment*time of season	$5.11_{1,15}$	0.04		$0.21_{1,13}$	0.72		$13.82_{1,12}$	**<0.01**		$0.23_{1,9}$	0.64	
		Plot number	$0.03_{1,15}$	0.87		$<0.01_{1,13}$	0.65		$< 0.01_{1,12}$	0.99		$3.44_{1,9}$	0.10	
	1994	Treatment	$1.30_{1,14}$	0.27	0.46	$0.21_{1,13}$	0.66	0.28	$1.05_{1,13}$	0.33	0.36	$0.75_{1,11}$	0.40	0.29
		Time of season	$2.81_{1,14}$	0.12		$3.69_{1,13}$	0.08		$0.13_{1,13}$	0.73		$2.27_{1,11}$	0.16	
		Treatment*time of season	$0.05_{1,14}$	0.83		$0.01_{1,13}$	0.92		$0.01_{1,13}$	0.97		$0.12_{1,11}$	0.73	
		Plot number	$8.42_{1,14}$	**0.01**		$1.25_{1,13}$	0.28		$3.61_{1,13}$	0.09		$1.11_{1,11}$	0.31	

Table 8 Factors affecting gross N transformation rates including the influence of the heating treatment. F-statistics$_{df}$ from three-way ancova with year, zone and treatment as categorical variables and soil temperature and moisture as the independent covariates. Interaction term not shown unless significant ($P < 0.050$)

	Gross mineralization			Gross nitrification			Gross immobilization			Gross NO_3^- consumption		
Source	$F_{d.f.}$	P	R^2	$F_{d.f.}$	P	R^2	$F_{d.f.}$	P	R^2	$F_{d.f.}$	P	R^2
Year	$1.69_{2,75}$	0.19	0.60	$0.08_{2,64}$	0.93	0.25	$0.23_{2,54}$	0.23	0.64	$0.92_{2,49}$	0.40	0.28
Zone	$0.18_{1,75}$	0.67		$0.42_{1,64}$	0.52		$0.38_{1,54}$	0.54		$0.02_{1,49}$	0.89	
Treatment	$3.67_{1,75}$	**0.05**		$0.13_{1,64}$	0.72		$3.81_{1,54}$	**0.05**		$1.14_{1,49}$	0.29	
Season	$32.40_{1,75}$	**<0.01**		$7.56_{1,64}$	**0.01**		$10.48_{1,54}$	**0.00**		$1.36_{1,49}$	0.25	
Year*treatment	$5.92_{2,75}$	**<0.01**		$0.08_{2,64}$	0.93		$5.17_{2,54}$	**0.01**		$0.10_{2,49}$	0.91	
Year*season	$4.47_{2,75}$	**0.01**		$0.15_{2,64}$	0.87		$0.93_{2,54}$	0.40		$1.14_{2,49}$	0.33	
Treatment*season	$6.41_{1,75}$	**0.01**		$0.04_{1,64}$	0.85		$7.79_{1,54}$	**0.01**		$0.38_{1,49}$	0.54	
Year*treatment*season	$5.75_{2,75}$	**<0.01**		$0.34_{2,64}$	0.72		$5.37_{2,54}$	**0.01**		$0.10_{2,49}$	0.91	
Zone*treatment*season	$0.33_{1,75}$	0.57		$0.35_{1,64}$	0.56		$0.84_{1,54}$	0.36		$0.21_{1,49}$	0.65	
Temperature	$10.19_{1,75}$	**<0.01**		$0.23_{1,64}$	0.63		$26.00_{1,54}$	**<0.01**		$0.52_{1,49}$	0.47	
Moisture	$0.87_{1,75}$	0.35		$0.09_{1,64}$	0.76		$0.84_{1,54}$	0.36		$0.64_{1,49}$	0.43	

Immobilization. Gross N immobilization rates were significantly different between zones, seasons and years (Tables 3 and 4). Gross N immobilization was significantly greater in the xeric zone compared to the mesic zone across all years (Tables 3 and 5). This is primarily the result of higher transformation rates in the xeric zone in the beginning of the growing season (Table 3). Gross immobilization rates differed from year to year, with the highest rates in 1992 (Table 5). The soil temperature significantly influenced immobilization (Table 4). Like gross mineralization rates, early growing-season rates were higher than late growing-season rates (Tables 3 and 7).

