Effects of elevated nitrogen and temperature on carbon and nitrogen dynamics in Alaskan arctic and boreal soils

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[1] Plant productivity in upland tundra and boreal forest is demonstrably limited by nitrogen (N) and indirect evidence from field studies suggests that decomposition by soil microbes may be similarly limited. As climate warms at high latitudes, understanding the response of soil organic matter (SOM) decomposition to increased soil temperature may be crucial for determining the net effect of warming on ecosystem carbon (C) balance because temperature directly affects decomposition but also because it has an indirect effect on C balance via nutrient mineralization. We incubated northern Alaskan soils at two temperatures (5°C and 15°C) and two levels of N addition (with and without) to directly test for N limitation of SOM decomposition and to explore the interaction between temperature and N limitation. Over the entire 924 day incubation of organic and mineral soils from two ecosystem types, we measured microbial respiration; over the initial 90 days of the incubation, we measured microbial biomass N, net N mineralization, and the isotopic signatures ($\delta^{13}C$ and $\Delta^{14}C$) of microbial respiration. Across soil layers and ecosystem types, temperature always had a strong positive effect on SOM decomposition rates, whereas N addition had positive, negative, and neutral effects. When C respiration rates were high, the positive N response was generally most strongly expressed, for example, in the organic soils, in the warmer incubation, and at the outset of the experiment. Negative N responses often occurred when C respiration rates were lower, predominantly in mineral soils and at the middle or end of the experiment. In the subset of soil types where we measured the radiocarbon age of respired CO_2, increased decomposition was related to increased use of older C. Net N mineralization and nitrification were not affected by temperature, but N addition increased net N immobilization in all soil layers and microbial biomass N in organic layers. Our data support the general idea that at least in these high-latitude organic soils, decomposition of labile carbon can be positively stimulated by added N, whereas decomposition of recalcitrant C is suppressed.

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1. Introduction

[2] More than 40% of global terrestrial carbon (C) pools reside in boreal and arctic soils, and these ecosystems are currently undergoing strong climatic changes [*Arctic Council*, 2005]. Current estimates place total soil C stocks in the northern circumpolar permafrost zone at 1672 Pg (1 Pg = 1 billion metric tons), with 277 Pg of that in peatlands [*Schuur et al.*, 2008]). This large C reservoir is likely to play a key role in climate change because of its potential release to the atmosphere in response to predicted climate warming [*Davidson and Janssens*, 2006; *Field et al.*, 2007; *Heimann and Reichstein*, 2008; *Schuur et al.*, 2009].

[3] The warming of high-latitude soils is expected to accelerate soil organic matter (SOM) decomposition and nutrient mineralization [*Nadelhoffer et al.*, 1991; *Hobbie*, 1996; *Rustad et al.*, 2001], with consequent effects on soil C storage. Because plant productivity in upland tundra and boreal forest is nitrogen limited [*Hobbie et al.*, 2002b], increased nitrogen (N) released from decomposing SOM could stimulate plant productivity, thereby increasing ecosystem C storage [*Shaver et al.*, 2006]. However, field evidence suggests that soil microbial activity and biomass may also be N limited in some ecosystems [*Kaye and Hart*, 1997; *Ekblad and Nordgren*, 2002; *Neff et al.*, 2002; *Schimel and Weintraub*, 2003; *Mack et al.*, 2004; *Nordin et al.*, 2004; *Rinnan et al.*, 2007]. Therefore, increased N released from decomposition of SOM could further stimulate microbial decomposer activity and decrease soil C storage. Because

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increased soil temperature has the potential to affect decomposition rates, N availability, microbial activity, and plant productivity, the net effect on C storage remains largely unknown [*Chapin et al.*, 2009].

[4] Many studies have evaluated the effects of temperature alone on SOM decomposition in northern ecosystems and found that warming generally increases C loss and decreases SOM turnover time [*Hobbie*, 1996; *Welker et al.*, 1999; *Hobbie et al.*, 2002b; *Dutta et al.*, 2006; *Czimczik and Trumbore*, 2007; *Allison and Treseder*, 2008; *Kane and Vogel*, 2009]. Other studies have tested for the effect of N alone or in combination with other nutrients on integrated ecosystem C cycling in northern or alpine ecosystems [*Makipaa*, 1995; *Neff and Hooper*, 2002; *Neff et al.*, 2002; *Mack et al.* 2004; *Knorr et al.*, 2005; *Yoshitake et al.* 2007a; *Allison et al.*, 2008, 2010; *Hyvonen et al.*, 2008; *Nowinski et al.*, 2008; *Hartley et al.*, 2010], but the results have been inconsistent. For example, in moist acidic arctic tundra near Toolik Lake, Alaska, results from a 20 year field fertilization experiment showed a net ecosystem C loss of 2 kg C m^{-2} over 20 years despite increased productivity, suggesting nutrient stimulation of decomposition [*Mack et al.*, 2004]. In contrast, a long-term fertilization experiment in boreal forests of Sweden and Finland saw soil C sequestration increased by 0.01–0.12 kg C m^{-2} yr^{-1} [*Hyvonen et al.*, 2008], presumably due to a 40% decline in the decomposition rate of SOM. The authors suggested that this decline was probably due to a reduction in heterotrophic respiration. *Franklin et al.* [2003] also reported an increase in soil C in a boreal pine forest in northern Sweden following N fertilization. They attributed a 70% reduction in SOM decomposition rates to an increase in decomposer efficiency. Finally, direct N addition to laboratory incubations of conifer forest soils revealed a decrease [*Persson et al.*, 2000; *Ramirez et al.*, 2010] or no effect on SOM decomposition rates [*Vance and Chapin*, 2001; *Michel and Matzner*, 2002; *Buckeridge and Grogan*, 2008; *Hartley et al.*, 2010]. This lack of consistency in field and laboratory studies may be explained by the fact that the effects of N addition on litter and SOM decomposition diverge depending on the stage of decomposition (i.e., early, late, and final stages). Thus, additions of N to fresh organic materials would stimulate the initial decomposition of labile C. In contrast, additions of N to humus (i.e., recalcitrant C) in final stage of decomposition would suppress microbial activity [*Berg and Matzner*, 1997].

[5] Despite the large number of studies testing the effects of either N addition or soil warming on C microbial decomposition, there are relatively few studies that isolate the mechanisms behind ecosystem level effects or explore the likely interactions among temperature, N availability, and SOM quality. To our knowledge, only few studies have looked at interactions between N availability and soil warming on decomposition of SOM under field [*Henry et al.*, 2005; *Bell et al.*, 2010] or controlled laboratory conditions [*Cusak et al.*, 2010; *Song et al.*, 2010], and their results were mixed. For example, *Cusak et al.* [2010] showed that for tropical mineral soils, N fertilization significantly suppressed microbial activity and oxidative enzymes but increased temperature sensitivity of recalcitrant C pools. In contrast, *Song et al.* [2010] observed no effect of N addition on microbial activity or temperature sensitivity in alpine meadow soils. Thus, the main objectives of our study were (1) to determine if decomposition of SOM from soils of northern Alaska is limited by N availability; (2) to explore how N limitation of SOM decomposition responds to temperature; and (3) to determine what SOM characteristics predict the response of SOM decomposition to N addition and temperature. Based on inferences from field studies [*Mack et al.*, 2004; *Allison et al.*, 2010], (1) N addition will stimulate SOM decomposition in soils of northern Alaska, and (2) soil warming will interact positively with N addition to stimulate losses of more labile C from organic soils. To test these hypotheses, we incubated organic and mineral soil layers from two high-latitude ecosystem types (Arctic Tundra and Boreal Forest) for 924 days under a factorial array of temperature (5°C and 15°C) and N addition. We examined the response of microbial respiration and biomass, salt-extractable net N mineralization and nitrification, water soluble organic and inorganic N and the isotopic signatures ($\delta^{13}C$ and $\Delta^{14}C$) of respired CO_2. The latter helped us to distinguish the decomposition of fresh material from that of old material to determine which parts of the soil organic C continuum were affected by N and temperature.

2. Materials and Methods

2.1. Site and Soil Description

[6] We sampled organic and mineral soil horizons from two high northern latitude ecosystems located in arctic tundra and boreal forests within Alaska (Table 1). Sites included recently burned (63°55′N; 145°44′W) and approximately unburned (>90 years old) black spruce forests near Delta Junction in interior Alaska (63°55′N; 145°44′W), moist acidic tussock tundra and nonacidic tundra near Toolik Lake, Alaska (68°38′N, 149°43′W). Soil sampling was conducted on 24 July 2001 for the tundra and 5–13 July 2006 for the black spruce forests, and soils were immediately placed on ice and frozen at −20°C until the beginning of this experiment. All sites experienced long, cold winters with average daily temperatures below freezing from September to May; daily mean air temperature during the growing season was 9.3°C and 11.8°C for the tundra and boreal sites, respectively. Total precipitation was 180 mm and 290 mm for these ecosystems, respectively.

