

Carbon allocation in boreal black spruce forests across regions varying in soil temperature and precipitation

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Abstract

A common hypothesis for northern ecosystems is that low soil temperatures inhibit plant productivity. To address this hypothesis, we reviewed how separate components of ecosystem carbon (C) cycling varied along a soil temperature gradient for nine well-drained, relatively productive boreal black spruce (*Picea mariana* Mill. [B.S.P.]) forests in Alaska, USA, and Saskatchewan and Manitoba, Canada. Annual soil temperature [expressed as soil summed degree days (SDD)] was positively correlated with above-ground net primary productivity (ANPP), while negatively correlated with total below-ground carbon flux (TBCF). The partitioning of C to ANPP at the expense of root processes represented a nearly 1:1 tradeoff across the soil temperature gradient, which implied that the amount of C cycling through these black spruce ecosystems was relatively insensitive to variation in SDD. Moreover, the rate at which C accumulated in the ecosystem since the last stand replacing fire was unrelated to SDD, but SDD was positively correlated to the ratio of spruce-biomass:forest-floor-mass. Thus, plant partitioning of C and the distribution of ecosystem C were apparently affected by soil temperature, although across regions, precipitation co-varied with soil temperature. These two factors likely correlated with one another because of precipitation's influence on soil heat balance, suggesting that a soil temperature–precipitation interaction could be responsible for the shifts in C allocation. Nonetheless, our results highlight that for this boreal ecosystem, ANPP and TBCF can be negatively correlated. In tropical and temperate forests, TBCF and ANPP have been reported as positively correlated, and our results may reflect the unique interactions between soil temperature, forest floor accumulation, rooting depth, and nutrient availability that characterize the black spruce forest type.

Keywords: allocation, biomass, black spruce, boreal, carbon, productivity, respiration, root, soil

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Introduction

The unknown effect of climate warming on the carbon (C) budgets of high latitude ecosystems creates a significant uncertainty for predicting the future concentrations of atmospheric carbon dioxide (CO₂) (Cox *et al.*, 2000). Scientists have predicted that climate warming

could increase heterotrophic respiration, or the rate that soil microbes decompose soil organic matter, resulting in greater CO₂ efflux to the atmosphere (Goulden *et al.*, 1998). High latitude ecosystems are expected to warm significantly during the next century in response to greenhouse gas climate forcing (ACIA, 2004), which may cause a decrease in the soil organic matter that has accumulated under cold and wet soil conditions (Harden *et al.*, 1992). The transfer of the high-latitude soil C pool to the atmosphere is a

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significant potential feedback to climate warming (Dixon *et al.*, 1994).

A key uncertainty for predicting ecosystem response to warming is whether any warming-mediated increase in heterotrophic respiration is offset by an associated increase in net primary productivity (NPP). Across forest ecosystems within the boreal biome, above-ground net primary productivity (ANPP) has been found to increase with soil (Van Cleve & Yarie, 1986) and mean air temperatures (Gower *et al.*, 2001). Increased NPP may be directly caused by warmer temperatures and longer growing seasons, or indirectly caused by the increased nutrient availability that co-occurs with greater microbial activity (Bonan, 1992). Thus, cold soil temperatures have been hypothesized to limit NPP in the boreal biome directly and indirectly (Van Cleve & Yarie, 1986; Bonan, 1992). Based on a soil warming experiment, cold soil temperatures have specifically been identified as a limiting factor to the ANPP of black spruce (*Picea mariana* Mill. [B.S.P.]) (Van Cleve *et al.*, 1990), one of the most common tree species in the North American boreal forest (Viereck & Johnston, 1990). In response to the soil warming treatment of Van Cleve *et al.* (1990), an increase in heterotrophic respiration likely exceeded that of NPP because after 3 years, the amount of C lost from soil organic matter was more than 10 times that stored in biomass via increased ANPP (estimated from data in Hom, 1986; Van Cleve *et al.*, 1990). In another study, eddy-covariance measurements showed that a mature black spruce forest lost C during warm years because ecosystem respiration increased while photosynthesis was relatively insensitive to warming (Goulden *et al.*, 1998). Because black spruce forests store more C than other forested boreal ecosystems (Gower *et al.*, 1997), heterotrophic respiration surpassing NPP in this ecosystem may cause a significant decline in the overall C storage of the North American boreal biome.

As temperatures increase, the balance between NPP and heterotrophic respiration could also be affected by how boreal plants allocate C among various tissues. Plant C allocation affects decomposition rates through litter composition (e.g. wood vs. leaves) and the spatial location of litter inputs (e.g. surface leaf litter vs. soil root litter) in ways that affect overall heterotrophic respiration (Giardina *et al.*, 2005; Ryan & Law, 2005). In boreal forests, plant allocation appears responsive to evaporative balance (Lapenis *et al.*, 2005), and to soil warming (Jarvis & Linder, 2000). However, the variability in C allocation and its potential influence on ecosystem C dynamics remains unclear because few studies have examined all components of ecosystem C cycling (Gower *et al.*, 2001).

