

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

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Abstract

Continuous half-hourly measurements of soil CO₂ 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 (θ). 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 θ 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 (θ_{fc} , $\sim 0.30 \text{ m}^3 \text{ m}^{-3}$): (1) R_{sN} was strongly reduced when θ decreased below θ_{fc} , which reflected a reduction in microbial decomposition, and (2) R_{sN} slightly decreased when θ increased above θ_{fc} , which reflected a restriction of CO₂ or O₂ 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 θ in the 0–15 cm soil layer, with a tendency of low R_{s10} and Q_{10R_s} values at low θ . Overall, the use of seasonal R_{s10} and Q_{10R_s} parameters led to an overestimation of daily ranges of half-hourly R_s (ΔR_s) during drought conditions, which supported findings that the short-term temperature sensitivity of R_s was lower during periods of low θ . The use of daily nighttime R_{s10} and Q_{10R_s} parameters greatly helped at simulating ΔR_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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1. Introduction

The efflux of carbon dioxide (CO₂) from the soil, referred to hereafter as soil respiration (R_s), is a major

component of CO₂ exchange between forest ecosystems and the atmosphere. On an annual basis, it accounts for more than two-thirds of the CO₂ released through ecosystem respiration (R_e) and about one half of the CO₂ 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 CO₂ sink strength of forest ecosystems and future atmospheric CO₂ 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 CO₂ by roots, mycorrhizal fungi, microorganisms and soil fauna throughout the soil profile, and the subsequent release of CO₂ 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 CO₂ and/or oxygen (O₂) 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⁻¹. 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⁻¹ 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⁻¹ (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 CO₂ 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⁻¹. 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 CO₂-free nitrogen gas (offset calibration) and a gas of known CO₂ concentration (~360 μmol mol⁻¹, 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 CO₂ m⁻² s⁻¹) was calculated using the following equation:

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

where ρ_a is the density of dry air in the chamber headspace (mol m^{-3}), V_e the effective volume of the chamber (m^3), A the area of ground covered by the chamber (m^2), ds_c/dt the time rate of change of the 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 s^{-1}) and t is the time (s). s_c was used in this calculation instead of the 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 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% CO_2 balance dry air) at a rate of 10 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:

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

where ds_{cl}/dt is the time rate of change of the CO_2 mixing ratio during gas injection over a 1-min interval following lid closure ($\text{mol CO}_2 \text{ mol}^{-1}$ dry air 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 (θ) 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 θ 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 θ (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°C (R_{s10}) or 283 K (R_{s283})) and temperature sensitivity parameters (relative change in R_s for a 10°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 θ 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 θ .

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., θ , 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°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 (θ)

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 (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 θ 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 ± 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 .

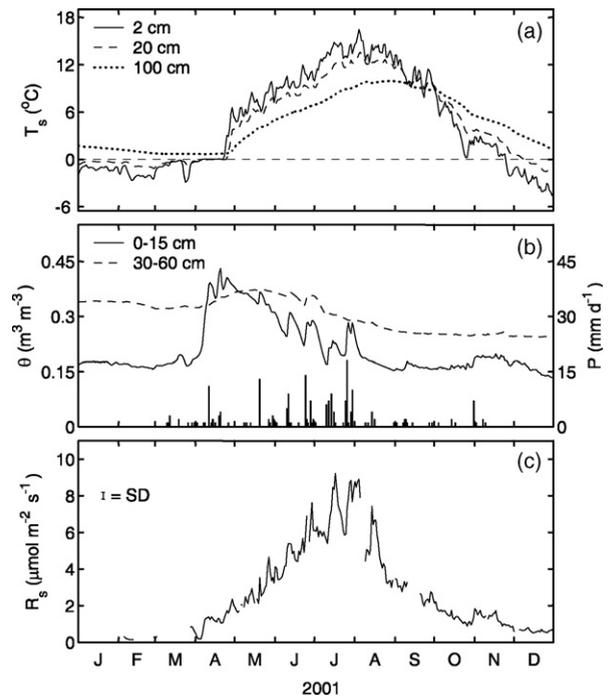


Fig. 1. Seasonal course of daily mean: (a) soil temperature (T_s) at the 2-cm (solid), 20-cm (dashed) and 100-cm (dotted) depths, (b) soil water content (θ) in the 0–15 (solid) and 30–60 cm layers (dashed), precipitation (P , right axis) and (c) soil respiration (R_s) in the aspen stand in 2001. The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

