

Growth and maintenance respiration rates of aspen, black spruce and jack pine stems at northern and southern BOREAS sites

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Summary We measured stem respiration rates during and after the 1994 growing season of three common boreal tree species at sites near the northern and southern boundaries of the closed-canopy boreal forest in central Canada. The growth respiration coefficient (r_g ; carbon efflux per μmole of carbon incorporated in structural matter) varied between 0.25 and 0.76, and was greatest for black spruce (*Picea mariana* (Mill.) B.S.P.), least for jack pine (*Pinus banksiana* Lamb.) and intermediate for trembling aspen (*Populus tremuloides* Michx.). There was a consistent trend for higher r_g at northern sites than at southern sites. Maintenance respiration rates at 15 °C (r_m) varied from 0.5 to 2.7 $\text{nmol C mol}^{-1} \text{C}_{\text{sapwood}} \text{ s}^{-1}$. Values of r_m were high at sapling-stage jack pine sites and mature black spruce sites, and low at mature trembling aspen and mature jack pine sites. We found significant relationships between annual maintenance respiration and sapwood relative growth rate and sapwood volume per unit of stem surface area that explained much of the within-stand and between-stand variability. Because of the large differences in parameter values among sites, we conclude that the use of stand-specific respiratory parameters may improve model predictions of ecosystem process models over the use of generic parameter values.

Keywords: autotrophic respiration, carbon cycle, climate warming, ecosystem process models, growth respiration coefficient, *Picea mariana*, *Pinus banksiana*, *Populus tremuloides*, sapwood relative growth rate, sapwood volume, stand-specific respiratory parameters.

Introduction

Knowledge of carbon cycling in the boreal biome is important because it may be the missing sink in the global C cycle (Tans et al. 1990), and because the boreal biome may switch from being a net C sink to become a net source if the predicted climate warming occurs. Annual net ecosystem storage of carbon depends on the balance between photosynthesis and respiration (autotrophic plus heterotrophic); however, this balance may change with climate warming because respiration is relatively more sensitive to temperature than photosynthesis (Ryan 1991, Amthor 1994). Stem growth is an important component of the carbon cycle of forested systems because

stems store carbon for long periods compared with foliage and fine roots. Although some of the carbon allocated to woody tissues is used for respiration, much is incorporated in new biomass. Stem carbon use efficiency, which describes the fraction of net photosynthetic production allocated to stems that is incorporated into new biomass, is an important indicator of how effectively the ecosystem sequesters carbon (Ryan et al. 1994, 1996).

The functional model of autotrophic respiration, which divides total respiration into growth and maintenance components (Amthor 1989, 1994), has become the standard basis for evaluating woody-tissue respiration (Sprugel and Benecke 1991, Sprugel et al. 1995). However, separating the growth and maintenance respiration components of total respiration is difficult because growing organs also contain mature tissues whose respiration is limited to the maintenance component. Theoretical methods for estimating the growth respiration coefficient, (r_g), have been developed (reviewed by Amthor 1989, 1994, Griffin 1994). Growth respiration can be estimated when r_g and growth are known, and maintenance respiration can then be calculated by subtracting growth respiration from total respiration. The mature tissue method (Amthor 1989) is an alternative method of dividing total respiration into growth and maintenance respiration. The mature tissue method assumes that respiration rates of mature tissues, or respiration rates measured when growth is minimal, can be used to estimate maintenance respiration rates of actively growing tissues, and growth respiration is then calculated as the difference between total respiration and maintenance respiration (Amthor 1989, and Sprugel and Benecke 1991). Sprugel and Benecke (1991) noted that estimates of growth respiration obtained by the mature tissue method tend to be greater than those calculated by theoretical methods, and suggested that there were demands for the products of growth respiration in addition to those included in the theoretical methods. Furthermore, several studies have found relationships between maintenance respiration rates and growth rates (Penning de Vries et al. 1979, Lavigne 1988, 1996), indicating that the assumption that they are independent is incorrect in at least some circumstances. Of the processes dependent on maintenance respiration, protein turnover of existing tissues is thought to create the largest demand (Penning de Vries 1975a, Amthor 1989). Based on the assump-

tion that nitrogen content is related to growth rate, Ryan (1991, 1995) and Ryan et al. (1996) used tissue nitrogen content as the basis for expressing maintenance respiration rates in an attempt to eliminate the effects of the relationship between maintenance respiration and growth.

