FIRE IN BOREAL BLACK SPRUCE (*PICEA MARIANA* MILL.) FORESTS: RESPIRATION, TEMPERATURE SENSITIVITY, AND BIOAVAILABILITY OF SOIL ORGANIC MATTER

By

Sarah Catherine Masco

RECOMMENDED:

Advisory Committee Chair

Chair, Forest Sciences Department

APPROVED:

Dean, School of Natural Resources and Agriculture Science

Dean of the Graduate School

April 15, 2005

Date

FIRE IN BOREAL BLACK SPRUCE (*PICEA MARIANA* MILL.) FORESTS: RESPIRATION, TEMPERATURE SENSITIVITY, AND BIOAVAILABILITY OF SOIL ORGANIC MATTER

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

Sarah Catherine Masco, B.S.

Fairbanks, Alaska

MAY 2005

Abstract

Boreal forests store large quantities of carbon (C) and currently act as atmospheric C sinks; however, predicted increases in temperature and fire frequency may change the boreal forest from a net C sink to a net source. This study evaluates the response of organic soil C and nitrogen (N) mineralization, and the bioavailability of C and N to burning in non-permafrost upland black spruce stands in interior Alaska. Two years after an experimental wildfire, burned soils were warmer than control soils at all depths measured, and decay of common substrates was greater in the burned than in the control soils. Burned soils had higher concentrations of total C, lignin, N, and mineral N, and lower concentrations of dissolved organic carbon (DOC) and soluble organic matter. However, apparent differences in organic matter quality did not correlate well with respiration metrics. In laboratory incubations, burned soils respired less than control soils, and this difference was entirely due to differences on the first day of the incubation. Mean Q_{10} values ranged from 2.1 to 2.5 and were greater in the burned soils than in the control soils.

Table of Contents

List of Figures

List of Tables

Acknowledgements

Heartfelt thanks are extended to Dr. David Valentine for sage advice, liters of red ink, hours of discussion, and limitless support. I also thank committee members Dr. Steve Sparrow and Dr. Roger Ruess for support, criticism, and all that falls in between. To my unofficial committee members Jason "get out there and do it" Vogel and Evan "just log transform it" Kane, thanks for providing a positive work environment, moral support, and a sounding board for my humble ideas. Special thanks to Dorte Dissing for GIS help, an occasional kick in the rear, and the best advice I ever received- "When you are lonely, don't be afraid to turn out the lights and look up at the stars." For my fruitful research time in Palmer, I thank all the faculty and staff at the Palmer research station, especially Gary Michaelson, Dr. Rudy Candler, and Laurie Wilson who helped me with lab work, ideas, and moral support. And last but not least, thanks to my father, Charley Masco, for endless love, encouragement and "what do you mean you don't want to get a job yet" fatherly advice. This research would not have been possible without funding from the National Science Foundation grant number DEB0080609.

1. Introduction[1]

Terrestrial ecosystems in boreal regions cover less than 17% of the Earth's land area, but contain more than 30% of all soil C in the terrestrial biome (Alexyev and Birdsey 1998, Apps et al. 1993). Presently the boreal forest serves as a net C sink of up to 1 Gt C yr^{-1} (Dong et al. 2003) due to slow decomposition rates related to low mean annual temperatures and poorly drained soils (Paavilainen and Paivanen 1995).

Changing temperature regimes, coupled with predicted increases in disturbance have the potential to turn the boreal forest from a net C sink to a source (Kasischke and Stocks 2000). Work by Kirschbaum (2000) suggests that boreal forest soils may respond more strongly to changes in temperature than temperate soils. Because of the large quantities of C stored in high-latitude soils, which are expected to warm more rapidly than those at lower latitudes, an understanding of temperature response of boreal soils is especially important.

Disturbance, particularly fire, is also predicted to increase in frequency and intensity in boreal forests (Kasischke and Stocks 2000). To fully understand the impact of disturbance on soil CO_2 losses, studies of disturbance impacts on soil properties such as chemical quality of litter, physical and chemical soil environment, soil microbiota, and soil N status are necessary. Changes in these variables contribute to changes in CO_2 fluxes (O'Neill et al. 2002), temperature sensitivity (Kirschbaum 2000), and soil organic matter (SOM) quality (Almendros et al. 1990).

---

[1] Masco, S.C. and Valentine D.W. (prepared for submission Canadian Journal of Forest Research) Fire in boreal black spruce forests: Temperature sensitivity of soil respiration and bioavailability of C.

The objectives of this study were 1) to determine impacts of fire on heterotrophic soil respiration potential, N status, and SOM pools in black spruce forests by comparing *in vitro* soil respiration in soils from different fire disturbance histories, and their relationship to soil temperature; 2) to determine relationship of soil temperature and N regimes to potential heterotrophic soil respiration. To accomplish these, I compared concentrations of nitrogen (N), carbon (C), dissolved organic carbon (DOC), ammonium (NH_4^+), nitrate (NO_3^-), proximate fraction, and mineralization variables (day one respiration rate, average respiration rate, total C respired, net N mineralization rate and net nitrification rate) between the burned and unburned soils. I used regression analyses to examine relationships between N concentration and net mineralization rates in the burned and control soils. In this paper, I examine heterotrophic respiration only and refer to this quantity as 'respiration'. The following hypotheses were tested:

H1: Lower concentration of labile C in the burned soils results in lower temperature sensitivity, because soil microbes are C limited and are less responsive to increases in temperature.

H2: Amount and form of C available for heterotrophic respiration depends on temperature: recalcitrant forms of C become more bioavailable as soils warm following fire.

H3: Lower concentration (g g^{-1}) of labile C in burned soils results in lower respiration rate in burned than in control soils.

2. Background

Aside from the direct effects of volatilization and release of C and nutrients from litter and SOM, deposition of ash, and creation of charcoal (DeBano 1998), fire indirectly affects nutrient cycling in the months and likely years following fire by altering the chemical and physical environment. Impacts of fire on soil properties include a decrease in soil respiration (O'Neill 2002, Pietikainen and Fritze 1992), creation of "pyromorphic humus" or fire altered SOM (Almendros et al. 1990), increase in soil temperature and moisture (Driscoll et al. 1999), decrease in temperature sensitivity (O'Neill 2002), and change in structure, function, and biomass of the microbial community (Andrews et al. 2000, Pietikainen et al. 2000, Fritze et al. 1998, Baath et al. 1995).

While both temperature and moisture are important in controlling soil respiration, temperature often plays the greater role in regulating CO_2 efflux (Buchmann 2000, Bowden et al. 1998, Russell and Voroney 1998). The Q_{10} value, or the magnitude of respiration rate change with a ten-degree temperature increase, has been used to measure temperature sensitivity of soils. It is expressed as:

Eqn 1: $$Q_{10} = \left(K_2 / K_1\right)^{\frac{10}{T_2 - T_1}}$$

Where K_2 and K_1 are the respiration rates at two temperatures T_2 and T_1 (Niklinska 1999, Winkler et al. 1996, Kirschbaum 1995). Others have fitted respiration and temperature data to an exponential model of the form:

Eqn. 2: $K = \beta_o e^{\beta_1 T}$

Eqn. 3: $Q_{10} = e^{10\times\beta_1}$

Where K is the respiration rate, β_0 and β_1 are fitted constants, and T is temperature (Buchmann 2000, Boone et al. 1998). Point-to-point comparisons are simpler to work with and can be calculated using only two temperatures, but assume that the relationship between temperature and respiration is linear. The fitted constants method requires respiration rates for at least three temperatures and involves more complex calculations, and assumes an exponential relationship between respiration rate and temperature.

Q_{10} values for boreal forest soils generally range from 1.5-7.0 across soil horizons and types (Ruess et al. 2003, Vogel 2004, Schlentner and Van Cleve 1985), although temperate organic soil Q_{10} values have been reported as high as 12.9 (reviewed in Kirschbaum 1995). In general, temperature sensitivity of soil respiration has been shown to decrease with increasing mean annual temperature (Reichstein et al. 2000, Ross et al. 1999, reviewed in Kirschbaum 1995).

Bioavailability of SOM has also been shown to affect temperature sensitivity of soil respiration (Dai et al. 2001, Andrews et al. 2000); Verburg et al. (1999) found that temperature sensitivity of decomposition rates decreased with decreasing substrate quality. Others have found that bioavailability of C is temperature sensitive. In arctic tundra soils, Dai et al. (2001) found that lignin degradation increased with temperature; Huang et al. (1998) found similar results for peat soils.

Fire effects on N dynamics have varied; following fire total N concentration has been shown to increase (Dyrness and Norum 1983), stay the same (Pietikainen and Fritze

1992, Dyrness et al. 1989, Dyrness and Norum 1983), or decrease (Smith et al. 2000, Dyrness and Norum 1983). Intensity, patchiness, and time since burn are major factors controlling post fire N status (Smith et al. 2000, Dyrness et al. 1989, Dyrness and Norum 1983). Mechanisms for N change are related to volatilization (DeBano 1998, Dyrness and Norum 1983), deposition of nutrients on soil surface in ash (Smith et al. 2000, Dyrness and Norum 1983), flush of N released from root mortality, lack of uptake of N by plants (Paul and Clark 1996), N losses due to leaching (Paul and Clark 1996), and lack of inputs of new C.

3. Study Area

Interior Alaska is bounded on the south by the Alaska Range and on the north by the Brooks Range; these mountains act as barriers to weather masses, contributing to the continental climate of interior Alaska (low annual precipitation, humidity, and cloudiness, as well as large daily and annual temperature ranges). Specifically, the study area is within the Yukon-Tanana uplands, a region of westward-trending highlands between the Yukon and Tanana rivers, with elevations ranging from 450 to 900 m (Wahrhaftig 1965).

Study sites are located in the 11 km^2 C4 watershed of the 104 km^2 Caribou-Poker Creeks Research Watershed (CPCRW) (65°N, 147°W), part of the Bonanza Creek Long Term Ecological Research (LTER) site, approximately 60 km northeast of Fairbanks, Alaska (Fig. 1). All sites in this study are closed canopy black spruce stands in areas of discontinuous permafrost.

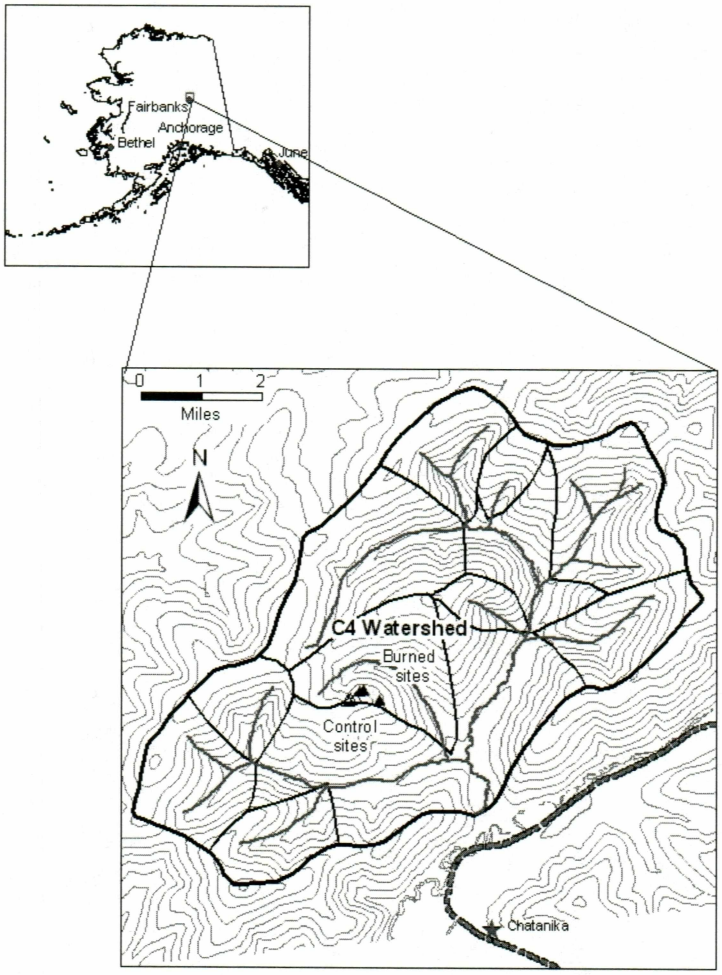

Fig. 1. Burned and Control sites within the C4 watershed at Caribou-Poker Creeks Research Watershed (CPCRW), near Chatanika, Alaska.

3.1 Climate

The mean annual air temperature at CPCRW is –3.3 °C; the watershed experiences cooler summer and warmer winter conditions than Fairbanks, which is 140 m lower than the lowest point in the watershed. Air temperature in Fairbanks ranges from -50 °C to +35°C. July is the warmest month with a mean daily temperature of 16.4 °C, while January is the coldest month with an average daily temperature of –24.9 °C (Haugen et al. 1982). Average annual precipitation in Fairbanks is 269 mm; most of this falls as rain in the summer months (June-August), with the highest monthly precipitation occurring in August (48 mm) (Slaughter and Viereck 1986).

3.2 Geology and Soils

CPCRW is underlain by the Yukon-Tanana metamorphic complex (formerly called Birch Creek schist) with sedimentary protoliths deposited in the late Precambrian to Paleozoic era. The complex in the watershed consists of greenschist facies, micaceous quartzites, garnet-mica schists, phyllites, and possible greenstone or impure marble (Chapman et al. 1971, Hawkins et al. 1982). Interior Alaska was not glaciated in the Illinoisan or Wisconsin glaciation, though it was affected by periglacial action. In quaternary time, wind blown silt from glacier outwash plains and river floodplains was deposited on the hills of interior Alaska. Loess was alternately deposited and eroded throughout the Quaternary era. Permafrost also developed and melted throughout this period (Péwé 1958).

Low mean annual temperature and insulating ground cover contribute to near-surface permafrost development in the study area. Eighteen percent of the C4 watershed is underlain by permafrost (Lotspeich and Slaughter 1977), though my study sites are generally permafrost free (Rieger et al. 1972). The lack of permafrost may be due in part to the shallowness of the forest floor (the soils are shallower than the active layer), but also could be due to warmer winter temperatures on these ridge tops. The soils of the C4 watershed are classified as Typic Cryorthents of the loamy-skeletal, mixed, non-acid family of the Olnes series. The soils in this series are well-drained, lightly weathered shallow soils, overlaying schistic parent material (Rieger et al. 1972).

3.3 Vegetation

Vegetation in the study area includes 60-90 year old stands of birch (*Betula papyrifera* Marsh.) and aspen (*Populus tremuloides* Mich.) on south facing slopes, and older even aged stands of black spruce (*Picea mariana* Mill.) exist on north facing slopes (Viereck et al. 1986). Stands included in this study are upland closed canopy mature black spruce (up to 200 year old), with lingonberry (*Vaccinium vitis idaea* L.), feathermoss species (*Hylocomium splendens* Hedw. B.S.G., *Pleurozium schreberi* (Brid) Mitt.), Labrador tea (*Ledum palustre* ssp. *Decumbens* L.), green alder (*Alnus viridis* ssp. *crispa* Vill.), and willow (*Salix sp.*) species in the understory. All sites in this study are in black spruce, the dominant vegetation type of interior Alaska.

3.4 Fire History

The fire return interval in the boreal forest is estimated to be 50-200 years (Viereck and Schandelmeier 1980, Heinselman 1978). Prior to 1999, the most recent fire in the C4 watershed occurred in 1924, when most of the watershed burned in a stand-destroying fire (Fastie 2000). The C4 watershed was burned in July of 1999 as part of the Frostfire project, a cooperative effort of the US Forest Service, Canadian Forest Service, Alaska Fire Service, Alaska Bureau of Land Management, and NSF-funded researchers at the University of Alaska Fairbanks. The burn was a light patchy burn, loosely defined as a burn that partially consumed the organic layer, and leaves a shallow ash layer on the soil surface (Dyrness and Norum 1983). The fire burned most intensely around the bases of spruce trees and least intensely in depressions (personal observation), resulting in patchiness of fire intensity (Valentine 2000, unpublished data).

4. Methods

4.1 Prefire Data

Pin flags were used to measure organic matter loss due to the experimental burn. The shaft of each flag was given a dogleg shape and then inserted vertically in the soil such that the horizontal portion of the shaft rested on the soil surface (1-meter grid). Following the burn, the distance was measured between the lower bend and the new soil surface. Following the fire, temperature probes were inserted at 5, 10, 20, 30, and 40 cm below the soil surface and data was collected using HOBO data collectors (Onset Corp, Bourne, MA).

4.2 Experimental Design

I used a nested design for this study: two treatments: burned (B) and control (C), three replicate sites per treatment (B1, B3, B4, C1, C2, C3), with five nested points per site. At each of the five randomly selected points I collected three soil cores, which I later bulked into one sample for that point (to reduce heterogeneity among soil sample analyses). Sample size was 15 (3 sites with 5 points each). Random selection resulted in selection of points that had differing burn intensity.

4.3 Soil core collection

I used a 15 cm diameter by 30 cm long stainless steel "cookie cutter" soil corer to collect the soil samples during September 2001. At time of collection, I separated the organic (O) layer qualitatively into three horizons: litter (L) layer consisting of clearly identifiable plant fragments, fiber (F) layer consisting of fibrous partially decomposed plant matter and some humic material, and humic (H) layer consisting of highly decomposed material and no identifiable plant parts (Canadian Soil Classification System, 3rd ed.). I measured the thickness of each layer at three points around the core to calculate volume, which was needed for bulk density determination. Soils were frozen within 6 hours of collection and remained frozen until time of analysis (January 2002- F layer, April 2002- H layer).

4.4 Common Substrates

I placed cellulose filter papers (75 mm Whatman qualitative, fast) and birch tongue depressors (2 cm by 12 cm, hemicellulose, cellulose, and lignin) at each of the sample points in the burned and control sites. Two tongue depressors were inserted vertically, end to end such that they encompassed the L, F, and H layers (they extended down approximately 30 cm). The filter papers were oven dried at 105 °C overnight, weighed, and then inserted into pre-sewn nylon mesh bags (2 filter papers per bag). The filter papers (sized 20 by 12 cm) were also inserted vertically into the organic layer. I collected them 1 year later and oven dried them for 4 days at 105 °C and then weighed, ashed, and re-weighed them to determine ash-free mass loss.

4.5 Laboratory Analyses

The frozen soil cores were weighed, thawed for 24 hours at 4 °C, weighed again, and sieved to 5.6 mm. The coarse and fine fractions were weighed and the coarse fraction was oven dried (105 °C) and reweighed. Moisture content was determined gravimetrically by weighing approximately 4 g (fresh weight) samples before and after drying at 105 °C. I bulked the three cores from each sample point and homogenized them by layer and then analyzed them for total C and N, extractable mineral N ($NH_4^+$and NO_3^-), dissolved organic C, proximate C fractions, and pH. Net N mineralization rates were calculated as the difference in pool size between the incubated and unincubated soils.