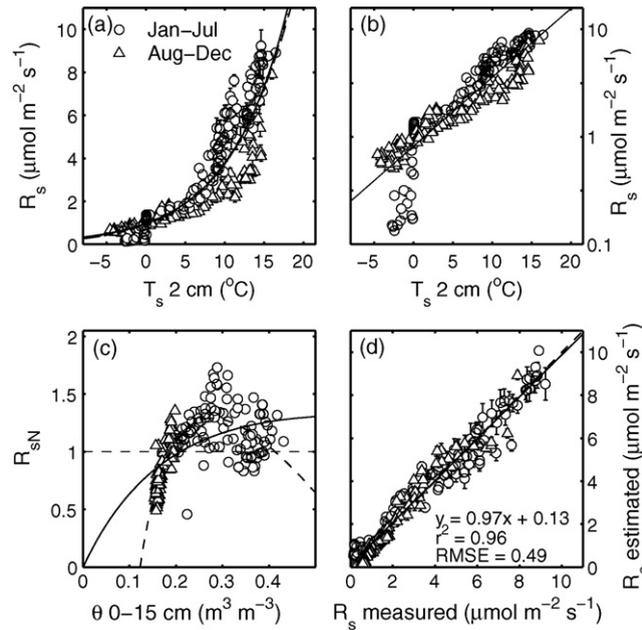


Fig. 2. Relationship between daily mean (a) soil respiration (R_s) and soil temperature (T_s) at the 2-cm depth, (b) logarithmically transformed R_s and T_s at the 2-cm depth, (c) daily temperature-normalized soil respiration (R_{sN}) and soil water content in the 0–15 cm layer (θ), and (d) estimated (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 ± 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). CO₂ 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 (θ)

Function name	Parameters						
	R_{s10} or R_{s283} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Q_{10R_s}	E_0 (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 ^a)	3.6	4.4			0.82	1.00	269
Arrhenius	3.8		89.3		0.82	1.00	269
Arrhenius (LT)	3.8		3534 ^b	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.

^a Calculated after a logarithmic transformation of daily R_s values following Morgenstern et al. (2004).

^b 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 θ in the 0–15 cm layer was below and above a threshold value of ~ 0.25 – $0.30 \text{ m}^3 \text{ m}^{-3}$ (Fig. 2c). Interestingly, this threshold value corresponded approximately to the soil water field capacity (θ_{fc}) in the 0–15 cm layer. The decrease in R_s below θ_{fc} most likely resulted from an inhibition of microbial activity in the organic layer because θ 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 θ was above θ_{fc} (Fig. 2c) and this response reflected a restriction in CO_2 transport out of the soil or an inhibition of CO_2 production due to a lack of O_2 (Bunnell et al., 1977).

Increases in θ 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 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 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 θ 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 θ 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 θ 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 (ΔR_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 ΔR_s was unexpected since daily ranges in T_s (ΔT_s) in the shallow soil layers remained relatively constant over the three periods (the average ΔT_s at the 2-cm depth was 2.5°C during the growing season, see Fig. 7). ΔR_s was positively correlated with daily mean R_s . There was a

