

# Interpreting the dependence of soil respiration on soil temperature and water content in a boreal aspen stand

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Received 16 November 2005; accepted 23 March 2006

## Abstract

Continuous half-hourly measurements of soil CO<sub>2</sub> efflux made between January and December 2001 in a mature trembling aspen stand located at the southern edge of the boreal forest in Canada were used to investigate the seasonal and diurnal dependence of soil respiration ( $R_s$ ) on soil temperature ( $T_s$ ) and water content ( $\theta$ ). Daily mean  $R_s$  varied from a minimum of 0.1  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in February to a maximum of 9.2  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in mid-July. Daily mean  $T_s$  at the 2-cm depth was the primary variable accounting for the temporal variation of  $R_s$  and no differences between Arrhenius and  $Q_{10}$  response functions were found to describe the seasonal relationship.  $R_s$  at 10 °C ( $R_{s10}$ ) and the temperature sensitivity of  $R_s$  ( $Q_{10R_s}$ ) calculated at the seasonal time scale were 3.8  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and 3.8, respectively. Temperature normalization of daily mean  $R_s$  ( $R_{sN}$ ) revealed that  $\theta$  in the 0–15 cm soil layer was the secondary variable accounting for the temporal variation of  $R_s$  during the growing season. Daily  $R_{sN}$  showed two distinctive phases with respect to soil water field capacity in the 0–15 cm layer ( $\theta_{fc}$ ,  $\sim 0.30 \text{ m}^3 \text{ m}^{-3}$ ): (1)  $R_{sN}$  was strongly reduced when  $\theta$  decreased below  $\theta_{fc}$ , which reflected a reduction in microbial decomposition, and (2)  $R_{sN}$  slightly decreased when  $\theta$  increased above  $\theta_{fc}$ , which reflected a restriction of CO<sub>2</sub> or O<sub>2</sub> transport in the soil profile.

Diurnal variations of half-hourly  $R_s$  were usually out of phase with  $T_s$  at the 2-cm depth, which resulted in strong diurnal hysteresis between the two variables. Daily nighttime  $R_{s10}$  and  $Q_{10R_s}$  parameters calculated from half-hourly nighttime measurements of  $R_s$  and  $T_s$  at the 2-cm depth (when there was steady cooling of the soil) varied greatly during the growing season and ranged from 6.8 to 1.6  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and 5.5 to 1.3, respectively. On average, daily nighttime  $R_{s10}$  (4.5  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and  $Q_{10R_s}$  (2.8) were higher and lower, respectively, than the values obtained from the seasonal relationship. Seasonal variations of these daily parameters were highly correlated with variations of  $\theta$  in the 0–15 cm soil layer, with a tendency of low  $R_{s10}$  and  $Q_{10R_s}$  values at low  $\theta$ . Overall, the use of seasonal  $R_{s10}$  and  $Q_{10R_s}$  parameters led to an overestimation of daily ranges of half-hourly  $R_s$  ( $\Delta R_s$ ) during drought conditions, which supported findings that the short-term temperature sensitivity of  $R_s$  was lower during periods of low  $\theta$ . The use of daily nighttime  $R_{s10}$  and  $Q_{10R_s}$  parameters greatly helped at simulating  $\Delta R_s$  during these periods but did not improve the estimation of half-hourly  $R_s$  throughout the year as it could not account for the diurnal hysteresis effect.

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**Keywords:** Carbon exchange; *Populus tremuloides*; Soil CO<sub>2</sub> efflux; Temperature sensitivity

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## 1. Introduction

The efflux of carbon dioxide (CO<sub>2</sub>) from the soil, referred to hereafter as soil respiration ( $R_s$ ), is a major

component of CO<sub>2</sub> exchange between forest ecosystems and the atmosphere. On an annual basis, it accounts for more than two-thirds of the CO<sub>2</sub> released through ecosystem respiration ( $R_e$ ) and about one half of the CO<sub>2</sub> assimilated through gross ecosystem photosynthesis ( $P_g$ ) (Black et al., 2005; Janssens et al., 2001; Valentini et al., 2000). Therefore, the way  $R_s$  responds to the on-going climate change (IPCC, 2001) is likely to have a significant impact on the CO<sub>2</sub> sink strength of forest ecosystems and future atmospheric CO<sub>2</sub> concentrations.

Predicting the response of  $R_s$  to climate change requires, in part, a thorough understanding of the dependence of this process on soil temperature and water content. Despite the abundant literature dealing with this subject, many questions remain unanswered because of the complexity of belowground respiration processes and their interaction with the environment.  $R_s$  integrates several biological and physical processes, including the production of CO<sub>2</sub> by roots, mycorrhizal fungi, microorganisms and soil fauna throughout the soil profile, and the subsequent release of CO<sub>2</sub> at the soil surface. Diurnal variations of  $R_s$  are usually highly correlated with temperature of the surface soil layers (e.g., Drewitt et al., 2002; Jassal et al., 2005). A few studies have, however, reported hysteresis-type behaviors and a decoupling between  $R_s$  and soil surface temperatures during drought conditions (Parkin and Kaspar, 2003; Subke et al., 2003; Xu and Qi, 2001b). At the seasonal time scale,  $R_s$  is also highly correlated with changes in soil temperature when water is not limiting (Curiel Yuste et al., 2003; Drewitt et al., 2002). Strong inhibition of  $R_s$  has often been observed at low soil water content (Borken et al., 1999; Griffis et al., 2004; Harper et al., 2005; Irvine and Law, 2002; Joffre et al., 2003) which has been mainly attributed to a reduction in decomposition due to microbial activity. A more subtle inhibition of  $R_s$  related to the transport and storage of CO<sub>2</sub> and/or oxygen (O<sub>2</sub>) in the soil may also play a role at high soil water contents (Bunnell et al., 1977), but datasets representing these conditions in the natural environment to support this hypothesis are still limited (Drewitt et al., 2002). Furthermore, the seasonal dependence of  $R_s$  on soil water content is still poorly understood because the variations in soil temperature and water content are often correlated and the independent effect of each variable is hard to detect or interpret (Davidson et al., 1998).

The use of the well known Arrhenius and  $Q_{10}$  functions to describe the exponential response of  $R_s$  to temperature has been criticized because of their constant temperature sensitivities over a wide range of soil temperatures (Lloyd and Taylor, 1994). There is

increasing empirical evidence that the temperature sensitivity of  $R_s$  decreases with increasing soil temperature within and among stands (Janssens and Pilegaard, 2003; Kirschbaum, 1995; Lloyd and Taylor, 1994; Reichstein et al., 2002, 2003). A loss of temperature control and a decrease in the temperature sensitivity of  $R_s$  (or  $R_e$ ) has also been found to occur during drought conditions (Borken et al., 1999; Curiel Yuste et al., 2003; Flanagan and Johnson, 2005; Janssens and Pilegaard, 2003; Lavigne et al., 2004; Palmroth et al., 2005; Qi et al., 2002; Reichstein et al., 2002, 2003; Xu and Baldocchi, 2004; Xu and Qi, 2001a,b). Although the exact nature of these interactions is not clear, potential mechanisms suggested to date include physiological acclimation of roots (Atkin et al., 2000), changes in microbial communities (Janssens and Pilegaard, 2003), switches from autotrophic to heterotrophic dominated respiration processes and switches from labile to recalcitrant substrates for microbial decomposition (Reichstein et al., 2002).

The recent development of automated chamber systems provides a great opportunity to measure  $R_s$  at fine temporal resolution and increase our understanding of the interaction between this process and the environment. In this study, we report on continuous half-hourly measurements of  $R_s$  made in 2001 in a mature boreal trembling aspen stand (*Populus tremuloides* Michx.). This unique dataset was characterized by a severe drought period beginning in the middle of the growing season, which lasted until the end of the year. Griffis et al. (2004) reported that soil temperature was the primary variable accounting for seasonal variations of  $R_s$ , bole ( $R_b$ ) and ecosystem ( $R_e$ ) respiration during that year but that drought resulted in a strong reduction of  $R_s$  and  $R_e$  late during the growing season. In this study, we built on the analysis of Griffis et al. (2004) and used the measurements to refine our understanding of the seasonal and diurnal dependence of  $R_s$  on these climate variables. The specific objectives were: (1) to determine how well different response functions described the seasonal dependence of  $R_s$  on soil temperature and water content, (2) to investigate whether the constant basal rate and temperature sensitivity of  $R_s$  derived from seasonal measurements were representative of the parameters derived at shorter time scales (i.e., diurnal), (3) to identify which environmental or biological factors influenced seasonal variations of the parameters derived at short time scales, and (4) to assess the capability of parameters derived at seasonal and diurnal time scales to simulate diurnal variations of half-hourly  $R_s$ .

## 2. Methods

### 2.1. Site description

This study was conducted in an 81-year-old (age in 2001) boreal trembling aspen (*P. tremuloides*) stand located in the Prince Albert National Park, Saskatchewan, Canada (53.7°N, 106.2°W). This stand has been studied intensively over the last decade as part of the Boreal Ecosystem-Atmosphere Study (BOREAS) and the Boreal Ecosystem Research and Monitoring Sites (BERMS) programs. It originated from fire disturbance in 1919 and is dominated by trembling aspen (~22 m in height), with sparsely distributed balsam poplar (*Populus balsamifera* L.) and a dense hazelnut understorey of about 2 m in height (*Corylus cornuta* Marsh.) with sparse alder (*Alnus crispa* (Alt.) Pursch.). The stand density in 1998 was ~830 stems ha<sup>-1</sup>. 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). The mineral soil is a loam to sandy clay loam and is covered by an 8–10 cm deep organic layer. Mean organic C contents of the organic and upper 20 cm mineral soil layers are 390 and 5 g C kg<sup>-1</sup> dry matter, respectively (Grant et al., 1999). Mean porosities of the organic and upper 20 cm mineral soil layers are approximately 0.85 and 0.50, respectively (Grant et al., 1999). Mean fine-root biomass (<2 mm) to a depth of 40 cm is 1.9 ± 0.6 Mg dry matter ha<sup>-1</sup> (average for 2003–2004) (Kalyn, 2005). Thirty percent of the fine roots are in the organic layer and an additional 60% are in the upper 20 cm of the mineral soil. The soil is well to moderately well drained.

