

# Soil and root respiration in mature Alaskan black spruce forests that vary in soil organic matter decomposition rates

Jason G. Vogel, David W. Valentine, and Roger W. Ruess

**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* (Mill.) B.S.P.) forests. We hypothesized faster decomposition correlates with greater amounts of both root and microbial contributions to soil respiration. Contrary to our prediction, the site with the coolest summer soil temperatures and slowest decomposition (site identification "high-np") had significantly ( $p < 0.05$ ) greater growing season soil respiration ( $485 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ) than the two other sites (372 and  $332 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ). Spruce C allocation to root respiration was significantly greater, and fine-root N concentration was 10% and 12% greater ( $p < 0.05$ ) at high-np than at the other two sites. High-np spruce foliage was also more enriched in  $^{13}\text{C}$  and depleted in  $^{15}\text{N}$ , suggesting either lower available moisture or slower N turnover. Either factor could drive greater C allocation to roots; however, a literature review suggests moisture deficit corresponds to greater C allocation to roots in black spruce forests across the boreal ecosystem. Controls on spruce C allocation need to be resolved before making the generalization that soil respiration will increase with warming in this forest type.

**Résumé :** Le réchauffement du climat aux latitudes élevées devrait augmenter la contribution tant des racines que des décomposeurs hétérotrophes à la respiration du sol. Les auteurs mesuré les composantes racinaires et hétérotrophes de la respiration du sol près de Fairbanks en Alaska, en 2000 et 2001, dans trois forêts d'épinette noire (*Picea mariana* (Mill.) B.S.P.) situées à différents endroits dans le paysage. Ils ont assumé qu'une décomposition plus rapide correspondrait à une plus grande contribution racinaire et hétérotrophe à la respiration du sol. Contrairement à leurs prédictions cependant, la respiration du sol pendant la saison de croissance était significativement plus élevée ( $p < 0,05$ ) dans le site avec les températures estivales du sol les plus froides et la décomposition la plus lente (site ID « np-élevé ») ( $485 \text{ g C}\cdot\text{m}^{-2}\cdot\text{an}^{-1}$ ) que dans les deux autres sites (372 et  $332 \text{ g C}\cdot\text{m}^{-2}\cdot\text{an}^{-1}$ ). L'allocation de C vers la respiration des racines était significativement plus élevée et la concentration de N dans les racines fines était 10 % et 12 % plus élevée ( $p < 0,05$ ) dans le site np-élevé que dans les deux autres sites. Le feuillage de l'épinette dans le site np-élevé était également plus riche en  $^{13}\text{C}$  et plus pauvre en  $^{15}\text{N}$ ; ce qui indiquait soit une plus faible disponibilité en eau, soit un remplacement plus lent de N. L'un ou l'autre de ces facteurs pourrait entraîner une plus forte allocation de C vers les racines. Cependant, une revue de la littérature indique qu'un déficit en eau correspond à une plus forte allocation de C vers les racines dans les forêts d'épinette noire partout dans l'écosystème boréal. Les facteurs qui contrôlent l'allocation de C chez l'épinette doivent être connus avant de pouvoir généraliser le fait que le réchauffement du climat entraînera une augmentation de la respiration du sol dans ce type de forêts.

[Traduit par la Rédaction]

## Introduction

Soil respiration generally increases with temperature, creating the possibility that the ongoing and predicted warming at high latitudes will increase soil respiration and decrease net boreal forest uptake of  $\text{CO}_2$  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

(C) balance. Root respiration in general consumes photosynthate recently fixed by the canopy (Högberg et al. 2001), thus this respiration has little influence on annual net ecosystem carbon balance and is sensitive to both canopy and soil conditions. Alternatively, microbial decomposition can affect ecosystem C balance by releasing  $\text{CO}_2$  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 2000). The decomposition of soil organic

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matter could drive a significant increase in atmospheric CO<sub>2</sub> 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 (Van Cleve et al. 1983), and a general hypothesis is that with soil warming, microbial decomposition will increase, releasing more nutrients to the plants, stimulating photosynthesis, and increasing overall plant productivity, including roots. If true, soil respiration should increase because of the stimulated contribution of both roots and microbes. However, experiments in other ecosystems indicate that soil respiration enhancement is not sustained at high levels in response to warming (Jarvis and Linder 2000; Rustad et al. 2001; Melillo et al. 2002). Root respiration 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 may instead result from the relatively quick depletion of easily decomposed soil organic matter (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 are accurate. 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, is the most prevalent and wide-ranging tree species in the boreal forest (Burns and Honkala 1990), and is 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 and predominance in wet, cool soils. Also, bryophytes can cover 100% of the forest floor underneath spruce, drastically lowering soil temperatures through the insulating properties of their tissue (Van Cleve et al. 1983).

Our objectives were to examine the relationship between decomposition and the two components of soil respiration, microbial and root respiration. We hypothesized that warmer soils favor faster decomposition and also higher rates of all components of soil respiration. Alternatively, a warmer soil and faster 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  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . We also measured moss gross photosynthesis

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

	High-np	Mid-dp	Low-sp
<b>Topography</b>			
Elevation (m)	580	184	124
Aspect (°)	340	180	195
Slope (%)	12	8	3
Active layer thickness (m) <sup>a</sup>	>1.5 <sup>b</sup>	0.85	0.64
<b>Overstory characteristics</b>			
Trees per hectare	6588	8000	6941
Basal area (m <sup>2</sup> ·ha <sup>-1</sup> )	28.6	26.0	30.4
Avg. diameter (cm)	7.4	6.2	7.6
Age (years)	110	75	120

**Note:** High-np, no permafrost; mid-dp, mid-elevation deep permafrost; low-sp, low-elevation shallow permafrost.

<sup>a</sup>Depth to permafrost was measured between 31 August and 9 February 1999.

<sup>b</sup>Permafrost was not found 1.5 m from the surface. It is unclear whether it existed below this depth.

and modeled moss respiration to constrain the influence of these on soil respiration results.

## Materials and methods

### Study areas

We selected a soil temperature gradient in a homogeneous vegetation type and therefore located similar black spruce forests near Fairbanks, Alaska, that varied in aspect and elevation. Sites included a high-elevation area with no permafrost (high-np), a mid-elevation deep permafrost area (mid-dp), and a low-elevation shallow permafrost (low-sp) area (Table 1). High-np 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.

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. 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 being 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).

Black spruce is the only canopy species, and feathermoss forms a near-continuous carpet. Feathermoss is a generic term for two species, *Hylocomium splendens* (Hedw.) B.S.G. and *Pleurozium schreberi* (Brid.) Mitt. The two species did not vary significantly in relative proportions among sites. Other cryptogams and bryophytes occupy <15% of the forest floor. Common to the understory of all sites are *Vaccinium vitis-idaea* 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 among the three sites, but variations occur in age and depth to permafrost (Table 1).

The soils are characterized by permafrost, an organic matter mat, and a loess parent material. The high-np site is without permafrost, which is common for high elevations with moderate slopes in interior Alaska. The organic matter mat is approximately 23 cm thick at the three sites. The mineral soil consists of loess that was blown from the Alaska Range and fluvial plains during the Holocene. It is patchily distributed across 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 approx. 1 m), and at high-np the loess cap is 50 cm thick.

