

# Influence of temperature and drought on seasonal and interannual variations of soil, bole and ecosystem respiration in a boreal aspen stand

David Gaumont-Guay<sup>a,\*</sup>, T. Andrew Black<sup>a</sup>, Tim J. Griffis<sup>b</sup>, Alan G. Barr<sup>c</sup>, Kai Morgenstern<sup>a</sup>, Rachhpal S. Jassal<sup>a</sup>, Zoran Nescic<sup>a</sup>

<sup>a</sup> *Biometeorology and Soil Physics Group, University of British Columbia, Vancouver, BC, Canada*

<sup>b</sup> *Department of Soil, Water and Climate, University of Minnesota, St. Paul, MN, USA*

<sup>c</sup> *Climate Research Branch, Meteorological Service of Canada, Saskatoon, Sask., Canada*

Received 16 November 2005; accepted 23 March 2006

## Abstract

Continuous half-hourly measurements of soil ( $R_s$ ) and bole respiration ( $R_b$ ), as well as whole-ecosystem  $\text{CO}_2$  exchange, were made with a non steady-state automated chamber system and with the eddy covariance (EC) technique, respectively, in a mature trembling aspen stand between January 2001 and December 2003. Our main objective was to investigate the influence of long-term variations of environmental and biological variables on component-specific and whole-ecosystem respiration ( $R_e$ ) processes. During the study period, the stand was exposed to severe drought conditions that affected much of the western plains of North America. Over the 3 years, daily mean  $R_s$  varied from a minimum of  $0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$  during winter to a maximum of  $9.2 \mu\text{mol m}^{-2} \text{s}^{-1}$  in mid-summer. Seasonal variations of  $R_s$  were highly correlated with variations of soil temperature ( $T_s$ ) and water content ( $\theta$ ) in the surface soil layers. Both variables explained 96, 95 and 90% of the variance in daily mean  $R_s$  from 2001 to 2003. Aspen daily mean  $R_b$  varied from negligible during winter to a maximum of  $2.5 \mu\text{mol m}^{-2} \text{bark s}^{-1}$  ( $2.2 \mu\text{mol m}^{-2} \text{ground s}^{-1}$ ) during the growing season. Maximum  $R_b$  occurred at the end of the aspen radial growth increment and leaf emergence period during each year. This was 2 months before the peak in bole temperature ( $T_b$ ) in 2001 and 2003. Nonetheless,  $R_b$  was highly correlated with  $T_b$  and this variable explained 77, 87 and 62% of the variance in  $R_b$  in the respective years. Partitioning of  $R_b$  between its maintenance ( $R_{bm}$ ) and growth ( $R_{bg}$ ) components using the mature tissue method showed that daily mean  $R_{bg}$  occurred at the same time as aspen radial growth increment during each growing season. This method led, however, to systematic over- and underestimations of  $R_{bm}$  and  $R_{bg}$ , respectively, during each year. Annual totals of  $R_s$ ,  $R_b$  and estimated foliage respiration ( $R_f$ ) from hazelnut and aspen trees were, on average, 829, 159 and  $202 \text{ g C m}^{-2} \text{ year}^{-1}$ , respectively, over the 3 years. These totals corresponded to 70, 14 and 16%, respectively, of scaled-up respiration estimates of  $R_e$  from chamber measurements. Scaled  $R_e$  estimates were 25% higher ( $1190 \text{ g C m}^{-2} \text{ year}^{-1}$ ) than the annual totals of  $R_e$  obtained from EC ( $949 \text{ g C m}^{-2} \text{ year}^{-1}$ ). The independent effects of temperature and drought on annual totals of  $R_e$  and its components were difficult to separate because the two variables co-varied during the 3 years. However, recalculation of annual totals of  $R_s$  to remove the limitations imposed by low  $\theta$ , suggests that drought played a more important role than temperature in explaining interannual variations of  $R_s$  and  $R_e$ .  
© 2006 Published by Elsevier B.V.

**Keywords:** Carbon exchange; *Populus tremuloides*; Soil water content; Soil  $\text{CO}_2$  efflux; Temperature sensitivity

\* Corresponding author at: University of British Columbia, Faculty of Land and Food Systems, 129-2357 Main Mall, Vancouver, BC, Canada V6T 1Z4. Tel.: +1 604 822 9119; fax: +1 604 822 2184.

E-mail address: [david.gaumontguay@ubc.ca](mailto:david.gaumontguay@ubc.ca) (D. Gaumont-Guay).

## 1. Introduction

Tower-based eddy covariance (EC) measurements of carbon dioxide ( $\text{CO}_2$ ) exchange made at more than 38 stands in the boreal forest have shown that this biome is, on average, a weak sink for atmospheric  $\text{CO}_2$  (Black et al., 2005), which is in agreement with large-scale  $\text{CO}_2$  concentration and isotope analyses (Ciais et al., 2005; Fan et al., 1998; Gurney et al., 2002; Sarmiento and Gruber, 2002). However, continuous monitoring in a few boreal coniferous and deciduous stands over the last decade has revealed large interannual variability in the  $\text{CO}_2$  sink strength or net ecosystem production (NEP) of these stands (Barr et al., 2006; Black et al., 2000; Goulden et al., 1998). The interannual variability in NEP has been mainly attributed to the direct effects of climate variability on  $\text{CO}_2$  assimilation through gross ecosystem photosynthesis ( $P_g$ ) and  $\text{CO}_2$  loss through ecosystem respiration ( $R_e$ ). Since recent studies have indicated that variation of  $R_e$  is a significant determinant of the sink-source status of forest stands (Barr et al., 2006; Griffis et al., 2004; Valentini et al., 2000), it is essential that we gain a better understanding of the environmental and biological controls on  $R_e$ .

Chamber measurements have proven very useful in assessing the contribution of soil ( $R_s$ ), wood ( $R_w$ ) and foliage ( $R_f$ ) respiration to  $R_e$  and to better understand how each component is affected by environmental and biological variables. On an annual basis,  $R_s$  accounts for more than two-thirds of  $R_e$ , the remainder being partitioned almost equally between  $R_w$  and  $R_f$  (Bolstad et al., 2004; Griffis et al., 2004; Lavigne et al., 1997). The seasonality of each component is highly correlated with variations of temperature (Drewitt et al., 2002; Gaumont-Guay et al., 2006; Griffis et al., 2004; Lavigne et al., 1997). Strong inhibitions of  $R_s$  have also been observed at low and high soil water contents (Gaumont-Guay et al., 2006; Griffis et al., 2004; Janssens et al., 2003) and have been mainly attributed to a reduction in decomposition by microbial activity and possibly to an alteration of transport and storage of  $\text{CO}_2$  and/or lack of oxygen ( $\text{O}_2$ ) in the soil, respectively (Bunnell et al., 1977; Gaumont-Guay et al., 2006).  $R_w$  and  $R_f$  have often been separated into their maintenance and growth components (Amthor, 1989). Despite the strong control of temperature on the maintenance component of  $R_w$  and  $R_f$ , seasonal variations have also been attributed to nitrogen content of the tissues and growth rates (Lavigne and Ryan, 1997; Lavigne et al., 1996, 2004; Maier, 2001; Maier et al., 1998; Ryan, 1991; Ryan et al., 1995; Vose and Ryan, 2002). Woody tissue growth respiration has

been shown to occur during periods of biomass increment and its magnitude to be proportional to the biomass synthesized (Lavigne et al., 2004; Maier, 2001; Vose and Ryan, 2002).

Although the EC technique allows the partitioning of NEP between  $P_g$  and  $R_e$ , large uncertainties remain in the annual integration of these components mainly because of measurement difficulties during high atmospheric stability at night (Baldocchi, 2003). The lack of turbulent mixing during nighttime causes an underestimation of the true biotic flux, i.e.,  $R_e$ . To overcome this problem, measurements under a threshold level of friction velocity ( $u_*$ ) are usually rejected and replaced with values determined from the relationship between  $R_e$  and soil temperature obtained under turbulent conditions (see Black et al. (1996) for an example of the method). Despite these corrections, annual totals of  $R_e$  derived from EC measurements are usually lower than those obtained from chambers (Bolstad et al., 2004; Drewitt et al., 2002; Goulden et al., 1996; Griffis et al., 2004; Lavigne et al., 1997; Law et al., 1999).

In this study, continuous half-hourly measurements of  $R_s$ , tree bole respiration ( $R_b$ ) and ecosystem  $\text{CO}_2$  exchange were made with automated chamber and EC systems between 2001 and 2003 in a mature boreal trembling aspen stand (*Populus tremuloides* Michx.) to investigate the influence of long-term variations of environmental and biological variables on component-specific and whole-ecosystem respiration processes. During the study period, the stand received approximately half of the normal yearly precipitation, which led to one the most severe droughts recorded to date (Hogg et al., 2005). The drought, which affected much of the western plains of North America, started in mid-2001 and lasted until the fall of 2003. The specific objectives of this study were to (1) quantify the seasonal variations of  $R_s$  and  $R_b$  during the 3-year period, (2) compare scaled-up chamber estimates of  $R_e$  with those obtained with EC, and (3) quantify the effects of the prolonged drought on interannual variations of  $R_e$  and its components.

## 2. Methods

### 2.1. Site description

This study was conducted in an 81-year-old (age in 2001) trembling aspen forest located at the southern edge of the Canadian boreal forest in the Prince Albert National Park, Saskatchewan, Canada (53.629°N, 106.200°W). This forest originated from fire disturbance in 1919 and is dominated by ~22-m high

trembling aspen (*P. tremuloides*) with a dense 2-m high hazelnut understory (*Corylus cornuta* Marsh.). The 30-year mean annual air temperature and precipitation measured at a nearby climate station (1934–1990, Waskesiu Lake, 53.6°N, 106.1°W) are 0.3 °C and 456 mm, respectively. The soil is classified as an orthic gray luvisol (Anderson, 1998) and consists of a loam to sandy clay loam covered by an 8–10 cm deep organic layer. A detailed description of the site can be found in Gaumont-Guay et al. (2006).

## 2.2. Chamber respiration measurements

Continuous half-hourly measurements of  $R_s$  and  $R_b$  were made with a non steady-state automated chamber system described in detail in Gaumont-Guay et al. (2006). The system consisted of four soil chambers and one tree bole chamber connected to temperature controlled housings (TCHs) containing data logging and pumping equipment. The 60-L transparent acrylic soil chambers were randomly located within a 15-m radius around the TCHs and consisted of a moveable lid attached by hinges to a fixed collar inserted between 3 and 4 cm into the soil. The lids were kept open when the chambers were not in use (83% of the time for each chamber) to allow rain, snow and litter to fall into the collar area. The ~95-L transparent tree bole chamber was attached to an aspen tree (~20 cm in diameter) at 1.2 m above the ground. The chamber, which was 50 cm in height, enclosed the entire circumference of the tree (0.33 m<sup>2</sup> bark area). The wall of the chamber was made of a clear flexible polyethylene sheet that was fixed on two painted plywood platforms forming the top and bottom of the chamber. Seals between the plywood platforms and the bole were achieved with expandable foam gaskets. When not in use, the chamber was flushed by blowing ambient air in and out of the chamber through small flap valves with a 120 V AC fan. All chambers were equipped with a 50-cm long pressure equilibration tube to eliminate any pressure difference between inside and outside the chamber and attenuate the potential pumping action of small fluctuations in ambient pressure (Widén and Lindroth, 2003). System operation (chamber selection, timing of lid opening and closing, activation of relays and solenoids, etc.) was achieved with dataloggers (Models 21X and CR10, Campbell Scientific Inc., Logan, UT, USA).