[7] The burned and unburned sites were distanced by approximately 4 km [*Treseder et al.*, 2004]. The unburned site in interior Alaska sites were dominated by black spruce (*Picea mariana*) with an understory of ericaceous shrubs and feather mosses (*Pleurozium schreberi* and *Hylocomium splendens*), while the recently burned site (soil BFM; Table 1) was dominated by graminoids (*Festuca altaica*, Carex *spp*.) and *Ceratodon purpurus* (i.e., fire moss). Soils from the burned site are classified as gelisols and were formed from loessal inputs carried by sediments of the Tanana River [*Richter et al.*, 2000]. Silt loams predominate, underlain by deposits of sand and gravel. In the area, permafrost is discontinuous and is not present in these sites [*Treseder et al.*, 2004]. The unburned site has a well-developed organic horizon of ~10 cm. The youngest site burned severely in 1999 leaving an organic horizon of less than 2 cm on average [*Treseder et al.*, 2004; *Lavoie and Mack*, 2011].

[8] The moist acidic tussock tundra and nonacidic tundra are less than 2 km apart. The site on the southern site of

Table 1. Chemical Properties (Mean ± SE) From a 924 day Laboratory Incubation of Soils at Temperatures 5°C and 15°C and Two Nitrogen Treatments (With or Without)[a]

Sites and Horizon Description	Code	Depth (cm)	pH	C (%)	N (%)	CN ratio
Boreal forest, Interior Alaska						
Unburned organic	BFUO	0–15	5.44	40.16 (0.28)	1.20 (0.25)	34.93 (7.14)
Unburned mineral	BFUM	5–15	5.23	2.93 (0.08)	0.13 (0.02)	22.63 (3.15)
Burned mineral	BFM	2–12	5.32	2.92 (0.28)	0.15 (0.01)	19.07 (1.20)
Tundra, northern Alaska						
Moist acidic organic	TAO	0–15	5.54	41.07 (0.48)	0.95 (0.12)	44.96 (7.05)
Moist acidic mineral	TAM	23–33	4.82	5.77 (1.18)	0.29 (0.07)	20.25 (0.58)
Moist nonacidic organic	TNAO	0–15	5.76	38.15 (2.18)	1.33 (0.38)	34.14 (10.48)
Moist nonacidic mineral	TNAM	23–33	6.82	3.49 (0.65)	0.23 (0.04)	14.50 (0.24)

[a]Soils were collected from organic and mineral horizons of moist acidic and nonacidic tundra near Toolik Lake and of boreal forests of interior Alaska.

Toolik Lake is located on the older (120,000–60,000 years) Itkillik I glacial surface [*Hamilton*, 2002]. Its vegetation is moist acidic tundra and is dominated by the tussock-forming sedge *Eriophorum vaginatum*, dwarf shrubs such as *Betula nana* and *Ledum palustre*, along with feather mosses and acidophilic mosses such as *Sphagnum* spp. [*Hobbie et al.*, 2002a]. The nonacidic site lies on the north side of the lake and is located on the Itkillik II glacial surface which is 25,000–11,500 years old [*Hamilton*, 2002]. The vegetation of the nonacidic tundra site is mainly composed of the dwarf shrubs *Dryas integrifolia* (i.e., crenulate mountain-avens), *Rhododendron lapponicum* (i.e., Lapland rosebay) and, *Salix arctica* (i.e., arctic willow) and minerotrophic mosses such as *Tomenthypnum nitens* [*Hobbie et al.*, 2002a]. Soils from the acidic and nonacidic tundra are classified as Gelisols [*Munroe and Bockheim*, 2001].

2.2. Incubation Design

[9] Three replicates (i.e., three spatially separated cores) of each soil were weighed (approx. dry weight: 5 g organic; 15–20 g mineral soil) into two subsets of 1 L Mason jars and assigned to dark incubation at two temperatures (5°C and 15°C) for 924 days. Both temperatures are in the range of summer soil temperature at these sites [*Hobbie and Chapin*, 1998; *Hobbie et al.*, 2002a; *Treseder et al.*, 2004]. The first subset of jars was used for respirometry and leaching and the second subset for N mineralization (see below) and microbial biomass. In the first subset, soils were placed in minilysimeter cups (i.e., Corning cup, Corning Inc., New York) on a layer composed of acid-washed nylon mesh, glass wool and a bed of 3 mm glass beads [*Nadelhoffer*, 1990]. In the second subset, soils were placed on the bottom of the jar.

[10] In half of the Mason jars, N (NH_4NO_3) was added every 2 weeks to increase the concentration of inorganic N (NO_3^- and NH_4^+) an order of magnitude above that found in unmanipulated tundra and boreal forest soils [*Mack et al.*, 2004, *Treseder et al.*, 2004]. We added in 5 or 2.5 mL of (0.07 or 0.1 μg N mL^{-1}) NH_4NO_3 to organic and mineral soils, respectively, for an addition rate of to 450 or 250 μg of N-NH_4NO_3 (gram dry weight)$^{-1}$. The same amount of distilled water was added to the control soils (i.e., no N addition).

2.3. Laboratory Measurements

2.3.1. Carbon Dioxide and Leaching of Soil N

[11] We measured CO_2 production (i.e., microbial respiration) from the samples for 924 days by sealing the Mason jars and measuring CO_2 accumulation in the headspace over ~24 h (first month) or 48 h (afterward) period. Air samples (10 mL) were taken at time 0 and at 24 or 48 h by syringe through a stopcock in the Mason jar lid and injected into a gas analyzer Li-Cor (Li-Cor, Nebraska). Carbon dioxide production in the Mason jar was expressed on total C basis (e.g., μg C CO_2 g C^{-1} h^{-1}). We calculated cumulative CO_2 flux from the soils over the course of the incubation by interpolating fluxes between successive measurement times.

[12] We measured dissolved inorganic N (DIN) and dissolved organic N (DON) monthly over the first 6 months of the incubation by adding 100 mL (2 × 50 mL) of distilled water to each corning cup and then applying a vacuum until the volume of water added was recovered. Leachate was filtered through a Whatman GF/F filter. The first leaching measurement occurred six days before the first N addition; thereafter, measurements were made at days 20, 32, 75, and 221. Dissolved inorganic N (NO_3^- and NH_4^+) in the leachate was determined colorimetrically using an Astoria-Pacific colorimetric autoanalyzer (Astoria, Oregon). Dissolved organic N in the leachate was determined by subtracting DIN from total N determined via persulfate oxidation and colorimetric analysis of resulting NO_3^- [*Sollins et al.*, 1999]. Native dissolved inorganic N produced was determined by subtracting dissolved inorganic N produced at days 20, 32, 75, and 221 from the cumulative amount of N added over that time period.

2.3.2. Net Nitrogen Mineralization and Microbial Biomass

[13] We used an aerobic laboratory incubation to estimate net nitrification and net N mineralization rates for each soil. Soils samples were analyzed for initial and final (3 months) pools of inorganic N (NH_4^+-N and NO_3^--N). For inorganic N determinations, approximately 5 g of organic and 10 g of field moist mineral soil were extracted with 0.5 M K_2SO_4 (ratio 1:5) [*Robertson et al.*, 1999]. The solutions were shaken for ~1 h, allowed to sit in an air-conditioned lab for 18–24 h (~23°C) and then filtered with a Whatman GF/A filter and vacuum pump. Ammonium and NO_3^- concentrations in soil extracts were also determined colorimetrically. Net N mineralization for the incubation period was calculated from the difference in initial and final inorganic N pools. All initial N pools and N flux were calculated on total N basis (e.g., μg N g N^{-1}).