### 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 independent methods: root exclusion via trenched plots and the total belowground carbon allocation (TBCA) method (Raich and Nadelhoffer 1989). The methods differ in their relative strengths and weaknesses. With trenched plots, researchers can track seasonal patterns of root respiration, but increase the pool of decomposing soil organic matter with the excision of live roots. Root exclusion generally also increases soil moisture. Alternatively, the TBCA approach 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 and 20 m apart along the slope of a stand. A 20 m × 20 m grid abutting the three trenched plots was used for randomly selecting points for placing decomposition materials, collecting litterfall, and removing soil cores. Control samples were assigned to one of the three trenched plots based on their location relative to the trenched plot.

The overstory stand characteristics, spruce biomass, and primary production were estimated with a prism (10 basal area factor (BAF)) and tree cores (Gower et al. 1997). A prism “sweep” was located near one randomly selected corner of each trenched plot at a site. The sweep center was located at a 45° angle 3 m from the corner. The diameter at breast height (DBH, 1.3 m) of each tree in the sweep and an allometric equation relating DBH to total tree biomass (M. Mack, unpublished data) were used to estimate the biomass of each tree. To estimate spruce production, 45–60 trees were cored at DBH along a 4 m × 20 m transect through the control plots. Tree-ring widths of 5-years’ growth (1997–2001) were measured with a microscope and digital micrometer. The 5-year mean ring width for trees within a 2-cm size class (e.g., 2.5–4.5 cm) was assigned to each equivalent tree in the prism sweep. Tree diameter change was estimated from the ring widths and scaled to biomass production using the allometric equation, and then multiplied by the number of trees per hectare (Gower et al. 1997).

Vascular understory biomass and production was estimated in August 2000. A 1-m<sup>2</sup> plot was randomly located within 5 m of each trenched plot at a site. The understory 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

A two-channel HOBO (Onset Corp, Bourne, Massachusetts) temperature sensor continuously logged soil temperature at 10- and 20-cm depths from the top of the moss surface, both within one randomly selected trenched plot and 3 m from the trenched plot. The loggers were left 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):

$$[1] \quad \text{SDD}(i) = \sum_{i=1}^n T_i \quad \text{when the daily } (i) \text{ maximum temperature } T > 0 \text{ } ^\circ\text{C}$$

During each soil respiration measurement period, soil temperature was also measured with a handheld Digisense™ sensor using type T (Cole Palmer) thermocouples affixed to a pole and inserted to depths of 10 ( $n = 6$  per site and 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. 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 a nondestructive method (e.g., TDR) in low-density organic matter requires calibration with harvested soil samples, causing substantial soil disturbance. Rather, the  $\delta^{13}\text{C}$  of canopy foliage was used to assess forest moisture status. Foliar  $\delta^{13}\text{C}$  can capture the influence of soil moisture, atmospheric moisture deficits, and soil temperature’s effects on hydraulic conductivity (Lajtha and Michener 1994). A direct altitudinal effect on  $\text{CO}_2$  internal partial pressure is possible but unlikely, because elevations only differed by 400 m (Körner et al. 1988).

We used foliar  $\delta^{15}\text{N}$  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 one-third 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 1999. A trench 0.5–1.0 m deep was dug around a 2.5 m × 3.0 m area. Trench depth was limited by permafrost depth or bedrock (high-np). Roots were kept from recolonizing the trenched plot interior area by a 0.2-mm thick polyethylene barrier placed to the depth of the trench. We located trenched plots between trees when possible, but at each site a black spruce tree (all <4.0 cm DBH) was removed from inside the plot. Also, all understory vascular plants were removed by cutting

at their base. The understory in the trenched plots was continuously clipped throughout the experiment.

Growing season (1 May – 30 September) soil respiration measurements were made between 1000 and 1200 hours about every 10 days between 1 June 2000 and 1 October 2001. We delayed measurements for 10 months after trenching to allow fine roots and the associated 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 approximately 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 not moved during the experiment. A 3-m boardwalk was used for 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™ (20 water : 1 herbicide) was 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<sup>-1</sup> 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 (approx. 8 cm above the surface of moss). Before the chamber was attached to the permanent collar, it was held 1 m above the soil surface so the CO<sub>2</sub> concentration in it was less than that at the soil surface. Light and darkened chamber measurements were made during a sampling period to determine feathermoss gross photosynthesis (see following section 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<sub>2</sub> concentrations at 3-s intervals. The chamber was left on the collar for 2 min, but only the CO<sub>2</sub> increase between 45 and 75 s was used in a regression between time and CO<sub>2</sub> concentration. Visual analysis of numerous 6-min intervals indicated this time-frame consistently provided linear and robust regressions of concentration change with time ( $\Delta\text{CO}_2/\text{s}$ ). Internal pressure, temperature, and  $\Delta\text{CO}_2/\text{s}$  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<sub>2</sub> and recording the increase in CO<sub>2</sub> concentration after 2 min of mixing. The average volume of the chamber–collar system was 5.1 L. Including collar specific volumes improved the  $R^2$  values of the temperature–respiration response equations by 3%.

Respiration was measured periodically during the winters of 2000–2001 and 2001–2002. Six locations were measured inside and outside trenched plots on the snow surface at a distance of at least 1 m from the operator's footprints. A rectangular chamber (0.0794 m<sup>2</sup>) was first pressed into the snow surface to create an imprint, then lifted approximately

1 m, and after 20 s placed again in the imprint. The time-frame used for regressions was the same as for summertime measurements.

### Moss gross photosynthesis and modeling respiration

To constrain the contribution of moss respiration ( $R_{s,m}$ ) to soil respiration, we measured moss gross photosynthesis ( $P_{s,m}$ ) and modeled moss respiration. The  $P_{s,m}$  was calculated as the difference between the flux under ambient light and that in a darkened chamber. Using the chamber air temperature, we estimated the  $R_{s,m}/P_{s,m}$  ratio using models developed from data in Skre and Oechel (1981). Models were developed for both *Hylocomium* and *Pleurozium*. Three seasonal time periods were modeled because moss photosynthetic capacity changes with the season (Skre and Oechel 1981). Time periods were snow-free to day 172, 173–210, and 211 to the first snow-fall. Trends in the ratio varied among time periods, so polynomial models were used because they most consistently provided significant relationships. The models were all of the form

$$[2] \quad R_{s,m}/P_{s,m} = a + bT + cT^2$$

where  $T$  is air temperature and the parameters  $a$ ,  $b$ , and  $c$  were curve-fit parameters generated in SAS with the NLIN procedure. We multiplied the modeled ratio by the  $P_{s,m}$  measurement to estimate  $R_{s,m}$ . *Hylocomium* and *Pleurozium* model results were weighted by the prevalence of each species at a site. The growing season estimates of  $P_{s,m}$  and  $R_{s,m}$  were derived by interpolating between measurements, and  $P_{s,m}$  estimates were corrected downwards by the number of hours that photosynthetic active radiation was less than the light compensation point for feathermoss (25  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) (Williams and Flanagan 1998). The light measurements were made at an 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  $P_{s,m}$  and  $R_{s,m}$  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 (usually 9–14 days) between measurements. Using respiration response to soil temperature and scaling to annual estimates with soil temperature data was not possible because moss photosynthesis and respiration were unrelated to soil temperature. Therefore, for consistency in scaling both moss and soil respiration, fluxes were interpolated. For soil respiration, using hourly soil temperatures at 10 cm to drive a model of respiration produced seasonal estimates that differed by 7%  $\pm$  5% ( $n = 6$ , trench and control) from interpolated values.