4.51 Nutrient Analyses

For total C and N analysis, approximately 0.1 g ball milled (F layer) or ground (H layer) soil subsamples were weighed into tin cups and analyzed on a Leco 1000 CHN analyzer (Leco Corp, St. Joseph, MI). Exchangeable inorganic N was determined by extracting 1.00 g air-dried sieved soil (2 mm) with 20 mL (F layer) or 10 mL (H layer) 2 N KCl and agitating for 30 minutes on an orbital shaker at 200 opm. Extracted solution was then filtered through S&S #710 filter paper into 4 mL plastic autoanalyzer vials. The vials were analyzed on an Orion Scientific auto-analyzer (Bremner 1982). Soil pH was determined on a 1:1 (10.0 g soil and 10.0 g distilled deionized water) using an Orion combination pH electrode (Orion Scientific Instruments).

To determine dissolved organic C, 4.00 g (F layer) or 8.00 g (H layer) air dried soil was added to 250 mL Nalgene centrifuge bottles, 40 mL distilled deionized water was then added and samples were centrifuged at 8000 rpm for 15 minutes. Samples were then vacuum filtered through Gelman Supor ® 450 0.45 micrometer membrane filters and the filtrate collected in 40 mL Kimble glass vials. Extracts were analyzed for dissolved organic C on a Model 700 TOC analyzer (OI Corp, College Station, TX) after diluting them 1:10 to bring concentrations within the measurement range of the TOC analyzer. The DOC analysis was performed on the air-dried soil ~3 months after the soil was thawed, sieved and air-dried.

4.52 Proximate Fraction Analysis

To assess the different forms of organic matter in the burned and control soils, I used a modified Van Soest Digest- the ANKOM Filter Bag Technique (ANKOM Technology Corporation, Macedon, NY; Komarek et al. 1996) to estimate proximate fractions. The analysis consists of a sequence of acid and neutral detergent and sulfuric acid digests, after each of which the remaining sample is weighed. The change in mass is used to calculate the portion of the sample in a particular fraction. Originally a forage fiber analysis technique (Goering and Van Soest 1970, Van Soest 1963), Van Soest digests have been used previously to estimate litter C fractions based on lability (Mafongoya et al. 1998, Sanger et al. 1998, Wieder et al. 1998, Ryan et al. 1990, Cromack 1973). Fractions include neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent lignin (ADL) (Table 1). Proximate fractions produced by Van Soest digests roughly correlate with plant tissue fractions- concentration of soluble, hemicellulose, cellulose, and lignin fractions are determined by difference (Table 1). The proximate fractions are only an estimate of digestibility, actual chemical composition of soil organic matter likely differs greatly from chemical composition of plant tissue fractions described by the digest.

The modified Van Soest technique developed by ANKOM Corporation automates the procedure so that large batches of samples can be run simultaneously, with minimal labor. The major difference is that samples are contained in filter bags that are easily run

Table 1. Proximate fractions estimated by ANKOM proximate carbon fraction analysis.

Fraction	Constituents
100%-NDF	Lipids, sugars, organic acids, pectins, starches, soluble protein, non-protein nitrogen
NDF	Lignocellulose, hemicellulose, cutin, silica
NDF-ADF	Hemicellulose
ADF	Lignin, cellulose, cutin, silica
ADF-ADL	Cellulose
ADL	Lignin, cutin, silica
ADL-ash	Lignin, cutin
ash	Silica

NDF = Neutral Detergent Fiber, ADF = Acid Detergent Fiber, ADL = Acid Detergent Lignin, Ash = mass of sample left after ashing at 550 °C for 8 hours.

Based on Van Soest (1994) and Ryan et al. (1990).

through several sequential procedures. I have not found mention in the literature of use of the filter bag technique on soils.

Prior to digestion, the soil was air-dried and ground through a Wiley Mill (20 Mesh) and then oven dried at 60 °C for 24 hours. A sub-sample was taken and oven dried at 105 °C for a dry matter correction. The filter bags were labeled, weighed and 0.50 g soil was added, and then the bags were sealed with a heat sealer. Bags and blanks were placed into the suspension basket and then into the digestion unit.

For the NDF analysis, 2 L of room temperature neutral detergent solution (sodium dodecyl sulfate, EDTA, disodium, sodium borate, sodium phosphate) was added to the vessel, and samples were then agitated in the digester for one hour at 100 °C. Samples were then rinsed with 8 L of 90 °C distilled water (four rinses in 2 L increments), excess water was pressed out of the bags, and they were immersed in acetone for 5 minutes. Bags were then placed on Kim-wipe covered trays in the fume hood for 30 minutes before drying in the oven overnight at 105 °C.

For the acid detergent fiber (ADF) analysis the post NDF samples were cooled in the desiccator, weighed, and then subjected again to the same procedure as above but using the acid detergent solution (cetyl trimethylammonium bromide in 1 N H_2SO_4).

For the acid detergent lignin (ADL) determination, the post ADF samples were weighed and then the ADL digest was performed by placing the bags and 250 mL of 72% H_2SO_4 into 4 L pickle jars and tumbling them at room temperature for 3 hours. Samples were then rinsed with 90 °C distilled water to remove all acid, then re-rinsed with acetone for 5 minutes and placed on Kim-wipe lined trays for 30 minutes.

Post ADL samples were oven dried overnight at 105 °C, reweighed, placed in pre-weighed crucibles and ashed in the muffle furnace at 550 °C for 8 hours. After allowing the samples to cool to 105 °C, they were placed in a desiccator, cooled to room temperature, and weighed.

For calculating proximate fractions (Komarek 1996):

Eqn. 4: $$\frac{((post\ wt)-(bag\ wt \times blank\ bag\ correction))\times 100}{sample\ wt \times oven\ dry\ mass\ correction}$$

4.53 Incubations

Immediately following thawing and sieving, bulked soils from each layer were sub-sampled and dried at 105° C for at least 12 hours to determine approximate water content at field condition. The remainder of the soil was kept at 4 °C until the start of incubation. Hourly respiration measurements were collected as soon as soils were brought to incubation temperature. Average time between thawing and first measurement was three days. Following sieving, soil samples were transferred to clean 250 mL I Chem ™ incubation jars with modified lids. The soils occupied approximately 20% of the volume of the jar (the mass of soil added to jars varied from 13-24 g soil oven dry weight equivalent for the H layer and 5-8 g soil oven dry weight for the F layer). Sufficient distilled deionized water was added to each jar to bring soils to 60% water holding capacity.

Water holding capacity was determined by placing sub-samples of dry soil in centrifuge tubes, adding water and letting excess drain for 24 hours. Centrifuge tubes

were narrower at the bottom so that the soil did not extend to the bottom. Water collected in the empty space, and the wet soil was scooped out of the tube and was weighed, dried (105 °C), and reweighed. Resulting values of 3.1 g g^{-1} were well within the literature values of 1.5 to 4 g H_2O g^{-1} soil for organic soil (Verburg et al. 1999, Andrews et al. 2000, Bowden et al. 1998). Moisture was maintained by monthly additions of distilled water (spray bottle application) to maintain constant weight.

F and H layers were incubated at 5, 15, and 25 °C for 205 (F) or 133 (H) days. Sampling was performed on the first day, approximately once a week for the first month, then every other week for 4 weeks, and then again after 4 weeks. Sampling was performed using a closed- cycle infrared gas analyzer (IRGA) (Micro-Oxymax Respirometer, Columbus Instruments; Columbus, Ohio). At each sampling date, CO_2 concentration in each chamber was measured once per hour for at least 5 hours, and this time series formed the basis to calculate an hourly respiration rate.

To combine hourly respiration rates and derive a daily respiration estimate, a trimmed means analysis was used on the hourly respiration rate data. All hourly rates were ranked for a given sample in a given day, then top and bottom 10% values were discarded. The remaining values were averaged to yield the respiration rate for that day.

I used two methods to estimate the total amount of C respired by each soil sample for the duration of the incubation: linear interpolation and integration, and regression of fitted nonlinear equation. For the linear interpolation analysis, I assumed that the respiration rate varied linearly between measurement dates. I multiplied the daily respiration rate (μg CO^2-C g C^{-1} day^{-1}) by the number of days between measurements for

each measurement interval and then summed those for the entire incubation period to arrive at a value for total C released over the incubation period.

For the nonlinear regression equation, I used PROC NLIN in SAS (SAS Institute, version 8, Cary NC) to fit the data to the form: $R = ct^b$. Where R is respiration rate (μg CO_2-C g C^{-1} d^{-1}), b and c are fitted constants, t is time (days), and R is total respired C (μg C). I integrated this equation to come up with total respired carbon.

I compared the nonlinear regression and linear interpolation methods and found that the results were of the same magnitude but that the non-linear regression method produced lower values. The R^2 values were not consistently high (some were less than 0.50) so I chose to use the linear interpolation method to estimate evolved CO_2-C.

4.6. Statistical Approach

I analyzed the data for normality using the Shapiro-Wilk test. Nearly all data were normalized with log or square root transformation. However, significance tests for both transformed and non-transformed data yielded the same results for all variables. Therefore, I used untransformed data for all further statistical analyses, unless otherwise noted. I used a nested ANOVA (main factor: treatment) to compare (separately) concentrations of total N, NO_3^-, $NH4^+$, total C, proximate fractions, dissolved organic C (DOC), bulk density (BD), and pH in the unincubated soil from control and burn sites. To accommodate the nested design and missing data from a misplaced soil core, I used the PROC GLM procedure in SAS (SAS Institute, version 8).

To analyze the post incubation data, I used a two-way nested ANOVA with interaction (main factors: treatment and temperature) to analyze the post-incubation values for NO_3^-, $NH4^+$, total mineral N ($NO_3^- + NH_4^+$), net N mineralization rate, net nitrification rate, proximate fraction, change in proximate fraction, average respiration rate, total C respired during entire incubation, and respiration rate on incubation day 1. I also used the 2-way nested ANOVA to compare NO_3^-, $NH4^+$, and total N before and after the incubation in the two treatments.

Removing the interaction term when there was no significant interaction improved the significance of the main effects only slightly, so all statistical results are from the models including interactions. Data presented are mean and standard error of the mean, unless stated otherwise.

5. Results

5.1 Soil Description

5.11 Fire Effects, Temperature Profile, and Common Substrates

Fire intensity was moderate to light (Fig. 2, Fig. 3), and some green trees persisted post burn in all sites. Post burn total organic layer thickness and F layer thickness were not different from control soils, though the L layer was significantly thinner and the H layer significantly thicker in the burned vs. control soils (Fig. 4). Burned sites were warmer than control sites at all depths measured, and the magnitude of difference increased with depth (Fig. 5). Both filter papers and tongue depressors decomposed faster

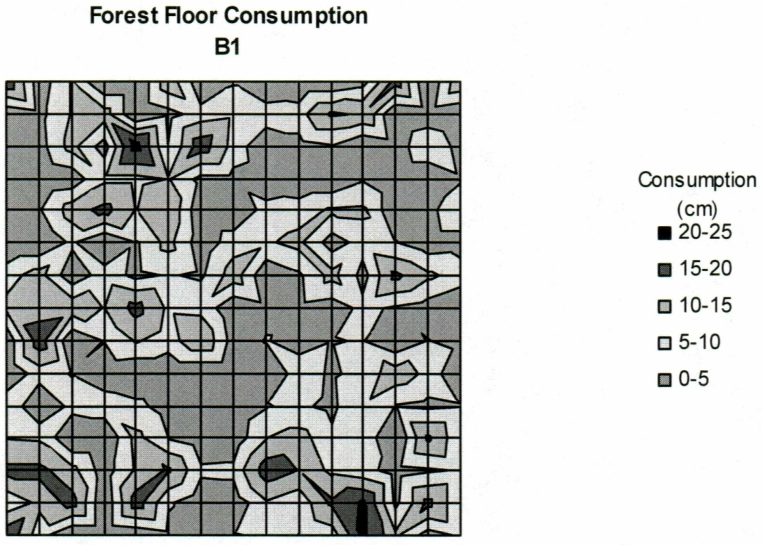

Fig. 2. Burn severity and forest floor consumption in site B1, CPCRW, Alaska as measured by pin flags placed pre-fire (Valentine, unpublished). Grid squares are 2 m by 2 m.

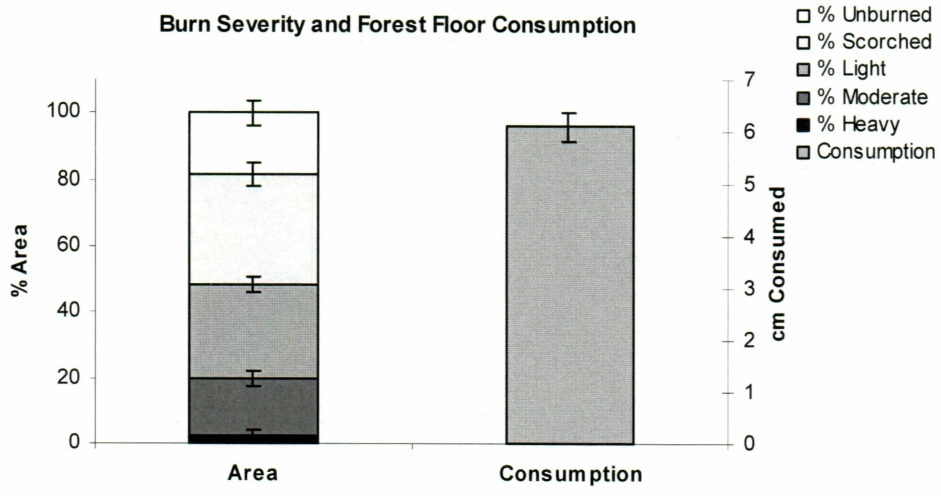

Fig. 3. Burn severity and forest floor consumption, CPCRW, Alaska. Intensity class as described in Dyrness and Norum (1983), n=3. Error bars are standard error of the mean.

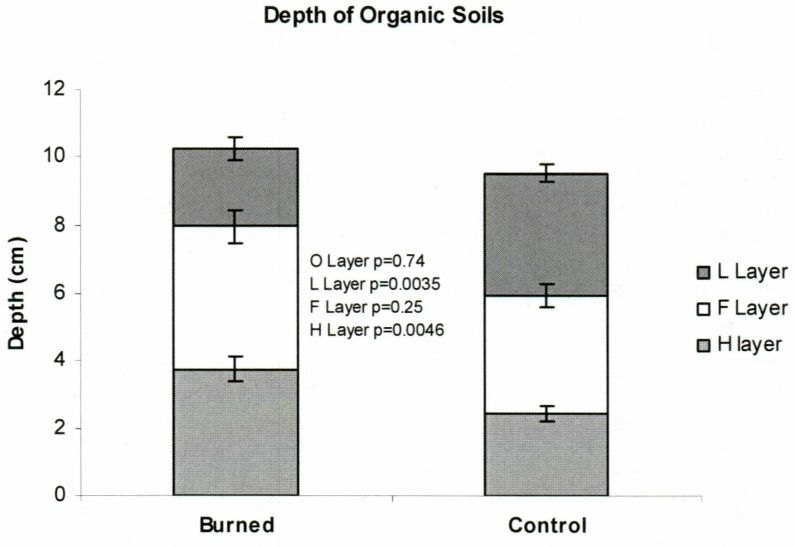

Fig. 4. Organic layer depth of soils from burned and control black spruce stands, CPCRW, Alaska. P values are from One-Way ANOVA, n=15. Error bars are standard error of the mean.

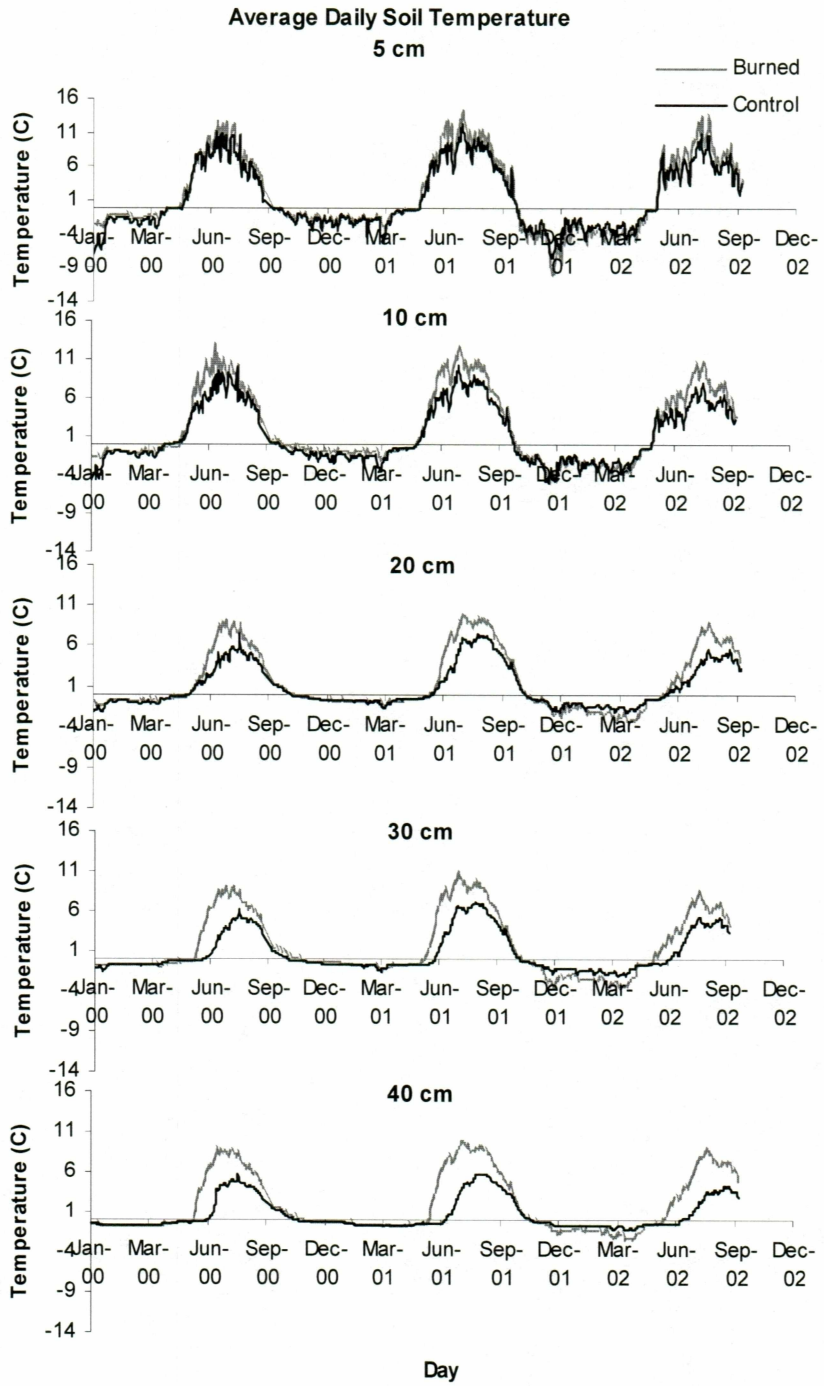

Fig. 5. Average daily temperature at 5-40 cm depths in soils from burned and control black spruce stands, CPCRW, Alaska, n=9.

in the burned stands than the control stands (Fig. 6). Mass loss of filter papers and tongue depressors in the burned soil was ~4 times faster than that in the control soil.