[14] Soil microbial biomass N (15°C only) was determined after a 3 month incubation from field-moist soil samples with the chloroform fumigation extraction method (CFE) [*Brookes et al.*, 1985]. The soil samples were fumigated for 1 day in chloroform vapor followed by extraction (K_2SO_4) and filtration. Extract subsamples (fumigated

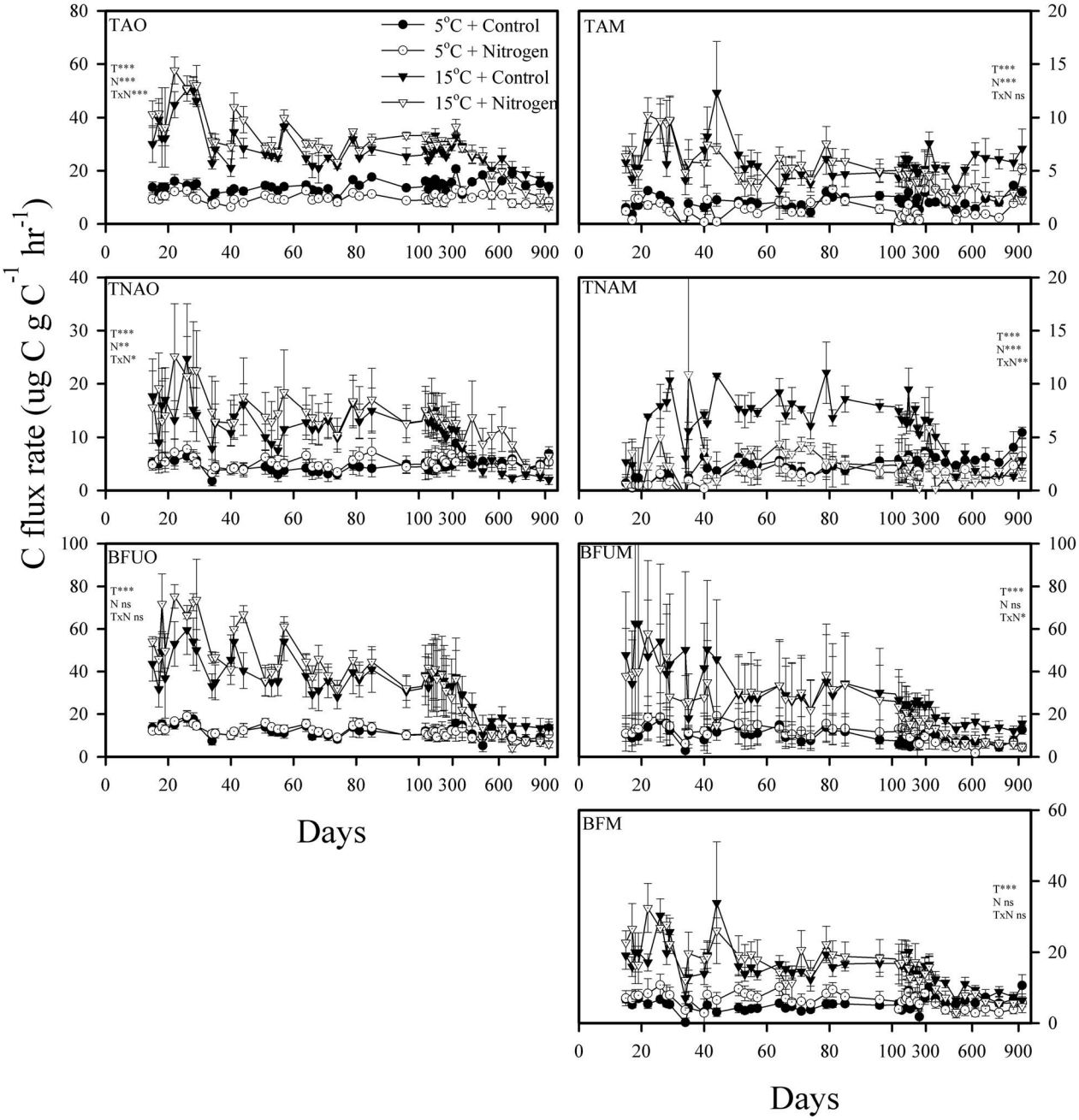

Figure 1. Mean (±SE) C flux rate (μg C g C^{-1} h^{-1}) during a 924 day laboratory incubation of soils at two temperatures (5°C and 15°C) and two N treatments (water addition and water plus N). Soils were collected from organic and mineral horizons of moist acidic and nonacidic tundra near Toolik Lake and of boreal forests in interior Alaska. Three asterisks indicate $P < 0.001$; two asterisks indicate $P < 0.01$; one asterisk indicates $P < 0.05$; NS indicates nonsignificant. Note that *y* axis values vary among soils.

and nonfumigated) were digested by persulfate oxidation and analyzed for NO_3^- colorimetrically. The microbial biomass was calculated by the difference between fumigated and nonfumigated with the recovery factor of 0.45 [*Vance et al.*, 1987].

2.3.3. Elemental Analysis

[15] Total soil C and N were measured on subsamples of initial soil cores using a Costech ECS 4010 Elemental Analyzer (Valencia, California) and calculated on a dry soil mass basis. Soil pH was measured with a pH meter using a soil:water ratio of 1:2.5 and 1: 10 for mineral and organic soils, respectively.

2.3.4. Isotope Measurements

[16] We performed isotope measurements for gaseous samples of $\delta^{13}CO_2$ and $\Delta^{14}CO_2$ respired (after 90 days of incubation time). Before making isotopic measurements of respiration CO_2, the headspace of the incubation jars was scrubbed with CO_2 free air to remove any atmospheric CO_2.

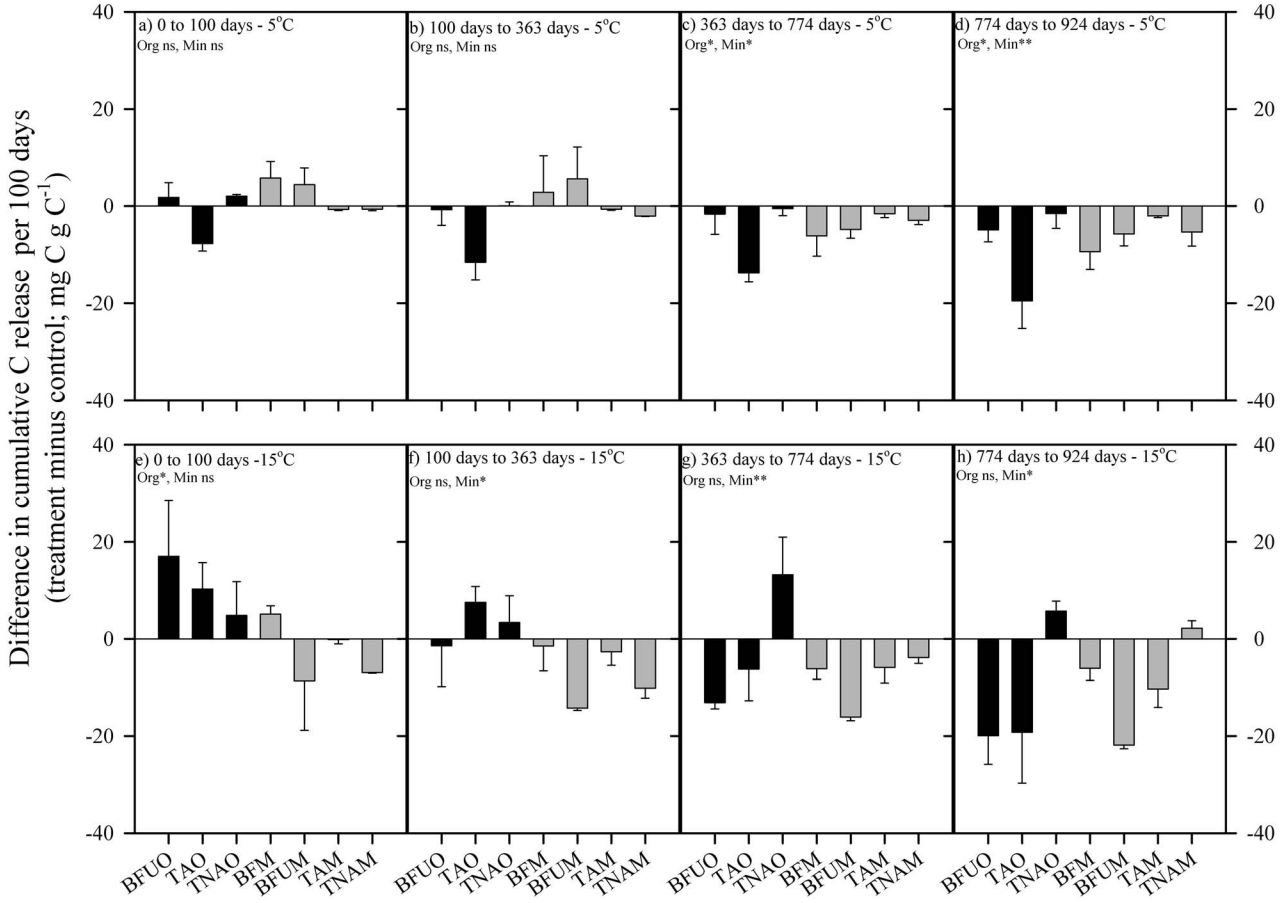

Figure 2. Mean difference (±SE) in cumulative microbial respiration (mg C g C^{-1}) between the N treatment (water plus N) and the control (water addition) (a, e) after 100 days, (b, f) between 100 and 363 days, (c, g) between 363 and 774 days, and (d, h) between 774 and 924 days during a laboratory incubation of soils at two temperatures (5°C and 15°C). Data presented are the difference between the nitrogen and control treatment. Data are also normalized on a 100 day scale. Soils were collected from organic and mineral horizons of moist acidic and nonacidic tundra near Toolik Lake and of boreal forests in interior Alaska. Three asterisks indicate $P < 0.001$; two asterisks indicate $P < 0.01$; one asterisk indicates $P < 0.05$; NS indicates nonsignificant.