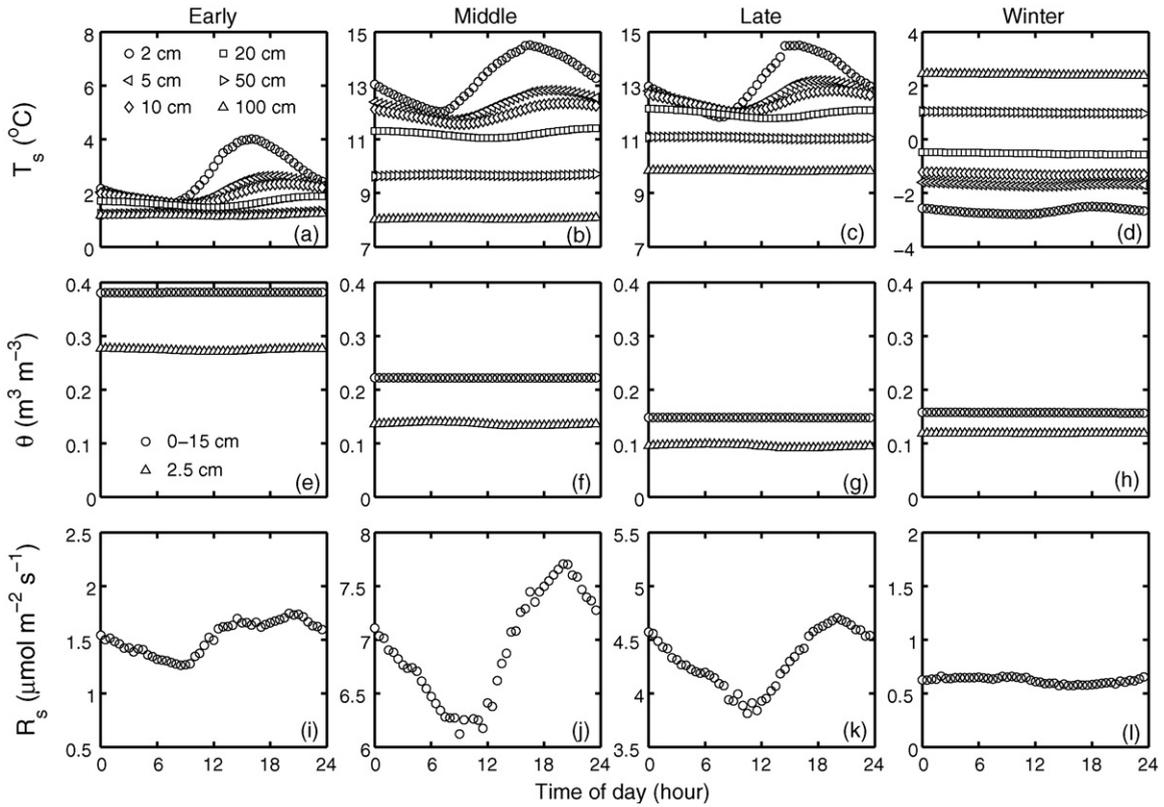


Fig. 3. Diurnal course of half-hourly soil temperature (T_s) at the 2-, 5-, 10-, 20-, 50- and 100-cm depths (a–d), soil water content (θ) in the 0–15 cm layer and at the 2.5-cm depth (e–h) and soil respiration (R_s) (i–l) in the aspen stand during the early (10 April–9 May), middle (1–30 July) and late (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 θ was low and T_s peaked in the surface soil layers. ΔR_s and ΔT_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