Here, we reviewed how black spruce allocation and C cycling varied along a soil temperature gradient that

spanned three regional study areas. The study areas included central Alaska (Ruess *et al.*, 2003; Vogel *et al.*, 2005; Schuur & Trumbore, 2006), southern Saskatchewan (O'Connell *et al.*, 2003a, b), and northern Manitoba (Wang *et al.*, 2002; Bond-Lamberty *et al.*, 2004a, c). The study areas also represent a regional precipitation gradient (Vogel *et al.*, 2005). However, soil temperature was treated as the independent variable because it was measured across studies, generally varies with precipitation in high latitudes (Zhuang *et al.*, 2001), and has been commonly used to formulate hypotheses regarding C cycling in boreal ecosystems (Van Cleve *et al.*, 1990; Bonan, 1992; Goulden *et al.*, 1998; Jarvis & Linder, 2000). Our objective was to examine whether warmer soils corresponded to shifts in plant C allocation, and increased forest productivity and soil CO₂ efflux. We also discuss other factors (precipitation and stand development) that could be affecting C allocation in the black spruce forest type.

Methods

Forest-type selected for review

We focused on studies where black spruce was the dominant canopy species and its C-cycling was greater than 40% of the total ANPP. This productivity criterion eliminated muskeg or paludified 'black spruce' forests that were poorly drained and open canopied, characteristics that allow Sphagnum mosses to dominate ecosystem NPP (Wang *et al.*, 2002; O'Connell *et al.*, 2003a). This criterion also led us to focus on mature forests (>70 years old) (Table 1), because black spruce generally regenerates concurrently with deciduous tree species after stand replacing fires (Viereck & Johnston, 1990), and this deciduous component can represent the majority of ecosystem productivity early in stand history (Bond-Lamberty *et al.*, 2004c).

We included both published ($n = 7$ study sites) and unpublished data ($n = 2$ study sites), but the unpublished data is available online (www.lter.uaf.edu, Appendix A). In order to be used in this comparison, a study needed to include growing season soil CO₂ efflux (in boreal forests this typically includes understory plant respiration as well as root respiration, and microbial respiration) and ANPP of the black spruce overstory, vascular understory, and mosses. Studies that approach this level of C budget detail in boreal forests are relatively rare (Gower *et al.*, 2001). Field measurements were conducted between 1998 and 2002 (Appendix B). The study sites had similar understory and moss species composition. For nearly all studies, feathermoss [*Hylocomium splendens* and *Pleurozium schreberii* (Bird.) Mitt.] formed a continuous ground cover. However, in

Table 1 General stand characteristics of the black spruce forests in this study

Region	Study no.	Age	Basal area	Average diameter (cm)	Trees ha ⁻¹	Soil temperature 10 cm	
Alaska	1	120	29	7.4	6588	784	
		75	26	6.4	8000	808	
		110	30	7.5	6940	838	
	2	78	15	3.9	12 800	696	
		3	75	8	5.4	3490	633
		4	180	12	9.3	1800	No data
Saskatchewan	5	120	44	8.9	7100	1032	
Manitoba	6	70	38	5.5	15 850	872	
		150	40	8.5	7100	1106	

Note: Basal area equals m²ha⁻¹ and soil temperature equals the sum of daily mean temperature at 10 cm soil depth when temperature >0 °C.

study 3, lichen species (*Cladonia* spp.) occupied between 30% and 50% of the ground surface (Mack *et al.*, 2008). Understory vascular plants that contributed the greatest amount to understory productivity were *Vaccinium vitis-idaea* (L.), *Ledum groenlandicum* (L.), and *Vaccinium uliginosum* (L.).

Each of the studies reported the mineral soil texture as silt loam, with studies 2 and 3 reporting rocks in the soil profile (Schuur & Trumbore, 2006). The silt loam soils accrued from either eolian (studies 1–3 in Table 1) or fluvial deposition processes (studies 4–6). Mineral weathering was described as minimal at all study sites, likely because of the cold soil temperatures and relatively young age (~10 000–15 000 years) of the soils (Harden *et al.*, 1992). Thick organic horizons (10–35 cm) of partially decomposed plant tissues were described for each study, a characteristic common to the black spruce forest type (Vioreck & Johnston, 1990). Because of deep organic layers and shallow permafrost depths, the soils of study sites in Alaska were classified as Typic Historthels (USDA Soil Conservation Service, Soil Survey Staff, 1999). For the Canadian sites, the lack of permafrost in the near surface soil horizon, and the presence of a water table within 100 cm of the soil surface, resulted in the sites being classified as Typic Cryaquepts.

Long-term seasonal air temperature and moisture patterns in each study area reflected the strong regional gradients in the North American boreal forest. In general, mean annual temperature declines with increasing latitude, while precipitation decreases from east to west (Vioreck & Johnston, 1990). For describing long-term patterns, monitoring stations at Fairbanks, AK; Thompson, Man.; and Prince Albert, Sask. were used. Each station recorded values for at least 20 years. Soil temperature was also monitored at 10 cm depth in each region by individual studies, and differences among sites within a region likely reflected local variation in

elevation, topographic position, and depth to permafrost (Zhuang *et al.*, 2001). The 10 cm depth was used to develop the temperature index 'summed soil degree days' (SDD) for each site, which was defined as the sum of all daily mean temperatures above 0 °C. For one study (Bond-Lamberty *et al.*, 2004c), the soil temperature from a nearby eddy-flux system (Goulden *et al.*, 1998; Dunn *et al.*, 2007) was used because onsite soil temperature measurements were only made intermittently over the growing season. Only soil temperatures from the year of CO₂ efflux measurements were used in the analysis.

