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Carbon cycling in three mature black spruce (*Picea mariana* [Mill.] B.S.P) forests in interior Alaska

A

THESIS

Presented to the Faculty
of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements
for the Degree of

Doctor of Philosophy

By

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Fairbanks, Alaska

May 2004

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CARBON CYCLING IN THREE MATURE BLACK SPRUCE (*PICEA MARIANA* [MILL.] B.S.P) FORESTS IN INTERIOR ALASKA

By

Jason Gene Vogel

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ABSTRACT

Climate warming in high latitudes is expected to alter the carbon cycle of the boreal forest. Warming will likely increase the rate of organic matter decomposition and microbial respiration. Faster organic matter decomposition should increase plant available nutrients and stimulate plant growth. I examined these predicted relationships between C cycle components in three similar black spruce forests (*Picea mariana* [Mill] B.S.P) near Fairbanks, Alaska, that differed in soil environment and *in-situ* decomposition.

As predicted, greater *in-situ* decomposition rates corresponded to greater microbial respiration and black spruce aboveground growth. However root and soil respiration were both greater at the site where decomposition was slowest, indicating greater C allocation to root processes with slower decomposition. It is unclear what environmental factor controls spruce allocation. Low temperature or moisture could cause spruce to increase belowground allocation because slower decomposition leads to low N availability, but foliar N concentration was similar across sites and root N concentration greater at the slow decomposition site. The foliar isotopic composition of ^{13}C indicated soil moisture was lower at the site with greater root and soil respiration. From a literature review of mature black spruce forests, it appears drier (e.g. Alaska) regions of the boreal forest have greater soil respiration because of greater black spruce C allocation belowground.

Organic matter characteristics identified with pyrolysis gas chromatography-mass spectrometry correlated with microbial processes, but organic matter chemistry less

influenced C and N mineralization than did temperature. Also, differences among sites in C and net N mineralization rates were few and difficult to explain from soil characteristics. Warming had a greater influence on C and N mineralization than the mediatory effect of soil organic matter chemistry.

In this study, spruce root C allocation varied more among the three stands than other ecosystem components of C cycling. Spruce root growth most affected the annual C balance by controlling forest floor C accumulation, which was remarkably sensitive to root severing. Predicting the response of black spruce to climate change will require an understanding of how spruce C allocation responds to available moisture and soil temperature.

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ACKNOWLEDGEMENTS

I thank my advisor, David Valentine, for his advice, patience, financial support and good humor in all stages of my thesis. He provided encouragement and skepticism throughout this process, and I believe I am a better scientist as a result. I use the pronoun "we" in all three chapters in reference to the input of David Valentine.

My committee members each deserve a special thank you. The insights of Roger Ruess guided much of this research, and his prior work excited my curiosity and encouraged this study in belowground C allocation. Roger Ruess is a co-author of the first chapter because of his input on the initial study design. Dave McGuire provided advice early in the research design, and during the later stages, encouragement and excellent reviews of the chapters. Steve Sparrow was always available for a discussion on organic matter quality and his generosity in lab resources was critical to my completing the incubation study. Jennifer Harden generously made the ^{14}C analysis possible and her encouragement and intellectual input always seemed timed to when I needed it most.

Others at the University of Alaska deserve mention. Dan White's lab conducted the pyrolysis analysis free of charge and answered numerous inquires on interpreting results. Rich Boone provided advice and encouragement in implementing the trenched plot method. The incubation study would have been "less" enjoyable without the advice and camaraderie of Rich Brenner. Terry Chapin loaned me his LI-COR infrared gas analyzer early in this research. The staff of Bonanza Creek LTER provided preliminary weather data and Ron Barry provided statistical advice. John Yarie shared his experience

and knowledge, and his home. Darleen Masiak of Steve Sparrow's lab was always a wonderful help. The Center for Global Change Research and the National Science Foundation's Long-Term Ecological Research (Bonanza Creek) program provided financial support for this research.

Kathy O'Neill shared her data and insights into C cycling in Alaskan forests. Colleagues from the University of Wisconsin-Madison also provided input and advice. Tom Gower made early suggestions and later, his research results available, which provided a larger perspective to the patterns I was observing. Sean Burrows and Kari Bisbee made suggestions on using SAS to manage and analyze data. The Land Trust Office of Alaska allowed me to conduct research on the lands they manage.

The staff of the Forest Soils Lab provided technical and collegial support. Lola Oliver's contribution is especially appreciated and my research, or perhaps any research in the lab, would not have been possible without her. Tim Quintal's brilliant inventions made innumerable steps in the data collection easier. Jason Downing and Jess Garron tolerated me as an office mate and provided ample assistance and friendship. Andrew Balser helped locate sites and was a good friend throughout. The undergraduate students who carried my research on their backs were critical to this study: Nate Pamperin, Desmond Johns, Paul Kephart, Dan Nidzgorski, and Andre Collins. Their hard work made mine easier.

The friends made within the community of graduate students and post-doctoral researchers are quite possibly the best outcome of my time in Alaska. Rich Brenner, Catherine Copass Thompson, Kevin Petrone, Evan Kane, and Martin Wilmking provided

great discussions on boreal ecology and life in general. The friendship and collegial input of Ted Schuur and Michelle Mack brought adventures and intellectual challenges that I will always treasure. I am deeply indebted to the friendship of Katey Walter; her adventurous spirit inspired me to push forward in the realms of research and life.

Finally, I lovingly thank my parents Gene and Janet Vogel for their guidance and encouragement throughout my life

GENERAL INTRODUCTION

The interaction between climate and boreal forest carbon (C) cycling has received increased attention because of ongoing climate warming in many high-latitude regions (Chapin et al. 2000, Serreze et al. 2000). The scientific community now generally agrees that part of the increase in temperature is "very likely" from the human derived greenhouse gases and that warming will continue with greenhouse gas buildup (Houghton et al. 2001). Projected warming is expected to be greatest at high-latitudes and the warming will likely alter a number of ecosystem processes in the boreal forest. Warming could increase the frequency of fire (Kasischke et al. 1995) and insect outbreaks (Parson et al. 2001), and also alter the balance between photosynthesis and respiration (Goulden et al. 1998). For the greenhouse gas carbon dioxide (CO_2), these ecosystem changes could significantly change the short- and long-term exchange of CO_2 between the forest and atmosphere.

In northern latitude ecosystems, photosynthesis often only slightly exceeds respiration on an annual basis (Janssens et al. 2001), but over long enough time periods the difference is enough to result in the accumulation of soil C. The boreal forest is the second largest forest biome and contains in its soils an estimated 182 Pg C (Post et al. 1982) or 24% of the current amount of atmospheric C. Much of the soil C has accumulated because low soil temperatures and excessive soil moisture limit decomposition (Harden et al. 2000), making it possible that a warming or drying climate will stimulate the decomposition of soil C (Kirschbaum 1995, McGuire et al. 1995, Chapin et al. 2000, Kirschbaum 2000). Alternatively, the warming would increase

decomposition, plant nutrient availability, growing season length and, as a result, forest growth. In this latter case, photosynthesis may remove more CO_2 from the atmosphere than the ecosystem loses from decomposition and the biome may increase its net C storage.

The potential of these alternative scenarios varies by vegetation type. Slow growing vegetation overlying substantial accumulations of soil C may not have the capacity to increase productivity to offset warming-induced decomposition. In Alaska, the most common tree species is black spruce (*Picea mariana* [Mill] B.S.P)(Labau and van Hees 1990), which is also the slowest growing tree species and co-occurs with the greatest amounts of soil C (Van Cleve et al. 1983, Gower et al. 1997). The only published soil warming experiment in black spruce reported that after 3 years, aboveground production increased 33% and forest floor mass decreased 20% in response to a 8-10 °C soil warming (Hom 1986, Van Cleve and Yarie 1986, Van Cleve et al. 1990). The absolute amount of forest floor decrease, however, was over 10x the increase in aboveground production (1800 vs. 128 g m^{-2}) (estimated from data in Hom 1986), suggesting decomposition can contribute significant amounts of C to the atmosphere with warming. Although climate warming is not expected to be this extreme (Houghton et al. 2001), model results (McGuire et al. 1995, Arain et al. 2002, Clein et al. 2002) and measurements with eddy-covariance systems (Jarvis et al. 1997, Goulden et al. 1998, Rayment and Jarvis 1999) have found that with moderate warming, respiration can temporarily exceed productivity in mature black spruce ecosystems.

The focus of this research is the relationships among plant primary production, decomposition, and root processes in mature black spruce forests that varied in *in-situ* decomposition rates and soil environment. Ecosystem C balance in black spruce is extremely sensitive to soil processes (Goulden et al. 1998, Ruess et al. in press), and these processes are the least understood and most difficult components of ecosystem C cycling to study (Gower et al. 1997). For example if increased decomposition causes soil C loss, then soil respiration should increase. However, both roots and microbes contribute to soil respiration and it is unclear if both respond similarly to environmental change. Delineating microbial respiration from root processes is necessary to monitor soil C loss (Boone et al. 1998) and for developing models of ecosystem response to climate change (Hanson et al. 2000). Root growth and mortality also contribute to the accumulation of soil C and an environmental factor that increases microbial respiration may also increase these root processes. The net result may be more soil C being stored.

Significant advances have been made in understanding the relationship between environment and root processes in black spruce ecosystems. As first reported by Tryon and Chapin (1983), the growth of roots in black spruce correlate seasonally to soil temperature (Steele et al. 1997; O'Connell et al. 2003; Ruess et al. (in press)) and the response of root elongation rate to temperature is greater for black spruce than other boreal tree species (Tryon and Chapin 1983, Steele et al. 1997). The peak in soil respiration coming from spruce roots also occurs during mid-summer and is greater than respiration from microbial decomposition (O'Connell et al. 2003). The seasonal course of root respiration may be from a change in root mass, an increased temperature

sensitivity of root respiration, or from increased photosynthate supply to roots due to more sunlight. In a Scots pine forest, root respiration decreased within two weeks of a tree girdling experiment (Högberg et al. 2001), suggesting a strong link between recent photosynthate and root respiration. Boone et al. (1998) found root respiration controlled the temperature sensitivity of soil respiration in temperate forests. In contrast to other ecosystems, a greater fraction of soil respiration is derived from roots in the boreal biome (Raich and Nadelhoffer 1989). Among Alaska forests, black spruce allocate proportionately more C belowground than other forest species (Ruess et al. 1996). Thus within a growing season, root processes in black spruce ecosystems likely dominate soil C flux and are sensitive to environmental factors.

Trees also shift allocation between above- and belowground plant parts in response to changing environment and nutrient availability (Gower et al. 1994), and this aspect of black spruce C dynamics is much less understood. However, for conifers a general understanding has developed for the relationship between nutrient availability and plant C allocation. With fertilization, absolute amounts of root production often decrease for a species (Kurz 1989; Gower et al. 1992; Haynes and Gower 1995), or root production decreases as a proportion of total plant production (Linder and Axelsson 1982). Also where species composition is constant and the forest canopy is no longer aggrading, natural gradients in fertility indicate greater root production where nutrient availability is low (Keyes and Grier 1981, Kurz 1989). In cross-species comparisons, however, belowground production increases with nutrient availability (Nadelhoffer et al. 1985). This may simply reflect greater overall C flux through the ecosystem.

Fewer studies have looked at environmental influences on C allocation per se, but lower moisture availability often increases the proportion of C allocated belowground in within species comparisons (Keyes and Grier 1981, Comeau and Kimmins 1989, Kurz 1989, Gower et al. 1992). Alternatively in cross-species comparisons, the total amount of C allocated to roots increases with mean temperature and precipitation (Raich and Nadelhoffer 1989, Vogt et al. 1990, Gower et al. 1994). There is a clear distinction between the response of one species to changing environment and nutrient availability, and the C allocation patterns of different species. No studies have looked specifically at the belowground production response of black spruce to variations in nutrient, moisture, or soil temperature. Alaskan studies, however, generally estimate a greater proportion of ecosystem primary production going to black spruce root growth (47-63%) (Ruess et al. 1996, Ruess et al. in press) than do studies in Canada (41-49%)(Gower et al. 1997, Steele et al. 1997, O'Connell et al. 2003a). Interior Alaska is drier than the Canadian study areas, which may explain this trend.

Changes in black spruce root processes may reflect the direct influence of climate on physiological processes. Black spruce roots adjust basal respiration, or acclimate, to average temperatures (Tjoelker et al. 1999). For roots acclimated to cold temperatures, a subsequent increase in temperature initially elicits a greater respiration response than for roots experiencing long-term warmer temperatures. However, if temperatures are warm long enough, root respiration decreases. This response may be an adaptation that allows for near constant maintenance respiration costs independent of temperature (Atkin et al. 2000), but how rapid acclimation occurs remains unknown (Tjoelker et al. 1999). It is

also unclear how respiration acclimation and root growth interact with fluctuating soil temperatures.

The interaction between root processes and climate change may be expressed in root N concentration. Across a mean temperature transect in temperate forests, root N concentration was positively correlated to respiration rates, but the trend was best explained by *in-situ* net N mineralization rates rather than site temperatures (Burton et al. 1996). Alternatively, root respiration and root N concentration were both lower in warm than cool biomes (Burton et al. 2002). Black spruce respiration is positively correlated to N concentration (Tjoelker et al. 1999, Ruess et al. in press), and N availability will likely increase with warming soil temperatures (Kirschbaum 1995). Both N availability and root N content could increase with warming and increase root respiration rates.

From the various observations of root function and its relationship to environment, it appears climate warming could have a positive, negative or neutral influence on C allocation to black spruce roots. A positive effect would occur if warming increases N availability, root N concentration, root growth and respiration rate. A negative if increased N availability from warming results in less C allocated belowground. A "no-effect" of climate warming would occur if C allocation to roots remained the same, with both root growth and respiration acclimating to the warmer temperatures. Rustad et al. (2001) reviewed soil-warming studies and found that in most cases, soil respiration and net N availability initially increased after warming but the increase was not sustained. Either root acclimation to warmer temperatures, decreased C

allocation to roots, or microbial depletion of easily decomposed organic matter may be responsible for this result (Rustad et al. 2001a).

The potential of a net soil C loss will also depend on the amount of soil C, its chemical characteristics, the temperature sensitivity of microbial decomposition, and the degree of temperature warming (Kirschbaum 1995, Niklinska et al. 1999, Kirschbaum 2000). Among forest species in Alaska, the soil organic matter of black spruce generally has the slowest decomposition rate (Flanagan and Van Cleve 1983, Vance and Chapin 2001). The organic matter is, however, capable of losing significant amounts of mass with little change in the rate of microbial decomposition (Sparrow and Cochran 1988, Vance and Chapin 2001, Neff and Hooper 2002). Thus, warming could result in a sustained loss in soil C, but concurrent with soil C mineralization is the conversion of organic nitrogen to forms that are available for plant uptake (Kirschbaum 2000). The chemical characteristics of the organic matter, or its quality, will mediate the relative rate of both mineralization processes.

Although a number of comparisons of organic matter quality have been made for different forest species (Flanagan and Van Cleve 1983, Vance and Chapin 2001), much less is known about the variability of organic matter quality within the black spruce ecosystem type. Long-term inhibition of decomposition by limiting temperature or moisture conditions may result in the buildup of organic matter that would otherwise be decomposed, and therefore, a change in soil environment may elicit a greater microbial response for this organic matter (Kirschbaum 1995, Niklinska et al. 1999). As microbes increase decomposition rates they can either produce CO_2 or incorporate the organic

matter into biomass. If microbial biomass increases, the rate of mineralization of N to plant available forms may decrease (Flanagan and Van Cleve 1983). The organic chemistry may also influence the rate of net N mineralization; the buildup of low N compounds could increase N immobilization in microbial biomass when environmental limitations are removed. The result would be a longer lag between when microbes release CO_2 and plant available N.

I focused my research on three stands in the Fairbanks area that are similar in stand structure (number of trees, tree size, and density, understory species composition) and soil characteristics (amounts of organic matter, loess soil cap). The site selection and approach was in part determined by my prior research experience in black spruce forests in Manitoba and Saskatchewan. Black spruce forests in different regions of the boreal forest are remarkable to the degree they resemble one another in structural characteristics. I questioned whether forests that appear similar actually cycle C in the same manner across the boreal forest. Significant environmental variability exists at the cross-biome scale, but also locally in Alaska, and I was curious how soil environment and ecosystem C cycling interact.

In Chapter 1, I examine the relationship between *in-situ* decomposition, microbial respiration, root respiration, and aboveground production of three black spruce forests near Fairbanks, Alaska. The general hypothesis is that where decomposition is faster, both components of soil respiration, microbial and root respiration are also greater. The faster decomposition of organic matter should also increase N availability and aboveground production. An alternative hypothesis is that faster decomposition results in

less belowground C allocation, and in this case, the respiratory processes will either stay the same or decrease. The possible environmental factors responsible for the patterns in plant allocation are examined both with foliar isotopes (^{13}C and ^{15}N) and soil temperature measurements.

The focus of Chapter 2 is the relationship between organic matter quality, microbial C and N mineralization, and the temperature sensitivity of these processes for the three sites. The experiment is based on laboratory incubations and the analysis of organic matter chemistry using pyrolysis gas chromatography-mass spectrometry. My objectives were to examine the interactive effect of temperature and organic matter chemistry on mineralization processes and also determine if the patterns in the laboratory could explain field observations of spruce C allocation and soil heterotrophic respiration. A specific organic matter characteristic, the proportion of primary polysaccharides, was hypothesized to reflect increased C mineralization potential and microbial respiration temperature sensitivity (Dai 2001, White et al. 2002). Conversely, I hypothesized the potential of net N mineralization would be inversely related to primary polysaccharides occurrence because the compounds identified have little nitrogen associated with them. This characteristic should increase microbial immobilization. The temperature sensitivity of processes was expected to be greatest for the low temperature site and be related to the primary polysaccharides.

The effect of root inputs on forest floor C balance is examined in Chapter 3. The high degree of belowground C allocation in black spruce led to the hypothesis that root exclusion should cause a divergence between control and trenched plot forest floor C.

The change in forest floor C of root exclusion areas is used to determine how root growth and decomposition influences the amount of C found in the forest floor. Independent estimates of root increment are derived from the "bomb" ^{14}C age of roots. A simple model of forest floor C balance and power analysis are used to propose improvements in the trenched plot methodology.

CHAPTER 1. Soil respiration in mature Alaskan black spruce forests that vary in soil organic matter decomposition rates

ABSTRACT

Climate warming at high latitudes is expected to increase root and microbial respiration and thus cause an increase in soil respiration. We measured the root and microbial components of soil respiration near Fairbanks, Alaska, in 2000 and 2001 in three black spruce (*Picea mariana*) forests. We hypothesized faster decomposition results in greater contributions of roots and microbes to soil respiration. Two independent methods of separating root and microbial respiration indicated roots contributed more to soil respiration than microbes, and the variation in root respiration drove between site differences in soil respiration. Thus, contrary to our prediction, the site with coolest summer soil temperatures and slowest decomposition (site ID "high-np") had significantly ($p<0.05$) greater growing season soil respiration (485 g C m^{-2} y^{-1}) than the two other sites (372 and 332 g C m^{-2} y^{-1}). At any given temperature, soil and root respiration were greatest at high-np, and two indirect measurements suggest root functional differences were responsible. Fine root N concentration was 10 and 12% greater ($p<0.05$) at high-np than at the other two sites, which is consistent with the greater root respiration rates. High-np spruce also had foliage more enriched in ^{13}C and depleted in ^{15}N than the other two sites, suggesting lower available moisture and possibly slower N turnover at this site, either of which may have resulted in greater allocation to roots.

Prepared for submission to Canadian Journal of Forest Research

Other components of soil respiration (winter soil respiration, heterotrophic respiration and moss photosynthesis and respiration) varied among sites, but had less influence on soil respiration than root respiration. Black spruce aboveground production (g C m^{-2}) generally decreased with increasing root and soil respiration. In an examination of our results in the context of other studies in black spruce ecosystems, we conclude moisture deficit may increase the amount of C cycling through roots in this forest type.

INTRODUCTION

Soil respiration generally increases with temperature, creating the possibility that the ongoing and predicted warming at high latitudes (Serreze et al. 2000) will increase soil respiration and decrease net boreal forest uptake of CO_2 from the atmosphere (Goulden et al. 1998). Both root and microbial respiration contribute to soil respiration and correlate with temperature, but the activity of each has different implications for ecosystem carbon balance. Root respiration in general consumes photosynthate recently fixed by the canopy (Högberg et al. 2001), thus this respiration has very little influence on annual net ecosystem carbon balance and is sensitive to both canopy and soil conditions. Alternatively, during decomposition microbes release CO_2 from soil organic matter that ranges in age from recent (e.g., fine root turnover) to years and millennia (e.g., litter and humified soil C) (Trumbore and Harden 1997, Trumbore 2000). In particular, the decomposition of boreal soil organic matter could drive a significant increase in atmospheric CO_2 because boreal soils store about 182 Pg of soil C (Post et al. 1982), equivalent to 24% of the current atmospheric pool.

Separating the root and microbial components of soil respiration is critical to monitoring the destabilization of soil C pools (Hanson et al. 2000), determining the relative sensitivities of roots and microbes to temperature or moisture (Boone et al. 1998, Melillo et al. 2002), and ultimately predicting how soil respiration will respond to a changing climate. Decomposition in boreal forests is very often temperature limited, and a general hypothesis for this forest is that with soil warming, microbial decomposition will increase, release more nutrients to the plants, stimulate photosynthesis and increase overall plant productivity, including roots. If true, soil respiration should increase because of the stimulated contribution of both roots and microbes. However, experiments indicate that soil respiration enhancement is not sustained at high levels in response to warming (Jarvis and Linder 2000, Rustad et al. 2001b, Melillo et al. 2002). The relative respiratory contribution of roots may decrease or stay the same with warming because of temperature acclimation or changing plant C allocation. Roots acclimate to warmer average temperatures by respiring less at a given temperature (Sowell and Spomer 1986, Tjoelker et al. 1999, Luo et al. 2001), also plants often decrease overall allocation to roots with increased nutrient availability (Haynes and Gower 1995). Microbes may also appear to acclimate to temperature (Flanagan and Veum 1974), but this result may instead may be from the relatively quick depletion of easily decomposed soil organic matter (Giardina and Ryan 2000, Melillo et al. 2002).

Although soil-warming experiments provide direct evidence of the potential influence of climate change on decomposition and soil respiration, natural climate gradients can be useful for examining whether predictions of the final carbon cycling

characteristics of a forest actually occur. The interpretive power of this approach is strengthened if the plant species community and soil characteristics remain relatively constant across environmental gradients. We used this approach, selecting a common overstory-understory species association found in the North American boreal forest. Black spruce (*Picea mariana* [(Mill) B.S.P]), the overstory species, occurs across the entire mean annual temperature range (7 to -11 °C) of the North American boreal biome, it is the most prevalent and wide ranging tree species in the boreal forest (Burns and Honkala 1990), and the most common in boreal Alaska (Labau and van Hees 1990). The greatest amounts of soil C occur under black spruce (Van Cleve et al. 1983, Gower et al. 1997), partly because of its poor tissue quality for decomposition and predominance in wet, cool soils. Also bryophytes can cover 100% of the forest floor underneath spruce and these bryophytes can drastically lower soil temperatures through the insulating properties of their tissue (Oechel and Van Cleve 1986). In this study, the associated bryophytes mostly consisted of feathermoss, which is a generic term for two species, *Hylocomium splendens* [(Hedw.) B.S.G.] and *Pleurozium schreberi* [(Brid.) Mitt.].

Our objectives were to examine the relationship between decomposition and the two components of soil respiration, microbial and root respiration. We predicted that conditions favoring faster decomposition will favor higher rates of all components of soil respiration. Alternatively, a soil environment that promotes decomposition may cause temperature acclimation in roots or decreased available organic matter for microbes, resulting in similar or lower soil respiration across a decomposition gradient. Possible physiological explanations for root respiration patterns are examined in the context of

foliage and fine root N concentration, and foliar isotopic differences in $\delta^{13}C$ and $\delta^{15}N$. We also measured moss gross photosynthesis and modeled moss respiration to constrain the influence of these on soil respiration results.

METHODS

Site selection and study area

We located a high elevation site with no permafrost (high-np) site, a mid-elevation site with deep permafrost (mid-dp), and a low elevation site with shallow permafrost (low-sp) site (Table 1). One of the sites is part of the Bonanza Creek Long Term Ecological Research (LTER) study within the Bonanza Creek Experimental Forest (64° 48'N, 147°, 52'W). No two sites are greater than 30 km apart. Information about Alaska LTER research is accessible online (http://www.lter.uaf.edu).

Seasonal variation in daily mean air temperatures is extreme, ranging from –24.9 °C in January to 16.4 °C June, with a mean average temperature of –3.3 °C. Substantial local variation in temperature occurs, driven by adiabatic altitude-temperature lapse rates, winter temperature inversions, and topographical sun-shading. The winter cold-air inversions driven by altitude are especially extreme; with high elevations up to 30 °C warmer on winter days. Annual precipitation (269 mm) is less than potential evapotranspiration (466 mm), and 65% of precipitation occurs during the growing season (Viereck et al. 1993).

At each site, black spruce is the only canopy species and feathermoss forms a near continuous carpet. Other cryptogams and bryophytes occupy <15% of the forest floor at any site. Few other vascular species represent significant biomass, but common to the

understory of all sites are *Vaccinium vitis idea* (L.) and *Cornus canadensis* [(L.) Graebn]. The two low elevation sites experience a mid-June flush of *Equisetum palustre* (L.), and high-np has three *Alnus crispa* [(Ait.) Pursh] bushes within the study area. The average diameter and stand density of the spruce are similar between the three sites, but variations occur in age and depth to permafrost (Table 1).

The soils of these stands are defined by permafrost, an organic matter mat, and a loessal parent material. Seasonal temperature patterns, soil moisture content, and soil texture control permafrost formation. In this study, the high-np site is without permafrost, which is common for higher elevations in interior Alaska because cold air drains to lower elevations during the winter. Thick organic matter mats accrue in black spruce forests and the majority of roots are found within the upper 20 cm of the soil profile (Tryon and Chapin 1983, Ruess et al. 1996, Ruess et al. (in review)), and mostly in the organic material. The mineral soil consists of loess that was blown from the glaciated areas in the Alaska Range and fluvial plains during the Holocene and covered parts of interior Alaska, which remained unglaciated (Péwé 1976). At the two permafrost sites, loess extends at least to the top of the permafrost (65 cm to ~1m), and at high-np, the loess cap is 50 cm thick and overlays a Cambrian schist.

Study design

Statistical comparisons are meant to test the relationships between decomposition, soil respiration and the components of soil respiration, and not the landscape features creating the variability in them. Each study area was kept small because slight changes in

elevation or aspect result in large differences in solar insolation, soil temperature or depth to permafrost.

Microbial and root respiration were separated from soil respiration using two methods: root exclusion via trenched plots, and the Total Belowground Carbon Allocation (TBCA) method (Raich and Nadelhoffer 1989). Trenched plots can track seasonal patterns of root respiration, but increase the pool of decomposing soil organic matter with the excision of live roots. The TBCA provides a check on the trenched plot approach because it leaves the soil system intact but it can only be applied at an annual or greater time-step.