Elevated CO₂ concentrations do not directly affect stem respiration parameters (Wullschleger et al. 1995, Carey et al. 1996), but they can indirectly influence respiration rates by changing the amount of carbohydrate available for stem growth. Possible global warming might affect the balance between growth and respiration because rising temperatures could increase maintenance respiration rates more than growth rates (Ryan 1991). Ryan et al. (1995) found that, for temperate conifer ecosystems, the proportion of net assimilation used for stem maintenance respiration increased linearly from 5 to 12% with increasing mean annual temperature.

The goal of the BOREal Ecosystem Atmosphere Study (BOREAS) was to assess the current and future roles of the boreal biome in the global carbon cycle (Sellers et al. 1995). We measured stem respiration during 1994 at sites near the southern and northern boundaries of the closed-canopy boreal forest in central Canada with the following objectives: (1) to determine whether respiratory parameters vary among three common boreal tree species (black spruce, *Picea mariana* (Mill.) B.S.P., jack pine, *Pinus banksiana* Lamb., and trembling aspen, *Populus tremuloides* Michx.), (2) to compare respiration parameters from the cold northern sites with those from the warmer, southern sites, and (3) to provide estimates of respiratory parameters for use in ecosystem process models. A companion study (Ryan et al. 1997) reports on foliar and root respiration, and examines complete autotrophic respiration budgets for these sites.

Methods

Study sites

We measured stem respiration and growth during the 1994 growing season at eight BOREAS sites with contrasting climates (Table 1). Four sites were located in the Southern Study Area, near the southern boundary of the boreal forest in central Canada, in the vicinity of Prince Albert, Saskatchewan (53°53' N, 104°53' W). The other four sites were located near the northern boundary of the boreal region, close to Thompson, Manitoba (55°53' N, 98°20' W) in the Northern Study Area. In each study area there was a mature aspen stand, referred to here as northern old aspen (NOA) and southern old aspen (SOA), a mature black spruce stand designated NOBS and SOBS, a mature jack pine stand called NOJP and SOJP, and a sapling-stage jack pine stand called northern young jack pine (NYJP) and southern young jack pine (SYJP). These sites are described in detail by Gower et al. (1997); important site characteristics for this study are summarized in Table 2.

Respiration measurements

We used automated, manifold systems to measure respiration rates. The data at the northern sites were supplemented with measurements made with a manual system. The manifold system used at the Northern Study Area differed from that used in the south, and so they are described separately. The manifold systems gave similar results to the portable system.

Southern Study Area The respiration system used in the south was similar to that described by Lavigne et al. (1996) and Lavigne (1996). Ambient air, drawn from 1 m above the ground, was pumped through 16 respiration chambers and

Table 1. Climatic norms for BOREAS study areas near Prince Albert, Saskatchewan, Canada (south) and Thompson, Manitoba, Canada (north).

Study area	Mean annual temperature (°C)	July average temperature (°C)	Annual precipitation (mm)	Growing season precipitation (mm)
South	0.1	14	390	160
North	-3.9	16	540	220

Table 2. Site characteristics of stands (OA = old trembling aspen, OJP = old jack pine, YJP = young jack pine, OBS = old black spruce) near the southern boundary of the boreal zone (Southern Study Area) and the northern boundary (Northern Study Area) in central Canada where stem respiration measurements were taken. The source of this information was Gower et al. (1997).

Site	Age (year)	DBH (cm)	Height (m)	Density (ha ⁻¹)	Sapwood volume (m ³ ha ⁻¹)	LAI	Soil texture
<i>Southern Study Area</i>							
OA	60	20.5	21	1000	327	3.3	Sandy loam
OJP	75	12.9	15	1200	57	1.3	Deep sand
YJP	16	3.2	5	10700	26	2.8	Deep sand
OBS	> 100	7.4	10	6200	61	5.6	Organic
<i>Northern Study Area</i>							
OA	-	11.6	-	2300	196	2.2	Sandy loam
OJP	60	11.1	11	1300	55	2.2	Deep sand
YJP	25	2.2	6	15200	13	1.8	Deep sand
OBS	90	8.5	12	5500	83	4.9	Organic

through the reference cell of the gas analyzer (LI-6252, Li-Cor, Inc., Lincoln, NE). A data logger (Model CR-10, Campbell Scientific Inc., Chatham, ON, Canada) controlled a series of solenoids that determined the order in which air was pumped through the 16 chambers. Each chamber was measured once during the 1.75-h measurement cycle. Air was pumped through each chamber for 20 minutes, and mean values for the last minute were recorded. Fans stirred air in the chambers while measurements were taken. The zero of the gas analyzer was checked regularly during the measurement cycle, and span was checked once. Stem temperature immediately under the bark was measured with a copper-constantan thermocouple inside the chambers while CO₂ flux was being observed.

