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Carbon and Nitrogen Cycling in Soils from Acidic and Nonacidic Tundra with Different Glacial Histories in Northern Alaska

Sarah E. Hobbie,* Tiffany A. Miley, and Marissa S. Weiss

Department of Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Circle, St. Paul, Minnesota 55108, USA

Abstract

Moist acidic and nonacidic tundra are two of the most common vegetation types of the tundra in the northern foothills of the Brooks Range, Alaska, and they differ considerably in vegetation, soil nutrient availability, and soil pH. Both occur on mesic, gentle slopes, but acidic tundra is more common on older glacial surfaces whereas nonacidic tundra is more common on younger surfaces. Although much prior research has focused on moist acidic tundra, nonacidic tundra is still relatively unstudied. We compared rates of soil carbon (C) and nitrogen (N) cycling and their response to warming and changes in moisture in moist acidic tundra on Itkillik I glacial drift (50,000–120,000 years old, pH = 3–4) and moist nonacidic tundra on Itkillik II glacial drift (11,500–60,000 year old, pH = 6–7). We hypothesized that rates of soil C and N cycling would be faster at the nonacidic site because it has a more favorable pH for microbial activity and higher-quality organic matter inputs arising from its greater herbaceous plant production relative to the acidic site. However, in contrast to our hypothesis, in situ soil respiration, as well as respiration, dissolved organic C production, and net N mineralization in laboratory incubations, was greater for soils from the acidic site. Nevertheless, the sites responded similarly to manipulations of temperature and moisture, exhibiting exponential increases in respiration with warming between 4°C and 15°C but surprisingly little sensitivity to changes in moisture between 300% and 700%. Slower soil organic matter decomposition at the nonacidic site likely results from the stabilization of soil organic matter by high concentrations of calcium.

Key words: Alaska; calcium; carbon; decomposition; mineralization; nitrification; nitrogen; pH; respiration; tundra.

Introduction

Boreal and arctic regions presently contain between 20% and 60% of the world's soil carbon (Schlesinger 1977; Post and others 1982, 1985; Gorham 1991; Chapin and Matthews 1992). Predicting the fate of this carbon (C) as the Earth's climate warms, and hence future tundra C balance, has motivated much of the research in tundra regions during the past decade (for example, Oechel and others 1993, 1998; Chapin and others 1995; Chapin and Shaver 1996; Hobbie 1996; Michelsen and others 1996; McKane and others 1997a, b; Hobbie and Chapin 1998; Shaver and others 1998; Jonasson and others 1999; Vourlitis and others 2000). In particular, this research has focused on determining whether arctic regions are likely to exhibit a net gain or loss of C as our climate changes and, if so, over what time scales (Shaver and others 1992; McKane and others 1997a). For example, given the strong nutrient limitation of net primary

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*Corresponding author: e-mail: shobbie@tc.umn.edu

production in arctic tundra, any initial C loss associated with the stimulation of decomposition by warming could be offset by a long-term C gain resulting from the greater plant growth that would arise due to higher nutrient availability (Shaver and others 1992).

Several uncertainties hinder our ability to predict the response of tundra C to climate warming. First, the balance between C gain and loss depends in large part on the sensitivity of decomposition to changes in soil moisture (Oechel and others 1993; McKane and others 1997b). Yet few studies have measured the effects of soil moisture on soil organic matter decomposition. Second, tundra landscapes are extraordinarily heterogeneous in the rates of the processes (net primary production, decomposition, fluxes of methane and dissolved organic C) that influence net ecosystem production (Nadelhoffer and others 1991; Shaver and Chapin 1991; Shaver and others 1996). Yet the underlying mechanisms responsible for this spatial variation remain poorly characterized (Hobbie 1999).

One potential influence on tundra C storage (and its response to climate change) that has received relatively little attention is soil pH. In northern Alaska, landscapes with different soil pH result from variations in a number of complex processes, including loess deposition, cryoturbation (frost heave), and landscape age (Walker and Everett 1991; Walker and others 1994, 1995, 1998; Bockheim and others 1998). In the foothills of the Brooks Range, Alaska, landscape age varies considerably because of the expansion and contraction of mountain glaciers from the Brooks Range during glacial periods (Hamilton 1986, 2002). Plant communities largely reflect this variation in surface age. For example, in the Toolik Lake region, gentle slopes on older landscapes of the Sagavanirktok and Itkillik I glacial advances are dominated by moist acidic tundra, whereas moist nonacidic (circumneutral) tundra occurs on gentle slopes of the younger Itkillik II glacial advance (Walker and others 1994). Moist acidic tundra is the dominant tundra type in the region, making up about 40% of the land area of the Upper Kuparuk River basin (Walker 1998) and has been the focus of a number of ecosystem studies (for example, Oechel 1989; Oechel and others 1994; Chapin 1995; Chapin and Shaver 1996; Hobbie and Chapin 1998; Shaver and others 2001). Moist- nonacidic tundra, the second most common vegetation type in the region, makes up about 17% of the Upper Kuparuk River basin (Walker 1998), but it has been less well-studied from an ecosystem perspective (Walker and others 1994, 1995; Gough and others 2000).

The objective of our study was to compare C and nitrogen (N) cycling, and their sensitivity to temperature and moisture, for soils from moist acidic and nonacidic tundra sites on landscapes with different glacial histories in the northern foothills of the Brooks Range, Alaska, near Toolik Lake. Specifically, we compared moist nonacidic tundra on the Itkillik II glacial drift (approximately 11,500–25,000 years old) with moist acidic tundra on the older (50,000–120,000 years old) Itkillik I drift (Hamilton 2002). Itkillik I and II glacial drifts, along with older glacial drifts, form mosaics of areas with different landscape ages in all of the major river valleys of the Central Brooks Range (Hamilton 1986). Because of the complex processes of cryoturbation that occur in this region, it is unlikely that these sites form a strict chronosequence. However, Itkillik I soils generally have greater profile development, as well as greater quantities of fine-textured particles and greater acidity, than Itkillik II soils, as would be expected in more weathered profiles (Munroe and Bockheim 2001). Parent material at both sites is glacial till with similar lithology (dominated by conglomerate and sandstone, with contributions of limestone) (Hamilton 1986). Because of the underlying permafrost soils are classified as Gelisols (Munroe and Bockheim 2001).