Net primary production (NPP) was estimated as the annual biomass increment of the overstory stems and branches, new foliage of the overstory and understory, bryophytes, and roots. None of the studies estimated herbivory, but it is generally assumed to be low in boreal forests except during major insect outbreaks (Gower *et al.*, 2001), which did not occur during any of the studies. All studies estimated overstory wood increment (stem + branch) (wood NPP) by collecting tree cores at 1.37 m from the ground, and then measuring the 5-year, average tree-ring increment. The increment was scaled to biomass with regional allometric relationships between tree diameter and tissue mass, and then the tissue amount was scaled to a unit area using stand density estimates. New foliage growth (foliage NPP) was estimated in two ways – (i) using new foliage allometric equations developed for each site or (ii) litterfall traps. In the latter case, the amount of foliage that annually falls as litter was assumed to equal the annual production of new foliage. In some studies, the litter was not separated into components, thus a ratio of litterfall to conifer foliage was developed from Gower *et al.* (1997) and Bond-Lamberty *et al.* (2004c). If a choice existed between litterfall and allometric equations, the litterfall estimate was used because it was the most consistently available across studies. Understory

NPP was collected from harvested plots and included both new twig and foliage growth. Bryophyte NPP was estimated using screens (O'Connell *et al.*, 2003a), cranked wires (e.g. Clymo, 1970; Bond-Lamberty *et al.*, 2004c), total moss growth referenced to *H. splendens* (Michelle C. Mack, unpublished) or annual estimates of moss net photosynthesis (Vogel *et al.*, 2005). A summary linking methods to each study site is available in Appendix A.

Forest floor mass was estimated by collecting organic material from the surface to the mineral soil layer for a known surface area. The forest floor layer was equivalent to the Oi and Oe soil horizon designation (USDA Soil Conservation Service, Soil Survey Staff, 1999). These horizons consisted of dead roots, moss fragments, and other identifiable tissues, but live coarse roots were removed from the samples. The forest floor layer generally accumulates between fire events that return on average at 75–120-year intervals (Bond-Lamberty *et al.*, 2004c; Kane *et al.*, 2005).

For estimating soil surface CO₂ efflux (R_s), all studies used a portable chamber system that was coupled to an infrared gas analyzer (IRGA). Each system was vented to allow for pressure equilibration, but was otherwise 'closed,' and all used a LICOR (Lincoln, NE) IRGA. The similarity in basic methodology and instrumentation likely minimized the potential for among-site differences to arise from differences in measurement technique (Janssens *et al.*, 2000). Researchers either scaled to annual estimates using efflux–temperature response curves and continuous soil temperature measurements, or by interpolating between time-points. The two scaling methods return similar results in this forest type because of the strong overlap in seasonal changes of soil temperature and CO₂ efflux (Vogel *et al.*, 2005). Most studies eliminated the respiratory contribution of mosses and understory vascular plants by clipping these plants at the soil surface. For those studies that included understory respiration in R_s , we used Ryan *et al.*'s (1997) estimates of the ratio between understory aboveground production and annual respiration in black spruce forests to calculate annual understory respiration (Appendix B). The understory respiration was then subtracted from the annual R_s estimate, and represented 5–15% of annual soil CO₂ efflux.

Spruce belowground allocation was determined from soil CO₂ efflux and litterfall measurements using the total belowground carbon flux (TBCF) method (Raich & Nadelhoffer, 1989; Litton *et al.*, 2007). In applying this method, the bulk of soil organic matter is assumed to be in steady state, and therefore, new litter inputs to the soil are matched by heterotrophic respiration outputs. Non-steady state conditions can also be examined if changes in C stocks (soil, roots) are taken into account

(Litton *et al.*, 2004; Ryan & Law, 2005); however, C stock changes are likely to be small for forests near the age we studied. We base this assumption on C-cycling measurements both with the eddy-covariance (Litvak *et al.*, 2003) and forest growth/heterotrophic respiration (Bond-Lamberty *et al.*, 2004c) techniques that indicate steady-state conditions develop at ~100 years of age in well-drained black spruce forests. Generally for black spruce forests, litterfall includes moss and understory production, and aboveground litterfall (Vogel *et al.*, 2005). TBCF was estimated by subtracting each of these litter inputs from soil CO₂ efflux. In addition to TBCF, each study also made direct estimates of the respiration of roots and heterotrophs. Researchers used different methods to separate components of soil CO₂ efflux, including root exclusion plots, isotope partitioning, or direct measurements of R_r . Estimates of R_r and heterotrophic respiration based on these methods were also compared across sites. The most commonly used separation method was the root exclusion technique ($n = 6$ study sites). Each study's partitioning and soil CO₂ efflux techniques are detailed in Appendix B.

Statistics

Statistical analysis was performed using STATISTICAL ANALYSIS SOFTWARE v. 9.0 (SAS Institute Inc., 1999). Regression analysis was used to test whether significant relationships ($P < 0.05$) existed between the components of the C cycle and soil temperature. Residuals were examined for heteroscedacity. Soil temperature (x -axis variable) was assumed to be measured with little error in comparison to the C-cycling measurements. To better examine shifts in allocation, Pearson's correlation analysis was used to examine the relationship between both TBCF and root respiration, and other components of the C cycle.

Results

The long-term mean annual air temperatures were identical for the Thompson, Mani. (−3.3 °C) and Fairbanks, AK (−3.3 °C) study areas, but the Prince Albert, Sask. area was considerably warmer (0.3 °C). However, Prince Albert and Fairbanks warmed faster in the spring than Thompson, while Fairbanks cooled faster in the fall than the other two areas (Fig. 1a). The regions also differed in annual precipitation, with Fairbanks (26 cm) receiving lower precipitation than Thompson (52 cm) or Prince Albert (42 cm) (Fig. 1b).

