Oecologia (2002) 132:374–381
DOI 10.1007/s00442-002-0987-4

ECOSYSTEMS ECOLOGY

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Environmental controls on carbon dioxide flux from black spruce coarse woody debris

Received: 1 March 2002 / Accepted: 23 May 2002 / Published online: 28 June 2002

Abstract Carbon dioxide flux from coarse woody debris (CWD) is an important source of CO_2 in forests with moderate to large amounts of CWD. A process-based understanding of environmental controls on CWD CO_2 flux (R_{CWD}) is needed to accurately model carbon exchange between forests and the atmosphere. The objectives of this study were to: (1) use a laboratory incubation factorial experiment to quantify the effect of temperature (T_{CWD}), water content (W_C), decay status, and their interactions on R_{CWD} for black spruce [*Picea mariana* (Mill.) BSP] CWD; (2) measure and model spatial and temporal dynamics in T_{CWD} for a boreal black spruce fire chronosequence; and (3) validate the R_{CWD} model with field measurements, and quantify potential errors in estimating annual R_{CWD} from this model on various time steps. The R_{CWD} was positively correlated to T_{CWD} (R^2=0.37, P<0.001) and W_C (R^2=0.18, P<0.001), and an empirical R_{CWD} polynomial model that included T_{CWD} and W_C interactions explained 74% of the observed variation of R_{CWD}. The R_{CWD} estimates from the R_{CWD} model excellently matched the field measurements. Decay status of CWD significantly (P<0.001) affected R_{CWD}. The temperature coefficient (Q_{10}) averaged 2.5, but varied by 141% across the 5–42°C temperature range, illustrating the potential shortcomings of using a constant Q_{10}. The CWD temperature was positively correlated to air temperature (R^2=0.79, P<0.001), with a hysteresis effect that was correlated to CWD decay status and stand leaf area index. Ignoring this temperature hysteresis introduced errors of –1% to +32% in annual R_{CWD} estimates. Increasing T_{CWD} modeling time step from hourly to daily or monthly introduced a 5–11% underestimate in annual R_{CWD}. The annual R_{CWD} values in this study were more than two-fold greater than those in a previous study, illustrating the need to incorporate spatial and temporal responses of R_{CWD} to temperature and water content into models for long-term R_{CWD} estimation in boreal forest ecosystems.

Keywords Carbon dioxide flux · Coarse woody debris · Boreal forest · Decomposition · Modeling

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Introduction

Boreal forests play a crucial role in the global carbon budget (Kasischke 2000). Wildfires, the dominant disturbance in many boreal forests (Goldammer and Furyaev 1997), produce a large amount of coarse woody debris (CWD) (Bond-Lamberty et al. 2002a), which significantly influences ecosystem structure and function (Harmon et al. 1986). CWD biomass has been quantified for numerous forest ecosystems (Frangi et al. 1997; Harmon et al. 1986; Krankina and Harmon 1995; Siitonen et al. 2000; Spies et al. 1988; Stewart et al. 1994; Stone et al. 1998), but direct measurements of CWD CO_2 flux (R_{CWD}) are limited (Chambers et al. 2001; Marra and Edmonds 1994; Yoneda 1975), especially for boreal forests (Bond-Lamberty et al. 2002a).

Bond-Lamberty et al. (2002a) estimated that the R_{CWD} comprised 1–54% of soil surface CO_2 flux for seven different-aged boreal black spruce stands comprising a fire chronosequence, with the maximum R_{CWD} occurring in a 12-year-old stand that contained the greatest CWD mass. They used an assumed Q_{10} to calculate annual R_{CWD}, but Q_{10} changes with temperature and water content (W_C) for soil surface CO_2 flux (Raich and Schlesinger 1992; Rayment and Jarvis 2000; Strömgren 2001; Wang et al. 2002) and decaying roots (Chen et al. 2000). The temperature dependence of Q_{10} for decaying CWD is not well studied. Bond-Lamberty et al. (2002a) also reported that R_{CWD} was moisture-limited below 43% W_C based on field measurements. Clearly, a controlled laboratory experiment to quantify the effects of temperature, W_C, and their interaction on R_{CWD} is needed.