Respiration chambers used in the Southern Study Area consisted of clear acrylic tubes and closed-cell neoprene (Lavigne et al. 1996 and Lavigne 1996). Chambers used on small diameter trees, including all trees at SYJP and some trees at SOBS, completely encircled the stem. Chambers on large diameter trees enclosed a portion of the stem circumference. One chamber per tree was attached to 16 trees in each stand. Tree diameters spanned the range of the stands (Table 3). Chambers were attached 1–2.5 m aboveground. Plate-like chambers on larger trees were attached on the sides of the trees that were most conducive to forming air-tight seals.

All stands were measured with the manifold system for 3–4 days early in the growing season, during the middle of the growing season, late in the growing season and after growth had ended for the year. Thirty to 50 measurements were made per chamber during each measurement period. Additional measurements were made with the manifold system at SOBS between the early growing season and mid-growing season

intensive field campaigns. Chambers were opened between measurement periods.

Northern Study Area Stem respiration was measured on 20 trees in the NOJP, NOBS, and NOA stands, and 10 trees in the NYJP stand; tree diameters spanned the range of the stand (Table 3). In the NOJP, NOBS, and NOA stands, aluminum chamber plates (110 cm²) with an external neoprene gasket were attached to the north side of the tree with putty after the removal of loose bark. Chambers were attached at a height of 1.2–1.4 m on four trees per stand, and additional chambers were placed at a height of 6 m. For CO₂ efflux measurements, a Plexiglas chamber was sealed to the chamber plate with an elastic cord. For measurements in the NYJP stand, split Plexiglas chambers (23 cm in length) enclosed the entire stem, with neoprene gaskets creating a seal. A small fan mixed the air in each chamber, and chambers were removed between measurements. Sapwood temperature was measured for each chamber with a copper-constantan thermocouple inserted 1 cm into the sapwood.

Two types of measurements were made in 1994. (1) During each intensive field campaign in the NOJP, NOBS, and NOA stands, CO₂ efflux was measured once per hour for 3–6 days on eight chambers per site (four trees with chambers located at heights of 1.3 and 6 m) to determine temperature response. At the NYJP stand, continuous measurements were made on six trees only during the midsummer intensive field campaign. (2) Point measurements of CO₂ flux were made every 2–3 weeks at all sites for all chambers. The continuous measurements were made using both a manifold and an open system (Field et al. 1991), controlled with a data logger (Model CR-21X, Campbell Scientific, Logan, UT). The manifold system had two gas circuits. When CO₂ efflux was being measured, inlet

Table 3. Stem characteristics where respiration chambers were attached at BOREAS sites near Prince Albert, Saskatchewan in the Southern Study Area, and near Thompson, Manitoba in the Northern Study Area. Abbreviations: OA = old trembling aspen stand, OJP = old jack pine stand, YJP = young jack pine stand, and OBS = old black spruce stand. Ranges are shown in parentheses.

Site	Diameter (cm)	Stem surface area (cm ²)	Sapwood volume (cm ³)	N (ppm)	Specific sapwood volume (cm ³ cm ⁻²)	Number of samples
<i>Southern Study Area</i>						
OA	17.9 (10.9–26.6)	307 (249–387)	638 (175–1140)	442 (32–670)	2.0 (0.7–3.2)	14
OJP	14.4 (9.2–21.2)	302 (215–402)	546 (232–1169)	245 (8–580)	1.7 (0.9–3.0)	15
YJP	5.5 (2.9–11.2)	187 (93–336)	228 (50–622)	575 (49–830)	1.1 (0.5–1.9)	16
OBS	8.8 (4.6–18.2)	280 (147–496)	186 (89–347)	305 (19–380)	0.7 (0.4–1.1)	12
<i>Northern Study Area</i>						
OA	13.6 (6.4–23.9)	110	277 (110–482)	404 (25–620)	2.5 (1.0–4.4)	24
OJP	12.5 (7.3–18.3)	110	179 (78–262)	267 (14–460)	1.6 (0.7–2.4)	24
YJP	4.6 (2.9–6.6)	326 (205–480)	246 (73–531)	332 (26–450)	0.7 (0.4–1.1)	8
OBS	10.7 (4.1–18.2)	110	75 (37–157)	343 (8–450)	0.7 (0.3–1.4)	24

air was drawn through a 20-liter mixing chamber (to provide a stable reference CO₂ concentration), pushed through the chamber at 270 μmol s⁻¹, and returned to the CO₂ analyzer (ADC LCA2, ADC, Hoddesdon, U.K.). Otherwise, inlet air was pushed through the chambers at 3.5 mmol s⁻¹, to keep CO₂ concentration in the chamber at < 5 μmol mol⁻¹ above ambient. The point measurements were made with an open system (Field et al. 1991) and an ADC LCA3 or LCA4 gas analyzer with an air flow of 270 μmol s⁻¹.