Sites with colder soil temperature had smaller diameter trees, which also resulted in basal area generally being lower in colder forests (Table 1). However, no correlation existed between site soil temperature and

stand density or age. This lack of correlation suggests that across these sites, soil temperature historically may have had a negative effect on tree size, but little discernible influence on forest stocking. Greater tree diameter in forests with warmer soils correlated to greater NPP of aboveground components of spruce growth (Tables 1 and 2). Stand basal area was also positively correlated with soil SDD ($R^2 = 0.84$, $P < 0.001$, not shown).

Wood and foliage NPP were positively correlated with soil SDD (Fig. 2a), as was total aboveground vascular production ($NPP = 0.19x - 68$, $R^2 = 0.81$, $P < 0.001$,

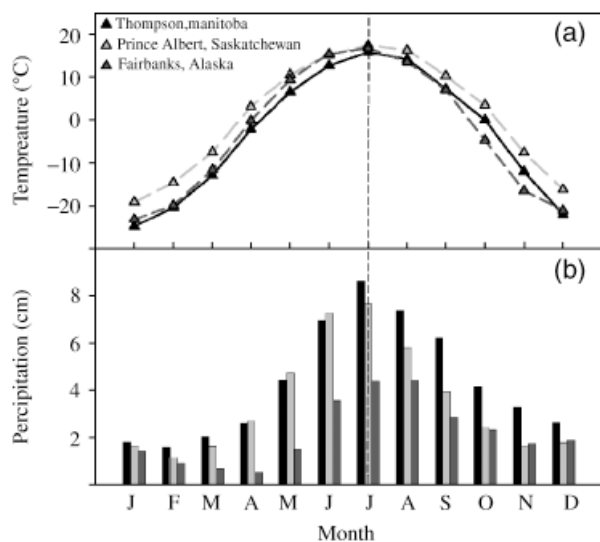


Fig. 1 Twenty-year mean monthly temperature (a) and precipitation (b) for Thompson, Manitoba; Prince Albert, Saskatchewan; and Fairbanks, Alaska. Study area color-coding is the same for panels (a) and (b).

not shown) and total aboveground ecosystem production (cryptogamic species included, $NPP = 0.19x - 55$, $R^2 = 0.74$, $P < 0.01$, not shown). Soil CO_2 efflux was negatively correlated with SDD, a relationship driven

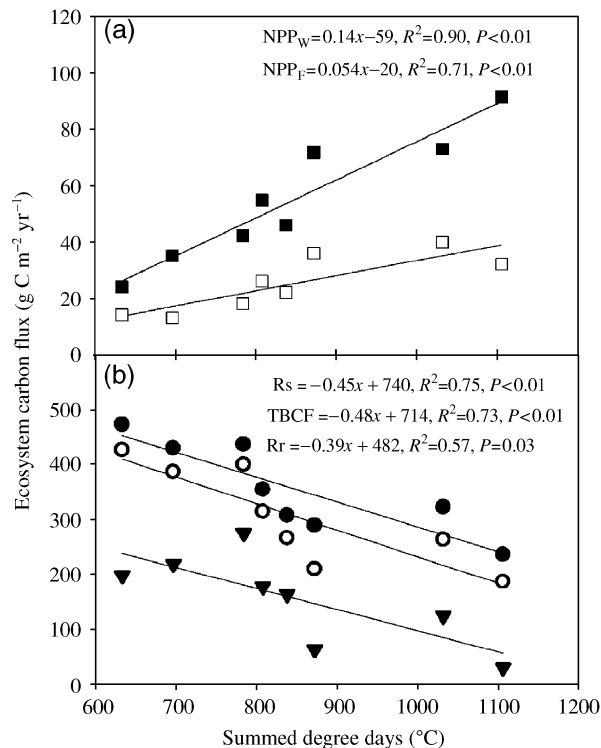


Fig. 2 Relationship between summed degree days ($^{\circ}C$) at 10 cm; and (a) aboveground wood production (wood NPP) (square, closed) and foliage (foliage NPP) (square, open), (b) soil carbon dioxide efflux (R_s) (circle, closed), total belowground carbon flux (TBCF) (circle, open) and root respiration (R_r) (triangle, closed) measured with a variety of methods.

Table 2 Root (R_r) and microbial (R_h) components of soil CO_2 efflux ($g C m^{-2} yr^{-1}$) separated with a variety of methods and total belowground C flux (TBCF) and net primary production ($g C m^{-2} yr^{-1}$) of stands in three regions

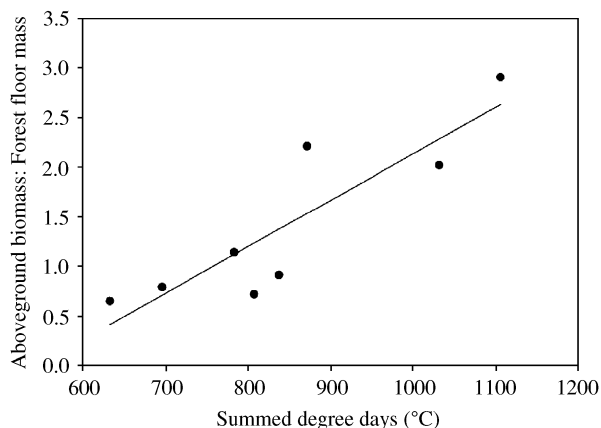
Region	Study no.	Soil CO_2 efflux				Net primary production (NPP)							
		Total soil	'Root' R_r	Microbial R_h	TBCF	NPP _W	NPP _F	NPP _U	NPP _B	NPP _{FR}	NPP _{CR}	NPP _{VA}	NPP _{TA}
Alaska	1	436	275	161	399	42	18	5	14	—	—	65	79
		354	177	177	314	55	26	1	13	—	—	82	95
		307	163	144	266	46	22	5	14	—	—	73	87
	2	429	219	210	386	35	13	15	15	—	—	63	78
Saskatchewan	3	472	198	274	426	24	14	19	13	—	—	57	70
	4	624	315	309	566	27	5	21	32	168	—	53	85
Manitoba	5	322	124	198	263	73	40	2	17	107	10	115	132
Manitoba	6	289	63	226	210	72	36	16	27	79	89	124	151
		236	30	206	186	92	16	23	12	37	36	130	142