Gross N immobilization was highly correlated with gross mineralization (Table 4, $r = 0.91$, $P < 0.001$). It is weakly correlated with NH_4^+-N concentrations in the soil ($r = 0.44$, $P = 0.01$), net mineralization ($r = 0.43$, $P = 0.01$) and net nitrification ($r = 0.39$, $P = 0.02$).

Effects of increased IR on nitrogen cycling

Inorganic pool sizes. Table 2 shows the average inorganic N concentrations in the soil by treatment at the time of the gross N transformation measurements. Extractable NH_4^+-N exceeded NO_3^--N in the heated and control plots at all dates across all years except for June 1994 when nitrate levels in the soil were higher. The heating treatment had no significant or consistent influence on the inorganic N pools (Table 2).

N transformation rates

Mineralization. **Analysis of heating treatment across years and zones:** When the heating treatment was included in the analysis, gross N mineralization was significantly different between treatments (higher with heating), seasons (higher in June) and years (higher in the early years of the experiment) but not zones (Tables 3 and 8). When the treatment was added to the analysis, the time of season became a significant factor because of the disproportionate increase in mineralization rates with heating in the early season; hence, a significant season*-treatment interaction ($F = 6.41$, $P = 0.013$; Table 8). There were also significant treatment*year and year*treatment*season interactions (Table 8).

Both treatment and temperature significantly affected gross mineralization (Table 8). Gross N mineralization was higher in the heated plots relative to the controls and this increase was influenced by the increase in temperature (Tables 3 and 8).

There was no significant treatment effect on net mineralization rates when the analysis combined all data (years, zones and time of season, Table 6). The treatment effect did not alter the significant influence of year and soil moisture on net mineralization (Tables 3 and 6).

Analysis of heating treatment by year within each zone: Although treatment and season significantly influenced gross mineralization in the first analysis, these factors were not always significant when each year is analysed separately. Treatment was significant only for 1992, but not for 1991 and 1994 (Table 7). Also, in both the xeric and mesic zones, the time of season remained significant for 1991 and 1992, but not for 1994 (Table 7).

When the net mineralization data were analysed by year within a zone, there were significant treatment effects. In the xeric zone, there was a significant increase in net mineralization in 1994, and a trend toward a treatment effect in 1991 and 1992 (Table 9). There were no

Table 9 Factors affecting net N transformation rates by zone and year. F-statistics$_{df}$ from ancova with treatment (heated or control) as categorical variable and plot number as the independent covariate. Plot number is used as a surrogate for snowmelt date and/or length of growing season. See Methods for complete explanation. Significant values ($P < 0.05$) shown in bold

			Net mineralization			Net nitrification		
Zone	Year	Source	$F_{\text{d.f.}}$	P	R^2	$F_{\text{d.f.}}$	P	R^2
Xeric	1991	Treatment	$3.18_{1,3}$	0.17	0.60	$0.52_{1,3}$	0.53	0.73
		Plot number	$0.32_{1,3}$	0.61		$5.7_{1,3}$	0.10	
	1992	Treatment	$3.90_{1,7}$	0.09	0.82	$0.79_{1,7}$	0.40	0.85
		Plot number	$24.30_{1,7}$	**<0.01**		$38.09_{1,7}$	**<0.01**	
	1994	Treatment	$8.63_{1,7}$	**0.02**	0.62	$2.06_{1,7}$	0.19	0.25
		Plot number	$1.19_{1,7}$	0.31		$0.06_{1,7}$	0.81	
Mesic	1991	Treatment	$0.05_{1,3}$	0.84	0.32	$0.02_{1,3}$	0.96	0.57
		Plot number	$1.40_{1,3}$	0.32		$3.73_{1,3}$	0.15	
	1992	Treatment	$< 0.01_{1,7}$	0.95	0.69	$0.23_{1,7}$	0.64	0.57
		Plot number	$15.13_{1,7}$	**0.01**		$9.37_{1,7}$	**0.02**	
	1994	Treatment	$0.93_{1,7}$	0.37	0.26	$0.31_{1,7}$	0.60	0.08
		Plot number	$1.15_{1,7}$	0.32		$0.43_{1,7}$	0.53	