### 2.2. Soil respiration measurements

Continuous half-hourly measurements of  $R_s$  were made between January and December 2001 using a non-steady-state automated chamber system. The system was installed in August 2000 and was equipped with four soil chambers connected to temperature-controlled housings (TCH) containing data logging and pumping equipment. All chambers, which were ~60 L in volume, were randomly located within a 15-m radius centered on the TCHs. The chambers were made of transparent acrylic and had a moveable lid attached by hinges to a fixed collar inserted between 3 and 4 cm into the soil. The lid was opened and closed using a nylon cord and a rotating pulley powered by a 12 V DC motor fixed on an aluminum frame. 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. Vegetation inside the chambers was clipped regularly during the growing season to avoid complication in the interpretation of the measurements. Collars were also cleared of snow regularly during winter to allow proper sealing of the lids. However, snow filled up the chambers to the height of the collar (~15 cm) during winter. 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 the 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).

The system measured the increase of CO<sub>2</sub> concentration in the headspace of each chamber over a 5-min interval sequentially allowing all chambers to be measured once every half-hour. When a chamber was selected, the air was circulated between the chamber and a closed-path infrared gas analyzer (IRGA, Model LI-6262, LI-COR Inc., Lincoln, NE, USA) with an AC linear pump (Model SPP-15EBS-101, Gast Manufacturing, Benton Harbor, MI, USA) at a rate of approximately 8 L min<sup>-1</sup>. The air in each chamber was mixed with two small fans. The total length of tubing (Synflex 1300, 4.0 mm i.d., Saint-Gobain Performance Plastics, Wayne, NJ, USA) for each chamber was ~30 m and the residence time of the air in the tubing circuit was short (<4 s). The IRGA was located in a separate TCH and its temperature was kept at 38 °C by controlling the heating (100 W custom heater) and cooling (120 V ac fans) of the TCH with a microprocessor (Model Pistic 3, Micromint Corporation, Longwood, FL, USA). The IRGA was calibrated daily by sequentially using CO<sub>2</sub>-free nitrogen gas (offset calibration) and a gas of known CO<sub>2</sub> concentration (~360 μmol mol<sup>-1</sup>, balance dry air) (gain calibration) from gas cylinders calibrated against a standard from the Meteorological Service of Canada, Downsview, Ont., Canada. The IRGA analogue signal was sampled at 5 Hz with the 21X datalogger, averaged every 5 s and transferred every half-hour to a PC system located in a hut. Data were downloaded daily via cellular phone to our laboratory for quality assessment and analysis.

Half-hourly  $R_s$  (μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>) was calculated using the following equation:

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

where  $\rho_a$  is the density of dry air in the chamber headspace ( $\text{mol m}^{-3}$ ),  $V_e$  the effective volume of the chamber ( $\text{m}^3$ ),  $A$  the area of ground 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 ( $\text{mol CO}_2 \text{ mol}^{-1}$  dry air  $\text{s}^{-1}$ ) and  $t$  is the time (s).  $s_c$  was used in this calculation instead of the  $\text{CO}_2$  mole fraction in  $\mu\text{mol CO}_2 \text{ mol}^{-1}$  moist air to account for the dilution effect of water vapor in the chamber headspace during measurements.

The geometric volume ( $V_g$ ) of the chambers varied seasonally with snow accumulation and changes in pressure and temperature (Drewitt et al., 2002; Griffis et al., 2004). To account for these changes and adsorption of  $\text{CO}_2$  on chamber walls and litter,  $V_e$  for each chamber was measured once each day using a gas injection technique described in detail in Drewitt et al. (2002). The technique consisted of injecting a high concentration gas (10%  $\text{CO}_2$  balance dry air) at a rate of  $10 \text{ ml min}^{-1}$  at Standard Temperature and Pressure with a range-adjustable mass flow controller (model 1179, MKS Instruments Inc., Wilmington, MA, USA) sequentially into each chamber air circulation circuit immediately following a regular  $R_s$  measurement by that chamber. The corresponding injection rate ( $I$ ) was  $0.74 \mu\text{mol CO}_2 \text{ s}^{-1}$ .  $V_e$  was then calculated using the following equation:

$$V_e = \frac{I}{\rho_a(ds_{cI}/dt - ds_c/dt)}, \quad (2)$$

where  $ds_{cI}/dt$  is the time rate of change of the  $\text{CO}_2$  mixing ratio during gas injection over a 1-min interval following lid closure ( $\text{mol CO}_2 \text{ mol}^{-1}$  dry air  $\text{s}^{-1}$ ). During summer,  $V_e$  was on average 16% higher than  $V_g$  but was approximately 30% less during winter due to the presence of snow in the collar area. In the winter of 2001–2002, a fixed volume plastic chamber (not inserted in the soil and permanently closed) was added to the system to detect leaks and to assess the accuracy and integrity of the measurements.  $V_e$  of that chamber was calculated daily and remained within 5% of  $V_g$ .

### 2.3. Climate and ancillary measurements

Half-hourly soil temperature ( $T_s$ ) was measured at depths of 2, 5, 10, 20, 50 and 100 cm with a copper–constantan thermocouple profile located near the automated chamber system. Soil volumetric water content ( $\theta$ ) was measured to a depth of 1.2 m every 4 h at the same location using MoisturePoint type B

segmented TDR probes (Model MP-917, ESI Environmental Sensors Inc., Victoria, BC, Canada). Measurements in the 0–15 and 30–60 cm soil layers were used in this analysis. Half-hourly  $\theta$  was obtained with linear interpolation between the measurements. Precipitation ( $P$ ) was measured with a weighing gauge (Model 3000, Belfort Instruments, Baltimore, MD, USA).

### 2.4. Data analysis

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 a representative half-hourly value for the stand. Missing data due to instrument failure, IRGA calibrations and poor quality measurements represented 40% of the dataset for the year (mostly during winter).

The functions used to quantify the dependence of  $R_s$  on  $T_s$  and  $\theta$  (see Section 3) are listed in Table 1.  $Q_{10}$  and Arrhenius-type functions were used to quantify the dependence of daily mean  $R_s$  on  $T_s$  at the 2-cm depth at the seasonal time scale and provide reference respiration rates ( $R_s$  at  $10^\circ\text{C}$  ( $R_{s10}$ ) or 283 K ( $R_{s283}$ )) and temperature sensitivity parameters (relative change in  $R_s$  for a  $10^\circ\text{C}$  change in  $T_s$  ( $Q_{10Rs}$ ) and activation energy ( $E_0$ )) (Eqs. (3)–(5)).  $T_s$  at the 2-cm depth was chosen because  $T_s$  measured at greater depth did not explain more of the variance in daily mean  $R_s$  (see Section 3). Two types of hyperbolic functions (Eqs. (6) and (7)) were used to quantify the dependence of the daily residuals of  $R_s$ , i.e. the ratios of observed to predicted values using the  $Q_{10}$  function and  $T_s$  at the 2-cm depth, on  $\theta$  in the 0–15 cm soil layer. Eqs. (3) and (7) were combined in Eq. (8) to predict daily mean  $R_s$  during the year using daily mean  $T_s$  and  $\theta$ .

Eq. (3) was also used to quantify the dependence of half-hourly nighttime  $R_s$  on  $T_s$  at the 2-cm depth at the diurnal time scale. Nighttime estimates of  $R_{s10}$  and  $Q_{10Rs}$  were derived for each day using a moving window (1-day time step) of 4 days. Nighttime data were used to insure that the measurements were characterized by a steady cooling of the soil and therefore minimize the effects of other environmental variables (e.g.,  $\theta$ , solar radiation and wind) that could make it difficult to interpret the diurnal changes of  $R_s$ . Moreover, to remove  $R_s$  measurements with a low signal-to-noise ratio and increase the robustness of the parameter estimations, only datasets that satisfied the following requirements were used in the analysis: (1) minimum daily range of nighttime  $T_s$  at the 2-cm depth of  $0.5^\circ\text{C}$ , (2) minimum coefficient of determination ( $r^2$ ) between  $R_s$  and  $T_s$  of

Table 1

Equations used in the analysis of the dependence of soil respiration ( $R_s$ ) on soil temperature ( $T_s$ ) and temperature-normalized  $R_s$  ( $R_{sN}$ ) on soil water content ( $\theta$ )

Function name	Equation	Reference
Soil temperature		
$Q_{10}$	$R_s = R_{s10} Q_{10R_s}^{(T_s-10)/10}$	Lloyd and Taylor (1994)
Arrhenius	$R_s = R_{s283} e^{(E_0/283.15R)(1-283.15/T_s)}$	Lloyd and Taylor (1994)
Arrhenius (LT)	$R_s = R_{s283} e^{E_0[1/(283.15-T_0)-1/(T_s-T_0)]}$	Lloyd and Taylor (1994)
Soil water content		
Bunnell	$R_{sN} = a[\theta/(b+\theta)][c/(c+\theta)]$	Modified from Bunnell et al. (1977)
Hyperbolic	$R_{sN} = a + b\theta + c/\theta$	This study
Soil temperature and water content		
$Q_{10}$ and hyperbolic	$R_s = (a + b\theta + c/\theta) R_{s10} Q_{10R_s}^{(T_s-10)/10}$	This study

Soil temperature functions:  $R_{s10}$  and  $R_{s283}$ ; soil respiration at 10 °C or 283 K ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $Q_{10R_s}$ ; temperature sensitivity parameter (unitless, relative change in  $R_s$  for a 10 °C change in  $T_s$ ),  $E_0$ ; temperature sensitivity parameter defined as the activation energy ( $\text{kJ mol}^{-1}$ ) in Eq. (4) and fitted parameter in Eq. (5) ( $K$ ),  $T_0$ ; fitted parameter ( $K$ ),  $R$ ; universal gas constant ( $8.314 \text{ J mol}^{-1} \text{ K}^{-1}$ ).  $T_s$  is expressed in °C in Eq. (3) and in K in Eqs. (4) and (5). Soil water content parameters:  $a$ ,  $b$  and  $c$  are fitted and  $\theta$  is expressed in  $\text{m}^3 \text{ m}^{-3}$  in Eqs. (6)–(8).  $R_{sN}$  is the temperature-normalized  $R_s$ .