Subscripts of NPP denote wood (W, stems + branches), foliage (F), understory (U), bryophytes (B), fine root (FR), coarse root (CR) production, vascular aboveground (VA), and total aboveground (TA) production. Citations for each study number are found in Appendix A.

Table 3 Pearson's correlation coefficients for significant linear relationships ($P < 0.05$) between total belowground carbon flux (TBCF) ($n = 9$) and other components of carbon cycle

Dependent variable	Independent variable	Intercept	Slope	r	P -value
TBCF	NPP _W	355	-3.35	0.88	**
	NPP _F	41.3	-0.11	0.88	**
	NPP _{VA}	658	-3.22	0.87	***

Note: P -values designated ** $P < 0.01$, *** $P < 0.001$. Definitions for independent variable abbreviations are found in Table 2.

**Fig. 3** The ratio of aboveground biomass to forest floor mass vs. summed soil degree days at 10 cm for mature black spruce forests.

by a significant decline in TBCF with increasing SDD (Fig. 2b). The vascular understory and bryophyte NPP were unrelated to SDD.

An increase in an aboveground component of ecosystem C cycling corresponded with a decrease in soil CO₂ efflux and TBCF. For example, TBCF was negatively correlated with wood, foliage, and total vascular NPP (Table 3). These same aboveground components of NPP were also negatively correlated to root respiration (R_r) ($P < 0.02$ in all cases, not shown), despite R_r being derived from multiple methods used to partition soil CO₂ efflux into components (Appendix B). Understory components of NPP were not significantly correlated to TBCF.

The aboveground and forest floor biomass distribution suggested that C cycling over the long-term appeared to be sensitive to soil temperature in a manner similar to that of the annual C cycle. The aboveground biomass to forest floor ratio increased significantly with soil temperature (Fig. 3); however, the rate of total C accumulation [(aboveground black spruce biomass + forest floor)/stand age] displayed no significant trend

Table 4 Aboveground spruce biomass (ABIO) and forest floor mass (FF) (gC m⁻²) for black spruce forests in three boreal regions

Region	Study	Mass		
		FF	ABIO	
Alaska	1	3890	4420	
		4730	3390	
		5070	4610	
	2	2160	1700	
		3	1790	1160
		5	3350	6760
Manitoba	6	2500	5520	
		2500	7250	

Note: Details of stand characteristics are found in Table 1. Study 4 is not included in this analysis because forest floor mass was not measured.

with SDD (not shown). Thus, the primary influence of soil temperature across the gradient was on ecosystem C distribution rather than the total rate of C accumulation (Table 4).

Discussion

Annual C cycling

If forest productivity in black spruce ecosystems is inhibited by cold soil temperatures that reduce the length of the growing season, or depress decomposition and limit nutrient availability (Van Cleve *et al.*, 1990; Bonan, 1992), then a reasonable hypothesis is that both aboveground primary productivity and root respiration should be greater in areas with warmer soils. In partial support of this hypothesis, total aboveground production increased with warmer soil temperatures (Fig. 2). However, spruce allocation belowground decreased, whether measured with TBCF or other methods for separating root respiration from soil CO₂ efflux. In this study, greater allocation belowground in colder soils could represent a general model of plant C allocation, where photosynthate is preferentially allocated to the plant organ (roots) responsible for acquiring some resource (e.g. moisture or nutrients) that is limiting in cold soils (Giardina *et al.*, 2005; Litton *et al.*, 2007).

The negative correlation in this study between aboveground productivity and TBCF is contrary to positive relationships between the two fluxes globally (Raich & Nadelhoffer, 1989; Giardina *et al.*, 2005; Litton *et al.*, 2007), although individual species and genera can exhibit a negative correlation between above- and belowground allocation (McDowell *et al.*, 2001; Reich & Bolstad, 2001; Rodeghiero & Cescatti, 2005; Palmroth

et al., 2006). In regional or global analyses, positive relationships between ANPP and TBCF may correspond to an overall increase in gross primary productivity (GPP) (Litton *et al.*, 2007). For an individual species, a regional change in canopy photosynthesis may have less of an effect on the ANPP:TBCF ratio than does a shift in allocation that compensates for nutrient or moisture limitations (Giardina *et al.*, 2005). These limitations can be particularly acute in black spruce ecosystems because of the resource limitations created by the thick organic layer. The organic soil layer in black spruce forests mostly consists of root and moss fragments (Trumbore & Harden, 1997), materials that effectively absorb available moisture and insulate deeper mineral soils. Both attributes keep soils deeper than ~50 cm frozen during most of the growing season (Zhuang *et al.*, 2001), which may be why fine roots in mature black spruce forests are found almost entirely in the forest floor (Steele *et al.*, 1997; Ruess *et al.*, 2003). Rooting in organic materials requires spruce to gain nutrients from substrates with high C:N ratios (Bonan, 1992). Thus, to overcome a slow rate of nutrient release, black spruce may need to allocate more C to root processes in areas where soil temperatures are cold.