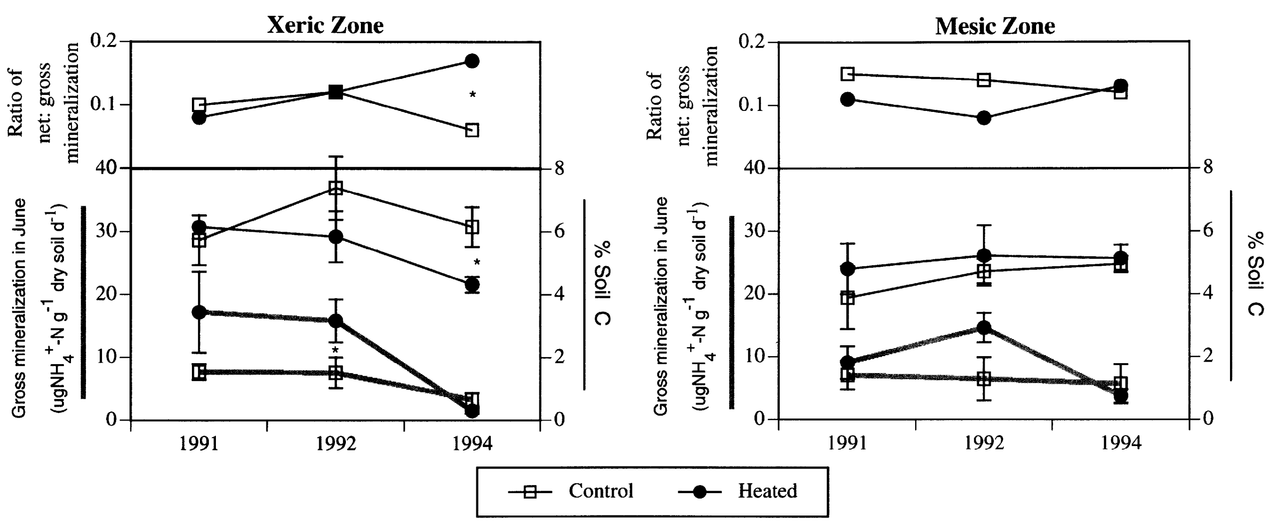

Fig. 3 Gross nitrogen mineralization (June), percent soil carbon (June) and the ratio of net to gross mineralization in the xeric and mesic zones, heated vs. control, in 1991, 1992, and 1994. In xeric zone, gross mineralization and % soil C decline in 1994. Because the decrease in gross immobilization is proportionally larger than that of gross mineralization in 1994, the ratio of net to gross mineralization increases significantly. In contrast, the mesic zone N transformation rates, soil C pool, and ratios remain relatively constant. *Indicates $P < 0.050$.

treatment effects in the mesic zone. In both the xeric and mesic zones, there were significant plot number effects in 1992 indicating that the date of snowmelt was an important factor (Table 9). Earlier snowmelt was correlated with higher mineralization rates (Table 4).

Analysis of heating treatment by season within each zone: In the xeric zone when all years were considered, gross mineralization rates were significantly higher with heating ($F = 3.43, P = 0.054$) and significantly higher in 1991 and 1992 ($F = 6.38$, $P = 0.021$, Fig. 3). There were no significant treatment or year effects on gross mineralization in the late growing season in August. Generally, gross mineralization rates were highest in the heated plots in the early season. In the xeric zone, percent soil carbon was a significant correlate with gross mineralization rates. There were no significant treatment effects in the mesic zone.

Like gross mineralization rates, xeric zone rates of net mineralization were significantly higher with the IR treatment ($F = 6.37$, $P = 0.021$) and significantly higher in years 1992 and 1994 ($F = 10.86$, $P = 0.001$). In these analyses, plot number was a significant covariate indicating the importance of earlier snowmelt date or increased growing season length on net mineralization rates ($P = 0.002$). None of these factors was significant in the mesic zone (Table 3).

Heating more than doubled the seasonally averaged ratio of net to gross mineralization rates in 1994 in the xeric zone and nearly doubled the ratio in 1992 in the mesic zone (Table 3). In the years 1991 and 1992, NH_4^+ turned over more rapidly (lower MRT) in the heated plots than in the controls, but by the fourth year of the study 1994, the controls exhibited higher NH_4^+ turnover rates.