5.12 C and N

Concentrations of most measured nutrients were significantly ($p<0.05$) higher in the burned than in the control organic soil layers (both F and H) (Table 2). Burned soils had greater concentrations of total C and N in both organic layers (Table 2). When scaled to a per area basis, C (kg m^{-2}) did not differ for F layer, and was greater in burned than in control H layer. There was no difference in N content (kg m^{-2}) between treatments for either soil layer (Table 2). DOC concentration was higher in the control than in burned H layer soils, but the reverse was true in the F layer. Burned soils had narrower C/N ratios than control soils, though the difference was only marginally significant in the H layer, ($p=0.059$, Table 2).

Initial mineral N contents also differed in burned and control soils. Concentrations of mineral ($NO_3^- + NH_4^+$) N were greater in burned than control soils for both layers (Fig. 7), and most of the mineral N occurred as NH_4^+. NO_3^- was low in all soils; in the F layer NO_3^- was significantly greater in burned than control soils, but not significantly different in the H layer ($p=0.10$).

Bulk density was not significantly different in burned (0.10 g cm^{-3} F layer, 0.24 g cm^{-3} H layer) and control (0.11 g cm^{-3} F layer, 0.28 g cm^{-3} H layer) soils and mean values were within the typical range for F and H layer soils (Soil Survey Staff 1999). Soil

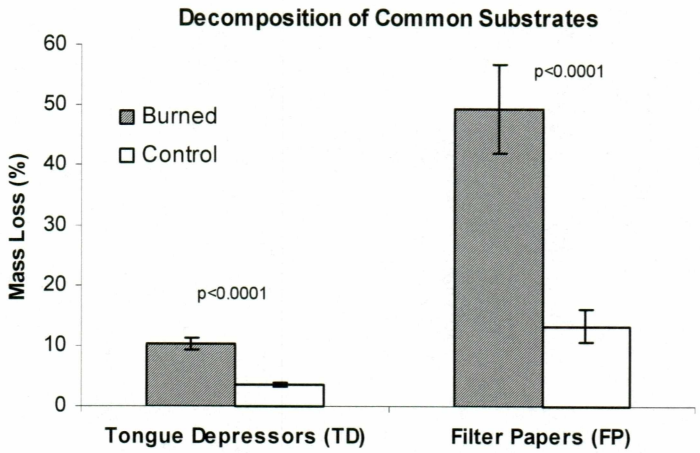

Fig. 6. Decomposition of common substrates at 20 (FP) or 30 (TD) cm depth in burned and control stands of black spruce, in situ 1 year, CPCRW, Alaska. P- values are from One-Way ANOVA, n=13 or 14 (filter paper burned and control) or n=15 or 14 (tongue depressor burned and control), data are mean and standard error of the mean.

Table 2. Nutrient data for unincubated soils from burned and unburned stands of black spruce, CPCRW, Alaska. One way ANOVA. N=15 for all F layer variables except BD where N=14, and N=14 for all H layer variables except BD where N=13. Error bars are standard error of the mean.

		NO_3^- ug N g^{-1}	NH_4^+ ug N g^{-1}	N cg g^{-1}	N kg m^{-2}	C cg g^{-1}	C kg m^{-2}	C:N	DOC mg g^{-1}	pH	BD g cm^{-3}
F layer	Burned	13.3 (3.5)	612.2 (202.3)	1.2 (0.1)	0.05 (0.01)	42.6 (1.2)	1.7 (0.9)	36.7 (1.7)	2.6 (0.6)	4.1 (0.1)	0.10 (0.01)
	Control	2.4 (0.4)	55.50 (3.9)	1.0 (0.03)	0.04 (0.00)	36.7 (1.2)	1.5 (0.6)	38.1 (1.4)	1.4 (0.1)	3.8 (0.1)	0.11 (0.01)
	p	*0.002*	*0.0002*	*0.003*	*0.30*	*0.0001*	*0.46*	*0.47*	*0.01*	*0.002*	*0.56*
H layer	Burned	8.0 (3.5)	290.3 (46.6)	0.86 (0.04)	0.06 (0.01)	20.9 (3.6)	0.3*	24.7 (0.9)	2.3 (0.1)	4.0 (0.1)	0.24 (0.03)
	Control	1.8 (0.2)	74.2 (5.9)	0.66 (0.03)	0.04 (0.01)	17.7 (3.1)	0.2*	27.0 (0.9)	2.9 (0.1)	3.9 (0.1)	0.28 (0.04)
	p	*0.10*	*<.0001*	*0.0003*	*0.09*	*0.009*	*0.05*	*0.059*	*0.003*	*0.37*	*0.44*

** Data log transformed to achieve normality, no error term available.*

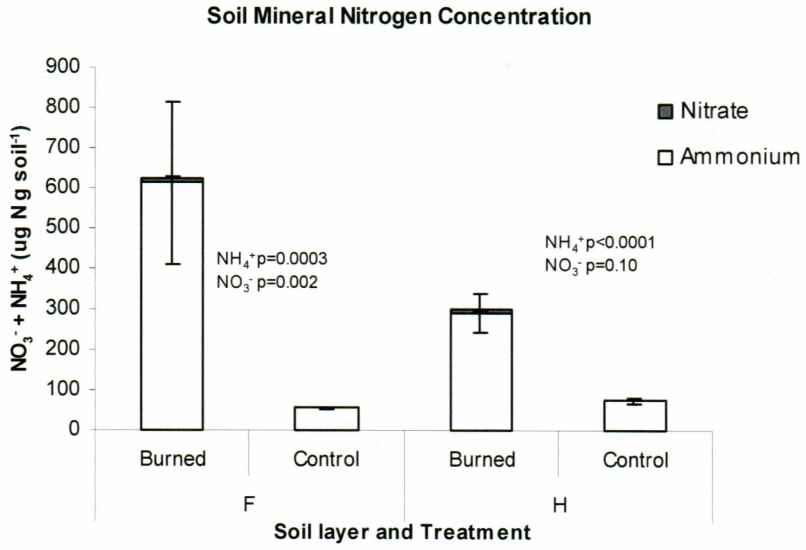

Fig. 7. Mineral nitrogen in unincubated soil from burned and control black spruce stands, CPCRW, Alaska. P- values are from One-Way ANOVA, n=15 (n=14 H layer control). Data are mean and standard error of the mean.

pH was higher in burned versus control F layer soils but not significantly different in the H layer ($p=0.37$, Table 2).

5.13 Proximate Fractions

Burned soils had smaller soluble and cellulose fractions and greater lignin fractions than control soils, but there was no significant difference in hemicellulose concentrations between the treatments ($p=0.42$) (Table 3). Lignin/N ratio was not different between burned and control soils ($p=0.21$, data not shown). Ash content was significantly higher in the burned than control soils ($p=0.03$, data not shown); all data for proximate fractions are expressed on an ash-free basis.

In the burned F layer soils, soluble fractions were negatively related to C/N ratio and to C concentration, and in the control soils were negatively correlated with C, DOC, and C/N ratio and negatively correlated with NH_4^+ (Table 4a). In the burned H layer soils, DOC was negatively related to NO_3^- concentration, and C/N ratio was negatively related to NH_4^+ concentration. In the control H layer soils, NO_3^- and NH_4^+ were positively related to total N concentration (Table 4b).

5.2 Incubations

5.21 C Mineralization

Respiration rate on the first day of the incubation was lower in burned soils than control soils for both soil layers at all temperatures and there was a significant interaction between temperature and treatment for both layers (Fig. 8). Day one respiration rate in the F layer

Table 3. Ash-free proximate fractions in F layer soils from burned and control black spruce stands incubated at 5, 15, and 25 °C. Two-way nested ANOVA, n=45 (burned post incubation), 44 (control post incubation), or 15 (unincubated). Error term in parentheses is standard error of the mean.

°C	Treatment	Soluble Fraction (g g Soil $^{-1}$)	Hemicellulose Fraction (g g Soil $^{-1}$)	Cellulose Fraction (g g Soil $^{-1}$)	Lignin Fraction (g g Soil $^{-1}$)
Unincubated	**Burned**	0.382 (0.015)	0.178 (0.008)	0.090 (0.004)	0.349 (0.009)
	Control	0.425 (0.012)	0.185 (0.004)	0.128 (0.008)	0.262 (0.014)
5	**Burned**	0.359 (0.011)	0.181 (0.005)	0.093 (0.005)	0.367 (0.009)
	Control	0.387 (0.021)	0.191 (0.007)	0.141 (0.02)	0.282 (0.014)
15	**Burned**	0.364 (0.015)	0.178 (0.008)	0.092 (0.005)	0.365 (0.008)
	Control	0.422 (0.015)	0.181 (0.006)	0.111 (0.007)	0.286 (0.015)
25	**Burned**	0.374 (0.018)	0.168 (0.008)	0.080 (0.005)	0.378 (0.011)
	Control	0.429 (0.014)	0.171 (0.007)	0.110 (0.008)	0.290 (0.012)
p	*treatment (pre)*	*0.013*	*0.4219*	*<.0001*	*<.0001*
p	*treatment*	*0.0003*	*0.3175*	*<.0001*	*<.0001*
p	*temperature*	*0.16*	*0.06*	*0.06*	*0.60*
p	*temperature*treat*	*0.55*	*0.84*	*0.27*	*0.89*

Table 4a. Pearson correlation coefficients for select variables, F layer burned (B) and control (C) soils, n=15.

		C	N	NO3	NH4	Soluble	Hemicellulose	Cellulose	Lignin	Soluble /N	Hemicellulose/N	Cellulose/N	Lignin /N	C/N	DOC
C	B	1	-	-		-0.73**	0.51*	0.68**	-	0.78**	-	-	-	-	-
	C	1	-	-	0.60*	-0.81**	-	-	0.85***	-0.83***	-0.60*	-	-0.57*	-	0.53*
N	B		1	-	0.75**	-	-	-	-	-0.72**	-0.59*	-0.70**	-0.85***	-0.81**	-
	C		1	-	0.63**	-	-	-	-	-0.82**	-	-0.88***	-0.92***	-0.52*	-
NO3	B			1	-	-	-0.51*	-	-	-	-0.61*	-	-	-	-
	C			1	-	-	-	-	-	-	-	-	-	-	-
NH4	B				1		-	-	-	-0.72**	-	-	-0.55*	-	0.57*
	C				1	-0.51*	-	-	0.54*	-0.75**	-	-0.54*	-0.63*	-	-
Soluble	B					1	-	-0.90***	-0.72**	0.64**	-	-0.67**	-	-0.56*	-
	C					1	-		-0.88***	0.67**	-		-	-0.65**	-0.56*
Hemicellulose	B						1		-	-	-	-	-	-	-
	C								-0.65**	-	0.90***	-	-	-	-
Cellulose	B							1	-	-0.55*	0.50*	0.75**	-	0.55*	-
	C							1	-	-	-	0.69**	-	-	-
Lignin	B								1	-	-	-	-	-	-
	C								1	-0.65**	-0.66**	-	-	0.63**	0.59*
Soluble/N	B									1	-	-	0.66**	-	-
	C									1	0.50*	0.61*	0.84***	-	-
Hemicellulose/N	B										1	0.76**	-	0.75**	-
	C										1	-	-	-	-
Cellulose/N	B											1	0.59*	0.92***	-
	C											1	0.77**	0.66**	-
Lignin/N	B												1	0.69**	-
	C												1	-	-
C/N	B													1	-
	C													1	-
DOC	B														1
	C														1

Table 4b. Pearson correlation coefficients for select variables, H layer burned and control soils. N= 15, alpha=0.05.

		C	N	Mineral N	NO_3^-	NH_4^+	C/N	DOC
C	Burned	1	0.78**	-	-	-	-	-
	Control		0.74**	-	-	-	-	-
N	Burned		1	0.69**	-	0.68**	-0.51*	-
	Control			0.55*	0.51*	0.53*	-	-
Mineral N	Burned			1	-	0.99***	-0.53*	-
	Control				-	0.99***	-	-
NO_3^-	Burned				1	-	-	-0.56*
	Control					-	-	-
NH_4^+	Burned					1	-0.52*	-
	Control						-	-
C/N	Burned						1	-
	Control							-
DOC	Burned							1
	Control							

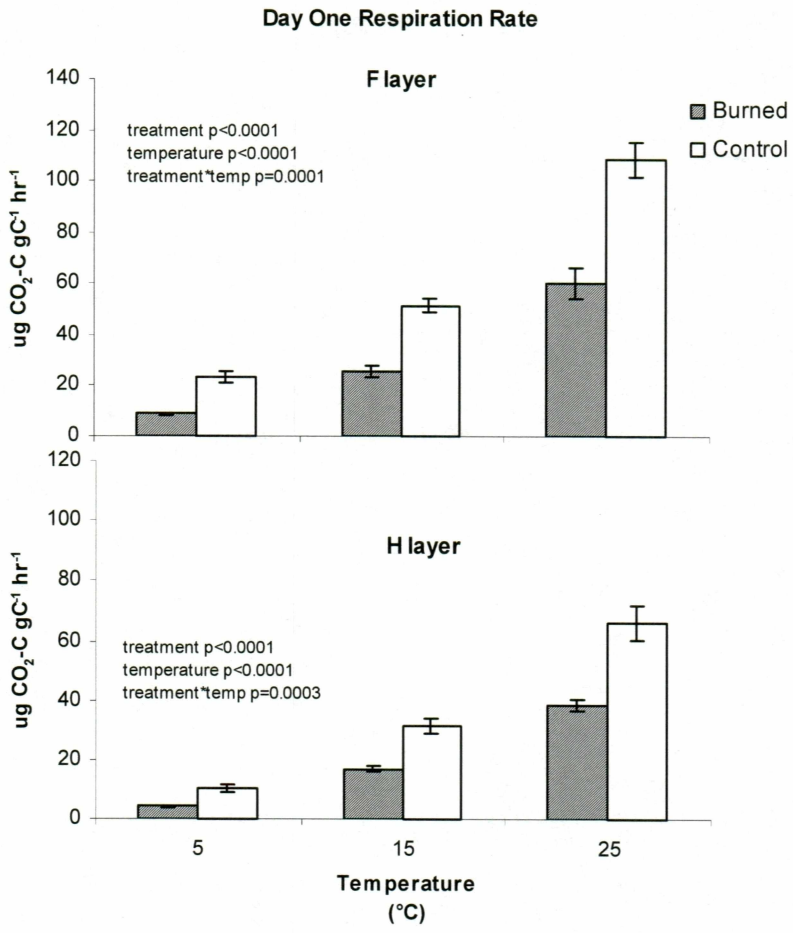

Fig. 8. Day one respiration rate in soils from burned and control black spruce stands, incubated 205 (F) and 133 (H) days at 5, 15, and 25 °C, CPCRW, Alaska. Two-way nested ANOVA, n = 45 and 42 (F layer burned and control) or n=44 and 43 (F layer burned and control), data are mean and standard error of the mean.

was almost twice that in the H layer for both treatments. After the first few days of the incubation, the rate dropped precipitously in all soils at all temperatures and then remained relatively constant for the duration of the incubation (Fig. 9, Fig. 10). In the F layer, average respiration rate was significantly lower in burned than control soils, but in the H layer burned and control soils they were not significantly different ($p=0.19$) (Fig. 11).

Control soils respired more C than burned soils based on integration of nonlinear regression equations (rate vs. time) at day one ($p<0.0001$ both F and H) and day 46 ($p<0.0001$, $p=0.02$) of the incubation, but there was no significant difference when integrated through day 130 ($p=0.69$, $p=0.87$) (Fig. 12). The linear interpolation method showed similar trends, though the cumulative values produced by linear methods were higher those produced by nonlinear methods for both treatments and layers (Fig. 13, Table 5). Total C respired on day one constituted 4 - 10% of the total through day 46, and 2 - 6% of the total through day 130. These percentages were significantly higher in control soils than burned soils for both time steps.

Relationships between mineralization rates and independent variables were stronger when examined by temperature and treatment independently than when relationships were examined across treatments because relationships between measured variables and respiration rate were dissimilar in burned and control soils.

In the burned F layer soils, respiration variables were positively related proximate fractions, and to indexes of lability such as soluble/N, hemicellulose/N (Fig. 14), and

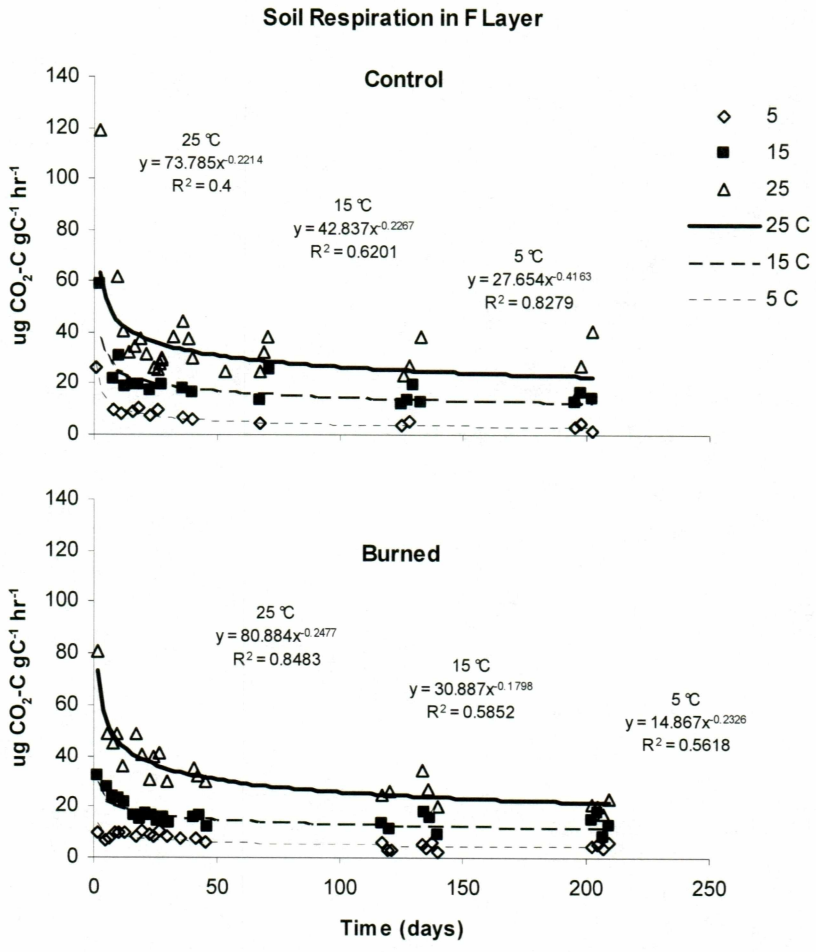

Fig. 9. Respiration rate over time in F layer soils from burned and control black spruce stands, incubated for 205 days at 5, 15, and 25 °C, CPCRW, Alaska.