Previous work at the two sites has revealed large differences in soil and plant characteristics that are typical of acidic and nonacidic sites in the region (Walker and others 1994; Munroe and Bockheim 2001). For example, soils at the younger site have a higher pH (around 6) (Gough and others 2000; Hobbie and Gough 2002), more total and available calcium (Ca) and magnesium (Mg), greater cation exchange capacity, higher percent base saturation and lower in situ net N mineralization rates than those at the older site (pH around 4) (Hobbie and Gough 2002). The soil pH measured at the nonacidic site is similar to that reported in other studies of nonacidic tundra and Itkillik II drift (Walker and others 1994; Munroe and Bockheim 2001). This pH is relatively high for its age, as compared to chronosequences on glacial and alluvial deposits in subarctic Alaska (Van Cleve and others 1993; Chapin and others 1994). The relatively high pH likely reflects the slow rate of weathering in soils that are frozen for the majority of the year and remain quite cold during the growing season (Tedrow and Brown 1962). In addition, it may be due to the presence of limestone in the drift (Hamilton 1986) and the influence of cryoturbation (frost churning), which may replenish the surface horizons with base cations and slow the rate of acidification and colo-

Table 1. Total Plant Biomass and Aboveground Net Primary Production (ANPP) and Estimates of Total Soil C Pools in Organic and Mineral Horizons (Active Layer Only) for the Two Sites Based on Previous Studies

	Site	
Parameter	Old, Acidic	Young, Nonacidic
Aboveground biomass (g/m^2)[a]	492 ± 11	375 ± 11
Belowground biomass (g/m^2)[a]	352 ± 62	229 ± 24
Total biomass (g/m^2)[a]	844 ± 62	604 ± 36
Vascular ANPP ($g\ m^{-2}\ y^{-1}$)[a]	147 ± 9	127 ± 15
Soil C (%)[b]		
Organic	34.8 ± 1.2	34.8 ± 1.0
Mineral	3.5 ± 0.2	3.7 ± 0.6
Bulk density (g/m^3)[b]		
Organic	0.08 ± 0.01	0.13 ± 0.02
Mineral	0.93 ± 0.10	1.00 ± 0.08
Horizon thickness (cm)[c]	13.4 ± 0.5	15.5 ± 0.4
Maximum thaw depth (cm)[c]	38.8 ± 0.8	38.4 ± 0.5
Total soil C (g/m^2)[d]		
Organic	373	701
Mineral	827	847

ANPP, aboveground net primary production
Values are means ± SE.
[a]*S. E. Hobbie, L. Gough, G. R. Shaver (unpublished); values are means of measurements made in 2000 and 2001. Belowground biomass includes rhizomes but excludes roots.*
[b]*Hobbie and Gough (2002)*
[c]*Gough and others (2000)*
[d]*Total soil C was estimated by multiplying the C concentration by the bulk density and the horizon thickness for each horizon. Mineral horizon thickness (in the active layer) was assumed to be equal to maximum thaw depth minus the organic horizon thickness.*

nization by *Sphagnum* mosses (Walker and others 1998).

The moist nonacidic site has relatively more diverse and abundant graminoids and forbs than the acidic site (Gough and others 2000). Dwarf shrubs such as *Dryas integrifolia, Rhododendron lapponicum*, and *Salix arctica* are present, along with minerotrophic mosses such as *Tomenthypnum nitens*. The acidic site is dominated by the tussock-forming sedge *Eriophorum vaginatum*, dwarf shrubs such as *Betula nana* and *Ledum palustre*, and acidophilic mosses such as *Sphagnum* spp. Such vegetation differences are typical of moist nonacidic and acidic tundra in the Toolik Lake region (Walker and others 1994) as well as areas further north (Walker and others 1998). Plant biomass (both above- and belowground) is higher at the acidic site (Table 1) (S. E. Hobbie, L. Gough, G. R. Shaver unpublished), consistent with higher Normalized Difference Vegetarian Index (NDVI0 and biomass in moist acidic tundra sites relative to nonacidic sites in the Toolik Lake region generally (Walker and others 1995). However, aboveground net primary production (ANPP) does not differ significantly between sites (Table 1) (S. E. Hobbie, L. Gough, G. R. Shaver unpublished).

We hypothesized that soil organic matter decomposition would be faster on the younger surface, both because of higher-quality organic matter inputs to soils (that is relatively more herbaceous production) and a more favorable pH for microbial activity. Herbaceous litter has been shown to decompose relatively quickly, whereas the *Sphagnum* mosses and woody litter produced by the dwarf shrubs common on the older site decompose very slowly (Hobbie 1996). Numerous studies have demonstrated that circumneutral pH promotes litter decomposition, microbial biomass, and soil respiration relative to acidic pH (Foster and others 1980; Cook and others 1985; Francis 1989; Persson and others 1989; Visser and Parkinson 1989; Bauhus and others 1993; Condron and others 1993; Andersson and others 1994, 2000; Baath and Arnebrandt 1994; Khanna and others 1994; Thirukkumaran and Morrison 1996; Anderson and Joergensen 1997; Neale and others 1997; Chan and Heenan 1999; Bergman and others 2000; Webster and others 2000).

To test our hypothesis, we measured in situ soil respiration at both sites during one growing season and performed short-term (28-day) and long-term (approximately 7-month) laboratory incubations

comparing soil respiration, net N mineralization, net nitrification, nitrification potential, and production of dissolved organic C (DOC) for the soils from the two sites. We also examined the temperature response of these processes, as well as the moisture response of soil organic matter decomposition at the two sites.

Materials and Methods

Site Description and Collection of Soils

We measured in situ respiration and collected soils for laboratory measurements of C and N cycling from two sites close to the Toolik Lake Research Station (68°38′N, 149°43′W, elevation 760 m), one on each of the two glacial surfaces. One site is located on the south side of Toolik Lake, on Itkillik I glacial drift (50,000–120,000 years old); the other is located on the north side of Toolik Lake, on Itkillik II glacial drift (11,500–25,000 years old) (Hamilton 2002). Both are upland sites on gentle, north-facing slopes with mesic soils as a result of underlying permafrost. The older site is characterized by moist acidic tussock tundra (Walker and others 1994, 1995) and has been the site of extensive prior research, as well as ongoing experiments by the arctic Long-Term Ecological Research (LTER) project (Hobbie and Chapin 1996, 1998; Gough and others 2000). The younger site is characterized by moist nonacidic tussock tundra (Walker and others 1994, 1995) and has been less well studied (but see Gough and others 2000; Hobbie and Gough 2002).