0.7, and (3) no rain events during the night. The average number of data points (half-hours) per night was  $19 \pm 4$ . Since daily changes in  $T_s$  at the 2-cm depth and  $R_s$  were negligible during winter (see Section 3), daily estimates of the parameters were obtained during the growing season only. 66% of the nighttime data available during the growing season met these criteria.

Curve fitting was done with the Nelder-Mead simplex method (constrained nonlinear least squares search procedure; Lagarias et al., 1998) and the statistical toolbox provided with the Matlab software (Version 6.5.1, The Mathworks Inc.).

### 3. Results and discussion

#### 3.1. Seasonal variations of soil respiration, temperature and water content

Half-hourly  $R_s$  averaged over the study period was  $2.9 \pm 2.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  ( $\pm$ standard deviation) in 2001 (excluding missing data). Daily mean  $R_s$  (24-h) showed strong seasonality and was at its lowest, but still positive, in February ( $\sim 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) (Fig. 1c). It reached a summer maximum of  $9.2 \mu\text{mol m}^{-2} \text{s}^{-1}$  in the middle of July, approximately 2 weeks before the peak in  $T_s$  in the surface soil layers (maximum daily mean  $T_s$  at the 2-cm depth was  $16.5 \text{ }^\circ\text{C}$  on 2 August, Fig. 1a). The highest value of  $R_s$  was similar to that reported by Russell and Voroney (1998) in the same stand in 1994 and by Bolstad et al. (2004) in an aspen stand in northern Wisconsin ( $9.3$  and  $8.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively). The replenishment of soil water following spring snowmelt (Fig. 1b) was immediately followed by a small increase of  $R_s$  even though  $T_s$  between 2 and 20 cm remained near freezing

during that period. Low precipitation from August to November (Fig. 1b) caused a severe drought in the stand during which  $R_s$  decreased more rapidly than expected with the decrease of  $T_s$ .

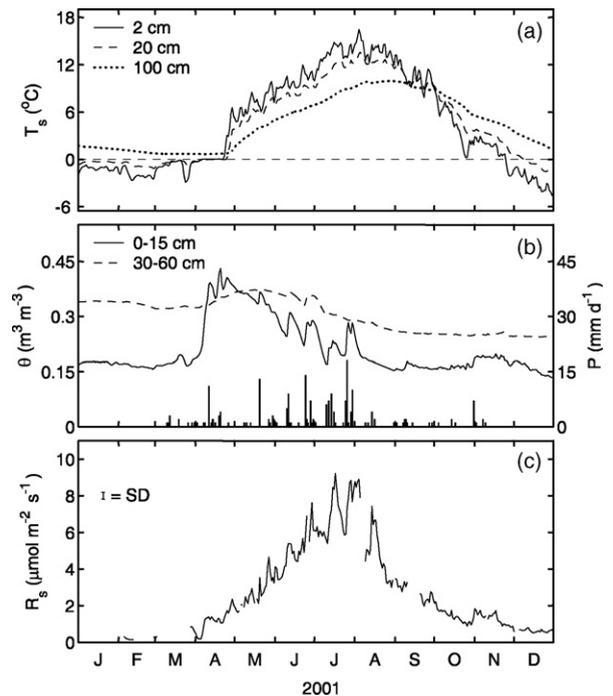


Fig. 1. Seasonal course of daily mean: (a) soil temperature ( $T_s$ ) at the 2-cm (solid), 20-cm (dashed) and 100-cm (dotted) depths, (b) soil water content ( $\theta$ ) in the 0–15 (solid) and 30–60 cm layers (dashed), precipitation ( $P$ , right axis) and (c) soil respiration ( $R_s$ ) in the aspen stand in 2001. The mean of all daily standard deviations (S.D.) calculated from the half-hourly measurements of  $R_s$  is presented for clarity.

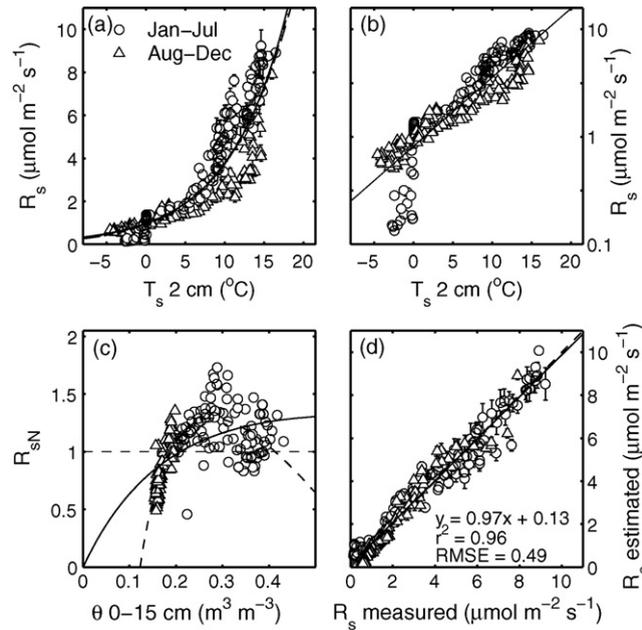


Fig. 2. Relationship between daily mean (a) soil respiration ( $R_s$ ) and soil temperature ( $T_s$ ) at the 2-cm depth, (b) logarithmically transformed  $R_s$  and  $T_s$  at the 2-cm depth, (c) daily temperature-normalized soil respiration ( $R_{sN}$ ) and soil water content in the 0–15 cm layer ( $\theta$ ), and (d) estimated (using Eq. (8)) and measured  $R_s$  in 2001 ( $n = 215$ ,  $P < 0.01$ ). Lines in panel (a) represent the best fits of Eqs. (3) (solid), (4) (dashed-dotted) and (5) (dashed) ( $P < 0.01$ ). The lines are almost indistinguishable from each other. Lines in panel (c) represent the best fits of Eqs. (6) (solid) and (7) (dashed) for the growing season only ( $P < 0.01$ ). The dashed and solid lines in panel (d) represent the 1:1 and the regression ( $P < 0.01$ ) relationships, respectively. Vertical bars represent  $\pm 1$  standard deviation from half-hourly measurements. Parameters in panels (a)–(c) are given in Table 2.

Daily mean  $R_s$  increased exponentially with  $T_s$  at the 2-cm depth but the relationship showed strong seasonal hysteresis (Fig. 2a). For example,  $R_s$  at 10 °C was higher early in the growing season rather than later and this difference was attributed to the limitation imposed by the late summer drought conditions on decomposition by microbial activity (see discussion below) or to high rates of fine-root production (Kalyn, 2005) and associated respiration early in the growing season. This pattern contrasted with the opposite hysteresis patterns observed by Drewitt et al. (2002), Goulden et al. (1998) and Morén and Lindroth (2000) in other forest stands. In these studies,  $R_s$  was lower in early summer than in late summer and the difference was attributed to the increased contribution of soil microbial activity during late summer in response to the warming of deeper soil layers.

There were no differences between the three temperature-response functions examined. Daily mean  $T_s$  at the 2-cm depth explained 82% of the seasonal variation in daily mean  $R_s$  in all cases (Table 2). The almost identical response of each function at low and high  $T_s$  contrasted with the findings of Lloyd and Taylor (1994) who suggested that Arrhenius and  $Q_{10}$  functions were inappropriate to accurately describe the dependence of  $R_s$  on  $T_s$  over this range of  $T_s$ . However, each

function overestimated  $R_s$  from January to March when the soil surface was frozen (Fig. 2a). CO<sub>2</sub> production was probably occurring deep in the soil during that period, though at low rates, because  $T_s$  at the 100-cm depth remained between 0 and 2 °C. Since no differences were observed between the temperature-response functions, the remainder of the analysis was done with the  $Q_{10}$  function because it is the most cited in the literature. The seasonal  $R_{s10}$  and  $Q_{10Rs}$  calculated with  $T_s$  at the 2-cm depth were 3.8  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and 3.8, respectively (Table 2). These estimates were well within the range of values (0.7–4.9  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for  $R_{s10}$  and 2.0–6.3 for  $Q_{10Rs}$ ) reported for other forest soils (Davidson et al., 1998; Janssens et al., 2003; Raich and Schlesinger, 1992). A logarithmic transformation of the daily  $R_s$  values following Morgenstern et al. (2004) yielded  $R_{s10}$  and  $Q_{10Rs}$  values of 3.6 and 4.4 (Table 2) but did not explain more of the variance in  $R_s$  or help in describing the relationship between  $R_s$  and  $T_s$  at the 2-cm depth from January to March (Fig. 2b).  $Q_{10Rs}$  calculated from the non-transformed data increased to 4.7 when  $T_s$  at the 20-cm depth was used because of the attenuation of the variation of  $T_s$  with depth. Using  $T_s$  at greater depths did not help to explain more of the variance in  $R_s$  and further enhanced the hysteresis effect described above.

Table 2

Response function parameters for the analysis of the dependence of daily mean soil respiration ( $R_s$ ) on soil temperature at the 2-cm depth ( $T_s$ ) and temperature-normalized  $R_s$  during the growing season ( $R_{sN}$ ) on soil water content of the 0–15 cm layer ( $\theta$ )

Function name	Parameters						
	$R_{s10}$ or $R_{s283}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$Q_{10R_s}$	$E_0$ ( $\text{kJ mol}^{-1}$ )	$T_0$ (K)	$r^2$	RMSE ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$n$
Soil temperature							
$Q_{10}$	3.8	3.8			0.82	1.00	269
$Q_{10}$ (–Log <sup>a</sup> )	3.6	4.4			0.82	1.00	269
Arrhenius	3.8		89.3		0.82	1.00	269
Arrhenius (LT)	3.8		3534 <sup>b</sup>	120.3	0.82	1.00	269
Function name	Parameters						
	$a$	$b$	$c$		$r^2$	RMSE	$n$
Soil water content							
Bunnell	0.61	0.61	5.27		0.39	0.22	215
Hyperbolic	4.93	–6.55	–0.51		0.63	0.17	215

All relationships were significant at the 99% probability level.