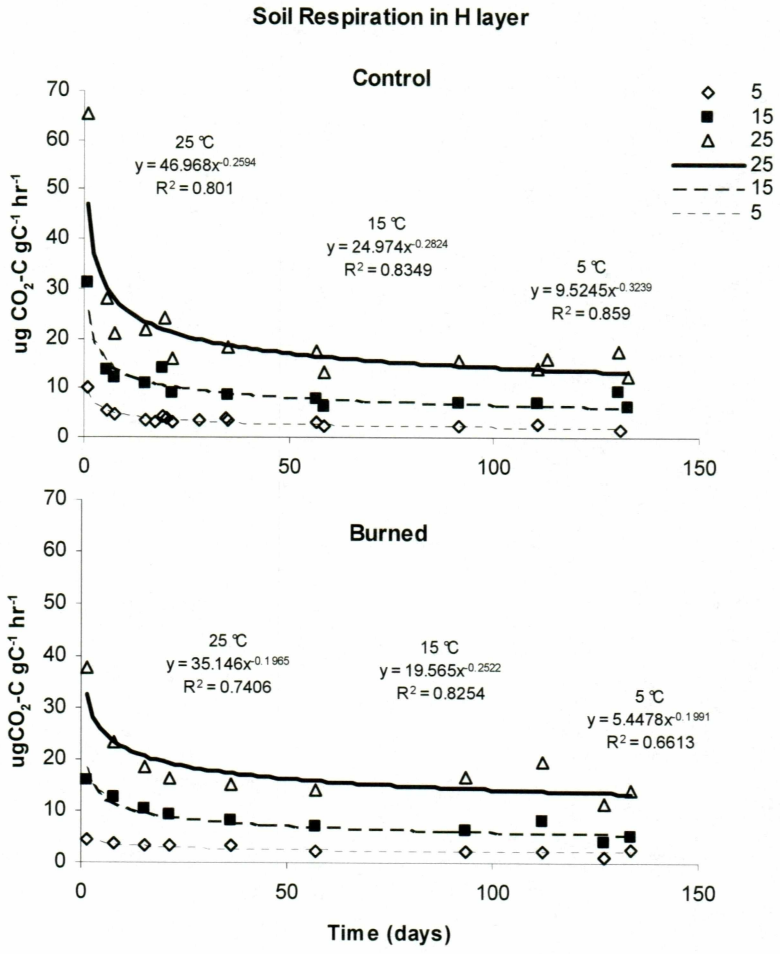

Fig. 10. Respiration rate over time in H layer soils from burned and control black spruce stands, incubated for 133 days at 5, 15, and 25 °C, CPCRW, Alaska.

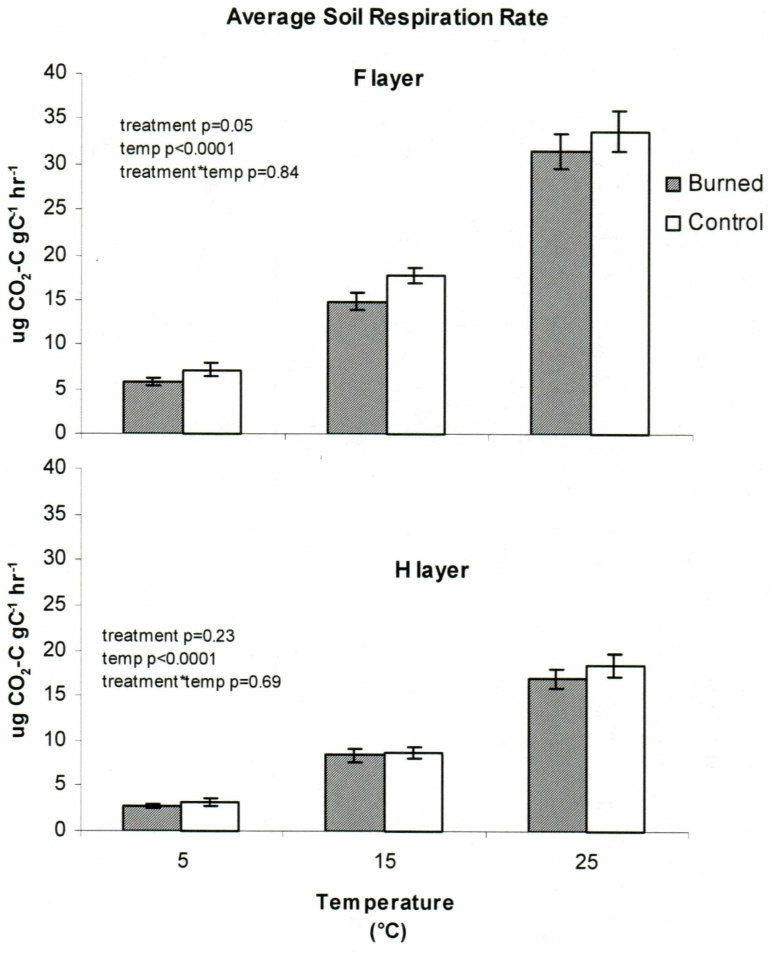

Fig. 11. Average hourly respiration rate over entire incubation in soils from burned and control black spruce stands, incubated for 205 (F) and 133 (H) days at 5, 15, and 25 °C, CPCRW, Alaska. Two-way nested ANOVA, n = 45 and 42 (F layer burned and control) or n=44 and 43 (F layer burned and control), data are mean and standard error of the mean.

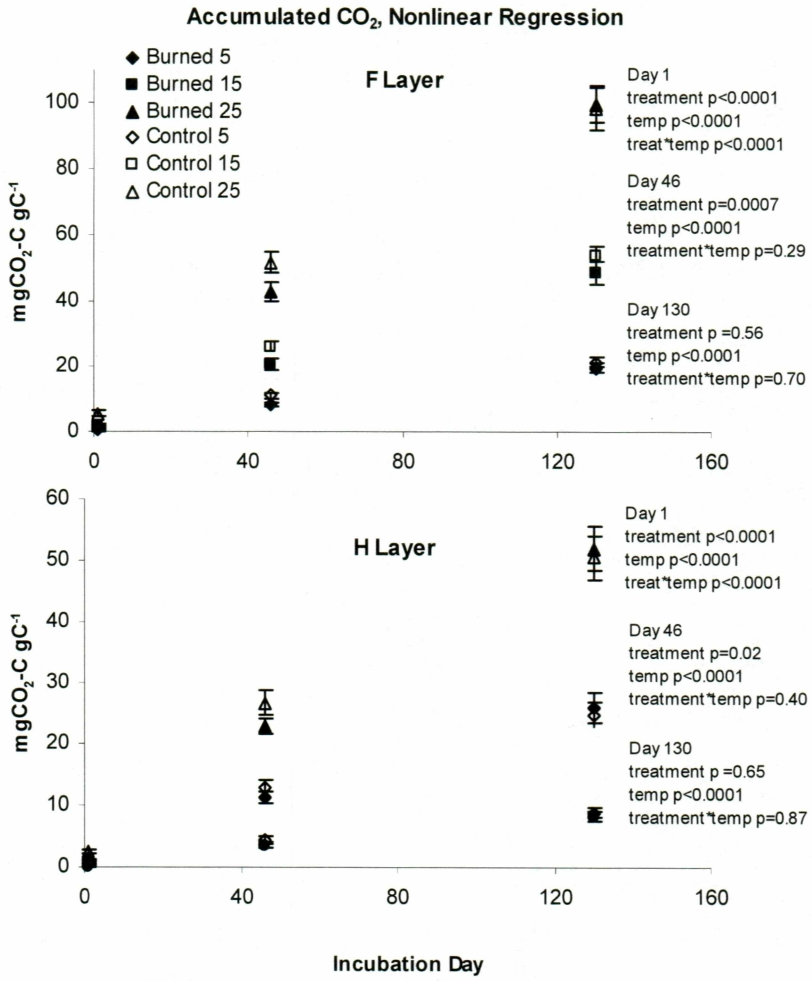

Fig. 12. Total carbon respired on day one, day one to day 46 and day one to day 130 in soils from burned and control black spruce stands, incubated for 205 (F) and 133 (H) days at 5, 15, and 25 °C, CPCRW, Alaska. Two-way nested ANOVA, n = 45 and 42 (F layer burned and control) or n=44 and 43 (F layer burned and control), data are mean and standard error of the mean.

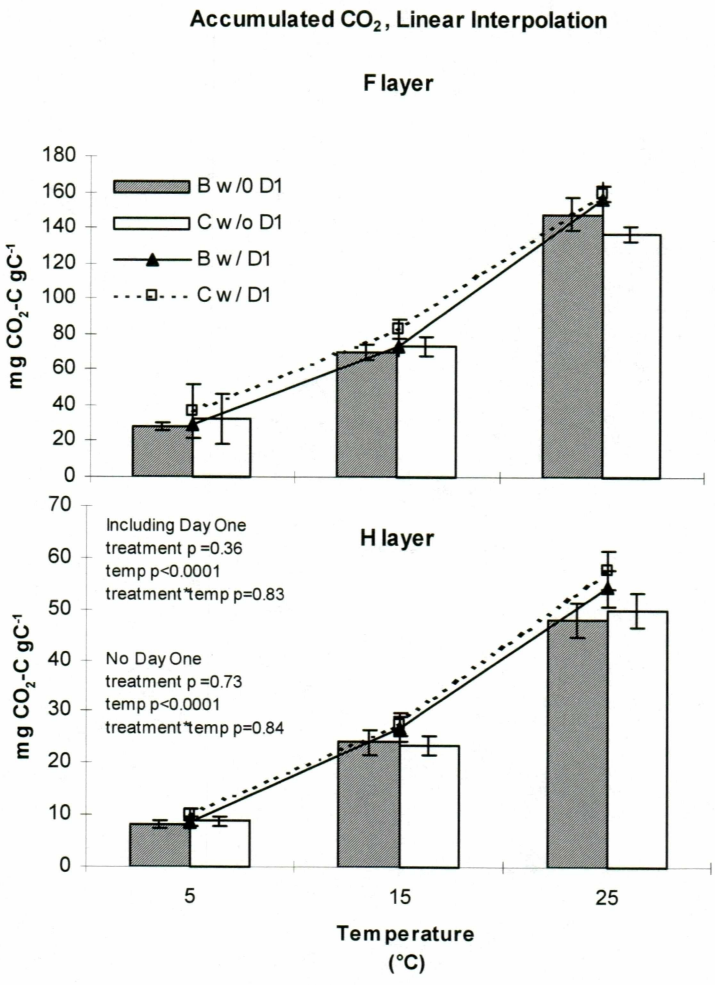

Fig. 13. Accumulated CO2 with and without day one respiration in soils from burned and control black spruce stands incubated at 5, 15, and 25 °C. Linear interpolation evaluated at 133 days, CPCRW Alaska. Two-way nested ANOVA, n = 45 and 42 (F layer burned and control) or n=44 and 43 (F layer burned and control), data are mean and standard error of the mean.

Table 5. Post incubation carbon and net nitrogen mineralization and inorganic nitrogen data for incubated soils from burned and control black spruce stands, Caribou-Poker Creeks Research Watershed, Alaska. Respiration values are integrated for the entire length of the incubation (205 days F, 133 days H), inorganic nitrogen is the pool size at the end of the incubation. Two-way nested ANOVA. n varies from 42 to 45. Error bars are standard error of the mean.

°C	Treatment	Day one respiration rate ug CO_2-C gC^{-1} hr^{-1}	Total Respired C mg CO_2-C g C^{-1} nonlinear regression	Total Respired C mg CO_2-C g C^{-1} linear interpolation	Percent Accumulated Day 1 *	Percent Accumulated Day 46 **	Average Respiration ug CO_2-C hr^{-1} $g C^{-1}$	NO_3^- ug N g $soil^{-1}$	NH_4^+ ug N g $soil^{-1}$	NO_3^-+NH_4^+ ug N g $soil^{-1}$	Net N Min. Rate ug N g^{-1} day^{-1}
F layer											
5	Burned	8.8 (3.5)	19.6 (1.6)	28.9 (2.3)	1.6 (0.1)	41.0 (0.6)	5.8 (0.5)	740.7 (247.5)	147.8 (65.1)	888.5 (264.9)	1.3 (0.9)
	Control	23.2 (11.7)	21.3 (1.7)	36.9 (5.2)	4.6 (0.4)	51.4 (1.1)	7.1 (0.8)	147.1 (104.8)	0.3 (0.1)	147.5 (104.8)	0.5 (0.5)
15	Burned	25.4 (10.8)	48.6 (3.4)	73.0 (4.6)	1.8 (0.2)	41.9 (0.8)	14.8 (1.0)	642.6 (233.0)	230.7 (106.3)	873.4 (289.6)	1.2 (1.0)
	Control	51.5 (34.0)	53.7 (3.0)	83.2 (4.3)	3.6 (0.4)	48.3 (1.2)	17.7 (0.9)	172.0 (46.4)	0.5 (0.2)	172.5 (46.5)	0.0 (0.2)
25	Burned	60.2 (31.7)	99.7 (5.7)	156.2 (9.6)	1.9 (0.3)	42.4 (1.0)	31.5 (2.0)	2159.0 (247.0)	218.0 (97.5)	2377.0 (295.3)	8.4 (1.3)
	Control	108.3 (65.6)	98.2 (6.5)	159.6 (10.5)	6.0 (0.9)	53.4 (1.8)	33.6 (2.2)	958.7 (256.2)	0.4 (0.2)	959.1 (256.2)	4.6 (1.3)
p	*treatment*	*<0.0001*	*0.56*	*0.18*	*<.0001*	*<.0001*	*0.05*	*<.0001*	*<.0001*	*<.0001*	*0.02*
p	*temp*	*<0.0001*	*<.0001*	*<.0001*	*0.002*	*0.02*	*<0.0001*	*<.0001*	*0.72*	*0.0001*	*<.0001*
p	*temp*treat*	*0.0003*	*0.70*	*0.87*	*0.01*	*0.04*	*0.88*	*0.14*	*0.72*	*<.0001*	*0.16*
H layer											
5	Burned	4.4 (0.4)	8.2 (0.8)	8.8 (0.8)	1.7 (0.1)	41.6 (0.7)	9.3 (1.0)	78.0 (29.3)	284.1 (63.5)	1.4 (0.3)	0.5 (0.2)
	Control	10.3 (1.0)	8.9 (0.9)	10.2 (1.1)	4.3 (0.3)	50.9 (0.7)	11.7 (1.3)	1.1 (1.7)	6.8 (2.7)	0.0 (0.0)	0.0 (0.0)
15	Burned	16.8 (0.9)	25.8 (2.4)	26.8 (2.4)	2.3 (0.2)	44.3 (0.8)	30.7 (2.8)	206.6 (63.1)	243.8 (58.0)	3.5 (0.7)	1.2 (0.5)
	Control	31.6 (2.6)	24.7 (2.0)	27.5 (2.2)	5.0 (0.3)	52.4 (0.7)	31.8 (2.6)	1.4 (1.6)	10.0 (3.4)	0.0 (0.0)	0.0 (0.0)
25	Burned	38.6 (2.0)	51.9 (3.7)	54.2 (3.5)	2.4 (0.2)	44.6 (1.1)	62.0 (4.1)	101.2 (41.2)	775.3 (152.4)	3.5 (0.7)	4.4 (1.1)
	Control	66.1 (5.8)	50.5 (3.5)	57.6 (3.8)	5.1 (0.4)	52.6 (1.0)	67.5 (4.6)	1.4 (0.4)	10.0 (3.4)	0.0 (0.0)	0.0 (0.0)
p	*treatment*	*<0.0001*	*0.65*	*0.36*	*<.0001*	*<.0001*	*0.19*	*<.0001*	*<.0001*	*<.0001*	*<.0001*
p	*temp*	*<0.0001*	*<.0001*	*<.0001*	*0.01*	*0.007*	*<0.0001*	*0.12*	*<.0001*	*<.0001*	*<.0001*
p	*temp*treat*	*0.0003*	*0.87*	*0.83*	*0.99*	*0.68*	*0.71*	*0.12*	*0.003*	*0.03*	*0.02*

* (CO_2 Accumulated on Day 1/ Total CO_2 Accumulated) *100

** (CO_2 Accumulated up to Day 46/ Total CO_2 Accumulated) *100

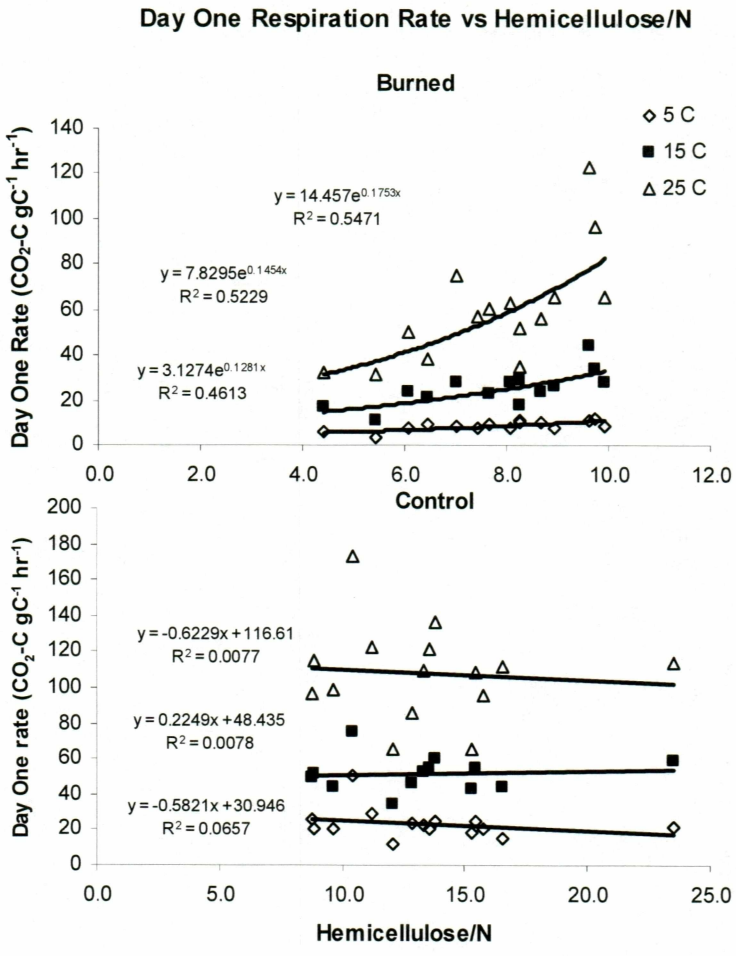

Fig. 14. Hemicellulose/N vs. day one respiration rate in F layer soils from burned and control black spruce stands, incubated for 205 days at 5, 15, and 25 °C, CPCRW, Alaska.

cellulose (Fig. 15) and negatively related to N (Fig. 16) and DOC (Fig. 17, Table 6a). In the control F layer soils, respiration variables were positively related to NH_4^+ at 5 °C and negatively related to cellulose at 15 °C and 25°C (Table 6a) and unrelated to any other measured variable.