Soils for the laboratory incubations were collected in August 1999 by obtaining three cores of peat from 10–15 locations spaced 5 m apart along transects at each site. Monoliths of O-horizon soils were collected using a serrated knife to a depth of 10 cm from the transition from live to dead moss. This transition was determined primarily by color (green versus brown), as well as the integrity of the tissues. The top 10 cm of soil contains more than 90% of root biomass (Hobbie and Chapin 1998) and is presumably the site of greatest biological activity in these cold soils. Organic matter depths are slightly deeper than 10 cm on average (Table 1) (Gough and others 2000). Soils were frozen, transported to the University of Minnesota, temporarily thawed to remove obvious roots and homogenize all soil cores within a site, and refrozen until early March 2000. Homogenization was necessary to make it feasible to establish the moisture treatments. These soils were frozen for approximately the same duration that they would have remained so in situ.

For the actual experiment, homogenized soils from each site were subsampled for long-term (approximately 7-month) incubations to determine soil respiration rates and dissolved inorganic N (DIN) and DOC production and for short-term (28-day) incubations to determine net N mineralization and nitrification potential with various treatments. In addition, three to five replicate subsamples from each site were used to determine gravimetric soil moisture, C and N (NA 1500 NCS Analyzer, Carlo-Erba Instruments, Milan Italy), organic matter content (by ashing for 1 h at 500°C), and pH in water and 0.01 M $CaCl_2$ (50 ml:5 g soil) (Orion 420A, Orion Instruments, Beverly, Massachusetts). Three replicate subsamples from each site were also analyzed for total phosphorus (P), Ca, potassium (K), and Mg by nitric acid digestion, followed by inductively coupled argon plasma optical emission spectrometery (ICP) (Applied Research Laboratory 3560, Thermo Electron, Franklin, Massachusetts) at the Research Analytical Laboratory, University of Minnesota, St. Paul, Minnesota.

Respiration

In August 1999, we installed PVC collars (10 cm deep, 10.16-cm diameter) at four points along each of two transects running perpendicular to the slope at each site. The points were located at least 6 m apart. At each of the eight points, a pair of adjacent collars was installed to serve as subreplicates. Measurements from adjacent collars were averaged for the statistical analyses. We installed the collars by cutting vertically into the peat with a serrated knife and placing them so that their tops were level with the moss surface. We clipped all vascular vegetation, as well as green moss biomass, to the soil or brown moss surface. We repeated clipping as needed during the subsequent growing season.

During summer 2000, we measured soil respiration on all collars nine times over the growing season (from mid-June until mid-August) using a LICOR 6400 infrared gas analyzer. Measurements were made at the young site on 18 June, 21–22 June, 28 June, 4–5 July, 12 July, 21 July, 22 July, 3 August, and 8 August and at the older site on 20 June, 23–24 June, 6–7 July, 11 July, 13 July, 18–19 July, 27 July, 4–5 August, and 8 August. Concurrent with the soil respiration measurements, we measured the soil temperature at 5 cm below the moss surface and thaw depth using a stainless steel probe (LI-COR, Inc., Lincoln, Nebraska). Although we did not measure soil moisture, previous work suggests that the sites differ little in soil moisture (L. Gough unpublished). Soil respiration was compared between sites with analysis of covariance

(ANCOVA) using means for each date as observations, with temperature and thaw depth as covariates.

To compare the substrate quality between the two sites more directly and to determine the influence of temperature and moisture on respiration, we conducted laboratory incubations with field-collected soils. Five-gram samples (dry weight equivalent) were placed into 120-ml polyethylene specimen cups that were in turn placed into one-quart wide-mouth Mason jars and covered with polyethylene film. Treatments were as follows: 4°C, 9°C, and 15°C; 300%, 500% (ambient), and 700% gravimetric moisture. Temperature and moisture treatments were crossed in a fully factorial manner. Six replicate jars were incubated for each treatment combination, for a total of 120 jars. We established temperature treatments using dark incubators (Percival Scientific, Perry, IA, USA). Soil moisture treatments were established by adding deionized water or by drying down soils to achieve the desired moisture content. Deionized water was added as needed throughout the experiment to maintain the moisture treatments. The 4°C temperature treatment approximates ambient soil temperature during the growing season in moist tundra (for example, see Hobbie and Chapin 1998); 9°C and 15°C represent warming treatments. The moisture treatments bracket ambient soil moisture at the two sites. Initial gravimetric moisture contents were 496% for the nonacidic site and 502% for the acidic site, similar to other growing season measurements made at the two sties (451 ± 44% and 537 ± 84% for the organic horizons of nonacidic and acidic tundra, respectively, L. Gough unpublished). Thus, 300% represents a drying treatment and 700% represents a wetting treatment at both sites.

We measured soil respiration after 7, 13, 26, 47, 75, 88, 174, and 216 days. At each date, we replaced the polyethylene film with a Mason jar lid fitted with a two-way stopcock. Initial and final (24 h) samples of the headspace were withdrawn using a syringe and immediately analyzed for CO_2 concentrations on a gas chromatograph (Shimadzu GC14A; Shimadzu Scientific Instruments, Wood Dale, IL, USA) using a thermal conductivity detector and a Poropak N column. We calculated the respiration rate from the change in CO_2 concentration in the headspace over time. Cumulative respiration was calculated by determining the average respiration rate for each interval between sampling, multiplying this rate by the duration of the sampling interval, and summing all intervals. We expressed rates on a per gram soil and per gram C basis. Rates expressed on a per gram C basis were corrected for respiratory C losses throughout the experiment. Between measurement dates, the lid of the Mason jar was replaced by polyethylene film.

DIN and DOC Production

To determine the influence of temperature and site on the production of inorganic N and dissolved organic C, additional 5-g subsamples were placed into modified Corning bottletop filtration units for repeated leaching with deionized water (Stanford and Smith 1972; Nadelhoffer 1990). Six replicate subsamples from each site were incubated at each of the three temperature treatments, 4°C, 9°C, and 15°C.