Nitrification. **Analysis of heating treatment across years and zones:** There was no significant treatment effect on gross or net nitrification rates (Table 6). Gross nitrification was generally lower in the late season relative to the early season ($F = 5.48$, $P = 0.008$, Table 6). Net nitrification rates were lower in 1994 than in the 1991 and 1992 ($F = 7.56$, $P = 0.008$, Table 6) and moisture played an important role ($F = 3.68$, $P = 0.062$, Table 6).

Analysis of heating treatment by year within each zone: For both the xeric and mesic zones, there was no significant treatment effect on gross or net nitrification in any year (7 and 9). The time of the growing season had a significant influence on gross nitrification rates only in 1991 in the xeric zone during ($F = 7.08$, $P = 0.029$; Table 7), with higher rates in the early growing season. Plot number is correlated with net nitrification in all years but 1994, suggesting that the date of snowmelt was an important factor for net, but not gross nitrification (Table 9).

Analysis of heating treatment by season within each zone: Gross rates of nitrification did not show any consistent effect of treatment or year within a season. In the xeric zone, net nitrification rates were significantly lower in 1994 relative to the two previous years ($F = 18.76$, $P = < 0.001$) and the plot number was a significant factor ($F = 9.55$, $P = 0.006$). In the mesic zone, only the plot number was significant in the analysis. There was a trend toward more rapid nitrate-N turnover rates (low MRT) in the mesic compared to the xeric zone in the early season (anova, $F = 2.18$; $P = 0.105$) as well as the late season (anova, $F = 1.70$; $P = 0.199$), but there was no effect of treatment.

Immobilization. **Analysis of heating treatment across years and zones:** Gross immobilization was influenced by many of the same factors as gross mineralization. Treatment, season and soil temperature significantly impacted immobilization rates. Like gross mineralization, there were a number of significant interactions, including year*treatment and season*treatment ($F = 3.57$, $P = 0.06$).

Analysis of heating treatment by year within each zone: In the xeric and mesic zones, there were significantly higher rates of gross immobilization in the early season and heating significantly increased gross immobilization in 1992 (Tables 3 and 7). There was a significant treatment*season interaction driven by the strong treatment effect in June that was not apparent in August (Table 3, treatment*time of season, $F = 13.82$, $P = 0.003$).

Analysis heating treatment by season within each zone: When analysed by time of season, it is clearer that the treatment effect on immobilization is primarily a consequence of the increased immobilization in the heated plots early in the growing season. When all years were combined, the heating treatment significantly increased rates of immobilization in the xeric, dry zone in June ($F = 6.29$, $P = 0.015$) but it had no effect in the mesic zone or in August. Like gross mineralization rates, the rates of immobilization were significantly higher in the first years of the study but declined significantly by 1994 ($F = 8.53$, $P = 0.014$).

Discussion

Summary of major findings

Average gross mineralization rates were 4.5 $\mu g\ N\ g^{-1}$ dry soil per day in the absence of the treatment. They were higher in the xeric zone than in the mesic zone, and were higher in the early part of the growing season relative to the late part in each year. In the early part of the growing season, ammonium produced by mineralization was partitioned roughly equally between immobilization and nitrification (in the absence of plant uptake), though nitrification declined significantly in the later part of the growing season. Gross mineralization and nitrification showed the strongest seasonality, and gross mineralization and ammonium immobilization showed the strongest year-to-year variation in response to climatic conditions. Net mineralization did not differ between zones but was highly influenced by the timing snowmelt from year to year. Earlier snowmelt resulted in greater net mineralization both under ambient variation and under the warming treatment.

The effect of heating was most pronounced in the xeric zone and in the early part of the growing season. Gross mineralization initially increased with heating, as did ammonium immobilization, leaving the ratio of net to gross mineralization unchanged but resulting in a decline in the mean residence time of N in the ammonium pool (Table 3, Fig. 3). This heating effect was diminished in the last year of the experiment as soil organic matter pools declined which led to a decline in gross mineralization rates and an even greater decline in gross immobilization rates. As a result, net mineralization rates, although generally higher with heating in all years of the study, did not show a significant increase with warming until 1994, the last year of the study (Table 3, Fig. 3). There were no significant heating effects on nitrification rates, or on nitrate consumption rates (immobilization + denitrification, in the absence of plant roots). No such patterns emerged in the mesic zone.

Further details of these results, along with elucidation of the underlying mechanisms driving these results, will be discussed below.