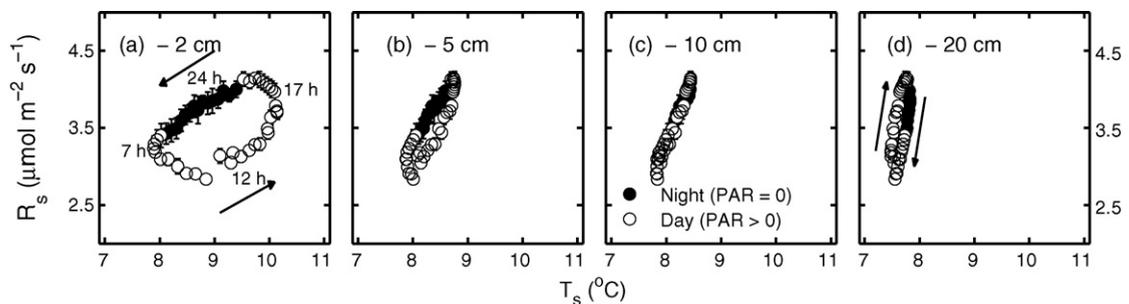


Fig. 4. Relationship between half-hourly soil respiration (R_s) and soil temperature (T_s) at the (a) 2-cm, (b) 5-cm, (c) 10-cm and (d) 20-cm depths for measurements made from June 4 to 8 2001 (ensemble average for each half-hour). Open and closed circles indicate daytime (PAR (photosynthetically active 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 ± 1 standard deviation from half-hourly measurements. Arrows in panels (a and d) indicate increasing time of day.

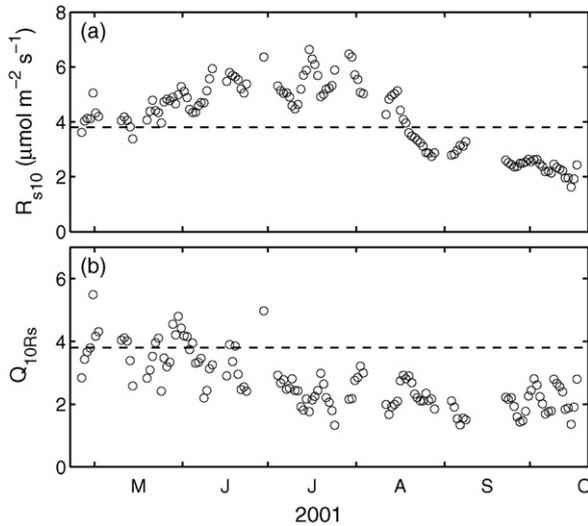


Fig. 5. Seasonal course of daily nighttime (a) soil respiration at 10 °C (R_{s10}) and (b) temperature sensitivity of R_s (Q_{10Rs}). Parameters for each day were estimated using half-hourly nighttime measurements of R_s and T_s at the 2-cm depth and a moving window (1-day time step) of 4 days. Dashed 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 ΔR_s , which was far larger than the reasonable biological Q_{10} of 2. Thus, these results suggest that most CO_2 production was still

occurring above 10 cm. Diurnal variations of θ at the 2.5-cm depth and in the 0–15 cm layer were negligible throughout the growing season (Fig. 3) indicating that θ 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 ΔR_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 θ ($\text{m}^3 \text{m}^{-3}$) 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 θ below and above θ_{fc} of the 0–15 cm layer with an optimal range