### 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  $\times$  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 (Soil Classification Working Group 1998) and included an A horizon and mineral soil to 5 cm depth.

The thickness of each horizon was measured and the horizon weighed dry (all materials were dried for 72 h 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 were hand sieved through a 2-mm screen, while organic material remaining on the screen was ground. All ground samples were analyzed with a LECO2000 CNS analyzer (St. Joseph, Michigan) for C and N concentrations.

From eight soil cores collected in July 2001, a subsample of live fine roots (<2 mm) was selected from the F–H horizon for C and N analysis. Roots from two cores were combined ( $n = 4$  per site). Roots were rinsed with deionized water, dried, and analyzed for C and N.

### Decomposition

We measured the 1-year mass loss of cellulose filter paper and spruce needle litter. Filter paper was used in control areas and trenched plots in 2000 and 2001, and spruce litter placed in control areas 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. The paper's center was 3.5 cm below the moss surface. Five bags were spaced haphazardly in each trenched plot and 15 filter papers were randomly located in the 20 m × 20 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 × 23 cm deep plastic mesh (mesh size 1 mm) birdseed bags (Quadel Industry, Coos Bay, Oregon). We opened a slit in the organic horizon with a flat spade and inserted the bag bottom to a depth of 24 cm, leaving approximately the top 1 cm below the surface. Spruce needle litter was collected near low-sp by shaking a tree gently so that necrotic needles fell on an underlying tarp (M. Mack, personal communication). Approximately 100 g of air-dried needles were sewn into 150- $\mu$ m silkscreen bags. We placed 15 bags vertically approximately 4 cm into the feathermoss layer at each site, a depth corresponding to where we observed the most litter. Locations were selected in the same manner as in 2000.

### Root respiration

The 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  $R_{sm}$  was subtracted during each measurement, and we calculated estimates with and without winter respiration. The equation is thus

$$[3] \quad TBCA (R_r) = \text{annual soil respiration} - (\text{litterfall} + \text{moss production})$$

Using trenched plots, root respiration is estimated as the annual or instantaneous difference between the trenched ( $R_{st} = R_{sm} + \text{heterotrophic microbial}$ ) and control ( $R_{sc} = R_{st} + \text{root}$ ) plot soil respiration, thus

$$[4] \quad R_r = R_{sc} - R_{st}$$

Both TBCA and trenched plot root respiration include the respiratory contribution of root maintenance and growth, mycorrhizal fungal respiration, and the heterotrophic respiration associated with annual root mortality and decomposition. Trenched plots include respiration from excised, previously live roots. We did not separate this extra heterotrophic respiration contribution, but hopefully minimized the differential influence of excised roots across sites by selecting for similar aboveground biomass and soil organic matter amounts.

Litterfall was estimated in 2000 and 2001. Six 1-m<sup>2</sup> wood-framed litter traps were randomly placed in the 20 m × 20 m plots and were elevated above the moss surface. Red squirrels used the collection screens as perches and, therefore, all squirrel-affected cones were removed. These represented 16% of the total litter mass. Litter was not further separated by component (i.e., foliage, twig, etc.). All vegetation was dried at 65 °C for 72 h and weighed. Litter biomass was multiplied by 0.48 to convert from dry 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-site 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' W test and visual inspection of normality plots) and homogeneity of variance (Levene's test). All data are presented as the mean  $\pm$  standard deviation (SD).

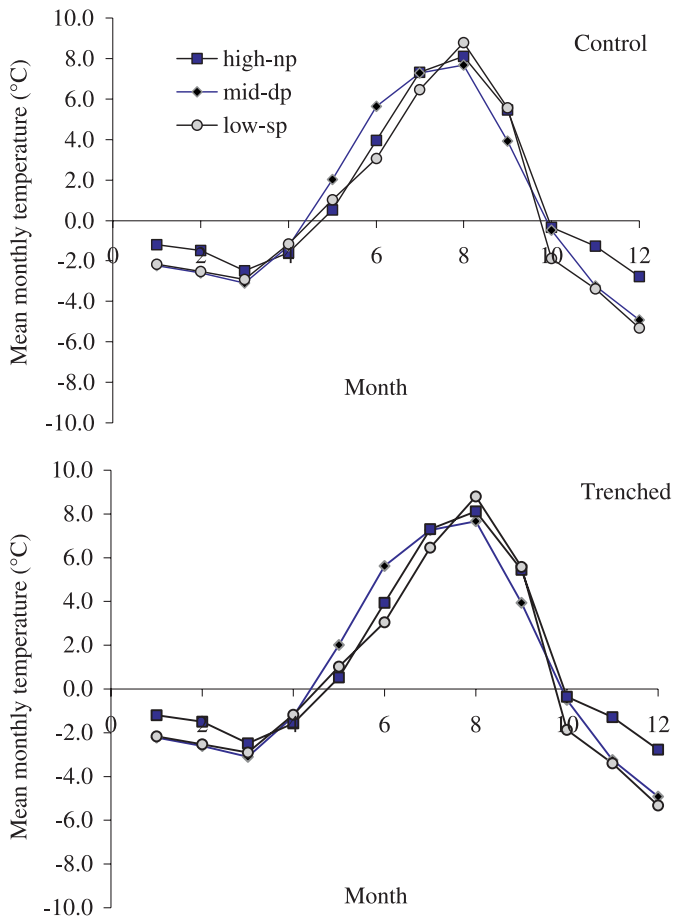
To determine whether site differences in seasonal soil respiration were a function of a temperature response differences, we fit temperature-response models for various model types (linear, exponential, quadratic) and examined residuals to determine which models did not violate the assumption of homogeneous variance. Based on the residual distribution, we decided on a linear model, although a second-order polynomial model would possibly better represent the response curves for the low-sp control and mid-dp trenched respiration.