Filtration units were modified by replacing the manufacturer's membrane with ashed Whatman GF/F filter paper and fitting a short piece of tubing with a two-way stopcock to the outlet port. We placed each filtration unit into a one-quart wide-mouth Mason jar and covered the jar with polyethylene. We measured soil respiration from these incubations similarly and on the same dates as those incubations previously described. In addition, 1 day after each respiration measurement, we leached each soil sample with deionized water by adding 100 ml of water to the incubation (equilibrated to the appropriate incubation temperature), allowing it to incubate for 1 h, and then letting it drain to field capacity (against gravity). The volume of leachate was recorded (always close to 100 ml), and the leachate was syringe-filtered through ashed GF/F filters and frozen for analysis.

We analyzed the leachate for DIN (NH_4^+ and NO_3^-) colorimetrically on an Alpkem autoanalyzer (OI Analytical, College Station, TX, USA). Dissolved organic C was determined on a Shimadzu TOC/TIC analyzer (Shimadzu Scientific Instruments). Concentrations of DIN and DOC were multiplied by the leachate volume to determine the total production of DIN and DOC at each sampling date. To determine cumulative DIN and DOC production, we summed production at all sampling dates. Cumulative respiration rates per gram soil C from leached soils were corrected for DOC losses throughout the experiment. Gravimetric soil moisture was measured on leached incubations after the final leaching.

Net N Mineralization and Nitrification

In addition to measuring the production of inorganic N over the course of the experiment by repeated leaching, we conducted short-term (28-day) laboratory incubations to measure net N mineralization and nitrification rates, as well as nitrification

Table 2. Soil Characteristics of Younger, Nonacidic and Older, Acidic Moist Tussock Tundra

Soil Characteristic	Site	
	Older Acidic	Younger Nonacidic
% Organic Matter	91.2	80.4
pH (0.01 M $CaCl_2$)	3.9	7.1
pH (H_2O)	4.7	7.4
% C	45.58	37.34
% N	1.09	1.55
C:N	41.90	24.09
% P	0.08	0.10
% Ca	0.27	3.30
% K	0.09	0.05
% Mg	0.07	0.16

C, carbon; N, nitrogen; P, phosphorus; Ca, calcium; K, potassium; Mg, magnesium
n = 3 *for total element and organic matter concentrations*
n = 2 *for pH*

potential. When the experiment was initiated, five 5-g (dry weight) subsamples of soil from each site were immediately extracted with 50 ml 2 M KCl, shaken for 2 h, and vacuum-filtered through preleached Whatman GF/A filter paper. Additional subsamples were incubated at 4°C, 9°C, and 15°C. Six replicate subsamples were incubated for each treatment. Soils were placed into polyethylene specimen cups and covered with polyethylene film for incubation. After 28 days, we extracted these samples with 2 M KCl. Extracts were analyzed for NH_4^+ and NO_3^- on an Alpkem autoanalyzer.

Six replicate samples from each site were incubated for 30 days at 4°C, 9°C, and 15°C, after which we determined their nitrification potential. We determined nitrification potential using a 24-h aerobic slurry in a neutral (pH 7.2) high NH_4^+ (18 mg N/L) potassium phosphate buffer (Hart and others 1994). We added 5 g dry soil equivalent to 100 ml of buffer and placed the flasks on a shaker table. After 2, 8, 14, and 24 h, we sampled 10 ml of slurry, centrifuged the slurry, and collected the supernatant for analysis of NO_3^-. Nitrification potential was calculated from the increase in NO_3^- over the 24-h period. Because samples incubated at higher temperatures exhibited nonlinear changes in NO_3^- over time, we report only nitrification potential results from the 4°C incubations.

Results

Soils from the younger site had lower organic matter content, higher pH, lower % C, lower C:N ratios, and 10-fold higher % total Ca than soils from the older site (Table 2). Site differences in total Ca and pH reported here are similar to previous work at these two sites that, in addition, demonstrated higher exchangeable Ca at the nonacidic site (Hobbie and Gough 2002).

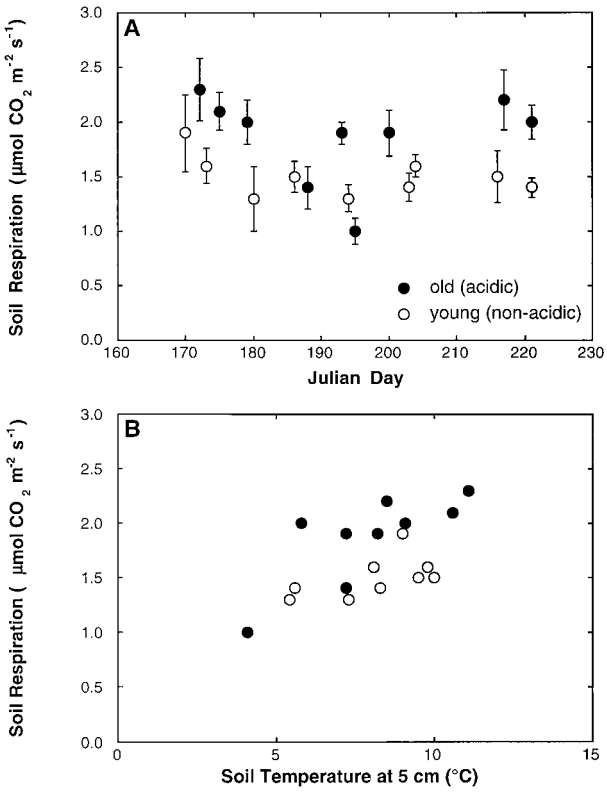

Figure 1. (**A**) Rates of in situ soil respiration were measured nine times during the growing season at the two sites. Values are means with standard error (SE) bars. (**B**) Rates of in situ soil respiration plotted against soil temperature at a depth of 5 cm below the moss surface. Values are means of all measurements made on a particular date and within a site. Respiration was significantly related to soil temperature, and the acidic site had significantly higher respiration rates than the nonacidic site (see Table 3).