Respiration in burned H layer soils was positively related to DOC and negatively related to NO_3^-, while in control soils respiration was positively related to net N mineralization rate and DOC (Table 6b). Net N mineralization rate was positively related to NH_4^+ and NO_3^- and negatively related to C/N in burned H layer soils, while in the control soils net N mineralization was negatively related to NH_4^+ and NO_3^-.

5.22 Temperature Sensitivity of Respiration

Regardless of Q_{10} calculation method, burned soils had higher Q_{10} values than control soils. Using point-to-point relative comparisons (see Kirschbaum 1995), H layer soils had slightly higher Q_{10} values than F layer soils (Fig. 18, Table 7). After 130 days, there was generally no difference between burned and control Q_{10} values, with the exception of 15 °C versus 25 °C in the H layer, where burned soils were more temperature sensitive than control soils. In the H layer, soils appeared to be slightly more temperature sensitive at day 130 than at day one, while in the F layer temperature sensitivity of day one rate and day 130 rate did not differ. The largest Q_{10} values for both day one and day 130 calculations resulted from the 5 °C vs. 15 °C comparison. Using nonlinear regression of rate across three temperatures to calculate temperature sensitivity (Boone et al. 1998) also produced greater Q_{10} values for burned than

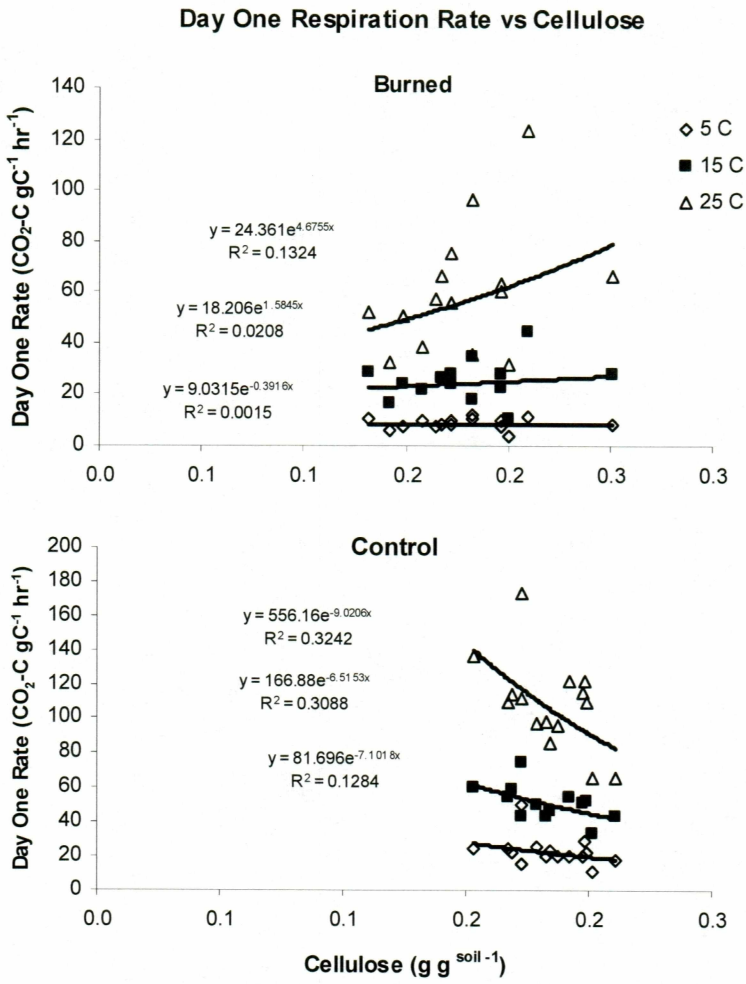

Fig. 15. Cellulose vs. day one respiration rate in F layer soils from burned and control black spruce stands, incubated for 205 days at 5, 15, and 25 °C, CPCRW, Alaska.

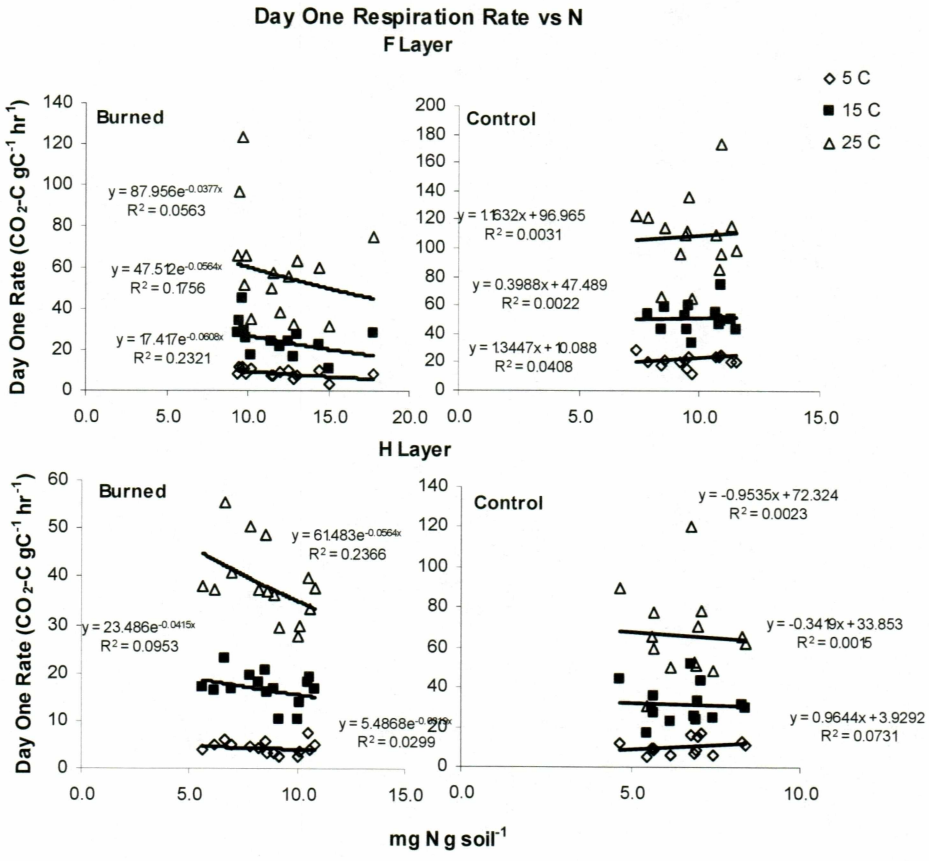

Fig. 16. Total percent N vs. day one respiration rate in F and H layer soils from burned and control black spruce stands, incubated for 205 days at 5, 15, and 25 °C, CPCRW, Alaska.

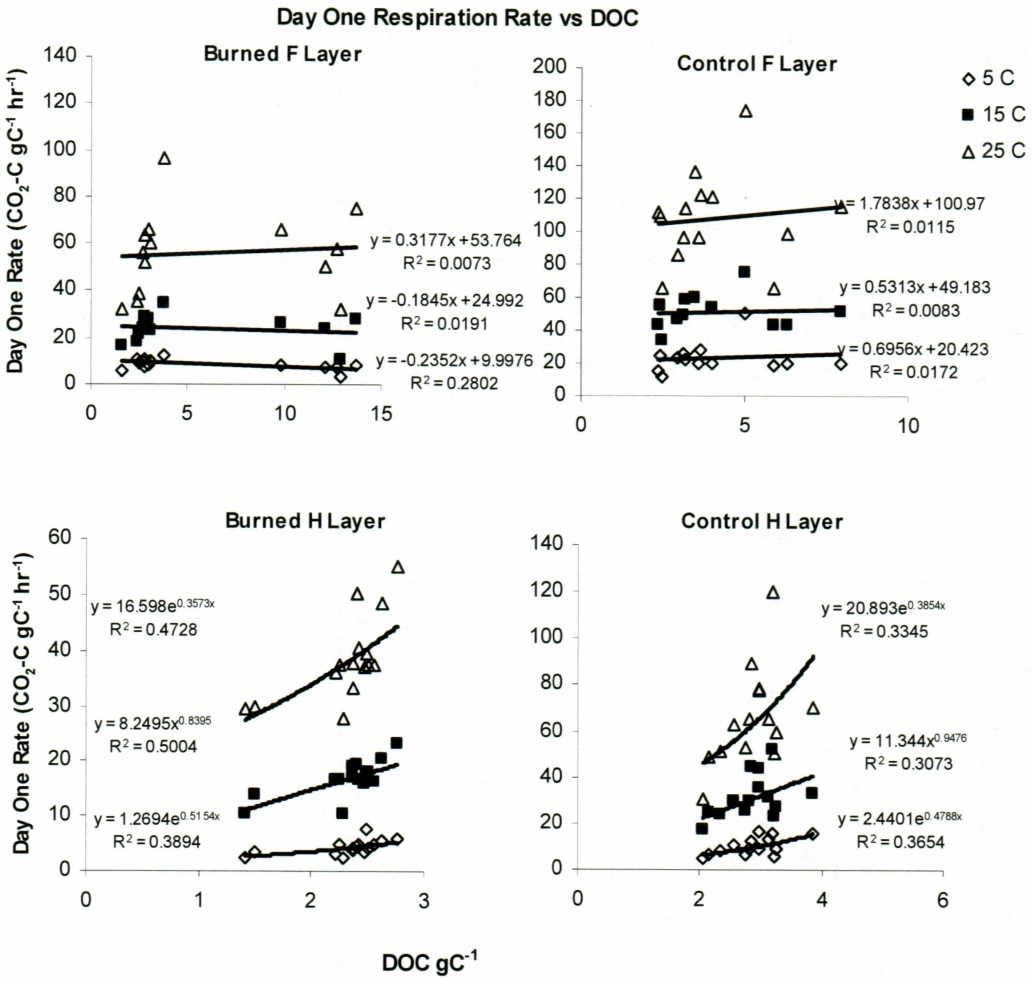

Fig. 17. Dissolved organic carbon (DOC) vs. respiration rate in soils from burned and control black spruce stands, incubated for 205 (F) and 133 (H) days at 5, 15, and 25 °C, CPCRW, Alaska.

Table 6a. Pearson correlation coefficients for C and N mineralization rates for burned and control F layer soils incubated at 5, 15 or 25 C, n=15 for B, 14 for C. Coefficients correspond to temperatures shown in parentheses.

		DOC	C	N	Net N Min. Rate	NH_4^+	Soluble Fraction	Hemi-cellulose Fraction	Cellulose Fraction	Lignin Fraction	Soluble/N	Hemi-cellulose/ N	Cellulose/ N	Lignin/ N
Day One Respiration Rate	**Burned**	-0.53* (5)	-	-0.50♣(5)	-0.60* (5)	-	-	-	-	-	0.53* (5)	0.69** (5)	0.49♣ (5)	-
	Control	-	-	-	-	0.58* (5)	-	-	-0.54* (15, 25)	-	-	-	-	-
Net N Min. Rate	**Burned**	-	0.58* (5)	-	-	-	-	-	-	-	-	-	-	-0.49♣ (15)
	Control	-	-0.66** (15)	-	-	-	0.61* (15)	0.66** 0.63* (5,15)	-	-0.56* -0.73** (5,15)	0.49♣ (15)	0.76** 0.67** (5,15)	-	-

* $p<0.05$

** $p<0.01$

♣$p<0.10$

Table 6b. Pearson correlation coefficients for net C and N mineralization rates (NminRt) for burned and control H layer soils incubated at 5, 15, or 25 C. n=15 for B, 14 for C.

		DOC	C	N	NminRt	NH4	NO3	C/N
Day One Respiration Rate	**Burned**	0.58* 0.73** 0.66**	-	-	-	-	-0.49* (5)	-
	Control	0.60* 0.65* (5, 15)	-	-	0.65* (25)	-	-	-
Net N Mineralization Rate	**Burned**	-	-	-	-	0.51* (25)	0.66** (5)	-0.49* (25)
	Control	-	-	-	-	-0.89*** -0.83** (5, 15)	-	-

* $p<0.05$
** $p<0.01$
*** $p<0.0001$

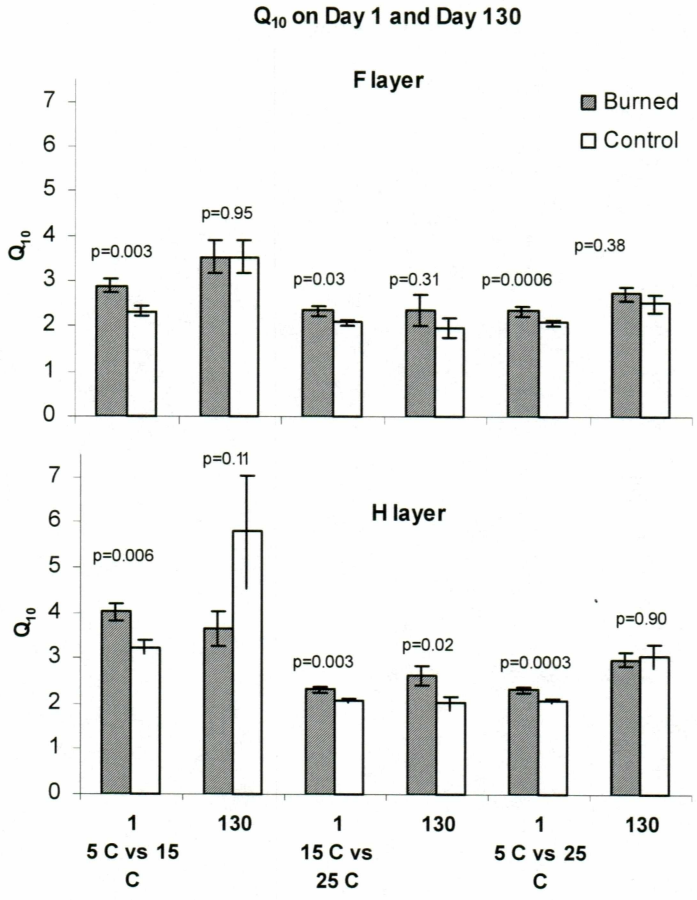

Fig. 18. Q_{10} $((R_2/R_1)^{10/(T2-T)})$ of respiration rate on day one and day 130 in soils from burned and control black spruce stands, incubated at 5, 15, and 25 °C, CPCRW, Alaska. Two-way nested ANOVA, n= 14 or n=15 (F layer burned), data are mean and standard error of the mean.

Table 7. Q_{10} of soil respiration in burned and control soils incubated at 5, 15, and 25 °C, sampled from CPCRW, Alaska. $R=B_o*e^{(B1*T)}$ and $Q_{10}=10*e^{(10*B1)}$. P values are for ANOVA of Q10 values, n=45, except for control H layer where n=42. Error term in parentheses is standard error of the mean.

		Day One Rate		**Total Respired C**		**Total Respired C (no day one)**	
		R^2	Mean	R^2	Mean	R^2	Mean
F layer	Burned	0.69	2.46 (0.10)	0.83	2.27 (0.09)	0.64	2.22 (0.08)
	Control	0.81	2.14 (0.05)	0.78	2.02 (0.08)	0.71	2.04 (0.09)
	p (treatment)		*0.002*		*0.03*		*0.09*
H layer	Burned	0.96	2.54 (0.06)	0.93	2.27 (0.05)	0.92	2.24 (0.05)
	Control	0.91	2.27 (0.04)	0.94	2.25 (0.06)	0.93	2.27 (0.07)
	p (treatment)		*0.0004*		*0.85*		*0.74*

R^2, $p<0.0001$

control soils though the values were not as large as those yielded by two-temperature comparisons. Calculations using day one rate and total released C both showed the same trend, but calculations excluding day one rates were not significantly different for either soil layer (Table 7).

An absolute index of temperature sensitivity (g CO_2-C gC^{-1} $°C^{-1}$):

Eqn. 5: $$\frac{R_2 - R_1}{T_2 - T_1}$$

(where R is respiration per gram C at temperatures 1 and 2) for burned and control soils resulted in higher values for control soils than burned soils for both soil layers (Table 8, Fig. 19). As with the Q_{10} point-to-point comparisons, the differences were only significant on day one, and the greatest differences occurred when comparing 5 and 15 °C.

5.23 Post Incubation Fiber Analyses

Percent change in proximate fraction over the incubation was calculated as

Eqn. 6: $$\left(\frac{post - pre}{pre}\right) \times 100$$

Lack of change in any fraction concentration meant that the fraction was consumed at the average rate of all the fractions in the sample, while decreasing and increasing concentrations implied faster or slower loss rates, respectively.

Following incubation, the distribution of soil proximate fractions differed between burned and control soils (Table 3). Soluble and cellulose fractions were smaller in burned vs. control soils. Within a treatment, proximate fraction did not differ by temperature

Table 8. Temperature sensitivity of incubated soils from burned and control stands of black spruce, CPCRW, Alaska. Error term in parentheses is standard error of the mean.