Three trenched plots were located between 9-20 m apart along the slope of a stand. A 20 x 20 m grid abutting the three trenched plots was used for randomly selecting points for placing decomposition materials, collecting litterfall, and removing soil cores. These control samples were then assigned to one of the three trenched plots based on the location of each relative to the trenched plot.

The overstory stand characteristics, spruce biomass and primary production were estimated with a prism (10 basal area factor (BAF)) (Gower et al. 1997). A prism sweep was located near each of the three trenched plots. A corner of trenched plot was randomly selected and the center of the prism sweep located at a 45° angle 3 m from the corner. The diameter at breast height (DBH) of each tree in the sweep was measured at 1.37 m and an allometric equation relating DBH to biomass used to estimate the biomass of each tree (Michelle Mack, unpublished data). To estimate spruce production, a tree core was collected at DBH from between 45-60 trees along a 4 m x 20 m transect through

the control plot in the fall of 2001. Tree rings were viewed using a microscope and 5 years (1998-2001) of ring width measured with a digital micrometer. The mean ring width for the 5 years and for all trees within a 2 cm size class (e.g. 2.5-4.5 cm) was assigned to each tree that represented the size class in the prism sweep. A change in tree diameter was estimated from the ring widths and scaled to biomass production using the allometric equation. The average increased tree size was multiplied by the number of trees per hectare in a size class as estimated with the prism (Gower et al. 1997).

Vascular understory biomass and production was estimated in August of 2000. A 1 m^2 plot was randomly located within 5 m of each trenched plot at a site. The understory biomass was clipped at the soil surface. Perennial plants were separated into new and old growth, dried and weighed. Annual plants were considered new growth.

Soil Temperature

At each site a two-channel HOBO (Onset Corp, Bourne, MA) temperature sensor continuously logged soil temperature at 10 and 20 cm depth from the top of the moss surface. HOBO's were placed both within one randomly selected trenched plot and within 3 m of the same trenched plot. The loggers were left in the same location continuously from August 1999 to June 2002. The 10 and 20 cm HOBO temperatures were used to compare sites using the temperature index, soil summed-degree-days (SDD):

$$SDD(i) = \sum_{i=1}^{n} Ti \qquad \text{when the daily (i) maximum temperature } T > 0\ ^{\circ}C. \qquad \text{Eqn.1}$$

During each soil respiration measurement period, soil temperature was also measured with a handheld Digisense^{TM} sensor using Type T (Cole Palmer) thermocouples affixed to a pole and inserted to depths of 10 (n = 6 each site/treatment), 20 (4), 30 (2), 40 (2), and 50 cm (2) from the moss surface. Estimates of SDD also were made from the Digisense sensor measurements, but only for 30, 40, and 50 cm depths. Some gaps in the HOBO data occurred because animals damaged the sensors, batteries failed, or sensors were launched improperly. Respiration response functions were examined using the handheld temperature data because they better incorporated spatial and temporal variation.

Isotopic indicators of forest moisture and N cycling

Soil moisture was not directly measured in 2000 and 2001 because non-destructive methods (e.g. TDR) in low density organic matter requires calibration with harvested soil samples, and we were attempting to minimize disturbance to these repeatedly measured areas. Rather, the moisture status of the trees was determined indirectly using the $\delta^{13}C$ of canopy foliage. Foliar $\delta^{13}C$ can incorporate soil moisture and atmospheric moisture deficits, and soil temperature through its effects on hydraulic conductivity (Lajtha and Michener 1994), but in our study a significant direct altitudinal effect on CO_2 internal partial pressure is unlikely because site elevations only differed by 400 m (Körner et al. 1988).

We used foliar $\delta^{15}N$ to determine whether soil N may be cycling differently among sites, but consider this an indirect measurement of numerous N cycling processes (Nadelhoffer and Fry 1994). In the fall of 2002, we collected current annual foliage from the south-facing, upper 1/3 canopy of four mature trees at each site. Foliage was removed from the stem, dried and ground with a roller ball mill. Samples were analyzed with a PDZ Europa 20-20 mass spectrometer at the Forest Soils Laboratory, University of Alaska-Fairbanks.

Soil respiration methods

The trenched plots were installed in August of 1999. A trench 80 mm wide by 0.5-1.0 m depth was dug around a 2.5 x 3.0 m area. Trench depth was limited by permafrost depth or bedrock (high-np). Roots were kept from re-colonizing the trenched plot interior area by a 0.2 mm thick polyethylene barrier placed to the depth of the trench. The trench was then backfilled with soil. We located trenched plots between trees when possible, but at each site a black spruce tree (all < 4.0 cm DBH) was found in one plot. These trees and all understory vascular plants were removed by cutting at the soil surface. Plots were clipped continuously throughout the experiment to keep non-bryophyte understory from re-growing in the trenched plot.

Growing season (May 1-September 30) soil respiration measurements were made between 10 am and 2 pm about every ten days between June 1, 2000 and October 1, 2001. We delayed measurements 10 months after trenching to allow fine roots and labile C to at least partially decompose. Two PVC respiration collars (15.2 cm diameter) were randomly located in each trenched plot and two others randomly placed 2-4 m away as

controls. Collars were inserted ~3 cm in the moss layer, and all vascular plants, cryptogams, and non-feathermoss bryophytes were clipped from within the collar. Feathermoss was not removed because it greatly influences soil temperature, moisture, and gas diffusion. The collars were left in place for the duration of the experiment. A 3 m boardwalk was placed on the approach to each collar to minimize the disturbance around it. In 2001, a "no-moss" treatment was implemented. Live, green moss in six new collars at each site was clipped, and diluted Roundup^{TM} (20 water:1 herbicide) applied to the remaining brown moss surface to prevent regrowth.

A clear acrylic chamber was constructed that could be clasped to the permanent collar. The chamber was vented to allow for pressure equilibration, but the system was otherwise closed. A Brailsford pump (model TD-4N-A) circulated air at 1 L min^{-1} between a LICOR 6262 infrared gas analyzer and the chamber. Air coming from the LICOR was sent to a manifold encircling the bottom of the chamber, air going to the gas analyzer was sampled at the top of the chamber (~8 cm above surface of moss). Before the chamber was attached to the permanent collar, it was held 1 m above the soil surface for 10 s so that the CO_2 concentration in it was less than that at the soil surface. Ambient light and darkened chamber measurements were made on each collar during a sampling period to determine feathermoss gross photosynthesis (see below for details). For a darkened chamber measurement, an opaque bucket was put over the top of the acrylic chamber.

A Hewlett Packard handheld computer logged the measured CO_2 concentrations at 3 s intervals. The chamber was left on the collar for 2 minutes, but to calculate flux

rate, only the CO_2 increase between 45 to 75 seconds was used in a regression between time and CO_2 concentration. Visual analysis of numerous 6-minute intervals indicated this timeframe consistently provided linear and robust regressions of concentration change with time.

Internal pressure, temperature, and $\Delta CO_2/s$ were used in the ideal gas law to calculate flux. Chamber air temperature was measured using a shaded thermocouple 3 cm above the moss surface. In 2001, each collar's volume was estimated by injecting into the chamber headspace 5 ml of 100% CO_2, allowing it to thoroughly mix, and recording the increase in CO_2 concentration after 2 minutes. The average volume of the chamber-collar system was 5.1 liters. Including collar specific volumes improved R^2's of the temperature-respiration response equations by about 3%.

Respiration was also measured periodically during the winters of 2000-01 and 2001-02. During each measurement period, six locations were selected in and outside trenched plots and a measurement made on the snow surface at a distance of at least 1 m from the operator's footprints. A rectangular chamber (0.0794 m^2) was first pressed into the snow surface to create an imprint, then lifted ~1 m, and after 20 s placed again in the imprinted snow. The timeframe used for regressions was the same as for summertime measurements. . Although the LICOR was encased in styrofoam insulation, the computer failed when the air temperature was less than –20 °C and therefore measurements are biased against extremely cold days.

Moss gross photosynthesis and modeling respiration

To constrain the contribution of moss respiration (Rs_m) to soil respiration, we measured moss gross photosynthesis (Ps_m) and modeled moss respiration using an empirical model. The Ps_m for each measurement period was calculated as the difference between the fluxes measured in an ambient light and darkened chamber. Then using the chamber air temperature, we estimated the Rs_m:Ps_m ratio using models we developed from data in Skre and Oechel (1981). Models were developed for both *Hylocomium* and *Pleurozium*, and over three seasonal time-periods because moss photosynthetic capacity changes over the growing season (Skre and Oechel 1981). Time periods were based on Skre and Oechel's measurement periods, and were snow-free to day 172, 173-210, and 211 to the first snowfall. Trends in the ratio varied, and polynomial models were used because they most consistently captured this variability. The models were of the form:

$Rs_m:Ps_m = a+bT+cT^2$, where T=air temperature. Eq 2.

The parameters a, b, and c were curve fit parameters generated in SAS with the NLIN procedure. Finally we multiplied the modeled ratio by the Ps_m measurement to estimate Rs_m. *Hylocomium* and *Pleurozium* model results were weighted by the prevalence of each species at a site. This approach freed us from tracking the moss density and weight in each collar. The growing season estimates of Ps_m and Rs_m were derived by interpolating between measurements, and Ps_m estimates were corrected downwards by the number of hours each day photosynthetic active radiation was less than the light compensation point for feathermoss (25 $\mu mol\ m^{-2}\ s^{-1}$) (Williams and Flanagan 1998). The light measurements used for the correction were made at a LTER weather station 5-

22 km from the sites. Moss net primary production for the growing season was calculated as the difference between the integrated Psm and Rsm values.

Estimates of annual soil respiration and moss photosynthesis

Annual estimates of moss respiration, photosynthesis and soil respiration were made by multiplying fluxes by the time period (usually 9-14 days) between measurements. An alternative approach is to use the flux response to soil temperature and scale upward to annual estimates based on soil temperature data, but significant regressions between moss photosynthesis and soil temperature were not found. Therefore, to remain consistent between moss and soil respiration flux we interpolated measurement between time periods. For soil respiration, using hourly soil temperatures at 10 cm to drive a model of respiration produced seasonal estimates that differed on average by 7 ± 5% (n=6, trench and control) from interpolated values, with values not consistently greater or less than one another

Soil and Root C and N

Soil cores were collected to estimate the soil C and N content for the trenched and control areas. In the fall of 2001, we removed ten, 5.5 cm diameter x 30 cm deep soil cores from random locations in the control plot. We dissected the cores into organic horizons that most closely resembled the Canadian L (litter), F (fibric) and H (humic) classification system (Canadian Soil Classification System, 3rd ed.), and included an A horizon and mineral soil to 5 cm depth. In this classification, the L layer was mostly comprised of live and dead moss. The F and H layers were not separated; but the F was live and dead fine roots, needles, and woody debris, and the H layer an amalgam of

highly decomposed organic matter, some roots, charcoal, and small amounts of mineral soil. The thickness of each horizon was measured and the horizon weighed dry (all materials were dried for 72 hours at 65 °C). The organic L and F/H horizons were ground in a Wiley mill using a 2 mm mesh screen. The A and mineral soil horizons were hand sieved through a 2 mm screen and the organic material remaining on the screen ground as before. Small pebbles were removed and the mineral and ground organic material thoroughly remixed for C and N analysis. All ground samples were analyzed with a LECO2000 CNS analyzer for C and N concentrations.

From a set of 8 soil cores collected in July of 2001, a subsample of easily identified live fine roots (< 2 mm) was selected from the F/H horizon of the core for C and N analysis. Roots from two cores were combined, for a total of 4 root samples per site. Roots were rinsed with deionized water, dried as for the soil, and analyzed for C and N with the CNS analyzer.

Decomposition

We measured the rate of mass loss of a common substrate, cellulose filter paper, and spruce litter at each site. Filter paper was used in control areas and trenched plots in 2000 and 2001, but spruce litter placed in control areas only in 2001. In 2000, we sewed cellulose filter papers (75 mm Whatman qualitative, fast) into nylon mesh bags (mesh size 2 mm) and put the bags vertically in the soil profile with the center of the paper at 3.5 cm below the moss surface. Five bags were spaced haphazardly in each trenched plot in each site and fifteen filter papers were randomly located in the 20x20 m grid area.

The depth interval covered by the filter papers was increased in 2001. Six filter paper disks were arrayed two wide and three deep in 15 cm wide by 23 cm deep plastic mesh (mesh size 2 mm) birdseed bags (Quadel Industry, Coos Bay, OR, (541) 267-2622). We opened a slit in the organic horizon with a flat spade and inserted the bag bottom to a depth of 24 cm, leaving the top ~1 cm below the surface. The filter papers and spruce needles were left to decompose for one year, beginning mid-June, 2001. Locations for both were selected in the same manner as 2000.

Spruce needle litter was collected near low-sp in 1998 by shaking a tree gently so that necrotic needles fell on a tarp placed underneath (Michelle Mack, pers. comm.). Approximately 100 g of air-dried black spruce needles were sewn into 150 μm silkscreen bags. We placed 15 bags vertically ~4 cm into the feathermoss layer at each site, a depth corresponding to where we observed the most needle litter. The dry weight of both materials before and after the 1 yr decomposition period was determined by drying for 72 hours at 65° C.

Root Respiration

The Total Belowground Carbon Allocation (TBCA) method provides an upper limit to root respiration when soil C is near steady state (Raich and Nadelhoffer 1989). In this study, the litter component includes moss litter, which we set equal to moss primary production (assuming live moss mass is constant). Instantaneous Rsm was subtracted during each measurement, and we calculated estimates with and without winter respiration. The equation is thus:

TBCA (Rr)=annual soil respiration – (litterfall + moss production). Eq. 3.

Using trenched plots, root respiration is estimated as the annual difference between the trenched (Rst=Rsm + heterotrophic microbial) and control (Rsc=Rst +root) plot soil respiration; thus

Rr=Rsc-Rst. Eq. 4.

Both the TBCA and trenched plot root respiration estimate includes the respiratory contribution of root maintenance and growth, mycorrhizal fungal respiration, and heterotrophic respiration associated with root decomposition. Trenched plots include respiration from excised, previously live roots but we did not separate this respiration contribution. Rather, we intended to minimize the differential influence of excised roots across sites by selecting for similar aboveground biomass and soil organic matter amounts, which assuming fixed root:shoot ratios, should result in similar initial root biomass inside the trenched plots for the three sites.

Litterfall was estimated at the three sites in 2000 and 2001. Six $1m^2$ wood-framed litter traps were randomly placed in the 20 x 20 m plot. The traps were elevated above the moss surface to minimize litter decomposition prior to collection periods and to prevent moss growth through the screen. We observed red squirrels using the collection screens as perches and depositing spruce cones into them. All squirrel-affected cones were removed from the litter estimates, which averaged 16% of the total litter mass. Otherwise the samples were not further separated by component (i.e. foliage, twig, etc.), and no coarse woody debris was captured in a litter trap. All vegetation was dried at

65°C for 72 hours and weighed. Litter biomass was multiplied by 0.48 to convert from mass to C (Gower et al. 1997).

Statistics

Statistical analyses were performed using Statistical Analysis Software v. 8.0 (SAS Institute, Inc. 1999). We used one-way ANOVA to compare among sites soil C content, filter paper decomposition, litterfall, $\delta^{13}C$, $\delta^{15}N$, foliage and root N concentration, and average soil respiration (average of individual collar or trenched growing season estimate). Data were tested for normality (Shapiro-Wilks and visual inspection of normality plots) and homogeneity of variance (Levene's). All data are presented as the mean ± standard deviation (S.D.).

To determine whether site differences in seasonal soil respiration were a function of a temperature response differences, we fit temperature-response models for various model types (linear, exponential, quadratic) and examined residuals to determine which could be used and not violate the assumption of homogeneous variance. Non-linear model fits were performed with PROC NLIN in SAS. Based on the residual distribution, we decided on a linear model. However, residuals indicated that second order polynomial model would better represent the temperature response curves for the low-sp control and mid-dp trenched respiration. Nevertheless for consistency we used the linear model for all comparisons.

We examined site and treatment differences in the relationship between soil temperature and respiration using a mixed model (PROC MIXED in SAS) and repeated measures. Mixed models re-create the covariance structure, which eliminates problems

associated with correlated variances and unequal temporal spacing of sampling periods (Littel et al. 1997). Treatment (site or trench), year (2000 or 2001), temperature, and all possible interactions were tested as fixed effects. Site or treatment(collar) and temperature*site/treatment(collar) were tested as random effects. The remaining subplot error (time*site/treatment(collar)) was analyzed with repeated-measures analysis with a spatial power variance structure to account for respiration and temperature measurements being taken on the same soil collars throughout the study.

RESULTS

Soil Temperature, biomass, and foliar isotopes

The monthly mean soil temperature at 10 cm from the moss surface ranged from -7.1 to 7.2 °C between June 2000 and July 2001 (Fig. 1). Soil temperature profiles (10 and 20 cm) could not be compared statistically because only one HOBO logger was deployed per site and treatment, however, HOBOs at both low-sp and mid-dp consistently reported much colder winter temperatures than in high-np. Although these winter temperatures would have a strong influence on annual mean temperature, they had no discernible influence on growing season soil temperature at 10 cm. The permafrost sites' summertime temperatures at 10 cm were warmer than in high-np in May and June and similar to high-np in July and August, but colder in September (Fig. 1). The summed-degree days (SDD_{10cm}) were least for the high-np site and greatest at low-sp (Fig. 2). Deeper than 30 cm, the two permafrost sites had colder soils than high-np. Trenched plots were warmer (SDD) at 30, 40, and 50 cm depths, but with substantially less effect at the two permafrost sites than at high-np. The high-np average deep

temperatures (30, 40 and 50 cm) were heavily influenced by the location of one of the two deep Digisense™ probes, which was in a particularly sunny area of the trenched plot. August and September temperatures averaged 2 °C cooler in 2000 than 2001 (not shown), but the ranking of site temperature for the 10 and 20 cm SDD did not change between years.

Foliar and root characteristics measured in high-np differed from those in the other two sites, which did not differ significantly from one another. The $\delta^{13}C$ of foliage was most enriched at high-np (Table 2), and marginally different ($p=0.08$) from low-sp, and mid-dp did not differ from either of the other two sites. The $\delta^{15}N$ was most depleted at high-np, but foliar N concentration did not differ across sites. Root N concentration was significantly greater at high-np than either of the other two sites (Table 2).

The overstory biomass of the two older sites was greater than that estimated for the younger mid-dp (Table 3). Understory biomass and production did not differ between high-np and low-sp, but there was much less vascular understory and production at mid-dp. The aboveground production differed significantly between sites (mid-dp>low-sp>high-np).

The C and N concentration and total C and N content of the L horizon decreased with elevation (Table 4). No significant general trend was found for other soil horizons. The C:N ratio of the F/H horizon at mid-dp was significantly lower than for either of the other two sites. The low-sp site had significantly more total soil C than did either of the two other sites (not shown), owing primarily to more C in the F/H and A horizons (Table 4). The mineral soil horizon to 5 cm depth did not differ between sites in element

concentration or mass, but the C:N ratio was greater at low-sp than mid-dp.

Decomposition

Filter paper (FP) decomposition was generally slowest at high-np for all depths and in both years (Table 5). Decomposition rates in the control areas of the two permafrost sites differed little from one another. In 2001, the shallow control FP (1-8.5 cm) decomposed significantly faster ($p=0.04$) at low-sp than high-np. Permafrost affected decomposition and soil temperature only below 20 cm (Fig. 2). The control FP decomposition rate decreased significantly ($p<0.05$) with increasing depth at high-np and low-sp (Table 5), reflecting the vertical soil temperature gradients (Fig. 2). In 2000, decomposition rates in trenched plots did not differ from control areas, but in 2001 trenching accelerated the decomposition rate for all FP depths at mid-dp, and for the 8.5-16 cm depth at low-sp. FP decomposition generally was slower in 2000 for surface filter papers than in 2001 (Table 5). Patterns in spruce foliage decomposition mirrored those for filter paper at similar depths in 2001.

Soil respiration, moss photosynthesis and root respiration

Soil CO_2 flux followed the seasonal soil temperatures at 10 cm during the growing season. The proportional contribution from roots occurred around the maximum in soil temperature (Fig. 3). Based on the difference between control soil respiration (Rsc) and trenched respiration (Rst), the amount of CO_2 coming from roots was ~20% less in the fall than the maximum root contribution observed in late July or early August. Darkened chamber Rsc in the 2001 growing season averaged 3.63 ± 1.56, 2.66 ± 1.06, 2.49 ± 1.18 μmoles CO_2-C m^{-2} s^{-1} at high-np, mid-dp, and low-sp, respectively, while Rst

averaged 1.40 ± 0.45, 1.67 ± 0.51, and 1.35 ± 0.43 μmoles CO_2-C m^{-2} s^{-1} across the same sites (Fig. 3). Moss gross photosynthesis (Psm) decreased the Rsc flux 14, 8, and 12% at the high-np, mid-dp, and low-sp sites. The percentage of *Pleurozium* was approximately 87% of the number of fronds counted in all collars at each site. The species percentage did not differ significantly between sites and the proportional distribution of moss did not describe the variability in the Psm of individual collars. Modeled moss respiration accounted for 5 of 10% of Rsc.

Winter fluxes decreased from the beginning of the winter until the snow-free season began in late April, but did not correlate with temperature at any depth (Fig. 4). The average winter fluxes for control areas were 0.11 ± .09 (n=4), 0.22 ± .07 (n=5), and 0.22 ± 0.10 (n=5) μmole CO_2-C m^{-2} s^{-1} and trenched plot fluxes averaged 0.10 ± .09, 0.15 ± 0.08, and 0.15 ± 0.15 μmole CO_2-C m^{-2} s^{-1} at high-np, mid-dp, and low-sp. Based on same-day comparisons, winter soil respiration at high-np was significantly less than the two sites on three occasions (Fig. 4), despite generally lower temperatures in the permafrost sites (Fig. 2). The two permafrost sites did not differ during their only overlapping measurement period. We estimated winter respiration for high-np and the two permafrost sites using separate curves relating the decrease in respiration with time (Fig. 4). Integrated winter estimates were derived separately for control high-np (31 g C m^{-2} y^{-1}) and the two permafrost sites (54 g C m^{-2} y^{-1}). Trenched plot winter flux did not differ between sites and one estimate was made for all sites (26 g C m^{-2} y^{-1}).

At every site, the integrated Rsc respiration was significantly greater than Rst, and the annual root respiration (Rsc-Rst), averaged 296 ± 55, 206 ± 67, and 192 ± 72 g C m^{-2}

y^{-1} at high-np, mid-dp and low-sp, respectively (Fig. 5). The Rsc at high-np was also significantly greater annually than mid-dp and low-sp (Fig. 5). This contradicted our prediction that greater decomposition rates would yield greater soil respiration. The Rst in mid-dp was significantly higher than in the other two sites, possibly because trenching artifacts increased decomposition rates at this site. The Rst and the average filter paper mass loss of the two deepest intervals (8.5-16 and 16-23.5 cm) were correlated (Fig. 6).

Faster decomposition in the trenched areas did not affect how sites were ranked based on decomposition and heterotrophic respiration. That is, when the relationship between trenched plot heterotrophic respiration and filter paper mass loss are used with control area filter paper decomposition (Fig. 6), the mid-dp heterotrophic respiration (172 g C m^{-2}) was still greater than for the other two sites (164 and 161 g C m^{-2}, low-sp and high-np, respectively). The amount of heterotrophic respiration was unrelated to the amount soil C, which may have reflected an interaction between organic matter quality and environment.

In 2001, Rsc from June-September was significantly greater than in 2000 at all sites (not shown), and the increase in Rst significant for two sites. Cooler soil temperatures at 10 cm in August and September of 2000 resulted in lower respiration. The interannual variability in temperature did not alter the rank order of growing season site respiration for control (high-np>mid-dp>low-sp) or trenched plots (mid-dp>low-sp>high-np).

Differences in annual Rsc and Rst among sites were a function of differences in the temperature response of soil respiration. At all sites, Rsc and Rst increased with

growing season 10 cm soil temperatures (Fig. 7a and b). The temperature sensitivity of Rsc was greater for high-np than low-sp, and Rst respiration at mid-dp was more temperature sensitive than for the other two sites (Table 6). The trenching significantly decreased the temperature sensitivity of respiration at all sites. The moss respiration (Rsm) did not affect trends in respiration across sites because of the uniformly low contribution of feathermoss to total soil respiration.

The two methods of estimating root respiration were related among sites, but the TBCA estimates were consistently higher (23-32%) than trenched plot estimates (Fig. 8). The components of TBCA (aboveground litter, moss production and winter respiration) varied between sites but did not affect overall trends. Aboveground litterfall (g C m^{-2} y^{-1}) was significantly greater ($p=0.02$) at mid-dp (58 ± 14, $n=6$) than at low-sp (41 ± 11), but neither differed from high-np (48 ± 11). Proportional root respiration varied from 50 to 63% of Rsc using the trenched plot method, and from 83 to 86% of Rsc using the TBCA method. Annual root respiration was significantly greater at high-np than at either permafrost site using the trenched plot method, and high-np root respiration greater than low-sp using the TBCA method (Fig. 8)

DISCUSSION

Soil environment and constraints on decomposition

Temperature and moisture both likely influenced patterns in filter paper decomposition. The slow rate of decomposition in the high-np site may have been due to lower soil temperature in the rooting zone during the early part of the growing season (Fig. 2), however, statistical inference cannot be drawn from this apparent relationship

because of the limited number of temperature loggers. Cellulose decomposition is extremely sensitive to temperature (Linkins et al. 1984), but soil moisture also may have affected decomposition. Although we have no direct measurement of soil moisture patterns, spruce needles in the high-np site were least depleted in foliar-^{13}C, suggesting greater moisture stress (Lajtha and Michener 1994). Lower soil moisture at high-np than the other two sites was expected because the permafrost at mid-dp and low-sp degrades slowly over the growing season and may provide soil moisture to the plants and microbes. Also the slope at high-np (12%) was much greater than at the other two sites (8 and 3%), which likely increased snowmelt runoff.

Nitrogen availability may also have affected filter paper decomposition. Lower N availability was implicated at high-np than the other two sites by the depleted foliage-^{15}N (Table 6), a phenomenon that often occurs with slower decomposition and greater N limitation (Garten and Van Miegroet 1994, Schuur and Matson 2001). However, foliar ^{15}N reflects numerous permutations of the N cycle that may not relate directly to plant available N (Nadelhoffer and Fry 1994). Foliar N concentration also was similar among sites, suggesting N availability did not differ for the three stands. Root N concentration was also greater for the high-np site than the other two sites. Nitrogen availability may have affected decomposition but it is difficult to discern its influence from the indirect methods employed in this study.

The filter paper decomposition captured between site variability in microbial respiration and also indicated, at two of the sites, decomposition potential was enhanced in 2001 because of trenching. The positive influence of trenching on the decomposition

rate of cellulose has been previously demonstrated and may be due to greater available moisture or nutrients to microbes (Fisher and Gosz 1986). Alternatively, temperatures at deeper depths also increased with trenching in our study and at the same depths as the greatest increase in decomposition. We suggest researchers using trenched plots to estimate microbial respiration also use a decomposition proxy in the plot to estimate the artifacts associated with the technique.