Half-hourly  $R_s$  and  $R_b$  ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) were calculated using the following equation:

$$R_i = \rho_a \frac{V_e}{A} \frac{ds_c}{dt}, \quad (1)$$

where  $R_i$  is the soil or bole respiration rate,  $\rho_a$  the molar density of dry air ( $\text{mol m}^{-3}$ ),  $V_e$  the effective volume of the chamber ( $\text{m}^3$ ),  $A$  the area of ground or bark covered by the chamber ( $\text{m}^2$ ),  $ds_c/dt$  the time rate of change of the  $\text{CO}_2$  mixing ratio in the chamber headspace over a 1-min interval following lid closure ( $\text{mol CO}_2 \text{ mol}^{-1} \text{ dry air s}^{-1}$ ) and  $t$  is the time (s).  $V_e$  was measured daily using a gas injection technique described in detail in Gaumont-Guay et al. (2006).  $V_e$  for the soil chambers was on average 14% higher than the geometric volume ( $V_g$ ) for the three summers, but was approximately 30% less during the winters due to the presence of snow in the collar area.  $V_e$  of the bole chamber was on average 10% higher than  $V_g$  over the 3 years.

Missing data due to instrument failure, IRGA calibrations and poor quality measurements represented 35 and 27% of the dataset for  $R_s$  and  $R_b$ , respectively, over the 3 years (mostly during winter). Since the spatial variability of  $R_s$  between chambers was low (coefficient of variation = 0.18, Griffis et al., 2004), half-hourly measurements made by the four chambers were averaged to obtain representative half-hour values for the stand.

## 2.3. Eddy covariance measurements

Continuous half-hourly whole-ecosystem  $\text{CO}_2$  flux measurements ( $F_c$ ) were made above the stand canopy with the EC technique (Chen et al., 1999). Vertical wind speed and  $\text{CO}_2$  mixing ratio were measured at 39 m above the ground with a three-dimensional sonic anemometer–thermometer (SAT, Model R3, Gill Instruments, Lymington, UK) and a closed-path IRGA (Model LI-6262), respectively. The IRGA was kept at 38 °C in a temperature controlled housing and calibrated daily using a procedure similar to that described for the automated chamber system (Gaumont-Guay et al., 2006). Air was sampled within 30 cm of the SAT and was pulled through a 4-m long  $\times$  4 mm i.d. heated tube (Synflex 1300, Saint-Gobain Performance Plastics, Wayne, NJ, USA) and the IRGA with a diaphragm pump (Model DOA-V191-AA, Gast Inc., Dayton, OH) at a flow rate of 9.5 L  $\text{min}^{-1}$ . The IRGA analogue signal was sampled at 125 Hz with a data acquisition system (Model DaqBook/200, Iotech Inc., Cleveland, OH, USA), down sampled to 20.83 Hz to match the SAT output and transferred every half-hour to the PC system in the hut. Data were downloaded daily via cellular phone to our laboratory for quality assessment and analysis.

Half-hourly block-averaged values of  $F_c$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) were calculated using the following equation:

$$F_c = \rho_a \overline{w's'_c}, \quad (2)$$

where  $\rho_a$  is the mean half-hourly molar density of dry air ( $\text{mol m}^{-3}$ ),  $w'$  and  $s'_c$  are the instantaneous fluctuations of vertical wind speed ( $\text{m s}^{-1}$ ) and  $\text{CO}_2$  mixing ratio ( $\mu\text{mol CO}_2 \text{ mol}^{-1}$  dry air), respectively. The over-bar indicates that the values of  $w's'_c$  were averaged over the 30-min period. The coordinate system for the SAT wind speed components was rotated to make the mean vertical and lateral components equal to zero. Half-hourly  $F_c$  values were corrected for the rate of change in storage of  $\text{CO}_2$  in the air column beneath the EC sensors ( $dS_c/dt$ ) using an eight-level  $\text{CO}_2$  sampling system (Yang et al., 1999) to give the ecosystem biotic flux or the net ecosystem  $\text{CO}_2$  exchange (NEE, i.e.,  $\text{NEE} = F_c + dS_c/dt$ ). NEE measurements were corrected for energy balance closure following Griffis et al. (2003). Missing  $F_c$  data due to instrument failure, IRGA calibrations and poor quality measurements represented 11.6, 11.2 and 7.2% of the dataset for the three respective years.

#### 2.4. Climate and ancillary measurements

Half-hourly air temperature ( $T_a$ ) was measured at 37 m above the ground with a chromel–constantan thermocouple in an aspirated radiation shield (Model 077, Met-One Instruments Inc., Grants Pass, OR, USA). Soil temperature ( $T_s$ ) was measured at depths of 2, 5, 10, 20, 50 and 100 cm (starting from litter surface) with a copper–constantan thermocouple profile located near the automated chamber system. Unless otherwise stated, the arithmetic average of  $T_s$  measurements made at the 2-, 5- and 10-cm depths was used in the analysis of the dependence of daily mean  $R_s$  on  $T_s$ . Tree bole temperature ( $T_b$ ) was measured within the chamber on the south and north sides of the tree by inserting fine-wire copper–constantan thermocouples at 2 mm beneath the outer surface of the bark. Soil volumetric water content ( $\theta$ ) was measured to a depth of 1.2 m every 4 h at the same location as the soil thermocouple profile using MoisturePoint type B segmented TDR probes (Model MP-917, ESI Environmental Sensors Inc., Victoria, BC, Canada). Measurements of  $\theta$  in the 0–15 and 30–60 cm soil layers were used in this analysis and half-hourly  $\theta$  was obtained by linear interpolation. Precipitation ( $P$ ) was measured with a weighing gauge (Model 3000, Belfort Instruments,

Baltimore, MD, USA). Photosynthetically active radiation (PAR) was measured above the forest canopy with a quantum sensor (Model 190-SB, LI-COR Inc., Lincoln, NE, USA). Leaf area index (LAI) was measured periodically during the 3 years using a LAI-2000 plant canopy analyzer (Chen et al., 1997) and was interpolated to fully describe all three growing seasons using an approach presented in Barr et al. (2004). Aspen radial growth increment was measured approximately every 2 weeks on two trees (27 and 16.3 cm in diameter) located near the bole chamber using manual band dendrometers attached at the 1.3-m height (Series 5, Agricultural Electronics Corporation, Tucson, USA).

#### 2.5. Estimation of annual respiration totals

Filling of gaps in records of daily values and calculation of annual totals for  $R_s$  were done with empirical relationships developed between  $R_s$ ,  $T_s$  in the 0–10 cm layer and  $\theta$  in the 0–15 cm layer (see Section 3). The seasonal relationship between daily mean  $R_s$  and  $T_s$  was first characterized for each year using a  $Q_{10}$  model:

$$R_s = R_{s10} Q_{10R_s}^{(T_s-10)/10}, \quad (3)$$

where  $R_{s10}$  is the soil respiration rate at 10 °C and  $Q_{10R_s}$  is the temperature sensitivity of  $R_s$ , defined as the relative increase in respiration for a 10 °C increase in  $T_s$ . A hyperbolic function (Gaumont-Guay et al., 2006) was then used to quantify the dependence of the daily residuals of  $R_s$  ( $R_{sN}$ ), i.e., the ratio of observed to predicted values using Eq. (3), on  $\theta$ :

$$R_{sN} = a + b\theta + \frac{c}{\theta}, \quad (4)$$

where  $a$ ,  $b$  and  $c$  are fitted parameters.

Filling of gaps in records of daily values and calculation of annual totals for  $R_b$  were done with empirical relationships developed between  $R_b$  and  $T_b$  at 2 mm beneath the outer surface of the bark for each year separately using Eq. (3) (rewritten in terms of  $T_b$ ). The mature tissue method (Amthor, 1989) was used to partition  $R_b$  into its components of maintenance ( $R_{bm}$ ) and growth ( $R_{bg}$ ) respiration. In the aspen stand, radial growth increment started with leaf emergence and was completed in early to mid-July (see Section 3). However, since small pulses in radial growth were observed in late summer and thickening of cell walls potentially continued after radial growth had stopped (Sprugel and Benecke, 1990), the radial growth increment period was extended until the end of

September during each year. The measurements of  $R_b$  made outside the radial growth increment period were assumed to reflect maintenance respiration ( $R_{bm}$ ) and those made during the radial growth increment period (from the time of leaf emergence to the end of September) were associated with maintenance and growth ( $R_{bg}$ ) respiration combined ( $R_{bmg}$ ). The relationship between daily mean  $R_{bm}$  and  $T_b$  at 2 mm beneath the outer surface of the bark was then used to estimate  $R_{bm}$  (using Eq. (3)) during the active growth period. The difference between daily mean  $R_{bmg}$  and  $R_{bm}$  was used to obtain daily mean  $R_{bg}$ .

The exponential relationship between daily mean nighttime  $R_f$  and  $T_f$  (Eq. (3) rewritten in terms of  $T_f$ ) determined using data obtained from an experiment conducted in 1996 in the aspen stand (Hogg et al., 2000) was used to estimate daily (from daily mean  $T_a$  in the aspen and hazelnut canopies, i.e., at the 18- and 2-m heights) and annual totals of  $R_f$  for aspen and hazelnut separately.  $R_{f10}$  and  $Q_{10Rf}$  parameters for aspen were  $0.31 \mu\text{mol m}^{-2}$  leaf (hemi- or projected surface area, HSA)  $\text{s}^{-1}$  and 2.0, respectively ( $r^2 = 0.57$ , RMSE = 0.05,  $n = 40$ ,  $P < 0.01$ ).  $R_{f10}$  and  $Q_{10Rf}$  parameters for hazelnut were  $0.12 \mu\text{mol m}^{-2}$  leaf (HSA)  $\text{s}^{-1}$  and 2.4, respectively ( $r^2 = 0.40$ , RMSE = 0.04,  $n = 39$ ,  $P < 0.01$ ). These estimates of  $R_f$  were likely an upper limit since they did not include the potential restricting effects of other environmental factors, such as soil water shortage, on respiratory capacity of leaves as well as the light inhibition of daytime dark respiration due to the Kok effect (Brooks and Fraquhar, 1985).

NEE measurements from EC made during the night represent  $R_e$ . Therefore, empirical relationships developed between half-hourly nighttime NEE when friction velocity ( $u_*$ ) was high ( $>0.35 \text{ m s}^{-1}$ , see Black et al., 2000) and  $T_s$  at the 2-cm depth were used to estimate half-hourly nighttime  $R_e$  during periods of low  $u_*$  and daytime half-hourly  $R_e$  (using a moving window procedure described in Barr et al., 2004). Half-hourly values for 24-h periods were averaged to get daily mean values. These values were then summed during each year to get annual totals. Half-hourly  $P_g$  was estimated as  $-NEE + R_e$  during daytime and the gaps filled by using a hyperbolic relationship between  $P_g$  and PAR (Krishnan et al., 2006). Gaps in NEE were filled using modeled  $P_g$  and  $R_e$ . Daily mean values of  $P_g$  and NEE were calculated by averaging half-hourly values over 24-h periods. These values were then summed during each year to get annual totals for these components. NEP was taken to be  $-NEE$ .