General trends in nitrogen cycling in the subalpine ecotone

Mineralization. Our gross mineralization rates in the absence of heating for the xeric zone exhibited a similar range of values (0.63–7.68 μgN g^{-1} dry soil day^{-1}) as those reported by others (Burke *et al.* 1989) for similar sage-brush steppe. Generally, rates were low in dry periods and higher when soils maintained considerable moisture. Estimation of net mineralization rates from other studies range from −0.5 to 1.6 μgN g^{-1} dry soil day^{-1} over 15-day incubation periods (Burke *et al.* 1989), from −0.1 to 0.3 μgN g^{-1} dry soil day^{-1} over 10-day incubation periods (Matson *et al.* 1991) in the sagebrush steppe dominated by *A. tridentata* ssp. *vaseyana*, and from approximately −0.06 to 0.10 μgN g^{-1} dry soil day^{-1} in the alpine tundra (Fisk & Schmidt 1995). The net mineralization rates found at this site in both zones were in the same range (0.18–0.48 μgN g^{-1} dry soil day^{-1}) as those measured for the sagebrush steppe (Burke *et al.* 1989; Matson *et al.* 1991) but much higher than rates in the alpine tundra (Fisk & Schimdt 1995). Unlike the results for the sagebrush system studied by Burke *et al.* and Matson *et al.* net mineralization rates were not negative in the subalpine ecotone because the measurements were integrated over the year.

Even though the two zones in our plots are distinct in vegetation and soil microclimate, there was no significant zone effect on net mineralization. We did not expect this, given the clear differences in soil microclimate. Although this lack of difference in mineralization rates among differing plant communities within an ecosystem type is not unprecedented (Fisk & Schmidt 1995), most comparative studies of this kind have documented significant ecosystem differences (Hart & Gunther 1989; Giblin *et al.* 1991).

Spatial variability within and among plots was high for both gross and net mineralization. This suggests that net N mineralization rates are influenced by factors interacting with or independent of the soil temperature and moisture gradient produced by vegetation cover or topography including differences in solar radiation (Greenland 1991), past disturbance by gopher activity (Thorn 1978) or rockiness.

Nitrification. Our gross nitrification rates ranged from 10.35 to 145.80 mg m^{-2} d^{-1} (or 0.23–3.24 μgN g^{-1} dry soil day^{-1}). These values are low to mid range for gross nitrification rates reported from other ecosystems such as oak woodland-grassland (73–420 mg m^{-2} d^{-1}; Davidson *et al.* 1990) and mature coniferous forest (*c.* 10–100 mg m^{-2} d^{-1}; Davidson *et al.* 1992).

Growing season net nitrification rates ranged from 1.88 to 4.19 g m^{-2} (or 0.93–2.07 μgN g^{-1} dry soil day^{-1}). These values were higher than nitrification rates measured in the alpine tundra (*c.* 0.05–1.30 g m^{-2}; Fisk & Schmidt 1995), old forests (0.50 g m^{-2}; Hart & Firestone 1989), and the sagebrush steppe (0.3 μgN g^{-1} dry soil day^{-1}, Matson *et al.* 1991) and equal to those measured in young forests (4.2 g m^{-2}; Hart & Firestone 1989). Based on the net nitrification rates alone, this subalpine system might be expected to exhibit gross nitrification rates that resembled young forests with high gross and net rates, but the gross rates observed here are much lower. The ratio of net nitrification to gross nitrification was near or above one in most cases (Table 5), indicating that the peak of gross nitrification was not captured in our measurements.

Although variable across many landscapes, nitrification rates are generally higher when soil NH_4^+ concentrations are high (Robertson & Vitousek 1981; Barford & Lajtha 1992), soil water content is low (Marrs *et al.* 1988), soil O_2 is high, pH is high (Focht & Verstraete 1977), allelopathic compounds are low (Rice & Pancholy 1974) and litter C:N is low (Robertson 1982; Rosswall 1982). Based on known controls on nitrification, we expected that rates of nitrification would have varied with changes in the soil environment. However, we observed no pattern in nitrification rates that indicated a significant relationship with changing soil microclimate conditions. Alternatively, our study might have lacked sufficient temporal resolution in the sampling to detect any pattern.

Net nitrification rates were higher in plots with earlier snowmelt dates. This is probably the result of the increase NH_4^+ concentration and in the soil immediately following snowmelt allowing nitrification in the absence of plant growth.