Respired CO_2 then reaccumulated in the jar and the headspace air in the incubation jars was sampled via a closed loop system pumped through a molecular sieve trap [*Bauer et al.*, 1992]. The CO_2 was extracted from the traps by baking them in a furnace (550°C) attached to a vacuum line where the air sample was purified as it passed through a water trap (at −70°C) and a liquid nitrogen (LN_2) trap. Purified CO_2 samples were sealed and stored in Pyrex tubes that had been prebaked at 550°C.

[17] For isotope analysis of solid, about 3 mg of the bulk organic soil samples and about 100 mg of the bulk mineral soil samples were combusted to obtain several milligrams of CO_2-C. For each sample, a 15 cm open ended quartz tube and 20 mg of cupric oxide wires were prebaked at 900°C in a muffle furnace. The soil samples were loaded and sealed with the CuO under vacuum into the prebaked quartz tubes and combusted in a muffle furnace at 900°C for 2 h. Combusted samples were purified in a vacuum line as described above. The primary standard for ^{14}C analysis was NIST Oxalic acid II (SRM 4990C, National Institute of Standards and Technology), while IAEA-C6 sucrose standard (International Atomic Energy Agency, Vienna, Austria) was analyzed as secondary standard. Anthracite coal cleaned with a standard acid-base-acid treatment was used as a blank. All standards and blanks used for ^{14}C measurements were combusted and purified similarly to the samples.

[18] For all ^{14}C measurements, a portion of the sample CO_2 was converted to graphite by reacting with H_2 in presence of Fe catalyst [*Vogel et al.*, 1987]. The graphite samples were pressed into targets and sent for analysis at the W. M. Keck Carbon Cycle Accelerator Mass Spectrometry facility at University of California, Irvine [*Southon et al.*, 2004]. All ^{14}C results were expressed as $\Delta^{14}C$ after correcting for any mass-dependent fractionation of ^{13}C [*Stuiver and Polach*, 1977]. Negative $\Delta^{14}C$ values of the samples indicate old C, whose ^{14}C content significantly decreased by radioactive decay, whereas positive values of $\Delta^{14}C$ indicate presence of excess nuclear bomb ^{14}C produced in the 1950s and early 1960s [*Trumbore et al.*, 1989]. Typical 1σ precisions of $\Delta^{14}C$ measurements for modern samples were

Table 2. Mean (±SE) Cumulative Microbial Respiration (g C kg C^{-1}) During a Laboratory Incubation of Soils at Temperatures 5°C and 15°C and Two Nitrogen Concentrations (Water Addition and Water Plus Nitrogen)[a]

	5°C				15°C			
Soil Types	100 days	363 days	774 days	924 days	100 days	363 days	774 days	924 days
				Control				
BFUO	23.8 (4.6)	101.2 (24.5)	202.6 (43.5)	245.6 (52.9)	78.1 (16.9)	304.3 (106.2)	476.5 (138.7)	536.9 (156.3)
TAO	**26.7 (2.4)**	**122.9 (5.7)**	**276.5 (9.9)**	**340.4 (12.3)**	58.3 (2.5)	238.7 (10.3)	465.7 (31.3)	537.0 (40.3)
TNAO	**8.3 (2.5)**	43.6 (13.4)	96.8 (25.8)	119.4 (30.8)	26.0 (6.7)	101.9 (22.5)	144.2 (33.4)	155.4 (36.8)
BFM	9.1 (1.2)	48.0 (5.6)	108.1 (20.5)	139.7 (26.4)	32.7 (4.4)	133.4 (19.7)	224.9 (28.0)	257.7 (33.6)
BFUM	21.8 (10.7)	75.0 (28.30	144.4 (49.8)	178.9 (57.4)	69.7 (44.3)	225.4 (91.2)	374.9 (123.0)	433.3 (135.0)
TAM	4.0 (0.5)	**18.0 (1.6)**	36.3 (2.9)	49.5 (3.6)	12.0 (2.6)	47.0 (4.5)	100.3 (8.6)	127.2 (13.1)
TNAM	3.8 (1.5)	21.7 (5.7)	49.1 (8.2)	66.5 (13.2)	**14.4 (0.6)**	**58.3 (7.2)**	81.5 (11.6)	89.0 (14.4)
				Nitrogen				
BFUO	25.6 (3.1)	100.9 (18.0)	195.5 (45.9)	231.1 (55.4)	95.1 (5.9)	317.5 (80.3)	435.8 (120.3)	466.3 (129.3)
TAO	**19.0 (0.8)**	**84.6 (5.2)**	**181.7 (11.0)**	**216.3 (16.8)**	68.5 (5.4)	269.0 (11.2)	470.3 (23.4)	512.7 (27.5)
TNAO	**10.4 (2.7)**	45.8 (14.7)	96.6 (30.7)	116.8 (36.1)	30.8 (10.6)	115.7 (34.3)	212.2 (68.1)	232.0 (67.9)
BFM	14.9 (4.2)	61.2 (22.6)	96.2 (36.6)	114.0 (41.1)	37.8 (5.5)	134.5 (34.1)	200.7 (49.4)	224.4 (54.7)
BFUM	26.2 (14.1)	94.2 (49.1)	143.8 (63.2)	169.7 (67.2)	61.1 (34.1)	178.9 (79.7)	262.2 (108.5)	287.7 (119.3)
TAM	3.2 (0.7)	**15.4 (1.3)**	27.1 (3.2)	37.3 (2.9)	11.8 (1.8)	39.7 (10.6)	68.7 (22.7)	80.1 (25.6)
TNAM	3.1 (1.2)	15.4 (5.2)	30.1 (11.0)	39.9 (11.7)	**7.5 (0.8)**	**24.5 (1.7)**	31.8 (1.2)	42.3 (1.6)

[a]Soils were collected from organic and mineral horizons of moist acidic and nonacidic tundra near Toolik Lake and of boreal forests in interior Alaska. A three-way mixed ANOVA nested model: temperature (factor) $F_{1, 282} = 64.2$, $P < 0.0001$; nitrogen (factor) $F_{1, 282} = 1.4$, $P = 0.2339$; depth (factor) $F_{1, 17} = 8.5$, $P = 0.0095$; the interaction of temperature and nitrogen was not significant. Means of cumulative microbial respiration for each soil type among days in bold ($P < 0.05$) indicate significant differences between the nitrogen and control treatments (n = 3, except for BFUM and TNAM n = 2).

better than ±3‰. The average background $\Delta^{14}C$ measured on coal blanks was −998.0 ± 0.5‰. Samples from Fourth International Radiocarbon Intercomparison (FIRI) exercise [*Scott et al.*, 2003] were analyzed to check the accuracy of the ^{14}C results, which agreed with their reported consensus values within 1σ limits of error.

2.4. Statistical Analysis

[19] We used a three-way mixed analysis of variance (ANOVA) model with repeated measurements to test the effect of soil layer (organic or mineral), temperature (5°C or 15°C) and N addition (with or without) on microbial respiration (CO_2 production). A one-way mixed ANOVA nested model was used to test the effect of N addition on (1) cumulative respiration for four periods, the first 100 days of the incubation, from the first 100 days to 363 days, from 363 days to 774 days, and from 774 days to 924 days; and (2) on daily C flux rate (C basis) over four periods based on the amount of C lost (expressed in percentage), 0–25% of C lost, from 25 to 50% of C lost, from 50 to 75% of C lost, and from 75 to 100% of C lost. The first test compares treatment effect on flux rates while holding sampling date constant; the second test compares treatment effects on flux rates while holding total C emissions constant. A three-way mixed ANOVA nested model was also used to test the effect of soil layer, temperature and N addition on dissolved organic N, microbial biomass (only soil layer and N addition) and isotopic measurements. Soil layer, temperature, N and their interactions were treated as fixed factors and with replicate (i.e., soil core) nested within soil type. The main effects of soil layer, temperature and N addition on net N nitrification and N mineralization rates (water and KCl extractions) were determined using nonparametric tests. The main effects of temperature and nitrogen were tested across all soils, ecosystems (boreal versus tundra) and individually for each soil. The degrees of freedom associated with appropriate F values were computed using Satterthwaite's approximation [*Littell et al.*, 2006]. Logarithmic transformation was performed when necessary to achieve normality. All statistical analyses were computed using SAS 9.1 (SAS Institute Inc., SAS OnlineDoc, 2003, available at http://support.sas.com/documentation/onlinedoc/91pdf/index.html).