## 2.6. Scaling up of chamber respiration measurements to the ecosystem level and comparison with eddy covariance measurements

$R_s$  was scaled up to the ecosystem level by multiplying daily mean values by the surface of ground not occupied by trees (0.98), based on an estimate of the average tree bole area at the ground level and stand density. Daily mean  $R_b$  was scaled up using the bark area index (BAI) for the site (0.89). To estimate the BAI, it was assumed that the trees had a truncated cone shape and had an average of 10 branches per tree.  $R_b$  was assumed to not vary with height based on measurements of  $R_b$  at the 1.3- and 6-m heights in this stand in 1994 (Ryan et al., 1997). Daily mean  $R_f$  for aspen and hazelnut were scaled up using interpolated estimates of the leaf area index of each species for each year.

Half-hourly estimates of nighttime  $R_e$  using chamber measurements were obtained as  $R_e = R_s + R_b + R_{fa} + R_{fb}$ , where  $R_{fa}$  and  $R_{fb}$  are aspen and hazelnut foliage respiration, respectively. These values were compared to nighttime half-hourly estimates of  $R_e$  obtained with EC. Half-hourly values of  $R_e$  from the two methods were averaged during the nighttime of each day (PAR above the forest canopy was  $<1 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ). Only half-hourly EC data when  $u_*$  was greater than  $0.35 \text{ m s}^{-1}$  were used in the analysis. Data collected during the 3 years were pooled for the comparison.

## 2.7. Evaluation of uncertainties in chamber and eddy covariance respiration estimates

An analysis was conducted to evaluate the uncertainties in the integrated annual carbon budgets obtained from chamber and EC measurements. Uncertainties in EC measurements originated mainly from: (1) random errors associated with the stochastic nature of turbulent transport and the varying location and extent of the flux footprint and (2) systematic errors mainly resulting from the insufficient nocturnal mixing and the associated gap filling procedure (Moncrieff et al., 1996). Random error in the annual NEP calculated via EC is usually small ( $<10\%$ ) due to the large number of half-hour measurements during the year (Morgenstern et al., 2004). To estimate a “worse case” uncertainty in the annual NEP, the random error of  $\pm 10\%$  was added to the average uncertainty in the corrections to the systematic errors ( $\pm 23\%$ ) for the aspen site calculated by Krishnan et al. (2006) for 1994–2005. To estimate the uncertainty in the annual totals of  $P_g$  and  $R_e$ , the average uncertainties reported by Black et al. (2000) for 1994, 1996–1998 were used,

i.e.,  $\pm 7\%$  for  $P_g$  and  $\pm 9\%$  for  $R_e$ . The magnitude of these uncertainties is similar to those reported for a Douglas-fir stand in British Columbia (Morgenstern et al., 2004). The uncertainties for the chamber technique originated mainly from random errors associated with spatial variability in the measurements. The uncertainty attributed to spatial variability of  $R_s$  was quantified using the coefficient of variation between chambers (18%). Since no measures of inter-tree variability for  $R_b$  were available and because significant variations of  $R_b$  with height, and between branches and boles, have been reported in the literature (e.g., Damesin et al., 2002), a conservative error estimate of 30% was assigned to this component. The average uncertainties associated with the estimates of leaf area index for aspen (11%) and hazelnut (5%) from 2001 to 2003 were used to estimate error in  $R_{fa}$  and  $R_{fb}$  for each year (Barr et al., 2004). The total “worse case” uncertainty in the integrated  $R_c$  estimates derived from chamber measurements was obtained by summing the absolute error for each component (i.e.,  $R_s$ ,  $R_b$ ,  $R_{fa}$  and  $R_{fb}$ ) for each year.

### 3. Results and discussion

#### 3.1. Phenological characteristics and climate conditions during the study period

Table 1 summarizes the phenological characteristics and the mean annual climate conditions during the 3-year study period in the aspen stand. The warmest and coldest years were 2001 and 2002, respectively, with mean annual  $T_a$  of  $3.0 \pm 11.9$  ( $\pm$ S.D.) and  $0.7 \text{ }^\circ\text{C} \pm 12.8$ , respectively. The wettest and driest years were also 2001 and 2002, respectively, with mean growing season  $\theta$  in the 0–15 cm layer of  $0.24 \pm 0.07$  and  $0.20 \pm 0.06 \text{ m}^3 \text{ m}^{-3}$ , respectively. Daily mean  $T_s$  of the 0–10 cm layer peaked in early to late August during each year ( $\sim 16 \text{ }^\circ\text{C}$ ) and was lowest in January ( $\sim -5 \text{ }^\circ\text{C}$ ) (Fig. 1a). Soil water content peaked just after snowmelt in each year and gradually decreased during the growing seasons (Fig. 1b). Low precipitation in late summer of 2001 (Fig. 1b) corresponded to the beginning of a severe drought in the stand. Precipitation was on average 200 mm less in the three years compared to the 30-year normal of 456 mm (Table 1). Barr et al. (2004) reported that the drought was associated with a reduction in maximum LAI for aspen and hazelnut in 2002 and 2003 (Table 1). Aspen leaf emergence was delayed by 3 weeks in 2002 due to a cold spring and these conditions resulted in the shortest growing season of the 3 years (Table 1).

Table 1

Phenological characteristics and mean annual climate conditions ( $\pm 1$  S.D. calculated from daily mean values) in the aspen stand from 2001 to 2003

Variable	2001	2002	2003
Phenology			
Max LAI aspen ( $\text{m}^2 \text{ m}^{-2}$ )	2.7	2.3	1.9
Max LAI hazelnut ( $\text{m}^2 \text{ m}^{-2}$ )	2.3	1.9	2.1
Aspen leaf emergence	26 April	23 May	30 April
Growing season length (days)	159	146	149
Temperature			
Mean $T_a$ (37 m, $^\circ\text{C}$ )	$3.0 \pm 11.9$	$0.7 \pm 12.8$	$1.9 \pm 14.2$
Mean $T_s$ (0–10 cm, $^\circ\text{C}$ )	$4.6 \pm 5.6$	$3.5 \pm 6.0$	$3.9 \pm 6.6$
Water			
Annual precipitation (mm)	240	289	254
Mean $\theta$ (0–15 cm, $\text{m}^3 \text{ m}^{-3}$ ) <sup>a</sup>	$0.24 \pm 0.07$	$0.20 \pm 0.06$	$0.22 \pm 0.07$
Mean $\theta^a$ (30–60 cm, $\text{m}^3 \text{ m}^{-3}$ )	$0.31 \pm 0.04$	$0.26 \pm 0.02$	$0.28 \pm 0.04$

LAI, leaf area index;  $T_a$ , air temperature;  $T_s$ , soil temperature (arithmetic average of  $T_s$  measured at 2, 5 and 10 cm);  $\theta$ , soil volumetric water content.

<sup>a</sup> Mean  $\theta$  was calculated during conditions when the soil was not frozen. Mean  $T_a$  and  $T_s$  are averages from 1 January to 31 December.

#### 3.2. Seasonal dependence of soil respiration on soil temperature and water content

Half-hourly  $R_s$  averaged during each year was  $2.9 \pm 2.4$  ( $\pm$ S.D.),  $2.3 \pm 1.9$  and  $2.5 \pm 2.0 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$  in 2001–2003, respectively (excluding missing data). Daily mean  $R_s$  (24-h) peaked in mid-July to late August ( $9.2$ ,  $7.6$  and  $8.6 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$  for each year, respectively) and was at its lowest during winter months ( $\sim 0.1 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ ), but still positive, when the soil surface was frozen (Fig. 1a and c).  $R_s$  generally followed the temporal trend of  $T_s$  in the 0–10 cm layer during each growing season. In spring of each year, the first signs of snowmelt were followed by a rapid increase in  $\theta$  in the 0–15 cm layer and a small increase in  $R_s$  (Fig. 1b and c). Interestingly, a small increase in  $R_s$  was measured at the end of March 2003 before the increase of  $T_s$  and  $\theta$ . This response may have been related to the microbial decomposition of leaves deposited the previous fall. Summer rain events usually resulted in strong positive pulses in  $R_s$ , especially in June, July and August when the

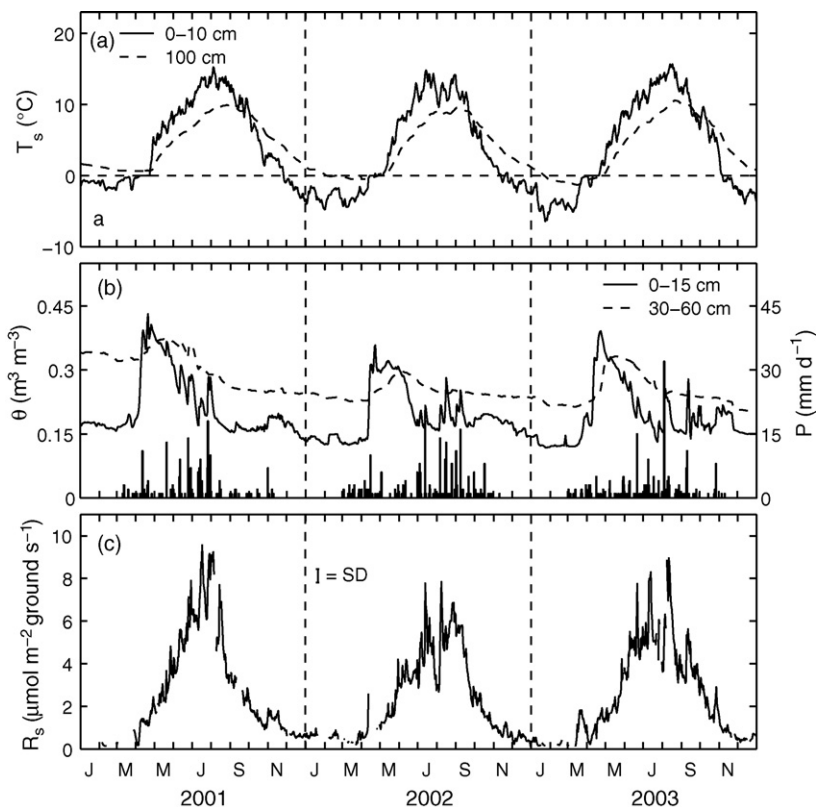


Fig. 1. Seasonal course of daily mean (a) soil temperature ( $T_s$ ) in the 0–10 cm layer (solid) and at the 100-cm depth (dashed), (b) soil water content ( $\theta$ ) between 0 and 15 (solid) and 30–60 (dashed) cm, precipitation ( $P$ , right axis) and (c) soil respiration ( $R_s$ ) in the aspen stand from 2001 to 2003. Only the mean of all standard deviations (S.D.) calculated from half-hourly measurements is presented for clarity.

soil was dry. For example, daily mean  $R_s$  increased rapidly from 3.6 to 9.0  $\mu\text{mol m}^{-2} \text{s}^{-1}$  following large rainfalls at the beginning of August 2003 (Fig. 2). As discussed in Gaumont-Guay et al. (2006), the sudden replenishment of soil water during these periods appeared to be associated with an instantaneous or sustained increase in  $\text{CO}_2$  production in the soil due to enhanced microbial decomposition of available carbon compounds and microbial population growth, respectively (Borken et al., 2002; Jassal et al., 2005; Lee et al., 2004; Xu and Baldocchi, 2004; Xu et al., 2004). There was a decoupling between  $R_s$  and  $T_s$  in the 0–10 cm layer late in the growing season of 2001 due to the onset of the drought (Fig. 1a and c). Episodic drying events during the growing seasons of 2002 and 2003 were also associated with reductions in  $R_s$  in both years. The dry surface soil layers combined with the drop in  $T_s$  in July 2002 resulted in the lowest mid-summer  $R_s$  measured during the 3 years.