Empirical models driven by environmental variables are commonly used to calculate annual R_{CWD} (Bond-Lamberty et al. 2002a). Coarse woody debris temperature (T_{CWD}) is not routinely measured, and therefore is often assumed to follow air temperature (T_A) (Bond-Lamberty et al. 2002a). The hysteresis effects of temperature and W_C on respiration, resulting from substrate thermal and hydrological conductivity and delayed biological response to environmental factors, are generally ignored (Bond-Lamberty et al. 2002a; Potter et al. 1993; Raich et al. 1991). However, the physical properties of wood might be critical to R_{CWD} because of its poor thermal conductivity (Campbell and Norman 1998). Furthermore, soil surface CO_2 flux displays nonlinear responses to environmental variables (Rayment and Jarvis 2000; Strömgren 2001; Wang et al. 2002). Presumably, R_{CWD}, also a product of microbial activity, behaves similarly. Therefore, using different modeling time steps may introduce bias in annual R_{CWD} estimates. Bond-Lamberty et al. (2002a) assumed that T_{CWD} followed T_A on a weekly time step, which has not been tested.

The objectives of this study were to: (1) quantify the effect of T_{CWD}, W_C, decay status, and their interactions on R_{CWD} for black spruce CWD; (2) measure and model spatial and temporal dynamics in T_{CWD} for a boreal black spruce fire chronosequence; and (3) validate the R_{CWD} model and quantify potential errors in estimating annual R_{CWD}.

Materials and methods

Site description and general experiment design

The CWD samples for incubation and temperature measurements were collected from a boreal black spruce fire chronosequence near Thompson, Manitoba (55°48′ N 97°52′ W). The chronosequence consisted of even-aged stands that originated from stand-killing wildfires in 1989, 1981, 1964, and 1870, containing 177.5±48.1, 58.2±21.6, 13.1±7.7, and 10.5±8.6 ton CWD ha^{-1}, respectively (Bond-Lamberty et al. 2002a). The stand ages were 12, 20, 37, and 131 years, respectively, at the time of investigation. All the stands were within 40 km^2. The stands were dominated by black spruce prior to wildfires, and had well-drained clay soils. Gower et al. (2002) provided detailed descriptions of the stands.

We addressed our objectives using a combination of measurements and modeling.

1. A laboratory factorial incubation experiment was used to quantify the effect of T_{CWD}, W_C, decay status, and their interactions on R_{CWD} for black spruce CWD.
2. In situ T_{CWD} and T_A were measured throughout the growing season to examine spatial and temporal T_{CWD} dynamics in the chronosequence.
3. The empirical R_{CWD} model developed from laboratory measurements was compared to field data.
4. The R_{CWD} model and T_{CWD} data were applied with various time steps to quantify potential errors in annual R_{CWD} estimates.

CWD incubation experiment

CWD samples for the incubation experiment were collected from the 12-year-old stand in November 2000. The stand was composed of trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh), jack pine (*Pinus banksiana* Lamb.), black spruce, and willow (*Salix* spp.) seedlings and saplings.

The experimental design of the incubation study was a two-factorial repeated measure design with seven temperatures and three CWD decay classes. The temperatures, selected to include a wide range of temperature between 0 and 45°C, were 5, 12, 17, 20, 26, 32, and 42°C. The decay classes were: class I – a knife could not penetrate into the sample; class II – a knife could slightly penetrate the sample with appreciable resistance; and class III – a knife could fully penetrate the sample with little resistance (Lambert et al. 1980).

A total of 36 samples, 12 from each decay class, were randomly selected in the field and carefully transported to University of Wisconsin – Madison. Each CWD sample was tagged and randomly assigned to one of two Conviron CMP3023 plant growth chambers (Conviron, Winnipeg, MB, Canada), with 6 of the 12 samples from each decay class in each growth chamber. Samples were exposed to 12:12 h of light and darkness each day. Each growth chamber was set to a treatment temperature, and the CWD samples were placed in the growth chamber for 48 h to equilibrate to the new temperature. Each sample was submerged in distilled water of the same treatment temperature for 48 h to achieve fiber saturation. They were removed from the water and incubated between 10 and 30 days, depending on the temperature, to produce a natural W_C gradient. The R_{CWD} measurements were started after the samples were removed from the water for 12–24 h, to minimize potential effect of CWD rewetting. The R_{CWD} was measured three to seven times during the drying period to obtain R_{CWD} at various W_C levels. At the end of the drying period a new treatment temperature was assigned to the growth chamber, and the measurement procedure was repeated.