We examined site and treatment differences in the relationship between soil temperature and respiration using a mixed model and repeated measures. Mixed models account for 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), temperature, and all possible interactions were tested as fixed effects. Site or treatment(collar) and temperature × site and temperature × treatment(collar) were tested as random effects. The remaining subplot error (time × site and time × treatment(collar)) was analyzed with repeated-measures analysis with a spatial power variance structure (O'Connell et al. 2003; Wang et al. 2002) to account for respiration and temperature measurements being taken on the same soil collars throughout the study. The mixed model used was

$$Y = X\beta + Z\gamma + \varepsilon$$

where  $Y$  denotes the vector of observed  $y_i$ 's,  $X$  is the known matrix of  $X_{ij}$ 's,  $\beta$  is the unknown fixed-effects parameter vector,

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



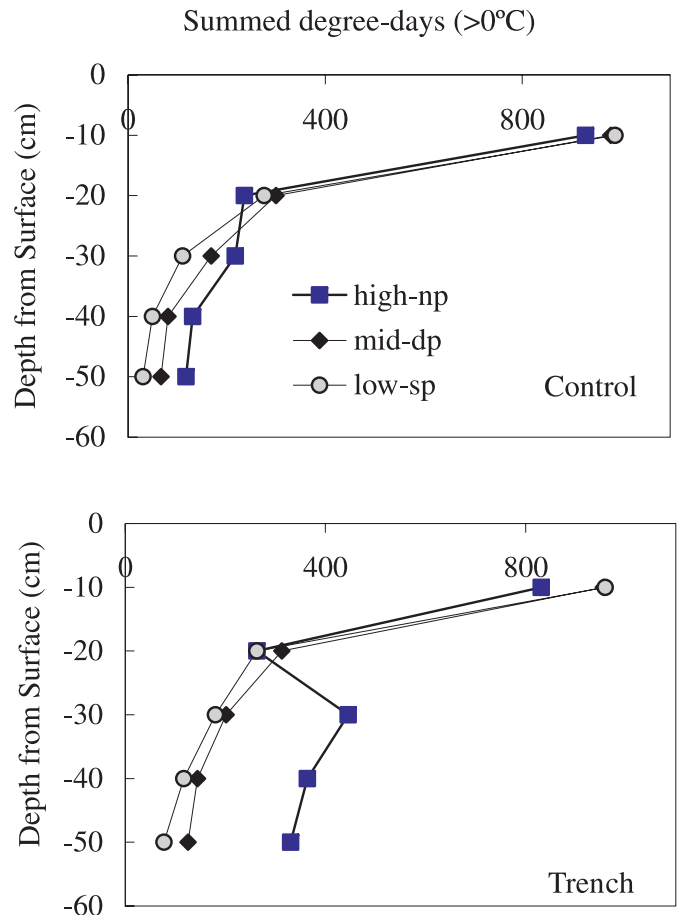
$Z$  is the known design matrix,  $\gamma$  is the vector of unknown random effects parameters, and  $\varepsilon$  is the unobserved vector of independent random errors.

## 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 (low elevation, shallow permafrost) and mid-dp (mid-elevation, deep permafrost) consistently reported much colder winter temperatures than those at high-np (high elevation, no permafrost). Summertime temperatures at the permafrost sites at 10 cm were warmer than those at high-np in May and June and similar to those at 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 at high-np. Trenched plots were warmer ( $SDD$ ) at 30-, 40-, and 50-cm depths. The high-np average deep temperatures (30, 40, and 50 cm) were heavily influenced by the location of one of the two deep Digisense

**Fig. 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.



**Table 2.** Isotopic signatures and N concentration of new foliage, and fine-root N concentration (mean  $\pm$  SD,  $n = 4$ ).

Site	Foliage		Root	
	$\delta^{15}N$	[N]	$\delta^{13}C$	[N]
High-np	$-6.07 \pm 0.54a$	$0.83 \pm 0.10$	$-27.5 \pm 0.66^*$	$1.05 \pm 0.01a$
Mid-dp	$-4.27 \pm 0.66b$	$0.84 \pm 0.06$	$-28.5 \pm 0.80$	$0.92 \pm 0.06b$
Low-sp	$-4.58 \pm 0.07b$	$0.84 \pm 0.05$	$-28.9 \pm 0.21^*$	$0.93 \pm 0.01b$

**Note:** High-np, no permafrost; mid-dp, mid-elevation deep permafrost; low-sp, low-elevation shallow permafrost. Means followed by the same letter are not significantly different at  $p < 0.05$ . \*, high-np > low-sp ( $p = 0.08$ ).

probes, which was in a particularly sunny area of the trenched plot. August and September temperatures were on average 2 °C cooler in 2000 than in 2001 (results not shown).

### Foliar, root, and biomass characteristics

Foliar and root characteristics measured in high-np often differed from those in the other two sites, which never differed significantly from one another. The  $\delta^{13}C$  of foliage was most enriched at high-np (Table 2) and was marginally different ( $p = 0.08$ ) from low-sp, but mid-dp  $\delta^{13}C$  did not differ from either of the other two sites. The  $\delta^{15}N$  was most de-

**Table 3.** Mean ( $\pm$  SD,  $n = 3$ ) aboveground biomass and productivity of black spruce and vascular understory.

Site	Black spruce		Understory	
	Biomass	Productivity	Biomass	Productivity
High-np	4422 $\pm$ 360a	42.3 $\pm$ 4.2c	7.9 $\pm$ 3.9a	4.8 $\pm$ 2.3a
Mid-dp	3394 $\pm$ 560b	54.8 $\pm$ 7.6a	1.0 $\pm$ 0.5b	0.9 $\pm$ 0.7b
Low-sp	4607 $\pm$ 230a	46.0 $\pm$ 5.2b	10.9 $\pm$ 4.2a	4.9 $\pm$ 3.6a

**Note:** High-np, no permafrost; mid-dp, mid-elevation deep permafrost; low-sp, low-elevation shallow permafrost. Means followed by the same letter are not significantly different at  $p < 0.05$  (one-way ANOVA, LSD). Biomass, g C·m<sup>-2</sup>; productivity, g C·m<sup>-2</sup>·year<sup>-1</sup>.

**Table 4.** Mean ( $\pm$  SD,  $n = 10$ ) C and N concentrations, C:N ratio, and total C and N for soil horizons.

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

**Note:** High-np, no permafrost; mid-dp, mid-elevation deep permafrost; low-sp, low-elevation shallow permafrost. Comparisons are between sites for a horizon (one-way ANOVA, LSD). Means followed by the same letter are not significantly different at  $p < 0.05$ . Soil includes coarse and fine roots. Mineral soil is measured to 5 cm below the A horizon.

pleted at high-np, but foliar N concentration did not differ across sites. Root N concentration was significantly greater at high-np than at 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 less vascular understory biomass and production at mid-dp. The spruce aboveground production differed significantly among sites (mid-dp > low-sp > high-np).

The C and N concentrations and total C and N contents 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 (results not shown), owing primarily to more C in the F–H and A horizons (Table 4).

## 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 at high-np. Permafrost affected decomposition and soil temperature 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).

In 2000, FP decomposition rates in trenched plots did not differ from control areas, but in 2001 the decomposition rate increased for mid-dp and low-sp at some depths. FP decomposition generally was slower in 2000 for surface filter papers than in 2001 (Table 5). Spruce foliage decomposition mirrored FP decomposition at similar depths in 2001.