Soil C Cycling

Contrary to our expectations, in situ soil respiration rates were lower at the younger site than at the older one (Figure 1A). The difference between the two sites was significant even when we adjusted for thaw depth and soil temperature using ANCOVA (Table 3). Respiration was positively related to soil temperature (soil temperature was a significant covariate), but respiration was higher at any given soil temperature at the older site than at the younger

Table 3. ANCOVA Comparing in situ Respiration Between Sites with Thaw Depth and Soil Temperature as Covariates

ANCOVA			Site	
Source	*F*	*P*	Acidic Tundra	Nonacidic Tundra
Site	11.05	0.005		
Thaw depth	0.08	0.79	22.2 ± 1.4	23.5 ± 1.0
Soil temperature	13.96	0.002	7.9 ± 0.4	8.2 ± 0.3

Means of all plots at a site for a sampling date were used as observations. When the model was run including the interaction terms between site and thaw depth and site and soil temperature, they were not significant. Seasonal means of temperature (°C) and thaw depth (cm) measured at the time of respiration measurements are indicated for both sites (values are means ± SE).

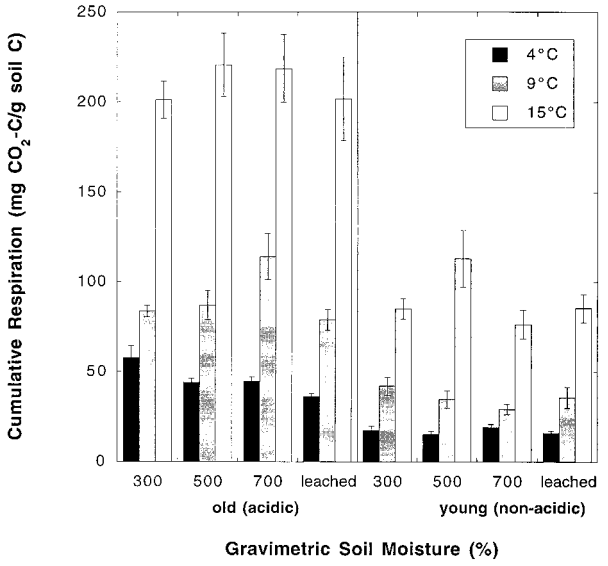

Figure 2. Cumulative C respired by the final sampling date for soils from the two sites incubated at three temperature and three moisture treatments. Data from soils that were repeatedly leached are also shown. Values are means with standard error (SE) bars.

one (Figure 1B, significant site effect in Table 3). In contrast to soil temperature, respiration rates were not affected by thaw depth. Neither seasonally averaged soil temperature nor thaw depth measured at the time of soil respiration measurements differed between sites (Table 3).

Although belowground biomass was higher at the older, acidic site (Table 1) (S. E. Hobbie, L. Gough, G. R. Shaver unpublished), the results from the laboratory incubations suggest that in situ differences resulted in large part from differences in substrate quality. Cumulative respiration per gram soil C was higher in soils from the older site and increased exponentially with temperature (Figure 2). Three-way analysis of variance (ANOVA) comparing ln-transformed respiration rates among sites, temperature treatments and moisture treatments (including leached samples) revealed highly significant site and temperature effects ($F = 501.68_{1,119}$ and $478.98_{2,119}$, respectively, $P < 0.0001$). The only other term in the model that was significant (although weakly so) was the three-way interaction among site, temperature, and moisture ($F = 2.25_{6,119}$, $P = 0.04$). The lack of a significant interaction between site and temperature was due to the ln-transformation of the data before analysis and reflected the exponential response of respiration to temperature at both sites.

Daily respiration rates initially declined, but they then began to increase for the warmer temperature treatments (9°C and 15°C) (Figure 3A, data presented for 500% moisture only). Thus, cumulative respiration did not exhibit the typical asymptotic pattern often observed in long-term incubations (for example, see Pastor and others 1993), but rather continued to increase linearly, and perhaps more than linearly in the 9°C and 15°C treatments for soils from the older site (Figure 3B).

Cumulative DOC leached from the lab incubations reflected site and treatment differences in soil respiration (Figures 4 and 5). DOC production was greater for soils from the older site and increased exponentially with temperature at both sites (two-way ANOVA using ln-transformed values: $F_{1,30} = 591.52$, $P < 0.001$; $F_{2,30} = 85.13$, $P < 0.0001$; $F_{2,30} = 0.18$, $P = 0.84$; for site, temperature, and their interaction, respectively). Cumulative DOC leached from soils during the incubation was significantly related to the cumulative amount of C respired from those same incubations, although C lost through DOC production was an order of magnitude less than C lost through respiration (Figure 5). The slope of the relationship between cumulative respiration and cumulative DOC production did not differ significantly between sites, but the acidic site had higher DOC production at any given level of respiration (Figure 5, ANCOVA of cumulative DOC production with site as a main effect and cumulative respiration as a covariate, $F_{1,45} = 74.70$ and $F_{1,45} = 52.03$, respectively, $P < 0.0001$ in both cases; when the model was run including the interaction term between site and respiration, it was not significant). Gravimetric moisture measured in leached soils after the final leaching were 900% (SE = 57) and 547% (SE = 29) for the acidic and nonacidic sites, respectively.