3. Results

3.1. Carbon Dynamics

[20] Respiration rates generally declined over the first 100 days, particularly for organic soils and those incubated at 15°C, and then remained relatively constant while declining only slightly over the remainder of the 924 day experiment (Figure 1).

[21] The interactions between soil layer, temperature, and N ($F_{4, 3615}$ value = 14.0; $P = 0.0002$) and between soil layer and N ($F_{3, 3615}$ value = 14.3; $P = 0.0002$) were highly significant. Organic soils had, on average, higher respiration (expressed on a C basis) rates than mineral soils across sites ($F_{1, 3619}$ value = 1159.4; $P < 0.0001$), and temperature increased CO_2 production for all soils (Figure 1; $F_{1, 3619}$ value = 1172.8; $P < 0.0001$). The effect of N addition on instantaneous microbial respiration was also significant ($F_{1, 3619}$ value = 12.0; $P = 0.0005$), but the sign of this effect was soil and temperature specific (Figure 1) with a significant increase in C mineralization rates for three soils at 5°C (BFM, BFUM, TNAO) and three organic soils at 15°C (BFUO, TAO, and TNAO), and a significant decrease in C mineralization rates for three soils at 5°C (TAM, TAO, TNAM) and for two mineral soils at 15°C (TNAM and BFUM). Within organic soils, boreal forest and acidic tundra sites had greater C mineralization rates than the nonacidic tundra site ($F_{2, 1720}$ value = 384.8; $P < 0.0001$). Within the mineral soils, boreal forest C mineralization rates were higher than both tundra sites ($F_{3, 1895}$ value = 183.2; $P < 0.0001$).

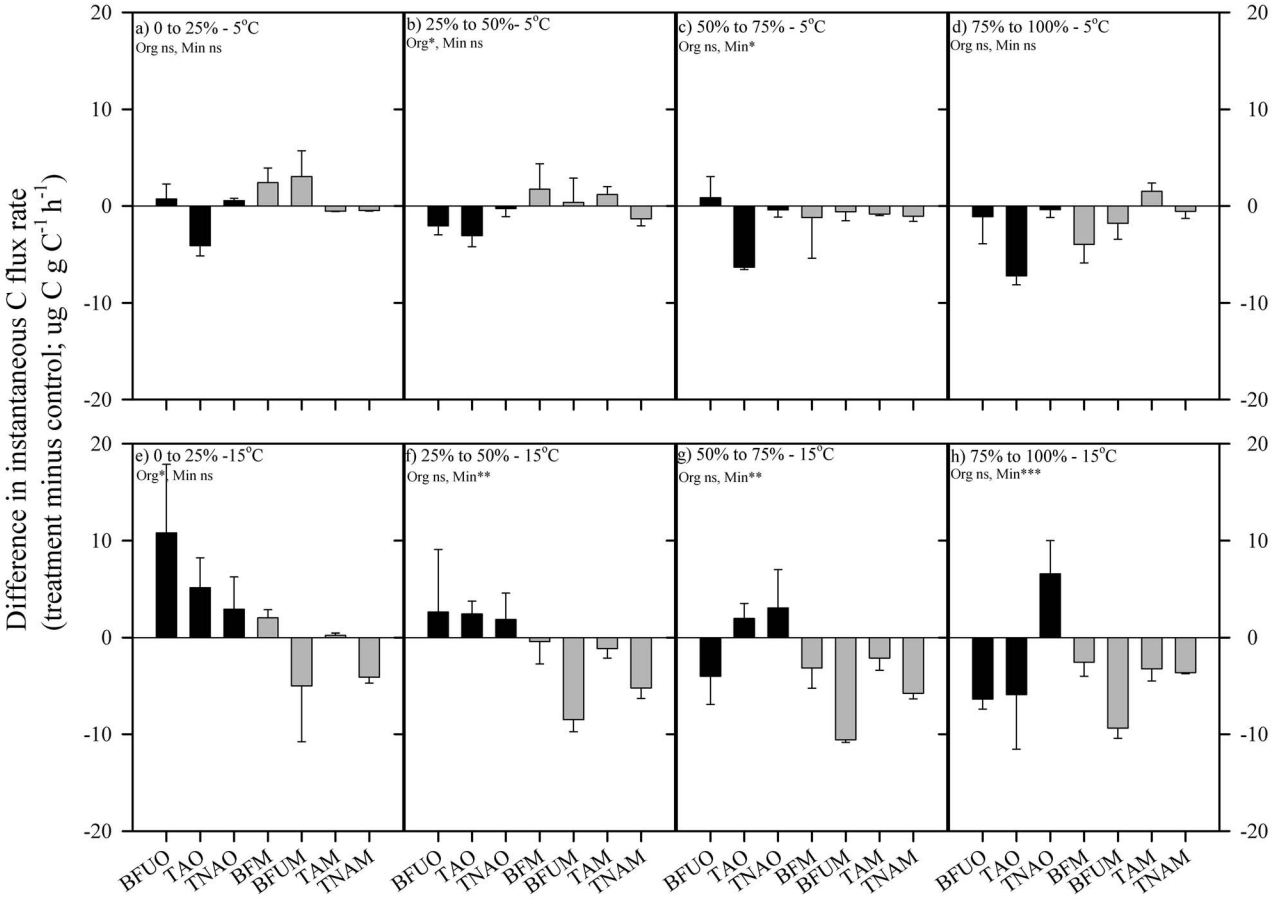

Figure 3. Mean difference (±SE) in instantaneous C flux rate (μg C g C^{-1} h^{-1}) between the N treatment (water plus N) and the control (water addition) (a, e) after 0–25% of C lost, (b, f) between 25% and 50% of C lost, (c, g) between 50% and 75% of C lost, and (d, h) between 75% and 100% of C lost during a laboratory incubation of soils at two temperatures (5°C and 15°C). Data presented are the difference between the nitrogen and control treatment. Soils were collected from organic and mineral horizons of moist acidic and nonacidic tundra near Toolik Lake and of boreal forests in interior Alaska. Three asterisks indicate $P < 0.001$; two asterisks indicate $P < 0.01$; one asterisk indicates $P < 0.05$; NS indicates nonsignificant.

[22] In an attempt to describe a general pattern, we calculated the effect of N on cumulative respiration per unit total C for four periods of time (i.e., 0–100 days, 100–363 days, 363–774 days, and 774–924 days; these periods were based on available measured sampling dates). During the first 100 days, there was only a positive significant effect ($F_{1,\ 8}$ value = 5.6; $P = 0.0458$) of N for the organic soils at 15°C (Figure 2e and Table 2). Between 100 and 363 days, the effect of N on cumulative respiration was negative ($F_{1,\ 9}$ value = 7.1; $P = 0.0261$) and limited to the mineral soil at 15°C (Figure 2f). During the periods between 363 and 774 days and between 774 and 924 days, the negative effect of N was significant for the mineral soils at 5°C (Figures 2c and 2d) ($F_{1,\ 9}$ value = 9.0; $P = 0.0152$ and $F_{1,\ 9}$ value = 15.1; $P = 0.0037$, respectively) and 15°C (Figures 2g and 2h) ($F_{1,\ 9}$ value = 18.6; $P = 0.0019$ and $F_{1,\ 9}$ value = 9.5; $P = 0.0130$, respectively), and for the organic soils at 5°C (Figures 2c and 2d) ($F_{1,\ 8}$ value = 4.5; $P = 0.0669$ and $F_{1,\ 8}$ value = 6.5; $P = 0.0344$, respectively).

[23] Using fixed sampling dates to compare treatment effects on instantaneous fluxes also incorporates the effects of treatment accumulated through time. To disentangle this, we tested the effect of N on instantaneous C flux rate over four periods based on the cumulative amount of C lost (i.e., 0–25%, 25% to 50%, 50% to 75%, and 75% to 100%, normalized to the treatment that lost the least total C set equal to 100%). During the first period (0–25% C lost), there was only a positive significant effect ($F_{1,\ 8}$ value = 6.1; $P = 0.0387$) of N for the organic soils at 15°C (Figure 3e). In the period where 25% to 50% C was lost, the effect of N on instantaneous C flux rate was negative and limited to the mineral soil at 15°C (Figure 3f) ($F_{1,\ 9}$ value = 8.2; $P = 0.0019$) and organic at 5°C (Figure 3b) ($F_{1,\ 8}$ value = 8.7; $P = 0.0019$). In the period where 50% to 75% of the C was lost, the negative effect of N on instantaneous C flux rate was significant for the mineral soils at 5°C (Figure 3c) ($F_{1,\ 9}$ value = 5.2; $P = 0.0485$) and 15°C (Figure 3g) ($F_{1,\ 9}$ value = 17.5; $P = 0.0024$). Finally, for the period where 75% to 100% of the C was lost, the negative effect of N was significant for the mineral soils at 15°C (Figure 3h) ($F_{1,\ 9}$ value = 30.9; $P = 0.0004$) and marginally significant for the organic soil at 5°C (Figure 3d) ($F_{1,\ 8}$ value = 3.9; $P = 0.0854$).