## Soil respiration, moss photosynthesis, and root respiration

Soil CO<sub>2</sub> flux followed the seasonal soil temperatures at 10 cm during the growing season. The maximum proportional contribution from roots occurred around the maximum in soil temperature (Fig. 3). Darkened-chamber R<sub>sc</sub> in the 2001 growing season averaged 3.63  $\pm$  1.56, 2.66  $\pm$  1.06, and 2.49  $\pm$  1.18  $\mu\text{mol CO}_2\text{-C}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  at high-np, mid-dp, and low-sp, respectively, while R<sub>st</sub> averaged 1.40  $\pm$  0.45, 1.67  $\pm$  0.51, and 1.35  $\pm$  0.43  $\mu\text{mol CO}_2\text{-C}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  across the same sites (Fig. 3). Moss gross photosynthesis (P<sub>sm</sub>) decreased the R<sub>sc</sub> flux 14%, 8%, and 12% at the high-np, mid-dp, and low-sp sites, respectively. Modeled moss respiration accounted for 5%–10% of R<sub>sc</sub>.

Winter respiration decreased from the beginning of the winter until the snow-free season began in late April (Fig. 4). The average winter fluxes for control areas were 0.11  $\pm$  0.09 ( $n = 4$ ), 0.22  $\pm$  0.07 ( $n = 5$ ), and 0.22  $\pm$  0.10 ( $n = 5$ )  $\mu\text{mol CO}_2\text{-C}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  at high-np, mid-dp, and low-sp, respectively, and trenched plot fluxes averaged 0.10  $\pm$  0.09, 0.15  $\pm$  0.08, and 0.15  $\pm$  0.15  $\mu\text{mol CO}_2\text{-C}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  at high-np, mid-dp, and low-sp, respectively. Based on same-day comparisons,

**Table 5.** Mean ( $\pm$  SD,  $n = 15$ ) 1-year decomposition (% mass loss) of filter papers and spruce litter inside and outside trench plots.

Site	Filter paper				Spruce litter
	2000	2001			2001
	1–8.5 cm	1–8.5 cm	8.5–16 cm	16–23.5 cm	~4 cm
<b>Control</b>					
High-np	11 $\pm$ 10b&	39 $\pm$ 24b&	14 $\pm$ 0.11	1 $\pm$ 9b	19 $\pm$ 10a
Mid-dp	46 $\pm$ 3a	49 $\pm$ 19ab*	25 $\pm$ 0.21*	17 $\pm$ 16a*	29 $\pm$ 10b
Low-sp	32 $\pm$ 23ab&	55 $\pm$ 17a&	22 $\pm$ 0.14*	10 $\pm$ 14a	25 $\pm$ 9ab
<b>Trench</b>					
High-np	17 $\pm$ 0.12b	24 $\pm$ 23b	11 $\pm$ 0.15b	9 $\pm$ 15b	nd
Mid-dp	54 $\pm$ 0.22a&	81 $\pm$ 14a*	54 $\pm$ 0.24a*	54 $\pm$ 19a*	nd
Low-sp	39 $\pm$ 0.19a&	60 $\pm$ 20a	44 $\pm$ 0.23a*	13 $\pm$ 10b	nd

**Note:** High-np, no permafrost; mid-dp, mid-elevation deep permafrost; low-sp, low-elevation shallow permafrost. Treatment means followed by the same letter are not significantly different at  $p < 0.05$ ; “\*” indicates a significant difference between trench and control; “&” indicates a between-year significant difference for surface filter paper. nd, no data.

winter soil respiration at high-np was significantly less than at 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 estimated for control high-np (36 g C·m<sup>-2</sup>·year<sup>-1</sup>) and the two permafrost sites (54 g C·m<sup>-2</sup>·year<sup>-1</sup>). Trenched plot winter flux did not differ among sites (26 g C·m<sup>-2</sup>·year<sup>-1</sup>).

At every site, the integrated Rsc (soil respiration, control) respiration was significantly greater than Rst (microbial respiration, trenched plot), and the annual root respiration (Rr = Rsc – Rst) averaged 296  $\pm$  55, 206  $\pm$  67, and 192  $\pm$  72 g C·m<sup>-2</sup>·year<sup>-1</sup> at high-np, mid-dp, and low-sp, respectively (Fig. 5). The Rsc at high-np was also significantly greater annually than at mid-dp and low-sp (Fig. 5). This contradicted our prediction that greater decomposition rates would yield greater soil respiration. The Rst at mid-dp was significantly higher than at the other two sites.

The Rst (microbial respiration, trenched plot) and the average FP mass loss of the two deepest intervals (8.5–16 and 16–23.5 cm) were correlated (Fig. 6). When the relationship between Rst and trenched plot FP mass loss are used with control area FP decomposition (Fig. 6), the mid-dp heterotrophic respiration (172 g C·m<sup>-2</sup>) was still greater than for the other two sites (164 and 161 g C·m<sup>-2</sup> at low-sp and high-np, respectively). Rst was unrelated to the amount of soil C.

In 2001, Rsc from June to September was significantly greater than in 2000 at all sites (results not shown), and the increase in Rst significant at two sites. Cooler soil temperatures at 10 cm in August and September 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

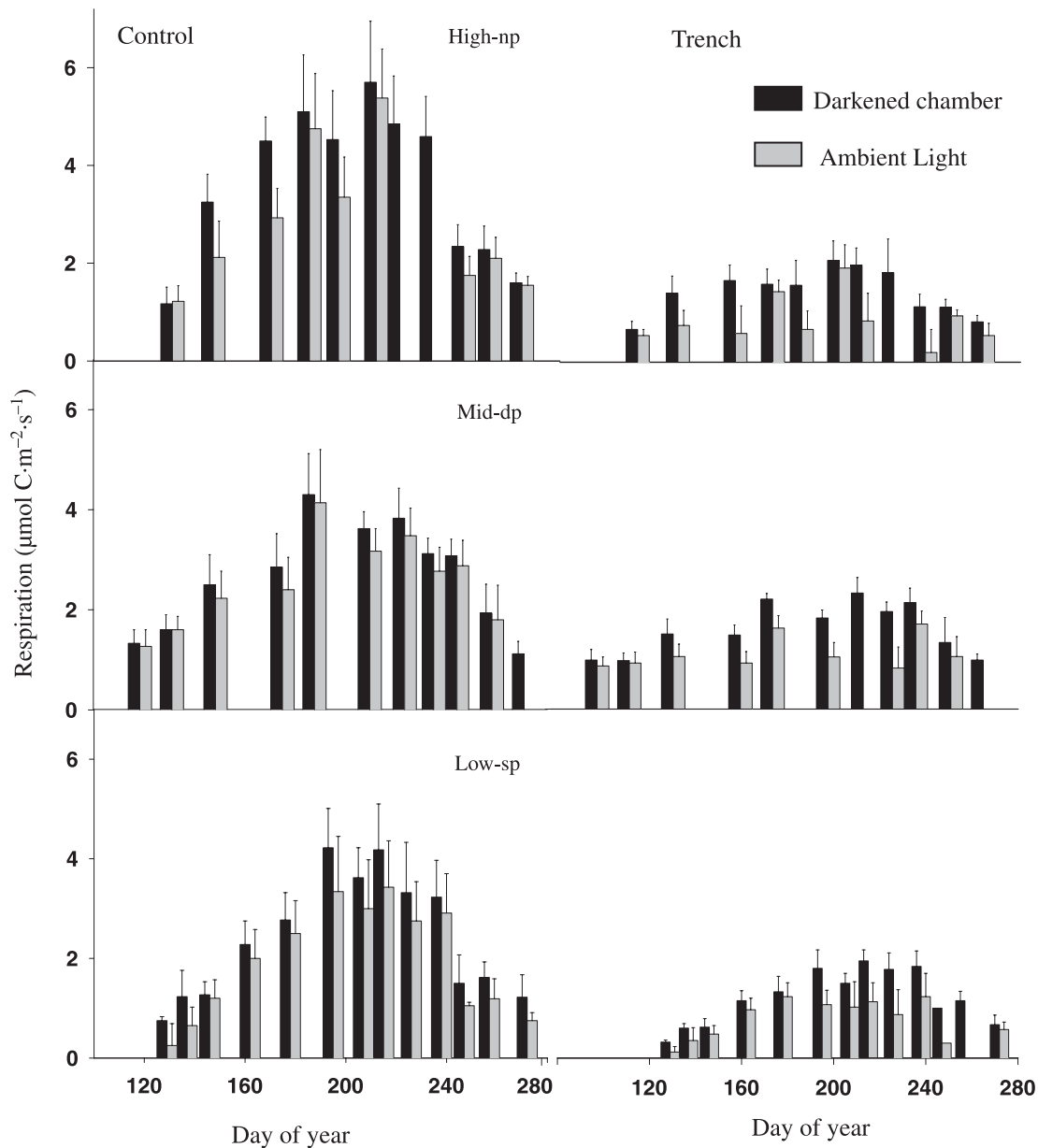
season 10-cm soil temperatures (Fig. 7a, 7b). The temperature sensitivity of Rsc was greater for high-np than for low-sp, and Rst respiration at mid-dp was more temperature sensitive than for the other two sites (Table 6). Trenching significantly decreased the temperature sensitivity of respiration at all sites. The moss respiration (Rsm) did not affect trends in respiration across sites. 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), and the components of TBCA did not affect overall trends. Aboveground litterfall was significantly greater ( $p = 0.02$ ) at mid-dp (58  $\pm$  14 g C·m<sup>-2</sup>·year<sup>-1</sup>,  $n = 6$ ) than at low-sp (41  $\pm$  11 g C·m<sup>-2</sup>·year<sup>-1</sup>), but neither differed from high-np (48  $\pm$  11 g C·m<sup>-2</sup>·year<sup>-1</sup>). Annual root respiration was significantly greater at high-np than at either permafrost site using the trenched plot method, and high-np root respiration was greater than at low-sp using the TBCA method (Fig. 8).