In each study area, we previously reported positive correlations between soil CO₂ efflux and soil temperature within a growing season (O'Connell *et al.*, 2003a; Bond-Lamberty *et al.*, 2004a; Vogel *et al.*, 2005); however, in this review greater annual soil CO₂ efflux occurred in areas with colder soils. Although this pattern appears unusual, it likely reflects that soil CO₂ efflux is both controlled by abiotic factors (temperature, moisture) and the carbohydrate supply to roots and soil heterotrophs (Ryan & Law, 2005). In a number of reviews, a positive relationship has not been found between mean annual temperature and soil CO₂ efflux for forested ecosystems (Janssens *et al.*, 2001; Campbell *et al.*, 2004; Bond-Lamberty *et al.*, 2004b); however, Raich *et al.* (2006) reported an increase in soil CO₂ efflux and TBCF with mean air temperature across tropical forests. In a study similar to ours, Rodeghiero & Cescatti (2005) found a parabolic relationship between mean annual soil temperature and mean soil CO₂ efflux. Initially, soil temperature and soil CO₂ efflux were negatively correlated, but the slope became positive after ~7°C (Rodeghiero & Cescatti, 2005). Soil warming studies have also found that soil CO₂ efflux will often acclimate, or change to a lower rate of respiration per degree temperature, after prolonged warming (Jarvis & Linder, 2000; Rustad *et al.*, 2001; Bronson *et al.*, 2008). The mechanism for this acclimation has been ascribed to changes in belowground allocation (Luo *et al.*, 2001; Bronson *et al.*, 2008) and to depletion of available soil organic matter for decomposition (Melillo *et al.*, 2002).

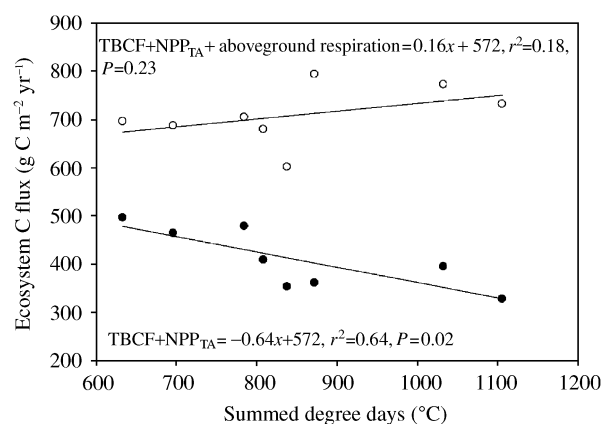


Fig. 4 The summed soil degree days vs. the total measured plant C flux (TBCF + NPP_{TA}) (closed circles), and an estimated C flux (open circles) that adds an indirect estimate of aboveground respiration (from Ryan *et al.*, 1997) to the measured fluxes.

One implication of our results is that spruce allocation could obscure relationships between soil temperature, aboveground productivity, and GPP. For example, because the ANPP and TBCF were negatively correlated across the gradient, and TBCF the greater flux, the sum of the two fluxes was negatively correlated to soil temperature (Fig. 4). This analysis of TBCF plus ANPP lacks aboveground respiration, and therefore, is not an estimate of GPP. However, an indirect estimate of aboveground respiration can be made with the aboveground productivity to aboveground respiration ratio (0.35) provided by Ryan *et al.* (1997) for black spruce forests. Summing the estimated aboveground respiration, TBCF, and aboveground productivity for each forest indicates that the sum of these fluxes is slightly increasing (slope NS) across the soil temperature gradient (Fig. 4). This 'summed plant C flux' is an indirect measure of GPP (Ryan *et al.*, 1997), and our observation resembles the analysis of Valentini *et al.* (2000), who found that GPP estimated with the eddy-covariance method was similar among European forests across a latitudinal and air temperature gradient. Long-term eddy-covariance monitoring for black spruce forests also suggest that GPP is disconnected from aboveground productivity. For the site with the greatest aboveground productivity (Manitoba, Table 2), 10 years of inter-annual variation in GPP was unrelated to changes in annual stem growth (Rocha *et al.*, 2006; Dunn *et al.*, 2007).

Long-term C cycling

Ecosystem C accumulation in the biomass and soil organic layers suggested that ecosystem C storage was insensitive to soil temperature, which is similar to

trends in tropical forests (Raich *et al.*, 2006). Rather, C storage was apparently partitioned aboveground in warmer areas at the expense of C in the forest floor (Fig. 3, Table 4). Based on the annual fluxes, reduced rates of forest floor C accumulation in areas with warmer forest soils could be from both greater rates of decomposition and lower rates of root litter production. Across an annual air temperature gradient, Reed & Nagel (2003) also found that *Pinus sylvestris* forests accumulated similar amounts of total ecosystem C, but that the relative distribution of C shifted between the forest floor and aboveground biomass. In contrast, Van Cleve & Yarie (1986) found ecosystem C storage increased with decreasing soil temperatures across boreal ecosystems dominated by different vegetation types. Their observation might reflect differences among plant functional types in tissue decomposability or photosynthetic capacity (O'Connell *et al.*, 2003a), rather than the direct effect of soil temperature on decomposition and plant productivity. Although our results suggest there will be little change in C storage with soil warming, the potential ecosystem response to soil warming cannot be fully discerned with a gradient study that assumes steady state conditions (Dunne *et al.*, 2004). Moreover, mineral soil C was not examined in this review because it was measured to different depths across studies; however, previous work has demonstrated that the mineral soil C in black spruce systems decreases with increased average soil temperatures (Kane *et al.*, 2005), and microbial decomposition within deeper layers is sensitive to soil warming (Goulden *et al.*, 1998).