Growth measurements

Increment cores were taken from enclosed portions of stems after chambers were removed. We measured bark thickness, phloem width, width of the 1994 xylem ring, and sapwood thickness on one increment core. Wood density and nitrogen concentration of sapwood were measured on a second increment core. We used the data to estimate sapwood volume beneath each chamber and growth on a dry weight basis. Growth estimates were converted to molar units by assuming a 50% carbon content for oven-dried wood (Carey et al. 1996). We computed sapwood relative growth rates (RGR_{sapwood}) as μmol mol⁻¹ C_{sapwood} year⁻¹ to facilitate comparing chambers of different sizes, and so that the units would be compatible with the respiration rate units.

Data analysis

We divided chamber flux by sapwood carbon enclosed in the chamber to calculate respiration rate. We regressed stem respiration rate against sapwood temperature for each chamber and intensive field campaign with the equation:

$$r = r_{15} Q_{10}^{(T - 15)/10}, \quad (1)$$

where r is stem respiration rate (nmol C mol⁻¹ C_{sapwood} s⁻¹), T is sapwood temperature (°C) recorded approximately 2 h earlier (see Ryan et al. (1996) and Lavigne et al. (1996) for explanations of the use of lagged sapwood temperature), r_{15} is a regression coefficient that estimates respiration rate at 15 °C, and Q_{10} is a regression coefficient that describes the change in respiration rate for a 10 °C change in sapwood temperature. Similar analyses have been described in detail by Lavigne (1987). We used the average Q_{10} for the stand to estimate the r_{15} of chambers where spot measurements were made.

The dates on which stem growth began and ended were estimated for each stand based on respiration measurements and phenological observations. We assumed that coefficients estimated with the post-growing season data were representative of the physiological state during the entire dormant season. Values of r_{15} and Q_{10} on each day of the growing season were estimated by linear interpolation between measured values. Sapwood temperature or air temperature was recorded hourly or half-hourly at most sites between Days 145 and 265 by groups making eddy covariance measurements. For times when temperatures were not collected on site, we used temperature records from nearby weather stations to make complete records of air temperature for the 1994 calendar year. Annual total respiration (R_{15} , mmol C mol⁻¹ C_{sapwood} year⁻¹)

was estimated by Equation 1 using daily values of r_{15} and Q_{10} with temperature records. Temperatures were not measured at NOA, so the temperature record for NYJP was used.

The mature tissue method (Amthor 1989) was used to estimate annual maintenance respiration (R_m), and to subdivide total respiration into maintenance and annual growth respiration (R_g). Values of r_{15} and Q_{10} estimated with post-growing season CO₂ flux measurements and the annual site-specific temperature records were used with Equation 1 to estimate R_m .

Two-way analysis of variance was used to compare respiration and growth among study areas and sites. When requirements for normality and homogeneity of variance were not met with data in its original units, the two-way ANOVA was performed on rank transformed data. A Fisher's LSD multiple comparison test was performed when significant differences ($P < 0.05$) were found. Sigastat version 2.0 (Jandel Inc., San Rafael, CA) was used for statistical analyses.

Results

Seasonal course of stem respiration rates

Stem respiration rates at the OJP and OA stands were lower than those at the YJP and OBS stands (Figure 1a). In the earliest measurements of the year, stem respiration rates of

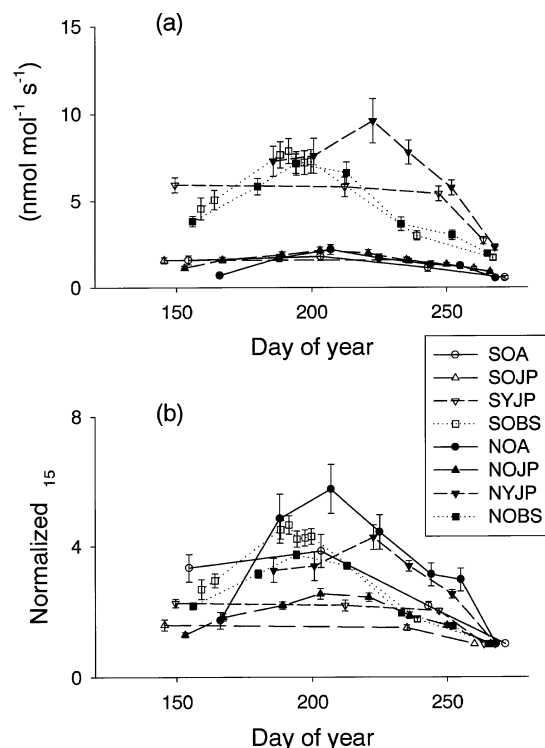


Figure 1. (a) Seasonal course of total stem respiration rates at 15 °C at BOREAS sites in the Southern and Northern Study Areas in central Canada. (b) Seasonal course of normalized total stem respiration rates at 15 °C (observed r_{15} during the growing season divided by the r_{15} observed after the growing season). Error bars are ± 1 standard error.