<sup>a</sup> Calculated after a logarithmic transformation of daily  $R_s$  values following Morgenstern et al. (2004).

<sup>b</sup> In K in the modified version of the Arrhenius function of Lloyd and Taylor (1994).

During the growing season, daily mean  $R_s$  normalized using the best fit of the  $Q_{10}$  function with  $T_s$  at the 2-cm depth ( $R_{sN}$ ) decreased when  $\theta$  in the 0–15 cm layer was below and above a threshold value of  $\sim 0.25$ – $0.30 \text{ m}^3 \text{ m}^{-3}$  (Fig. 2c). Interestingly, this threshold value corresponded approximately to the soil water field capacity ( $\theta_{fc}$ ) in the 0–15 cm layer. The decrease in  $R_s$  below  $\theta_{fc}$  most likely resulted from an inhibition of microbial activity in the organic layer because  $\theta$  in the 30–60 cm layer was relatively constant during the year (Fig. 1b). Moreover, the soil water limitation in the 0–15 cm layer started in August (open triangles in Fig. 2a and c) when most of fine-root growth had probably stopped (Kalyn, 2005) and it is unlikely that these conditions led to a reduction in autotrophic respiration.  $R_s$  also decreased when  $\theta$  was above  $\theta_{fc}$  (Fig. 2c) and this response reflected a restriction in  $\text{CO}_2$  transport out of the soil or an inhibition of  $\text{CO}_2$  production due to a lack of  $\text{O}_2$  (Bunnell et al., 1977).

Increases in  $\theta$  following large episodic summer rain events were associated with positive pulses of  $R_s$  (Fig. 1). This type of response has been discussed in detail in other studies and has been mainly attributed to an instantaneous or long-term increase in  $\text{CO}_2$  production in the soil due to enhanced 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). The enhancement of  $\text{CO}_2$  production could have partly originated from the increased metabolic activity of root-associated microorganisms, as rhizo-

sphere priming effects have been found to occur in a boreal black spruce stand following large rainfalls (Gaumont-Guay, 2005).

The reduction in  $R_{sN}$  at low and high  $\theta$  was best described by a hyperbolic function (Eq. (7), Table 2 and Fig. 2c) and the shape of the relationship suggests that  $R_{sN}$  was strongly inhibited when  $\theta$  in the 0–15 cm layer was less than  $0.12 \text{ m}^3 \text{ m}^{-3}$ . This threshold value corresponded approximately to the permanent wilting point in the 0–15 cm layer. The Bunnell function (Eq. (6)) performed poorly at describing the seasonality of  $R_{sN}$  and forced the calculated values through zero, which seems unrealistic for this type of soil. Overall,  $T_s$  at the 2-cm depth and  $\theta$  in the 0–15 cm layer explained 96% of the variance in daily mean  $R_s$  in 2001 when using Eq. (8) (Fig. 2d).

### 3.2. Diurnal variations of soil respiration, temperature and water content

Fig. 3 shows the diurnal variation of  $T_s$  in the soil profile and the corresponding variation of  $R_s$  during the growing season and winter of 2001. Mean monthly daily ranges in  $R_s$  ( $\Delta R_s$ ) were 0.5, 1.7 and  $0.9 \mu\text{mol m}^{-2} \text{s}^{-1}$  during the early, middle and late parts of the growing season, respectively. This variation of  $\Delta R_s$  was unexpected since daily ranges in  $T_s$  ( $\Delta T_s$ ) in the shallow soil layers remained relatively constant over the three periods (the average  $\Delta T_s$  at the 2-cm depth was  $2.5^\circ \text{C}$  during the growing season, see Fig. 7).  $\Delta R_s$  was positively correlated with daily mean  $R_s$ . There was a

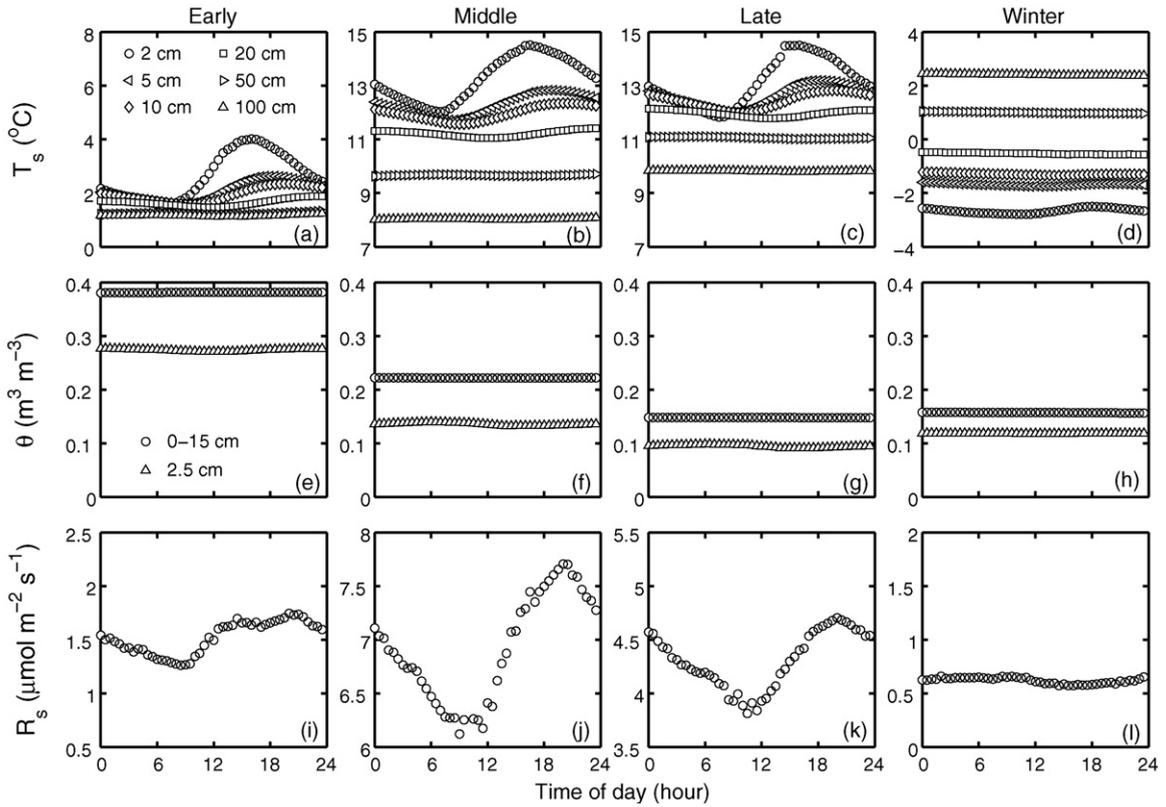


Fig. 3. Diurnal course of half-hourly soil temperature ( $T_s$ ) at the 2-, 5-, 10-, 20-, 50- and 100-cm depths (a–d), soil water content ( $\theta$ ) in the 0–15 cm layer and at the 2.5-cm depth (e–h) and soil respiration ( $R_s$ ) (i–l) in the aspen stand during the early (10 April–9 May), middle (1–30 July) and late (10 August–9 September) parts of the growing season and winter (1–29 December) of 2001. Half-hour values are an ensemble average of 29 days during each period. Only the mean for each half-hour is presented for clarity. The range on the y-axis is the same magnitude for each variable but the absolute values for  $T_s$  and  $R_s$  are different for each period.

marked reduction of both variables late in the growing season when  $\theta$  was low and  $T_s$  peaked in the surface soil layers.  $\Delta R_s$  and  $\Delta T_s$  at all depths were negligible during winter.

Diurnal variations of  $R_s$  were usually out of phase with  $T_s$  at the 2-cm depth (Fig. 3).  $R_s$  peaked at around

20 h during the early, middle and late parts of the growing season, which was 4, 3.5 and 5 h, respectively, later than  $T_s$  at the 2-cm depth. This resulted in significant hysteresis in the relationship between half-hourly  $R_s$  and  $T_s$  at the 2-cm depth. For example,  $R_s$  was higher during the cooling part of the day than during the

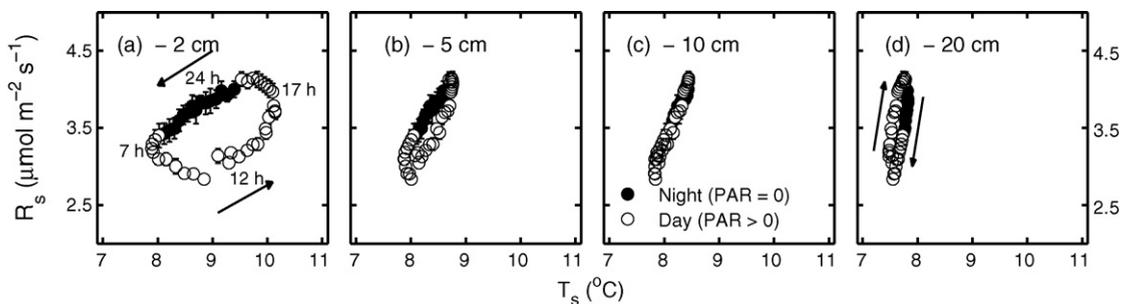


Fig. 4. Relationship between half-hourly soil respiration ( $R_s$ ) and soil temperature ( $T_s$ ) at the (a) 2-cm, (b) 5-cm, (c) 10-cm and (d) 20-cm depths for measurements made from June 4 to 8 2001 (ensemble average for each half-hour). Open and closed circles indicate daytime (PAR (photosynthetically active radiation)  $> 0 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and nighttime (PAR =  $0 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) measurements, respectively. Vertical bars represent  $\pm 1$  standard deviation from half-hourly measurements. Arrows in panels (a and d) indicate increasing time of day.