			Relative			Absolute		
			5 °C vs.15 °C	15 °C vs. 25°C	5 °C vs. 25°C	5 °C vs.15 °C	15 °C vs. 25°C	5 °C vs. 25°C
F Layer	Day 1	**Burned**	2.89 (0.16)	2.35 (0.10)	2.35 (0.10)	1.75 (0.17)	3.50 (0.48)	2.57 (0.30)
		Control	2.33 (0.11)	2.09 (0.07)	2.09 (0.07)	3.10 (0.33)	5.67 (0.55)	4.26 (0.27)
			0.0033	*0.0304*	*0.0006*	*0.0022*	*0.0032*	*<.0001*
	Day 130	**Burned**	3.54 (0.36)	2.34 (0.34)	2.72 (0.16)	7.93 (1.15)	13.99 (2.01)	10.96 (1.05)
		Control	3.53 (0.36)	1.98 (0.22)	2.52 (0.19)	10.21 (1.32)	12.36 (2.45)	11.29 (1.17)
			0.9482	*0.2218*	*0.3793*	*0.1297*	*0.5870*	*0.8188*
H Layer	Day 1	**Burned**	4.01 (0.19)	2.32 (0.07)	2.32 (0.07)	1.24 (0.07)	2.18 (0.13)	1.71 (0.09)
		Control	3.24 (0.15)	2.07 (0.04)	2.07 (0.04)	2.15 (0.18)	3.33 (0.33)	2.79 (0.25)
			0.0060	*0.0026*	*0.0003*	*<.0001*	*0.0032*	*0.0002*
	Day 130	**Burned**	3.66 (0.38)	2.64 (0.21)	2.98 (0.14)	4.93 (0.81)	9.32 (0.70)	7.12 (0.66)
		Control	5.78 (1.26)	2.01 (0.14)	3.05 (0.25)	5.33 (0.75)	6.28 (0.97)	5.63 (0.72)
			0.1025	*0.0238*	*0.9007*	*0.7910*	*0.0092*	*0.0796*

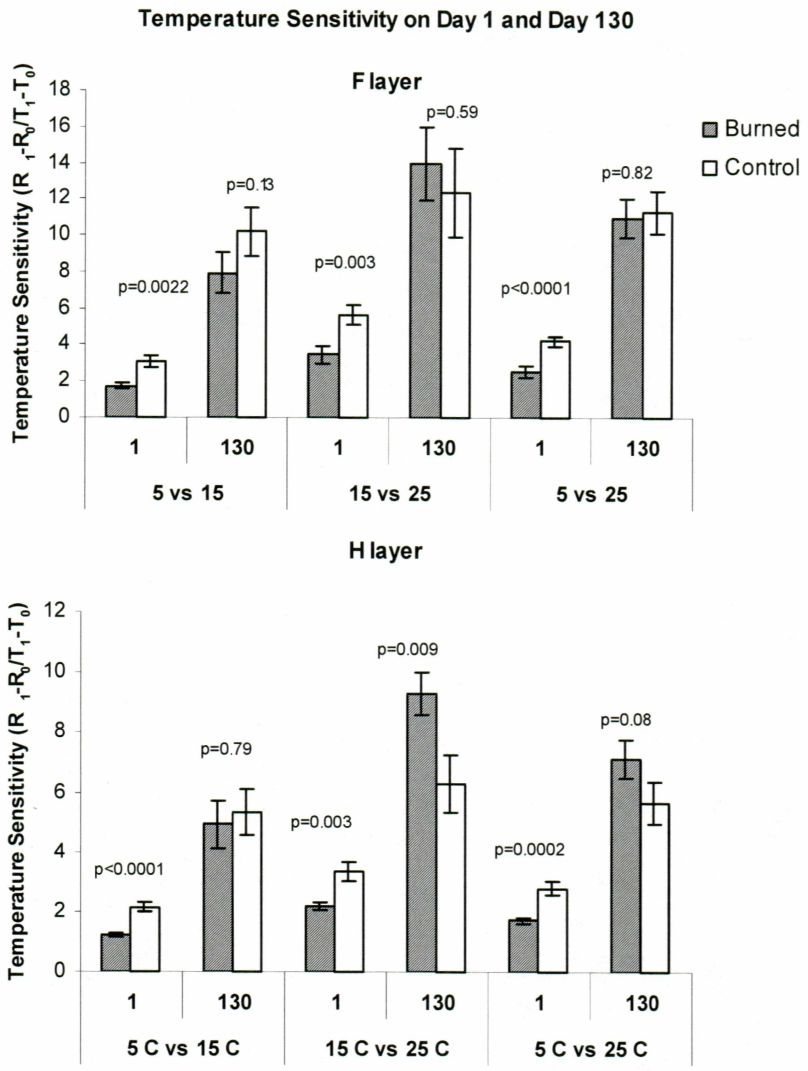

Fig. 19. Temperature sensitivity $(R_2/R_1)/(T_2-T_1)$ of day one and day 130 respiration rate in soils from burned and control soils black spruce stands, incubated at 5, 15, and 25 °C, CPCRW, Alaska. Two-way ANOVA, n= 14 or n=15 (F layer burned), data are mean and standard error of the mean.

following incubation, though percent change in some SOM fractions did (Table 9, Fig. 20). Lignin concentration increased in all treatments and temperatures, but the increase was significantly greater in the control soils. Change in soluble, hemicellulose and cellulose fractions varied but generally soluble and hemicellulose decreased and cellulose remained the same. Losses of hemicellulose and cellulose fractions increased with temperature (Fig. 21).

5.24 Nitrogen

Following incubation, concentrations of NH_4^+ in both F and H layer soils were greater in burned than control soils, and there was a significant interaction between temperature and treatment (Table 5). Total post incubation mineral N was orders of magnitude higher in burned than control soils for both layers and there was a significant interaction between treatment and temperature in both layers (Table 5). As in the unincubated soils, NH_4^+ was the dominant form of mineral N.

In both soil layers, total net N mineralization rates were orders of magnitude greater in burned than control soils (Fig. 22). Net N immobilization occurred in the control H layer soils at 5 and 15 °C, but not in any of the other soils. When analyzed across treatments, net N mineralization exhibited weak relationships with soil N content (Table 6a). In the control F layer soils at 5 and 15 °C there was a positive relationship between net N mineralization rate and lignin/N ratio (Fig. 23). In the burned F layer soils at all temperatures, cellulose was negatively correlated with net mineralization rate (Fig. 24). In the H layer, nitrogen concentration was positively related to net N mineralization

Table 9. Change in proximate fractions in incubated F layer soils from burned and control black spruce stands incubated at 5, 15, and 25 °C. Two-Way Nested ANOVA, n=45 (burned) or 44 (control). Error term in parentheses is standard error of the mean.

°C	Treatment	Soluble Fraction (g g Soil $^{-1}$)	Hemicellulose Fraction (g g Soil $^{-1}$)	Cellulose Fraction (g g Soil $^{-1}$)	Lignin Fraction (g g Soil $^{-1}$)
5	**Burned**	-5.0 (2.9)	3.7 (3.9)	2.3 (2.4)	5.3 (1.8)
	Control	-8.6 (4.6)	8.8 (11.2)	3.8 (4.1)	8.4 (2.4)
15	**Burned**	-4.1 (2.9)	4.1 (5.9)	0.8 (4.4)	4.9 (1.6)
	Control	-0.7 (2.3)	-12.7 (3.4)	-1.4 (3.6)	9.8 (2.6)
25	**Burned**	-1.9 (3.1)	-10.3 (3.8)	-4.8 (4.4)	8.2 (1.7)
	Control	1.4 (2.7)	-13.1 (5.2)	-7.0 (3.3)	13.1 (5.0)
p	*treatment*	*0.68*	*0.34*	*0.75*	*0.05*
p	*temperature*	*0.11*	*0.02*	*0.06*	*0.31*
p	*temperature* * *treatment*	*0.45*	*0.20*	*0.84*	*0.92*

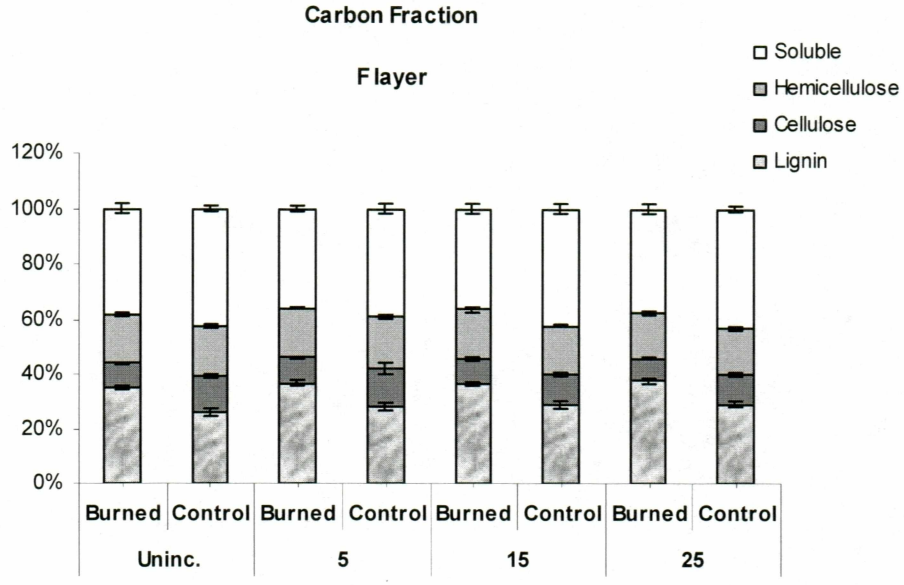

Fig. 20. Proximate fractions in F layer soils from burned and control black spruce stands, incubated for 205 days at 5, 15, and 25 °C, CPCRW, Alaska. Two-way nested ANOVA. Unincubated soils: n=15, incubated soils: n=45 and n=44 (burned and control) data are mean and standard error of the mean. See Table 3 for p values.

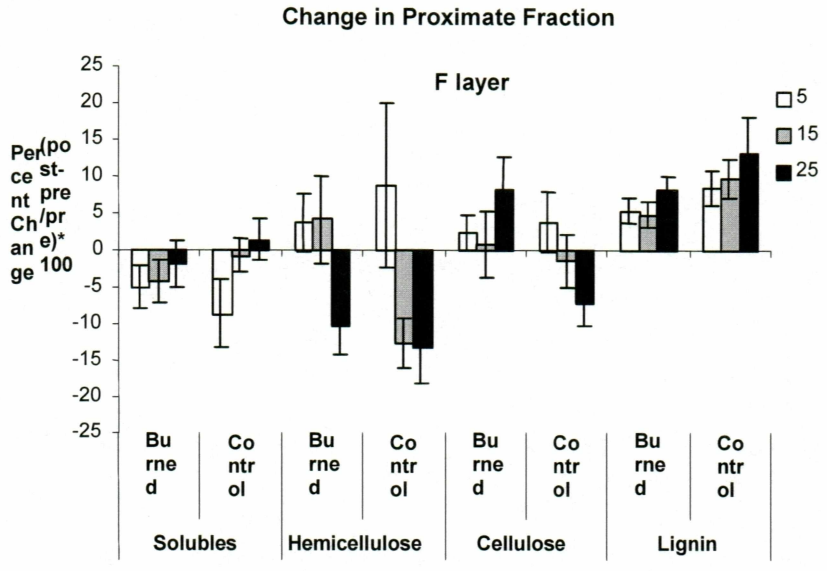

Fig. 21. Change in proximate fractions in F layer soils from burned and control black spruce stands, incubated for 205 days at 5, 15, and 25 °C, CPCRW, Alaska. Two-way nested ANOVA. Unincubated soils: n=15 (n=14 H layer control), incubated soils: n=45 and n=44 (burned and control) data are mean and standard error of the mean. See Table 9 for p values.

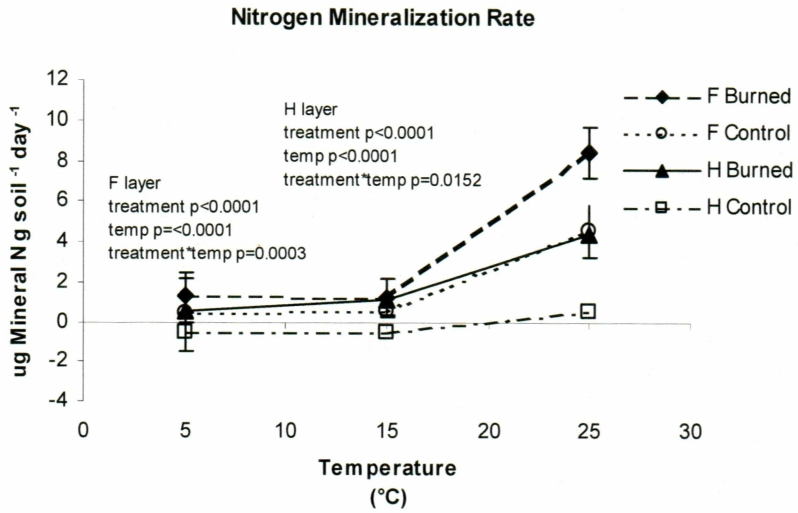

Fig. 22. Nitrogen mineralization rate in soils from burned and control black spruce stands, incubated for 205 (F) and 133 (H) days at 5, 15, and 25 °C, CPCRW, Alaska. Two-way ANOVA, n=45 (n=42 H layer control), data are mean and standard error of the mean.

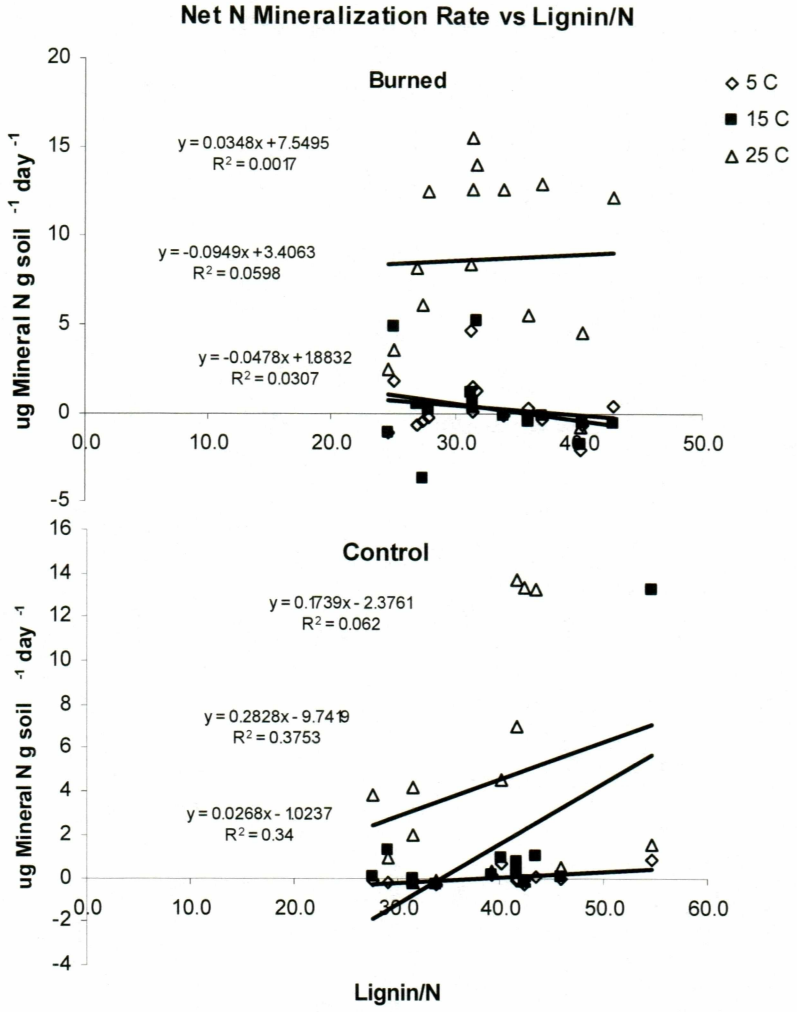

Fig. 23. Lignin/N vs.net nitrogen mineralization rate, burned and control F layer soils from black spruce stands, incubated for 205 days at 5, 15, and 25 °C, CPCRW, Alaska.

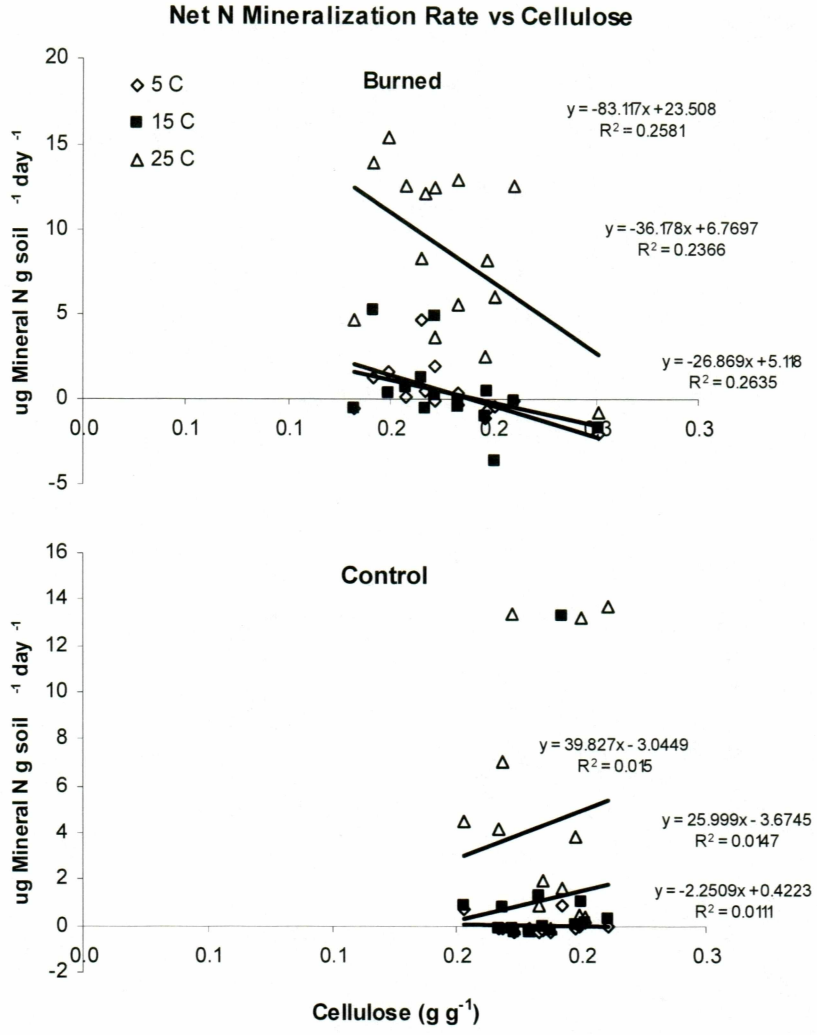

Fig. 24. Cellulose concentration vs. net nitrogen mineralization rate in soils from burned and control black spruce stands, incubated for 205 (F) days at 5, 15, and 25 °C, CPCRW, Alaska.

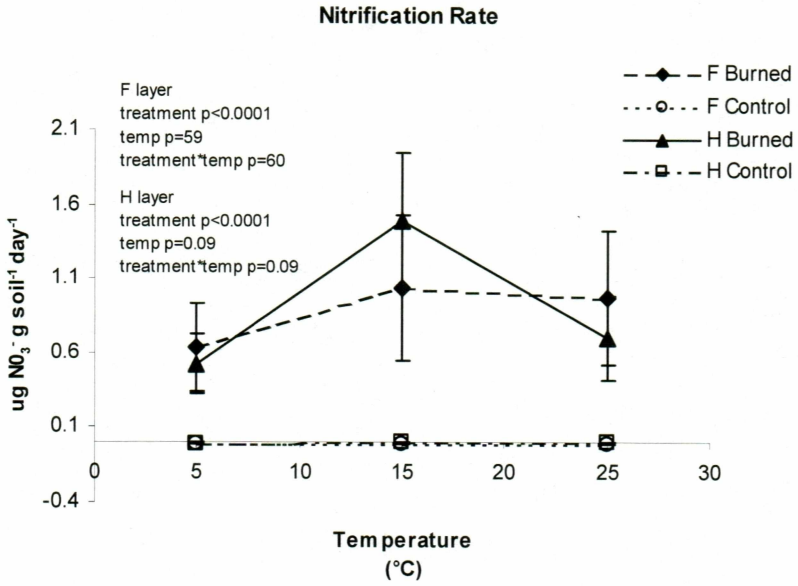

Fig. 25. Nitrification rate, burned and control soils black spruce stands, incubated for 205 (F) and 133 (H) days at 5, 15, and 25 °C, CPCRW, Alaska.

but in the control soils net N mineralization was negatively correlated to N concentration (Table 6b). Net nitrification rate was greater in burned than control soils for both layers and the highest rates for both layers occurred at 15 °C (Fig. 25).