southern sites were already much greater than dormant season rates (Figure 1b). In contrast, the earliest measurements of respiration rates at northern sites were only slightly greater than dormant season rates, and rates increased substantially during the following 30–70 days (Figure 1b). Respiration rates at SOJP and SYJP showed little variation during the growing season (Figures 1a and 1b); respiration rates declined from growing season rates to dormant season rates during a relatively short period. Respiration rates at NOJP and NYJP varied more during the growing season than their southern counterparts and the decline from growing season maximal rates to dormant-season rates began earlier than at the southern sites. Respiration rates at Northern and Southern OBS and OA stands showed substantial seasonal variation that differed between species (Figures 1a and 1b). Respiration increased to maximal rates between Days 180–190 at OBS stands, and after Day 200 at OA stands.

Among the forest stands studied, respiration rates varied least with temperature in aspen stands (Table 4), but there were no other statistical differences among stands or between Northern and Southern Study Areas.

Annual respiration rates

Annual total respiration rates did not vary significantly ($P > 0.05$) between Northern and Southern Study Areas, but did vary significantly between sites ($P < 0.001$, Table 5). The R_t rates were greatest at the YJP stands, followed by the OBS,

Table 4. Values of temperature response coefficients (Q_{10}) measured during BOREAS intensive field campaigns early in the growing season (IFC-1, May 23 to June 16), mid-growing season (IFC-2, July 19 to August 8), late growing season (IFC-3, August 29 to September 20), and after the growing season had ended (September 27 to October 10). Standard errors of the means are given in parentheses.

Site	Q_{10}			
	IFC-1	IFC-2	IFC-3	Post-growing season
<i>Southern Study Area</i>				
OA	1.2 (0.05)	1.3 (0.04)	1.2 (0.06)	1.0 (0.10)
OJP	1.6 (0.04)	–	1.5 (0.05)	1.7 (0.05)
YJP	1.7 (0.03)	1.7 (0.07)	1.5 (0.05)	1.7 (0.04)
OBS	1.8 (0.06)	1.7 (0.03)	1.7 (0.10)	2.2 (0.08)
<i>Northern Study Area</i>				
OA	1.4 (0.10)	1.4 (0.09)	1.7 (0.06)	–
OJP	2.4 (0.20)	1.6 (0.01)	1.8 (0.02)	–
YJP	–	1.7 (0.03)	–	–
OBS	1.5 (0.05)	1.6 (0.06)	1.8 (0.07)	–

OJP, and OA stands. Average annual maintenance respiration rates varied significantly between sites ($P < 0.001$), but not between Northern and Southern Study Areas (Table 5). The order of stands from highest to lowest R_m followed that for R_t .

Annual growth respiration rates (R_g) varied significantly between Northern and Southern Study Areas ($P < 0.001$), between stands ($P < 0.001$), and the interaction between study area and stand was also significant ($P = 0.008$, Table 5). Sapwood relative growth rates (RGR_{sapwood}) did not vary significantly between Northern and Southern Study Areas, but did vary significantly between stands ($P < 0.001$, Table 5). Young Jack Pine stands had the highest growth rates, OBS stands had significantly greater growth rates than those of OJP and OA stands, but growth rates of OJP stands did not differ significantly from those of OA stands. Stem carbon use efficiency (CUE), calculated as the ratio of carbon used for growth to carbon used for growth and respiration ($RGR_{\text{sapwood}} / (RGR_{\text{sapwood}} + R_t)$), differed significantly between sites ($P < 0.001$), and these site differences were not the same at Northern and Southern Study Areas ($P = 0.026$, Table 5). Old Aspen and YJP stands were among the most efficient users of carbon in Northern and Southern Study Areas, and the OBS stand was least efficient in both study areas. The YJP stand was significantly more efficient than the OJP stand in the Southern Study Area, but not in the Northern Study Area.