Annual soil, root, and microbial respiration

Contrary to our prediction, soil respiration was not greater where microbial respiration and filter paper decomposition were greater. From literature estimates of black spruce soil respiration, a relationship similar to ours between decomposition and soil respiration is difficult to identify because the two have rarely been measured together (Table 7). Our three-site mean growing season estimate for soil respiration of 366 g C m^{-2} y^{-1} fits between the median (287 g C m^{-2} y^{-1}) and the mean (393± 200 g C m^{-2} y^{-1}, n=18) of other reported values in mature black spruce (Schlentner and Van Cleve 1985, Moosavi and Crill 1997, Nakane et al. 1997, O'Neill 2000, Rayment and Jarvis 2000, Swanson and Flanagan 2001, Wang et al. 2002, O'Connell et al. 2003b, Ruess et al. 2003, in press) (Table 7).

The greater soil respiration in high-np is the result of greater root respiration and based on the foliar ^{13}C results, may have been due to increased moisture stress and greater belowground C allocation by black spruce at high-np. This hypothesis would fit a trend observed in the literature, where moisture deficit, or growing season precipitation minus potential evapotranspiration (Thornthwaite 1948), and soil respiration appear

positively correlated in mature black spruce forests across Manitoba, Saskatchewan, and Alaska (Fig. 9) We restricted our literature review to mature (>70 years) black spruce forests, but did not control for variability in methodology (Table 7.) The fourth study in Nova Scotia was also conducted in black spruce but no information was provided on stand age, so we cannot eliminate this as a confounding factor (Risk et al. 2002) The trend also support the "wet-dry" comparison of Wang et al. (2002) where greater soil respiration was found in drier black spruce sites. Growing season mean or maximum temperatures, annual mean temperatures, and precipitation did not suggest as strong a trend across studies.

The total allocation to fine roots has been shown to increase in xeric conditions (Keyes and Grier 1981, Gower et al. 1992), but more often the proportional allocation is greater where soil moisture is limiting (Santantonio and Hermann 1985, Comeau and Kimmins 1986). The mean proportional root contribution reported by studies is 55 ± 11% (n=9) without including TBCA estimates, which agrees with the trenched plot average of 55% for the three sites in this study (Table 7). However, given the differences in total respiration among studies, our estimate of the absolute amount of C cycling through roots is considerably higher than for both Saskatchewan and Manitoba (O'Connell et al. 2003 Wang et al. 2002) and overall the studies indicate Alaskan black spruce forests allocate substantially more C belowground than elsewhere (Fig. 9). Neither soil or root respiration has, to our knowledge, been examined with root production in forests across gradients in moisture; therefore it is not possible to speculate how these processes actually scale with one another.

Decreased C allocation belowground has also been observed in N fertilization studies (Gower et al. 1992), along natural gradients in nutrients (Keyes and Grier 1981), and in one study both fine root production and soil respiration were depressed by the addition of N fertilizer (Haynes and Gower 1995). In this study, the black spruce aboveground production was unrelated to soil respiration but followed the trend in microbial respiration (mid-dp>low-sp>high-np), suggesting black spruce shifted allocation from aboveground to belowground processes with depressed decomposition. Faster soil organic matter turnover may indicate greater N availability, increased aboveground growth and spruce allocating less C belowground when N availability is greater.

The greater root N concentration in high-np than the other two sites may indicate an adaptation by roots to the lower soil temperatures and may explain the greater root and soil respiration at the site (Burton et al. 1996). Root respiration rate and root N concentration are generally positively correlated in tree species (Burton et al. 1996, Pregitzer et al. 1998, Burton et al. 2002). Because more enzymes and proteins are necessary for cold weather function (Atkin et al. 2000), increased tissue N concentration may signify adaptation to low temperature. Alternatively, our root N concentrations may have captured varying patterns in root morphology among sites. That is, during our sampling we collected roots <2 mm but if within that category the size distribution varied with environmental factors, then fine root N concentration would also vary because root N concentration is generally negatively related to root diameter (Burton, Pregitzer et al. 2002).

The discrepancy between the root respirations (Rr) estimated from the TBCA method and trenched plots may have reflected artifacts associated with either technique. The decomposition of excised roots in the trenched plots could partly explain the discrepancy. Other researchers have constrained the artifact of excised root decay by applying decomposition constants to root biomass and estimating the resulting heterotrophic contribution (Bowden et al. 1993, Lavigne et al. 2003). This correction is necessary when the heterotrophic respiration from trenched plots is used for ecosystem carbon budget analysis. The TBCA and trenched plots may also differ because we did not account for an important litter component (e.g. past coarse woody debris), or possibly the soil C pool is degrading at these sites (Raich and Nadelhoffer 1989). However, where TBCA could be estimated in other studies it consistently provided greater estimates of root respiration than where trenched plot (O'Connell et al. 2003b) or even direct measurements of root respiration (Ruess et al. in press) were employed (Table 7). As suggested by Hanson et al. (2000), further direct comparisons of methods to estimate root respiration are necessary to understand why divergent estimates of root respiration occur using methods that should provide similar results.

Our estimated winter (snow-cover season) respiration of 36-54 g C m^{-2} $winter^{-1}$ was similar to values reported in Winston et al. (1997) for black spruce and jack pine forests (40-55 g C m^{-2} $winter^{-1}$) and by Wang et al. (2003) (25-35 g C m^{-2} $winter^{-1}$, Table 7) for Manitoba black spruce. The extremely high value (321 C m^{-2} $winter^{-1}$) reported by O'Connell et al. (2003) is likely an outlier due to the method used to separate winter and growing season respiration. The lower winter respiration at high-np than the two

permafrost sites was surprising (Fig. 7), considering the warmer winter soil temperatures and thicker layer of non-frozen soil at this site (Fig. 2). This result may be due to differences in organic matter quality or available soil moisture (Clein and Schimel 1995, Dioumaeva et al. 2002, Michaelson and Ping 2003).

The exclusion of roots also influenced winter respiration at two of the sites, however, we do not know if the effect is due to black spruce roots respiring at very low soil temperatures (-6 to –1 °C) because we are aware of no direct root respiration measurements at temperatures below freezing. The indirect influence of roots on winter respiration has also been demonstrated for arctic tundra (Grogan et al. 2001). The influence of root exclusion on winter soil respiration may hinge on how much the cessation of annual fine root mortality reduces C availability to microbes and macrofauna rather than the direct reduction in root respiration. For example, in the control areas we have observed active macroinvertebrates in minirhizotrons during most of the winter (Ruess et al., unpublished data), organisms that likely take advantage of the fine roots that senesce during the fall and winter (Steele et al. 1997, Ruess et al. in press).

Soil, microbial and root response to temperature

Seasonally and inter-annually within a site, growing season soil, root, and microbial respiration covaried with temperature in our study. The peak of soil, microbial, and root respiration occurred in late July and early August, coinciding both with the maximum 10 cm soil temperature and a well-identified maximum in black spruce fine root growth (Tryon and Chapin 1983, Steele et al. 1997, Ruess et al. in press). The temperature sensitivity of soil respiration was more affected by root than microbial

respiration, which is consistent with other studies in forest ecosystems (Boone et al. 1998, Lavigne et al. 2003, O'Connell et al. 2003b).

The warmer soil temperatures in 2001 than 2000 elicited a greater increase in respiration from control than trenched areas at all sites. This observation might also reflect the greater temperature sensitivity of root respiration or that trenched plot respiration was beginning to decrease with substrate limitation from 2000 to 2001. O'Neill (2000) reported inter-annual soil respiration variability for mature Alaskan black spruce forests; however, Ruess et al. (in press) found no significant inter-annual variation in soil respiration despite considerable between year soil temperature differences. Whether a significant increase in soil respiration is observed in a warm year may be dependent on how quickly the system adjusts to the warmer temperature. For example, Jarvis and Linder (2000) and Mellilo et al. (2002) reported fairly rapid temperature acclimation of soil respiration in forests that were experimentally warmed. If acclimation occurs annually in ecosystems, it might explain why some studies observe inter-annual increases in soil respiration with natural warming but others do not.

Annual moss photosynthesis and respiration

Moss function did not differ greatly from other experiments in boreal systems or explain between site differences in soil respiration for this study. In control collars, the decrease in soil respiration by moss gross photosynthesis (Psm) of 8-14% is considerably less than the 35% reduction reported for black spruce forests in Saskatchewan (Swanson and Flanagan 2001), but closer to the 20% reduction in a Swedish spruce/pine forest (Moren and Lindroth 2000). Mean growing season Psm for all sites (0.53 μmole m^{-2} s^{-1})

was on the low end of the range 0.5-1.0 μmole m^{-2} s^{-1} reported in Goulden and Crill (1997) in Manitoba black spruce and less than the seasonal average of 0.75 μmole m^{-2} s^{-1} of Swanson and Flanagan (2001) in Saskatchewan. Because moss is highly sensitive to moisture deficit (Skre and Oechel 1981, O'Neill 2000), the lower growing season precipitation in interior Alaska (175 mm) than at the locations of the other two studies (352 mm and 302 mm) is consistent with our lower values.

Modeled average moss respiration (Rsm) contribution to soil respiration (5-10%) compared well with the 7% moss contribution estimated by Swanson and Flanagan (2001). Moss primary production for the three sites averaged 14 ± 3 g C m^{-2} y^{-1}, lower than the 24 g C m^{-2} y^{-1} reported for a central Saskatchewan forest (O'Connell et al. 2003b), but similar to the 14-15 g C m^{-2} y^{-1} measured 166 km southeast of our study area (Jennifer Harden pers. comm.). Although our production and Psm values are similar to other studies, in this study 6% of measurements during the two growing seasons indicated a Psm of zero, which would result in zero Rsm using our approach. This is likely an inaccurate description of moss function and under certain conditions may pose a significant difficulty in using gross photosynthesis to constrain moss respiration.

CONCLUSIONS

Although heterotrophic respiration correlated significantly with decomposition rates, total soil respiration did not. Instead, variations in the much larger rates of root respiration drove landscape and inter-annual patterns in total respiration. The greater allocation belowground at the high-np site could be related to decreased moisture availability, as the trend in Fig. 9 indicates for different areas in North America. A causal

factor may be the differences in root N concentration, which is consistent with between site differences in root respiration. Burton et al. (1996) also found root N concentration explained root respiration patterns in a temperate forest but they also observed that greater net N mineralization co-occurs with greater root N concentration. Our indirect estimates of nitrogen availability (similar foliage N concentration and lower $\delta^{15}N$ and lower decomposition rate at high-np) suggest the root N concentration was an adaptation to its environment and not a result of greater N availability. Rather, because soil temperature is cooler and available soil moisture likely less at the site with greater root N concentration, it may be the high N concentration and root respiration are an expression of a combination of cold weather acclimation and moisture limitation. These hypotheses need to be tested with experimental soil warming research and moisture manipulations, which should track both microbial and root respiration with concomitant measurements of root N concentration and N availability (both organic and inorganic). If these soil respiratory patterns are indicative of changes that might occur with climate change, then increases in soil respiration might be from a net soil C loss, but more likely any increase will be due to adjustments in root respiration.

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Table 1-1. General topographic, soil and vegetation characteristics of the three study sites.

	High-np	Mid-dp	Low-sp
Topography			
Elevation (m)	580	184	124
Aspect (degrees)	340	180	195
Slope (%)	12	8	3
Active layer thickness (m)[1]	>1.5?	0.85	0.64
Overstory characteristics			
Trees per hectare	6,588	8,000	6,941
Basal Area ($m^2 ha^{-1}$)	28.6	26.0	30.4
Ave. Diameter (cm)	7.4	6.2	7.6
Age (years)	110	75	120

[1]depth to permafrost measured between 8/31 and 9/2/99

Table 1-2. Isotopic signatures and N concentration of new foliage, and fine root N concentration (mean ± SD, n=4). Significant ($p<0.05$) differences noted by different letters.

	Foliage			Root
Site	$\delta^{15}N$	N concentration	$\delta^{13}C$	N concentration
high-np	-6.07 ± 0.54a	0.83 ± 0.10	-27.5 ± 0.66*	1.05 ± 0.01a
mid-dp	-4.27 ± 0.66b	0.84 ± 0.06	-28.5 ± 0.80	0.92 ± 0.06b
low-sp	-4.58 ± 0.07b	0.84 ± 0.05	-28.9 ± 0.21*	0.93 ± 0.01b

*high-np>low-sp ($p=0.08$)

Table 1-3. Mean (n=3) aboveground biomass (g C m^{-2}) and productivity (g C m^{-2} y^{-1}) of black spruce and vascular understory (mean±standard deviation). Different letters represent differences between sites (one-way ANOVA, LSD).

	Black spruce		Understory	
Site	Biomass	Productivity	Biomass	Productivity
high-np	4,422 ± 360a	42.3 ± 4.2c	7.9 ± 3.9a	4.8 ± 2.3a
mid-dp	3,394 ± 560b	54.8 ± 7.6a	1.0 ± 0.5b	0.9 ± 0.7b
low-sp	4,607 ± 230a	46.0 ± 5.2b	10.9 ± 4.2a	4.9 ± 3.6a

Table 1-4. Values are mean (± standard deviation) C and N concentration, C:N, and total C and N (g m^{-2}) for soil horizons. Comparisons are between sites for a horzion (one-way ANOVA, LSD). Soil includes coarse and fine roots.

Site	Horizon	%C	%N	C:N	Total C	Total N
High-np	L	46.0 ± 1.8a	1.0 ± 0.24a	47 ± 10b	428 ± 174a	10 ± 5a
	F/H	39.5 ± 6.6	0.67 ± 0.11b	59 ± 9a	4409 ± 1483	74 ± 17
	A	9.30 ± 2.9b	0.37 ± 0.14b	25 ± 6	1441 ± 518b	58 ± 30
	Min[1]	3.20 ± 1.00	0.16 ± 0.04	21 ± 3.0ab	1180 ± 410	63 ± 11
Mid-dp	L	40.6 ± 4.0b	0.91 ± 0.11b	45 ± 10b	353 ± 232a	8 ± 5a
	F/H	41.6 ± 2.6	0.88 ± 0.12a	47 ± 9b	4679 ± 1836	101 ± 46
	A	9.32 ± 5.8b	0.33 ± 0.11b	28 ± 3	1565 ± 1047b	72 ± 61
	Min	2.90 ± 1.30	0.16 ± 0.05	17 ± 3.0a	1333 ± 429	74 ± 18
Low-sp	L	39.0 ± 5.6c	0.74 ± 0.21c	55 ± 10a	186 ± 62b	3 ± 2b
	F/H	41.6 ± 2.20	0.67 ± 0.09b	63 ± 10a	5260 ± 1204	86 ± 26
	A	17.5 ± 4.2a	0.63 ± 0.11a	28 ± 4	2379 ± 463a	87 ± 17
	Min	2.80 ± 1.30	0.19 ± 0.13	25 ± 5.6b	1378 ± 180	94 ± 77

[1]Mineral soil to 5 cm below the A horizon

Table 1-5. Mean (± standard deviation, n=15) 1yr decomposition (% mass loss) of filter papers and spruce litter in and outside trenched plots. Comparisons are between sites within treatment[1], control vs. trench[2], and years for surface filter paper[3].

Year	2000	2001			2001
Material	Filter Paper	Filter Paper			Spruce litter
Depth (cm)	1-8.5	1-8.5	8.5-16	16-23.5	~4
Site		Control			
high-np	11 ± 10b&	39 ± 24b&	14 ± 0.11	1 ± 9b	19 ± 10a
mid-dp	46 ± 3a	49 ± 19ab*	25 ± 0.21*	17 ± 16a*	29 ± 10b
low-sp	32 ± 23ab&	55 ± 17a&	22 ± 0.14*	10 ± 14a	25 ± 9ab
		Trench			
high-np	17 ± 0.12b	24 ± 23b	11 ± 0.15b	9 ± 15b	no data
mid-dp	54 ± 0.22a&	81 ± 14a*	54 ± 0.24a*	54 ± 19a*	"
low-sp	39 ± 0.19a&	60 ± 20a	44 ± 0.23a*	13 ± 10b	"

[1]different letters indicate significant difference between sites within treatment ($p<0.05$)

[2](*), signifcant difference between trench and control

[3](&), between year significant differences for surface filter paper

Table 1-6. Linear regression coefficients of respiration (umole C m^{-2} s^{-1}) increase with temperature, R^2 (coefficient of variation), and number of sample periods x replicates. Significant difference between sites denoted by different letters. Trenched and control temperature sensitivity differed for all sites.

Site	Treatment	b0	b1	R^2	n
High-np	Control	0.93	0.29a	0.76	57
Mid-dp		0.63	0.27ab	0.70	38
Low-sp		0.62	0.22b	0.83	54
High-np	Trench	0.52	0.11b	0.59	57
Mid-dp		0.54	0.16a	0.70	38
Low-sp		0.52	0.10b	0.75	54

Table 1-7. Literature estimates of soil respiration during winter and the growing season (GS) and proportional contribution of moss and roots in mature black spruce forests. Descriptions of the methods employed by other studies for soil respiration and for estimating root respiration not found in this paper. Reviews of methodology can be found in Norman et al. (1997) and Hanson et al. (2001).

		Flux (g C m^{-2} y^{-1})		% contribution		
Study	Location	GS[1,2]	Winter	Moss	Root[3]	GS+winter
Schlenter and Van Cleve (1985)	Alaska	$369^{SL,U}$				
O'Neill (2000 and submitted)[4]	Alaska	$627^{IC,M}$		14	74^{RI}	
		505		21	63	
Ruess et al. (in press)	Alaska	$616^{IC,NM}$			57^{DR}, 86^{T}	
		624			57^{DR}, 82^{T}	
		501			57^{DR}, 90^{T}	
This Study	Alaska	$436^{IC,NM}$	36	5	63^{TP}, 86^{T}	62, 85
		354	54	7	50^{TP}, 83^{T}	51, 81
		307	54	10	53^{TP}, 85^{T}	54, 83
Valentine, D.W. unpublished data	Alaska	$500^{IC,M}$	70			
Nakane et al. (1997)	Saskatchewan	$368^{AA,NM}$				
		283				
Swanson and Flanagan (2001)	Saskatchewan	$287^{IC,MP}$		7		
Rayment and Jarvis (2000)	Saskatchewan	$896^{IO,M}$				
O'Connell et al. (2003)	Saskatchewan	$242^{IC,NM}$	321		69^{TP}, 67^{T}	32, 86
Wang et al. (2003)	Manitoba	250	25		50^{BU}	
		225	20		46^{BU}	
		210	35		46^{BU}	
		230	20		48^{BU}	
Trumbore (2000)[5]	Manitoba	200			45^{14C}	
Moosavi and Crill (1997)	Manitoba	$259^{SC,M}$				

[1]Respiration technique:soda lime (SL), IRGA closed system (IC), alkali absorption (AA), IRGA open system (IO), static chamber (SC)

[2]Moss treatment: Unknown (U), moss included (M), removed (NM), or moss photosynthesis included (MP)

[3]Root respiration method: burn vs. unburn (BU), direct measurement of roots (DR), trench plots (TP), TRCA (T), bomb carbon (14C), reconstruction from laboratory incubation (RI)

[4]Proportions of moss and root are part of submitted paper

[5]Study reports recent carbon and not necessarily root, also the "recent carbon" is actually 40-50%

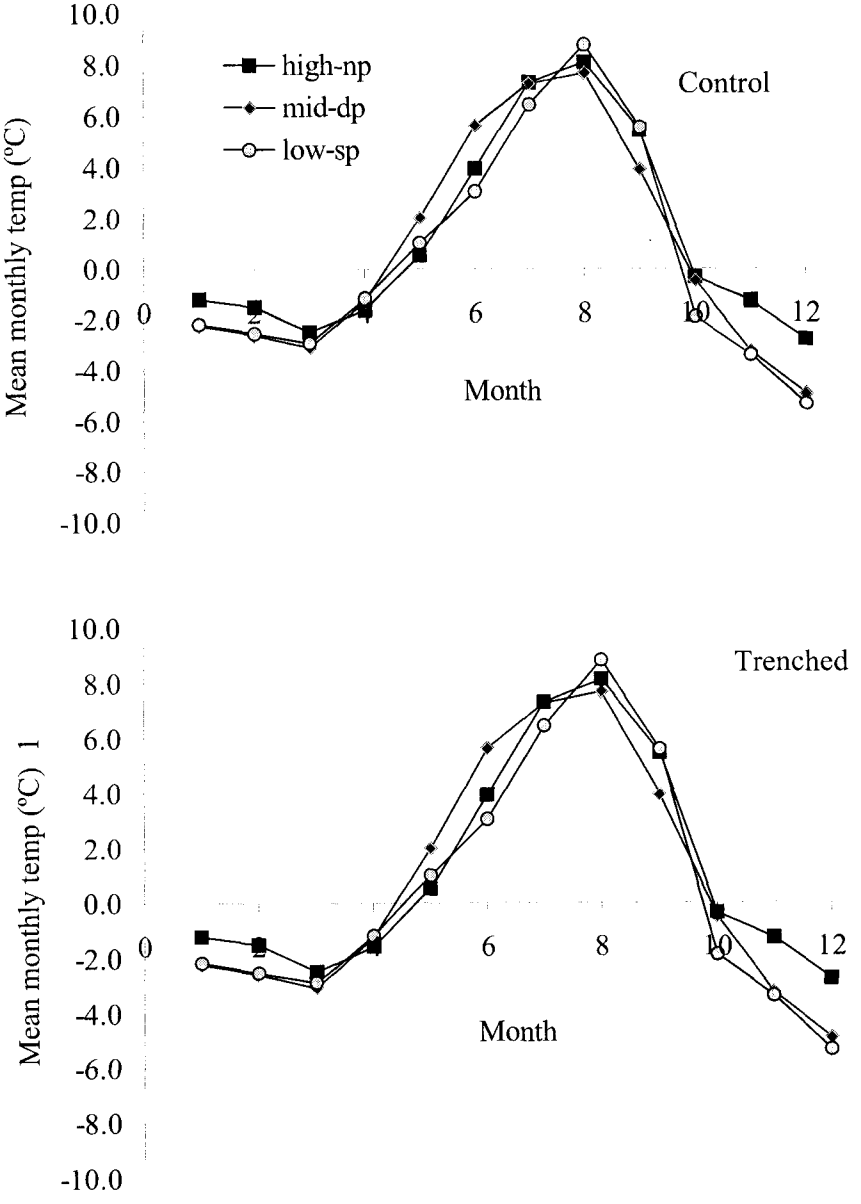

Figure 1- 1. Trenched plot and control area seasonal course of mean monthly temperatures (September 30, 2000 to October 1, 2001) at 10 cm depth.

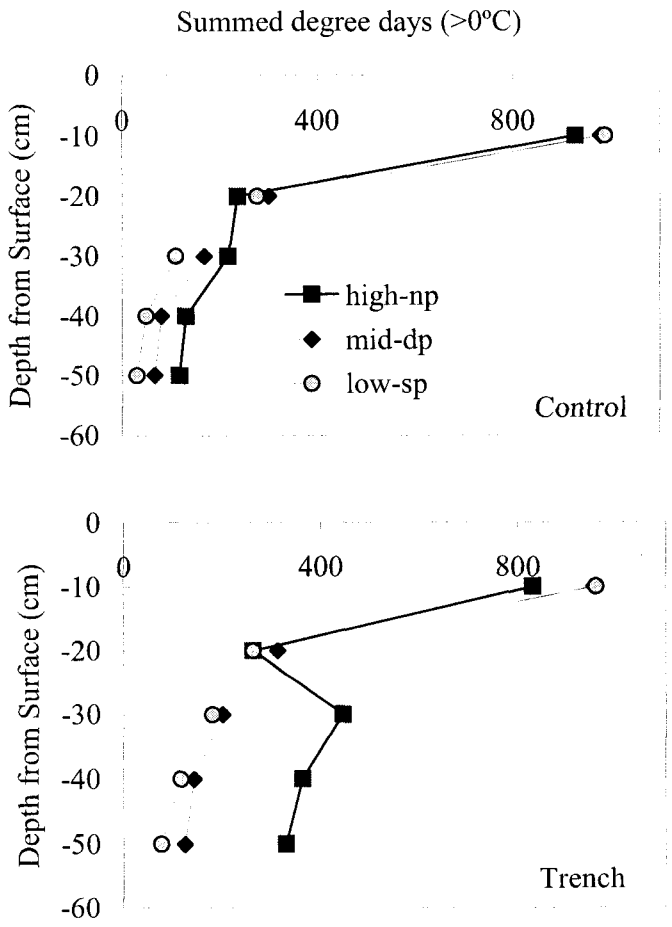

Figure 1- 2. Growing season summed soil degree-days for five depths. The high-np deep temperatures were greatly influenced by one probe in a sunny area of the trenched plot.

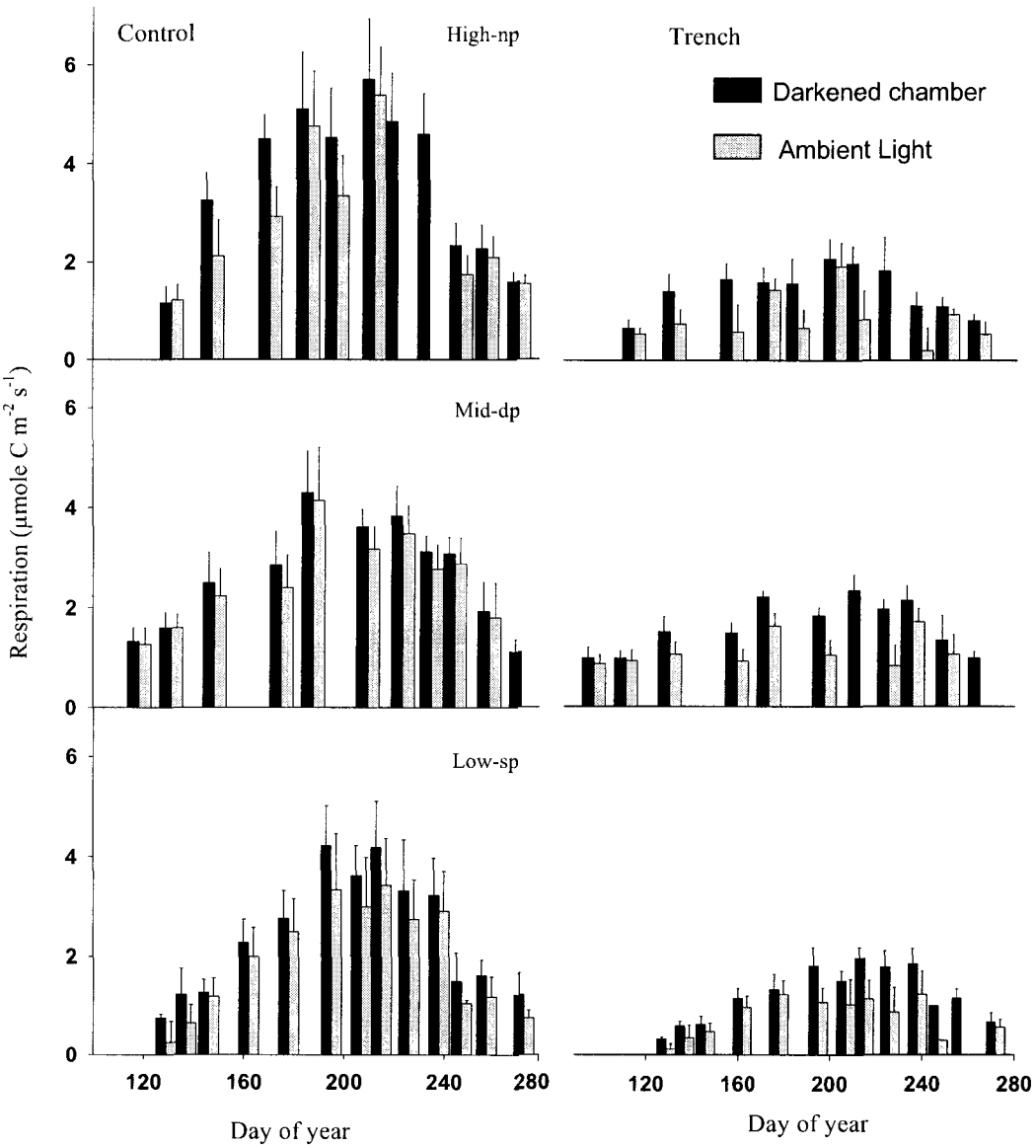

Figure 1- 3. Seasonal (2001 only) dynamics of measured darkened chamber and ambient light soil respiration (μmol CO_2-C m^{-2} s^{-1}) efflux.