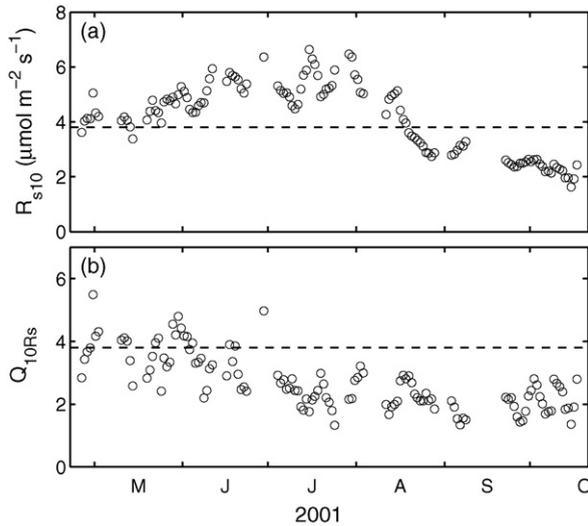


Fig. 5. Seasonal course of daily nighttime (a) soil respiration at 10 °C ( $R_{s10}$ ) and (b) temperature sensitivity of  $R_s$  ( $Q_{10Rs}$ ). Parameters for each day were estimated using half-hourly nighttime measurements of  $R_s$  and  $T_s$  at the 2-cm depth and a moving window (1-day time step) of 4 days. Dashed horizontal lines represent the  $R_{s10}$  (top panel) and  $Q_{10Rs}$  (bottom panel) values derived at the seasonal time scale (see Fig. 2a).

warming part of the day in early June (Fig. 4). Interestingly, inversion of the  $R_s$ – $T_s$  hysteresis loops occurred at the 20-cm depth during that period indicating that 10 cm was the depth at which the correlation between  $R_s$  and  $T_s$  was maximum. Assuming that diurnal variations of  $R_s$  were entirely driven by  $T_s$  at the 10-cm depth, the range of  $T_s$  measured during that period at that depth would have required an unusually large  $Q_{10}$  (>150) to explain  $\Delta R_s$ , which was far larger than the reasonable biological  $Q_{10}$  of 2. Thus, these results suggest that most  $\text{CO}_2$  production was still

occurring above 10 cm. Diurnal variations of  $\theta$  at the 2.5-cm depth and in the 0–15 cm layer were negligible throughout the growing season (Fig. 3) indicating that  $\theta$  was not responsible for the hysteresis behavior. Since recent studies have suggested that the rhizospheric component of  $R_s$  could be more controlled by carbohydrate production and within-tree transport than by diurnal variations of environmental variables (Gaumont-Guay, 2005; Tang et al., 2005), it is possible that the diurnal variations in rhizospheric respiration could have been a significant factor in explaining the hysteresis behavior observed in this study.

### 3.3. Short-term temperature sensitivity of soil respiration

In order to examine whether variations of the temperature sensitivity of  $R_s$  could have been a significant factor in explaining seasonal variations of  $\Delta R_s$ , we estimated  $R_{s10}$  and  $Q_{10Rs}$  for each day (with Eq. (3)) using nighttime measurements of  $R_s$  and  $T_s$  at the 2-cm depth and a moving window (1-day time step) of 4 days (see Section 2). Daily nighttime  $R_{s10}$  and  $Q_{10Rs}$  showed strong seasonality and ranged from 6.8 to 1.6  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and 5.5 to 1.3, respectively (Fig. 5). On average, daily nighttime  $R_{s10}$  (4.5  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and  $Q_{10Rs}$  (2.8) were higher and lower, respectively, than the values obtained from the seasonal relationship (see Table 2). There was a strong correlation between  $R_{s10}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and  $\theta$  ( $\text{m}^3 \text{m}^{-3}$ ) in the 0–15 cm layer ( $R_{s10} = 29.0 - 45.6\theta - 3.0/\theta$ ,  $r^2 = 0.76$ , RMSE = 0.59  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , Fig. 6a). The shape of the relationship was similar to the one observed for daily mean  $R_s$  (Fig. 2c) and showed reductions of  $R_{s10}$  for  $\theta$  below and above  $\theta_{fc}$  of the 0–15 cm layer with an optimal range

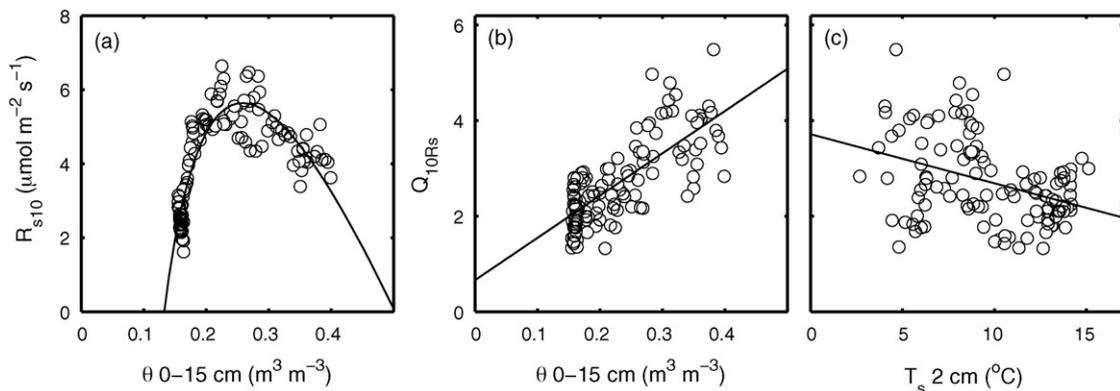


Fig. 6. (a) Relationship between daily nighttime soil respiration at 10 °C ( $R_{s10}$ ) and soil water content ( $\theta$ ) in the 0–15 cm layer; relationship between daily nighttime temperature sensitivity of  $R_s$  ( $Q_{10Rs}$ ) and (b)  $\theta$  in the 0–15 cm layer and (c) soil temperature ( $T_s$ ) at the 2-cm depth. The line in the left panel represents the best fit of Eq. (7) ( $P < 0.01$ ). Lines in the middle and right panels represent the best fits of linear regressions between  $Q_{10Rs}$  and the respective environmental variables ( $P < 0.01$ ).  $n = 110$  for  $R_{s10}$  and  $Q_{10Rs}$ . Parameters are given in the text.

between 0.20 and 0.30 m<sup>3</sup> m<sup>-3</sup>.  $Q_{10Rs}$  increased with  $\theta$  ( $Q_{10Rs} = 9.01\theta + 0.62$ ,  $r^2 = 0.55$ , RMSE = 0.62, Fig. 6b) and decreased slightly with  $T_s$  (°C) at the 2-cm depth ( $Q_{10Rs} = -0.12T_s + 3.94$ ,  $r^2 = 0.19$ , RMSE = 0.82, Fig. 6c).

A strong dependence of  $Q_{10Rs}$  (or  $Q_{10Re}$ ) on soil water content has been observed in many ecosystems (Borken et al., 1999; Curiel Yuste et al., 2003; Davidson et al., 1998; Flanagan and Johnson, 2005; Harper et al., 2005; Janssens and Pilegaard, 2003; Reichstein et al., 2002; Qi et al., 2002; Widén, 2002; Xu and Qi, 2001a,b). Reichstein et al. (2002) reported a reduction of  $Q_{10}$  for  $R_e$  from about 2.5 to 1 with increasing drought severity in three Mediterranean evergreen stands. They speculated that it could be due to a switch in the carbon pool being respired ( $Q_{10}$  of labile substrates is higher than that of recalcitrant substrates) and/or to an inactivation of the rhizosphere ( $Q_{10}$  of rhizosphere respiration is higher than of microbial decomposition). Although the temperature sensitivity of rhizosphere respiration could be higher than that for microbial decomposition at the seasonal time scale (Boone et al., 1998; Gaumont-Guay, 2005), there is no consensus on the difference in the temperature sensitivities of labile and recalcitrant carbon pools (Bååth and Wallander, 2003; Bol et al., 2003; Coûteaux et al., 2001; Fang et al., 2005; Giardina and Ryan, 2000; Knorr et al., 2005; Liski et al., 1999; Reichstein et al., 2005b). In a spruce stand, a lower  $T_s$  sensitivity of  $R_s$  was observed during drought and the increased sensitivity following rewetting of the soil was attributed to an increase in carbon availability for microbial processes (Borken et al., 1999). This hypothesis was also used to explain the high temperature sensitivity of  $R_s$  observed following spring snowmelt in a mixed Scots pine and Norway spruce stand in Sweden (Widén, 2002).

The interpretation of the relationship between  $Q_{10Rs}$  and  $\theta$  was complicated by the finding that this parameter also varied with  $T_s$  and that both climate variables were highly correlated during the growing season ( $r = 0.82$ ). A decrease in  $Q_{10}$  with increasing  $T_s$  has been observed at the organ level (Tjoelker et al., 2001), within forest stands (Janssens and Pilegaard, 2003; Palmroth et al., 2005; Qi et al., 2002; Xu and Qi, 2001a) and in studies at larger spatial and temporal scales (Kirschbaum, 1995; Reichstein et al., 2003). A reduction in  $Q_{10}$  with temperature could be attributed to a direct physiological acclimation of the roots to the changing temperature regime of the soil (e.g. Atkin and Tjoelker, 2003). In a recent synthesis paper, Atkin et al. (2005) suggested that the acclimation of root respiration to temperature was an important process at low temperatures, which was

mediated by a limitation of enzymatic capacity. They also suggested that at moderate to high temperatures, root respiration was more limited by substrate availability, and that the transition from enzymatic controls to limitations by substrate supply was associated with a reduction of  $Q_{10}$ . However, several authors have reported little or no acclimation of root respiration to seasonal changes in temperature (Burton and Pregitzer, 2003; Sowell and Spomer, 1986; Weger and Guy, 1991).