Table 3. Mean Microbial Biomass (±SE) (μg N g C^{-1}) During a Laboratory Incubation of Soils at 15°C and Two Nitrogen Concentrations (Water Addition and Water Plus Nitrogen)[a]

Soil Types	15°C, Control	15°C, Nitrogen
	Organic Soils	
BFUO	1983.9 (988.1)	2172.3 (692.9)
TAO	1684.2 (275.4)	3771.5 (1505.2)
TNAO	1727.9 (697.7)	2075.9 (1098.1)
	Mineral Soils	
BFM	2051.7 (409.7)	1512.9 (169.5)
BFUM	1912.6 (770.5)	2311.3 (880.9)
TAM	328.8 (123.6)	432.8 (174.9)
TNAM	410.4 (75.3)	584.4 (41.5)

[a]Soils were collected from organic and mineral horizons of moist acidic and nonacidic tundra near Toolik Lake and of boreal forests in interior Alaska. A two-way mixed ANOVA nested model: nitrogen (factor) $F_{1,\ 19} = 2.5$, P = 0.1289; depth (factor) $F_{1,\ 19} = 109.3$, $P < 0.0001$; the interaction of nitrogen and depth was not significant.

[24] Microbial biomass N was only measured at 15°C in the 3 month incubation; on per carbon basis, it was significantly higher in organic than mineral soils (F value = 7.2; $P = 0.0105$; Table 3). In organic soils, microbial biomass was significantly higher in samples with added N; microbial biomass increased from 1983.9 (i.e., control) to 2172.3 μg N g C^{-1} (i.e., with N), 1684.2 to 3771.5 μg N g C^{-1}, and 1727.9 to 2075.9 μg N g C^{-1} for BFUO, TAO, and TNAO soils, ($F_{1,\ 8}$ value = 6.1; P = 0.0384). Within the mineral soils, boreal soils showed higher microbial biomass than tundra soils ($F_{1,\ 10}$ value = 18.7; P = 0.0015).

[25] For logistic and financial reasons, isotopic measurements were determined on a subset of samples. The solid organic matter δ^{13}C isotope values from Toolik Lake were −26.6 (±0.2), −27.5 (±0.4), −25.8 (±0.7), and −26.5 (±1.0) for the acidic mineral, organic and nonacidic mineral and organic, respectively. Estimated bulk ^{14}C age computed from the soil C isotope value at the same site was 1510 years (±227) for TAM, 3278 years (±386) for TNAM, modern for TAO and TNAO. For respired CO_2, the isotope δ^{13}C-CO_2 across all soil types (boreal and arctic) displayed a soil layer difference ($F_{1,\ 16.6}$ value = 8.1; P = 0.0113) with more depleted values found for the organic soils (Table 4). A direct comparison of the δ^{13}C-CO_2 values over both temperature treatments should take into account that microbes at higher temperatures may be using different C substrates at a fixed time point during the experiment compared to the lower temperature treatment by virtue of the fact that they have respired more cumulative C [*Waldrop and Firestone*, 2004]. To account for this, we also compared the δ^{13}C-CO_2 values using ANCOVA with cumulative respiration as a covariate. Using the ANCOVA, the isotope δ^{13}C-CO_2 neither displayed a temperature nor N effect but still showed a soil layer effect ($F_{1,\ 16.5}$ value = 10.0; P = 0.0027). There was no significant difference between boreal and tundra soils, but when individually tested, TAM showed a marginally significant ($F_{1,\ 7}$ value = 5.0; P = 0.0612) effect of temperature on δ^{13}C-CO_2 values, with more depleted values at 15°C (Table 4).

[26] We tested also the effect of N on Δ^{14}C for all Toolik Lake soils (TAM, TNAM, TNAO, and TAO) and the interaction of nitrogen and temperature on TAO soils only using ANCOVA, with cumulative C respired as a covariate. Mineral soils showed more depleted values than organic soils reflecting the older C ages of these deeper soil layers (Figure 4; $F_{1,\ 7.7}$ value = 37.8; P = 0.0408). Overall, there was no significant effect of N alone on Δ^{14}C ($F_{1,\ 16.8}$ value = 0.4; P = 0.5597). But more specifically, TAO showed a significant temperature and N interaction ($F_{1,\ 8}$ value = 4.8; P = 0.0428), with younger C (higher isotope values) respired at 15°C in the N treatment, while younger C appeared to be respired at 5°C in the control treatment (Figure 4), a result consistent with the C flux data we measured. The $\Delta^{14}CO_2$ also exhibited a general relationship with cumulative respiration; older C was respired with increasing cumulative respiration (R^2 = 0.465; $P < 0.0001$; data not shown).

3.2. Nitrogen Dynamics

[27] To understand the changing effect of added N on N mineralization, we measured multiple aspects of soil N cycling across the experiment to determine differences among soil types. First, the results of a 16 week laboratory incubation of repeatedly leached soils showed no effect of temperature or type of ecosystem (i.e., boreal versus tundra) on cumulative dissolved inorganic N (DIN) production. In addition, N addition had a significant negative effect on net NO_3^- release (χ^2_1 value = 36.4; $P < 0.0001$) and stimulated total inorganic N immobilization (accounting for what was added) (χ^2_1 value = 21.1; $P < 0.0001$) in organic and mineral soils (Figure 5). The results also showed higher NO_3^- immobilization at 15°C and higher NO_3^- (χ^2_1 value = 11.1; P = 0.0009) and inorganic N immobilization (χ^2_1 value = 7.3; P = 0.007)

Table 4. Mean (±SE) Isotopic Measurements of Respiration CO_2 During a Laboratory Incubation at Temperatures 5°C and 15°C and Two Nitrogen Treatments (With or Without)[a]

	5°C, Control		5°C, Nitrogen		15°C, Control		15°C, Nitrogen	
Soil Types	δ^{13}C	Δ^{14}C	δ^{13}C	Δ^{14}C	δ^{13}C	Δ^{14}C	δ^{13}C	Δ^{14}C
BFUO	nd	nd	nd	nd	−24.68 (1.76)	nd	−24.83 (1.01)	nd
TAO	−24.97 (0.59)	184.4 (9.0)	−25.24 (0.80)	138.2 (16.9)	−26.13 (0.53)	153.3 (16.6)	−25.72 (0.56)	198.1 (14.9)
TNAO	−22.36 (1.77)	nd	−22.36 (1.37)	nd	−24.26 (0.82)	65.0 (5.4)	−23.36 (0.71)	69.8 (18.5)
BFM	−20.03 (1.80)	nd	−23.57 (0.53)	nd	−23.74 (0.97)	nd	−23.28 (1.24)	nd
BFUM	nd	nd	nd	nd	−22.47 (1.94)	nd	−21.94 (1.57)	nd
TAM	−20.19 (0.85)	nd	−17.09 (1.81)	nd	−23.01 (1.70)	−96.3 (30.0)	−22.08 (1.78)	−58.6 (19.2)
TNAM	−19.83 (3.20)	nd	−24.13 (2.04)	nd	−19.29 (1.97)	−25.9 (31.9)	−24.17 (3.02)	−89.3 (59.8)

[a]Soils were collected from organic and mineral horizons of moist acidic and nonacidic tundra near Toolik Lake and of boreal forests of interior Alaska; nd, not determined.