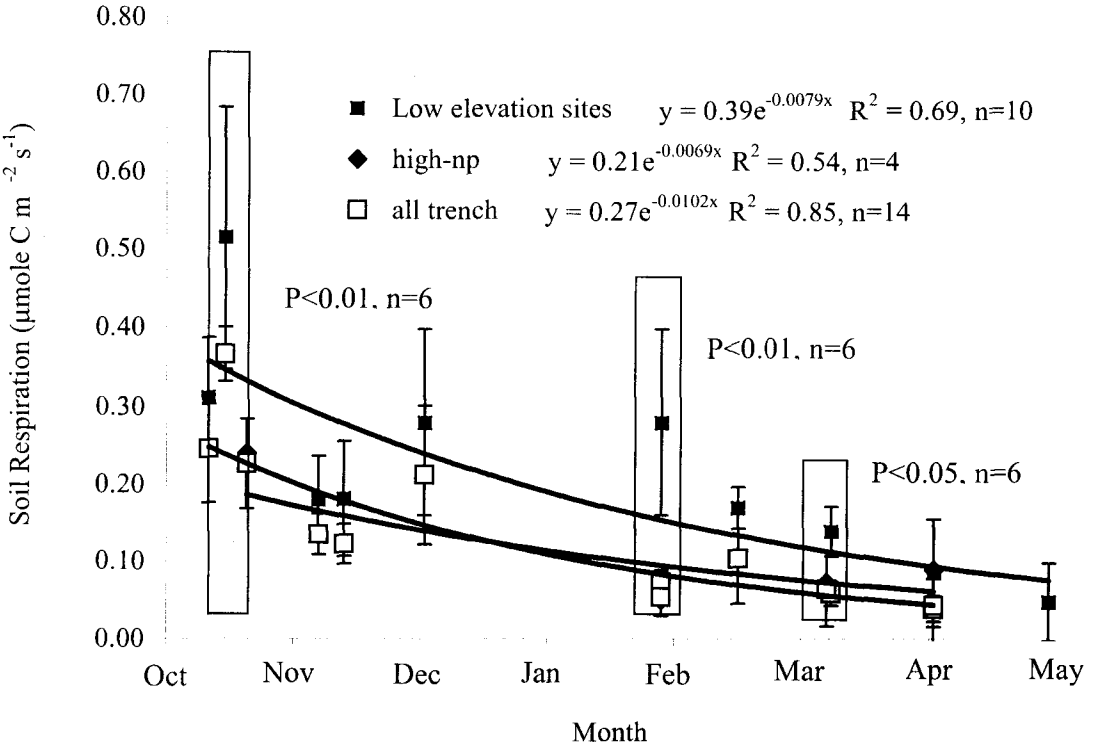

Figure 1- 4. Winter trend in soil respiration for the control areas of the two permafrost sites, high-np, and the trenched plots of all sites. Bars represent measurement periods where a control high-np measurement overlapped with one of the two low elevation sites and the difference between the two was significant. The (x) in each regression is the number of days since Oct 10, 2000; the day after the first significant snowfall.

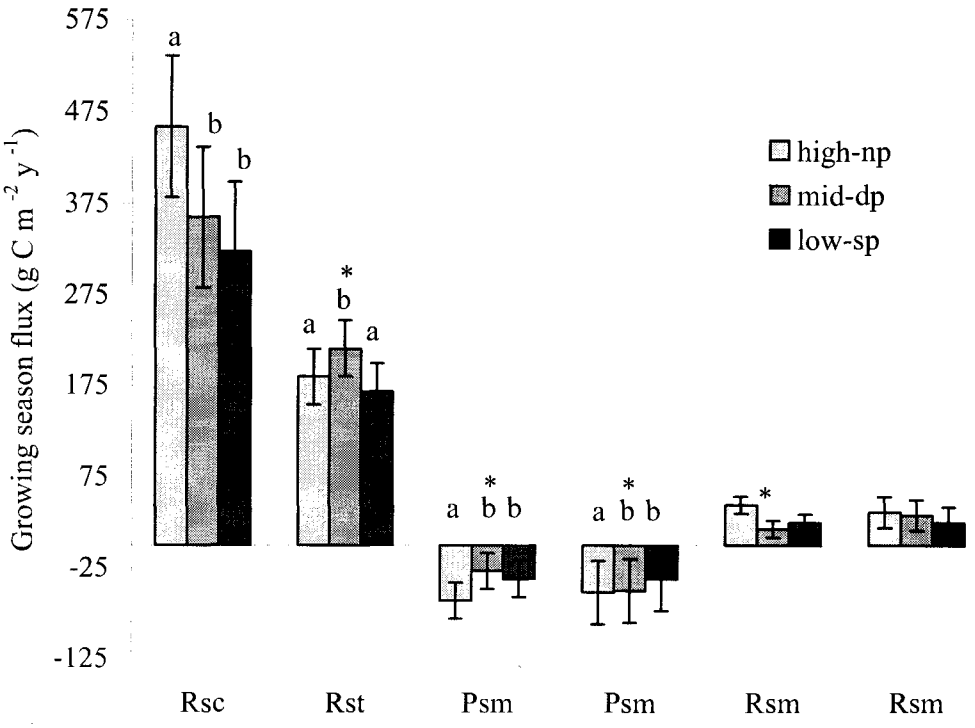

Figure 1- 5. Respiration from control soil (Rsc), trench/microbial (Rst), moss (Rsm), and moss gross photosynthesis (Psm). Significant differences between sites denoted by different letters (n=6, ±SD), significant influence of trench treatment indicated with (*) (n=3, ±SD).

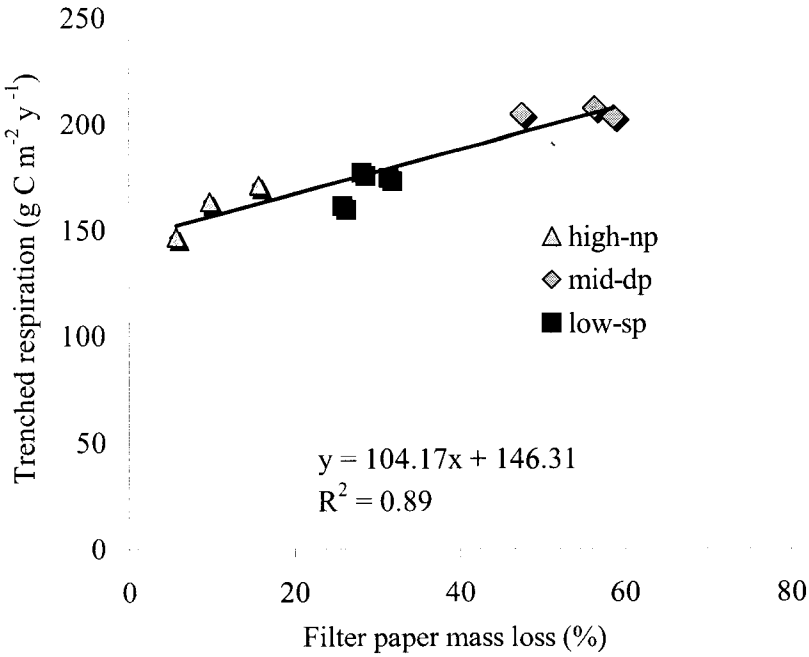

Figure 1- 6. Relationship between annual trenched plot soil respiration and average percent mass loss of filter papers at two depths (8.5-16 and 16-23.5 cm from moss surface) for 2001.

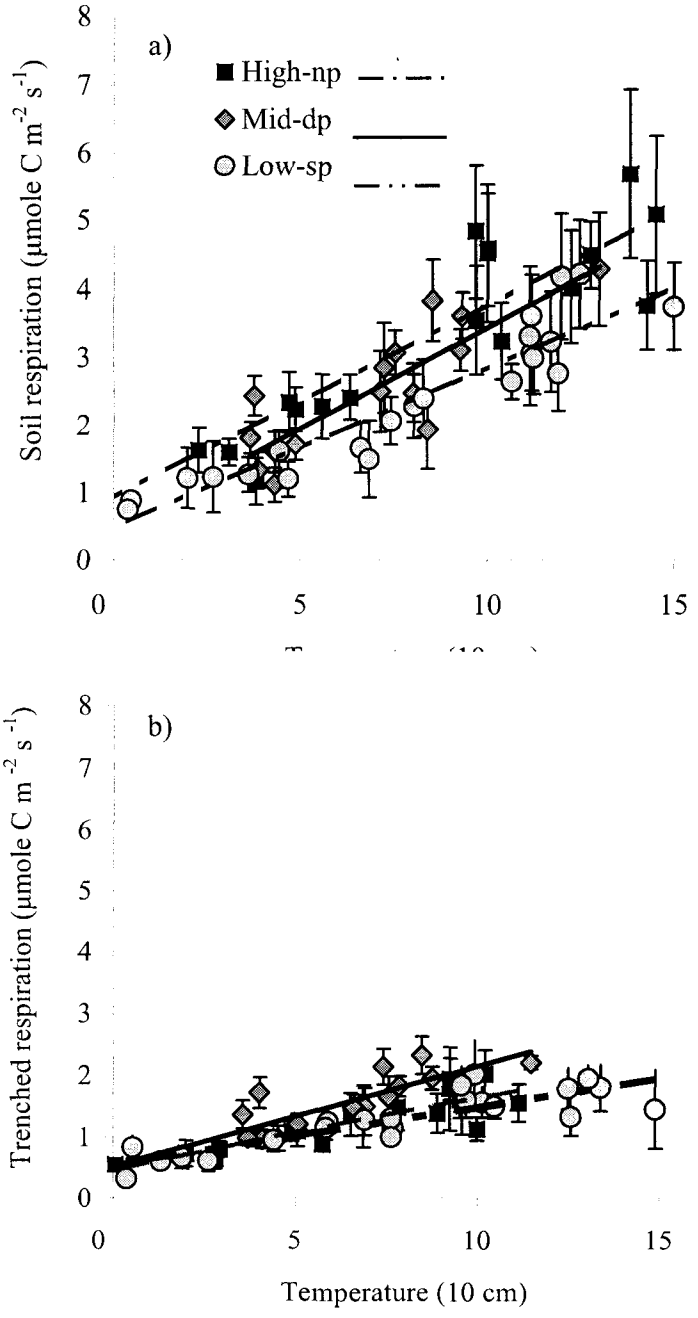

Figure 1- 7. Darkened chamber respiration (µmol CO_2-C m^{-2} s^{-1}) increase with temperature in (a) control (n=6) and (b) trench areas (n=3).

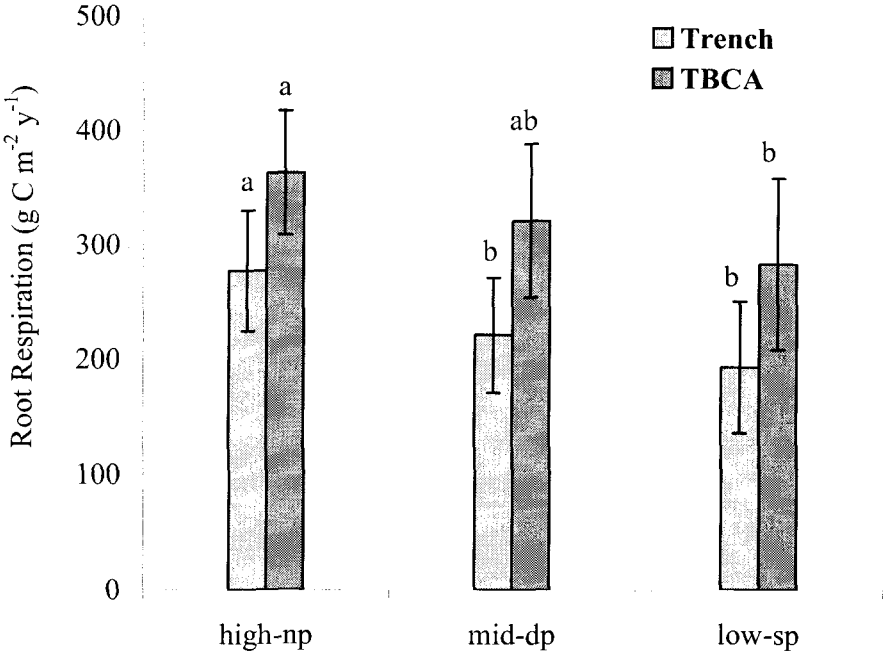

Figure 1- 8. Annual root respiration (g C m^{-2} y^{-1}) (n=3 ± SD), estimated with trenched plots and TBCA method for 2001. Significant differences ($p<0.05$) among sites denoted with different letters.

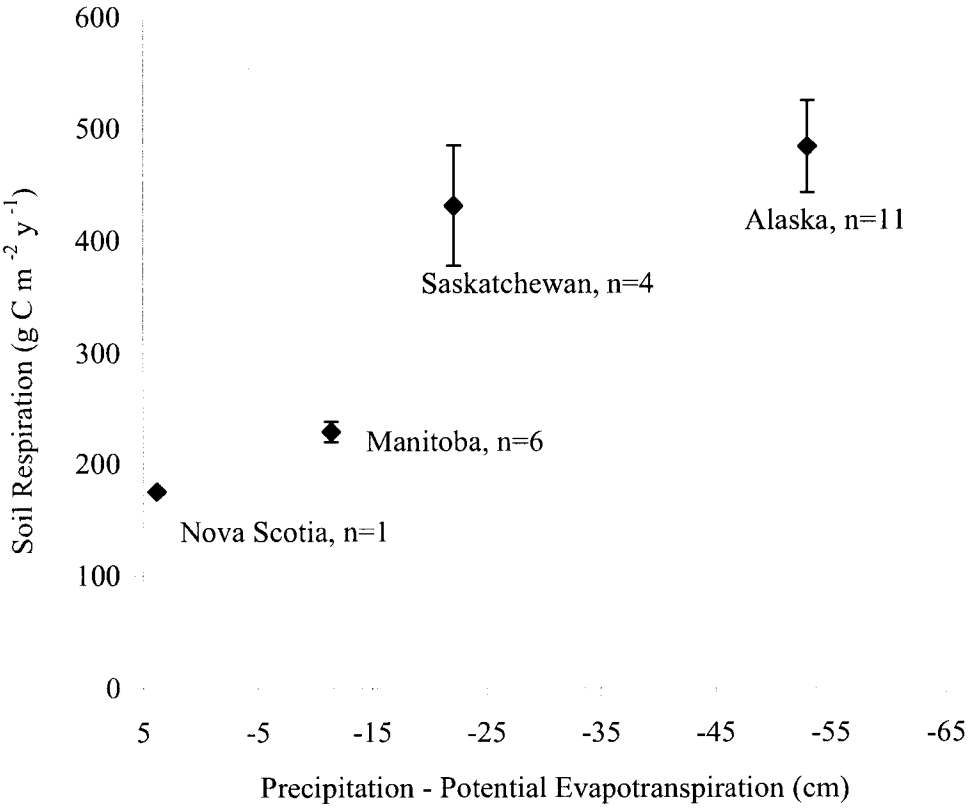

Figure 1- 9. Relationship between moisture deficit (precipitation-potential evapotranspiration) and growing season soil respiration (mean±standard error) for mature black spruce studies in Manitoba, Saskatchewan, Nova Scotia and Alaska. Table 7 describes the studies in more detail.

CHAPTER 2. The influence of temperature and organic matter quality on C and net N mineralization in the organic horizons of black spruce soils

ABSTRACT

In boreal ecosystems, the rate of C and N mineralization in surface organic soils plays a critical role in ecosystem C balance. Climate warming will likely increase these mineralization processes. We studied how C and net N mineralization vary with temperature, organic matter chemistry, and microbial dynamics for black spruce organic soils from three sites that differed in *in-situ* decomposition rates. Laboratory incubations were conducted at five temperatures (0, 5, 10, 15 and 20°C) for 188 days. Warming increased both mineralization processes. The respiration rate increase in C mineralization between temperature intervals (Q_{10}) decreased with warmer temperatures. Net N mineralization also generally increased with warming and cumulative C loss, but within a temperature treatment, the C lost did not constrain the amount of N mineralized. Sites did not differ in microbial biomass or microbial turnover time (biomass/respiration rate), but both indices were significantly greater at 5 than 15 °C for all sites. Thus, temperature was a consistent positive influence on mineralization processes, but site differences in these processes were difficult to explain from soil characteristics or *in-situ* decomposition rates.

For most temperature treatments, microbial respiration was correlated to the relative contents of polysaccharides (negative) and phenols and lignins (positive) determined through pyrolysis-gas chromatography/mass spectrometry. These results

Prepared for submission to Soil Biology and Biochemistry

were contrary to our original hypothesis that labile polysaccharides would be positively related to respiration. However, the polysaccharide pool size was correlated positively to microbial biomass at 5 and 15 °C. Polysaccharides also decreased to a greater degree over the course of the incubation than other compounds, suggesting they were preferentially consumed but turned into biomass or microbial secondary-products and not CO_2. Thus, CO_2 production may not track compound specific decomposition dynamics. For polysaccharides, their residence time in microbial biomass or the decomposition to other organic compounds (e.g. phenols, polypeptides) appear to be an important intermediate step in decomposition. We conclude soil warming will increase the rate of C and N mineralization, however, microbial dynamics and organic matter characteristics interact to modify the production of CO_2 and mineral N.

INTRODUCTION

Boreal forest soil C represents an estimated 24% of the atmospheric pool (Post et al. 1982), and much of this soil C is considered "reactive" or potentially sensitive to warming (McGuire et al. 1995). Regions of the boreal forest have been warming for the past 100 years (Serreze et al. 2000), which is likely increasing soil organic matter (SOM) mineralization to CO_2 and plant available N. Some boreal ecosystems can experience a net carbon (C) loss with warming temperature due to enhanced microbial decomposition outstripping net primary production (Goulden et al. 1998; Janssens et al. 2001). If this were to become widespread, the current atmospheric CO_2 increase could accelerate. Concurrent nitrogen (N) mineralization with warming will likely stimulate plant growth (Kirschbaum 1995), but the available evidence suggests that in boreal systems CO_2

production proceeds at a much greater rate than net N mineralization (Vance and Chapin 2001).

Warming increases mineralization processes, and in some studies, the total potential amount of C or N mineralized (Ellert and Bettany 1992; MacDonald et al. 1995; Dalias et al. 2001). In the latter case, a warmer soil temperature allows microbes to mineralize organic matter that may never be mineralized at lower temperatures. This may be due to microbial community change with warming (Zogg et al. 1997; Andrews et al. 2000) or because the optimal temperatures for certain microbial enzyme function is reached with warming (Linkins et al. 1984). Thus at cooler temperatures, organic matter may accumulate that has a greater potential to lose soil C under a warmer climate (Niklinska et al. 1999, Dalias et al. 2001). A clear link has not been made, however, between a SOM characteristic and the potential temperature response of mineralization processes.

Investigators using pyrolysis-gas chromatography/mass spectrometry (PY-GC/MS) have reported strong positive relationships between the relative abundance of certain indicator compounds, such as primary polysaccharides, and microbial respiration (White et al. 2002). Where SOM decomposition is inhibited, primary polysaccharides could accumulate and increase the potential for future C mineralization. Alternatively, the microbial consumption of a substrate can generate microbial biomass, respiratory CO_2 or other by-products of metabolism. The amount and rate that each end product is produced is to some degree dependent on the chemistry of the original substrate (Sugai and Schimel 1993, Nicolardot et al 1994). Substrate chemistry could also influence N

dynamics (Weintraub and Schimel 2003). For example, the decomposition of N-free primary polysaccharides could enhance microbial N immobilization, thereby depressing the rate of net N mineralization (Vance and Chapin 2001).

We studied organic soils from black spruce (*Picea mariana* [(Mill) B.S.P])-feather moss (*Pleurozium schreberi* (Brid.) Mitt. and *Hylocomium splendens* (Hedw.) B.S.G) forests. Black spruce is the most prevalent tree species in Alaska (Labau and van Hees 1990) and co-occurs with the greatest amounts of soil C (Van Cleve et al. 1983). The forest type spans the mean annual temperature range of the North American boreal forest (Burns and Honkala 1990), which likely means the spruce- and moss-derived SOM found across this temperature gradient will not be mineralized uniformly in response to a temperature increase (Kirschbaum 1995).

Our overall objective was to examine the relationships between soil characteristics and microbial processes. Traditional indices (pH, C:N ratio) of soil organic matter quality and specific organic compounds (polysaccharides, lignin, phenolics) identified with PY-GC/MS were related to microbial processes. We hypothesized that where cold temperatures depress *in-situ* decomposition, relatively labile organic compounds (e.g., 1° polysaccharides) accumulate. We predicted that with warming, soil polysaccharide content would correlate to greater microbial biomass, respiration, and the ratio of C mineralized to N mineralized. We also hypothesized that the temperature sensitivity (indexed by the Q_{10} coefficient) and rates of net N mineralization would be negatively correlated to the abundance of polysaccharides.

METHODS

Site descriptions and soil sampling

The association of black spruce and feathermoss is common in the boreal forest and prevalent in areas of interior Alaska where black spruce is relatively productive (Viereck et al. 1993). We attempted to maintain this vegetation association across a gradient in the rate of *in-situ* decomposition. In a subsequent examination of the field data, we found two of the sites were similar in *in-situ* temperature and decomposition. Complete site descriptions can be found in Chapter 1, but sites were designated "high-np", "mid-dp" and "low-sp", for high, mid, and low elevation sites; the postscripts, -np, -dp, and -sp reflect "no-", "deep-", and "shallow-" permafrost depths. General site characteristics are summarized in Table 1.

In November 2001, 5 soil monoliths (~225 cm^2) that extended from the moss surface down to mineral soil were collected from 5 random points located within a 20x20m plot at each site. We collected samples in the fall because this is when the greatest amount of "fresh" organic matter is available for microbial use due to fine root mortality and other tissue senescence (Ruess et al. in press). The litter or L layer was removed, and the F and H layers (The Canadian system of soil classification, 1998) were combined and sieved through a 3 mm mesh screen while still partially frozen. Large roots (>2 mm) and detritus that passed through the sieve were picked from the soil. Sieved soils were immediately refrozen (~-5 C) until all soils were sieved. The combined F and H layers were used for the incubations.

Water-holding capacity

Water-holding capacity (WHC) was determined for each sieved soil and then all soils were either dried or wetted to reach 50% WHC. To estimate WHC, a 15 cm length glass vial was filled with soil, water applied in drips until it pooled at the bottom, the surface to 5 cm soil scooped, weighed wet, then dried for 48 hours at 65 °C and finally weighed dry. The moisture content of the field samples was measured, and if needed, deionized water added to bring the sample to 50% WHC. Three soils needed drying and were put into an open plastic bag and then in an incubator set to 1 °C. Soils were dried between 2 and 5 days, and turned twice a day to prevent differential drying. All other soils were placed in the same incubator in closed bags. The duration of drying varied between 2 and 5 days. The soils were then thoroughly remixed and pre-incubated for 5 days at 0 °C to reduce the CO_2 signal associated with sample preparation. The 50% WHC was maintained throughout the incubation by adding water when necessary.

C mineralization

For the C mineralization experiment, 5 temperature treatments (0, 5, 10, 15, and 20°C) were maintained for 188 days. Fifty grams of wet soil were placed in glass mason jars (volume=910 mL for 10, 15, 20°C, volume=455 mL for 0 and 5°C). Each jar had a rubber septum embedded in the jar lid. At the beginning of each measurement period, the jar was held in front of a fan and then capped. Each jar was immediately over-pressurized using a syringe containing 20 mL of ambient air. Then 20 mL of headspace was drawn and analyzed with a LICOR 6262 infrared gas analyzer connected to a pressurized sample loop. The jars were allowed to accumulate CO_2 between 1 and 3 days

before a second sample was drawn. No air was injected before drawing the second sample. The slope of concentration increase with time, the incubation air temperature, jar volume, and air pressure were used in the ideal gas law to calculate flux rate. Air pressure was recorded from the LICOR system. Rates were estimated immediately after putting the jars into temperature controlled incubators, and then at 3, 5, 12, 20, 37, 51, 67, 80, 100, 134 and 188 days later. Between sampling periods, the jars were left opened but covered with a plastic extra cling Saran® wrap, a type of wrap which repels H_2O but allows CO_2 to pass through the membrane. The time between sample field collection and the beginning of the incubation was 23 days.

Net N mineralization

A second experiment was simultaneously prepared for estimating net N mineralization and microbial biomass C (detailed in next section) using the same soils. Forty grams (g) of soil were transferred into 100 mL plastic cups, and 10 cups for each site incubated at 5, 10 or 15 °C. Each cup was covered with the plastic wrap to avoid moisture loss. Five replicate cups were used for an initial mineral N extraction and five for a second mineral N extraction. The first extraction for mineral N occurred 20 days after the start of the incubation and the second extraction at staggered intervals after the first (15°C-80 days, 10°C-92 days, 5°C-108 days). The second extraction was staggered to standardize among the temperature treatments by the amount of CO_2 lost.

Before an extraction, two 10-g soil subsamples were removed from the cup to measure moisture content and microbial biomass (second extraction only). Then 100 mL of 0.5 M K_2SO_4 was combined with the remaining 20 g of soil (5:1 ratio of soil to

K_2SO_4). The slurry was shaken by hand for 20 seconds, and placed in an incubator for 24 hours at 0 °C. When removed from the incubator, the slurry was shaken as before and then extracted with a Falcon filtering system through a glass fiber filter with 1.0 μm pore size (GFA-VWR). The entire extract solution was suctioned through the filter. The C mineralization rate was also measured for these N mineralization samples with essentially the same methodology to the C-mineralization experiment. The concentrations of NH_4^+ and NO_3^- in extracts were estimated colormetrically using a modified dual channel Technicon II Autoanalyzer system. Method details are found in Vance and Chapin (2001).