In this study, part of the temporal variability of daily nighttime  $R_{s10}$  and  $Q_{10Rs}$  during the growing season could be attributed to the error associated with the application of a nonlinear function (Eq. (3)) to the nighttime measurements of  $R_s$  and  $T_s$  at the 2-cm depth. This error arises from the assumption that the relationship between the two variables was exponential and that the calculations were performed with small variations of  $T_s$  (Fig. 3) that often differed greatly from the reference  $T_s$  of 10 °C. However, calculations of daily  $R_{s10}$  and  $Q_{10Rs}$  with the intercepts and slopes after logarithmically transforming the nighttime data (Morgenstern et al., 2004) yielded results almost identical to those using the nonlinear method and did not change the values of  $R_{s10}$  and  $Q_{10Rs}$  (data not shown). Another source of seasonal variability could be the use of  $T_s$  measurements at a fixed depth, in this case at the 2-cm depth. The occurrence of diurnal hysteresis between  $R_s$  and  $T_s$  at the 2-cm depth suggests that the respiratory activity could be controlled by  $T_s$  at greater depth. If that were the case, expressing  $R_s$  as a function of  $T_s$  at the 2-cm depth would result in a lower apparent  $Q_{10}$ , because the diurnal variations in  $T_s$  near the soil surface are larger than those deeper in the soil.

### 3.4. Estimating daily ranges and diurnal variations of half-hourly soil respiration

The seasonal course of daily  $\Delta R_s$  was estimated using three methods: (1) using the seasonal  $R_{s10}$  and  $Q_{10Rs}$  derived from the relationship between daily mean  $R_s$  and  $T_s$  at the 2-cm depth (Eq. (3)), (2) using the same relationship as described in (1) together with the seasonal relationship between daily temperature-normalized  $R_s$  and  $\theta$  in the 0–15 cm layer (Eq. (8)), and (3) using the daily nighttime  $R_{s10}$  and  $Q_{10Rs}$  values derived from nighttime half-hourly measurements of  $R_s$  and  $T_s$  at the 2-cm depth.  $\Delta R_s$  was calculated using Eq. (9), which was obtained by taking the first derivative of  $R_s$  in either Eq. (3) or (8) with respect to  $T_s$ :

$$\Delta R_s \approx \frac{\Delta T_s R_s \ln Q_{10Rs}}{10}, \quad (9)$$

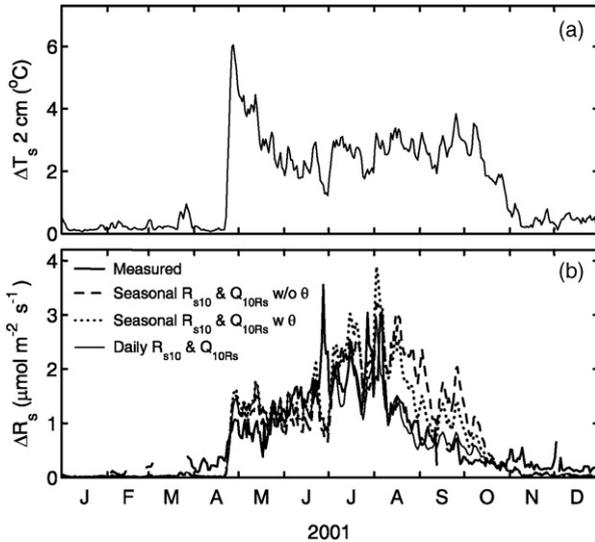


Fig. 7. Seasonal course of daily ranges in (a) soil temperature at the 2-cm depth ( $\Delta T_s$  2 cm) and (b) measured and estimated soil respiration ( $\Delta R_s$ ) in 2001.  $\Delta R_s$  was estimated with Eq. (9) using: (i) seasonal  $R_{s10}$  and  $Q_{10R_s}$  parameters obtained using daily mean  $R_s$  and  $T_s$  (Eq. (3)), (ii) the same as in (i) together with soil water content ( $\theta$ ) in the 0–15 cm layer (Eq. (8)) and (iii) daily nighttime  $R_{s10}$  and  $Q_{10R_s}$  parameters.

where  $\Delta T_s$  is the measured daily range in  $T_s$  at the 2-cm depth and  $R_s$  is the daily mean value calculated using Eqs. (3) and (8) for methods 1 and 2, respectively (parameters used in the equations are given in Table 2). For method 3, daily mean  $R_s$  was calculated using the daily nighttime  $R_{s10}$  and  $Q_{10R_s}$  values, which were estimated using the parameterization with  $\theta$  in the 0–15 cm layer (see Section 3.3 and Fig. 6a and b). As shown in Fig. 7,  $\Delta R_s$  calculated with Eq. (3) (i.e., using only  $T_s$  at the 2-cm depth) were similar to the measured values until the end of July (see the “Seasonal  $R_{s10}$  &

$Q_{10R_s}$  w/o  $\theta$ ” curve). During August, September and October when  $\theta$  was low, Eq. (3) overestimated  $\Delta R_s$  by 0.5–2.0  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . With the inclusion of  $\theta$  in the 0–15 cm layer (i.e., Eq. (8)), the estimation of  $\Delta R_s$  during the low  $\theta$  period was slightly improved but did not agree with the measured values (see the “Seasonal  $R_{s10}$  &  $Q_{10R_s}$  w  $\theta$ ” curve). The use of daily nighttime  $R_{s10}$  and  $Q_{10R_s}$  greatly improved the estimation of  $\Delta R_s$  during the drought period (see the “Daily  $R_{s10}$  and  $Q_{10R_s}$ ” curve). These results support the hypothesis that the short-term temperature sensitivity of  $R_s$  during periods of low  $\theta$  was lower than that calculated using parameters derived at the seasonal time scale.

The same three methods were used to estimate half-hourly  $R_s$  throughout the year. As shown in Fig. 8, the inclusion of  $\theta$  in the 0–15 cm layer (method 2) was essential to obtain a precise estimation of half-hourly  $R_s$  in 2001. Although method 3 was superior to method 2 at high  $R_s$ , it greatly overestimated  $R_s$  during winter. This was because of the overestimation of daily nighttime  $R_{s10}$  when the soil was frozen. Method 3 also systematically overestimated daytime  $R_s$  during the growing season because it could not account for the diurnal hysteresis observed between  $R_s$  and  $T_s$  at the 2-cm depth.

### 3.5. Implications of the results

The results obtained in this study suggest that care should be taken when interpreting and comparing  $Q_{10R_s}$  derived at different times scales because they do not necessarily represent the same processes (Curiel Yuste et al., 2004; Davidson et al., 2006; Janssens and Pilegaard, 2003).  $Q_{10R_s}$  derived at seasonal time scale incorporates the instantaneous control of temperature on enzymatic activity (or any other process controlled

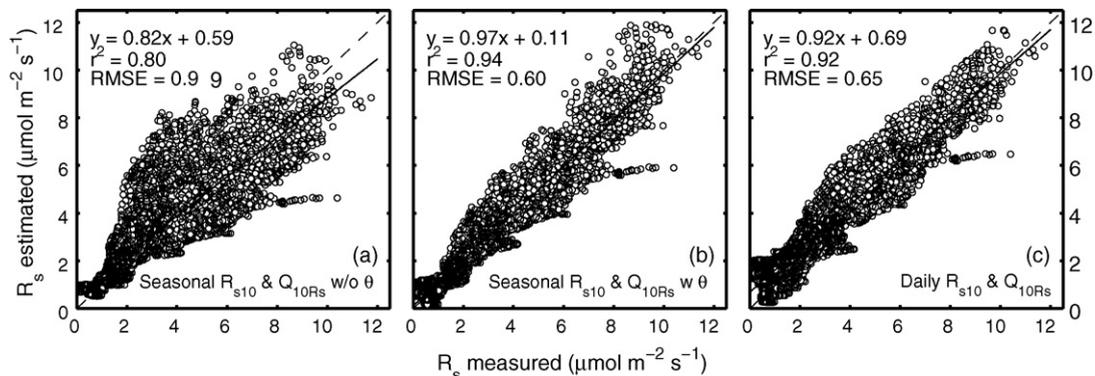


Fig. 8. Relationship between estimated and measured half-hourly soil respiration ( $R_s$ ) using: (a) seasonal  $R_{s10}$  and  $Q_{10R_s}$  parameters (Eq. (3)), (b) the same as in (a) together with soil water content ( $\theta$ ) in the 0–15 cm layer (Eq. (8)) and (c) daily nighttime  $R_{s10}$  and  $Q_{10R_s}$  parameters. The dashed and solid lines represent the 1:1 and the regression ( $P < 0.01$ ) relationships, respectively.

by temperature) as well as the long-term phenological control of root growth dynamics and microbial population changes. Other variables, like  $\theta$  and substrate supply, also have the potential to influence seasonal changes in  $R_s$  and consequently,  $Q_{10R_s}$ . For example, the strong dependence of  $R_s$  on  $\theta$  resulted in a strong interannual variation of  $Q_{10R_s}$  in the aspen stand from 2001 to 2003 (Gaumont-Guay et al., this issue).

$Q_{10R_s}$  derived at short time scale mostly represents the control of temperature on a fixed population of roots and decomposers. As shown in this study, there were strong variations in short-term  $R_{s10}$ , which was an indication of the amount of respiring biomass with regard to phenology and water restrictions. Low  $\theta$  was also associated with a reduction in short-term  $Q_{10R_s}$  and this response possibly resulted from a change in the vertical source strength distribution of  $CO_2$  production in the soil profile. Seasonal variations of short-term  $Q_{10R_s}$  could also have originated from a change in the partitioning of  $R_s$  between its autotrophic and heterotrophic components or to changes in microbial communities throughout the growing season. Monson et al. (2006) reported recently that forest soil microbial communities adapted to cold conditions exhibit a stronger temperature response than the ones in warm summer conditions and this could have been a

significant factor in explaining the decrease in  $Q_{10R_s}$  observed in our study from spring to summer. It is important to note that the use of a constant  $Q_{10R_s}$  derived from a long-term dataset (e.g. seasonal) when the differences between the long- and short-term  $Q_{10R_s}$  are large (e.g. Janssens and Pilegaard, 2003; Rayment and Jarvis, 2000; Widén, 2002) can result in erroneous estimates of  $R_s$  at short time scales. This method is often used with the eddy covariance technique to get half-hourly estimates of  $P_g$  from nighttime  $R_e$  relationships (Baldocchi, 2003) and can lead to large errors in the estimation of these terms (Reichstein et al., 2005a).