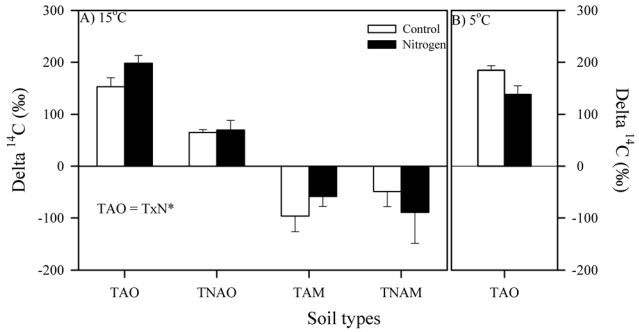

Figure 4. Carbon isotope ratio ($\Delta^{14}C$) of microbial respiration at two incubation temperatures (5°C and 15°C) and two N concentrations (water addition and water plus N) after 90 days into the 924 day laboratory incubation experiment. Soils were collected from organic and mineral horizons of moist acidic and nonacidic tundra near Toolik Lake, Alaska. Three asterisks indicate $P < 0.001$; two asterisks indicate $P < 0.01$; one asterisk indicates $P < 0.05$; NS indicates nonsignificant.

rates in organic than mineral soils. In contrast, effects of added N on leached DON were more variable; soil layer, temperature and N all had significant effects on DON production ($F_{1, 19}$ value = 50.2; $P < 0.0001$, $F_{1, 387}$ value = 7.1; $P = 0.0188$ and $F_{1, 387}$ value = 19.8; $P < 0.0001$, respectively). In general, dissolved organic N was highest in the organic soils (average of five leaching measurements: 78.1 (±6.3) versus 19.2 (±5.8)), at 15°C (53.6 (±6.1) versus 43.7 (±6.1)) and with N addition (61.6 (±6.1) versus 35.7 (±6.1)). No significant difference in DON between boreal and tundra ecosystems were detected ($F_{1, 18}$ value = 3.0; $P = 0.1003$).

[28] In another metric of N cycling, the results of the 3 month laboratory incubation of unleached soils showed, on per unit N basis, higher N mineralization (χ^2_1 value = 4.9; $P = 0.02$) rates in the mineral as compared to the organic soils. This study also showed that in the N addition treatment, net N immobilization increased in all soil layers (χ^2_1 value = 51.8; $P < 0.0001$) with organic soils expressing stronger net N immobilization rates (Figure 6). This result is generally consistent with the effect of added N on respiration in organic soils for the first 100 days. The results showed also no effect of temperature or type of ecosystem on net N nitrification and net N mineralization rates in any soils (Figure 6).

3.3. Substrate Quality and N Cycling Controls Over Respiration

[29] The effects of temperature and added N on patterns of respiration were variable across soils types and through time, and are likely a result of differing quality of soil organic C available for decomposition. There was an overall positive effect of total C on cumulative C mineralization across all soils ($R^2 = 0.491$; $P < 0.0001$) (data not shown). However, when organic and mineral soils were analyzed individually there were no correlations between cumulative C mineralization rates with total C. Likewise, there was an overall negative effect of net N mineralization on cumulative respiration across all soils ($R^2 = 0.479$; $P = 0.001$) (data not shown), but cumulative C mineralization rates from mineral or organic soils alone were not correlated with net

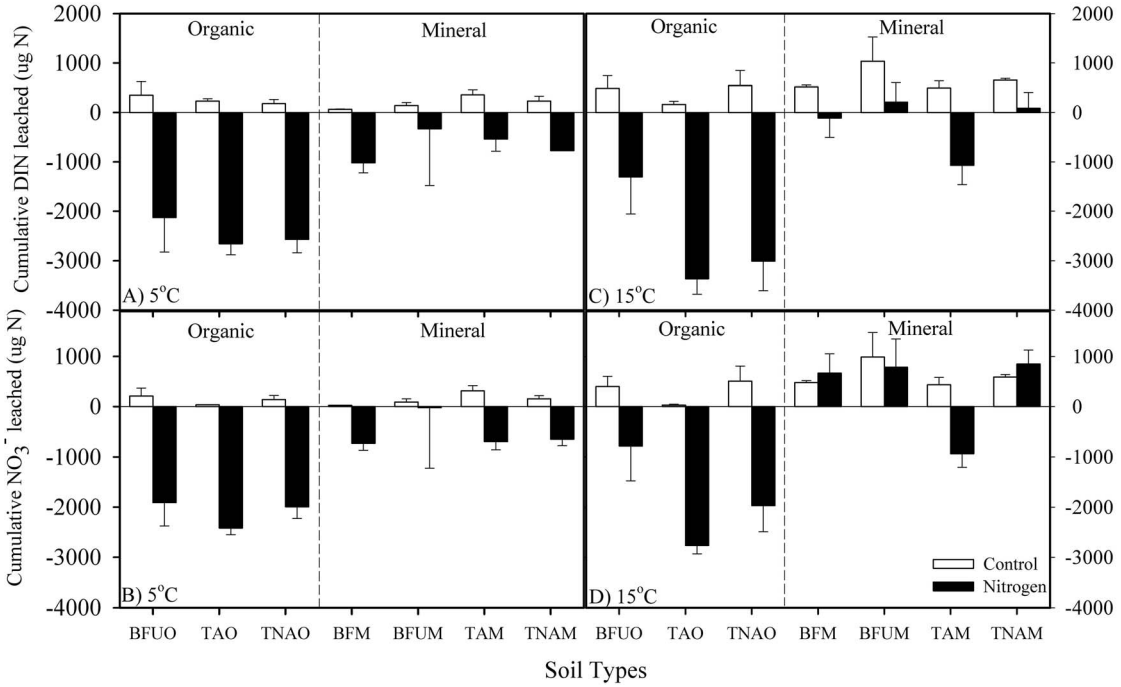

Figure 5. Cumulative dissolved nitrate (NO_3^--N) and inorganic N (NO_3^--N + NH_4^+-N) (μg N) leached from a 16 week laboratory incubation at two temperatures (5°C and 15°C) and two N concentrations (water addition and water plus N). Soils were collected from organic and mineral horizons of moist acidic and nonacidic tundra near Toolik Lake and of boreal forests in interior Alaska.

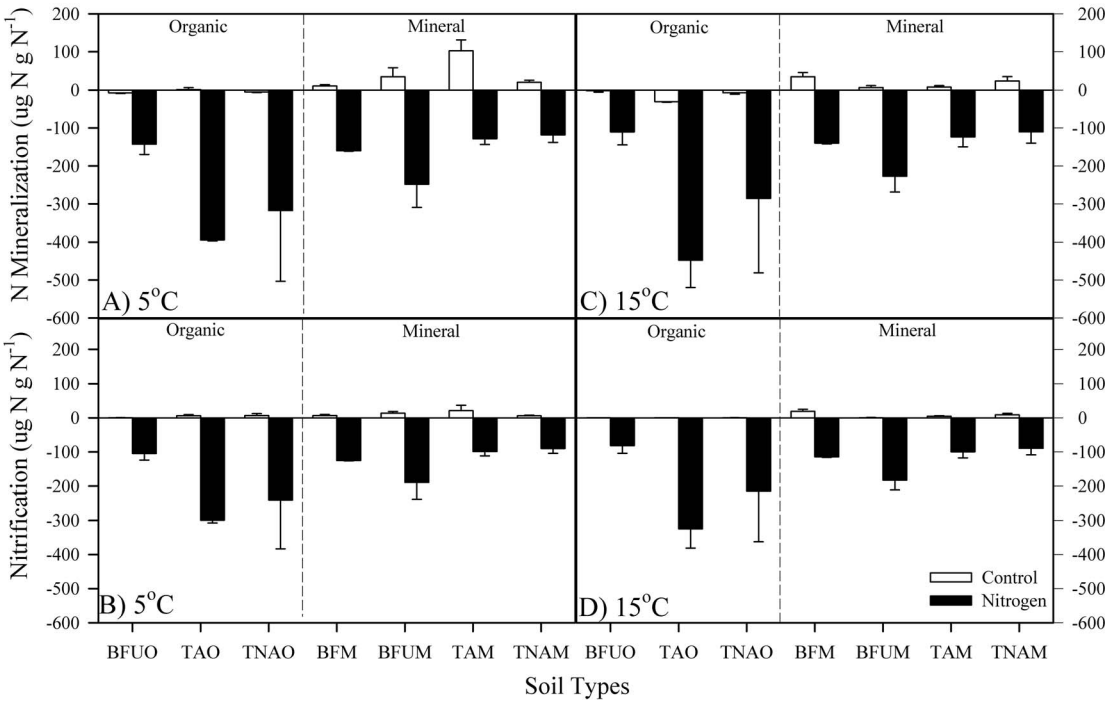

Figure 6. Mean (±SE) cumulative nitrate (NO_3^--N) and inorganic N (NO_3^--N + NH_4^+-N) (μg N g dw^{-1}) from a 3 month laboratory incubations at two temperatures (5°C and 15°C) and two N concentrations (water addition and water plus N). Soils were collected from organic and mineral horizons of moist acidic and nonacidic tundra near Toolik Lake and of boreal forests in interior Alaska.

N mineralization (data not shown). Furthermore, cumulative C mineralization was positively related to bulk soil C:N ratio (R^2 = 0.061; P = 0.0182), preleached dissolved organic (R^2 = 0.542; P < 0.0001) or inorganic N (R^2 = 0.217; P < 0.0001) (before the first N addition), leached dissolved organic (R^2 = 0.437; P < 0.0001) or inorganic N (R^2 = 0.542; P < 0.0001) (average of five measurements), but only when mineral and organic soils were combined (data not shown). There was no relationship between cumulative C mineralization, and initial extractable inorganic N (data not shown).