6. Discussion

6.1 Respiration

In the "snapshot view" provided by laboratory incubation of our soils 2 years after the fire, the burned soils initially respired less than the control soils. Though this value may not accurately represent respiration potential *in situ* (due to the disturbance from thawing, aerating and watering the soils) the salient point is that both soils received identical treatment but produced very different initial quantities of CO_2. I hypothesize that the initial pulse in respiration measured in this study, which was greater in the control soils, was due to the presence of labile root-derived C. In the control sites, the presence of an intact canopy and understory continuously contributed to a pool of labile soil C while in the burned soils, lack of plant activity resulted in few C additions to offset losses. Research by Burke et al. (1997) supports this concept. They found no difference in *in situ* soil respiration in burned and unburned soils for up to 2 years following fire, but found that 2-7 years following fire, respiration in the burned soils was lower than that in the control soils. They hypothesized that for the first 2 years following fire, lack of autotrophic respiration and fine root inputs were balanced by decomposition of deep soil SOM and/or metabolization of fire-released C. Following depletion of these C reserves

and prior to revegetation (2-7 years since fire), respiration in burned soils dropped below that in control soils.

The difference in carbon inputs to control and burned soils from absence of vegetation is potentially large. In trench plot experiments in similar black spruce soils, Vogel (2004) found that 3 years following trenching, the trenched plots contained less C than untrenched plots. Burning would have a similar effect on soil C supply, resulting in reductions in organic matter input. Reduction in concentration of labile SOM could result in the lower respiration rates in the burned soil, as measured in this study.

Researchers have linked the labile pool of organic matter to root activity. For example, in boreal forests Ruess et al. (1996, 2003) estimated that variations in C allocation to roots accounted for 62% of the variation in soil respiration *in situ* and that 56% of soil respiration was derived from fine root respiration. Other researchers have also linked high initial laboratory respiration rates to root-derived C. Verburg et al. (1998) used ^{14}C labeled root exudates to identify sources of respired C and found that the signatures of initial respiration measurements correlated well with those of the root-derived C, but that the relationship disappeared as the incubation progressed. They estimated that *in situ* respired root exudates alone were responsible for up to 50% of total soil respiration. Similar results were noted by Frank and Hamilton (2001) who found higher respiration rates and greater concentration of C in rhizosphere soils than bulk soils in pulse-chase ^{13}C experiments.

The day one pulse in respiration rate measured in this study cannot be entirely attributed to the decomposition of roots and root related C, because the estimated

decomposition rate of roots is approximately 49 days (Ruess et al. 2003). However, it is estimated that 23% of fine root mass consists of water-soluble C (Chen et al. 2002), which may decompose faster than the entire root and thus could contribute to a short-term pulse in respiration seen in this study. In addition to differences in quantities of fine roots between burned and control soils, there likely were differences in root exudates present in soil at time of collection, also contributing to differing respiration potential. Because I did not measure the presence of fine roots, I can only speculate on their impact. However, in similar stands of spruce in interior Alaska, O'Neill et al. (2002) observed lower root metabolism and microbial activity in soils from burned stands than those in unburned stands (O'Neill et al. 2002).

In addition to affecting plant growth, fire has also been shown to alter microbial population composition, size, and activity. Fritze et al. (1998) found that DOC extracted from burned soils was chemically different than that from unburned soils and that when this DOC was applied to unburned soils, the soil microbial structure changed and respiration decreased by 20%. When the same DOC was added to burned soils, no change in respiration or microbial structure was observed. They concluded that the increase in pH and in toxic compounds following fire resulted in a shift in the microbial community to microbes more tolerant of the post-burn conditions. Microbes residing in unburned soils were not able to thrive in the presence of the burned DOC. Other researchers noted a decrease in microbial biomass following soil heating, as well as evidence of differential substrate usage and C limitation in the heated soils (Pietikainen et al. 2000). It is possible that differences in pools of SOM and in respiration were caused

by differing microbial communities in the burned and control soils, but because I did not assess the microbial community, I cannot determine the involvement of microbes in this study.

Though the results of this study partially support the initial hypothesis of greater respiration in control than burned soils and presence of greater concentrations of labile SOM in the control soils, we were unable to develop a clear relationship between respiration and lability. I found only weak relationships between measured variables and respiration. Though the rates measured in this study followed the same pattern observed by other researchers- initially high rates followed by lower and more consistent rates, my measures of labile C were only weakly related to initial respiration rate. Previous researchers (Melillo et al. 1982, Aber et al. 1990, Verburg 1998) have attributed initially high respiration rates to processing of labile C, while the slow and steady rates measured in the latter stages of the incubation were thought to represent the decomposition of recalcitrant and uniform SOM quality. The results of this study are contrary to the assumptions that respiration rates can be explained by the measures of lability I used, and that the process of decomposition is a linear path beginning with respiration of labile organic matter and continuing indefinitely with breakdown of recalcitrant organic matter.

There are at least three possible reasons for the observed departure from the assumed relationship between estimated lability and respiration: CO_2 efflux is not an accurate proxy for microbial activity; our concepts of what constitutes the labile (DOC) or recalcitrant (lignin) fractions are incorrect; or that the Ankom analysis is too crude to approximate lability with respect to soil microbes.

Because of the difficulty inherent in measuring gross transformations of SOM, net CO_2 efflux is frequently used as an estimate of bioavailability of organic matter and decomposition rates in soil. However it is likely that organic matter cycles between microbial biomass and SOM without being released as CO_2. Vogel (2004) advanced this hypothesis, based on the examination of organic matter pools and soil respiration in black spruce soils. Using pyrolysis-GC/MS, he found that polysaccharides were positively related to changes in phenolics but negatively related to respiration, indicating that decomposition of polysaccharides resulted in production of phenolics rather than CO_2.

In our study, the soluble fraction decreased as the lignin fraction increased, this relationship was similar in the burned and control soils, indicating that there is little difference in processes occurring in the two soils. The decrease in the soluble fraction and increase in lignin over the course of the incubation indicate that these fractions approximated lability and recalcitrance –respectively. The lignin fraction was the only fraction to increase in concentration over the course of the incubation, and it did not correlate with any measure of respiration. This lack of relationship could be due to the difficulty in measuring lignin. The lignin measured in this study likely contains both the lignin of plant structural material, and the "lignin" of microbial byproducts. These chemically very different compounds probably are not equally available to microbes, and presence of both in the same "pool" could mask any relationship of one or the other compound has with respiration.

Proximate fractions estimated by the Van Soest technique have been shown to correlate well with the forest products fractionation technique, also used for estimating

lability (Ryan et al. 1990), and though the Ankom technique has not been used previously on soils, our results fit well with the published values derived from Van Soest digests of forest litter and organic soil (Sanger et al. 1998, Ryan et al. 1990, Aber et al. 1990). The digest is traditionally used on fresh litter, so the fractions measured may be qualitatively different than those produced when analyzing fresh litter and consequentially result in different relationships with respiration. Additionally, the forage fiber technique is a procedure developed with the purpose of analyzing the digestibility of feed for livestock. While there are similarities between the digestibility of organic matter to ruminants and the digestibility to soil microbes, there are also potentially large differences.

In order to examine litter quality and decomposition of fresh litter and SOM, soil scientists have adapted the Van Soest technique from its original forage fiber application, and in this study I have further stretched the applicability by using a "modified Van Soest" (the Ankom procedure), to examine SOM. It is likely that the lack of relationships between our measured organic matter 'pools' and soil CO_2 efflux is a consequence of adapting an animal science technique to soils- where the technique may not produce relevant fractions for estimating lability in partially humified soil. Lack of correlation between fractions and respiration variables indicates that though there may be differences in pools of organic matter, those differences don't strongly translate to large changes in bioavailability of SOM or large differences in respiration.

Because I did not find any relationship between change in a particular proximate fraction and incubation temperature, we can conclude no relationship between the bioavailability of Ankom SOM fraction and temperature. This may be because

bioavailability is not temperature sensitive in these soils, or due to the large error observed in the mass change numbers. Researchers (Huang et al. 1998, Dai et al. 2001) who have noted the dependence of bioavailability on temperature used a more precise and possibly more accurate analytical tool- Py-GC-MS and may have had greater ability to detect changes in SOM pools. It is also possible that error stemmed from comparisons of incubated and unincubated samples rather than analyzing proximate fraction before and after incubation.

6.2 N Pools and Net Fluxes

Two years after fire, total N and mineral N concentrations were greater in burned than unburned soils. The mineral N pool consisted almost entirely of NH_4^+, consistent with research showing the low nitrification potential of boreal forest soils (Van Cleve et al. 1993, Munson and Timmer 1991, Weber and Van Cleve 1984). Previous studies have related this low nitrification potential to low pH (Martikainen 1984), chemical inhibition (Wardle et al. 1998), and C limitation (Wheatley et al. 2001). Even so, some of our soils exhibited net nitrification.

Rates of net nitrification in laboratory incubations were several orders of magnitude greater in burned soils than in control soils. NO_3^- accumulation was not temperature sensitive, though changes in NH_4^+ concentration were. The lack of response in net nitrification to either temperature or NH_4^+ concentration suggests that nitrifiers likely were limited by something other than temperature and NH_4^+ availability. Threshold pH values for nitrification generally are assumed to be around 4 (Paul and

Clark 1996). The burned soils had significantly higher pH than unburned soils, and only the pH in the burned F layer soils was above 4. It is possible that the slightly higher pH in the burned soils facilitated more rapid rates of nitrification. The low net nitrification rates in the control soils generally suggest that NO_3^- leaching may not be a large loss of N from undisturbed soils. However, high concentrations of NH_4^+ and NO_3^- in the burned soils indicate that they have the potential to export NO_3^- from the watershed.

N mineralization rate has been shown in some studies to be inhibited by high lignin/N ratio in SOM (Flanagan and Van Cleve 1983, Van Cleve et al. 1993, Scott and Binkley 1997), but not in others (Thomas and Prescott 2000), however lack of relationship between lignin/N ratio and net N mineralization rate could be due to error in estimating the "lignin" fraction using the Ankom technique.

Schimel et al. (2004) discuss four conceptual models of N availability and transformation, ranging from dominance of organic N as the major source of N to plants to the dominance of NO_3^- as available N. In environments with low available N, the N cycle is dominated by organic N, because negligible net N mineralization occurs and there is little mineral N available for plant uptake; both plants and microbes are N limited. As the availability of N increases, microbes meet their N demands and excrete NH_4^+, which, given proper conditions, is nitrified. Sites in this study support this model. The control sites were at the N-limited end, where organic N dominates and pools of

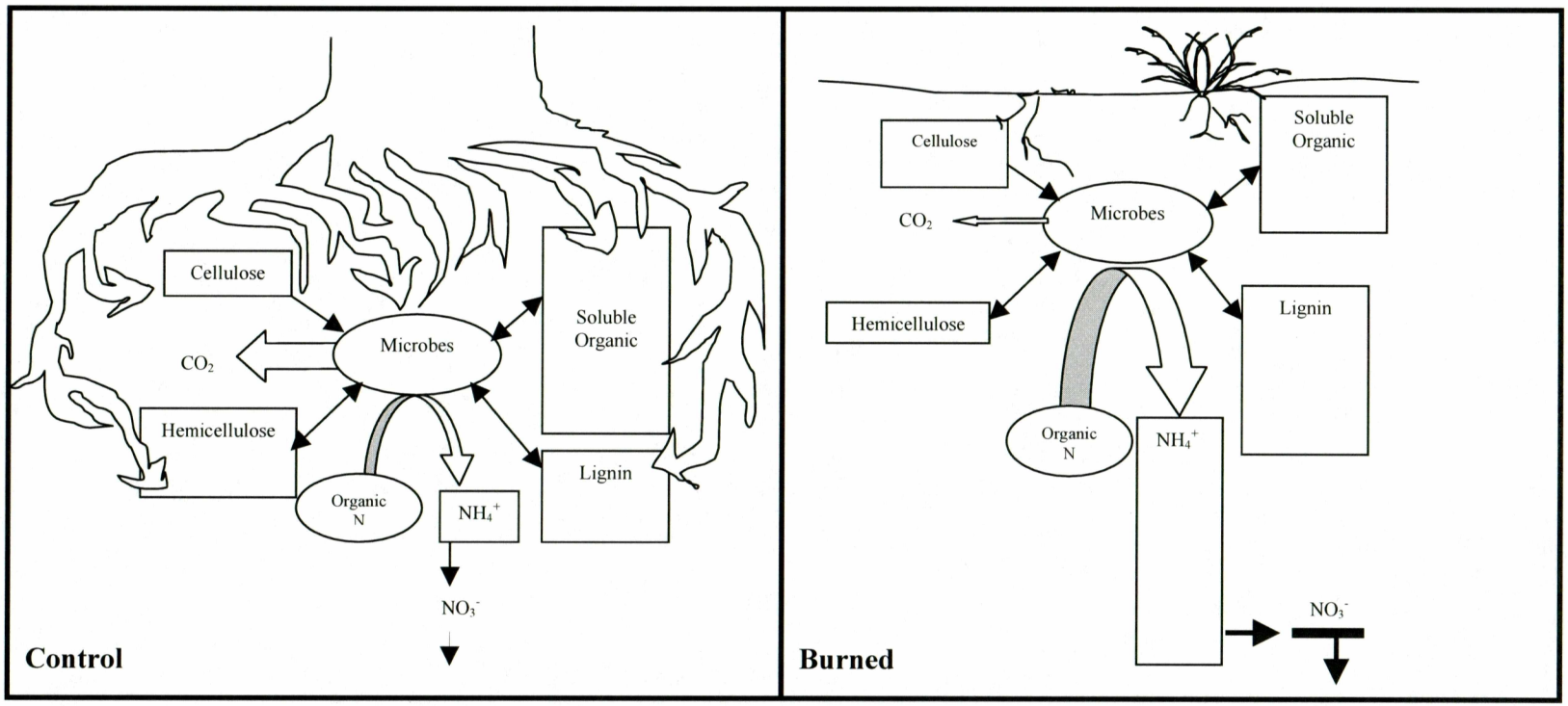

Fig. 26. Conceptual model of carbon and nitrogen cycling in burned and control stands of black spruce, interior Alaska.

mineral N are small, and the burned sites were at the N rich end of the continuum, where N availability meets or exceeds biotic demand and larger pools of mineral N exist, including NO_3^- (Fig. 26).

6.2 C and N Dynamics

Burned and control soils displayed distinct C and N cycles. In the burned soils, pools and net fluxes of available N were high as was recalcitrant SOM, while labile SOM concentration and initial respiration were lower. Positive relationship between respiration and lability indexes (soluble fraction/N, hemicellulose fraction/N, cellulose fraction/N) hints at C limitation in the burned soils. This is supported by the negative relationship between N and respiration and net N mineralization rate and respiration. It is also indirectly supported by the pool size of NH_4^+ and presence of nitrate in the burned soils- if the soils were N limited, little N would be present. If respiration in the burned soils was limited by C availability, we would expect net N mineralization rate to be negatively related to C.

In the control soils, the reverse was true: total and available N concentration and net flux were low, as was recalcitrant SOM, and concentration of labile C and initial respiration were greater than in burned soils. The positive relationship between NH_4^+ and respiration and the negative relationship between cellulose and respiration indicate that availability of N may limit respiration in the unburned soils.

However, the inconsistencies in the relationship of net N mineralization rate and other measured variable indicate complexity in C and N dynamics that far outreach the

ability of this study to characterize the relationship. The lack of relationship between net nitrogen mineralization rate in the burned soil and any measured variable is curious. If burned soils were C limited, we would expect to find an inverse relationship between C and net N mineralization rate- because as C became available, microbes would mineralize less N, instead incorporating both C and N into biomass. Examining the C/N ratios does not further clarify the relationship. In the control soils, net N mineralization rate is positively related to SOM fractions and lability indexes. If control soils were truly N limited, net N mineralization rate would be inversely related to indexes of lability.

Because net N mineralization does not measure all transformations of N, it is difficult to determine the relationship between SOM fractions and N transformation. The difficulty is further exacerbated by the inaccuracy and imprecision of the techniques used to determine SOM lability. So even though there were large and significant differences in nutrient and SOM pools, relationships between pools and fluxes across treatment and temperature are difficult to discern. Because the difference in respiration only existed early in the incubation, we have to assume that any differences in organic matter quality or C and N dynamics were not significant enough to affect mid- to long- term bioavailability of SOM and consequent ability of the soil to release C.

6.3 Temperature Sensitivity

As noted by other researchers (Burke et al. 1997, Dyrness et al. 1986), the burned soils had warmer growing season and cooler winter temperatures than the control soils,

which probably resulted in the accelerated decomposition of common substrates in burned stands relative to control stands.

The method for Q_{10} calculation (point to point comparisons versus nonlinear regression) had an effect on the magnitude of the values but not in the trends between burned and control soils, burned soils always produced greater Q_{10} values than control soils. The nonlinear regressions were not relatively insensitive to the larger difference in respiration rate change from 5 to 15 °C, which was evident in the point-to-point comparisons. This is probably because the nonlinear regression method produces a single number explaining temperature sensitivity through a given range, and some accuracy is lost through the regression method, even with R^2 of 0.91 or greater.

In this study, by the end of the incubation there was little or no difference in temperature sensitivity of the soils, hinting that their organic matter was similarly available to microbes. However, because Q_{10} calculated in this study only evaluates the net result of decomposition (CO_2 efflux), it is insensitive to internally cycled organic matter and doesn't shed light on the gross transformations of SOM.

I had hypothesized that the presence of labile C in the control soils would increase temperature sensitivity and that microbial C limitation in the burned soils would reduce temperature sensitivity. However I did not find this to be true, based on the lack of relationship between labile C (as measured in this study) and Q_{10}, and the fact that temperature sensitivity was greater in the burned soils.

It is possible that the Q_{10} method may be inappropriate for assessing relative organic matter quality when respiration rates to be compared are of greatly differing

magnitudes. At 5 °C in the burned soils respiration was very low, and even small increases in respiration at 10 °C resulted in high Q_{10} values. In the control soils, higher respiration rates necessitate much larger increases in respiration rate to produce large Q_{10} values. Calculating the increase on an absolute basis in C respired with temperature (CO_2-C gC^{-1} $°C^{-1}$) alleviates this problem by removing the impact of the differences in rates. Although the warming of burned soils produced a greater increase in CO_2 production relative to that produced at cooler temperatures, the absolute increase in CO_2 production was much larger in unburned soils for all comparisons for both layers. The control soils had the potential to release a larger quantity of CO_2 per degree than the burned soils, even though the burned soils were more responsive to temperature change.