To provide an indication of the level of decoupling between  $R_s$  and  $T_s$  in the surface soil layers, the depth at which the correlation between  $R_s$  and  $T_s$  was maximum ( $z_m$ ), i.e. no diurnal hysteresis was observed, was calculated for each day during the growing season. To obtain  $z_m$ , correlation coefficients ( $r$ ) between half-hourly  $R_s$  and  $T_s$  at the soil surface (taken as air temperature at the 1-m height) and at the 2-, 5-, 10- and 20-cm depths were calculated for each day using the same type of moving window as described previously (see insert in Fig. 9). A third-order polynomial function was then fitted between  $r$  and the depth of  $T_s$  measurements to estimate the maximum  $r$  (which varied from 0.45 to 1.0 throughout the growing season)

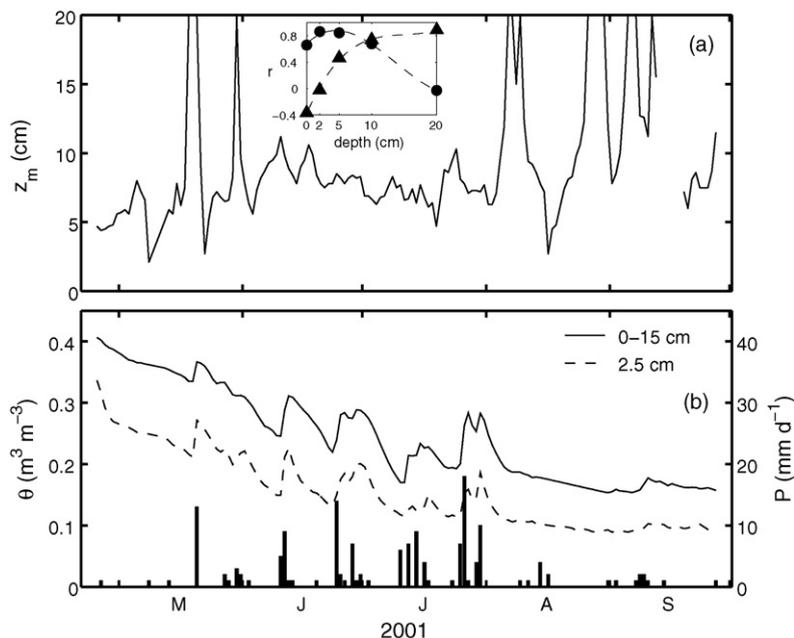


Fig. 9. Seasonal course of (a) depth of maximum correlation ( $z_m$ ) between soil respiration ( $R_s$ ) and soil temperature ( $T_s$ ), (b) daily mean soil water content ( $\theta$ ) in the 0–15 cm layer and at the 2.5-cm depth and daily precipitation ( $P$ , right axis) in 2001.  $z_m$  was calculated using a moving window (1-day time step) of 4 days by calculating the correlation coefficients ( $r$ ) between half-hourly  $R_s$  and  $T_s$  at the soil surface (taken as air temperature at the 1-m height) and at the 2-, 5-, 10- and 20-cm depths. Correlation coefficients ( $r$ ) obtained at each depth for two contrasting days is presented in panel (a) (insert):  $z_m \approx 3$  cm on 17 August (closed circles) and  $z_m > 20$  cm (closed triangles) on 26 August.

and  $z_m$ . As shown in Fig. 9, there was a strong temporal variation in  $z_m$  during the growing season. Maximum values of  $z_m$  (>15 cm) were observed in May and August, two periods showing contrasting soil water availabilities. When  $\theta$  was high (May), strong rain events caused  $z_m$  to increase, which suggested low  $\text{CO}_2$  production near the soil surface due to restricted  $\text{O}_2$  supply resulting from near saturation conditions. When  $\theta$  was low (August), strong rain events tended to bring  $z_m$  back to the soil surface even when  $\theta$  at the 2.5-cm depth remained unchanged. This response was likely related to the activation of dormant decomposers associated with the coarse litter fraction and the upper soil layers. The seasonal variation of  $z_m$  observed in this study raises further concerns about the validity of using  $T_s$  measurements at a fixed depth (usually at a shallow depth) to estimate  $R_s$  at short time scales. A better estimation of half-hourly  $R_s$  could be achieved with the use of a multi-layer process-based model (e.g. Jassal et al., 2004), which takes into account the production of  $\text{CO}_2$  at multiple depths in the soil profile and the subsequent transport of  $\text{CO}_2$  at the soil surface. It could also be achieved with the use of a multi-layer empirical fitting procedure like the ones suggested by Reichstein et al. (2005b) and Swanson and Flanagan (2001). Although such a procedure fitted the data well in this study, it yielded unrealistic basal rates and temperature sensitivities for independent soil layers (data not shown). The interpretation of the temporal variations of  $z_m$  as well as the seasonal and diurnal hysteresis between  $R_s$  and  $T_s$  will require further research into the vertical distribution of soil  $\text{CO}_2$  production.

#### 4. Conclusions

Correctly interpreting the dependence of  $R_s$  on environmental variables still remains a challenging task due to the complex nature of belowground respiration processes. Continuous measurements of  $R_s$  made with an automated chamber system in a mature boreal aspen stand provided, however, new insights into the control of  $R_s$  by these variables at seasonal and diurnal time scales. The major findings of this study are:

- (1) There was a strong dependence of daily values of  $R_s$  on  $T_s$  at the 2-cm depth and no significant differences were found between three temperature-response functions examined. The seasonal values of the  $R_{s10}$  and  $Q_{10R_s}$  parameters derived from a  $Q_{10}$  model were  $3.8 \mu\text{mol m}^{-2} \text{s}^{-1}$  and 3.8, respectively. A reduction of  $\theta$  in the 0–15 cm soil

layer that occurred from August to November resulted in hysteresis-like behavior in the  $R_s$ – $T_s$  relationship. The use of a hyperbolic function greatly improved our ability to predict the reductions of  $R_s$  at low and high  $\theta$ .

- (2) Although diurnal variations of half-hourly  $R_s$  closely resembled those of  $T_s$  at the 2-cm depth,  $R_s$  generally lagged  $T_s$  by 4–5 h. The hysteresis resulting from this lag was not related to diurnal variations of  $\theta$  in the surface soil layers and disappeared when using  $T_s$  at greater depths.
- (3) Daily values of  $R_{s10}$  and  $Q_{10R_s}$  calculated from nighttime measurements of  $R_s$  and  $T_s$  at the 2-cm depth showed strong seasonality and were, on average, higher ( $4.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and lower (2.8), respectively, than those derived from the seasonal relationship.  $R_{s10}$  and  $Q_{10R_s}$  were highly correlated with changes in  $\theta$ . The results indicated a reduction in the short-term temperature sensitivity of  $R_s$  with increasing soil water limitation.
- (4) The parameterization of daily nighttime  $R_{s10}$  and  $Q_{10R_s}$  values using seasonal changes in  $\theta$  was successful in estimating daily ranges in  $R_s$ , especially during the drought period. It was not successful, however, in estimating half-hourly  $R_s$  throughout the year because it could not account for the diurnal hysteresis between  $R_s$  and  $T_s$  in the surface soil layer. Careful interpretation of the lag and hysteresis effects will require further studies of the vertical distribution of soil  $\text{CO}_2$  production.

#### Acknowledgments

This research was funded by the Fonds de Recherche sur la nature et les Technologies du Québec (FCAR) in the form of a three-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 and the support from Dave Wieder and 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