Microbial biomass

Microbial biomass C (MBC) was determined using the chloroform-fumigation extraction method (Brookes et al. 1985), except that derived MBC values were not increased by a factor relating to "true" microbial biomass because no such factor has been developed for this soil type. The 10-g soil subsample removed from the N-extraction cup was fumigated for 4 hours and then extracted in the same manner as outlined in the previous section. These post-fumigation extracts and extracts from the pre-fumigation were digested (detailed in next paragraph). The microbial C was estimated from the C difference between the two extracts.

Extracts were digested in 100 mL serum vials. Five mL of extract and 5 mL of an oxidizing potassium persulfate digest were combined in each serum vial, which was then immediately sealed with a rubber septum and a crimped aluminum seal (Cabrera and Beare 1993). Vials were then placed in a drying oven set to 85 °C for 24 hours. After

allowing the vials to cool to room temperature, the serum vial headspace was sampled with a syringe and the concentration of CO_2 determined on the LICOR 6262 system. Six phenylalanine standard solutions, ranging from 0 to 300 ppm of solution C, also were digested and the CO_2 concentration in the headspace regressed against the solution C concentration to develop a standard curve. We expected phenylalanine's aromatic structure to make its recalcitrance representative of the organic matter in solution (Brenner et al. submitted). The standard curve was linear with an R^2 equaled 0.99.

Respiration rates were expressed as mg C g soil C^{-1} day^{-1}, and rates increased by the amount of soil C previously mineralized as estimated by multiplying respiration rates by the time between measurement periods (Hobbie et al. 2002). The rate increase with temperature of C and net N mineralization processes was examined using the Q_{10} function:

$$Q_{10}= (k_2/k_1)^{[10/(t2-t1)]} \quad \text{Eq. 1;}$$

Where k_2 and k_1 equal the process rates at temperatures $t_{2(warm)}$ and $t_{1(cool)}$ (Van't Hoff 1898). Q_{10}'s were examined at 5 °C intervals and the "rates" used were estimated from the accumulated CO_2 during the course of the incubation, or in the case of net N mineralization, the interval between the first and second extraction. The net N mineralization rates were expressed as μg N g soil N^{-1} day^{-1}.

Soil analysis

A pre-incubation subsample of dried soil was prepared for pH, total C and N, and PY-GC/MS analysis by grinding in a roller ball mill for 24 hours. For the pH

measurement, deionized water and the ground oven-dried soil were combined at a 20:1 w/w ratio. Total C and N were measured on a LECO CNS analyzer.

PY-GC/MS was used in organic matter quality analysis. Details of the methodology are found in White et al. (2002). Briefly, a subsample of dried soil containing about 200 μg carbon was pyrolyzed in a quartz sample tube. Pyrolysis was performed on a CDS Analytical Pyroprobe 2000/AS2500. The pyrolyzer was connected to an HP 6890 gas chromatograph in tandem with an HP 5973 mass selective detector operated in electron impact mode. Compounds were separated in the gas chromatograph using a Restek Rtx35-MS column (30 m x 0.32 mm x 0.25 μm). Helium was the carrier gas and the flow rate held constant at 2.0 ml/min. Mass spectra were identified using the Wiley 275 library. Clean sample tubes were run every fourth sample to prevent or detect any carry-over (White et al. 2002).

An index of 30 compounds were identified from each chromatogram and grouped into 9 classes based on the probable origin of each compound (Bracewell et al. 1989, White et al. 2002) (Table 2). The compound designation represents the relative abundance of a class of compounds in the index but not the total amount of the class in the organic matter. The chromatographic areas of all 30 index compounds in each chromatogram were summed to find the total index area for that chromatogram, and each class was then divided by the total index area to develop a proportional estimate. Some post-incubation samples were also analyzed, eleven from the 5 °C and six from the 20 °C incubation. A full sampling of all temperature treatments was not possible due to limited access to the gas chromatograph-mass spectrometer.

Statistical Analysis

All statistical analyses were performed with SAS statistical software v. 9.0. One-way ANOVA was used to compare the C and N mineralization amounts and microbial biomass among sites and between temperatures, and means were compared using the Least Significant Difference (LSD) method. A two-way ANOVA was used to examine site and temperature interactions. Normality of data was tested with the Shapiro-Wilk's statistic (α=0.05). Both net N mineralization and the C:N mineralization ratio needed to be log-transformed, and means reported are untransformed and weighted. Pearson's correlation coefficients were examined to test hypotheses regarding the interaction between initial PY-GC/MS chemical compounds, the mineralization process rates, and microbial biomass and tunover. Process rates and microbial dynamics also were examined in correlation to one another and, in this case, a Bonferroni correction was applied to the p-value of correlations to avoid Type I errors since no *a-priori* hypotheses were formulated for these relationships. In subsequent statistical analyses only the four classes of compounds (primary and secondary polysaccharides, lignin, and phenols) were significantly related to microbial processes. Therefore, only these relationships are reported. The change over the course of the incubation of organic compounds was examined relative to microbial processes using correlation analysis. Stepwise multiple regression analysis was also performed but results are not reported because the procedure consistently selected the variable with the highest correlation coefficient but did not combine variables in novel ways. Time-series repeated measures analysis of respiration rates did not reveal significant differences that were not observed by comparing the

estimated total amount of C lost, which is likely due to their being no consistent trend in respiration rates with time across sites.

RESULTS

Site comparisons

For traditional indices of organic matter quality, few site differences in soil characteristics were evident. The organic matter from each site was similar in C and N concentration, C:N ratio, and water holding capacity, but the pH of the high-np soil was slightly lower than for the other two sites (Table 1). The pyrolysis analysis did indicate some site differences in organic matter quality. As predicted, the site (high-np) with the slowest *in-situ* decomposition had a higher relative proportion of polysaccharides, which were greater than either mid-dp ($p=0.064$) or low-sp ($p=0.081$), but other compound groups did not differ significantly among sites (Table 3).

Site differences in respiration rate were few for all temperature, but temperature affected the temporal dynamics of respiration rate and the amount of C lost. The maximum respiration rate rarely occurred at the beginning of the experiment, and for most temperatures, the respiration rate did not decrease predictably with time or C loss (Fig. 1). The exceptions were the 15 and 20 °C incubations for low-sp, and the 0 °C respiration rates for high-np. In these cases, respiration decreased steadily as C content declined (Fig. 1). The estimated total C lost increased significantly with temperature for all sites ($p=0.03$ to $p<0.001$), but the only site difference in cumulative C loss was at 0 °C where low-sp lost more C than the other two sites (Fig. 2).

The temperature sensitivity of respiration (Q_{10}) varied among sites for low incubation temperatures and Q_{10} generally decreased with increasing temperature. We predicted the site with the slowest *in-situ* decomposition (high-np) would have the greatest temperature sensitivity, but this prediction only held for the lowest temperature interval (Fig. 3). Q_{10} at the two coldest temperature intervals (5/0 and 10/5) was significantly higher than the Q_{10} based on either of the warmest temperatures (15/10 and 20/15) for all sites.

Both temperature and site influenced the rate of net N mineralization. The net N mineralization was greater for mid-dp than low-sp at both 10 and 15 °C, but no significant differences were observed among sites at 5 °C (Fig. 4a). A two-way ANOVA for all sites indicated both temperature ($F_{2,15}$ =4.82, p=0.02) and site ($F_{2,15}$=4.82, p=0.02) significantly influenced net N mineralization, but the interaction term was not significant. However, for individual sites, net mineralization only increased significantly with temperature for the mid-dp site. Net nitrification did not occur at any temperature.

Organic matter chemistry or shifting microbial function were expected to differentially affect the ratio of C mineralization to net N mineralization (Cmin:Nmin) with changing temperature and organic matter chemistry, however, the ratio did not vary with temperature and site differences were difficult to explain based on soil characteristics. We predicted the site with the most polysaccharides (high-np) would have the greatest Cmin:Nmin ratio because of microbial immobilization of N, however, the Cmin:Nmin ratio was only greater for low-sp than mid-dp at 10 and 15 °C (Fig. 4b). Microbial function was expected to vary with temperature, but for all sites, the

Cmin:Nmin ratio was similar among temperatures. The Q_{10} of net N mineralization between temperature intervals also did not vary with temperature (Fig. 5). Thus, there does not appear to be a differential influence of temperature on net N mineralization. However in all of these comparisons, the extreme variability of net N mineralization may have obscured relationships.

Microbial dynamics were more sensitive to temperature than to site soil characteristics. Microbial biomass (MBC) did not differ among sites for a given temperature (Table 4), but the amount of MBC was significantly less at 15 than 5 °C at all sites. This temperature difference was significant even when microbial mass was expressed on a per-gram soil C basis that had the estimated amount of C previously lost from the soil removed. At all sites, microbial turnover time (MBC/respiration rate) decreased significantly with warming from 5 to 15 °C.

Correlations among soil characteristics, mineralization rates and microbial biomass

The compounds within either a labile (e.g. polysaccharides) or recalcitrant (e.g. lignin) group were positively correlated to one another (i.e. lignin vs. phenols), and between groups compounds were negatively correlated (i.e. primary polysaccharides vs. phenols). We also examined whether pyrolysis compound correlated with other soil characteristics and how soil characteristics covaried with one another. Primary polysaccharides were negatively correlated to pH ($p=0.07$), and lignin was weakly negatively correlated to N concentration ($p=0.08$, $n=13$), and (Table 5). Water holding-capacity (WHC) was the soil characteristic most strongly correlated to pyrolysis groups.

The labile group was negatively correlated, and the resistant group positively correlated to WHC ($p<0.01$).

Microbial respiration and biomass were generally significantly correlated with pyrolysis compounds (Table 6). Contrary to our prediction, however, the presumed labile primary and secondary polysaccharides were negatively correlated to microbial respiration at most temperatures. Lignin and phenols were expected to be resistant to microbial breakdown but were positively correlated to respiration. Of the two, phenols were more strongly positively correlated with respiration than lignin at all temperatures. Microbial biomass and microbial turnover time (MTT) were positively correlated to the polysaccharides and both microbial indices were negatively correlated to lignin and phenols (Table 6). The Q_{10} of respiration for any given temperature interval did not correlate with pyrolysis products.

Indices of microbial function (i.e. mineralization rates, temperature sensitivity) and microbial biomass were only marginally linked in correlations analysis. The mineralization rates and index of microbial function generally were not correlated to one another unless they shared variables (Table 7). The only marginally significant correlation between independent variables was at 15 °C, where net N mineralization was negatively correlated to MTT ($r=-0.61$, $p=0.09$).

Changes in the proportions of compounds in the pyrolysis index during incubations indicate relative rates of consumption, production, or preservation. The most significant change at both 5 and 20°C was the net decrease of primary polysaccharides within the index (Table 8). However, the temperature treatment did not result in a greater

net decrease in polysaccharides. The correlation between the relative changes in compounds may indicate whether the preferential consumption of one corresponds to a net preservation or production of another compound (Dai 2001). Significant correlations were found at 5°C between the change in polysaccharides and an increasing proportion of phenols (n=11, p=0.002) and polypeptides (n=11, p=0.02) (Fig. 6). The mean absolute peak area decreased for the polypeptides but increased for phenols, suggesting there was a net production of phenols. The polypeptides may have decreased over the incubation but at a slower rate than the polysaccharides. The change in polysaccharides at 20°C did not significantly correlate with the change in another compound.

The change in the pyrolysis index over the course of the incubation at 5°C was not correlated to most microbial processes. Only when one sample was rejected as an outlier was net N mineralization (r=0.82, p=0.003) correlated to the decrease in primary polysaccharides (Fig. 7). Although the initial concentrations of pyrolysis compounds described microbial processes, the change in the pyrolysis index was a poor indicator of most microbial functions during the course of the incubation. Also, the pyrolysis makeup at the end of the experiment for the 5°C and 20°C did not correlate with processes during the course of the incubation (not shown).

DISCUSSION

C mineralization

The high capacity for C loss that we observed is a definitive characteristic of black spruce organic horizons in particular (Sparrow and Cochran 1988; Vance and

Chapin 2001; Dioumaeva et al. 2002; Neff and Hooper 2002) and high latitude organic soils in general (Nadelhoffer et al. 1991; Niklinska et al. 1999; Hobbie et al. 2002; Weintraub and Schimel 2003). For the black spruce organic soils in this study and others (Sparrow and Cochran 1998; Dioumaeva et al. 2002; Neff and Hooper 2002) it is also apparent that soil C mineralization rates can persist largely independent of C loss for most temperatures (Fig. 1). However, the respiration rate of the fastest decomposition site (low-sp) did decrease slightly over the course of the experiment at the two warmest temperatures. Niklinska et al. (1999) also found respiration decreased predictably for organic soils collected from southern forests at warmer incubation temperatures but for northern forests, respiration persisted without a noticeable decrease. A larger gradient in temperature or decomposition environment may be necessary to fully develop the influence of these site factors on mineralization potential for black spruce forests.

Based on the parameters of first order kinetic models fit to respiration trends with time, McDonald et al. (1995) proposed that the available pool size for microbial decomposition increases with warmer temperatures. The implication of this finding is that warming increases the total potential C loss from a soil, not simply the respiration rate. We could not address this hypothesis with the kinetic models of McDonald et al. (1995) because respiration rate did not express a definitive time-trend. Instead we examined the respiration rate trends as a function of estimated C loss. Using this approach, we hypothesized that if the C available was larger at the warmer temperature, the respiration rate would begin to decrease after more C had been lost from the soil in warmer than cooler incubations. For two of the sites (mid-dp, low-sp) respiration rate for

the 10°C incubation did not change appreciably past the C loss point of initial C where the 15 and 20°C incubations began to decrease (~4.5 to 6%)(Fig. 1). This did not indicate the available pool size increased at the two warmer temperatures. The contrary findings of McDonald et al. (1995) may be specific to mineral soils, or a longer incubation of an organic soil horizon may be necessary to address this hypothesis.

We hypothesized that microbial respiration would be more temperature sensitive at the colder site. Our hypothesis was supported by the Q_{10}'s at the lowest temperature interval (5/0), or the temperature range most relevant to growing season soil temperatures, but for no other. Kirschbaum's (1995) literature review indicated microbial respiration was increasingly temperature sensitive with decreasing average temperatures. As a result, he proposed high-latitude ecosystems might lose more soil carbon with warming temperatures than other ecosystems. However the absolute rates from various studies were not reported (Kirschbaum 1995) and we found that the site with faster *in-situ* decomposition lost more C at colder temperatures than the site with depressed *in-situ* decomposition. Thus in our study the temperature sensitivity difference (slower decomposition site Q_{10} >faster decomposition site Q_{10}) was primarily a function of lower respiration at colder temperatures at the slow-decomposition site (Fig. 2 and 3). This agrees with the work of Niklinska et al. (1999) who found generally lower respiration at 5 °C for incubated soils from more northerly, colder sites than southern, warmer forests.

Contrary to our prediction, the Q_{10}'s of C and net N mineralization were not related to the relative abundance of primary polysaccharides, or to any other soil

characteristic. Our results also suggest there is no relationship between mineralization temperature sensitivity and the substrate consumed. However, the Q_{10} index may not adequately capture microbial growth, respiration and thus temperature sensitivity (Ellert and Bettany 1992, MacDonald et al. 1995). There are also difficulties in estimating the parameter. The depletion of available C proceeds at a different time-step for each temperature treatment. Thus, calculating Q_{10}'s based on instantaneous rates is extremely sensitive to the changing pool size and possibly microbial response to initial sample preparation (Niklinska et al. 1999). To address the first difficulty, we attempted to match respiration rates in time (i.e. 1 week after start of incubation) and percent C lost (i.e. after 2% loss) but still found no relationships between Q_{10} and soil characteristics. The only significant relationships with Q_{10} were microbial biomass C at 15°C and respiration rate at 10 °C, indicating microbial function are better predictors of temperature sensitivity. Linking soil organic matter characteristics to the temperature sensitivity of mineralization processes may require a more detailed understanding of microbial dynamics than that provided by measuring respiratory CO_2 or mineralized N (Ellert and Bettany 1992, Nicolardot et al. 1994, MacDonald et al. 1995).

Pyrolysis compounds and microbial processes

The role of organic matter chemistry in influencing microbial processes was difficult to discern at the site level, and correlations between processes and individual samples provided results contrary to our original hypotheses. We hypothesized the proportion of polysaccharides would be positively correlated to microbial respiration, similar to the results of White et al. (2000, 2003). Instead, we found the opposite to be

true at most temperatures. Alternatively, microbial biomass and the microbial turnover time were positively related to the proportion of polysaccharides. One possible implication of our observations is that the microbial processing of a substrate is not necessarily reflected in CO_2 production. Studies where ^{14}C-labeled substrates are added to soils suggest that the proportion of substrate released as CO_2 vs. converted to microbial biomass or secondary microbial product is dependent on temperature (Nicolardot et al. 1994) and substrate chemistry (Sugai and Schimel 1996). The nutrients available to microbes may also determine whether microbes process available C to CO_2. Vance and Chapin (2001) found that in black spruce soils, the amount of added cellobiose and cellulose converted to CO_2 increased with the amount of added N. We note again that White et al. (2002, 2003) found a positive relationship between the same primary polysaccharide index we used and microbial respiration. Perhaps the reason for their result is that by adjusting nutrients, temperature, moisture, and pH to an optimal level, they selected for a microbial community that preferentially converted the polysaccharides to CO_2 in a relatively short time-frame, or created conditions favoring the conversion of polysaccharides to CO_2.

Microbial biomass was a relatively small fraction of soil C and it is unlikely polysaccharides consumed during the incubation could be solely retained in this pool. Rather, the production of phenols during decomposition may represent the fate of consumed polysaccharides (Fig. 6). In the incubations of arctic soils published in White et al (2002), the index changes were much more dramatic with primary polysaccharides decreasing nearly 70% as a percent of index, and phenolics increasing by nearly 70%.

However, since lignin also produces methylphenol when pyrolyzed, the increase in the relative abundance of phenolics cannot be strictly tied to microbial metabolism. Some amino acids also produce phenols when pyrolyzed (Chefetz et al. 2002). The increase in the phenolic index may represent the change in multiple compounds.

We unexpectedly found that water holding capacity (WHC) was positively correlated to microbial biomass and turnover time, but negatively to microbial respiration (not shown). Soil WHC was also strongly correlated with the classes of pyrolysis compounds (Table 5). We found no relationship between soil water content and microbial respiration. Thus WHC in of itself may be an important influence on microbial dynamics or one that integrates multiple factors influencing microbial processes. The possible influence of WHC on microbial processes requires further research.

Net N mineralization

Net N mineralization generally increases with the decrease in available C and microbial immobilization of N; thus, we predicted primary polysaccharides would be negatively correlated to net N mineralization. The initial proportion of polysaccharides was negatively correlated to N mineralization at 15°C (Table 6), however, at 5 and 10°C the initial polysaccharides and net N mineralization were not correlated. The relationship's temperature dependence may reflect that N mineralization depends more on the decomposition of available C rather than initial C quality (Schimel and Weintraub 2003). This appears to be the case for the 5°C incubation, where the relative decrease in polysaccharides over the duration of the incubation was positively correlated to net N mineralization (Fig 7.). We also expected that if C processing and N mineralization are

correlated, cumulative C mineralization should explain variability in net N mineralization for a given temperature. However, only when all temperatures were included in the analysis was the relationship between C and N mineralization significant. The lack of a significant relationship within a temperature may reflect the order of magnitude difference in the two rates, the lack of sensitivity of the measurements, or again, that microbial processing of organic matter is not solely expressed in CO_2 loss.

Organic matter chemistry after the incubation

The proportional decrease in primary polysaccharides was not directly related to the amount of C lost at both 5 and 20°C. The reason for this result could vary for the two temperatures (the only two analyzed for pyrolysis products both before and after the incubation). As discussed earlier, for the 5 °C incubation the production of phenols may be a significant end-product of processed polysaccharides. For the 20°C, the lack of a correlation between the decreasing polysaccharides and increase in other compounds may reflect that the polysaccharides were used very early in the incubation and the subsequent respiration was the result of the simultaneous metabolism of multiple organic fractions. Weintraub and Schimel (2002) found for organic soil incubations conducted at 20°C, the proportions of organic matter fractions (cellulose, hemi-cellulose, acid-insoluble lignin) did not change significantly between the beginning and end of a yearlong incubation for most of the arctic soils they studied. They also found the soluble fraction was the best predictor of microbial respiration throughout the study. Whether organic matter fractions change significantly in relation to one another may depend on the incubation temperature or the amount of C lost.

Conceptual model

We organized the various results from this study around a simple conceptual model that relates the transformation of specific organic matter constituents, the production of microbial biomass or CO_2, and the dynamics of N (Fig. 8). We found support for our original hypothesis that polysaccharides are preferentially consumed. Within the timeframe of our study, however, we propose consumption resulted more in the transformation of polysaccharides to another compound class (phenolics) than it did in the production of CO_2. The phenolics may be produced and then consumed again and converted to CO_2, which is reflected by the lower (faster) microbial turnover time in soils having more phenolic compounds. Microbial biomass becomes C limited with a decrease in polysaccharides, leading to net N mineralization. Thus, net N mineralization is dependent on the degree polysaccharides are consumed rather than the initial amount of polysaccharides. Although similar to more traditional concepts of soil C dynamics in that C availability and decomposition are linked, the model diverges from past models in that C availability does not relate to CO_2 production. Also, the increase in N mineralization is dependent on the consumption of specific compounds and not CO_2 production.

Our conceptual model is sensitive to the limitations of the PY-GC/MS method. The most substantial pyrolysis limitation reflects the inability to directly relate the chromatographic peaks in PY-GC/MS to the mass of compounds (Bracewell et al. 1989). Therefore, a complete test of the model we propose will require the inclusion of wet chemistry methods (Dai 2001) or a study-design that combines pyrolysis and C additions of different compounds to soils. Also, the apparent temperature dependence of compound

production and consumption may be a function of temperature or of C loss. These alternatives could be addressed by harvesting and analyzing incubated soil samples during the course of incubations conducted at different temperatures.

CONCLUSIONS

Microbes in black spruce organic soils can sustain C mineralization rates for prolonged periods of time. This result suggests these soils may be more likely than soils from other ecosystems to experience a net loss of soil C with warming (Giardina and Ryan 2001). However unlike estimated C loss, the temperature sensitivity of respiration offers counterintuitive information regarding potential soil C loss. This is because indices of relative temperature sensitivity, such as Q_{10}, are highly sensitive to the CO_2 evolution rates at the lowest temperatures. Also, within the narrow range of organic matter we studied, temperature sensitivity was not linked to an organic matter characteristic. With these considerations in mind, we urge caution in interpreting Q_{10} values in the context of soil C loss potential with warming temperatures.

Organic matter characteristics modified the influence of temperature on mineralization processes and in a consistent manner across temperatures. Thus, there does not appear to be a differential effect of organic matter chemistry on microbial processes with changes in temperature. Although our study suggests that long-term inhibited *in-situ* decomposition could result in organic matter chemistry differences, the resulting differences among sites had little effect on C mineralization potential and net N mineralization within the timeframe of our study. A larger gradient of *in-situ* environment or decomposition may be required for understanding their effects on

potential mineralization processes. Finally, our results for the change in compounds at 5°C and 20°C highlight that decomposition is not simply the transformation of organic matter to CO_2, but rather a multi-step transformation process.

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Table 2-1. *In-situ* temperature and decomposition, and the soil characteristics of organic matter incubated in this study. Different letters represent significant ($p<0.05$) between site differences. Least significant difference (LSD) used for comparisons.

site	SDD[1]	Mass loss (%)[2]	%C	%N	C:N	pH	WHC[3]
high-np	929	13a	41	0.80	51	4.2 ± 0.15a	535 ± 102
mid-dp	979	23b	41	0.94	44	4.5 ± 0.12b	512 ± 56
low-sp	988	20b	38	0.82	46	4.5 ± 0.16b	524 ± 55

[1]summed daily maximum temperature > 0 °C based on one temperature logger placed at 10 cm soil depth during 2000 and 2001 (Chapter 1).

[2]One-year decomposition of filter paper placed between 7.5 and 15.0 cm depth (Chapter 1)

[3]water holding capacity, g H_2O/g dry soil

Table 2-2. Grouping of organic molecules identified with pyrolysis gas chromatography (White et al. 2002).

Category	Specific molecules identified
primary polysaccharides	furfural; hydroxyfuran; methyl hydantion; 1,4:3,6-dianhydro-α-d-glucopyranose
secondary polysaccharides	methylfurfural; 2-propyl furan
polypeptides	indole; pyridine
lignin	2-methoxyphenol; 4-ethyl-2-methoxy phenol; 4-vinyl-2-methoxy phenol
phenols	phenol; 2-methyl phenol; 4-methyl phenol; dimethyl phenol
lipids	1-tridecene; 1-pentadecene;1-hexadecene; 1-heptadecene; 1-octadecene
alkanes & napthalene	decane; un-, do-, tri-, penta-, hexadecane; napthalene
cyclopentones	methylcyclopentenone; dimethylcyclopentenone

Table 2-3. Percent of index area for chemical compounds found in incubated soils (mean±standard error).

	polysaccharides			
Site	primary	secondary	lignin	phenols
high-np (n=4)	50.6 ± 2.4*	11.0 ± 0.7	12.6 ± 1.8	16.0 ± 1.0
mid-dp (n=5)	46.3 ± 0.7	11.3 ± 0.6	13.0 ± 1.0	17.4 ± 0.5
low-sp (n=4)	45.9 ± 1.2	9.9 ± 0.3	14.7 ± 1	18.4 ± 0.5

*high-np>mid-dp, p=0.064, one-way ANOVA, LSD

*high-np>low-sp, p=0.081

Table 2-4. Microbial biomass[1] and turnover time[2] for the three sites and temperatures (mean±standard error). Different letter represent between temperatures differences for a site ($p<0.05$). No significant differences among sites for a temperature were found.

Site	Temperature	Microbial C[1] (mg FE-C/g soil C)	Microbial Turnover time[2] (days)
high-np	5	10.2 ± 1.00 a	34.4 ± 6.1 a
	10	8.5 ± 1.37 ab	21.2 ± 7.0 ab
	15	6.5 ± 1.05 b	9.3 ± 2.5 b
mid-dp	5	10.3 ± 0.33 a	33.7 ± 2.2 a
	10	9.5 ± 0.51 a	16.4 ± 0.6 b
	15	7.2 ± 0.44 b	8.7 ± 0.8 c
low-sp	5	9.1 ± 0.67 a	29.1 ± 3.8 a
	10	9.3 ± 0.84 a	14.8 ± 1.4 b
	15	6.8 ± 0.39 b	7.6 ± 0.8 c

[1,2] Definitions of terms found in Table 6, or methods

Table 2-5. Pearson's correlation coefficients between pyrolysis products and soil attributes are shown if significant.

Soil	polysaccharides		lignin	phenols
Attribute	primary	secondary		
%C	--	--	--	--
%N	--	--	-0.49*	--
C:N	--	--	--	--
pH	-0.51*	--	--	0.67***
WHC[1]	0.79***	0.63**	-0.68***	-0.79***

*p<0.10, **p<0.05, ***p<0.01

[1]water holding capacity

Table 2-6. Pearson correlation coefficients between microbial processes and pyrolysis compounds. Levels of signifigance denoted by * ($p<0.1$), **($p<0.05$), and ***($p<0.01$).