## Discussion

### Decomposition and soil respiration

Contrary to our prediction, soil respiration was lower where microbial respiration and filter paper decomposition were the greatest. From literature estimates of black spruce soil respiration, a relationship similar to the one we found 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<sup>-2</sup>·year<sup>-1</sup> fits between the median (287 g C·m<sup>-2</sup>·year<sup>-1</sup>) and the mean (393  $\pm$  200 g C·m<sup>-2</sup>·year<sup>-1</sup>,  $n = 18$ ) 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. 2003; Ruess et al. 2003) (Table 7).

The greater soil respiration at high-np (high elevation, no permafrost) is the result of greater root respiration, and based on the foliar <sup>13</sup>C results, it 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

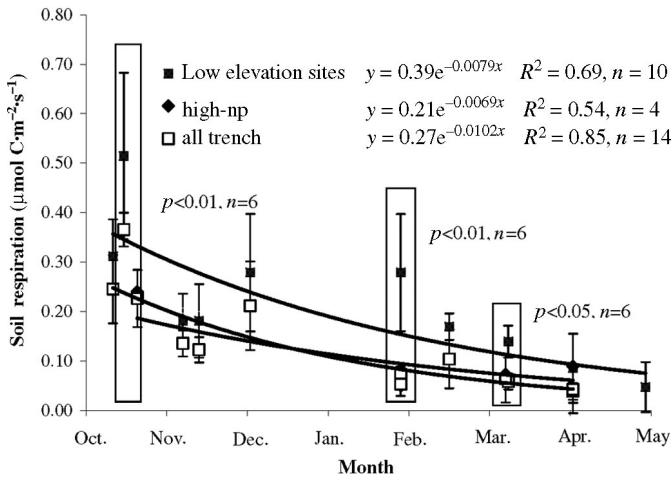
**Fig. 3.** Seasonal (2001 only) dynamics of measured darkened chamber and ambient light soil respiration ( $\mu\text{mol CO}_2\text{-C}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) efflux.

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 conducted in a 71-year-old dense ( $49 \text{ m}^2\cdot\text{ha}^{-1}$ ) red spruce stand (Risk et al. 2002). The general trend supports 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.

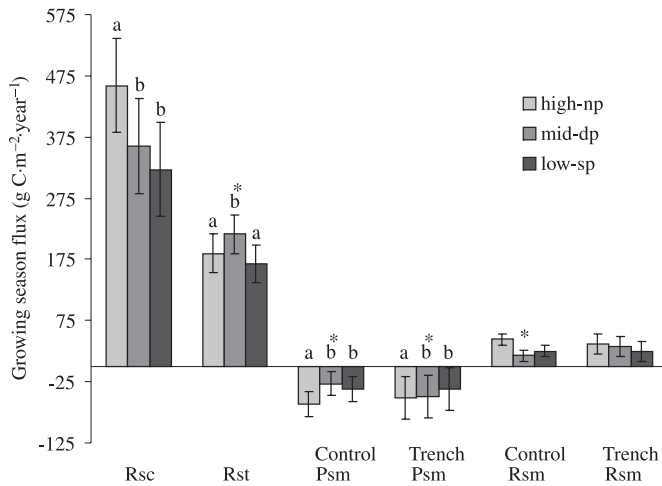
The total allocation to fine roots has been shown to increase in xeric conditions (Keyes and Grier 1981; Gower et al. 1992), but more often the proportional allocation is greater

where soil moisture is limiting (Santantonio and Hermann 1985; Comeau and Kimmins 1989). The latter trend in production is consistent with the proportional respiration trend in this study (Table 7). For all black spruce studies, the mean proportional root contribution reported is  $55\% \pm 11\%$  ( $n = 9$ ), without including TBCA estimates, which agrees with the trenched plot average of 55% for the three sites in the present study (Table 7). The studies located in Manitoba, where precipitation is greater, reported lower proportional contributions from roots (mean = 49%) than studies in Alaska (mean = 60%). However, given the differences in total respiration among regions, the absolute amount of C cycling through roots appears considerably higher in Alaska than in both Saskatchewan and Manitoba (O’Connell et al. 2003; Wang et al. 2002). To our knowledge, neither soil or root respiration has been examined with root production in forests across gradients in moisture; therefore, it is not possible

**Fig. 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 10 October 2000, the day after the first significant snowfall.