- Anderson, D., 1998. BOREAS TE-01 soils data over the SSA tower sites. Available online at: <http://www-eosdis.ornl.gov/>.
- Atkin, O.K., Edwards, E.J., Loveys, B.R., 2000. Response of root respiration to changes in temperature and its relevance to global warming. *New Phytol.* 147, 141–154.
- Atkin, O.K., Tjoelker, M.G., 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends Plant Sci.* 8, 343–351.
- Atkin, O.K., Bruhn, D., Hurry, V.M., Tjoelker, M.G., 2005. The hot and the cold: unraveling the variable response of plant respiration to temperature. *Funct. Plant Biol.* 32, 87–105.
- Bååth, E., Wallander, H., 2003. Soil and rhizosphere microorganisms have the same  $Q_{10}$  for respiration in a model system. *Global Change Biol.* 9, 1788–1791.
- 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.
- 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  $CO_2$  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.
- Bol, R., Bolger, T., Cully, R., Little, D., 2003. Recalcitrant soil organic materials mineralize more efficiently at higher temperatures. *J. Plant Nutr. Soil Sci.* 166, 300–307.
- 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.
- Boone, R.D., Nadelhoffer, K.J., Canary, J.D., Kaye, J.P., 1998. Roots exerts a strong influence on the temperature sensitivity of soil respiration. *Nature* 396, 570–572.
- Borken, W., Xu, Y.-J., Brumme, R., Lamersdorf, N., 1999. A climate change scenario for carbon dioxide and dissolved organic carbon fluxes from a temperate forest soil: drought and rewetting effects. *Soil Sci. Soc. Am. J.* 63, 1848–1855.
- 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.
- 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., 2003. Field measurements of root respiration indicate little to no seasonal temperature acclimation for sugar maple and red pine. *Tree Physiol.* 23, 273–280.
- Coûteaux, M.M., Bottner, P., Anderson, J.M., Berg, B., Bolger, T., Casals, P., Romanya, J., Thiery, J.M., Vallejo, V.R., 2001. Decomposition of  $C^{13}$ -labelled standard plant material in a latitudinal transect of European coniferous forests: differential impact of climate on the decomposition of soil organic matter compartments. *Biogeochemistry* 54, 147–170.
- Curiel Yuste, J., Janssens, I.A., Carrara, A., Meiresonne, L., Ceulemans, R., 2003. Interactive effects of temperature and precipitation on soil respiration in a temperate maritime forest. *Tree Physiol.* 23, 1263–1270.
- Curiel Yuste, J., Janssens, I.A., Carrara, A., Ceulemans, R., 2004. Annual  $Q_{10}$  of soil respiration reflects plant phenological patterns as well as temperature sensitivity. *Global Change Biol.* 10, 161–169.
- Davidson, E.A., Belk, E., Boone, R.D., 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biol.* 4, 217–227.
- Davidson, E.A., Janssens, I.A., Luo, Y., 2006. On the variability of respiration in terrestrial ecosystems: moving beyond  $Q_{10}$ . *Global Change Biol.* 112, 154–164.
- Drewitt, G.B., Black, T.A., Nescic, Z., Humphreys, E.R., Jork, E.M., Swanson, R., Ethier, G.J., Griffis, T., Morgenstern, K., 2002. Measuring forest-floor  $CO_2$  fluxes in a Douglas-fir forest. *Agric. For. Meteorol.* 110, 299–317.
- Fang, C., Smith, P., Moncrieff, J.B., Smith, J.U., 2005. Similar response of labile and resistant soil organic matter pools to changes in temperature. *Nature* 433, 57–59.
- Flanagan, L.B., Johnson, B.G., 2005. Interacting effects of temperature, soil moisture and plant biomass production on ecosystem respiration in a northern temperate grassland. *Agric. For. Meteorol.* 130, 237–253.
- Gaumont-Guay, D., 2005. Analysis of environmental and biological controls on soil respiration in boreal deciduous and coniferous stands. Ph.D. Thesis. University of British Columbia, Vancouver, BC, unpublished.
- Giardina, C.P., Ryan, M.G., 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature* 404, 858–861.
- 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.
- Grant, R.F., Black, T.A., den Hartog, G., Berry, J.A., Neumann, H.H., Blanken, P.D., Yang, P.C., Russell, C., Nalder, I.A., 1999. Diurnal and annual exchanges of mass and energy between an aspen-hazelnut forest and the atmosphere: testing the mathematical model *ecosys* with data from the BOREAS experiment. *J. Geophys. Res.* 104, 27699–27717.
- Griffis, T.J., Black, T.A., Gaumont-Guay, D., Drewitt, G.B., Nescic, 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.
- Harper, C.W., Blair, J.M., Fay, P.A., Knapp, A.K., Carlisle, J.D., 2005. Increased rainfall variability and reduced rainfall amount decreases soil  $CO_2$  efflux in a grassland ecosystem. *Global Change Biol.* 11, 322–334.
- IPCC, 2001. *Climate change 2001*. In: *Third Assessment Report of the IPCC*, Cambridge University Press, Cambridge, UK, pp. 183–237.
- Irvine, J., Law, B.E., 2002. Contrasting soil respiration in young and old-growth ponderosa pine forests. *Global Change Biol.* 8, 1183–1194.
- Janssens, I.A., Lankreijer, H., Matteucci, G., Kowalski, A.S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grunwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E.J., Grelle, A., Rannik, U., Morgenstern, K., Oltchev, S., Clement, R., Gudmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N.O., Vesala, T., Granier, A., Schulze, E.D., Lindroth, A., Dolman, A.J., Jarvis, P.G., Ceulemans, R., Valentini, R., 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biol.* 7, 269–278.
- Janssens, I.A., Pilegaard, K., 2003. Large seasonal changes in  $Q_{10}$  of soil respiration in a beech forest. *Global Change Biol.* 9, 911–918.
- Janssens, I.A., Dore, S., Epron, D., Lankreijer, H., Buchmann, N., Longdoz, B., Brossaud, J., Montagnani, L., 2003. Climatic influ-

- ences 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., Drewitt, G.B., Novak, M.D., Gaumont-Guay, D., Nestic, Z., 2004. A model of the production and transport of CO<sub>2</sub> in soil: predicting soil CO<sub>2</sub> concentrations and CO<sub>2</sub> efflux from a forest floor. *Agric. For. Meteorol.* 124, 219–236.
- 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.
- Joffre, R., Ourcival, J.-M., Rambal, S., Rocheteau, A., 2003. The key-role of topsoil moisture on CO<sub>2</sub> efflux from a Mediterranean *Quercus ilex* forest. *Ann. For. Sci.* 60, 519–526.
- 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.
- Kirschbaum, M.U.F., 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. *Biogeochemistry* 27, 753–760.
- Knorr, W., Prentice, I.C., House, J.I., Holland, E.A., 2005. Long-term sensitivity of soil carbon turnover to warming. *Nature* 433, 298–301.
- Lagarias, J.C., Reeds, J.A., Wright, M.H., Wright, P.E., 1998. Convergence properties of the Nelder-Mead simplex method in low dimensions. *SIAM J. Optimiz.* 9, 112–147.
- Lavigne, M.B., Foster, R.J., Goodine, G., 2004. Seasonal and annual changes in soil respiration in relation to soil temperature, water potential and trenching. *Tree Physiol.* 24, 415–424.
- 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.
- Liski, J., Iivesniemi, H., Makela, A., Westman, C.J., 1999. CO<sub>2</sub> emissions from soil in response to climatic warming are over-estimated—the decomposition of old soil organic matter is tolerant of temperature. *Ambio* 28, 171–174.
- Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. *Funct. Ecol.* 8, 315–323.
- Monson, R.K., Lipson, D.L., Burns, S.P., Turnipseed, A.A., Delany, A.C., Williams, M.W., Schmidt, S.K., 2006. Winter forest soil respiration controlled by climate and microbial community composition. *Nature* 439, 711–714.
- Morén, A.-S., Lindroth, B.A., 2000. CO<sub>2</sub> exchange at the floor of a boreal forest. *Agric. For. Meteorol.* 101, 1–14.
- 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.
- Palmroth, S., Maier, C.A., McCarthy, H.R., Oishi, A.C., Kim, H.S., Johnsen, K.H., Katul, G.G., Oren, R., 2005. Contrasting responses to drought of forest floor CO<sub>2</sub> efflux in a Loblolly pine plantation and a nearby Oak-Hickory forest. *Global Change Biol.* 11, 421–434.
- Parkin, T.B., Kaspar, T.C., 2003. Temperature controls on diurnal carbon dioxide flux: implications for estimating soil carbon loss. *Soil Sci. Soc. Am. J.* 67, 1763–1772.
- Qi, Y., Xu, M., Wu, J., 2002. Temperature sensitivity of soil respiration and its effects on ecosystem carbon budget: nonlinearity begets surprises. *Ecol. Model.* 153, 131–142.
- Raich, J.W., Schlesinger, W.H., 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B, 81–99.
- Rayment, M.B., Jarvis, P.G., 2000. Temporal and spatial variation of soil CO<sub>2</sub> efflux in a Canadian boreal forest. *Soil Biol. Biochem.* 32, 35–45.
- Reichstein, M., Tenhunen, J.D., Rouspard, O., Ourcival, J.M., Rambal, S., Miglietta, F., Peressotti, A., Pecchiari, M., Tirone, G., Valentini, R., 2002. Severe drought effects on ecosystem CO<sub>2</sub> and H<sub>2</sub>O fluxes at three Mediterranean evergreen sites: revision of current hypotheses? *Global Change Biol.* 8, 999–1017.
- Reichstein, M., Rey, A., Freibauer, A., Tenhunen, J., Valentini, R., Banza, J., Casals, P., Cheng, Y.F., Grunzweig, J.M., Irvine, J., Joffre, R., Law, B.E., Loustau, D., Miglietta, F., Oechel, W., Ourcival, J.M., Pereira, J.S., Peressotti, A., Ponti, F., Qi, Y., Rambal, S., Rayment, M., Romanya, J., Rossi, F., Tedeschi, V., Tirone, G., Xu, M., Yakir, D., 2003. Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. *Global Biogeochem. Cy.* 17, 1–15.
- Reichstein, M., Falge, E., Baldocchi, D.B., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T., Granier, A., Grunwald, T., Havrankova, K., Iivesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J.M., Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D., Valentini, R., 2005a. On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global Change Biol.* 11, 1424–1439.
- Reichstein, M., Subke, J.-A., Angeli, A.C., Tenhunen, J.D., 2005b. Does the temperature sensitivity of decomposition of soil organic matter depend upon water content, soil horizon, or incubation time? *Global Change Biol.* 11, 1–14.
- Russell, C.A., Voroney, R.P., 1998. Carbon dioxide efflux from the floor of a boreal aspen forest. I. Relationship to environmental variables and estimates of C respired. *Can. J. Soil Sci.* 78, 301–310.
- Sowell, J.B., Spomer, G.G., 1986. Ecotypic variation in root respiration rate among elevational populations of *Abies lasiocarpa* and *Picea engelmannii*. *Oecologia* 68, 375–379.
- Subke, J.-A., Reichstein, M., Tenhunen, J.D., 2003. Explaining temporal variation in soil CO<sub>2</sub> efflux in a mature spruce forest in Southern Germany. *Soil Biol. Biochem.* 35, 1467–1483.
- Swanson, R.V., Flanagan, L.B., 2001. Environmental regulation of carbon dioxide exchange at the forest floor in a boreal black spruce ecosystem. *Agric. For. Meteorol.* 108, 165–181.
- Tang, J., Baldocchi, D.B., Xu, L., 2005. Tree photosynthesis modulates soil respiration on a diurnal time scale. *Global Change Biol.* 11, 1–7.
- Tjoelker, M.G., Oleksyn, J., Reich, P.B., 2001. Modelling respiration of vegetation: evidence for a general temperature-dependent  $Q_{10}$ . *Global Change Biol.* 7, 223–230.
- Valentini, R., Matteucci, 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.
- Weger, H.G., Guy, R.D., 1991. Cytochrome and alternative pathway respiration in white spruce (*Picea glauca*) roots. Effects of

- growth and measurement temperature. *Physiol. Plantarum* 83, 675–681.
- Widén, B., 2002. Seasonal variation in forest-floor CO<sub>2</sub> exchange in a Swedish coniferous forest. *Agric. For. Meteorol.* 111, 283–297.
- 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., Qi, Y., 2001a. Spatial and seasonal variations of  $Q_{10}$  determined by soil respiration measurements at a Sierra Nevadan forest. *Global Biogeochem. Cy.* 15, 687–696.
- Xu, M., Qi, Y., 2001b. Soil-surface CO<sub>2</sub> efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California. *Global Change Biol.* 7, 667–677.
- 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.