Potential limitations due to measurement or design

Since this is a review of studies mostly designed independently of one another, there is the potential that methodological differences could have affected results. For some measurements, significant overlap existed in methodology (e.g. wood and understory NPP, soil CO₂ efflux) (Appendix A, B), thus the relationships based on these measures are likely to be robust. In the case of bryophyte NPP, methodology and intensity of measurement varied significantly among studies; however, bryophytes were a relatively small fraction of ecosystem NPP and measurement discrepancies were unlikely to have significantly affected overall results. For foliage NPP, estimates from the two methods employed (litterfall traps and allometric equations) have been reported to be significantly correlated in black spruce forests, but the relationship was not 1:1 (Bond-Lamberty *et al.*, 2004c). In the case of conifers, deviation from unity may reflect that litterfall is an integrated measure of foliage production, whereas allometric equations only capture foliage growth for the year of tree harvest. In

effect, the new foliage growth and litterfall could be functioning at a different timestep to one another.

Our ability to infer direct causality between soil temperature and spruce C allocation is limited because each region has different patterns of precipitation (Fig. 1), and soil moisture availability may also affect spruce C allocation (Vogel *et al.*, 2005). However, in these relatively well-drained black spruce forests, soil temperature effectively integrates both precipitation and air temperature (Zhuang *et al.*, 2001). During the winter, snow cover decreases soil heat loss because snow insulates the soil (Hinkel & Hurd, 2006). During the summer, rainfall increases soil heat content by increasing soil thermal conductivity, and by directly transferring the atmosphere's heat content to the soil (Zhuang *et al.*, 2001). This precipitation–soil temperature interaction is likely why the Manitoba sites have warmer soils than the Alaskan sites, even though the mean annual temperatures of the two areas are similar (Fig. 1). Despite this inherent interaction, natural soil temperature gradients have formed the foundation for many observational studies (Van Cleve & Yarie, 1986; Kane *et al.*, 2005).

Manipulative studies will ultimately determine the relative sensitivity of aboveground productivity and spruce C allocation to soil temperature or moisture. For black spruce, Van Cleve *et al.* (1990) found that in an extreme warming, aboveground productivity and canopy N content increased with soil warming, but no measures of belowground processes or soil moisture were reported. For a warming plus irrigation study in boreal Norway spruce (*Picea abies*), irrigation caused an increase in aboveground productivity, but soil warming plus irrigation resulted in a growth response 2 × greater than irrigation alone (Strömberg *et al.*, 2002). This growth response could have been in part due to the lower allocation to fine roots in the warming plus irrigation than the irrigation alone treatments (Majdi & Ohrvik, 2004). In an ongoing study of a 17-year-old black spruce forest, Bronson *et al.* (2008) reported that soil warming and soil + air warming caused a decrease in spruce allocation to fine roots over 2 years. The shift in allocation may have contributed to a decrease in annual soil CO₂ efflux in the soil + air warming treatment. The soil warming only treatment resulted in a nonsignificant increase in soil CO₂ efflux. In both warming treatments, irrigation was used to maintain soil moisture to a similar level of the control, which may have been the reason why this study's soil CO₂ efflux results differed from other soil warming studies which did not have similar control (Rustad *et al.*, 2001). These various manipulative studies suggest that spruce C dynamics are highly sensitive to soil temperature, but that soil moisture is likely also important. Both preci-

precipitation and temperature are expected to increase in the boreal forest during the next century (ACIA, 2004), suggesting the interaction between soil temperature and moisture deserves further study.

Conclusions

For many tree species, aboveground productivity and TBCF are positively correlated (Raich *et al.*, 2006; Litton *et al.*, 2007), but black spruce appears to be one of a number of species where the two growth processes can be negatively correlated across climatic gradients (Giardina *et al.*, 2005). As a result, any proposed relationship between climate and black spruce productivity should account for both above- and belowground processes. For example, if we had only studied the relationship between soil temperature and aboveground productivity, we would have supported the hypothesis that soil temperature in some way controls ecosystem primary productivity. Rather, the key measurements (NPP, soil CO₂ efflux, TBCF, ecosystem C distribution) that were similar in methodology across studies suggested that soil temperature is a determinant of spruce and ecosystem C allocation, but soil temperature appears to have only a marginal effect on the absolute amount of C cycling through the vegetation. Given the overlay of precipitation with soil temperature, it is likely that the two abiotic factors are interacting to affect spruce allocation, but new manipulative studies are needed to disentangle the effects of each factor. In regards to ecosystem C balance, methodological differences among studies for heterotrophic respiration, and the lack of mineral soil C data, prevented a robust assessment of soil temperature's long-term influence on soil and ecosystem C cycling. However, this study is the first to examine black spruce C allocation across a significant soil temperature gradient, and provides an impetus for further study of belowground processes as they interact with soil temperature, and also nutrient availability and available moisture.