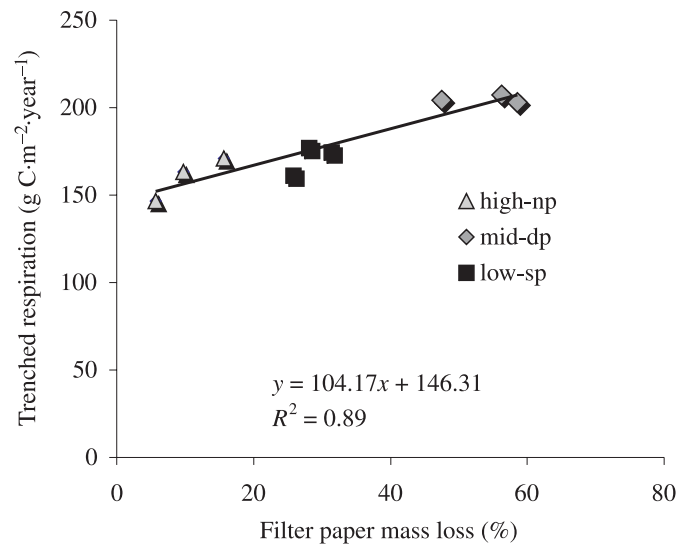
**Fig. 5.** Mean ( $\pm$  SD) respiration ( $\text{g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ) from control soil (Rsc), trench and microbial (Rst), moss (Rsm), and moss gross photosynthesis (Psm). Significant differences between sites are denoted by different letters ( $n = 6$ ); a significant influence of trench treatment is indicated with an asterisk (\*) ( $n = 3$ ).



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 where both fine-root production and soil respiration were depressed by the addition of N fertilizer (Haynes and Gower 1995). In N-limited systems, however, above-ground production generally increases with N fertilization. In the present study, the black spruce aboveground production was unrelated to soil respiration but followed the trend in microbial respiration (mid-dp > low-sp > high-np) and decomposition. The  $^{15}\text{N}$  of foliage was also most depleted at

**Fig. 6.** Relationship between annual trenched plot soil respiration ( $\text{g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ) and annual percent mass loss of filter papers at two depths (average of filter papers at 8.5–16 and 16–23.5 cm from moss surface) for 2001.



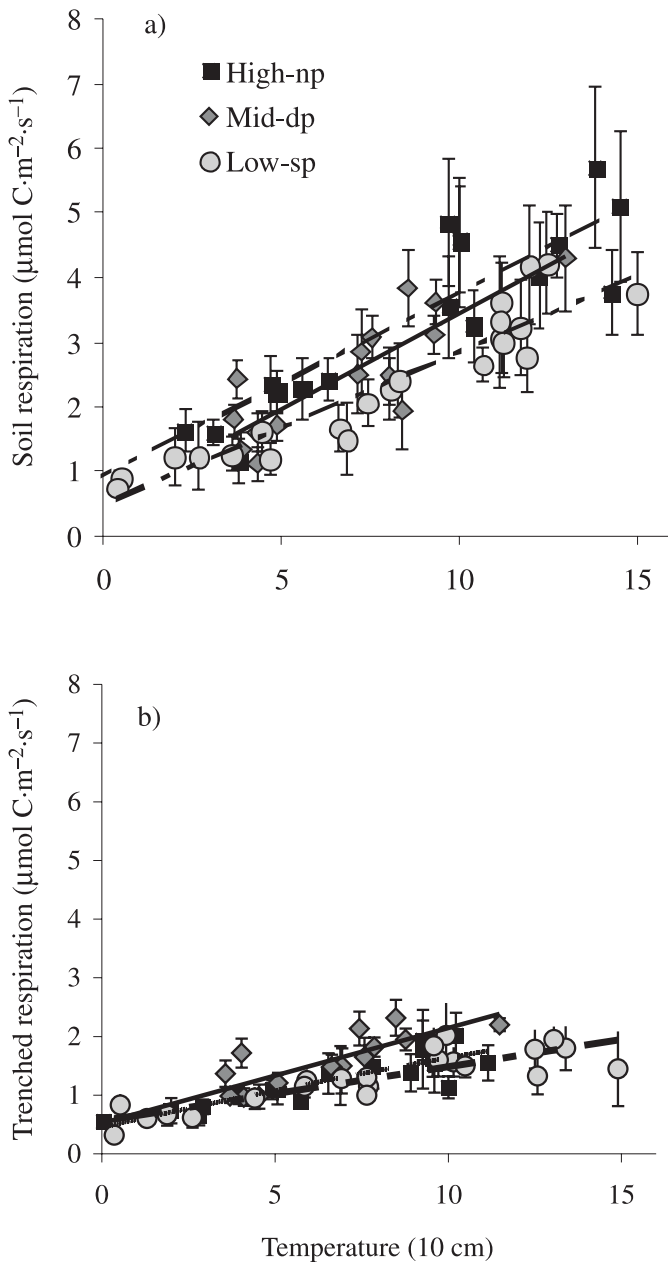
high-np, suggesting less available N (Garten and Van Miegroet 1994). Faster soil organic matter turnover may result in greater N availability and increased aboveground growth, but less C allocation to roots.

**Soil environment and constraints on decomposition**

Temperature and moisture may have influenced patterns in filter paper decomposition. The slow rate of decomposition in the high-np (high elevation, no permafrost) 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 at the high-np site were least depleted in foliar  $^{13}\text{C}$ , suggesting greater moisture stress (Lajtha and Michener 1994). Lower soil moisture at high-np than at the other two sites was expected, because the frost at mid-dp (mid-elevation, deep permafrost) and low-sp (low elevation, shallow permafrost) degrades over the growing season, possibly providing soil moisture to the plants and microbes. Also, the slope at high-np (12%) was greater than at the other two sites (8% and 3%), resulting in increased snowmelt runoff.

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 (Fisher and Gosz 1986). Researchers using trenched plots should consider using a decomposition proxy to estimate any decomposition artifacts caused by root exclusion.

**Fig. 7.** Darkened chamber respiration ( $\mu\text{mol CO}_2\text{-C}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) increase with temperature in (a) control ( $n = 6$ ) and (b) trench areas ( $n = 3$ ).



**Winter respiration**

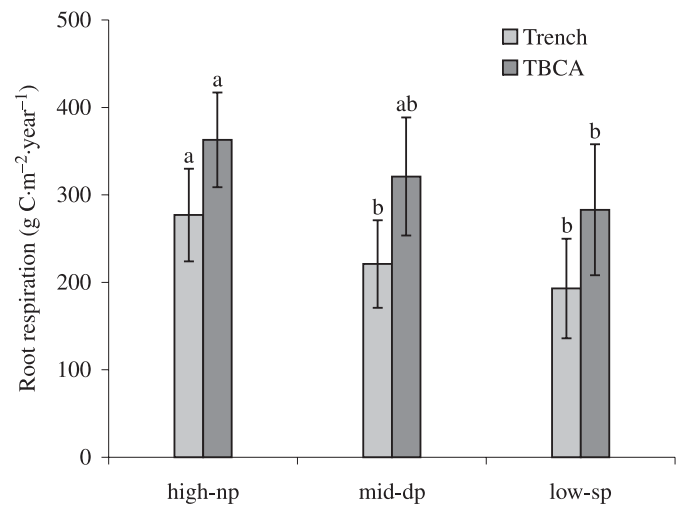
Our estimated winter (snow-cover season) respiration of 36–54  $\text{g C}\cdot\text{m}^{-2}$  was similar to values reported in Winston et al. (1997) for black spruce and jack pine forests (40–55  $\text{g C}\cdot\text{m}^{-2}$ ) and by Wang et al. (2002) (25–35  $\text{g C}\cdot\text{m}^{-2}$ ; Table 7) for Manitoba black spruce. The lower winter respiration at high-np than at the two permafrost sites was surprising (Fig. 7), considering the warmer winter soil temperatures and thicker layer of nonfrozen 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; Michaelson and Ping

**Table 6.** Linear regression coefficients of respiration ( $\mu\text{mol C}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) increase with temperature,  $R^2$  (coefficient of variation), and number of sample periods  $\times$  replicates.