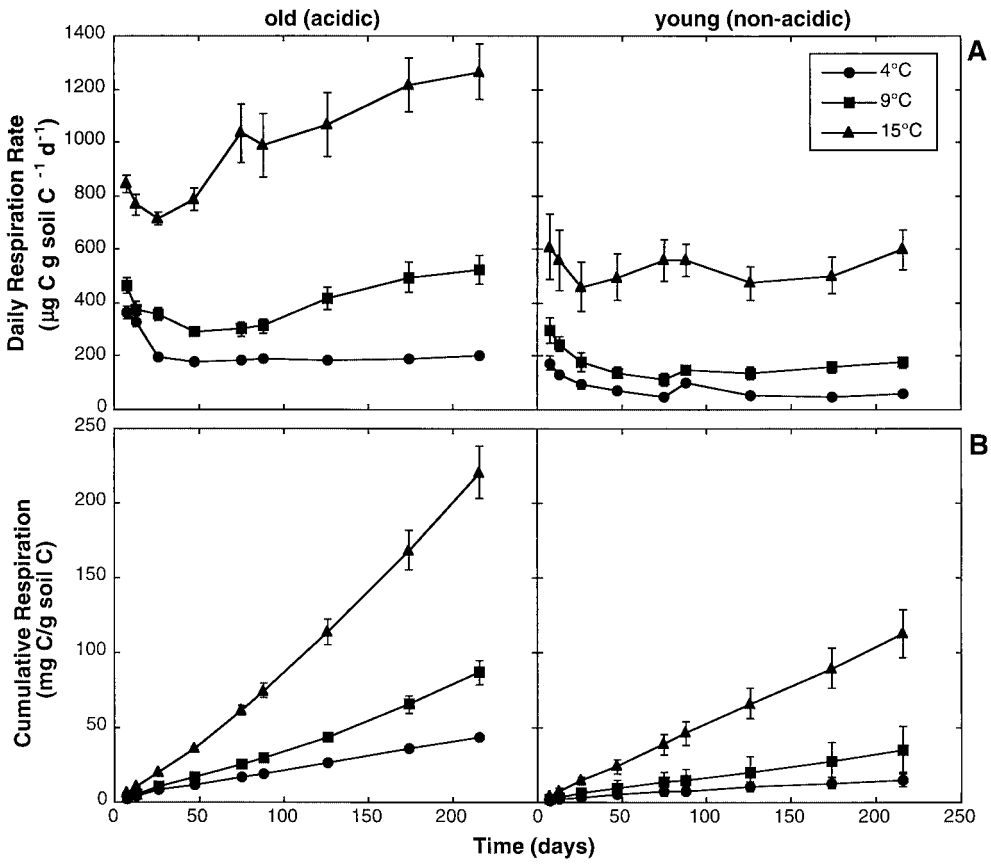

Figure 3. (A) Daily respiration rates and (B) cumulative respiration measured in laboratory incubations at three temperatures for soils from the two sites. For simplicity, and because there was little difference among moisture treatments, only the data for the 500% moisture treatment are presented. Values are means with standard error (SE) bars.

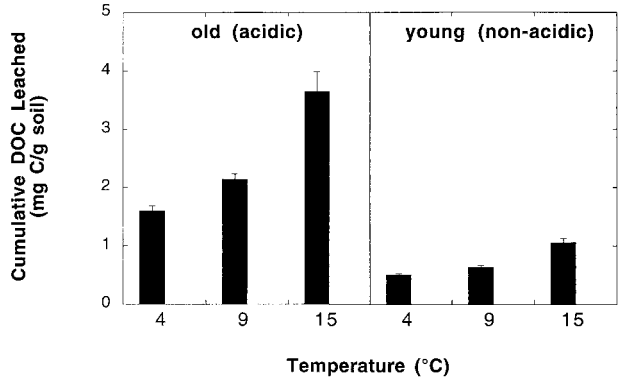

Figure 4. Cumulative dissolved organic C leached from incubations by the final sampling date for soils from the two sites that were incubated at three temperatures.

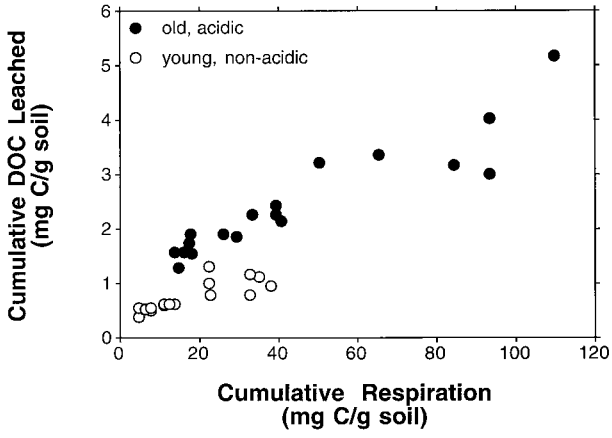

Figure 5. Dissolved organic C leached plotted against C respired. Data from all three temperature treatments are included for each site and represent cumulative C leached or respired from incubations by the final sampling date. There was a significant relationship between cumulative DOC leached and cumulative C respired, as well as a significant difference between sites adjusting for site differences in respiration (ANCOVA of cumulative DOC production with site as a main effect and cumulative respiration as a covariate, $F_{1,45} = 74.70$ and $F_{1,45} = 52.03$, respectively, $P < 0.0001$ in both cases; when the model was run including the interaction term between site and respiration, it was not significant).

N Cycling

During the 28-day incubations, soils from both sites exhibited net N immobilization at all temperatures (Figure 6). However, soils from the younger sites showed greater net N immobilization than soils from the older site, and temperature did not significantly affect N immobilization at either site (two-way ANOVA: $F_{1,30} = 506.89$, $P < 0.0001$; $F_{2,30} =$

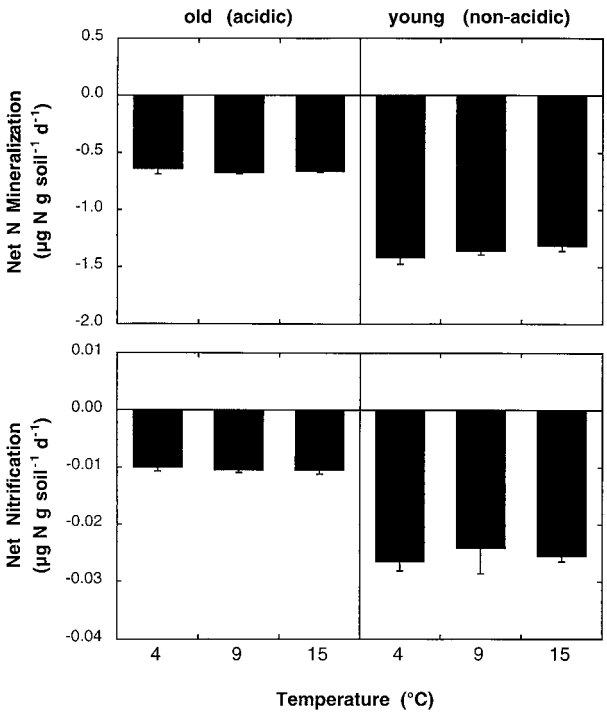

Figure 6. Net N mineralization and nitrification rates from short-term (28-day) aerobic incubations of soils from both sites incubated at three temperatures. Values are means with standard error (SE) bars.