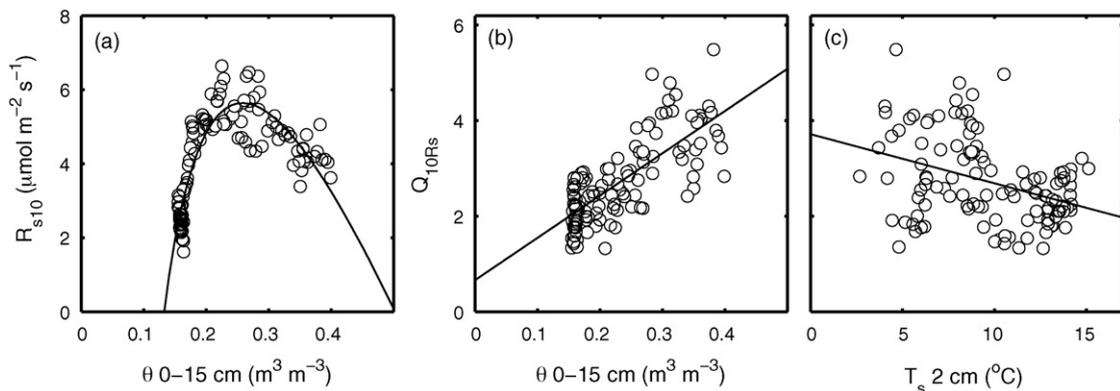


Fig. 6. (a) Relationship between daily nighttime soil respiration at 10 °C (R_{s10}) and soil water content (θ) in the 0–15 cm layer; relationship between daily nighttime temperature sensitivity of R_s (Q_{10Rs}) and (b) θ in the 0–15 cm layer and (c) soil temperature (T_s) at the 2-cm depth. The line 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 m³ m⁻³. Q_{10Rs} increased with θ ($Q_{10Rs} = 9.01\theta + 0.62$, $r^2 = 0.55$, 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 θ 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 ΔR_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 θ 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. ΔR_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 :

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

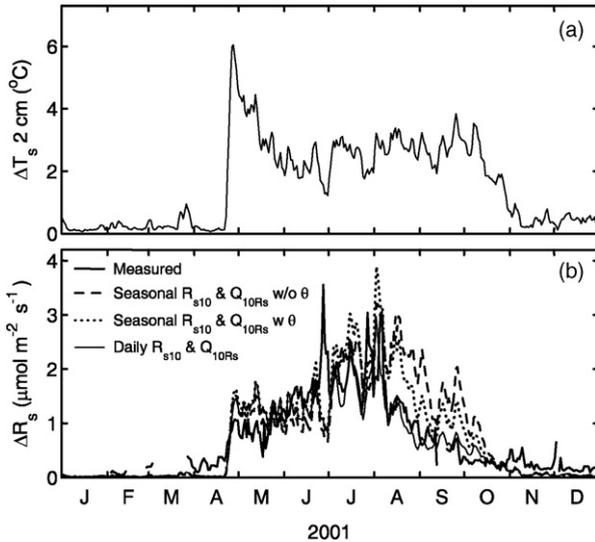


Fig. 7. Seasonal course of daily ranges in (a) soil temperature at the 2-cm depth (ΔT_s 2 cm) and (b) measured and estimated soil respiration (ΔR_s) in 2001. ΔR_s was estimated with Eq. (9) using: (i) seasonal R_{s10} and Q_{10Rs} parameters obtained using daily mean R_s and T_s (Eq. (3)), (ii) the same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

where ΔT_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_{10Rs} values, which were estimated using the parameterization with θ in the 0–15 cm layer (see Section 3.3 and Fig. 6a and b). As shown in Fig. 7, ΔR_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_{10Rs} w/o θ ” curve). During August, September and October when θ was low, Eq. (3) overestimated ΔR_s by 0.5–2.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$. With the inclusion of θ in the 0–15 cm layer (i.e., Eq. (8)), the estimation of ΔR_s during the low θ period was slightly improved but did not agree with the measured values (see the “Seasonal R_{s10} & Q_{10Rs} w θ ” curve). The use of daily nighttime R_{s10} and Q_{10Rs} greatly improved the estimation of ΔR_s during the drought period (see the “Daily R_{s10} and Q_{10Rs} ” curve). These results support the hypothesis that the short-term temperature sensitivity of R_s during periods of low θ 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 θ 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_{10Rs} 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_{10Rs} derived at seasonal time scale incorporates the instantaneous control of temperature on enzymatic activity (or any other process controlled