The relationship between daily mean  $R_s$  and  $T_s$  in the 0–10 cm layer for each of the 3 years was well described by a  $Q_{10}$  model (Fig. 3). There was a reduction of  $R_{s10}$  in

2002 and 2003 as compared to 2001 ( $R_{s10}$  values were 4.1, 3.7 and 3.7  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for the respective years, Table 2). A gradual reduction in the temperature sensitivity of  $R_s$  was also observed over the 3 years ( $Q_{10R_s}$  values were 4.1, 3.6 and 3.3 for the respective years, Table 2). The relationship between  $R_s$  and  $T_s$  in the 0–10 cm layer showed strong seasonal hysteresis in 2001 (Fig. 3a). This pattern was attributed to the limitation imposed on microbial activity by the late summer drought conditions or to high rates of fine root production and associated respiration early in the growing season (Gaumont-Guay et al., 2006). The seasonal hysteresis was not observed in 2002 or 2003.

Daily mean  $R_s$  normalized using the best fits of the  $Q_{10}$  functions during the growing seasons ( $R_{sN}$ ) decreased when  $\theta$  in the 0–15 cm layer was below and above a threshold value of  $\sim 0.25$ – $0.30 \text{ m}^3 \text{ m}^{-3}$  during each year (Fig. 3). This value corresponded approximately to the soil water field capacity ( $\theta_{fc}$ ) in the 0–15 cm layer. The dependence of daily  $R_{sN}$  on  $\theta$  was well described with a hyperbolic function (Eq. (4), parameter values for each year are given in Table 2). As

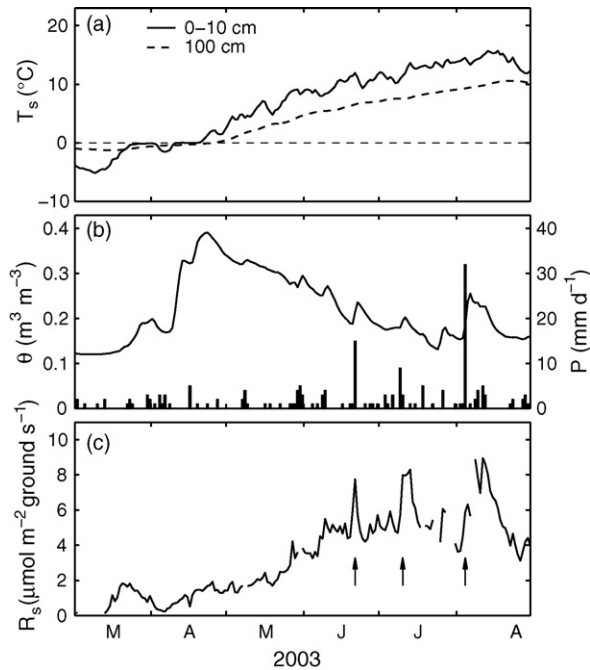


Fig. 2. Seasonal course of daily mean (a) soil temperature ( $T_s$ ) in the 0–10 cm layer (solid) and at the 100-cm depth (dashed), (b) soil water content ( $\theta$ ) in the 0–15 cm layer, precipitation ( $P$ , right axis) and (c) soil respiration ( $R_s$ ) in the aspen stand from March to August 2003. Arrows indicate pulses in  $R_s$  following large rainfalls.

discussed in Gaumont-Guay et al. (2006), the strong reduction in  $R_s$  below  $\theta_{fc}$  in 2001 probably resulted from an inhibition of heterotrophic respiration in the organic layer because  $\theta$  in the 30–60 cm layer was relatively constant during the year. The low  $\theta$  conditions in the organic layer during 2001 likely did not induce a reduction in root respiration because fine-root growth was probably over by that time. However, since the water limitation started earlier in 2002 and 2003 (i.e., June–July, see Fig. 1b), it is possible that respiration associated with fine root growth was reduced during those 2 years (Bryla et al., 1997, 2001; Burton et al., 1998). The reduction in  $R_s$  above  $\theta_{fc}$  during each year likely reflected a restriction in soil  $\text{CO}_2$  transport or an inhibition of  $\text{CO}_2$  production due to a lack of oxygen ( $\text{O}_2$ ) (Bunnell et al., 1977; Gaumont-Guay et al., 2006). Overall,  $T_s$  in the 0–10 cm layer and  $\theta$  in the 0–15 cm layer explained 96, 95 and 90% of the variance in daily mean  $R_s$  for the respective years (Table 2).

### 3.3. Seasonal dependence of bole respiration on bole temperature

Half-hourly  $R_b$  averaged during each year was  $0.6 \pm 0.5$  ( $\pm$ S.D.),  $0.5 \pm 0.5$  and  $0.5 \pm 0.5 \mu\text{mol m}^{-2}$

Table 2

Response function parameters, with their  $\pm 95\%$  confidence limits, for the analysis of the dependence of (i) daily mean soil respiration ( $R_s$ ) on soil temperature ( $T_s$ ) in the 0–10 cm layer, (ii) daily temperature-normalized  $R_s$  during the growing season ( $R_{s,N}$ ) on soil water content ( $\theta$ ) in the 0–15 cm layer and (iii) both climate variables combined for 2001–2003

Year	$T_s$ (i)		$\theta$ (ii)		$T_s - \theta$ (iii)	
	$R_{s,10}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$r^2$	$Q_{\text{tors}}$	$n$	$a$	$b$
2001	$4.1 \pm 0.2$	$0.79$	$4.1 \pm 0.5$	269	$5.3 \pm 0.6$	$-6.9 \pm 1.1$
2002	$3.7 \pm 0.1$	$0.90$	$3.6 \pm 0.2$	310	$5.3 \pm 1.2$	$-8.2 \pm 2.5$
2003	$3.7 \pm 0.1$	$0.83$	$3.3 \pm 0.3$	311	$5.3 \pm 1.0$	$-8.5 \pm 2.0$
			RMISE <sup>a</sup> ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )		$c$	RMSE
			1.1		$-0.56 \pm 0.07$	0.15
			0.6			0.15
			0.9			0.23
						$n$
						215
						201
						200
						$r^2$
						0.74
						0.41
						0.19
						0.96
						0.95
						0.90

All relationships were significant at the 99% probability level. Parameters are defined in the text.

<sup>a</sup> Root mean square error.



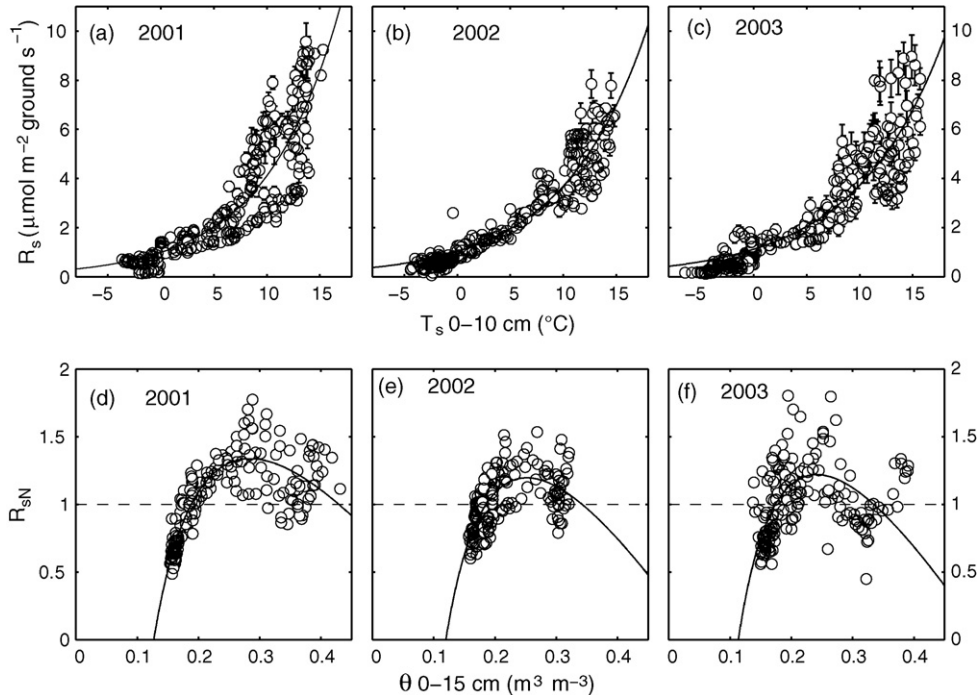


Fig. 3. (Top panels) Relationship between daily mean soil respiration ( $R_s$ ) and soil temperature ( $T_s$ ) in the 0–10 cm layer for (a) 2001, (b) 2002 and (c) 2003. Lines represent the best fits of Eq. (3) ( $P < 0.01$ ). (Bottom panels) Relationship between daily temperature-normalized soil respiration ( $R_{sN}$ ) and soil water content ( $\theta$ ) in the 0–15 cm layer during the growing season of (d) 2001, (e) 2002 and (f) 2003.  $R_s$  was normalized with the  $R_s$ – $T_s$  relationships obtained for each year separately. Lines represent the best fits of Eq. (4) ( $P < 0.01$ ). Vertical bars in the top panels represent  $\pm 1$  S.D. from half-hourly measurements. Parameters are given in Table 2.

bark  $s^{-1}$  for 2001–2003, respectively (excluding missing data). Daily mean  $R_b$  peaked in June during each year (1.8, 2.5 and 2.4  $\mu\text{mol m}^{-2}$  bark  $s^{-1}$  for the respective years), but in contrast to  $R_s$ , maximum values were recorded at least 2 months before the peak in  $T_b$  at the 2-mm depth in 2001 and 2003 (compare Figs. 1a and c and 4a and c). The decoupling between  $R_b$  and  $T_b$  was not an artifact of the depth of temperature measurement inside the bole, as  $T_b$  at the 4- and 8-cm depths only lagged by a few hours that at 2 mm (data not shown). Interestingly, the peak in  $R_b$  occurred at the end of the aspen leaf emergence period during each year, which corresponded to the end of the radial growth increment period for the aspen trees (Fig. 4b). Therefore, the response of  $R_b$  appeared to reflect an increase in energy demand for growth processes.

Daily mean  $R_b$  increased exponentially with  $T_b$  at the 2-mm depth during each year (Fig. 5a–c) and the seasonal relationships were well described by a  $Q_{10}$  model (Eq. (3) rewritten in terms of  $T_b$ ).  $R_b$  was almost negligible when  $T_b$  was less than  $-5^\circ\text{C}$ , but was still positive between  $-5$  and  $0^\circ\text{C}$ . Again, this response could not be attributed to the depth of  $T_b$  measurement because daily variations in  $T_b$  at the 4- and 8-cm depths were only slightly out of

phase with those at 2 mm (as indicated above).  $R_{b10}$  was constant over the 3 years (mean value of 0.55  $\mu\text{mol m}^{-2}$   $s^{-1}$ , Table 3) but  $Q_{10Rb}$  decreased in 2003 due to the low  $R_b$  values measured in fall (Fig. 5c).