To measure R_{CWD}, a CWD sample was removed from the growth chamber and immediately inserted into a custom chamber connected to a Li-Cor 6200 infrared gas analyzer (IRGA) (Li-Cor, Lincoln, Neb.). The IRGA chamber consisted of a clear acrylic tube 125 cm in length by 15 cm in diameter, sealed at both ends. Two small internal fans were installed to ensure uniform CO_2 concentration inside the chamber. A plastic sampling tube was connected to the IRGA, and spiraled the entire length of the chamber along the interior wall, ensuring that a representative air sample was obtained. The CO_2 concentration inside the chamber was scrubbed down to about 50 µmol mol^{-1} below ambient, and R_{CWD} was measured as the CO_2 concentration rose back through ambient. The IRGA configuration used was: total system volume 22,000 cm^3, flow rate 1,100 cm^3 s^{-1}, one measurement every 30 s, five measurements in total. Ambient temperature, CO_2 concentration, and relative humidity were recorded at the time of each measurement. CWD samples were weighed (±0.1 g) at the completion of each R_{CWD} measurement, to calculate W_C of each CWD sample, and returned to the appropriate growth chamber. At the end of the

Table 1 Physical properties of the black spruce coarse woody debris (*CWD*) for the incubation study. (*N* sample size, SL_{CWD} specific CWD area, $\bar{x}$ mean)

Decay class	N	Diameter (cm)		Length (cm)		Dry mass (g)		Density (g cm^{-3})		SL_{CWD}(cm g^{-1})	
		$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
I	12	8.5	2.3	70.3	7.8	1,676	792	0.41	0.06	1.35	0.45
II	12	7.8	1.2	66.3	10.4	1,084	400	0.34	0.05	1.69	0.36
III	12	8.7	1.1	62.6	9.3	1,044	327	0.28	0.05	1.83	0.35

incubation experiment, each CWD sample was oven-dried at 70°C to a constant mass and weighed (±0.1 g). The sample length and diameters in two perpendicular directions at both ends were measured. We calculated the surface area, volume, density, and specific CWD area (SL_{CWD}, defined as the CWD surface area to mass ratio) by assuming each sample was a cylinder (Table 1).

Statistical models relating R_{CWD} to T_{CWD}, W_{C}, and SL_{CWD} were developed using SAS software version 8.2 (SAS 2001). The mixed effect procedure (PROC MIXED) was used for the repeated measure analysis, assigning SL_{CWD}, T_{CWD}, W_{C}, and all possible interactions as fixed effects. CWD samples within each T_{CWD} and W_{C} combination were treated as a random effect, and used to test for autocorrelation between measurements. A spatial power covariance matrix was chosen for autocorrelation based on SBC (Schwarz's Bayesian Criterion). Natural logarithm transformation of R_{CWD} was used to achieve homoscedasticity. A backward elimination procedure was performed to remove insignificant terms (α=0.05) in the models. An analysis of covariance (ANCOVA) was conducted to test the effect of decay class on R_{CWD} by setting T_{CWD} and W_{C} as covariates.

The Q_{10} was calculated as

$$Q_{10} = (R_{\mathrm{CWD2}}/R_{\mathrm{CWD1}})^{[10/(T_2-T_1)]} \tag{1}$$

where R_{CWD1} and R_{CWD2} were the R_{CWD} at temperatures T_1 and T_2. To explore the relationships among Q_{10}, T_{CWD}, and W_{C}, we arbitrarily binned W_{C} to the nearest 10%. We calculated Q_{10} within temperature ranges of 5–20, 20–32, and 32–42°C, and each W_{C} level. The Q_{10} values for the temperature ranges of 20–32 and 32–42°C were statistically combined (df=49, t=–1.21, P=0.234). Analysis of variance (ANOVA) was conducted to test the effects of decay class, T_{CWD}, and W_{C} on Q_{10}.

In situ T_{CWD}

The T_{CWD} was measured continuously in the field at the four stands using type T (copper-constantine) thermocouples connected to Campbell Scientific CR 10X dataloggers (Campbell Scientific, Logan, Utah, USA). Six CWD samples (>5 cm in middle length diameter), two for each decay class, were randomly selected at each stand. Thermocouples were installed in a 2-cm-deep hole in the top of each CWD sample, and the hole was sealed with silicon adhesive. At the 12-year-old stand, we examined the heterogeneity of T_{CWD} within CWD. Thermocouples were installed in the top and bottom of four CWD samples in each decay class. T_{A} at each site was measured at a nearby (<20 m) meteorological station (Gower et al. 2002). Temperatures were measured every minute, and averaged for each half-hour period, from late May through early October 2001.

We examined T_{CWD} diurnal patterns based on the half-hour interval measurements at the four stands. A paired t-test was used to test the differences in T_{CWD} temporal patterns among stands and decay classes. The seasonal differences among stands, decay classes, and heterogeneous positions were tested on daily, weekly, and monthly time steps, respectively. A PROC MIXED procedure was used to develop empirical models of T_{CWD} against T_{A} on a daily time step. A first order autoregressive model was required (z=–5.97, P<0.001) for autocorrelation in time series temperature measurements.