The R_g rates were significantly correlated to RGR_{sapwood} (Figure 2a, Table 5). The growth respiration coefficient (r_g , Table 5), which was estimated as the ratio of annual growth respiration rate to sapwood relative growth rate ($R_g / RGR_{\text{sapwood}}$), varied significantly between study areas ($P < 0.001$) and sites ($P < 0.001$), and there was a significant interaction between study area and site ($P = 0.003$). Values of r_g were highest for OBS stands and lowest for JP stands. Values of r_g tended to be higher at northern sites than at southern sites, and the differences between study areas were statistically significant ($P < 0.05$) for the YJP and OJP stands.

Maintenance respiration rates

There were no significant relationships between maintenance respiration rate and sapwood nitrogen concentration within stands or for all stands combined. The RGR_{sapwood} explained much of the within-stand and between-stand variations in maintenance respiration rates (Figure 2b). A nonlinear relationship between annual maintenance respiration (R_m ; $\text{mmol mol}^{-1} C_{\text{sapwood}} \text{ year}^{-1}$) and sapwood relative growth rate (RGR_{sapwood} ; $\text{mmol mol}^{-1} C_{\text{sapwood}} \text{ year}^{-1}$),

$$R_m = 71.4 (1 - \exp(-0.0105 RGR_{\text{sapwood}})), \quad (2)$$

explained 55% of the variation ($r^2 = 0.55$, standard error of estimate = $12.8 \text{ mmol mol}^{-1} C_{\text{sapwood}} \text{ year}^{-1}$). The nonlinear equation produced accurate estimates over the entire range of observed RGR_{sapwood} , in contrast to a simple linear equation that consistently overestimated maintenance respiration rates at low RGR_{sapwood} . Within-stand relationships between RGR_{sapwood} and R_m differed from the relationship that existed when data from all stands were pooled (Figure 2b). Relation-

Table 5. Mean sapwood relative growth rate (RGR_{sapwood} ($\text{mmol mol}^{-1} C_{\text{sapwood}} \text{ year}^{-1}$)), annual total, maintenance and growth respiration rates (R_t , R_m and R_g ($\text{mmol mol}^{-1} C_{\text{sapwood}} \text{ year}^{-1}$)), maintenance respiration coefficient (r_m ($\text{nmol mol}^{-1} C_{\text{sapwood}} \text{ s}^{-1}$)), growth respiration coefficient (r_g ($\mu\text{mol } \mu\text{mol}^{-1}$)) and stem carbon use efficiency (CUE).

Site	RGR_{sapwood}	R_t	R_m	R_g	r_m	r_g	CUE
<i>Southern Study Area</i>							
OA	31.5 (7.3)	20.9 (3.6)	11.9 (2.2)	9.0 (1.7)	0.54 (0.10)	0.29 (0.08)	0.57 (0.04)
OJP	24.2 (3.3)	26.4 (2.2)	20.5 (2.0)	5.9 (0.9)	1.09 (0.11)	0.24 (0.05)	0.46 (0.03)
YJP	122.0 (8.3)	84.9 (5.8)	54.6 (4.6)	30.3 (2.6)	2.70 (0.20)	0.25 (0.02)	0.59 (0.01)
OBS	45.9 (4.3)	63.6 (5.5)	30.6 (2.7)	33.0 (3.3)	1.70 (0.15)	0.72 (0.07)	0.42 (0.03)
<i>Northern Study Area</i>							
OA	27.9 (4.4)	19.2 (2.1)	8.7 (1.1)	10.5 (1.6)	0.53 (0.08)	0.38 (0.10)	0.57 (0.03)
OJP	32.8 (3.1)	29.7 (2.0)	18.7 (1.3)	11.0 (0.9)	0.89 (0.08)	0.34 (0.03)	0.51 (0.02)
YJP	82.7 (6.4)	75.4 (5.6)	43.0 (3.8)	32.3 (2.4)	2.31 (0.18)	0.39 (0.11)	0.48 (0.04)
OBS	39.1 (4.4)	62.6 (4.8)	32.9 (2.9)	29.6 (2.1)	1.96 (0.18)	0.76 (0.08)	0.37 (0.02)