The mature tissue method (Amthor, 1989) was used to partition  $R_b$  into its components of maintenance ( $R_{bm}$ ) and growth ( $R_{bg}$ ) respiration (see Section 2).  $R_{bm10}$  decreased slightly from 2001 to 2003 ( $R_{bm10}$  values were 0.43, 0.42 and 0.39  $\mu\text{mol m}^{-2}$   $s^{-1}$  for the respective years, Table 3) but  $Q_{10Rbm}$  remained constant at around 2.6 (Table 3). The 3-year average  $Q_{10Rbm}$  value was approximately twice as high as values obtained previously in the same stand (Lavigne and Ryan, 1997; Ryan et al., 1997). It was also in the upper range of values (1.7–2.5) reported for other deciduous and coniferous species (Ceschia et al., 2002; Damesin et al., 2002; Edwards and Hanson, 1996; Lavigne et al., 1996; Maier, 2001; Maier et al., 1998; Ryan et al., 1995).  $R_{bm10}$  and  $Q_{10Rbm}$  parameters calculated for each year were used to estimate seasonal variations in daily mean  $R_{bm}$  throughout the study period. Seasonal variations in  $R_{bg}$  were then calculated by taking the difference between daily mean  $R_b$  and estimated  $R_{bm}$ . According to the partitioning analysis,  $R_{bm}$  almost entirely dominated  $R_b$  during the 3

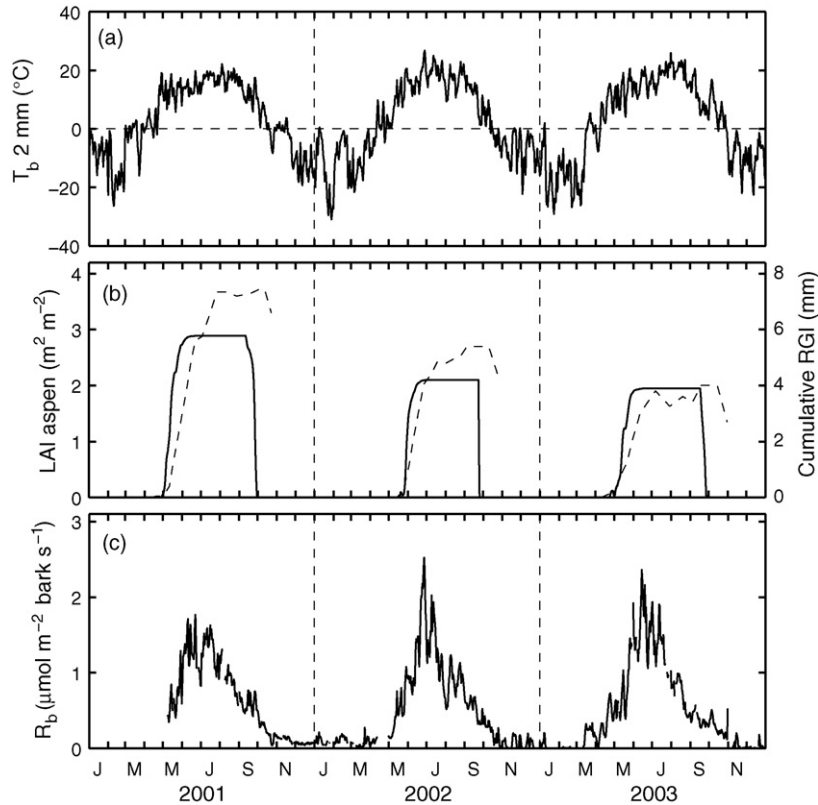


Fig. 4. Seasonal course of daily mean (a) bole temperature ( $T_b$ ) at 2 mm beneath the outer surface of the bark, (b) aspen leaf area index (LAI), aspen cumulative radial growth increment (RGI) and (c) bole respiration ( $R_b$ ) in the aspen stand from 2001 to 2003.

years (Fig. 6a).  $R_{bg}$  generally followed the same temporal trend as aspen radial growth increment (Fig. 6b). The higher  $R_{bg}$  in June and July 2003 was unexpected, as radial growth increment decreased in response to drought during that year (see Fig. 4b and Barr et al., 2006). Interestingly, the mature tissue method did not identify the increased  $R_b$  during the first months of the active

growth period in each year as being due to  $R_{bg}$  (Fig. 6b). Instead, it indicated that the increase was due to  $R_{bm}$ . Differences in  $R_b$  at a reference temperature have been observed between spring and fall periods (usually higher in spring than fall) in other studies (see Lavigne et al., 2004, and references therein) and these were attributed mainly to the metabolic requirements for cambial

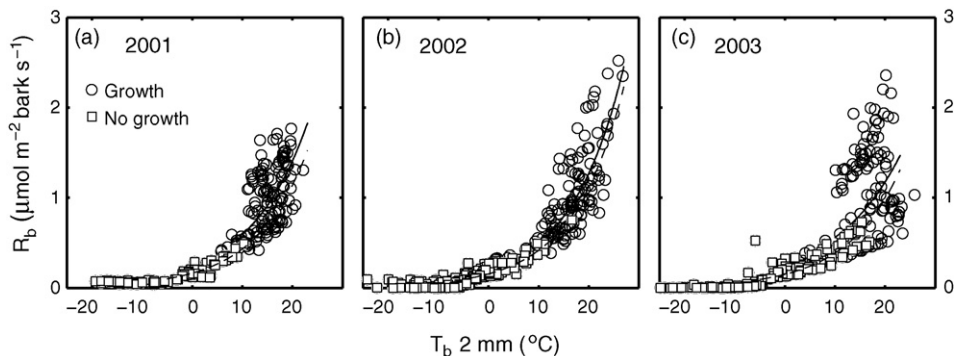


Fig. 5. Relationship between daily mean bole respiration ( $R_b$ ) and bole temperature ( $T_b$ ) at 2 mm beneath the outer surface of the bark during (a) 2001, (b) 2002 and (c) 2003. Open circles and squares represent measurements made during (growth) and outside (no growth) the aspen radial growth increment periods, respectively. Solid and dashed lines represent the best fit of Eq. (3) (rewritten in terms of  $T_b$ ) for each measurement period, respectively ( $P < 0.01$ ). Parameters are given in Table 3.

Table 3

Response function parameters, with their  $\pm 95\%$  confidence limits, for the analysis of the dependence of (i) daily mean bole respiration ( $R_b$ ) and (ii) daily mean bole maintenance respiration ( $R_{bm}$ ) on bole temperature ( $T_b$ ) at 2 mm beneath the outer surface of the bark for 2001–2003

Year	Bole respiration ( $R_b$ )					Bole maintenance respiration ( $R_{bm}$ )				
	$R_{b10}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$Q_{10Rb}$	$r^2$	RMSE <sup>a</sup> ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$n$	$R_{bm10}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$Q_{10Rbm}$	$r^2$	RMSE ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$n$
2001	$0.59 \pm 0.04$	$2.4 \pm 0.3$	0.77	0.24	230	$0.43 \pm 0.03$	$2.6 \pm 0.2$	0.86	0.04	90
2002	$0.49 \pm 0.03$	$2.6 \pm 0.2$	0.87	0.20	327	$0.42 \pm 0.02$	$2.7 \pm 0.2$	0.83	0.05	189
2003	$0.56 \pm 0.05$	$2.1 \pm 0.2$	0.62	0.34	329	$0.39 \pm 0.02$	$2.6 \pm 0.2$	0.86	0.07	196

Units of  $R_{b10}$  and  $R_{bm10}$  are given on bark area basis. All relationships were significant at the 99% probability level. Parameters are defined in the text.

<sup>a</sup> Root mean square error.

reactivation during spring and to the entry of cambium into rest following cessation of cambial growth in late summer. These results show the difficulties in accurately partitioning respiration between its maintenance and growth components and suggest that care should be taken when interpreting annual totals derived from such procedures. Due to the uncertainties associated with the partitioning method, realistic annual totals for  $R_{bm}$  and  $R_{bg}$  were not calculated.

### 3.4. Ecosystem respiration and its components

The sums of scaled-up daily nighttime  $R_s$ ,  $R_b$  and  $R_f$  were highly correlated with nighttime  $R_e$  measurements made using EC above the forest canopy over the 3 years ( $r^2 = 0.83$ , Fig. 7). There was a significant over-estimation of scaled-up chamber estimates of  $R_e$  above

$5 \text{ g C m}^{-2} \text{ d}^{-1}$  when  $R_f$  was included in the comparison (Fig. 7b). This could have originated from the possible overestimation of  $R_f$  for aspen and hazelnut because the procedure used in this study to calculate  $R_f$  did not take into account the potential restricting effects of drought, or other limitations such as the light inhibition of daytime dark respiration (Brooks and Fraquhar, 1985), on this process. Abnormally high values of  $R_e$  ( $> 10 \text{ g C m}^{-2} \text{ d}^{-1}$ ) were measured using EC on some occasions during each growing season (Fig. 7a and b). Yang et al. (1999) attributed these pulses to sudden releases of  $\text{CO}_2$  from the canopy following periods of high atmospheric stability with high  $\text{CO}_2$  concentrations below the EC sensors. It is unlikely that these bursts were related to real biotic fluxes. When these data were not included in the comparison, the intercept of the linear regression between chamber-based (including  $R_f$ )

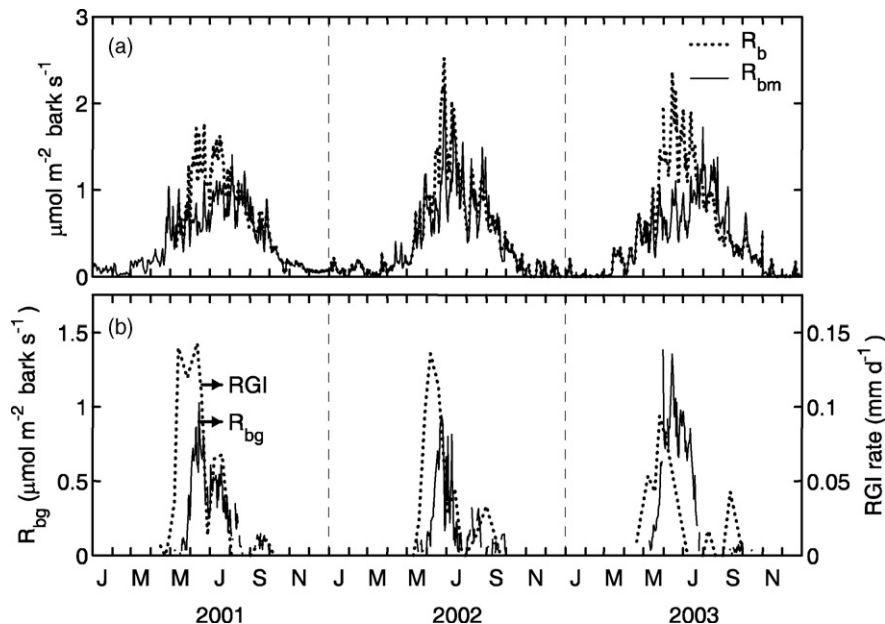


Fig. 6. Seasonal course of daily mean (a) total bole ( $R_b$ , dotted line), maintenance ( $R_{bm}$ , solid line) and (b) growth ( $R_{bg}$ , solid line) respiration in 2001–2003. The seasonal course of aspen radial growth increment (RGI, dotted line) rate is also presented in panel (b) (right axis).