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Appendix A

Table A1 Methods used to estimate the net primary production (NPP) of black spruce stems and branches (NPP_w), foliage (NPP_F), vascular understorey (NPP_U), bryophytes (NPP_B), and coarse root (NPP_{CR}) and fine root growth (NPP_{FR})

Study (region)	Study no.	NPP _w	NPP _F	NPP _U	NPP _B	NPP _{CR}	NPP _{FR}
(1) Vogel <i>et al.</i> (2005) (Alaska)	1	Fixed area plots (40 m ²), 20–40 trees cored, allometric equations from nearby forest (Mack <i>et al.</i> , 2008)	Six traps baskets per site; each 0.25 m ² . Foliage estimate from ratio in Gower <i>et al.</i> (1997)	Three plots (1 m ²)	Six collars per site (181 cm ²). Modeled from feathermoss gross photosynthesis and respiration. Other bryophytes were not measured	Not measured	Not measured
(2) Mack <i>et al.</i> (2008) (Alaska)	2	Fixed area plots (144 m ² , 4–16 per site), 5–10 trees per site were cored, site-specific allometric equations	Foliage estimate from site-specific allometric equation	12 plots (1 m ²)	Production estimated by multiplying total green moss biomass of all species by the ratio of new growth per total green biomass of <i>Hylocomium splendens</i>	Not measured	Not measured
(3) Mack <i>et al.</i> (2008) (Alaska)	3	Fixed area plots (144 m ² , 4–16 per site), 5–10 trees cored, site-specific allometric equations	Foliage estimate from site-specific allometric equation	Six plots (1 m ²)	Production estimated by combining per cent cover estimates (20, 1 m ² per site) with a fluorescent dye method for estimating annual growth increment (Harden <i>et al.</i> , in preparation)	Not measured	Not measured
(4) Ruess <i>et al.</i> (2003)* (Alaska)	4	Fixed area plots (90 m ²), 10 trees cored, allometric equations from Van Cleve <i>et al.</i> (1983)	Relationship between biomass and litterfall developed from data in Van Cleve <i>et al.</i> (1983). Foliage estimate from ratio in Gower <i>et al.</i> (1997)	Created regression between per cent cover and biomass or growth. 20 plots (0.25 m ²)	Monitored shoot growth of 10 feathermoss fronds in 20–40 subplots per site (each 0.25 m ²). All other cryptograms growth estimated by multiplying by feathermoss growth	Not measured	Estimated with 5 minirhizotron tubes monitored throughout growing season

(5) O'Connell <i>et al.</i> (2003a,b) (Saskatchewan)	5	Variable radius plot (basal area factor $2 \text{ m}^2 \text{ ha}^{-1}$), all trees found in plot (5–20), site-specific allometric equations	Three litter traps per site; each 0.25 m^2 . Foliage estimate from ratio in Gower <i>et al.</i> (1997)	Six 0.10 m^2 plots	Five mesh squares per site (100 cm^2) for feathermoss. Lichens not reported	Coarse root (> 1.5 mm) growth estimated with tree cores and allometric equations from Foster (1985)	Estimated with minirhizotrons (30 total) monitored throughout growing season
(6) Bond-Lamberty <i>et al.</i> (2004a,c) (Manitoba)	6	Fixed area plots (50 m^2), 15–20 trees randomly selected and cored, site-specific allometric equations	Eight litter traps per site; each (0.25 m^2). Litter sorted into component	Five plots (0.25 m^2)	Five mesh squares per site (100 cm^2) for feathermoss. Lichens not reported	Coarse roots (> 5 mm diameter) measured with site-specific allometric equations. Coarse roots between 2 and 5 mm estimated with sequential coring (see NPP _{FR})	Fine roots growth estimated with sequential coring (2 timepoints, 10 cores, each core 16.6 cm^2 and 50 cm deep)

*Only one of three stands is used in this analysis because the other two sites had less than 40% of aboveground production attributed to black spruce.

Appendix B

Table B1 Details of soil respiration methods used in each study

Study no. and citation	Year measured	Licor model	Chamber area (m ²)	Root respiration	Moss respiration	Understory respiration	Growing season length
(1) Vogel <i>et al.</i> (2005)	2000, 2001	6262	0.018	Root exclusion	Modeled and removed	Clipped from collar area	May 10 to snowfall (9/20/2000 or 10/2/2001)
(2) D.W. Valentine (unpublished data)	2002	6262	0.17	Bomb ¹⁴ C*	Removed w/NPP from Mack <i>et al.</i> †	Removed w/NPP from Mack <i>et al.</i> †	May 10 to October 1
(3) Schuur & Trumbore (2006)	2001	6262	0.051	Bomb ¹⁴ C	Removed w/NPP from Mack <i>et al.</i>	Removed w/NPP from Mack <i>et al.</i>	June 1 to August 30
(4) Ruess <i>et al.</i> (2003)	1998, 1999	6000–09	0.0078	Direct root	Clipped from collar area	Clipped from collar area	May 15 to September 15
(5) O'Connell <i>et al.</i> (2003b)	1998, 1999	6200	0.018	Root exclusion	Clipped from collar area	Clipped from collar area	May 15 to September 22
(6) Bond-Lamberty <i>et al.</i> (2004a)	2001, 2002	6200	0.085	Root exclusion	Removed w/NPP	Clipped from collar area	May 15 to September 15

Study numbers correspond to study numbers in Table 1.

*Root respiration partitioning found in Schuur & Trumbore (2006).

†Understory or moss NPP values used to estimate respiration with the NPP:annual respiration ratio created by Ryan *et al.* (1997) for species in black spruce forests.