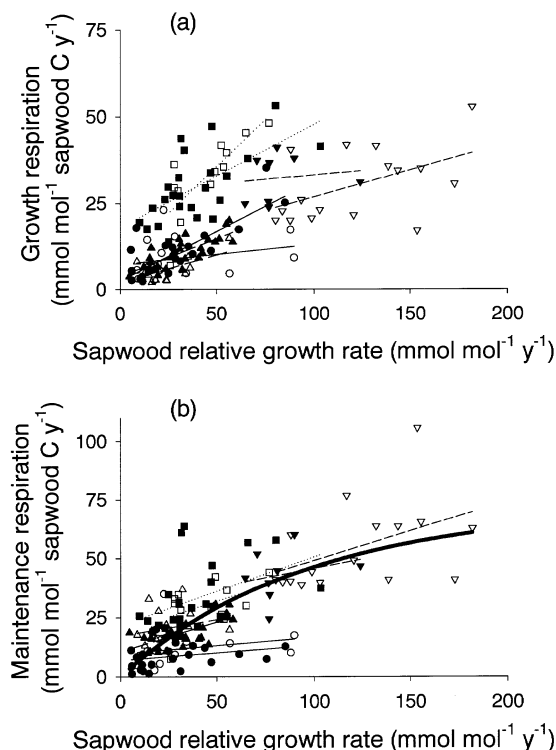


Figure 2. (a) Relationships between annual stem growth respiration rate and sapwood relative growth rate and (b) between annual stem maintenance respiration rates and sapwood relative growth rates at BOREAS sites in the Southern and Northern Study Areas in central Canada. Growth and maintenance respiration rates were estimated by the mature tissue method. Regression lines are shown for each site. Symbols and lines correspond to sites defined in Figure 1. The thick, solid line is the regression line for all data, see Equation 2.

ships between maintenance respiration and sapwood volume per unit of stem surface (SSV; $\text{cm}^3 \text{ cm}^{-2}$) existed for individual stands and for all stands combined (Figure 3). A nonlinear relationship between annual maintenance respiration and SSV,

$$R_m = 27.2 \text{ SSV}^{-0.58}, \quad (3)$$

based on data from all stands, explained 28% of the total variation ($r^2 = 0.28$, standard error of estimate = $15.0 \text{ mmol mol}^{-1} C_{\text{sapwood}} \text{ year}^{-1}$) and fit the data well over the entire range of SSVs. We tested numerous regression models using both RGR_{sapwood} and SSV to predict R_m , and obtained the best fit ($r^2 = 0.65$, standard error of estimate = $11.4 \text{ mmol mol}^{-1} C_{\text{sapwood}} \text{ year}^{-1}$) when the nonlinear models used for RGR_{sapwood} and SSV were combined:

$$R_m = 59.5 \text{ SSV}^{-0.38} (1 - \exp(-0.0139 \text{ RGR}_{\text{sapwood}})). \quad (4)$$

Discussion

With the mature tissue method, we obtained estimates of r_g that were substantially higher than theoretical estimates reported for the same or similar species. For example, Carey et al. (1996) determined that the theoretical r_g for *Pinus ponderosa* Dougl. ex Laws. was 17, which is lower than the values we estimated for jack pine (Table 5). Chung and Barnes (1977) estimated r_g theoretically for black spruce at 12, which is much less than our estimates (Table 5), and the r_g of 0.25 calculated for generic wood by Penning de Vries (1975b) is lower than our estimates for trembling aspen. Edwards and Hanson (1996) found that predicted respiration, based on theoretical

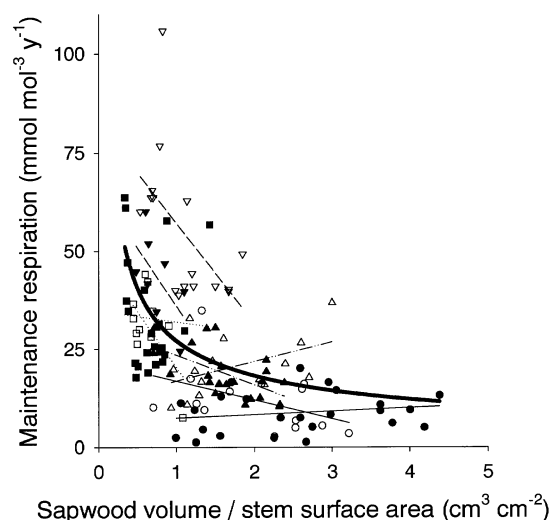


Figure 3. Relationships between annual maintenance respiration rates, estimated by the mature tissue method, and specific sapwood volumes (sapwood volume per unit of stem surface area) at BOREAS sites. Regression lines are shown for each site. Symbols and lines correspond to sites defined in Figure 1. The thick, solid line is the regression line for all data, see Equation 3.

estimates of r_g , underestimated observed respiration rates during the growing season for *Quercus alba* L. and *Acer rubrum* L. but not for *Quercus prinus* L. Sprugel and Benecke (1991) noted that mature tissue estimates of r_g were generally higher than theoretical estimates. Griffin (1994) reported that published theoretical estimates of r_g for stem wood ranged from 0.08 to 0.50 for a variety of species, and our estimates by the mature tissue method ranged from 0.25 to 0.76 (Table 5). Sprugel and Benecke (1991; p 335) argued that theoretical estimates of r_g should be considered the minimum realistic estimates, because “growth-related maintenance respiration and other “hidden costs” of wood production” are not included. The extent to which our estimates of r_g differed from theoretical estimates varied between species, as was found by Edwards and Hanson (1996).