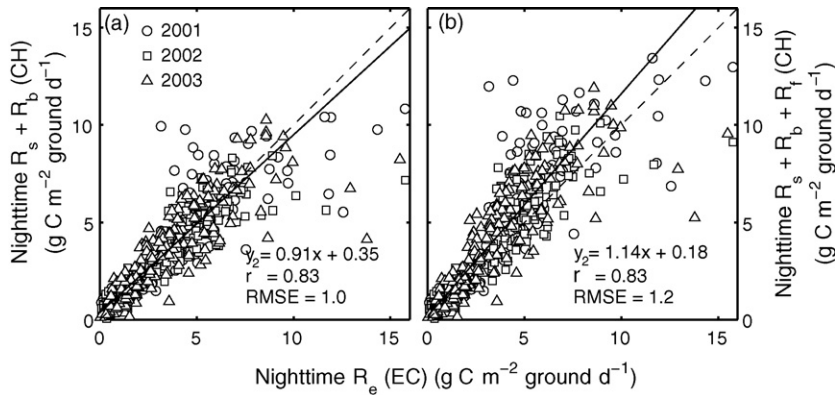


Fig. 7. Comparison between scaled up (a) daily nighttime average soil and bole respiration measured with chambers ( $R_s + R_b$  (CH)) and (b) daily nighttime average soil and bole respiration measured with chambers and estimated foliage respiration (aspen and hazelnut combined) ( $R_s + R_b + R_f$  (CH)) and daily nighttime average ecosystem respiration measured above the canopy with the eddy covariance technique ( $R_e$  (EC)). Only nighttime EC measurements lower than  $10 \text{ g C m}^{-2} \text{ d}^{-1}$  for friction velocity ( $u^*$ )  $> 0.35 \text{ m s}^{-1}$  and non gap-filled data were used in the analysis. Solid and dashed lines represent the best fit of the linear regressions ( $P < 0.01$ ) and the 1:1 lines, respectively.

and EC-based respiration measurements was not significantly different than zero ( $P = 0.03$ ) but the slope was significantly larger than 1 (95% confidence interval between 1.10 and 1.18) (Fig. 7b).

Annual totals of  $R_e$  derived from chamber measurements, including nighttime and daytime respiration, were on average 25% higher than those obtained with EC over the 3 years (Table 4). The values were, however, in agreement given the uncertainty of each measurement technique. Several studies have reported higher estimates of  $R_e$  derived from chamber measurements (Bolstad et al., 2004; Drewitt et al., 2002; Goulden et al., 1996; Griffis et al., 2004; Lavigne et al., 1997; Law et al., 1999), while others have reported good agreement between the two techniques (Law et al., 2001; Wallin et al., 2001). In our study, although the spatial variability between soil chambers was low, the overestimation could have originated from the limited spatial representation of the soil and bole chamber measurements in the tower footprint. The smaller annual totals of  $R_e$  obtained from EC could also be attributed to possible systematic errors in estimates of nighttime  $R_e$ , possibly because advective  $\text{CO}_2$  transport was not being completely accounted for by using high  $u^*$  EC  $\text{CO}_2$  flux measurements (Griffis et al., 2004).

Studies using a combination of micrometeorological and chamber techniques have shown that  $R_s$  usually accounts for more than two-thirds of annual  $R_e$  in forest stands (Bolstad et al., 2004; Goulden et al., 1996; Griffis et al., 2004; Lavigne et al., 1997; Law et al., 1999; Shibistova et al., 2002), which is in agreement with our study (Table 4). On average,  $R_s$ ,  $R_b$  and  $R_f$  contributed  $70 \pm 0.6$ ,  $14 \pm 0.6$  and  $16 \pm 1.1\%$  of annual  $R_e$  calculated from the chamber measurements over the

3 years (Table 4). However, the “true”  $R_b$  was likely underestimated slightly because aspen stems can assimilate some of the  $\text{CO}_2$  produced by respiration during daytime (Foote and Schaedle, 1976, 1978). Annual totals of each component varied markedly between years (Table 4). There were strong reductions in  $R_s$  and  $R_b$  in 2002, the coldest and driest year. The

Table 4

Annual estimates ( $\pm$  uncertainty<sup>a</sup>) of net ecosystem productivity (NEP), gross ecosystem photosynthesis ( $P_g$ ), ecosystem respiration ( $R_e$ ) and its components ( $\text{g C m}^{-2} \text{ ground year}^{-1}$ ) obtained from eddy covariance (EC) and scaled-up chamber (CH) measurements in 2001–2003

Variable	2001	2002	2003
NEP	$361 \pm 119$	$134 \pm 44$	$97 \pm 32$
$P_g$	$1385 \pm 97$	$1017 \pm 71$	$1037 \pm 73$
$R_e$ (EC)	$1024 \pm 92$	$882 \pm 79$	$940 \pm 84$
$R_s$	$914 \pm 165$	$745 \pm 134$	$827 \pm 149$
$R_b$	$167 \pm 50$	$147 \pm 44$	$163 \pm 49$
$R_{fa}^b$	$187 \pm 21$	$128 \pm 14$	$133 \pm 15$
$R_{fb}^b$	$56 \pm 3$	$45 \pm 2$	$58 \pm 3$
$R_e$ (CH) <sup>c</sup>	$1324 \pm 239$	$1065 \pm 194$	$1181 \pm 216$
$R_e$ (CH)/ $R_e$ (EC)	1.29	1.21	1.26
$R_s/R_e$ (CH)	0.69	0.70	0.70
$R_b/R_e$ (CH)	0.13	0.14	0.14
$R_{fa}/R_e$ (CH)	0.14	0.12	0.11
$R_{fb}/R_e$ (CH)	0.04	0.04	0.05
$R_b/P_g$	0.12	0.14	0.16

<sup>a</sup> The procedure used to estimate the “worse case” uncertainty of each component is given in Section 2: NEP  $\pm 33\%$ ,  $P_g \pm 7\%$ ,  $R_e \pm 9\%$ ,  $R_s \pm 18\%$ ,  $R_b \pm 30\%$ ,  $R_{fa} \pm 11\%$  and  $R_{fb} \pm 5\%$ .

<sup>b</sup>  $R_{fa}$  and  $R_{fb}$  are estimates of nighttime and daytime foliar dark respiration for aspen and hazelnut, respectively, and were calculated with measurements of  $T_a$  at the 18-m height in the aspen canopy and the 2-m height in the hazelnut canopy.

<sup>c</sup>  $R_e$  (CH) =  $R_s + R_b + R_{fa} + R_{fb}$ .

substantial reductions in  $R_f$  observed for aspen and hazelnut in 2002 were due to the decrease in LAI for both species in response to drought (Table 1).  $R_f$  increased in 2003 for both species due to higher  $T_a$  but the decrease in LAI for aspen during that year kept the annual total similar to that in 2002. There was an increase in the  $R_b/P_g$  ratio in 2002 and 2003 but the average value ( $0.13 \pm 0.01$ ) (Table 4) was similar to that observed for temperate conifers (Ryan et al., 1995).

The contribution of each component also varied markedly during the year (Fig. 8a). The maximum contribution of  $R_s$  occurred in August, which corresponded to the time of the peak in near-surface  $T_s$ . The maximum contribution of  $R_b$  occurred between May–July and corresponded to the active growth period of the aspen trees.  $R_f$  contributed mostly between July and September. The trend in  $R_f$  contrasted with that observed in a boreal Scots pine stand in central Siberia (Shibistova et al., 2002). These authors reported a bimodal pattern in  $R_f$  (peaks in spring and autumn) that was not only associated with the seasonality of  $T_a$  but also with the foliar respiratory capacity during the two periods. Bolstad et al. (2004) found that maximum  $R_b$  occurred in early summer and corresponded to maximum cambium activity and the development of new xylem elements. In our study,  $R_e$  during the winter was almost completely dominated by  $R_s$  as the stand is deciduous and there is a strong reduction in bole metabolic activity during winter. When the daily sums

of the components were compared with the EC estimates of  $R_e$ , it was found that there was a close correspondence in the seasonal patterns in spite of the systematic overestimation of chamber-based measurements as mentioned earlier (Fig. 8b).

### 3.5. Role of drought in explaining interannual variation of ecosystem respiration

Considerable interannual variability in the  $\text{CO}_2$  sink strength (NEP) has been observed in the aspen stand over the last 10 years (Barr et al., 2004, 2006; Black et al., 2005). Krishnan et al. (2006) reported that NEP varied from a minimum of  $4 \text{ g C m}^{-2} \text{ year}^{-1}$  in 2004 to more than  $361 \text{ g C m}^{-2} \text{ year}^{-1}$  in 2001. NEP has been found to be negatively correlated with the date of leaf emergence, which in turn was negatively correlated with spring  $T_a$  (Black et al., 2005). The high NEP in 2001 was associated with early leaf emergence and the short-term effects of the initial stage of the drought on  $\text{CO}_2$  exchange in the stand.  $P_g$  was relatively unaffected by soil water limitation but  $R_e$  decreased considerably, likely as a result of reduced heterotrophic respiration (Griffis et al., 2003). Year 2002 was the coldest and driest of the last 10 years and these conditions led to the lowest annual  $R_e$  measured in the stand, reflecting reductions in both heterotrophic and autotrophic respiration.  $P_g$  was also affected by the drought through a reduction in maximum LAI, length of growing season

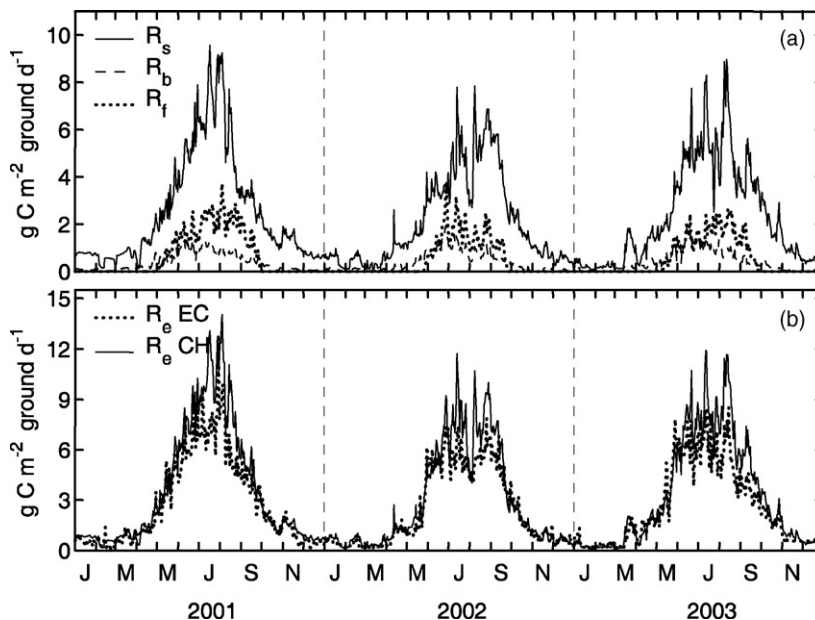


Fig. 8. Seasonal course of (a) daily mean scaled-up soil ( $R_s$ ), bole ( $R_b$ ) and foliage ( $R_f$ , aspen and hazelnut combined) respiration, and (b) daily mean ecosystem respiration ( $R_e$ ) obtained from the sum of scaled-up chamber (CH) and eddy covariance (EC) measurements from 2001 to 2003.