Temperature	Process	polysaccharides primary	polysaccharides secondary	lignin	phenols
0	Respiration[1]	-0.61 **	-0.64 **	0.62 **	0.64
5	Respiration	-0.77 **	-0.64 **	0.69 **	0.82 **
	Microbial C[2]	--	--	-0.53 *	--
	Turnover[3]	0.82 ***	0.70 **	-0.76 ***	-0.80 **
	Cmin:Nmin[4]	--	--	--	--
	Nmin[5]	--	--	--	--
	Q_{10}[6]	--	--	--	--
10	Respiration	--	--	--	--
	Microbial C	0.80 ***	0.66 **	-0.86 ***	-0.74 **
	Turnover	0.76 **	0.62 **	-0.61 **	-0.75 **
	Cmin:Nmin	--	--	--	--
	Nmin	--	--	--	--
	Q_{10}	--	--	--	--
15	Respiration	-0.63 **	-0.58 **	--	0.59 **
	Microbial C	0.50 *	0.52 *	-0.68 **	--
	Turnover	0.80 ***	0.72 **	-0.71 **	0.70 **
	Cmin:Nmin	--	--	--	--
	Nmin	-0.55 *	--	--	--
	Q_{10}	--	--	--	--
20	Respiration	-0.64 **	-0.51 *	0.62 **	0.65 **
	Q_{10}	--	--	--	--

[1] average respiration rate for the duration of experiment

[2] Chloroform fumigation extraction microbial C (CFE), not true biomass (s methods for details)

[3] turnover time of microbial biomass (CFE/respiration rate)

[4] ratio of cumulative C respired to N mineralized

[5] Net N mineralization

[6] The Q_{10} was developed from the respiration at this temperature and the next lowest

Table 2-7. Pearson correlation coefficients between microbial processes. Level of signifigance denoted by * ($p<0.1$) and **($p<0.05$). A Bonferroni correction is applied to the p-values of these relationships.

Temperature	Process[1]	C_{min}:N_{min}	N_{min}	Resp	Microbial C	Turnover
5	C_{min}:N_{min}					
	N_{min}	-0.92 **				
	Resp	- -	- -			
	Microbial C	- -	- -	- -		
	Turnover	- -	- -	-0.83 **	0.75 **	
	Q_{10}	- -	- -	- -	- -	- -
10	C_{min}:N_{min}					
	N_{min}	-0.89 **				
	Resp	- -	- -			
	Microbial C	- -	- -	- -		
	Turnover	- -	- -	-0.85 **	0.81 **	
	Q_{10}	- -	- -	0.84 **	- -	-0.60 *
15	C_{min}:N_{min}					
	N_{min}	-0.93 **				
	Resp	- -	- -			
	Microbial C	- -	- -	- -		
	Turnover	- -	-0.61 *	-0.83 **	0.64 *	
	Q_{10}	- -	- -	- -	0.61 *	- -

[1]see Table 6 for definitions of processes

Table 2-8. Mean (±standard deviation) proportional change (%) in compounds after a 188 day incubation at 5 °C (n=11) and 20 °C (n=6).

	polysaccharides							
Temperature	primary	secondary	polypeptides	lignin	phenols	lipids	alkanes	cyclopentones
5	-5.77 ± 0.91	-0.15 ± 0.46	0.77 ± 0.23	1.91 ± 0.51	2.43 ± 0.80	0.46 ± 0.20	0.22 ± 0.25	0.13 ± 0.15
20	-7.94 ± 1.03	-0.61 ± 0.36	0.81 ± 0.24	1.26 ± 0.45	4.07 ± 0.63	-0.12 ± 0.23	0.30 ± 0.23	0.06 ± 0.16

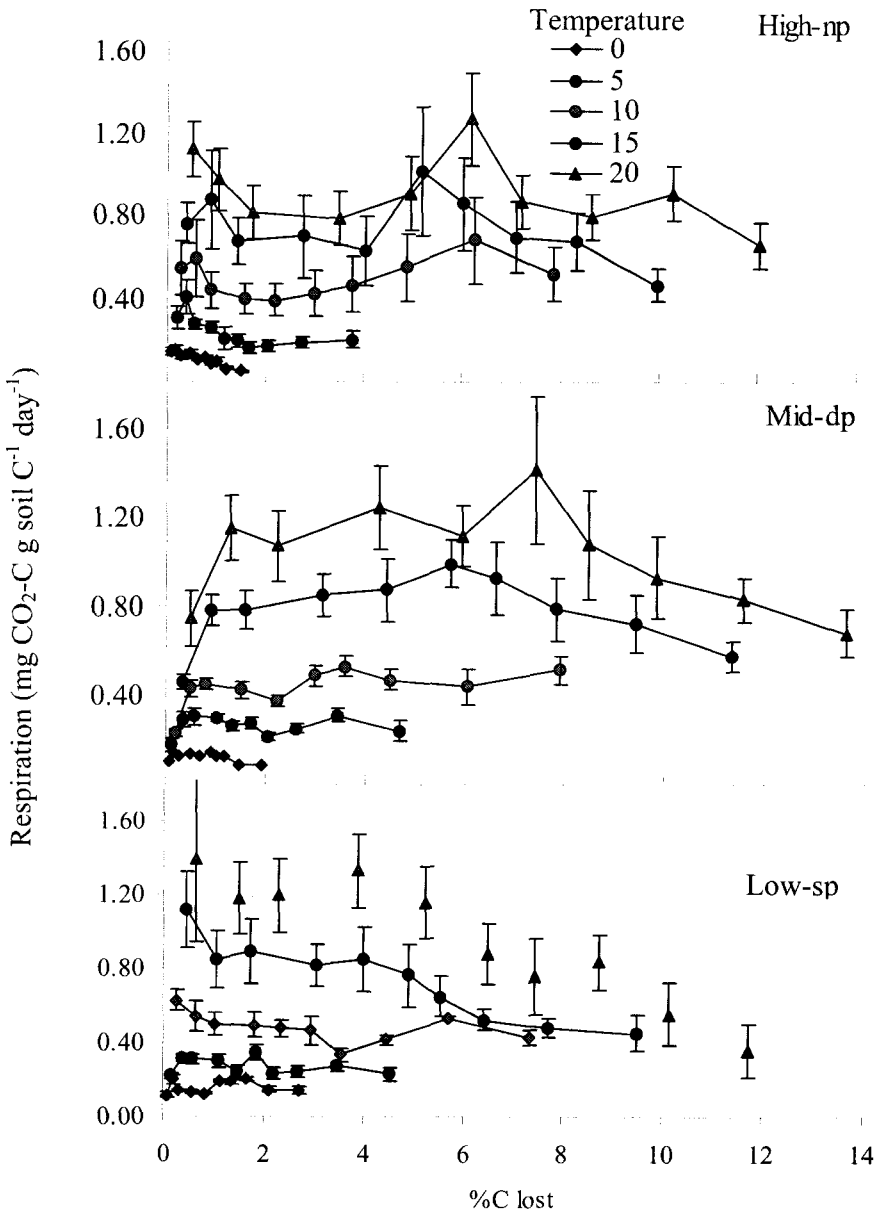

Figure 2- 1. Respiration (mg CO_2-C g soil C^{-1} day^{-1}) (mean of 5 samples±stderr) expressed as a function of the estimated C lost for the three sites and five temperature treatments. Percent C loss was estimated from the respiration rates

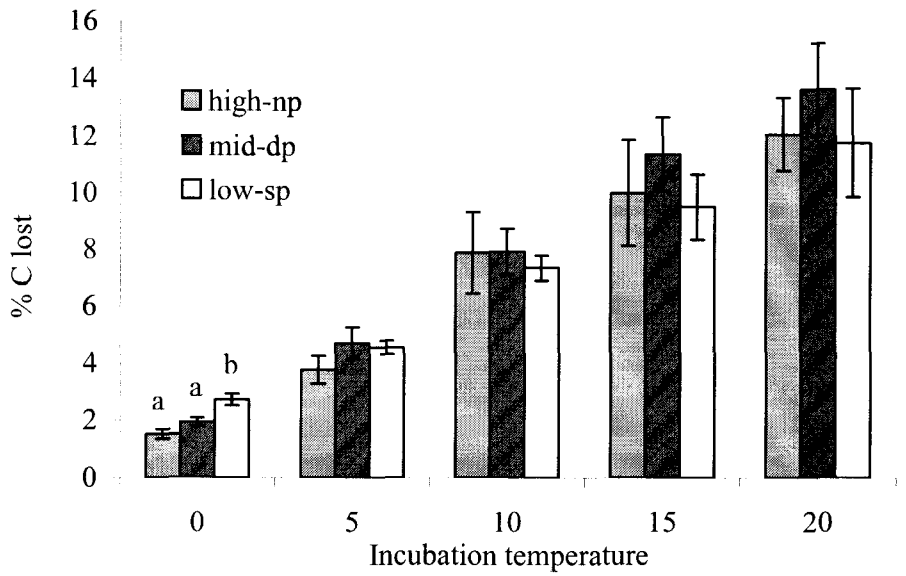

Figure 2- 2. The percentage of initial total C estimated to have been lost from each temperature treatment and site over the course of 188 days. Different letters represent differences among sites for a temperature treatment, the increase between 5 °C temperature intervals was significant for each site. One-way ANOVA and least squares difference used for all comparisons.

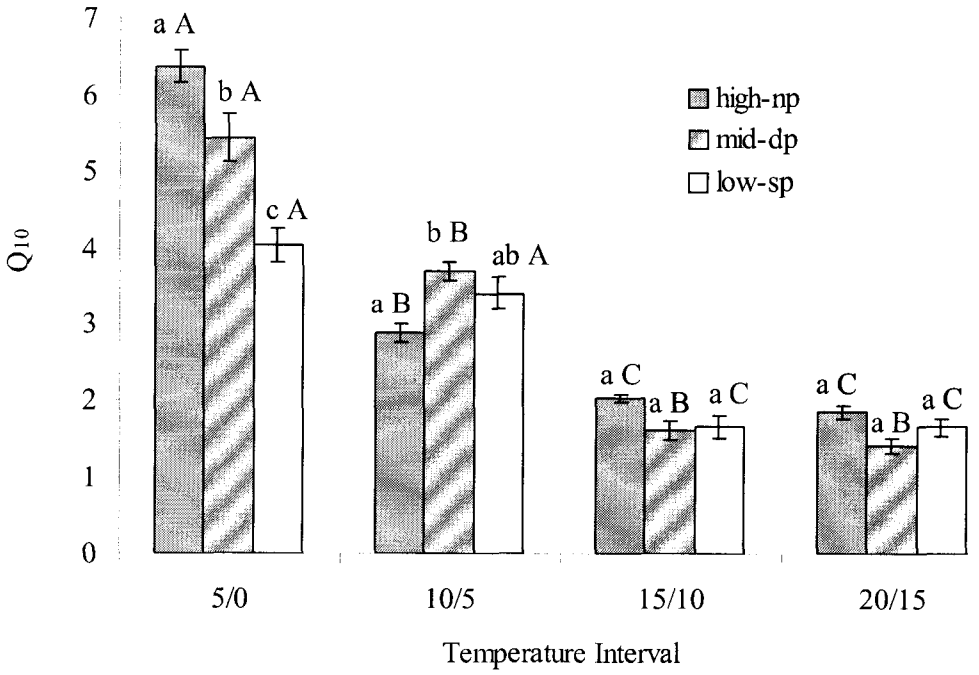

Figure 2- 3. Change in respiration Q_{10} with temperature interval. Calculated from the total mass loss during the incubation. Mean (±standard error) of 5 incubated soils per site. Different letters represent significant differences among sites ($p<0.05$) within a temperature interval (lower case) and between temperatures for a given site (upper case).

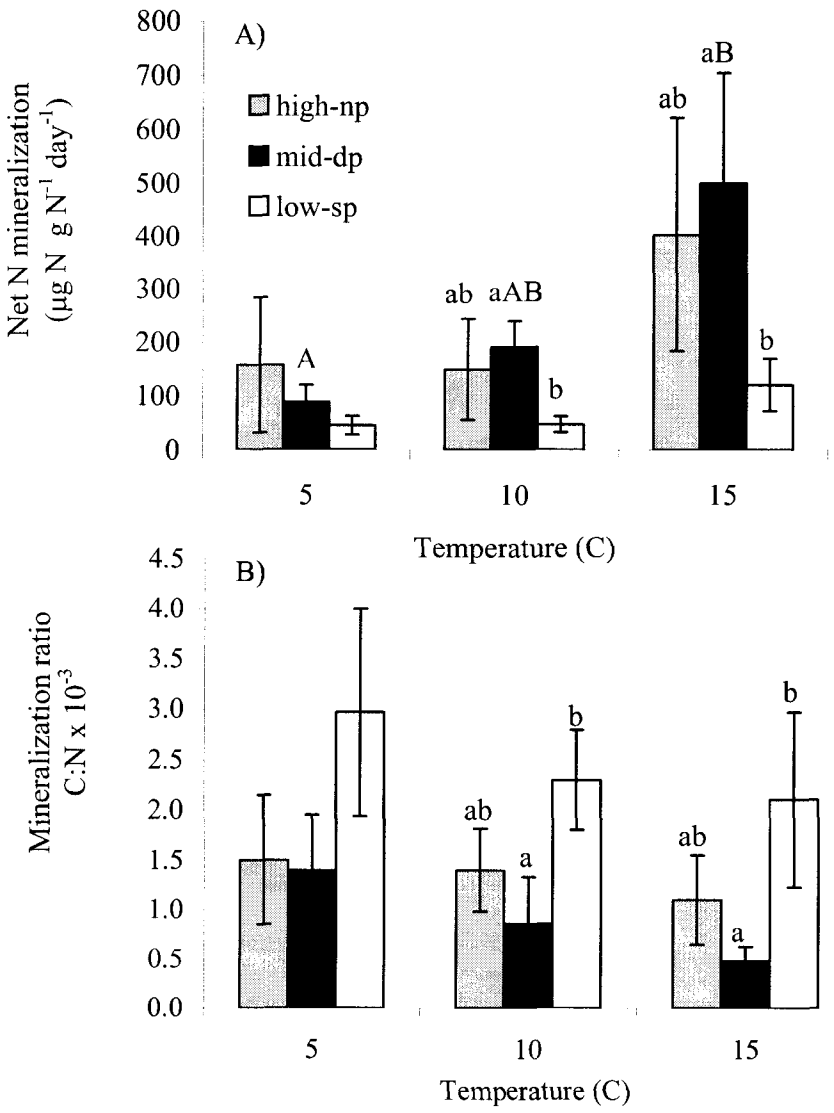

Figure 2- 4. Net N mineralization (A) and the ratio of C:N mineralized (B) for three temperatures. Different lower case letters represent significant differences between sites ($p<0.05$) for a temperature, upper case letters represent between temperature differences for a site. A two-way ANOVA indicated both site and temperature were significant.

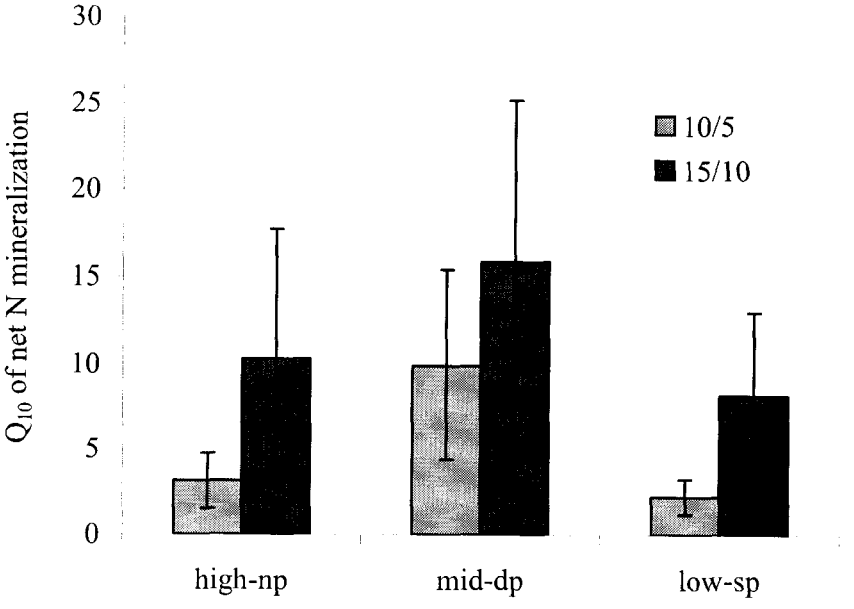

Figure 2- 5. The temperature sensitivity of net N mineralization for each site and two temperature intervals. No significant differences were observed between sites or temperatures treatments.

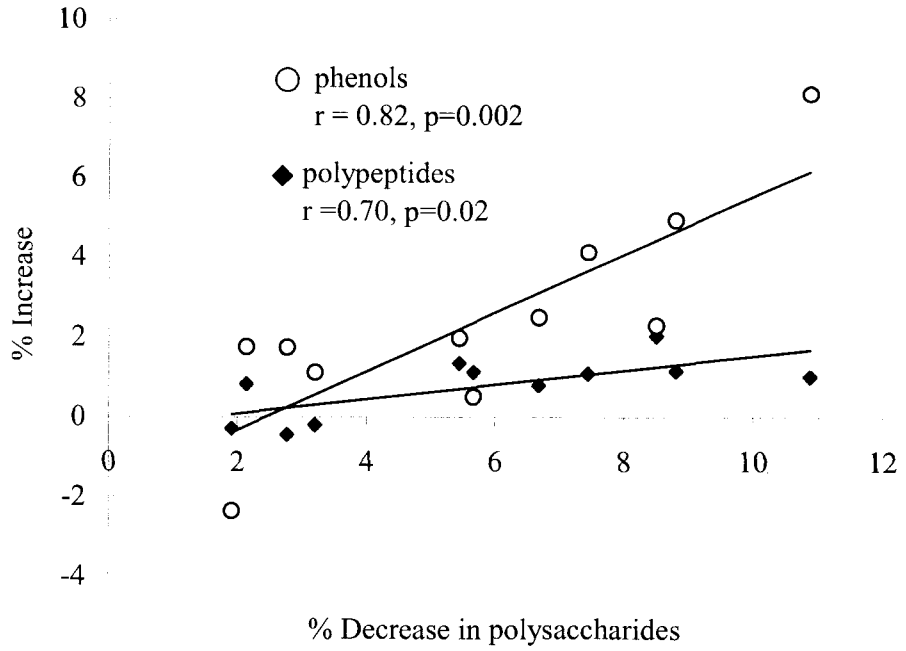

Figure 2- 6. The proportion of phenols and polypeptides increased as a function of the decrease in primary polysaccharides for the 5°C incubation.

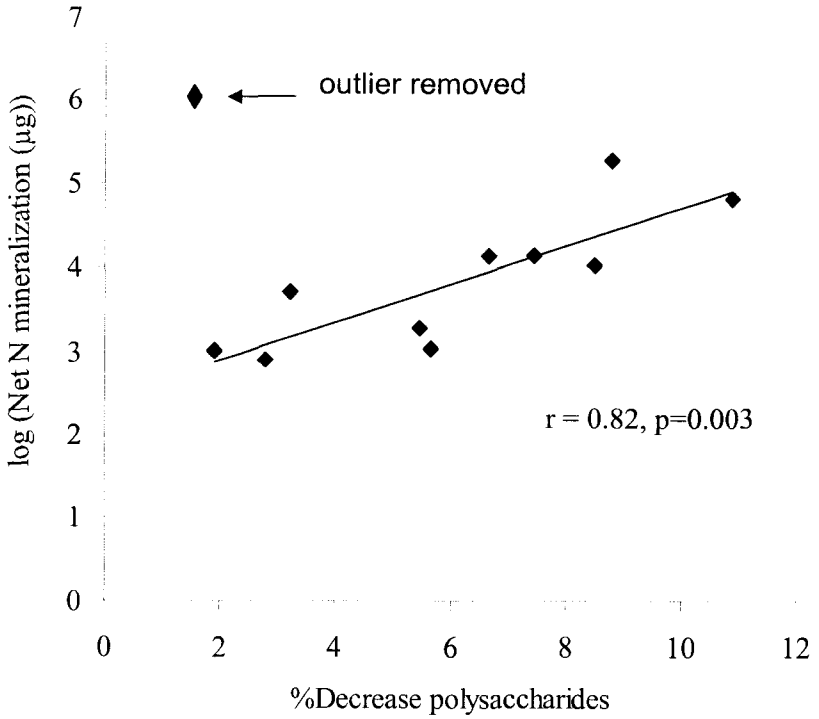

Figure 2- 7. The relationship between the decrease in primary polysaccharides and net N mineralization for the 5°C incubation.

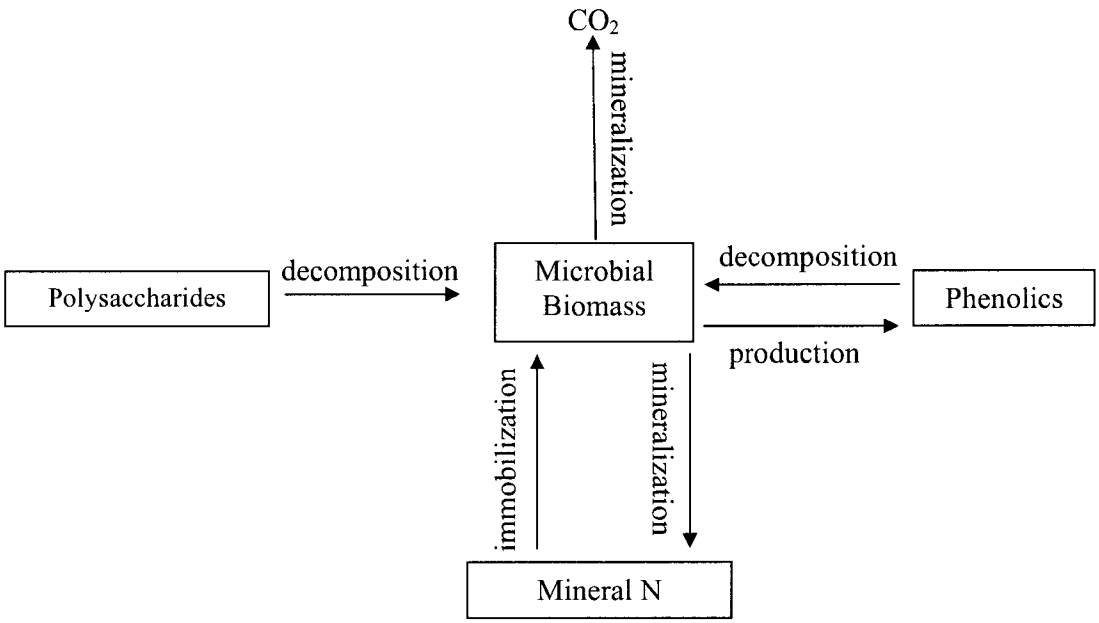

Figure 2- 8. Conceptual diagram of the relationship between polysaccharides, microbial biomass, phenolics and mineral N. Results suggest polysaccharides are consumed and converted to phenolics, which are then mineralized. The decomposition of polysaccharides results in increased net N mineralization.

CHAPTER 3. Roots determine the forest floor carbon balance of black spruce ecosystems

ABSTRACT

We examined the root contribution to forest floor carbon (C) balance in three mature black spruce forests using three complimentary techniques. For one technique, we estimated net root increment (NRI) from the change in forest floor C inside trenched plots after three years of root exclusion. The NRI estimate is equivalent to root production, plus root senescence, minus C lost through root decomposition. NRI estimates ranged between 216 to 583 g C m^{-2} y^{-1} and were sensitive to assumptions regarding root decomposition. In an alternative approach, we used the root pool's bomb ^{14}C age to estimate root increment at two of the sites. The combined live and dead root pool increment estimated with ^{14}C was much lower (121 and 130 g C m^{-2} y^{-1}) than the trenched plot NRI estimates. The trenched plot estimates may include senescent root contributions to forest floor organic matter or indicate that the dissolved organic flux from severed roots is substantial. Finally, a forest floor turnover time of 29-34 years was estimated from heterotrophic respiration and forest C in the control areas. This turnover time is much less for this forest type than has been previously estimated based on aboveground litter. These results suggest root processes are an important contribution to heterotrophic respiration and that the black spruce forest floor is more dynamic than has been previously estimated.

Prepared for submission to Canadian Journal of Forest Research

INTRODUCTION

The belowground carbon (C) allocation of forests remains one of the least understood components of ecosystem C cycling. Fine roots, mycorrhizae, coarse roots, and rhizosphere organisms receive an annual allocation of C that varies in relative proportions and in absolute amounts over the course of a growing season and within a soil profile. The complexity of the soil-root-heterotrophic system makes it difficult to make precise measurements of all belowground components, which then confounds C budget analysis. Most often an estimate of dry matter production or respiratory flux is by necessity made at a small scale and extrapolated to an annual estimate using an environmental or temporal scaling factor. The conclusions of a study are therefore highly dependent on the scaling method used, yet the error terms that reflect each component of the scaling are unknown or unreported. As a result, conclusions regarding belowground C cycling developed in one study are difficult to compare across studies (Kurz and Kimmins 1987, Publicover and Vogt 1993, Vogt et al. 1998).

In this study, we used root exclusion areas or trenched plots and a mass balance approach to estimate belowground C allocation in black spruce forests. After the insertion of root impenetrable barriers, trenched plots exclude new root growth. With time, the control and trenched plot area will differ in soil C because of root growth in the control area and C loss from the trenched plots. If C loss from the trenched plots is measured, then new root growth, the conservation of senesced roots, minus the decomposition of senesced roots can be calculated for the controls areas. The strength of the technique is that mass change is integrated over multiple years, it takes into account all components of

plant and mycorrhizae growth, and the resulting control and trenched plot errors of measurement can be calculated. One weakness is that unless individual components of the root and soil system are identified at the outset and end of experiment, the net increment of any one component cannot be identified. When researchers do identify specific belowground components, the trenched plot method can be used in conjunction with compartment flow models to estimate production, mortality and root decomposition (Santantonio and Grace 1987).

Yanai et al. (2003) reviewed the literature and determined that for most studies, a change in forest floor C of at least 20% is necessary to detect significant change with a reasonable number of samples. Aspects of black spruce growth may make this change attainable in a relatively short amount of time with root exclusion. For example, mature spruce roots are found almost entirely in the forest floor (Tryon and Chapin 1983) and the species allocates between 41-63% of annual production to root growth (Steele et al. 1997; Ruess et al. (in review)).

The objectives of this study are to measure the importance of root inputs to forest floor C balance using multiple complimentary techniques. Because of the high degree of belowground C allocation in these forests, we hypothesized that forest floor C balance would be extremely sensitive to root exclusion. From the difference in forest floor C, we estimated net root increment and used a mass balance model to account for other components of the soil C cycle that may have influenced results. We also estimated root increment from the ^{14}C content of the fine root pools. The forest floor turnover time was also examined to determine the root inputs necessary to maintain heterotrophic flux.