NH_4^+ and NO_3^- immobilization. In this system, in the absence of plant uptake, the primary pathways of consumption of NH_4^+-N are microbial immobilization and nitrification. In many cases, gross immobilization was greater than gross mineralization (Table 3). If the inorganic NH_4^+-N concentrations are high, this relationship can exist, but cannot be sustained.

Overestimation of N immobilization is likely to occur in the process of NO_3^--N consumption (Table 5). There were other pathways of NO_3^--N loss from this system including denitrification and leaching. In the pool dilution cores, leaching was not a possibility. The ratio of NO_3^--N consumption to NO_3^--N production was greater than 1 in most cases (Table 5). It is possible that denitrification contributed to this consumption in excess of production when the soil moisture was high, but it cannot explain the high consumption rates in the xeric zone in the late season when denitrification would be low or nonexistent. For this reason, we suspect that NO_3^- consumption may have been stimulated by the addition of $^{15}NO_3{}^-$ N in the pool dilutions (Davidson *et al*. 1991).

The higher rates of gross NH_4^+-N consumption relative to gross $NO_3{}^-$ N consumption are consistent with studies in systems dominated by an ammonium economy including a mature coniferous forest (Davidson *et al*. 1992), a northern hardwood forest (Zak *et al*. 1990), and an Alaskan taiga forest (Clein & Schimel 1995). Even so, NO_3^- assimilation is significant at this site and is probably most important in microsites where NH_4^+ is not readily available.

Effects of increased IR on nitrogen cycling in a subalpine ecotone

Nitrogen transformations. In the absence of increased IR, internal N cycling did not differ greatly between the two zones, even though they differed markedly in initial vegetation and soil-moisture content. The xeric and mesic zones did differ significantly in their N cycling responses to the increased IR. The xeric and mesic zones were not distinct from one another in net mineralization rates, but were very different in the response of the net mineralization rates to the heating treatment. In the mesic zone, heating had no significant effect on the rate of net N mineralization while in the xeric zone, heating increased net mineralization in the 1992 and 1994 (Table 3). The heated plots still maintained higher net mineralization rates than the controls in the fourth year of our study (1994), even though both heated and control rates were lower relative to the second year. These results are different from those of another warming study at the Harvard Forest where researchers documented an immediate increase and an eventual decline of the magnitude of a warming effect on net N mineralization rates over a three-year period (Peterjohn *et al*. 1994).

Rates of gross mineralization were higher in the xeric zone relative to the mesic zone and the impact of heating was greater in the xeric zone. In the xeric zone, gross mineralization rates exhibited the opposite pattern to net mineralization rates, showing the largest increase as a result of heating in the first two years and declining by the fourth year in which there was no difference between heated and control. This is because gross mineralization was roughly equalled by gross immobilization in 1991 and 1992. In 1994, when microbial demand for N declined, possibly as a consequence of C limitation as SOM declined with increased IR, more N was released resulting in significantly higher net N mineralization rates in the heated plots relative to the controls. This mechanism provides an explanation for a delay in increased net mineralization in response to warming that other studies have documented.

The impact of heating was most pronounced early in the growing season. With heating, the highest gross mineralization rate in the xeric zone was 17.19 μgN g^{-1} dry soil day–1, or 1.5 times that measured in the absence of heating and three times as large as that measured the sagebrush steppe ecosystem (Burke *et al*. 1989). It is possible that the additional IR to the soil surface early in the growing when there is little plant cover provides conditions more favourable to microbial activity (e.g. higher temperatures). Indeed, temperature was a significant positive correlate with gross mineralization and immobilization. In contrast, moisture, and not temperature, was a significant positive correlate with net mineralization. These results, although not overwhelming, provide some explanatory power for the changes in N cycling. These relationships, along with other factors such as SOM content, may help in the prediction of ecosystem response to warming

In contrast to net and gross mineralization, nitrification rates were not significantly or consistently affected by the heating treatment or by the differences in soil microclimate across zone or years. Net nitrification rates were also significantly lower in the fourth year of the study (Table 5). This could have been because of the higher gross NO_3^- consumption rates that year. Others have shown a decrease in net nitrification with warming (Binkley *et al*. 1994; Robinson *et al*. 1995), most likely as a result of decreasing soil osmotic potential (Low *et al*. 1997).