0.66, $P = 0.52$; $F_{2,30} = 1.36$, $P = 0.27$; for site, temperature, and their interaction, respectively). Soils from both sites also immobilized nitrate, exhibiting negative net nitrification rates over the 28-day incubation (Figure 6). As with net N mineralization, net nitrification did not respond to increased temperature (two-way ANOVA: $F_{1,30} = 120.22$, $P < 0.0001$; $F_{2,30} = 0.15$, $P = 0.86$; $F_{2,30} = 0.28$, $P = 0.76$; for site, temperature, and their interaction, respectively). Despite more negative nitrification rates in the 28-day incubations in soils from the younger site, these soils had four times greater potential nitrification than soils from the older site ($t = 2.22$, $P = 0.05$) (Table 4).

In contrast to the results of the short-term incubations, cumulative DIN leached from the incubations was greater for soils from the younger site and responded strongly to increased temperature (Figure 7), (two-way ANOVA on ln-transformed data: $F_{1,30} = 9.14$, $P = 0.005$; $F_{2,30} = 31.59$, $P < 0.0001$; $F_{2,30} = 2.34$, $P = 0.11$; for site, temperature, and their interaction, respectively). Greater cumulative DIN leached from warmer incubations resulted from large increases in DIN leached late in the incubation, particularly at the younger site. In fact, the temperature treatments did not differentiate in terms of cumulative DIN production until after about 100 days (Figure 7). The ratio of nitrate to ammonium in cumulative DIN leached by the end of the incubation was essentially zero for soils

Table 4. Nitrate: Ammonium Ratio in Cumulative DIN Leached from Soils from the Two Sites by the End of the Incubation and Nitrification Potentials Determined for Soils from Each Site

	Site	
Parameter	Older Acidic	Younger Nonacidic
Nitrate:Ammonium		
4°C	0.01 ± 0.01	0.71 ± 0.40
9°C	0.00 ± 0.00	4.43 ± 2.03
15°C	0.01 ± 0.01	140.99 ± 43.75
Nitrification potential (μg N g soil^{-1} h^{-1})	0.02 ± 0.01	0.08 ± 0.03

Values are means ± SE.

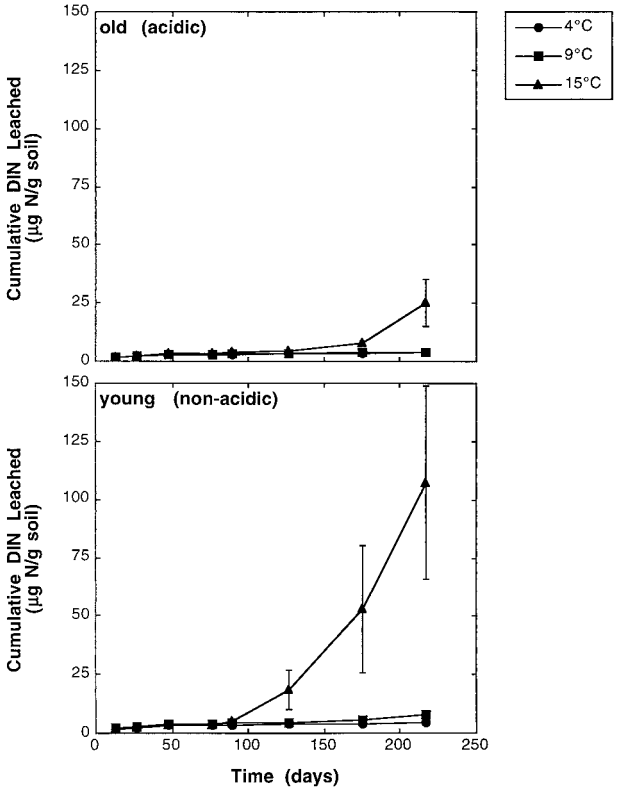

Figure 7. Cumulative dissolved inorganic N leached during laboratory incubations at three temperatures for soils from the two sites. Values are means with standard error (SE) bars.

from the older acidic site (that is, very little nitrate was leached from these soils) (Table 4). However, this ratio was positive for soils from the nonacidic site and increased greatly with increased temperature.

Discussion

Response of C and N Cycling to Climate Change

Despite large differences in C cycling, soils from the two sites responded similarly to increased temperature with exponential increases in respiration, DOC production, and DIN leaching, as has been found in numerous studies of respiration in arctic tundra both in laboratory incubations and in situ (Nadelhoffer and others 1991; Oberbauer and others 1991, 1992, 1996; Hobbie 1996; Grogan and Chapin 1999; Neff and Hooper 2002). In contrast, soil respiration at both sites was insensitive to changes in moisture. Previous studies of litter respiration in the arctic have found that at some sites, litter decomposition declined over the same range of moisture content manipulated here (Flanagan and Veum 1974; Heal and French 1974); while at another site, litter respiration increased between 300% and 500% and remained constant with further increases in moisture (Flanagan and Veum 1974). In situ respiration also responds inconsistently to changes in soil moisture. Some sites exhibit little or no relationship to variation in soil moisture, whereas others exhibit significant correlations with moisture (Oberbauer and others 1991, 1992, 1996). Soil respiration may be less sensitive than litter respiration to changes in moisture because the range of soil water content manipulated here may reflect minimal changes in soil water potential (Gulledge and Schimel 1998). Our results suggest that changes in soil moisture resulting from climate change may be less important in influencing future soil organic matter decomposition than previously assumed (Oechel and others 1993; McKane and others 1997a; Le Dizes and others unpublished). Rather, the direct effects of temperature change on respiration may be more important than the effects of changes in soil moisture, at least within the range of moistures manipulated here.

Patterns of DOC production, as measured by repeated leaching of soils, closely followed those of organic matter decomposition, with greater DOC production at warmer temperatures and at the older site relative to the younger site. DOC production and respiration were tightly correlated across treatments, and warming increased both respiration and DOC production. The tight correlation between CO_2 and DOC production has previously been found in some sites but not in others (reviewed in Neff and Asner 2001). This effect could arise because microbial decomposition simultaneously produces both CO_2 and soluble C compounds or because DOC is a substrate for microbial activity. Alternatively, the same processes that stabilize particulate soil organic matter and make it resistant to decay could also stabilize DOC. Greater stabilization of DOC in soils from the nonacidic site relative to the acidic site is very likely, given the high concentrations of exchangeable Ca^{2+} in the nonacidic soils (Hobbie and Gough 2002). Increasing soil Ca^{2+} concentrations have been shown to reduce DOC concentrations because of sorption and precipitation processes (Romkens and others 1996; Romkens and Dolfing 1998; Oste and others 2002).