7. Conclusions

In situ, burned soils were warmer, had higher pH, and decomposed common substrates more quickly than the control soils. In laboratory incubations, burned soils mineralized more net N, contained higher concentrations of total and mineral N and total C, and lower concentrations of labile C. Because respiration rates between soils from burned and unburned stands only differed on day one of the incubation, when the soil most closely resembled field conditions, and because persistent differences in measured variables did not account for substantial variation in respiration for the duration of the experiment, I hypothesize that the main effects of this fire on soil N dynamics resulted from the removal of vegetation and associated substrate supplies to microbial communities.

Though temperature sensitivity was greater in the burned soils than control soils, the salient point is that control soils had more labile C to process, respired more C over the very short-term, and respiration rate increased with temperature more (in absolute terms) than burned soils. Also, Q_{10} values for lab incubations are not equivalent to field studies, as the absence of roots changes temperature sensitivity dynamics. O'Neill et al. (2002) found lower Q_{10} values in burned than control stands, possibly because of the greater temperature sensitivity of root respiration (Boone et al. 1998).

Another factor affecting Q_{10} values is choice of time frame. If evaluated early on in the incubation, accuracy of values is compromised by the effects of thawing, sieving and aerating. However, early on in an incubation the soil more closely resembles its field condition than it does later in the incubation, so if the purpose of the experiment is to study real world conditions, an early evaluation of Q_{10} is recommended. In the advanced stages of incubation, disturbance effects are minimal, but the soil has been incubating for some period of time without fresh inputs and likely does not resemble the soil in its *in situ* condition. If the purpose of the study were to examine the amount of recalcitrant organic matter and its temperature sensitivity, then Q_{10} evaluation at the end of the incubation might be the better choice.

Conclusions from laboratory incubations are not directly applicable to *in situ* processes, because moisture and temperature are held constant and there are no inputs to the soil. In the field, the net ecosystem release of C in either system will depend on the amount of C fixed by vegetation, so the net result of these fluxes will also determine whether the sites are C sources or sinks with respect to atmospheric CO_2 concentrations

(Goulden et al. 1998). *In situ*, CO_2 release in burned soils is not balanced by uptake of CO_2 by plants, thus they have the potential to export CO_2 to the atmosphere. Also, because soils from burned sites were more temperature sensitive, they have the potential to release more C to the atmosphere if sufficiently warmed.

The Ankom proximate fraction analysis showed differences in C pools and changes in these pools over the incubation, but these changes were only weakly related to mineralization variables. Use of more sensitive analyses may provide insight into relationships among SOM pools, fluxes, and associated microbial communities, but our data only hint at those relationships.

Further study should include a vegetation removal treatment to compare the effects of burning vs. cessation of fresh litter inputs. And because microbes are responsible for the net release of C from soils, future research should focus on the effects of fire on microbial community dynamics and the relationship between microbes, lability of C, respiration, and fire.

8. References

Aber, J. D. Melillo J. M. McClaugherty C. A. 1990. Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. Canadian Journal of Botany 68:2201-2208.

Alexyev, V. A. and Birdsey R. A. Carbon Storage in Forests and Peatlands of Russia. 1998. Radnor, PA, USDA Forest Service, Northeastern Forest Experiment Station.

Almendros, G. Gonzalez-Vila F. J. Martin F. 1990. Fire induced transformation of soil organic matter from an oak forest: an experimental approach to the effects of fire on humic substances. Soil Science 149, no. 3:158-168.

Andrews, J. A. Matamala R. Westover K. and Schlesinger W. H. 2000. Temperature effects on the diversity of soil heterotrophs and the del 13C of soil-respired CO2. Soil Biology and Biochemistry 32:699-706.

Apps, M. J. Kurz W. A. Luxmoore R. J. Nilsson L. O. Sedjo R. A Schmidt R. Simpson L. G. and Vinson T. S. 1993. Boreal forests and Tundra. Water Air and Soil Pollution 70:39-53.

Baath, E. Frostegard A. Pennanen T. and Fritze H. 1995. Microbial community structure and pH response in relation to soil organic matter quality in wood-ash fertilized, clear-cut or burned coniferous forest soils. Soil Biology and Biochemistry 27, no. 2:229-240.

Boone, R. D. Nadelhoffer K. J. Canary J. D. Kaye J. P. 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. Nature 396:570-572.

Bowden, R. D. Newkirk K. M. and Rullo G. M. 1998. Carbon dioxide and methane fluxes by a forest soil under laboratory-controlled moisture and temperature conditions. Soil Biology and Biochemistry 30, no. 12:1591-1597.

Bremner, J. M. 1982. Extraction of Exchangeable Ammonium, Nitrate, and Nitrite. In Methods of Soil Analysis, Chemical and Microbiological Properties. Agronomy Monograph 9, Part 2., edited by Black, C. A. Evens D. D. White J. L. Ensminger L. E. Clarke F. E. (Madison,WI: American Society of Agronomy).

Buchmann, N. 2000. Biotic and abiotic factors controlling soil respiration rates in Picea abies stands. Soil Biology and Biochemistry 32:1625-1635.

Burke, R. A. Zepp R. G. Tarr M. A. Miller W. L. Stocks B. J. 1997. Effect of fire on soil-atmosphere exchange of methane and carbon dioxide in Canadian boreal forest sites. Journal of Geophysical Research 102, no. D24:29289-29300.

Chapman, R. M Weber F. R. and Taber B. 1971. Preliminary geologic map of Livengood quadrangle. Open File Report 483. scale 1:250,000. U.S. Geological Survey.

.

Chen, H. Harmon M. E. Sexton J. Fasth J. 2002. Fine root decomposition and N dynamics in coniferous forests of the Pacific Northwest, U.S.A. Canadian Journal of Forest Research 32:320-331.

Cromack, K. 1973. Litter production and litter decomposition in a mixed hardwood watershed at Coweeta Hydrologic Station, North Carolina. Ph.D. Dissertation. Athens, Georgia: University of Georgia.

Dai, X. Y. Ping C. L. Candler R. Haumaier L. and Zech W. 2001. Characterization of soil organic matter fractions of tundra soils in Arctic Alaska by Carbon-13 Nuclear Magnetic Resonance Spectroscopy. Soil Science Society of America Journal 65, no. 1:87-93.

DeBano, LF. 1998. Fire: it's effect on soil and other ecosystem resources. Edited by Neary, DG Ffolliott PF. 1 ed. New York: John Wiley & Sons, Inc.

Dong, J. Tucker C. J. Kauppi P. E. et al. 2003. Remote sensing estimates of boreal and temperate forest woody biomass: Carbon pools, sources, and sinks. Remote Sensing of Environment 84, no. 3:393-410.

Driscoll, K. G. Arocena J. M. Massicotte H. B. 1999. Post-fire soil nitrogen content and vegetation composition in Sub-Boreal spruce forests of British Columbia's central interior, Canada. Forest Ecology and Management 121:227-237.

Dyrness, C. T. and Norum R. A. 1983. The effects of experimental fires on black spruce forest floors in interior Alaska. Canadian Journal of Forest Research 13:879-893.

Dyrness, C. T. Van Cleve K. and Levison J. D. 1989. The effect of wildfire on soil chemistry in four forest types in interior Alaska. Canadian Journal of Forest Research 19:1389-1396.

Dyrness, CT Viereck LA Van Cleve K. 1986. Fire in taiga communities of interior Alaska. In Ecological Studies: analysis and synthesis, Vol. 57, (New York: Springer-Verlag).

Fastie, C. L. 2000. Fire history of the C4 and P6 basins of the Caribou-Poker Creeks Research Watershed, Alaska. The Role of Fire in the Boreal Forest and its Impacts on Climatic Processes, INE/WERC Report No. 00.03.21-23. University of Alaska Fairbanks, Fairbanks, AK.

Flanagan, P. W. and Van Cleve K. 1983. Nutrient cycling in relation to decomposition and organic matter quality in taiga ecosystems. Canadian Journal of Forest Research 13, no. 5:795-817.

Frank, D. A. and Hamilton E. W. 2001. Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. Ecology 82, no. 9:2397-2402.

Fritze, H. Pennanen T. and Kitunen V. 1998. Characterization of dissolved organic carbon from burned humus and its effects on microbial activity and community structure. Soil Biology and Biochemistry 30, no. 6:687-693.

Goering, H. K Van Soest P. J. 1970. Forage fiber analysis (apparatus, reagents procedures, and some applications). USDA Agricultural Handbook No. 379.

Goulden, M. L. Wofsy S. C. Harden J. W. Trumbore S. E. Crill P. M. Gower S. T. Fries T. Daube D. C. Fan S. M. Sutton D. J. Bazzazz A. Munger J. W. 1998. Sensitivity of boreal forest carbon balance to soil thaw. Science 279:214-217.

Haugen, R. K. Slaughter C. W. Howe K. E. and Dingman S. L. Hydrology and climate of the Caribou-Poker Research Watershed, Alaska. CREL Report 82-86. 1982. Hanover, NH.

Hawkins, D. B. Forbes R. B. Hok C. I. and Dinkel D. 1982. Arsenic in the water, soil, bedrock, and plants of the Ester Dome area of Alaska. Report IWR-103. 82 pp. University of Alaska. Fairbanks, Alaska. Institute of Water Resources.

Heinselman, M. L. 1978. Fire intensity and frequency as factors in the determination and structure of northern ecosystems. Preliminary draft ed.

Huang, Y. Eglinton G. Van der Hage E. R. E. Boon J. J. Bol R. and Ineson P. 1998. Dissolved organic matter and its parent organic matter in grass upland soil horizons studied by analytical pyrolysis techniques. European Journal of Soil Science 79:1-15.

Kasischke, E. S. and Stocks B. J. 2000. Fire, Climate Change, and Carbon Cycling in the Boreal Forest. Edited by Kasischke, E. S., Ecological Studies. New York, NY: Springer-Verlag.

Kirschbaum, M. U. F. 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. Soil Biology and Biochemistry 27, no. 6:753-760.

Kirschbaum, M. U. F. 2000. Will changes in soil organic carbon act as a positive or negative feedback on global warming? Biogeochemistry 48:21-51.

Komarek, A. R. Manson H. and Thiex N. 1996. Crude fiber determinations using the ANKOM system. Publication 102, ANKOM Technology Corporation, Fairport, NY.

Lotspeich, C. W. and Slaughter F. B. 1977. Caribou-Poker Creeks Research Watershed Alaska. Arctic Bulletin 2, no. 10:182-188.

Mafongoya et. al. 1998. 1998. Mineralization of nitrogen from decomposing leaves of multipurpose trees as affected by their chemical composition. Biology and Fertility of Soils 27, no. 2:143-148.

Martikainen, P. J. 1984. Nitrification in two coniferous forest soils after different fertilization treatments. Soil Biology and Biochemistry 16:577-582.

Melillo, J. M. Aber J. D. Muratore J. F. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63, no. 3 :621-626.

Munson, A. D. and Timmer V. R. 1991. Site-specific growth and nutrition of planted Picea mariana in the Ontario clay belt V. Humus nitrogen availability. Canadian Journal of Forest Research 21:1194-1199.

Niklinska, M Maryanski M. and Laskowski R. 1999. Effect of temperature on humus respiration rate and nitrogen mineralization: Implications for global climate change. Biogeochemistry 44:239-257.

O'Neill, K. P. Kasischke E. S. and Richter D. D. 2002. Environmental controls on soil CO2 flux following fire in black spruce, white spruce, and aspen stands of interior Alaska. Canadian Journal of Forest Research 32:1525-1541.

Paavilainen, E. and Paivanen J. 1995. Peatland Forestry., Ecological Studies. New York: Springer-Verlag.

Paul, E. A. Clark F. E. 1996. Soil Microbiology and Biochemistry. 2nd ed. San Diego, CA: Academic Press.

Péwé, T. L. Geology of the Fairbanks (D-2) Quadrangle, Alaska. 1958. Department of the Interior, U.S. Geological Survey.

Pietikainen, J. Hiukka R. Fritze H. 2000. Does short-term heating of forest humus change its properties as a substrate for microbes? Soil Biology and Biochemistry 32:277-288.

Pietkainen, J. and Fritze H. 1992. Microbial biomass and activity in the humus layer following burning: short-term effects of two different fires. Canadian Journal of Forest Research 23:1275-1285.

Reichstein, M. Bednorz F. Broll G. and Katterer T. 2000. Temperature dependence of carbon mineralisation: conclusions from a long-term incubation of subalpine soil samples. Soil Biology and Biochemistry 32:947-958.

Rieger, S. Furbush C. E. Schoephorster D. B. Summerfield H. Jr. Geiger L. C. 1972. Soils of Caribou-Poker Creeks Research Watershed, Interior Alaska. Technical Report 236, Army Corp of Engineers, US CRREL, Hanover, NH.

Ross, D. J. Kelliher F. M. Tate K. R. 1999. Microbial processes in relation to carbon, nitrogen and temperature regimes in litter and a sandy mineral soil from a central Siberian Pinus sylvestris L. forest. Soil Biology and Biochemistry 31:757-767.

Ruess, R. W. Hendrick R. L. Burton A. J. Pregitzer K. S. Sveinbjornsson B. Allen M. F. Maurer G. E. 2003. Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. Ecological Monographs 73, no. 4:643-662.

Ruess RM, Van Cleve K Yarie J Viereck LA. 1996. Contributions of fine root production and turnover to the carbon and nitrogen cycling in taiga forests of the Alaskan interior. Canadian Journal of Forest Research 26, no. 8:1326-1336.

Russell, C. A. and Voroney R. P. 1998. Carbon dioxide efflux from the floor of a boreal aspen forest. I. Relationship to environmental variables and estimates of C respired. Canadian Journal of Forest Research 78:301-310.

Ryan, M. G. Melillo J. M. Ricca A. 1990. A comparison of methods for determining proximate carbon fractions of forest litter. Canadian Journal of Forest Research 20:166-171.

Sanger, L. J., P. Cox, P. Splatt, M. Whelan, and J. M. Anderson. 1998. Variability in the quality and potential decomposability of Pinus sylvestris litter from sites with different soil characteristics: acid detergent fiber (ADF) and carbohydrate signatures. Soil Biology and Biochemistry 30, no. 4:455-461.

Schimel, J. P. and Bennett J. 2004. Nitrogen Mineralization: Challenges of a changing paradigm. Ecology 85, no. 3:591-602.

Schlentner, R. E. and Van Cleve K. 1985. Relationships between CO_2 evolution from soil, substrate temperature, and substrate moisture in four mature forest types in interior Alaska. Canadian Journal of Forest Research 15:97-106.

Scott, N. A. and Binkley D. 1997. Foliage litter quality and annual net N mineralization: Comparison across North American forest sites. Oecologia 111, no. 2:151-159.

Slaughter, C. W. and Viereck L. A. 1986. Climatic characteristics of the taiga in interior Alaska. In Forest Ecosystems in the Alaskan Taiga: A synthesis of Structure and

Function, edited by Van Cleve, K. Chapin F. S. III. Flanagan P. W. Viereck L. A. Dyrness C. T. (New York: Springer-Verlag).

Smith, C. K. Coyea M. R. and Munson A. D. 2000. Soil carbon, nitrogen, and phosphorous stocks and dynamics under disturbed black spruce forests. Ecological Applications 10, no. 3:775-778.

Soil Survey Staff. Soil Taxonomy Handbook. United States Natural Resources Conservation Service. Agricultural Handbook No 436. 1999. Washington DC, US Government Printing Office.

Thomas, K. D. and Prescott C. E. 2000. Nitrogen availability in forest floors of three tree species on the same site: The role of litter quality. Canadian Journal of Forest Research 30:1698-1706.

Valentine, DW. 2000. Unpublished Data.

Van Cleve, K. Yarie J. Erickson R. Dyrness C. T. 1993. Nitrogen mineralization and nitrification in successional ecosystems on the Tanana River floodplain, interior Alaska. Canadian Journal of Forest Research 23:970-978.

Van Soest, P. J. 1963. Use of detergents in the analysis of fibrous feeds. II. A rapid method for the determination of fiber and lignin. J. Assoc. Off. Anal. Chem 46:829-835.

Van Soest, P. J. 1994. Nutritional Ecology of the Ruminant. Edited by . US: Cornell University Press.

Verburg, P. S. J. Gorissen A. and Arp W. J. 1998. Carbon allocation and decomposition of root-derived organic matter in a plant-soil system of Calluna vulgaris as affected by elevated CO2. Soil Biology and Biochemistry 30, no. 10/11:1251-1258.

Verburg, P. S. J. Van Dam D. Hefting M. M. Tietema A. 1999. Microbial transformations of C and N in a boreal forest floor as affected by temperature. Plant and Soil 208, no. 2:187-197.

Viereck, L. A. and Schandelmeier L. A. 1980. Effects of fire in Alaska and adjacent Canada : a literature review . U.S. Department of the Interior, Bureau of Land Management, Alaska State Office. Anchorage, AK.

Viereck, L. A. Van Cleve K. Dyrness C. T. 1986. Forest ecosystem distribution in the taiga environment. In Forest ecosystems in the Alaskan taiga: a synthesis of structure and function, edited by Van Cleve, K. Chapin F. S. Flanagan P. W. Viereck L. A. and Dyrness C. T. (New York: Springer Verlag).

Vogel, J. G. 2004. Carbon Cycling in three mature black spruce (Picea mariana [Mill.] B.S.P.) forests in interior Alaska. Carbon Cycling in three mature black spruce (Picea mariana [Mill.] B.S.P.) forests in interior Alaska, University of Alaska-Fairbanks, Fairbanks, Alaska.

Wahrhaftig, C. 1965. Physiographic divisions of Alaska. U.S. Geological Survey Professional Paper 482.

Wardle, D. A. Zackrisson O. and Nilsson M. C. 1998. The charcoal effect in Boreal forests: mechanisms and ecological consequences. Oecologia 115:419-426.

Weber, M. G. and Van Cleve K. 1984. Nitrogen transformations in feather moss and forest floor layers of interior Alaska black spruce ecosystems. Canadian Journal of Forest Research 14:278-290.

Wheatly, R. E. Ritz K. Crabb D. and Caul S. 2001. Temporal variations in potential nitrification dynamics in soil related to differences in rates and types of carbon and nitrogen inputs. Soil Biology and Biochemistry 33:2135-2144.

Wieder, R. K. Starr S. T. 1998. Quantitative determination of organic fractions in highly organic, Sphagnum peat soils. Communications in Soil Science and Plant Analysis 29, no. 7/8:847-857.

Winkler, J. P. Cherry R. S. and Schlesinger W. H. 1996. The Q_{10} relationship of microbial respiration in a temperate forest soil. Soil Biology and Biochemistry 28, no. 8:1067-1072.