Table 5

Total precipitation ( $P$ ), mean soil temperature ( $T_s$ ) at the 2-cm depth and total soil respiration ( $R_s$ ) for each month of the growing season and during winter of 2001–2003

Period	Total $P$ (mm month <sup>-1</sup> )			Mean $T_s$ (°C)			Total $R_s$ (g C m <sup>-2</sup> month <sup>-1</sup> )		
	2001	2002	2003	2001	2002	2003	2001	2002	2003
April	26	26	18	0.7	-0.8	0.2	36	29	30
May	24	16	25	6.5	3.1	6.1	85	54	69
June	45	16	31	9.3	9.3	9.9	150	101	138
July	69	46	32	12.5	12.8	12.5	219	141	166
August	9	60	59	13.4	12.0	14.0	173	164	169
September	10	47	27	10.5	9.9	10.1	87	124	113
October	11	20	12	5.0	10.1	6.5	45	55	66
January–March	28	37	38	-1.0	-3.0	-3.5	59	36	36
November–December	18	21	12	-0.2	-0.7	-1.7	60	41	40
Total/average <sup>a</sup>	240	289	254	4.6	3.5	3.9	914	745	827

<sup>a</sup> Annual totals for  $P$  and  $R_s$  are in mm year<sup>-1</sup> and g C m<sup>-2</sup> year<sup>-1</sup>, respectively. The 30-year annual mean value for  $P$  is 456 mm year<sup>-1</sup>.

and a likely direct effect of water stress, and this led to a strong reduction in NEP in 2002. There was a small increase of  $R_e$  in 2003 due to higher temperature but  $P_g$  remained low, which resulted in the third lowest NEP measured in the stand during the last decade.

In this study, the independent effects of temperature and  $\theta$  on  $R_e$  and its components were difficult to separate because the two variables co-varied during the 3 years (Table 1). Separation of the effects of the two variables on  $R_s$ , the dominant respiration component in the stand, was undertaken by recalculating annual totals of this component based on  $T_s$  only, i.e., without the limitation imposed by low or high  $\theta$ . Since the seasonal  $R_{s10}$  and  $Q_{10R_s}$  parameters for each year already included the effect of soil water limitation on  $R_s$ , they were recalculated for the drought-free period of 2001, i.e., prior to August (Table 5). These coefficients (5.0  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and 4.0 for  $R_{s10}$  and  $Q_{10R_s}$ , respectively) were used to estimate daily  $R_s$  values for the 3 years based on the measured seasonal variations of  $T_s$  in the 0–10 cm layer. The resulting annual totals of  $R_s$  were 1168, 1045 and 1160 g C m<sup>-2</sup> year<sup>-1</sup> for 2001–2003, respectively. Based on these calculations, it appears that  $T_s$  accounted for only 11 and 1% of the reduction in annual  $R_s$  in 2002 and 2003, respectively, as compared to 2001. The greater reduction in 2002 was likely due to the 3-week delay in spring warming and to lower  $T_a$  and  $T_s$  from August to September (Table 5). Comparison of annual totals of  $R_s$  in Table 4 with the above values indicated that low  $\theta$  resulted in reductions of annual  $R_s$  of 21, 29 and 29% in 2001–2003 with respect to their non-limiting soil water values.

Part of the effects of drought on  $R_s$  and  $R_e$  is likely related to the timing and frequency of rain events rather

than to the amount of precipitation during a growing season. Although total precipitation was highest during the growing seasons of 2002 and 2003 (Table 1), soil water shortage following spring snowmelt occurred more rapidly in these 2 years (see Fig. 1). This was related to lower precipitation during June and July (Table 5). Total  $R_s$  was significantly lower during these 2 months in 2002 and 2003. Since a substantial fraction of fine-root growth occurs during this period in the aspen stand (Kalyn, 2005), it is possible that these conditions led to a reduction in the contribution of autotrophic respiration to  $R_s$ . The significant drop in precipitation for August, September and October 2001 led to a gradual reduction in  $R_s$  during that year. In contrast,  $R_s$  continued to increase in August 2002 and 2003 due to the replenishment of soil water and high  $T_s$ .

#### 4. Conclusions

- (1) Daily mean  $R_s$  varied from 0.1 to 9.2  $\mu\text{mol m}^{-2} \text{s}^{-1}$  over the 3 years.  $R_s$  was highly correlated with  $T_s$  at the 0–10 cm depth during individual years but was also strongly reduced during periods of low and high  $\theta$  in the 0–15 cm layer.  $R_s$  reached its maximum when  $T_s$  was highest in late July–early August.
- (2) Daily mean  $R_b$  varied from negligible during winter to a maximum of 2.5  $\mu\text{mol m}^{-2} \text{bark s}^{-1}$  (2.2  $\mu\text{mol m}^{-2} \text{ground s}^{-1}$ ) during the growing season. In all 3 years,  $R_b$  peaked at the end of the radial growth increment and leaf emergence period, which was 2 months before the peak in  $T_b$  at the 2-mm depth in 2001 and 2003. Partitioning of  $R_b$  between its maintenance ( $R_{bm}$ ) and growth ( $R_{bg}$ ) components revealed that seasonal variations in  $R_{bg}$

were in phase with aspen radial growth increment. This method was, however, inadequate to provide realistic annual totals for each component.

- (3) On average over the 3 years, annual totals of  $R_s$ ,  $R_b$  and  $R_f$  were 829, 159 and 202 g C m<sup>-2</sup> year<sup>-1</sup>, respectively, which corresponded to 70, 14 and 16%, respectively, of the annual totals of  $R_e$  calculated from chamber measurements. The sums of scaled-up daily nighttime  $R_s$ ,  $R_b$  and  $R_f$  were highly correlated with  $R_e$  estimates obtained from EC measurements. Over the 3 years, chamber-based annual totals of  $R_e$  were, however, 25% higher than annual totals obtained from EC.
- (4) Drought appears to have played a more important role than temperature in explaining year-to-year variability of  $R_s$  and  $R_e$ . The effect of drought during each year was more related to the timing and frequency of rain events rather than to the amount of precipitation.

## Acknowledgments

This research was funded by the Fonds de Recherche sur la Nature et les Technologies du Québec (FCAR) in the form of a 3-year graduate scholarship to DGG and the Natural Sciences and Engineering Research Council of Canada (NSERC) through an operating grant to TAB. Additional support was provided by the Fluxnet Canada Research Network (through NSERC, the Canadian Foundation for Climate and Atmospheric Sciences (CFCAS) and BIOCAP, Canada) and the Meteorological Service of Canada through a Contribution Agreement to the University of British Columbia. The authors sincerely acknowledge the technical assistance of Andrew Sauter for the development of the automated chamber system, Ted Hogg for providing dendrometer measurements of aspen radial growth increment and Dave Wieder (Parks, Canada) for maintaining the equipment in the field. The authors also wish to thank Michael Novak, Robert Guy, Cindy Prescott and two anonymous reviewers for constructive reviews of the manuscript.

## References

- Amthor, J.S., 1989. Respiration and Crop Productivity. Springer-Verlag, New York, p. 215.
- Anderson, D., 1998. BOREAS TE-01, soils data over the SSA tower sites. Available online at <http://www.eosdis.ornl.gov/>.
- Baldocchi, D.B., 2003. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Global Change Biol.* 9, 479–492.
- Barr, A.G., Black, T.A., Hogg, E.H., Kljun, N., Morgenstern, K., Nestic, Z., 2004. Interannual variability in the leaf area index of a boreal aspen-hazelnut forest in relation to net ecosystem production. *Agric. For. Meteorol.* 126, 237–255.
- Barr, A.G., Black, T.A., Hogg, E.H., Griffis, T.J., Morgenstern, K., Kljun, N., Theede, A., Nestic, Z., 2006. Climatic controls on the carbon and water balances of a boreal aspen forest, 1994–2003. *Global Change Biol.* 12, 1–16.
- Black, T.A., den Hartog, G., Neumann, H.H., Blanken, P.D., Yang, P.C., Russell, C., Nestic, Z., Lee, X., Chen, S.G., Staebler, R., Novak, M.D., 1996. Annual cycles of water vapour and carbon dioxide fluxes in and above a boreal aspen forest. *Global Change Biol.* 2, 219–229.
- Black, T.A., Chen, W.J., Barr, A.G., Arain, M.A., Chen, Z., Nestic, Z., Hogg, E.H., Neumann, H.H., Yang, P.C., 2000. Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. *Geophys. Res. Lett.* 27, 1271–1274.
- Black, T.A., Gaumont-Guay, D., Jassal, R.S., Amiro, B.D., Jarvis, P.G., Gower, S.T., Kelliher, F.M., Dunn, A., Wofsy, S.C., 2005. Measurement of CO<sub>2</sub> exchange between boreal forest and the atmosphere. In: Griffiths, H., Jarvis, P.G. (Eds.), *The Carbon Balance of Forest Biomes*. Taylor and Francis Group, Oxon, UK, pp. 151–178.
- Bolstad, P.V., Davis, K.J., Martin, J., Cook, B.D., Wang, W., 2004. Component and whole-system respiration fluxes in northern deciduous forests. *Tree Physiol.* 24, 493–504.
- Borken, W., Xu, Y.-J., Davidson, E.A., Beese, A., 2002. Site and temporal variation of soil respiration in European beech, Norway spruce, and Scots pine forests. *Global Change Biol.* 8, 1205–1216.
- Brooks, A., Fraquhar, G.D., 1985. Effects of temperature on the CO<sub>2</sub>/O<sub>2</sub> specificity of ribulose-1,5-bisphosphate carboxylase/oxygenase and the rate of respiration in the light. *Planta* 165, 397–406.
- Bryla, D.R., Bouma, T.J., Eissenstat, D.M., 1997. Root respiration in citrus acclimates to temperature and slows during drought. *Plant Cell Environ.* 20, 1411–1420.
- Bryla, D.R., Bouma, T.J., Hartmond, U., Eissenstat, D.M., 2001. Influence of temperature and soil drying on respiration of individual roots in citrus, integrating greenhouse observations into a predictive model for the field. *Plant Cell Environ.* 24, 781–790.
- Bunnell, F.L., Tait, D.E.N., Flanagan, P.W., vanCleve, K., 1977. Microbial respiration and substrate weight loss. I. A general model of the influence of abiotic variables. *Soil Biol. Biochem.* 9, 33–40.
- Burton, A.J., Pregitzer, K.S., Zogg, G.P., Zak, D.R., 1998. Drought reduces root respiration in sugar maple forests. *Ecol. Appl.* 8, 771–778.
- Ceschia, E., Damesin, C., Lelaube, S., Pontailler, J.Y., Dufrene, E., 2002. Spatial and seasonal variations in stem respiration of beech trees (*Fagus sylvatica*). *Ann. For. Sci.* 59, 801–812.
- Chen, J.M., Blanken, P.D., Black, T.A., Guilbeault, M., Chen, S., 1997. Radiation regime and canopy architecture in a boreal aspen forest. *Agric. For. Meteorol.* 86, 107–125.
- Chen, J.M., Black, T.A., Yang, P.C., Barr, A.G., Neumann, H.H., Nestic, Z., Blanken, P.D., Novak, M.D., Eley, J., Ketler, R.J., Cuencas, R., 1999. Effects of climatic variability on the annual carbon sequestration by a boreal aspen forest. *Global Change Biol.* 5, 41–43.
- Ciais, P., Janssens, I., Shvidenko, A., Wirth, C., Malhi, Y., Grace, J., Schulze, E.-D., Heimann, M., Phillips, O., Dolman, A.J., 2005. The potential for rising CO<sub>2</sub> to account for the observed uptake of carbon by tropical, temperate, and Boreal forest biomes. In: Griffiths, H., Jarvis, P.G. (Eds.), *The Carbon Balance of Forest Biomes*. Taylor and Francis Group, Oxon, UK, pp. 109–149.
- Damesin, C., Ceschia, E., Le Goff, N., Ottorini, J.M., Dufrene, E., 2002. Stem and branch respiration of beech: from tree measurements to estimations at the stand level. *New Phytol.* 153, 159–172.