METHODS

Site selection

We selected three sites that differed in elevation and the depth from the soil surface to underlying permafrost. Sites were designated high elevation no permafrost (high-np), mid-elevation deep permafrost (mid-dp), and low elevation shallow permafrost (low-sp). The mid-dp site is a younger stand (75 vs. 110 years for high-np and 120 for low-sp) with slightly lower overstory biomass (3.9 kg C m^{-2}) than high-np (4.4 kg C m^{-2}) and low-sp (4.9 kg C m^{-2}) (Chapter 1). The sites were selected to represent the local variation in temperature that is driven by altitude, winter temperature inversions, and topographical sun-shading. At each site, black spruce is the only canopy species and feathermoss forms a near continuous carpet. At the two permafrost sites, loess extends at least to the top of the permafrost (65 cm to ~1m), and at high-np, the loess cap is 50 cm thick and overlays a Cambrian schist (Chapter 1).

The trenched plots were installed between late-July and mid-August of 1999. A trench 80 mm wide by 0.5-1.0 m depth was dug around a ~2.0 x 3.0 m area. Trench depth was limited by the depth to permafrost or bedrock. Roots were kept from re-colonizing the trenched plot interior area by a 0.2 mm thick polyethylene barrier placed to the depth of the trench. The vascular understory in the trenched plots was clipped continuously throughout the experiment. Details of trenched plot installation are found in Chapter 1.

Trenched plot overview

Researchers have used root exclusion areas, or trenched plots, to examine root and heterotrophic respiration (O'Connel et al. 2003, Melillo et al. 2002, Boone et al. 1998, Haynes and Gower 1995, Bowden et al. 1993) and root decomposition (Publicover and Vogt 1993, Santantanio and Grace 1987). The technique has also been used to examine the influence of roots on soil C pools (Hart and Sollins 1998) and N cycling (Fisher and Gosz 1986).

Trenching may cause environmental artifacts that subsequently increase heterotrophic respiration. Trenching areas often opens the canopy and allows greater radiation to reach the forest floor, increases nutrient availability to microbes, and increases soil moisture (Fisher and Gosz 1986). To account for these artifacts, in Chapter 1 we used a decomposition proxy in and outside trenched plots. The proxy (cellulose filter paper) tracked heterotrophic respiration in the trenched plots, but at two of the sites (low-sp and mid-dp) the proxy decomposition rate in trenched plots was faster than the control area proxy. We corrected downwards the heterotrophic respiration from the control areas by using a correlation between filter paper mass loss and heterotrophic respiration from trenched plots ($y = 104.17x + 146.31$, $r^2 = 0.89$). Excised live roots also contribute to heterotrophic respiration and this flux is also accounted for (detailed in later section).

Soil C and N

Soil cores were collected to estimate the soil C and N content for the trenched and control areas. In the fall of 2001, we removed 10, 5.5 cm diameter x 30 cm deep soil

cores from random locations in the control area. We dissected the cores into L (litter), and a combined F (fibric) and H (humic) organic horizon (Canadian soil classification system 3rd ed). We also identified an A horizon and the mineral soil to 5 cm below the A horizon. In August 2002, 3 soil cores were collected from each trenched plot and were processed in the same manner as the control collars. The C and N concentration of each soil horizon was determined with a LECO CNS2000 analyzer. Details about methods used to analyze the cores are found in Chapter 1.

Root biomass

Root biomass was estimated from three soil cores collected in early June 2000 from the control areas of high-np and low-sp. The soil horizons were identified as for the soil C and N analysis. Each horizon was hand-washed over a fine mesh screen (125 μm). The organic material remaining on the screen (roots+detritus) was put into a plastic bag filled with distilled water. The bag was then poured and swirled onto a shallow (40-cm diameter) circular pan until organic material appeared homogeneously distributed (Steele et al. 1997). The pan was divided into 16th's and 3 sections randomly selected for the L, A, and the mineral soil horizons. The F+H horizon was subsampled to a greater degree (detailed in next section). Roots were separated into coarse (>2 mm) and fine (<2 mm) size classes and also into a live and dead root fraction. Live and dead roots were differentiated by color and consistency. Extremely fine roots (<0.75 mm) were judged live or dead strictly by coloration, with dark roots considered dead and white and tan roots considered live. Darkened roots greater than ~0.75 mm in diameter were not

assumed dead, but if a firm consistency was felt, the roots were pulled apart to determine if a live inner cambial region existed.

The F+H horizon had the greatest mass of roots and required a greater degree of subsampling. Three sections were randomly selected, removed from the pan, and the organic material remaining on the pan discarded. The three sections were then swirled back onto the pan's surface, divided into 16^{ths} and 5 sections again randomly selected for sorting. Each core required 14-18 hours of processing time. The washed root samples for mid-dp were accidentally warmed for an unknown amount of time, and therefore were discarded without being sorted.

Subsamples of live and dead roots were dry-ashed at 450°C for 12 hours to determine the organic matter percent. The organic matter was assumed to have a C concentration of 45% because samples were too small for direct C and N analysis. Subsamples of live and dead roots were also sent to Lawrence Livermore laboratory for ^{14}C analysis on an accelerator mass spectrometer and prepared following the procedure outlined in Trumbore and Harden (1997) and (Vogel 1992). After dry ashing, there was not enough root material from one of the high-np cores for ^{14}C analysis.

Estimating net root increment with trenched plots

In this experiment the variable of interest is the divergence in forest floor C between trenched plots and control areas after three years of root exclusion. However, the control area was sampled about 9 months before the third year. The estimate of forest floor C includes both live and dead roots. In the control area, any forest floor change (ΔFF_C) is the net result of inputs to the soil (net root increment (NRI), moss production

(NPPm), understory litter and root production (NPP_{UC}), and litterfall (L)) and outputs (heterotrophic respiration (Rh) dissolved organic carbon export (fDOC) and particulate organic matter export (fPOM) (Fig 1.). NRI is equivalent to root net primary production plus root detritus production, minus the amount of heterotrophic respiration coming from root turnover. This balance can be expressed for the control area:

$$FF_{C(t)} - FF_{C(0)} = (NRI + NPPm + NPP_{UC} + L) - (Rh + fDOC + fPOM); \quad \text{Eq. 1.}$$

In the trenched plots, the trenched plot forest floor C change (ΔFF_T) includes a component not in the ΔFF_C equation: the heterotrophic respiration from excised root decomposition (Rhr). Also, the NRI in the trenched plot is zero. The equation is:

$$FF_{T(t)} - FF_{T(0)} = (NPPm + L) - (Rh + Rhr + fDOC + fPOM); \quad \text{Eq. 2.}$$

We assumed equality for the initial forest floor conditions in the trenched plot and control areas and also that the shared variables were equal. The equation for the difference between the control forest floor C and trenched plots at time (t) is then:

$$FF_{C(t)} - FF_{T(t)} = NRI + Rhr; \quad \text{Eq. 3.}$$

Thus the difference between trenched plot and control forest floor C represents the sum of net root increment in the control areas and the artifact of previously live roots being excised and decomposed in the trenched plots.

Vascular understory biomass was eliminated from the trenched plots. Therefore its litter and belowground production was not part of the trenched plot input term and does not cancel (Fig. 1). The primary production of the control understory (NPPuc) ranged from 0.9-4.8 g C m^{-2} y^{-1}, and was mostly new foliage growth (Chapter 1). We assumed understory production approximated annual litterfall and that there was a 1:1 ratio between above- and belowground production (Steele et al. 1997).

Including understory production and rearranging Eq. (3) we estimated NRI as follows.

$$NRI = FF_{C(t)} - FF_{T(t)} - Rhr - NPPu_C ; \quad \text{Eq. 4.}$$

Estimating the contribution of excised roots soil C loss

In the first approach to constraining Rhr, we used a published estimate of fine root decomposition rate (k) for Engelmann spruce in Pacific Northwest forests (Chen et al. 2002). The decomposition rate was applied to the fine live root biomass estimated for the control areas in the spring of 2000. The exponential decay function was used to model the mass loss with time:

$Y_t = Y_0 \exp^{-kt}$

where Y_0 is the fraction of initial fine root mass, Y_t is the fraction of initial mass remaining at year t, and k is the turnover rate ($year^{-1}$). When developing models parameters from observed data, Chen et al. (2002) did not force Y_0 to be the initial root mass. Therefore, Y_0 was not 100%, but rather 79% of initial root mass and k=0.172 (Chen et al. 2002). We selected Engelmann spruce fine roots because they had a similar N concentration (1.0 to 1.2%) to the fine roots in this study (Chapter 1). We assumed that coarse roots decomposed at half the rate of fine roots and that the decomposed left the soil system. For the mid-dp site, the average aboveground biomass to belowground biomass ratio of the other two sites was used to estimate belowground biomass.

In the second approach to constrain Rhr, we assumed the decomposition of roots occurred at the same rate as the bulk soil organic matter. The live roots comprised 17% of the soil carbon (average of high-np and low-sp), which if scaled directly would represent 17% of heterotrophic flux from the trenched plots. In Chapter 1, we reported Rh+Rhr values for the trenched plots for 2000 and 2001. The Rh+Rhr estimates for 1999 and 2002 were based on the average of 2000 and 2001 values. The 2002 Rh+Rhr estimate was set to the average of the 2000 and 2001 trenched plot respiration. The 1999 Rh+Rhr estimates were also assumed to equal the average of 2000 and 2001, but the estimates were weighted downwards by the amount of time before the trenched plots were installed. We likely underestimated Rh+Rhr for 1999 because the excised roots were decomposing at their fastest rate and overestimated the flux for 2002 because a significant decrease in soil C had previously occurred.

Estimating root increment with ^{14}C signatures of live and dead roots

An alternative root increment can be estimated from a ^{14}C age of roots. The pool of live and dead roots have a ^{14}C signature associated with the "bomb" spike, or the influx of ^{14}C to the atmosphere as the result of aboveground nuclear testing during the 1950's and early 1960's (Trumbore and Harden 1997). The historical track of atmospheric ^{14}C has been estimated directly for northern latitudes (Burcholadez et al. 1989, Trumbore and Harden 1997) but in this study the ^{14}C for 1997-2000 was modeled based on a general decrease in atmospheric concentrations. The radiocarbon values are expressed as $\Delta^{14}C$, which is the difference in parts per thousand (per mil or ‰) between the $^{14}C/^{12}C$ ratio in the sample and that of a universal standard (oxalic acid I, decay corrected to 1950). The $\Delta^{14}C$ values are corrected by the plant tissues $^{13}C/^{12}C$ ratio to account for discrimination against the isotopes during photosynthesis.

Only the live and dead roots from the F/H horizon were analyzed for ^{14}C. For live roots, the ^{14}C age represents the time-integrated, continual input of new root production minus annual root mortality. The ^{14}C age of dead roots represents the age of newly dead roots plus the residual age of the dead root mass as it decomposes (Gaudinski et al. 2001). Gaudinski et al. (2001) proposed a one-pool, steady state model to estimate the mean age of roots, but they found the results were not significantly different from an age directly estimated from the root position along the atmospheric ^{14}C curve. We chose the latter approach because of its simplicity (Fig. 2), and applied it to the combined live and dead pool as a whole rather than each individually because of uncertainty in separating live and dead roots. Also, the pools did not differ significantly from one another in $\Delta^{14}C$

(Appendix 1). Using this approach, the increment of the root pool is the pool size divided by the ^{14}C age. Thus, we assume a normal distribution of root mass around the ^{14}C age and that the same amount of C annually leaving the pool through decomposition enters the root live and dead pools again through root production and mortality. Although necessary for estimating increment, we note these assumptions are poorly tested and are sensitive to the multi-pool nature of root matter (Gaudinski et al. 2001). Root pools from mineral soil horizons and the coarse root size classes were assumed to be accumulating C since the beginning of stand initiation.

The turnover time index of forest floor dynamics

The impact of root processes on forest floor C dynamics can also be examined from indices of forest floor decomposition. One useful index in this regard is forest floor turnover time. Turnover time is estimated as forest floor C (g C m^{-2}) divided by heterotrophic respiration (g C m^{-2} y^{-1}). Many past studies have used this index, but have only used aboveground litter as a proxy for heterotrophic respiration. Alternatively, either directly measured heterotrophic respiration or multiple litter components can be used to estimate turnover time. We used aboveground litter, heterotrophic respiration and belowground increment and compared these turnover times to literature estimates with and without belowground production.

Statistical Analyses

Statistical analysis was performed using Statistical Analysis Software v. 8.0 (SAS Institute, Inc. 1999). A mixed model was used for the analysis of forest floor C because the comparison between the trenched plot treatments and control forest floor was

unbalanced (n=3 trenched plots, n=10 control). Comparisons between treatment and control for a site and across sites were also performed. The sites and treatment were designated fixed effects and the replicates for forest floor sampling or the trenched plots were considered random. Data were tested for normality (Shapiro-Wilks) and homogeneity of variance (Levene's).

Using power analysis, we estimated how many samples would be needed at different years after initial trenching to detect a decrease in forest floor C in the trenched plot and a possible accumulation of C in the control area. We used two approaches for estimating C accumulation in the control forest floor. The first was based on the estimated net root increment (Eq. 3), and the measured litter, understory and moss production minus the heterotrophic respiration (Rh) from the trenched plots (excised root respiration (Rhr) and extra Rh from trench artifacts are both removed). Forest floor accumulation rate was also estimated from the forest floor mass divided by the stand age minus 40 years. Forty years was removed because a chronosequence study in Alaska indicated little forest floor C accumulation occurs prior to this point in stand history (O'Neill 2000). The average rates for the three sites are used in the analysis.

The power analysis was performed using the three site average variance of both the control and trench forest floor C. Power analysis was based on a one-tailed test because the trenched plots could only lose C relative to the control. The number of replicates needed was estimated for both α=0.05 and α=0.10, and the power (β) set to (0.75) (Yanai et al. 2003). Because the standard deviations are known, we used the Z-test for analysis (Steidl and Thomas 2001).

RESULTS AND DISCUSSION

Root biomass

The identifiable roots represented a sizeable fraction of the forest floor mass. The live coarse plus fine root biomass comprised 17% of forest floor C in high-np and 14 % in low-sp (Table 1 and 2). For any soil horizon, the live and dead root pools of the two sites did not differ significantly from one another for any size class. Including the dead root pool, total root mass comprised 24% in high-np and 28% in low-sp of the forest floor C. Tryon and Chapin (1983) reported a live root biomass of 1230 g m^{-2} for a mature black spruce forest in Alaska, which was 16% of the forest floor mass (Van Cleve et al. 1983). Two and three times more root mass was found in the forest floor L and F/H than in the mineral soil (Table 1). We may have underestimated root biomass because the water-soluble fraction was lost during root washing. Although washing is a necessary and common practice in spruce forest studies (Steele et al. 1997, Ruess et al. in press), researchers in other systems have found the water-soluble C to represent nearly 23% of fine root mass (Chen et al. 2002).

Control and trench soil C and N

Trenching significantly reduced soil C content overall after 3 years ($p=0.024$). The trenched plot forest floor C was significantly lower ($p=0.03$) than the control area forest floor C at the low-sp site (Fig. 3), but these differences were not significant within the other two sites. The mean difference between trenched plot and control forest floor C (28%) was greater than the necessary 20% effect size Yanai et al. (2003) estimated would be necessary for most studies to detect significant changes in forest floor C. Our results

differed from those of Hart and Sollins (1998), who found no discernible effect of root exclusion on soil C in a mature Douglas-fir forest 13 years after initial trenching. This apparent discrepancy may reflect the nature of black spruce root growth and C allocation. As indicated by the distribution of roots in this study (Table 1), most black spruce root growth occurs in the forest floor (Tryon and Chapin 1983, Ruess et al. 1996, Steele et al. 1997, Ruess et al. (in review)). This growth characteristic restricts the root exclusion effect of trenching to the forest floor where the highest decomposition rates also occur. The forest floor is easier to sample than the entire mineral soil and the root growth characteristic reduces the probability that roots will grow under the trench barriers and recolonize the trenched plot. Finally, the high C allocation to roots by black spruce may make their exclusion disproportionately important. For example, the ratio of belowground production to aboveground litterfall has been estimated to be between 90:1 (Ruess et al. 1996) and 13:1 in Alaskan black spruce (Ruess et al. in press), which is far greater than for most other forests (Vogt et al. 1986).

The amount of C loss did not increase by including the mineral A horizon or the mineral soil horizon to 5 cm below the A horizon (not shown). This result is consistent with the observation of greater root inputs in organic horizons than in the mineral. There was a non-significant trend of N decrease across sites when the A horizon was included (Fig. 4). We mention this because with direct measurements of N flux, trenched plots may provide valuable information on the role roots and available C play in maintaining soil N in these ecosystems.

Estimating net root increment

Given the change in forest floor C over three years and the two estimated losses from excised root decomposition (Rhr), the net increment of roots (NRI) was between 216 and 583 g C m^{-2} y^{-1} (Table 2). These values are much higher than root production estimates from other studies of mature black spruce, where values have ranged between 110 and 168 g C m^{-2} y^{-1} (Ruess et al. 1996, Steele et al. 1997, O'Connell et al. 2003b, Ruess et al. in press). NRI includes annual root production and the accumulation of annually senesced roots, but should be lower than root production because it includes the decomposition of annual root turnover.

The NRI estimates was extremely sensitive to how the respiration or mass loss of excised roots (Rhr) was calculated. The NRI estimate based on root decomposition rates were closer to published estimates of root production than the method based on CO_2 loss from the trenched plots (Table 2). The decomposition method would capture the potential flux of dissolved organic matter (fDOC) or particulate organic matter (fPOM), although we did not measure any water-borne C flux. These fluxes would have to be substantially elevated due to trenching to account for the differences in NRI. Watershed-level measurements have indicated that only 1.0 g C m^{-2} y^{-1} is lost through fDOC from permafrost watersheds in Alaska (MacClean et al. 1999). This analysis only includes C leaving the watershed and misses C transported within the soil profile or the watershed and is likely a low estimate. An alternative approach for estimate the influencing of trenching is to estimate how the lack of transpiration could increase fDOC from the trenched plots. Arain et al. (2002) reported that a mature black spruce forest in central

Saskatchewan evapotranspired 320 mm/year. Assuming a similar value for the forests in our study and that half the water lost is transpired and half evaporated, then a lack of transpiration could result in an excess 160 mm/year of water in the soil profile of a trenched plot. Shibata et al. (2003) reported that the DOC concentration in suction lysimeters under an Alaskan black spruce forests floor averaged 65 mg C L^{-1} over a growing season. If this DOC concentration is lost with the excess water then the estimated excess fDOC is 10 g C m^{-2} $year^{-1}$ from the trenched plot. Soil DOC and POM concentrations also may have been elevated in trenched plots because of soluble C loss from severed fine roots (Chen et al. 2002), however, it is difficult to account for the discrepancy between the two methods for estimating Rhr given our current understanding of water-borne C flow through these soils.

The highest reported values of black spruce root growth are from Ruess et al. (in press) where the litter to fine root belowground production for three Alaskan black spruce forests was between 13 and 17:1. Applying these two ratios to our litter estimates (41-58 g C m^{-2} y^{-1}) would give fine root production estimates of between 533 and 986 g C m^{-2} y^{-1}. The Ruess et al. sites are considerably older than ours, which means the actual ratios for our and their study likely differ. It is noteworthy, however, that they did not estimate net coarse root production or mycorrhizae growth, both of which would be captured by our estimate.

The old ^{14}C age of the fine root (live and dead) pool indicated the pools measured in this study do not turn over annually in relationship to annual inputs of atmospheric ^{14}C (Table 3). Annual turnover would be necessary for the NRI estimates at low-sp to be

valid because the fine root pool size is only slightly larger than the NRI estimate (Table 1 and 2). Using the ^{14}C age of root pools, Gaudinski et al. (2001) also estimated root turnover would have to be longer than 1 year for a temperate forest. Because of our sampling time (first week of June), the root pools we sampled may represent an older cohort than that of annual production. For example, Ruess et al. (in press) reported a significant fraction of black spruce fine roots that appeared during the growing season in minirhizotrons decomposed within the same year, but that as roots aged and grew in diameter, the likelihood they would die and decompose decreased exponentially. Also, the seasonal maximum in root biomass generally occurs in late July and early August (Steele et al. 1997, Ruess et al. in press). Therefore, the age distribution of the sampled roots in our study is likely weighted toward the older fraction of roots.

Much younger ^{14}C ages would be necessary for trenched plots NRI estimates (based on decomposition) to agree with ^{14}C method root increment. The estimated root pool age would have to be 3.9 years for high-np and 2.4 years for low-sp. One possible reason for the older ^{14}C age is that the amount of soluble C stored by the live and dead fine roots is mostly lost during root washing, making the root pools appear older because only the root structural C is left behind. Alternatively, the fraction of roots that do turnover annually may become part of the soil organic matter that is not clearly distinguishable from other detritus. The contribution to forest floor organic matter by these roots would not be captured by the ^{14}C method. For the ^{14}C root increment and the NRI estimates to agree, the contribution of decomposing roots to forest floor C would have to be 95 and 350 g C m^{-2} y^{-1} for high-np and low-sp, respectively,. The turnover

time of control forest floor C provides some insight into whether this amount of flux from decomposing roots is possible.

Forest floor turnover and relationship to net root increment

The turnover time of the forest floor suggests a much faster decomposition rate in black spruce forests than has been previously reported. Van Cleve et al. (1983) as modified by Ruess et al. (1996) estimated the forest floor turnover time of a spruce forest to be 167 years, but this estimate was based solely on the input of aboveground litter. Our turnover time estimates using overstory litterfall, understory production and moss litter are less than the Van Cleve et al. (1983) estimates, ranging between 63 and 102 years (Table 4). The estimates of forest floor turnover time from heterotrophic respiration are even less, ranging between 29 and 34 years for the control areas. Ruess et al. (1996) made a similar observation of a lower forest floor turnover time in black spruce forests. Based on their fine root production (assuming root litter=root production) and aboveground litter fall estimates, the forest floor residence time in their study was ~25 years. Including the NRI estimates from Table 2 reduced the forest floor turnover time in our study to values less than that estimated from heterotrophic respiration (Table 4). The difference in turnover using heterotrophic respiration versus the NRI estimates may reflect the deviation from steady state, in other words, the net increment of forest floor C. The results also suggest root inputs can have a large influence on the rate of forest floor turnover in these systems.

Estimated effect size and sample size

. From our power analysis and the estimated effect size, we determined the number of samples needed at different years past initial trenching to detect a divergence in forest floor C. The effect size is the amount of C accumulated in the control area and the total amount lost from inside the trenched plot. The net amount of C accumulated in the control area equals inputs minus outputs. Inputs to forest floor C include net root increment (NRI), litter (L), and moss and understory productivity (NPPm and NPPuc). The NRI estimate was based on the decomposition approach in Table 2. The carbon output equals heterotrophic respiration (Rh). The trenched plot loses carbon at a rate equal to Rh plus the extra decomposition of previously live roots (Rhr). For comparison purposes, we include an average forest floor C accumulation rate (FFA) estimated from the forest floor C divided by stand age minus 40 years (87±26 g C m^{-2} y^{-1}, n=3). We subtract 40 years because O'Neill (2000) reported forest floor C accumulation only began after this period in a chronosequence study of interior Alaska black spruce forests and that the rate of accumulation averaged 100 g C m^{-2} y^{-1}. The potential divergence between trenched plots and control areas is diagrammed in Figure 5, with 2003 values projected from prior estimates of Rh and Rhr (Chapter 1). The variance in the trenched plot forest floor C was lower than control area C; as a result, a study design based on this variance would require less sampling intensity (Table 5). The true variance of a study would reflect a combination of control and trenched plot variance, which would result in an intermediate sampling intensity.

The difference in variance between the trenched plot and control areas may indicate either an actual change that occurs with trenching or an aspect of the sampling scheme. As decomposition proceeded in the trenched plots, the variability in forest floor C may have decreased as the organic matter approached a similar chemical makeup. For example, the trenched plots may begin with variable proportions of soluble organic matter, cellulose, and lignin, but as microbes preferentially consumed soluble organic matter and cellulose, all trenched plots would eventually begin to consist of mostly lignin. Variability caused by annual inputs of root C would then be reduced. Alternatively, the spatial distribution of control and trenched forest floor sampling differed and therefore the reduced variability in the trenched plots might reflect that they are in fact sub-populations of the control area. The most likely sub-population scenario would be that forest floor samples from a trenched plot were on average farther away from large tree roots, which may cause increased variability in the control samples. We addressed this possibility by correlating forest floor C from each trenched plot subsample to the distance to the nearest tree, but did not find a significant correlation. We could not relocate the cored control areas because numerous other samplings had occurred at the sites. Liski et al. (1995) reported greater mineral soil C nearer to a tree base than further. This observation may not apply to mature black spruce forests because their coarse roots spread laterally from the tree base.

Assumptions and recommendations

Implicit in the net root increment estimate was the assumption the control and trenched plot forest floor C were initially similar, which we do not know because we did

not wish to disturb the trenched plots at the beginning of the experiment by collecting soil cores. Also, by sampling the trenched plot and control areas 9 months apart, we may have underestimated NRI. Finally we did not measure overstory litter inside the trenched plots, and therefore do not know if litter amounts are similar. If they differ slightly, however, it would have little effect because NRI is between five and ten times greater than the aboveground litter inputs.

Yanai et al. (2003) found that paired designs generally increased the power and decreased the number of samples needed in studies of forest floor C change, which reflects the positive influence pairing has on the power of a study design (Steidl and Thomas 2001). A paired design could be implemented by collecting control samples at the beginning of an experiment that are equidistant to the surrounding trees in reference to the trenched plots, and then using distance as a pairing mechanism. We have found that 0.15 m diameter root exclusion collars (effectively 0.07 m^2 trenched plots) provided similar heterotrophic respiration estimates as the large trenched plots (6 m^2) (Vogel, unpublished data). This means trench size could be reduced and plots spaced more evenly between trees. Small trenched plots could also make the measurement of fDOC easier because the entire underside of the trenched plot could be underlain by a lysimeter. An improved approach to our decomposition method would be to sort and weigh the live and dead pool at the beginning and end of the experiment and estimate live root mass loss (Santantonio and Grace 1987). This approach introduces the error of root sorting but would provide an estimate of Rhr that includes fDOC. Also if a researcher used the latter approach, then the trenched plot barriers could be made permeable to water movement in

the soil profile since control area gas flux would no longer be a confounding factor. Unfortunately, the rooting and allocation characteristics of black spruce may make trenched plots uniquely suited to it, but difficult to successively employ in other forest types (Hart and Sollins 1998).

CONCLUSIONS

Black spruce forest floor turnover time is less than previously reported when root growth and decomposition are accounted for, and overall, forest floor C balance is extremely sensitive to the exclusion of new root growth and root severing. For the three sites, the minimum estimate for net root increment (216, 290, 493 g C m^{-2} y^{-1}, Table 2) is higher than root production reported for Canadian black spruce (101-120 g C m^{-2} y^{-1}) (Steele et al. 1997, O'Connell et al. 2003b), but are closer to estimates for Alaskan black spruce (120-168 g C m^{-2} y^{-1}) (Ruess et al. 1996, Ruess et al. in press). This might reflect the high degree of belowground C allocation in Alaskan forests (Chapter 1), or that coarse root primary production, soluble C stored in live roots, or the conservation of senesced roots and mycorhizzae in the forest floor are more important to soil C balance than previously accounted for.