Site	$b_0$	$b_1$	$R^2$	$n$
<b>Control</b>				
High-np	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
<b>Trench</b>				
High-np	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

**Note:** High-np, no permafrost; mid-dp, mid-elevation deep permafrost; low-sp, low-elevation shallow permafrost. Means followed by the same letter are not significantly different at  $p < 0.05$ . Trenched and control temperature sensitivity differed for all sites.

**Fig. 8.** Annual root respiration ( $\text{g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ) (mean  $\pm$  SD,  $n = 3$ ), estimated with trenched plots and total belowground carbon allocation method for 2001. Significant differences ( $p < 0.05$ ) among sites are denoted with different letters.



2003). The negative effect of root exclusion on winter respiration at two of the sites is consistent with results for arctic tundra (Grogan et al. 2001), but the exact causal relationships are unclear.

**Soil, microbial, and root response to temperature**

The warmer soil temperatures in 2001 than in 2000 elicited a greater increase in respiration from control than trenched areas at all sites. This observation might reflect the temperature sensitivity of root respiration (Boone et al. 1998; Lavigne et al. 2003; O’Connell et al. 2003) or that microbes were becoming substrate limited in 2001. O’Neill (2000) reported interannual soil respiration variability for mature Alaskan black spruce forests; however, Ruess et al. (2003) found no significant interannual variation in soil respiration despite considerable between-year soil temperature differences. A soil respiration response in a warm year may be dependent on how temperature and moisture interact (Ruess et al. 2003)

**Table 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.

Study	Location	Flux ( $\text{g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ )		% contribution		GS+winter
		GS <sup>a,b</sup>	Winter	Moss	Root <sup>c</sup>	
Schlenter and Van Cleve 1985	Alaska	369 (SL,U)				
O'Neill 2000 <sup>d</sup>	Alaska	627 (IC,M)		14	74 (RI)	
		505		21	63	
Ruess et al. 2003	Alaska	616 (IC, NM)			57 (DR), 86 (T)	
		624			57 (DR), 82 (T)	
		501			57 (DR), 90 (T)	
Present 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
D.W. Valentine, 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)	
		200			55 ( <sup>14</sup> C)	
Trumbore 2000 <sup>e</sup>	Manitoba	200				
Moosavi and Crill 1997	Manitoba	259 (SC, M)				

**Note:** Descriptions of the methods employed in other studies for measuring soil respiration and for estimating root respiration not found in the present paper. General reviews of methodology can be found in Norman et al. (1997) and Hanson et al. (2000).

<sup>a</sup>Respiration technique: soda lime (SL), IRGA closed system (IC), alkali absorption (AA), IRGA open system (IO), static chamber (SC).

<sup>b</sup>Moss treatment: unknown (U), moss included (M), removed (NM), or moss photosynthesis included (MP).

<sup>c</sup>Root respiration method: burn versus unburn (BU), direct measurement of roots (DR), trench plots (TP), total belowground carbon allocation (T), bomb carbon (<sup>14</sup>C), reconstruction from laboratory incubation (RI).

<sup>d</sup>Proportions of moss and root are part of submitted paper.

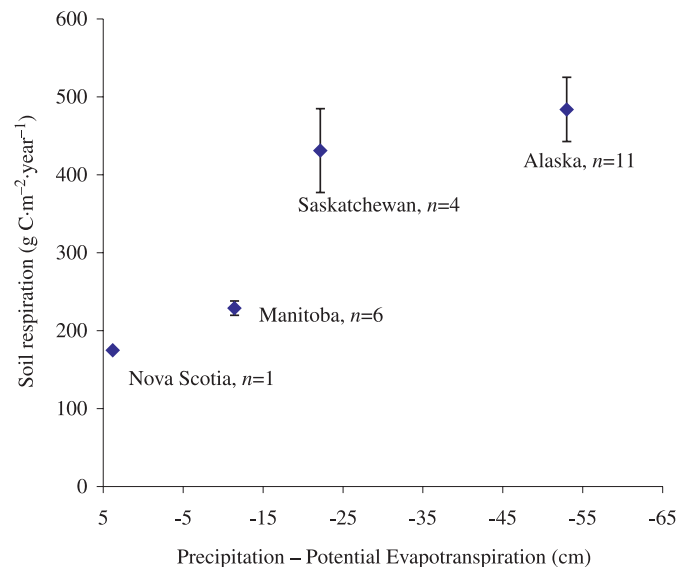
<sup>e</sup>Study reports recent carbon and not necessarily root, also the "recent carbon" is actually 50%–60%.

or on how quickly roots acclimate or microbes deplete C. For example, Jarvis and Linder (2000) and Mellilo et al. (2002) reported fairly rapid temperature acclimation of soil respiration in experimentally warmed forests. Acclimation may occur quickly with natural warming, which explains why soil respiration responds in some studies but not others.

### Annual moss photosynthesis and respiration

Moss function in our study was similar to that in other experiments in boreal systems, and moss gas exchange did not explain between-site differences in soil respiration. 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). 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 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  $14 \pm 3 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ , lower than the  $24 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  reported for a central Saskatchewan forest

**Fig. 9.** Relationship between moisture deficit (precipitation – potential evapotranspiration) and growing season soil respiration (mean  $\pm$  SE) for mature black spruce studies. Table 7 describes the studies in more detail.



(O'Connell et al. 2003), but similar to the 14–15 g C·m<sup>-2</sup>·year<sup>-1</sup> measured 166 km southeast of the study area (J. Harden, personal communication). Although our production and Psm values are similar to those in other studies, we note that 6% of measurements during the two growing seasons indicated a Psm of zero, which would result in zero Rsm.

## 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 interannual patterns in total respiration. The greater allocation below ground at the high-np (high elevation, no permafrost) site could be related to decreased moisture availability, as the trend in Fig. 9 indicates for different areas in North America, or root respiration variation among sites may simply reflect the differences in root N concentration. Burton et al. (1996) also found root N concentration explained root respiration patterns in a temperate forest, but they observed that greater net N mineralization co-occurs with greater root N concentration. Our indirect estimates of N availability (similar foliage N concentration and lower  $\delta^{15}\text{N}$  and lower decomposition rate at high-np) suggest the root N concentration at high-np was an adaptation to environment and not the 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 that the high root N concentration and greater respiration are an expression of a combination of cold weather acclimation, moisture limitation, and root morphology. If these soil respiratory patterns are indicative of changes that might occur with climate change, then increases in soil respiration might result from a net soil C loss, but more likely any increase will be due to adjustments in root respiration.

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