4. Discussion

[30] This experiment showed that high-latitude SOM decomposition responded positively and consistently to temperature while the response to N addition was more variable through time and across soil types. Interestingly, there were both significant positive and negative effects of N addition. The positive N response was generally most strongly expressed when C respiration rates were high, for example in the organic soils, in the warmer incubation, and at the outset of the experiment. Negative N responses often occurred when C respiration rates were lower, predominantly in mineral soils and at the middle or end of the experiment. In organic soils, where C flux rates responded positively to N addition, we observed high rates of N immobilization.

[31] The amount of respired C was substantially larger in the higher temperature treatments as reported previously in many other laboratory incubation studies [e.g., *Kirschbaum*, 2006; *Reichstein et al.*, 2000; *Rustad et al.*, 2001; *Hobbie et al.*, 2002a; *Dioumaeva et al.*, 2002; *Fierer et al.*, 2003; *Fang et al.*, 2005; *Melillo et al.*, 2002; *Davidson and Janssens*, 2006; *Dutta et al.*, 2006; *Vanhala et al.*, 2008]. In this experiment, a 10°C increase resulted approximately in 2.5 fold change in respiration rate (q^{10} for mineral = 2.55; organic = 2.73) as measured by the amount of cumulative C loss after 1 year of incubation. However, this should be interpreted as the apparent rather than physiological q^{10}. It was within the high-temperature treatment that we observed positive responses to added N. The magnitude of the N response to this rate of N addition was relatively small compared to the effect of a 10°C increase in temperature (Figure 2). The positive response to added N was confined to organic soils and most pronounced within the first 100 days of the experiment when respiration fluxes were highest. These same soils had an inherently high demand for N; they exhibited net N immobilization both in control and N addition treatments. Also, microbial biomass N tended to increase following N addition in the organic soils incubated at the higher temperature, which could indicate that concurrent with increased respiration, there was either an increase in total microbial biomass, or a decrease in the biomass:N ratio. From these results it appears that N limitation of microbial respiration was most apparent when other factors controlling microbial activity (C lability, temperature) were at their maximum within our experiment. This result is consistent with the findings of other studies in temperate [*Månsson and Falkengren-Grerup*, 2003; *Allen and Schlensinger*, 2004) and boreal (*Illeris and Jonasson.*, 1999; *Vance and Chapin*, 2001; *Allison et al.*, 2009] ecosystems but in contrast with other studies that show a lack [*Yoshitake et al.*, 2007a, b; *Buckeridge and Grogan*, 2008] or a negative [*Treseder*, 2008; *Allison et al.*,

2010] effect of N addition on microbial biomass and activity. The opposing responses across these studies may be due to changes in soil organic quality and the opposing effects of N on labile versus recalcitrant C as documented across the range of soil types in this study.

[32] In our experiment, the negative responses of microbial respiration to added N occurred largely in mineral soils and later in the experimental period when respiration fluxes were lower. This negative response manifested earlier in the higher temperature treatment, although it was not detectable at the outset of the experiment. By late in the experiment, the negative effect of N was present in both high- and low-temperature treatments. Mineral soils showed no or low net release of N and addition of N resulted in a stimulation of net N immobilization (after the added N was accounted for) and may reflect increasing microbial growth efficiency in response to increasing availability of exogenous N, although invoking this hypothesis here deserves further scrutiny [*Agren et al.*, 2001; *Fisk and Fahey*, 2001].

[33] There were two soil types that were notable exceptions to the general contrasting pattern between mineral and organic soil types. First, there was a *negative* effect of added N in an *organic* soil (TAO) at the cooler temperature (Figures 2a–2d). Second, there was a *positive* effect of added N in a *mineral* soil (BFUM) at the cooler temperature (Figure 2a–2d). In the TAO soil, this negative response was relatively large in magnitude and consistent over time compared to N effects in other soil types (i.e., TNAO and BFUO). Moreover, this negative response to added N at the cooler temperature was exactly opposite of a relatively strong positive N effect at the warmer temperature in the same soil. Though counterintuitive, the pattern of response in the respiration was corroborated by what we observed with radiocarbon dating of soil respiration. For the TAO at the higher temperature treatment, higher radiocarbon values corresponded to higher cumulative flux within added N. This supports the idea that older, decadally aged C was respired as younger labile C pools were exhausted. This pattern between cumulative respired C and higher radiocarbon values was similar in the TAO incubated at the cooler temperature; higher radiocarbon values corresponded to high cumulative flux, albeit the higher flux was from the control, not the N addition, soil. As for the BFUM soil, this positive effect of N was also relatively important in magnitude compared to N effects in other soil types (e.g., TAM and TNAM) but persisted only through the first year of the experiment.

[34] The results for the organic and mineral soils together support the general idea that decomposition of labile C can be positively stimulated by added N, whereas decomposition of recalcitrant C is generally suppressed [*Neff et al.*, 2002; *Bradford et al.*, 2008]. Because soils contain a mixture of different C pools across a continuum of lability and recalcitrance, the changing response of soils across the incubation period likely represent the changing influence of different pools during different time periods. Indeed, *Cusak et al.* [2010] showed for tropical mineral soils that an increase in soil C following N addition was not uniform among soil C pools. The authors observed that the active labile soil C pool decomposed faster with N fertilization, while the slow recalcitrant C pool had longer turnover times. *Allison et al.* [2010] also inferred a similar pattern in boreal forest soils with an initial loss of soil labile C followed by substrate depletion and lower soil CO_2 respiration. In the same way, the neutral or negative response of mineral soils to added N in our study may have been caused by the negative response of a large recalcitrant pool that masked any response of the labile pool. The negative radiocarbon values of respiration from the two mineral soils that we sampled support the idea that old, slow turnover C dominates this flux in mineral soil.

[35] The temporal pattern of the incubation showed increasing N suppression of respiration over time. By day 100, the labile pool had been largely respired and the whole soil exhibited a negative response to added N; this process took longer in the lower temperature treatment, perhaps because it took longer to deplete the labile pool when microbial rates were lower. In reverse, the positive effect of N that occurred at the outset of the experiment disappeared as the labile pool was depleted. Overall, we expect that N limitation to SOM decomposition will be most pronounced when labile pools are large; this conclusion is supported by the net N immobilization (high N demand due to high C availability) observed in these soils, a finding similar to that of *Vance and Chapin* [2001].

[36] With this general model, it still remains unclear why two soils (i.e., TAO and BFUM) showed opposite effects of N at low versus high temperature. For the BFUM, we could invoke the same model as above, with the idea that the net positive effect of the smaller labile pool is only visible when a small cumulative amount of C has been respired. If the negative effect of N predominates over the course of the incubation for that soil, then that effect might already dominate the first time period at 15°C where there is already more C flux as compared to the 5°C incubation for the same time period, which could still be exhibiting the positive effect of N for the small labile pool.

[37] This model, however, does not explain the response of TAO, where N stimulated respiration at the high temperature, but suppressed respiration at the low temperature, which is probably closer to the field temperature regime for deep soils. The mineral soils from this ecosystem, by contrast, were unresponsive to N addition. The original motivation for this study was to examine the direct effects of added N on the decomposition of soils from moist acidic tundra, where field additions of N and P stimulated C loss from deep organic and mineral soils [*Mack et al.*, 2004]. It is intriguing that direct nutrient limitation of decomposition, as assayed by the lab experiment, does not fully explain the patterns observed in the field. Other possible mechanisms at work include direct effects of P on decomposition [*Buckeridge and Grogan*, 2008; *Lagerstrom et al.* 2009; *Hartley et al.*, 2010], changes in rhizosphere processes driven by altered plant species composition and rooting depth [*Sullivan et al.*, 2007], and complex changes in microbial community composition [*Fisk and Fahey*, 2001; *Schmidt et al.*, 2004; *Allison et al.*, 2008; *Demoling et al.*, 2008] and extracellular enzyme activity [*Carreiro et al.*, 2000; *Waldrop et al.*, 2004; *Allison et al.*, 2008; *Cusak et al.*, 2010].

5. Conclusion

[38] Our study provides evidence for N limitation of decomposition in high-latitude soils, but this was observed

only under specific conditions: higher temperatures, organic soils, and when labile C availability is high. Nitrogen actually suppressed decomposition when labile C pools were low or had become depleted: the mechanistic explanation for this effect is more challenging to reconcile. The positive and negative effects of N on SOM decomposition together may help explain the variable responses to added N observed across a range of ecosystems that are likely to differ in organic matter quality.

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