We believe the net root increment (NRI) estimate is too high for one site (low-sp), possibly because of the influence of permafrost on soluble C loss and overall the NRI estimates likely include an extra dissolved organic C flux. However, for two sites, the average forest floor C accretion rate we estimate is 166 g C m^{-2} y^{-1} when using the net root increment estimates from the decomposition approach. This forest floor accretion rate is only greater by 66 g C m^{-2} y^{-1} from chronosequence work in Alaska (O'Neill

2000). For the two forests where NRI seems reasonable, combining aboveground production estimates from Chapter 1 with the C accretion in the forest floor suggests the forests sequester 212 g C m^{-2} y^{-1}. This degree of C accumulation differs from most studies of mature black spruce which have indicated they annually gain small C amounts or even lose C (Goulden et al. 1998, O'Connell et al. 2003b, Ruess et al. in press), but one eddy-covariance study reported an annual uptake of 222 g C m^{-2} y^{-1} (Rayment and Jarvis 1999). With the methodological improvement we suggest, the impact of roots on forest floor C balance may be more easily examined with trenched plots than other methods that scale fluxes up to annual estimates. Reliable estimates of root contributions to ecosystem C balance in mature black spruce forests may be attainable within 3-4 years of trenching if a paired design is employed in forests aggrading forest floor C.

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Table 3- 1. Root distribution (g C m^{-2}) between live and dead, and fine (<2mm) and coarse (>2mm) roots for the different soil layers in the control areas. Values represent mean (±standard error, n=3). Root estimates were not made for site mid-dp

		Fine Roots		Coarse roots	
Site	Soil Layer	Live	Dead	Live	Dead
		----------g C m^{-2}----------			
high-np	L	10 ± 3	8 ± 4	0 ± 0	0 ± 0
	F/H	538 ± 153	293 ± 116	262 ± 72	35 ± 9
	A	42 ± 8	130 ± 19	120 ± 61	13 ± 6
	mineral	55 ± 22	105 ± 25	64 ± 60	19 ± 14
	Total	645 ± 161	536 ± 139	447 ± 164	67 ± 15
low-sp	L	9 ± 2	11 ± 6	1 ± 1	4 ± 3
	F/H	427 ± 93	682 ± 152	336 ± 205	48 ± 16
	A	86 ± 56	100 ± 4	22 ± 9	51 ± 48
	mineral	5 ± 1	26 ± 3	3 ± 2	6 ± 2
	Total	527 ± 145	819 ± 145	362 ± 196	108 ± 49

Table 3- 2. Net root increment (NRI) estimates based on the difference in forest floor (ΔFF) 3 years after trenching. The three year cumulative estimate of trenched plot respiration (Rh+Rhr) is used to estimate excised root decomposition (Rhr)[a]. In an alternative method, the decomposition of excised roots is estimated from root biomass and a published decomposition rate[b]. Understory production (NPP_{UC}) is not found in the trenched plots and is subtracted from the forest floor change. The cumulative RI estimates are divided by 3 years for an annual estimate.

	Forest floor (g C m^{-2})		ΔFF	Rh+Rhr	NPP_{UC}	Rhr (g C m^{-2})		NRI=ΔFF-Rhr-NPP_{UC}		NRI (g C m^{-2} y^{-1})	
Site	Control	Trench	(g C m^{-2})	(g C m^{-2})	(g C m^{-2})	Resp[a]	Decomp[b]	Resp	Decomp	Resp	Decomp
high-np	4837	3669	1168	451	29	77	490	1063	649	354	216
mid-dp	5031	3774	1257	537	5	103	383	1149	869	383	290
low-sp	5427	3537	1890	495	30	81	410	1779	1450	593	483

[a]Excised root decomposition (Rhr) estimated as 17% of trenched plot respiration

[b]Excised root decomposition estimated from exponential decay of fine and coarse roots (Chen et al. 2002).

Table 3- 3. The average root pool mass (g C m^{-2})(fine roots[a] and other roots[d]) and ^{14}C age of pools. Root increment is calculated from the fine root pool divided by the pool's ^{14}C age. An increment is also estimated from pool size of coarse roots and other fine roots in the A and mineral horizon divided by stand age. The two increments are summed to estimate total NRI. The $\Delta^{14}C$ for individual live and dead pools and instrument precision found in Appendix 1.

site	Fine Roots[a] live+dead	$\Delta^{14}C$	^{14}C age[b] (years)	^{14}C Fine[c] NRI	Other roots[d] live+dead	Other roots[e] NRI	Total NRI
high-np	849	155 ± 4	7.5 ± 1	113	845	8	121
low-sp	1149	173 ± 26	9.3 ± 3	124	687	6	130

[a] fine root mass (g C m^{-2}) of L and F/H horizon, from Table 1.

[b] estimated from Fig. 2, difference between year sampled (June of 2000) and root age on ^{14}C curve.

[c] Fine root pool/^{14}C age

[d] Coarse roots and live and dead fine roots (g C m^{-2}) in A and mineral soil, from Table 1.

[e] NRI = "other root pool"/stand age.

Table 3- 4. The turnover time (years) of the forest floor (L,F, and H) estimated from dividing control forest floor C (g C m^{-2}) by either litter, heterotrophic respiration or litter+root increment (g C m^{-2} y^{-1})

	Turnover Time (years)		
site	Litter	Control	Litter+RI
high-np	76	29	16
mid-dp	63	29	14
low-sp	102	34	10

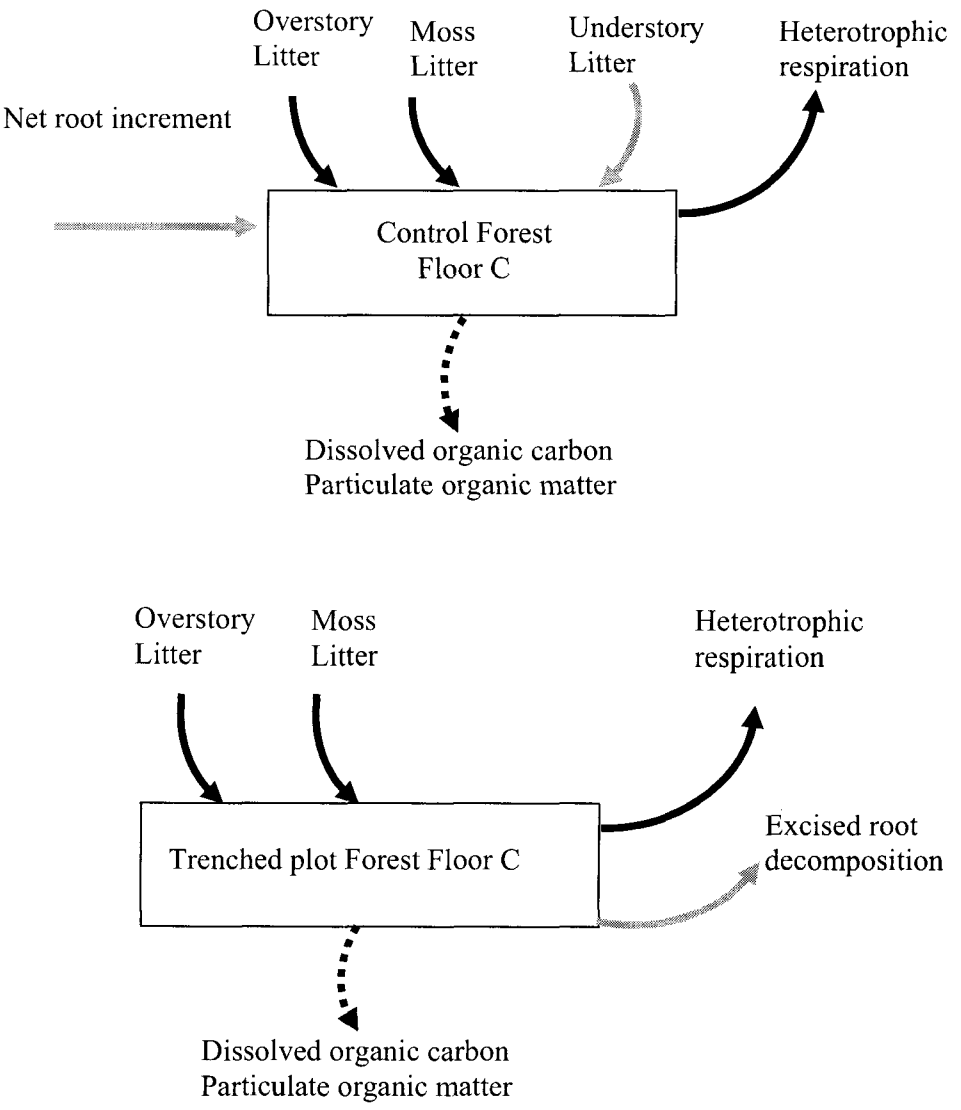

Figure 3- 1. Carbon cycle components contributing to forest floor carbon balance in- and outside trenched plots. The gray arrows (net root increment, excised root decomposition, and understory litter) are fluxes not shared by the other pool. The dashed arrows represent fluxes not directly measured (dissolved organic carbon and particulate organic matter) but which may differ between trenched plots and control areas

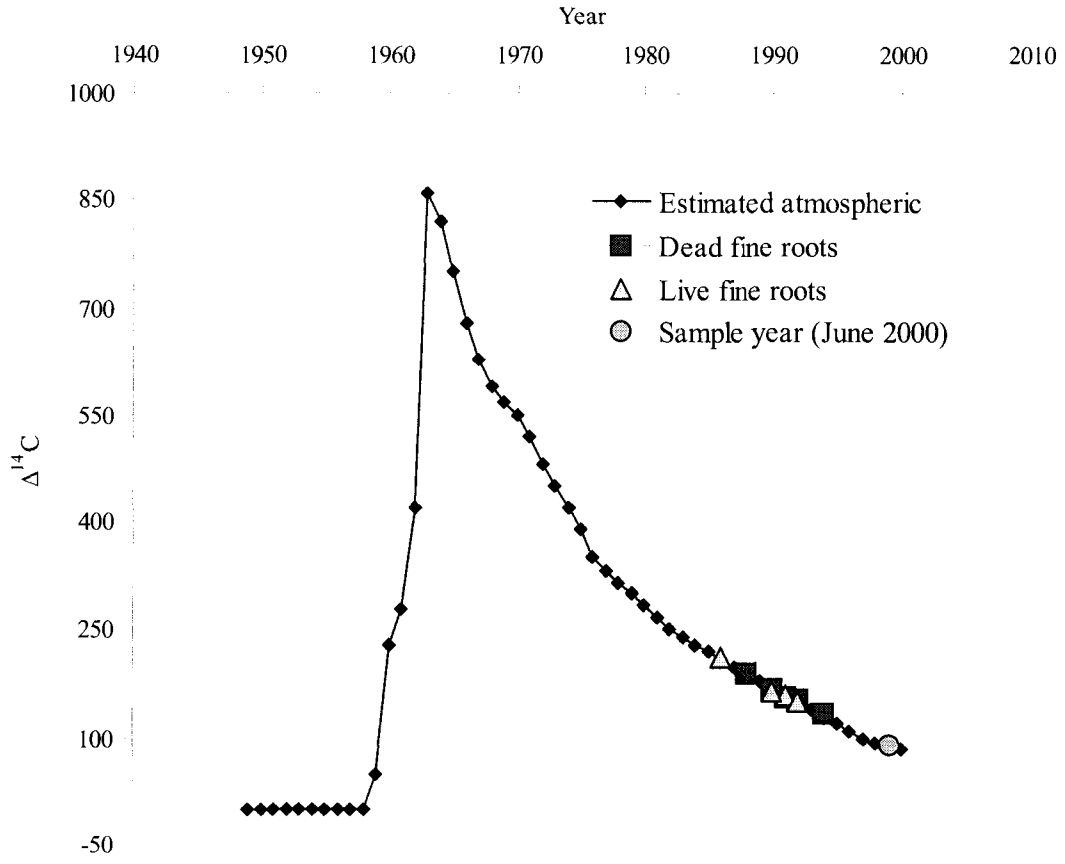

Figure 3- 2. Atmospheric $\Delta^{14}C$ and the probable year position of live and dead roots sampled from the F/H horizon of two sites. There are 5 live and dead root samples but most overlap with one another and are not individually detectable in graph. The period of root sampling was the first week of June 2000.

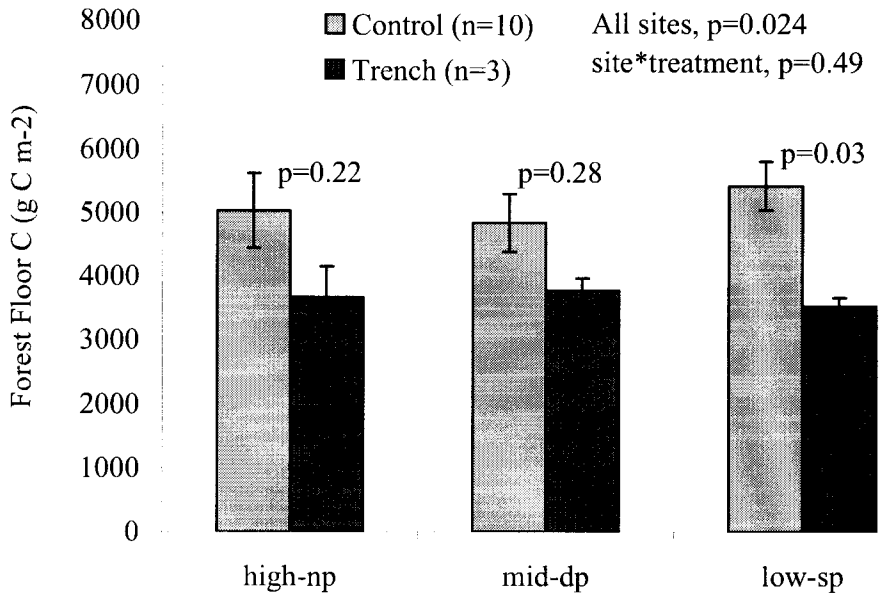

Figure 3- 3. The control area and trenched plots total forest floor C (L, F, and H horizon) for the three sites (mean ± standard error). P-values above bars represent within site comparisons, and the p-value from comparing all trenched plot and control areas across sites is in the upper right hand corner.

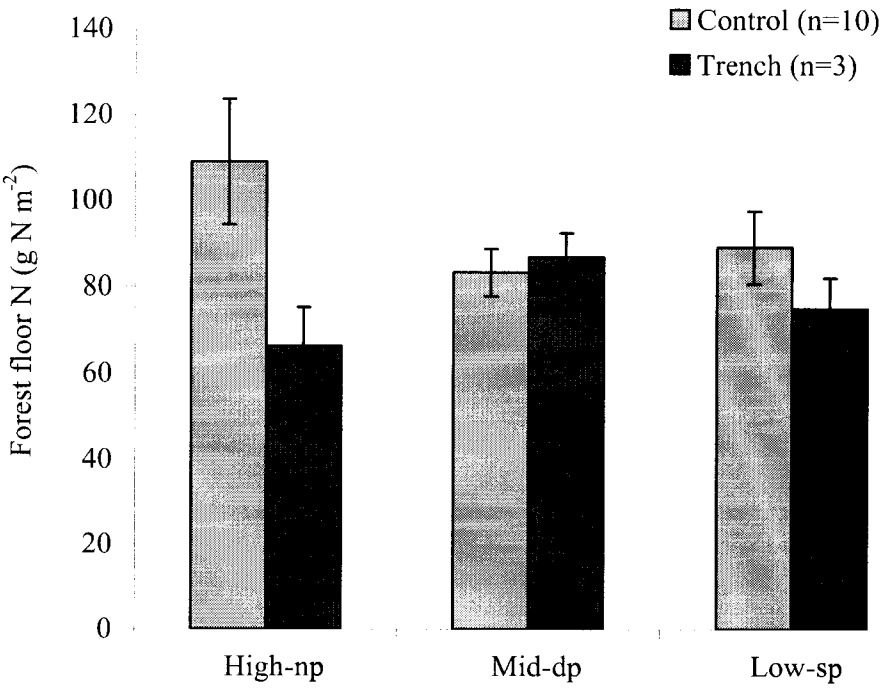

Figure 3- 4. The control area and trenched plots total forest floor N (L, F, and H horizon) for the three sites (mean ± standard error). Treatment and control area are not significantly different from one another

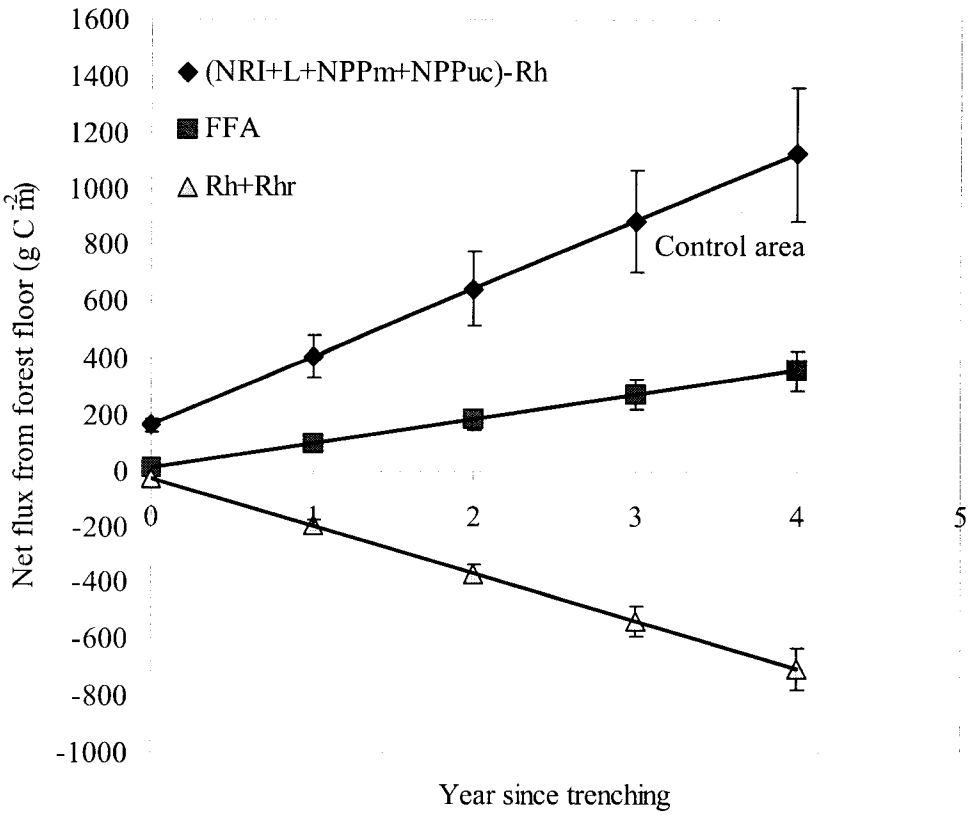

Figure 3- 5. Estimated divergence between trenched plot and control forest floor C, or effect size (g C m^{-2}) with time since trenching. Forest floor accumulation for control areas is from the sum of net root increment (NRI, Table 2, decomp method), litter (L), and moss and understory productivity (NPPm and NPPuc) minus heterotrophic respiration (Rh). An estimate of average forest floor C accumulation rate (FFA) in the control area is used for comparison. Trenched plots lose C from the sum of Rh and the decomposition of newly dead roots (Rhr). Values are mean (±standard error) of estimates for the three sites.

Appendix 1. The $\Delta^{14}C$ of live and dead root pools for two of the sites. Value in parentheses are 1 SD of the accelerator mass spectrometry (AMS) radiocarbon measurement.

Site	Sample	Live $\Delta^{14}C$	Dead $\Delta^{14}C$
high-np	1	159 (6)	154 (5)
	2	151 (5)	157 (5)
low-sp	1	212 (6)	134 (5)
	2	166 (6)	191 (6)
	3	167 (6)	168 (5)

SUMMARY AND SUGGESTED FUTURE WORK

Climate warming at high latitudes is generally expected to increase decomposition rates, soil respiration, heterotrophic respiration, and plant primary production (Chapin et al. 2000). From this study, it appears faster decomposition rates do result in greater heterotrophic respiration and aboveground plant primary production. Soil respiration, however, may not increase with warming because it is dominated by root respiration in black spruce forests. Root respiration and soil respiration were both greater at the site with the slowest decomposition and least aboveground production. This suggests the amount of C allocation to roots will control soil respiration in black spruce forests and that this aspect of C cycling will need to be understood before general predictions on ecosystem response to environment can be made.

The environmental factor that controls C allocation was difficult to discern from the three sites in this study, but across the biome, moisture deficit was the most apparent control. The site with slower decomposition was only marginally cooler than the other two sites and the difference only apparent during May and early June. Decomposition rates may have affected nutrient availability, as suggested by the more depleted foliar ^{15}N at the slow decomposition site. This may have resulted in greater belowground C allocation by spruce. Foliar N concentration, however, did not differ among sites and root N concentration was greater at the slow decomposition site. Soil moisture deficit may have been a factor for both decomposition and plant C allocation; the slow decomposition site had greater ^{13}C content in the foliage than the shallow permafrost site. A soil moisture deficit effect best fits this study into the cross biome trend apparent from a

literature review. That is, soil and root respiration greatly increase with moisture deficit across the boreal biome and because Alaska is drier than most other regions, the black spruce here cycle a greater amount of C through the root system.

Winter soil respiration trends indicated this component of ecosystem C cycling deserves further study. Although winter soil respiration was only 5 to 15% of annual soil respiration, it was less at the site with warmer winter soil temperatures, which suggests some other environmental factor (i.e. moisture) or organic matter characteristic is affecting winter efflux. Root exclusion also decreased winter respiration at two of the sites, indicating either root detritus as a C supply to microbes or root maintenance respiration affect winter soil respiration. Climate warming is expected to be greater during the winter season in high-latitude regions (Houghton et al. 2001), but based on the results from this study, controls on winter respiration may require further investigation before it can be concluded that winter soil respiration will increase simply as a function of temperature.

Based on the rate of microbial respiration in the incubation study, very little difference existed among sites in organic matter quality. The only respiration differences occurred at the lowest incubation temperature (0 °C), where the trends followed the *in-situ* winter soil respiration measurements. One hypothesis in Chapter 2 was that microbial respiration from the site with the slowest *in-situ* decomposition would have the greatest temperature sensitivity. This occurred, but was a function of less microbial respiration at low temperatures and not greater respiration at warmer. The temperature sensitivity index (Q_{10}) of microbial respiration did not correlate to any aspect of soil

organic matter chemistry. The sensitivity of Q_{10} to the low temperature mineralization rates and the difficulties in determining how to calculate Q_{10}, make it a poor tool for understanding the links between temperature sensitivity, microbial processes, and organic matter chemistry.

Organic matter chemistry influenced microbial processes in unexpected ways. I hypothesized that the accumulation of polysaccharides due to inhibited decomposition would result in greater microbial respiration. Although microbes did preferentially consume polysaccharides during the course of the incubation, microbial respiration and microbial biomass were negatively and positively correlated, respectively, to the proportion of polysaccharides. These results suggest microbes used polysaccharides but they were converted to biomass and not CO_2. The decomposition of an organic matter compound may not directly relate to the production of CO_2 because of lags caused by microbial turnover time.

Temperature influenced mineralization processes to a greater degree than did the organic matter attributes for a site. Across sites, the proportion of polysaccharides consumed during the incubation was positively correlated to net N mineralization, suggesting a link between organic matter quality and N availiability. Differences in net N mineralization among sites did not suggest N availability was the reason for greater allocation belowground at the lowest decomposition site, however, *in-situ* measurements of N availability would better address this possibility.

The importance of root processes on soil C balance was also apparent based on the results in Chapter 3. Although it is generally assumed that the amount of soil C is

relatively insensitive to C inputs on annual basis, a significant difference was observed between the forest floor C in- and outside root exclusion areas after three years. From the difference in C between treatment and control and using two different modeling approaches, I estimated net root increment (root production minus decomposition) for the three stands to range between 216 and 583 g C m^{-2} y^{-1}. An alternative analysis based on the ^{14}C age of the live and dead root pools, indicated root increment was 120 and 131 g C m^{-2} y^{-1} at two of the sites. The difference between the two methods may indicate that a significant fraction of annual root turnover is converted to soil organic matter or that trenched plots result in an extraordinary loss of dissolved organic carbon. Nonetheless, the forest floor turnover time of black spruce forests appear much lower than past estimates have indicated (Van Cleve et al. 1983).

The high degree of belowground C allocation in these ecosystems and the concentration of roots near the soil surface may make the trenched plot method a valuable new tool in determining the role roots play in maintaining forest floor C balance in black spruce ecosystems. The method can be improved, however, from the approach I used. Foremost, trenched plots need not be as large as the ones in this study (6 m^2). Very small trenched plots (0.07 m^2) inside and outside large trenched plots provided heterotrophic respiration estimates indistinguishable (6% less, n=6) from the large trenched plots. Small trenched plots would be superior to large plots because they can be spaced more evenly between trees and the flux of dissolved organic carbon easily measured with a lysimeter underlying the trenched plot. A second improvement to the method would be estimating root mass at the beginning and end of the experiment in and outside the

trenched plot. Although this introduces the expense and error of measuring root mass, root decomposition and accumulation estimates would be more firmly grounded. Finally, small trenched plots should be paired to control sample areas by the distance to the nearest tree(s). Pairing generally increases the power of a study design (Steidl and Thomas 2001, Yanai et al. 2003), and using tree distance may reduce the variability in forest floor C sampling. In a black spruce forest aggrading forest floor C, a significant difference between trenched plot and control area forest floor C may be detectable within 3-4 years of installation with a reasonable number of trenched plots.

Black spruce as a species is generally slow growing and adapted to cool and wet soil environments (Van Cleve et al. 1983, Viereck et al. 1993). The environmental conditions that define its habitat in the boreal biome will change with proposed climate warming and alter the C cycle of these forests. Each component of C cycling in black spruce ecosystems will likely also change, but of these, soil respiration and root respiration are the most variable across environmental gradients and may respond to climate warming in unexpected ways. From this study, it appears inhibited decomposition results in greater C allocation to the root system of black spruce and greater soil respiration. Thus, faster decomposition with climate warming may result in *less* soil respiration, despite heterotrophic respiration and aboveground production increasing. It is unclear from this study whether allocation shifts annually in response to environment, but if it does, this would have implications for interpreting tree ring response to environment and for using empirical soil respiration models over multiple years for a given location.

The environmental mechanism controlling shifts in allocation may be temperature or moisture availability but it is difficult to determine which factor is preeminent. Environmental control on allocation may actually represent nutrient availability control because of decomposition dynamics. Manipulative experiments that adjust soil moisture and temperature, and that measure both above- and belowground components of the C cycle, are necessary in black spruce ecosystems. At a minimum in a manipulative study, root respiration should be separated from total soil respiration, but ideally root growth and changes in root N concentration would also be monitored. Root growth and mortality have a substantial influence on ecosystem and soil C balance, and these aspects of black spruce growth require further study in manipulated environments. The experimental design should also include a priori measurements of soil C that have enough statistical power to detect the changes in soil C that will likely occur with a warming experiment (Hom 1986).

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