The r_g of stands at each southern site was lower than for the comparable stand in the Northern Study Area (Table 5), showing that stem growth was more efficient in the south than in the north. We speculate that the differences in r_g could be related to subtle, inherent differences in the seasonal course of growth rates (Figures 1a and 1b), the contributions of respiration that have not previously been assigned to growth, and the weather during the 1994 growing season, which was warmer than usual, particularly in the north, and drier than usual, especially in the south.

Maintenance respiration rates differed greatly between stands (Table 5). The OA stands had the lowest r_m , possibly because stem photosynthesis recycled some of the CO_2 produced by respiration (Foote and Schaedle 1976, 1978). Relationships between sapwood volume per unit of stem surface area (SSV) and R_m existed for some sites, but not for the aspen sites (Figure 3), and this difference might also have been

associated with stem photosynthesis. Site differences were not simply species-related; OJP stands had relatively low r_m , whereas YJP stands had relatively high r_m . The r_m did not differ significantly between Northern and Southern Study Areas.

Lavigne (1996) found no differences in stem maintenance respiration rates between northern and southern provenances of jack pine growing together in a common garden at a southern site. Growth rates of trees selected to represent northern provenances were similar to those representing southern provenances. These results and the findings presented here show that stem maintenance respiration of jack pine does not exhibit genetically related latitudinal trends.

Differences in maintenance respiration between and within sites could be explained partly by differences in $\text{RGR}_{\text{sapwood}}$ and SSV, although the significance and nature of the relationships varied between sites (Figures 2b and 3). A relationship between maintenance respiration rate and sapwood relative growth rate similar to that observed at the BOREAS sites was observed for jack pine growing in eastern Canada (Lavigne 1996), and trends between maintenance respiration and stem growth and SSV similar to those found here have been observed for *Abies balsamea* (L.) Mill. (Lavigne 1988, Lavigne et al. 1996). However, these relationships do not always exist. For example, relationships were insignificant at the OA stands, and relationships with SSV were nonexistent at the SOBS and SOJP stands (Figure 3). Moreover, Ryan (1990), Sprugel (1990) and Edwards and Hanson (1996) found that only sapwood volume correlated with chamber differences in maintenance respiratory fluxes.

Although it has been assumed that no relationship exists between maintenance respiration rate and growth rate (Amthor 1989), we consistently observed such relationships at our sites (Figure 2b), suggesting that the manner in which the functional subdivision of respiration is applied may need to be modified. One possibility is to develop individual relationships between r_m for maintenance respiration and specific sapwood volume and sapwood relative growth rate, rather than assuming the same value for all trees of a species; however this will require a better understanding of maintenance respiration. A better understanding of growth respiration is also required to explain why estimates of r_g by the mature tissue method are greater than the theoretical estimates, and this, in turn, might lead to a revision in our understanding of total respiration and its growth and maintenance components.

Because the calculations of stem carbon use efficiency did not require dividing respiration into its growth and maintenance components, the comparisons of stands were not subject to the associated uncertainties. Among stands, the black spruce stands used the carbon allocated to stems least efficiently (Table 5). Black spruce stands also had the lowest carbon use efficiencies based on conversion of net photosynthetic production to net primary production (Ryan et al. 1997). Aspen stands had the highest carbon use efficiency, but the true efficiency could be lower if some respired CO_2 was recycled by stem photosynthesis. The SYJP stand had higher stem carbon use efficiency than the SOJP stand, indicating an effect of stand age. However, our data do not unequivocally demonstrate that

stem carbon use efficiency changed with stand age for jack pine, because the NYJP stand was not more efficient than the NOJP stand, as a result of the high r_g of the NYJP stand.

Conclusions

Most process models use three parameters: the growth coefficient (r_g ; $\mu\text{mol C respired per } \mu\text{mol C incorporated in woody biomass}$), the maintenance respiration rate per unit of sapwood C (or N) at some reference temperature (r_m ; $\text{nmol C mol}^{-1} \text{C}_{\text{sapwood}} \text{ s}^{-1}$ at 15 °C) and a dimensionless temperature coefficient (i.e., Q_{10}). We found that each of these parameters varied substantially among stands, and therefore, using stand-specific parameters may improve model predictions compared with using generic parameter values. The large variations in these parameters highlight the need for a better understanding of stem growth and maintenance respiration processes. The results cast doubt on the assumption that stem maintenance respiration rate is independent of stem growth rate.

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