Hart *et al*. (1994) suggested that the best measure of the dynamics of the NH_4^+ and NO_3^- pools is not net or gross mineralization rates, but the mean residence time of an N atom in a particular pool (MRT). The mean residence time integrates the dynamic interactions between the inorganic N pools and N transformations. A smaller MRT indicates faster turnover in the N pool. The MRT of an N atom is generally a few days in the NH_4^+ and NO_3^- pools and 1–2 months for the microbial biomass pool (Davidson *et al*. 1992; Hart *et al*. 1994). The heating treatment, through its influence on both transformation rates and pool sizes, impacted the mean residences time of N in this system. Mean residence times were generally shorter in the NH_4^+ pool in the heated plots indicating a more rapid turnover of N in these pools. The NH_4^+ turnover time was higher in June than August indicating greater activity in the early growing season, but there was not a difference across zones. The MRT of the N atom in the NO_3^- pool was not consistently influenced by the heating treatment.

Plant community and soil microclimate differences. The two zones, represent two different plant communities and soil microclimates. The differing responses in gross N mineralization rates of the two zones to the increased infrared radiation are most certainly the result of differences in initial soil microclimate conditions and vegetation type and cover. (Harte *et al*. 1995). The heaters raised the soil temperatures in drier, less-vegetated xeric zone more than in the moister, more-densely vegetated mesic zone (Harte *et al*. 1995). This soil microclimate variability, in space and time, most certainly influenced the patterns of change in the N transformations. Indeed, the effect of heating on mineralization was more pronounced in the early growing season when moisture levels were sufficient to allow microbial activity, vegetation cover was low so that the increased radiative flux of the heaters was delivered directly to the surface of the soil and not intercepted, and there was an abundant supply of substrate. The impact of heating on N transformation rates was greatest in the early growing season in the xeric zone, and the timing and magnitude of the effect of this heating on soil microclimate was mediated by vegetation cover (Harte *et al*. 1995). During the early growing season, the mesic zone soil moistures were very high, so the increased IR flux to the surface served to increase evaporation, not increase soil temperature. The impact of heating on N transformation rates in the mesic zone therefore was dampened relative to the xeric zone. In the late growing season, the soil in the xeric zone was too dry and the vegetation cover in the mesic zone too great to allow for a significant impact of increased IR on N transformations.

Vegetation type has been shown to also play an important role in N turnover and availability (Rehder & Schäfer 1978; Burke *et al*. 1989; Hart & Gunther 1989; Giblin *et al*. 1991; Hobbie 1996). This influence can be exerted by vegetation via influences on soil moisture, temperature, as mentioned above, and soil organic matter accumulation and quality. Vegetation type also influences accumulation of soil organic matter, which influences rates of N transformations. Soils from areas of greater organic matter accumulation have a greater potential for high mineralization rates, if the system does not become substrate limited. Burke *et al*. (1989) found significantly higher rates of N mineralization and immobilization in plant communities dominated by *Artemisia tridentata* ssp. *vaseyana* compared to plant communities characterized by the prevalence of two other subspecies of sagebrush. The increase is attributed to higher productivity in *A. tridentata* ssp. *vaseyana* communities that resulted in higher organic matter accumulation and more favourable soil microclimate conditions (Burke *et al*. 1989).

Harte & Shaw (1995) documented a compositional shift in aboveground biomass among growth forms (shrubs, graminoids and forbs) with heating at this site. This shift favoured increased aboveground biomass of shrubs (woody-species) over forbs (highly decomposable long-lived perennials) over the four years in the heated plots relative to the controls in both the xeric and mesic zones (Harte & Shaw 1995). Total aboveground biomass did not change with heating. But this change in aboveground composition produced a decrease in litter production and quality in the heated plots relative to the controls (Shaw, unpubl. data), resulting in a decrease in SOM by the fourth year of the study. This decrease in SOM may explain the observed decline of gross mineralization and N turnover rates in the xeric-zone heated plots.