- Drewitt, G.B., Black, T.A., Nestic, Z., Humphreys, E.R., Jork, E.M., Swanson, R., Ethier, G.J., Griffis, T., Morgenstern, K., 2002. Measuring forest-floor CO<sub>2</sub> fluxes in a Douglas-fir forest. *Agric. For. Meteorol.* 110, 299–317.
- Edwards, N.T., Hanson, P.J., 1996. Stem respiration in a closed-canopy upland oak forest. *Tree Physiol.* 16, 433–439.
- Fan, S., Gloor, M., Mahlman, J., Pacala, S., Sarmiento, J., Takahashi, T., Tans, P., 1998. A large terrestrial carbon sink in North America implied by atmospheric and oceanic dioxide data and models. *Science* 282, 442–446.
- Foote, K.C., Schaedle, M., 1976. Diurnal and seasonal patterns of photosynthesis and respiration by stems of *Populus tremuloides* Michx. *Plant Physiol.* 58, 651–655.
- Foote, K.C., Schaedle, M., 1978. The contribution of aspen bark photosynthesis to the energy balance of the stem. *For. Sci.* 24, 569–576.
- Gaumont-Guay, D., Black, T.A., Griffis, T.J., Barr, A.G., Jassal, R.S., Nestic, Z., 2006. Interpreting the dependence of soil respiration on soil temperature and water content in a boreal aspen stand. *Agric. For. Meteorol.* 140, 220–235.
- Goulden, M.L., Munger, J.W., Fan, S.-M., Daube, B.C., Wofsy, S.C., 1996. Measurements of carbon sequestration by long-term eddy covariance: methods and critical evaluation of accuracy. *Global Change Biol.* 2, 169–182.
- Goulden, M.L., Wofsy, S.C., Harden, J.W., Trumbore, S.E., Crill, P.M., Gower, S.T., Fries, T., Daube, B.C., Fan, S.M., Sutton, D.J., Bazzaz, A., Munger, J.W., 1998. Sensitivity of boreal forest carbon balance to soil thaw. *Science* 279, 214–217.
- Griffis, T.J., Black, T.A., Morgenstern, K., Barr, A.G., Nestic, Z., Drewitt, G.B., Gaumont-Guay, D., McCaughey, J.H., 2003. Ecophysiological controls on the carbon balances of three southern boreal forests. *Agric. For. Meteorol.* 117, 53–71.
- Griffis, T.J., Black, T.A., Gaumont-Guay, D., Drewitt, G.B., Nestic, Z., Barr, A.G., Morgenstern, K., Kljun, N., 2004. Seasonal variation and partitioning of ecosystem respiration in a southern boreal aspen forest. *Agric. For. Meteorol.* 125, 207–223.
- Gurney, K.R., Law, R.M., Denning, A.S., Rayner, P.J., Baker, D., Bousquet, P., Bruhwiler, L., Chen, Y.H., Ciais, P., Fan, S., Fung, I.Y., Gloor, M., Heimann, M., Higuchi, K., John, J., Maki, T., Maksyutov, S., Masarie, K., Peylin, P., Prather, M., Pak, B.C., Randerson, J., Sarmiento, J., Taguchi, S., Takahashi, T., Yuen, C.W., 2002. Towards robust regional estimates of CO<sub>2</sub> sources and sinks using atmospheric transport models. *Nature* 415, 626–630.
- Hogg, E.H., Saugier, B., Pontailier, J.Y., Black, T.A., Chen, W., Hurdle, P.A., Wu, A., 2000. Response of trembling aspen and hazelnut to vapour pressure deficit in a boreal deciduous forest. *Tree Physiol.* 20, 725–734.
- Hogg, E.H., Brandt, J.P., Kochtubajda, B., 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951–2000. *Can. J. For. Res.* 35, 610–622.
- Janssens, I.A., Dore, S., Epron, D., Lankreijer, H., Buchmann, N., Longdoz, B., Brossaud, J., Montagnani, L., 2003. Climatic influences on seasonal and spatial differences in soil CO<sub>2</sub> efflux. In: Valentini, R. (Ed.), *Canopy fluxes of Energy, Water and Carbon dioxide of European Forests*. Springer-Verlag, Berlin, pp. 253–256.
- Jassal, R.S., Black, T.A., Novak, M.D., Morgenstern, K., Nestic, Z., Gaumont-Guay, D., 2005. Relationship between soil CO<sub>2</sub> concentrations and forest-floor CO<sub>2</sub> effluxes. *Agric. For. Meteorol.* 130, 176–192.
- Kalyn, A.L., 2005. Fine root biomass and net primary production in black spruce, aspen and jack pine forests in Saskatchewan. M.Sc. Thesis. University of Saskatchewan, Saskatoon, SK, unpublished.
- Krishnan, P., Black, T.A., Grant, N.J., Barr, A.G., Hogg, E.H., Jassal, R.S., Morgenstern, K., 2006. Impact of changing soil moisture distribution on net ecosystem productivity of a boreal aspen forest during and following drought. *Agric. For. Meteorol.* 139, 208–223.
- Lavigne, M.B., Franklin, S.E., Hunt, E.R., 1996. Estimating stem maintenance respiration rates of dissimilar balsam fir stands. *Tree Physiol.* 16, 687–695.
- Lavigne, M.B., Ryan, M.G., 1997. Growth and maintenance respiration rates of aspen, black spruce and jack pine stems at northern and southern BOREAS sites. *Tree Physiol.* 17, 543–551.
- Lavigne, M.B., Ryan, M.G., Anderson, D.E., Baldocchi, D.D., Crill, P.M., Fitzjarrald, D.R., Goulden, M.L., Gower, S.T., Massheder, J.M., McCaughey, J.H., Rayment, M., Striegl, R.G., 1997. Comparing nocturnal eddy covariance measurements to estimates of ecosystem respiration made by scaling chamber measurements at six coniferous boreal sites. *J. Geophys. Res.* 102, 28977–28985.
- Lavigne, M.B., Little, C.H.A., Riding, R.T., 2004. Changes in stem respiration rate during cambial reactivation can be used to refine estimates of growth and maintenance respiration. *New Phytol.* 162, 81–93.
- Law, B.E., Ryan, M.G., Anthoni, P.M., 1999. Seasonal and annual respiration of a ponderosa pine ecosystem. *Global Change Biol.* 5, 169–182.
- Law, B.E., Kelliher, F.M., Baldocchi, D.D., Anthoni, P.M., Irvine, J., Moore, D., van Tuyl, S., 2001. Spatial and temporal variation in respiration in a young ponderosa pine forest during a summer drought. *Agric. For. Meteorol.* 110, 27–43.
- Lee, X., Wu, H.-J., Sigler, J., Oishi, C., Siccama, T., 2004. Rapid and transient response of soil respiration to rain. *Global Change Biol.* 10, 1017–1026.
- Maier, C.A., 2001. Stem growth and respiration in loblolly pine plantations differing in soil resource availability. *Tree Physiol.* 21, 1183–1193.
- Maier, C.A., Zarnoch, S.J., Dougherty, P.M., 1998. Effects of temperature and tissue nitrogen on dormant season stem and branch maintenance respiration in a young loblolly pine (*Pinus taeda*) plantation. *Tree Physiol.* 18, 11–20.
- Moncrieff, J.B., Malhi, Y., Leuning, R., 1996. The propagation of errors in long-term measurements of land-atmosphere fluxes of carbon and water. *Global Change Biol.* 2, 231–240.
- Morgenstern, K., Black, T.A., Humphreys, E.R., Griffis, T.J., Drewitt, G.B., Cai, T.B., Nestic, Z., Spittlehouse, D.L., Livingstone, N.J., 2004. Sensitivity and uncertainty of the carbon balance of a Pacific Northwest Douglas-fir forest during an El Niño La Niña cycle. *Agric. For. Meteorol.* 123, 201–219.
- Ryan, M.G., 1991. Effects of climate change on plant respiration. *Ecol. Appl.* 1, 157–167.
- Ryan, M.G., Gower, S.T., Hubbard, R.M., Waring, R.H., Gholz, H.L., Cropper, W.P., Running, S.W., 1995. Woody tissue maintenance respiration of four conifers in contrasting climates. *Oecologia* 101, 133–140.
- Ryan, M.G., Lavigne, M.B., Gower, S.T., 1997. Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. *J. Geophys. Res.* 102, 28871–28883.
- Sarmiento, J.L., Gruber, N., 2002. Sinks for anthropogenic carbon. *Phys. Today* 55, 30–36.
- Shibistova, O., Lloyd, J., Zrazhevskaya, G., Arneth, A., Kolle, O., Knohl, A., Astrakhantceva, N., Shijneva, I., Schmerler, J., 2002. Annual ecosystem respiration budget for a *Pinus sylvestris* stand in central Siberia. *Tellus* 54B, 568–589.



- Sprugel, D.G., Benecke, U., 1990. Measuring woody-tissue respiration and photosynthesis. In: Lassoie, J.P., Hinckley, T.M. (Eds.), *Methods and Approaches in Tree Ecophysiology*. CRC Press, Boca Raton, USA, pp. 329–355.
- Valentini, R., Matteuci, G., Dolman, A.J., Schulze, E.D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grunwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, U., Berbigier, P., Loustau, D., Guomundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Jarvis, P.G., 2000. Respiration as the main determinant of European carbon balance. *Nature* 404, 861–865.
- Vose, J.M., Ryan, M.G., 2002. Seasonal respiration of foliage, fine roots and woody tissues in relation to growth, tissue N and photosynthesis. *Global Change Biol.* 8, 182–193.
- Wallin, G., Linder, S., Lindroth, A., Rantfors, M., Flemberg, S., Grelle, A., 2001. Carbon dioxide exchange in Norway spruce at the shoot, tree and ecosystem scale. *Tree Physiol.* 21, 969–976.
- Widén, B., Lindroth, A., 2003. A calibration system for soil carbon dioxide efflux measurement chambers: description and application. *Soil Sci. Soc. Am. J.* 67, 327–334.
- Xu, M., Baldocchi, D.B., 2004. Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California. *Agric. For. Meteorol.* 123, 79–96.
- Xu, M., Baldocchi, D.B., Tang, J., 2004. How soil moisture, rain pulses and growth alter the response of ecosystem respiration to temperature. *Global Biogeochem. Cy.* 18, GB4002 doi:10.1029/2004GB002281.
- Yang, P.C., Black, T.A., Neumann, H.H., Novak, M.D., Blanken, P.D., 1999. Spatial and temporal variability of CO<sub>2</sub> concentration and flux in a boreal aspen forest. *J. Geophys. Res.* 104, 27653–27661.