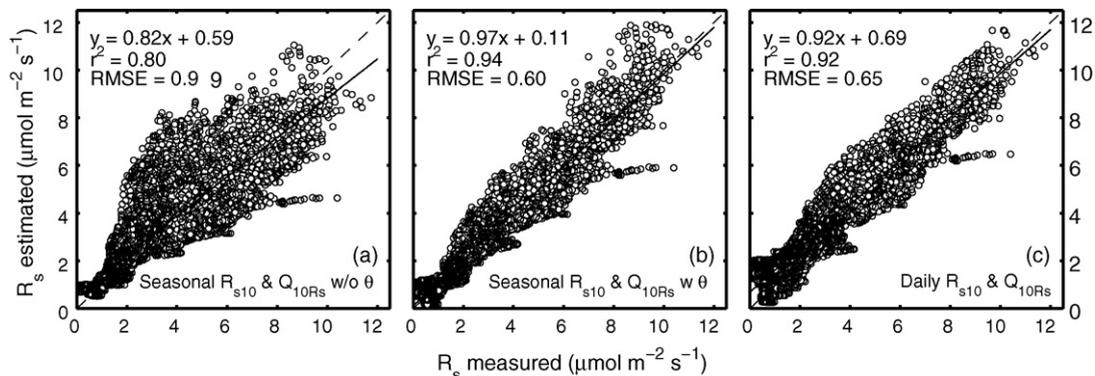


Fig. 8. Relationship between estimated and measured half-hourly soil respiration (R_s) using: (a) seasonal R_{s10} and Q_{10Rs} parameters (Eq. (3)), (b) the same as in (a) together with soil water content (θ) in the 0–15 cm layer (Eq. (8)) and (c) daily nighttime R_{s10} and Q_{10Rs} parameters. The 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 θ 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 θ 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 θ 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)

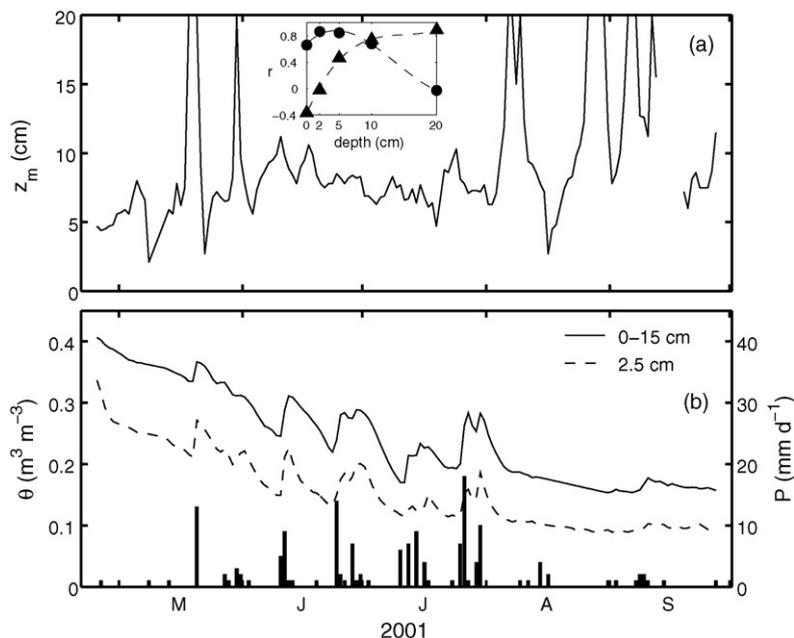


Fig. 9. Seasonal course of (a) depth of maximum correlation (z_m) between soil respiration (R_s) and soil temperature (T_s), (b) daily mean soil water content (θ) in the 0–15 cm layer and at the 2.5-cm depth and daily precipitation (P , right axis) in 2001. z_m was calculated using a moving window (1-day 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 θ was high (May), strong rain events caused z_m to increase, which suggested low CO_2 production near the soil surface due to restricted O_2 supply resulting from near saturation conditions. When θ was low (August), strong rain events tended to bring z_m back to the soil surface even when θ 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 CO_2 at multiple depths in the soil profile and the subsequent transport of 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 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 θ 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 θ .

- (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 θ 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 θ . 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 θ 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 CO_2 production.

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