In the present study, changes in SOM with heating exert some influence on rates of gross mineralization and immobilization. A multivariate general linear model including SOM content, treatment, season, zone and temperature accounted for a significant portion of the variation in rates of gross mineralization and immobilization ($R^2 = 0.625$). Indeed, both soil temperature and SOM content were significant factors determining rates of gross mineralization ($P = 0.002$ and $P = 0.053$, respectively). In the xeric zone, SOM content declined over the four-year study as did gross mineralization rates. This decline in mineralization rates can be understood by compartmentalization of the SOM pool. Assuming there are two major components to the SOM pool, a fast-turnover active pool and a slow-turnover recalcitrant pool, the fast pool includes the newer litter inputs with a relatively high C:N ratio relative to slow-turnover pool. With an increase in temperature and no carbon limitation, gross mineralization and immobilization rates are increased with no significant change in net mineralization. This results in higher rates of both gross mineralization and immobilization rates in the early season in heated plots for the first two years of the study. By the fourth year of the study, however, the bulk of the SOM residing in the soil in the heated plots may have been a more recalcitrant pool, creating an environment of C limitation, slowing rates of microbial activity, resulting in inorganic N release and significantly higher net mineralization rates in the heated plots in the xeric zone. In addition, total inorganic N flux from the surface litter layer decreased by 1994, suggesting that the changes in litter production and quality were influencing litter breakdown (Shaw, unpubl. data). Further investigations are needed to elucidate the mechanisms underlying the changes in mineralization.

Implications for global climate change

Some studies in the arctic tundra have shown significant positive responses of microbial activity to increased temperatures (Billings *et al*. 1982, 1983). It is assumed that this increased microbial activity will ultimately result in significant nutrient release (Melillo *et al*. 1990). Others studies have shown, through the use of greenhouses, that an atmospheric temperature increase of 4–5 °C will not exert a strong enough influence on soil temperatures to alter nutrient availability (Jonasson *et al*. 1993; Robinson *et al*. 1995). Similarly, Nadelhoffer *et al*. (1992) have shown significant increases in N mineralization in the moist tundra with increases in soil temperature between 9 and 15 °C, but not below 9 °C. The actual response of soil microclimate to a changing climate will depend not only on the convective heat transfer resulting from an increase in atmospheric temperature, but on the absorption of the increased IR incident on the soil surface and the initial soil microclimate. The results from these other studies may not be readily applicable to the subalpine ecotone because the simulated perturbation and the initial soil microclimate conditions were so different. In our study, the actual soil temperature and moisture changes with increased IR varied widely through the course of the experiment. If microbial populations respond to these changes, the spatial and temporal variations in nutrient release should also vary widely. In this system, the heating treatment significantly affected rates of N cycling in the beginning of the growing season and at the beginning of the experimental manipulation.

The most significant response of the subalpine ecosystem to simulated climate warming was the temporary increase in gross N mineralization and turnover, followed by a return to predisturbance levels of mineralization. Because N is the limiting nutrient, these results suggest that an increase in N turnover could temporarily stimulate primary production and carbon storage. This stimulation of primary production will happen only if the increase in mineralization is not accompanied by an equivalent increase in microbial N immobilization. If the depletion of the fast turnover C pool results in the subsequent decline of N mineralization, primary production would decline as well. We did not see an increase in primary production in the heated plots suggesting that increases in gross mineralization were accompanied by increases in gross immobilization in the presence of plant growth. The concomitant increase in atmospheric concentrations of carbon dioxide, however, may lead to a period of increased primary production and mineralization through increases in high quality inputs to the soil. Higher concentrations of CO_2 have been shown to increase high-quality C compounds into the soil through root exudation, stimulating microbial activity (Ineson *et al*. 1996; Rouhier *et al*. 1996; Moorhead & Linkins 1997). This mechanism could allow for further stimulation of N cycling and an increase in N availability to plants.

This study, in conjunction with another focusing on aboveground biomass with heating, suggests that there may be increases in carbon storage only through a plant compositional shift to growth forms with woody biomass (Harte & Shaw 1995; Chapin *et al*. 1996), and not through increased biomass production with nutrient release. If N is limiting to both plant and microbial growth, an increase in N mineralization with global warming will enhance primary productivity and carbon storage only if microbial immobilization is not also enhanced. This study shows that, in the absence of plant uptake, microbial immobilization does increase with increased mineralization with no net change in nitrogen availability. It is unclear how N availability to plants will change with global warming. The magnitude and direction of the long-term change of the N supply in the subalpine and other ecosystems will depend on the balance between the process of mineralization and the opposing processes of microbial N immobilization and plant uptake, and how these processes are affected by other components of climate change including the availability of water.

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