The response of net N mineralization to increased temperature was less straightforward. Although cumulative DIN production from repeated leaching increased with temperature, short-term (28-day) net N mineralization did not increase, despite a significant increase in respiration with warming over the same time period, suggesting simultaneous increases in both mineralization and immobilization. Production of inorganic N measured by repeated leaching over the same time period also did not differ among temperature treatments (Figure. 7). Previous studies of acidic tussock tundra soils have also found that temperature has little influence early in incubations, especially when the temperature increases are relatively small (Marion and Black 1986; Hobbie 1996). The effects became greater as the incubation progressed, presumably because the store of readily available C was depleted, especially at high temperature and in soils from the nonacidic site, leading to lower immobilization and greater temperature effects on net N mineralization later in the incubation. Greater DIN leaching from the soils of the younger nonacidic site likely also resulted from greater nitrification of mineralized N in the nonacidic soils, since these soils had higher nitrification potentials and much higher nitrate:ammonium ratios in leachate, consistent with their higher pH. Nitrate would leach more easily in water extracts than ammonium because these soils have a relatively high cation exchange capacity.

Our results suggest that tundra soils contain large pools of relatively labile C that have been protected from decomposition by cold temperatures that inhibit microbial activity. Further evidence for this interpretation comes from the time course of respiration during the experiment. At higher tempera-

tures, soils exhibited an initial decline in respiration followed by an increase, rather than the gradual decline in respiration reported from other incubation studies (for example, Pastor and others 1993), suggesting that proportionally more of the organic matter pool decomposed as the incubation progressed. Similar results have been found in other studies of arctic soils (Neff and Hooper 2002; J. P. Schimel personal communication) and stand in sharp contrast to the results reported for temperate and tropical soils. In these warmer soils, there was only a small amount of labile C whose decomposition was sensitive to warming (Giardina and Ryan 2000). These unusual results could be explained by a number of different mechanisms that could not be distinguished in our study, such as lagged expansion of the microbial population, a shift in microbial community structure toward microbes capable of using different C substrates or toward less efficient microbes, or the activation of enzymes by warming (Linkins and others 1984).

Site Differences in C and N Cycling

Rates of respiration (per gram soil and per gram C), DOC production, and short-term net N mineralization were higher at the older acidic site than at the younger nonacidic site, contradicting our hypothesis that microbial activity would be higher in soils from the younger site because of higher substrate quality and a more favorable pH. In fact, respiration rates both in situ and in laboratory incubations, as well as DOC production in laboratory incubations, were much higher in soils from the older site despite its acidic pH, higher C:N ratio, and relatively high abundance of woody species and *Sphagnum* mosses and thus (presumably) low-quality litter inputs. Similarly, short-term net N mineralization rates were higher at the older site, consistent with in situ buried-bag measurements (Hobbie and Gough 2002). Differences between sites in soil organic matter decomposition cannot be explained by differences in environmental conditions such as temperature, moisture, or thaw depth, since soils in laboratory incubations (where those factors were controlled) showed similar between-site differences in respiration. Furthermore, environmental parameters measured here and in other studies (Gough and others 2000; L. Gough unpublished) did not differ between sites. Slower organic matter decomposition at the nonacidic site helps explain the larger soil C pools at that site, despite similar C inputs (that is, ANPP) at the two sites (Table 1).

Higher C losses from the acidic site are somewhat surprising, given the numerous field and laboratory studies demonstrating that increasing pH in acidic soils stimulates microbial biomass and/or activity (Cook and others 1985; Persson and others 1989; Andersson and others 1994; Baath and Arnebrandt 1994; Khanna and others 1994; Kreutzer 1995; Anderson and Joergensen 1997; Neale and others 1997; Chan and Heenan 1999; Webster and others 2000). Nevertheless, some laboratory studies have found that the initial stimulation of respiration by high pH ultimately declines or becomes inhibited as the incubations progress (Muneer and Oades 1989a; Persson and others 1989; Kreutzer 1995; Neale and others 1997). One possible explanation for the contrasting short- versus long-term effects of pH on microbial respiration is that although increasing the pH of acidic soils initially makes conditions more favorable for microbial activity, higher base cation concentrations stabilize organic matter over time. For example, high concentrations of divalent base cations (Ca^{2+} and Mg^{2+}) increase the resistance of soil organic matter to decomposition by forming stable cation bridges among particulate and dissolved organic matter or between organic matter and mineral surfaces (Oades 1988; Muneer and Oades 1989b, 1989a; Romkens and others 1996; Chan and Heenan 1999; Oste and others 2002). This cation stabilization of soil organic matter likely explains why microbial activity was lower at the younger site, since exchangeable Ca^{2+} concentrations are an order of magnitude higher in both the organic and mineral horizons of soils at the younger nonacidic site than they are at the older acidic site (Hobbie and Gough 2002). The slightly higher mineral content of the soils at the younger site (Table 2) may further stabilize soil organic matter at that site relative to the older site, although interactions between organic matter and mineral surfaces are likely minimal in these organic soils.

Conclusions

Despite their similar climates, acidic and nonacidic tundra on adjacent sites with different glacial histories differed greatly in their rates of soil respiration, soil organic matter decomposition, DOC production, net N mineralization, and nitrification. Respiration from soils of both sites increased with warming in situ and in laboratory incubations. In contrast, soil respiration in laboratory incubations was insensitive to both drying and wetting, suggesting that changes in soil moisture arising from future climate warming may have smaller effects on tundra C balance than previously assumed. Production of DOC was strongly related to microbial respiration at both sites. Contrary to our initial hypothesis, the younger nonacidic site had slower rates of soil or-

ganic matter decomposition and net N mineralization (in 28-day laboratory incubations) than the older acidic site. These results indicate that pH differences associated with variation in substrate age may have strong effects on ecosystem C and N cycling and storage, likely because the organic matter in nonacidic soils is stabilized by high concentrations of exchangeable Ca^{2+}. The two sites studied here are similar in plant species composition and soil pH to other acidic and nonacidic sites on the Itkillik I and II surfaces, respectively. Therefore, our results are representative of these different tundra types. Landscape age and its effects on soil pH appear to be an underappreciated source of variation in ecosystem processes in Alaskan tundra.

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