Potential errors in modeling annual R_{CWD}

The laboratory empirical R_{CWD} model was compared to the field measurements of R_{CWD}, T_{CWD}, W_{C}, and CWD physical properties (Bond-Lamberty et al. 2002a). We did not measure W_{C} in situ, but, for comparison, employed the W_{C} models at the same sites by Bond-Lamberty et al. (2002a), i.e. W_{C}=4.6244–0.3083 T+0.0054 T^2, W_{C}=13.119–0.8816 T+0.0155 T^2, and W_{C}=29.062–1.9911 T+0.0349 T^2 for CWD decay I, II, and III, respectively; where T was the week of year.

We focused on two sources of error in annual R_{CWD} estimates: (1) ignoring T_{CWD} hysteresis to T_{A}; and (2) using various T_{CWD} modeling time steps. The R_{CWD} was calculated from the R_{CWD} model driven by W_{C} and T_{CWD} or T_{A}. The R_{CWD} estimates from T_{CWD} and T_{A} were denoted as R_{TCWDijk} and R_{TAijk}, where i=1, 2, 3 for decay classes; j=1, 2, 3, 4 for stands; and k=8,760, 365, 52, and 12 for hours, days, weeks, and months per year, respectively. The sources of error were evaluated as follows:

Error in annual R_{CWD} estimates caused by ignoring T_{CWD} hysteresis to T_{A} at j stand (E_{Hj}) was calculated as:

$$E_{\mathrm{Hj}} = \{\sum_{i=1}^{3}[(\sum_{k=1}^{8,760} R_{\mathrm{TCWDijk}} - \sum_{k=1}^{8,760} R_{\mathrm{TAijk}})/ \sum_{k=1}^{8,760} R_{\mathrm{TCWDijk}}]\}/3 \tag{2}$$

Errors in annual R_{CWD} due to different modeling time steps were calculated as: (1) hourly versus daily: R_{Th}–R_{Td} /R_{Th}, (2) hourly versus weekly: R_{Th}–R_{Tw} / R_{Th}, (3) hourly versus monthly: R_{Th}–R_{Tm} / R_{Th}; where R_{Th}, R_{Td}, R_{Tw}, *and* R_{Tm} were annual R_{CWD} means of the three decay classes in the four stands estimated on hourly, daily, weekly, and monthly time steps, respectively.

Results and discussion

Environmental and substrate controls on R_{CWD} in boreal forests

The R_{CWD} was positively correlated to T_{CWD} (n=636, R^2=0.37, P<0.001) and W_{C} (R^2=0.18, P<0.001) (Fig. 1). A polynomial model that included T_{CWD} and W_{C} interactions explained 74% (P<0.001) of the observed variation in R_{CWD} in the laboratory (Table 2).

CWD decay class significantly affected R_{CWD} (df=3, 615, F=271.3, P<0.001). The pairwise comparisons indicated that the R_{CWD} for decay I was significantly less than that for decay II (df=615, t=–3.70, P<0.001) and decay III (t=–3.64, P<0.001), and the R_{CWD} for decay II and III did not differ (t=–0.41, P=0.685). However, the relationship between R_{CWD} and W_{C} did not differ significantly (P=0.179 for the intercepts and P=0.389 for the slopes) among the decay classes (Fig. 1b). $\mathrm{SL_{CWD}}$ was 1.83, 1.69, and 1.35 cm^2g^{-1} for decay class I, II, and III, respectively. The $\mathrm{SL_{CWD}}$ for decay I was significantly less than for decay II (P=0.037) and III (P=0.004) (Fig. 2a). The R_{CWD} increased with increasing $\mathrm{SL_{CWD}}$ (Fig. 2b).

Temperature and $W_{\mathrm{C}}$are two major environmental factors that influence microbial activity and decomposition rates of organic matter (Boddy 1983a; Chen et al. 2000; Flanagan and Veum 1974; Moore 1986; O'Connell 1990; Wang et al. 2002). Temperature is commonly the more important environmental factor influencing R_{CWD}, but W_{C} strongly interacted with T_{CWD} on R_{CWD} across a broad W_{C} gradient (from 10 to 190%) (Table 2, Fig. 1b). The R_{CWD} variability increased with either T_{CWD} or W_{C} until a certain level, and then tended to decline (Fig. 1), which suggested that either temperature or W_{C} could become the dominant environmental control on R_{CWD} in extreme conditions. This result is corroborated by previous studies (Boddy 1983a; Bond-Lamberty et al. 2002a;

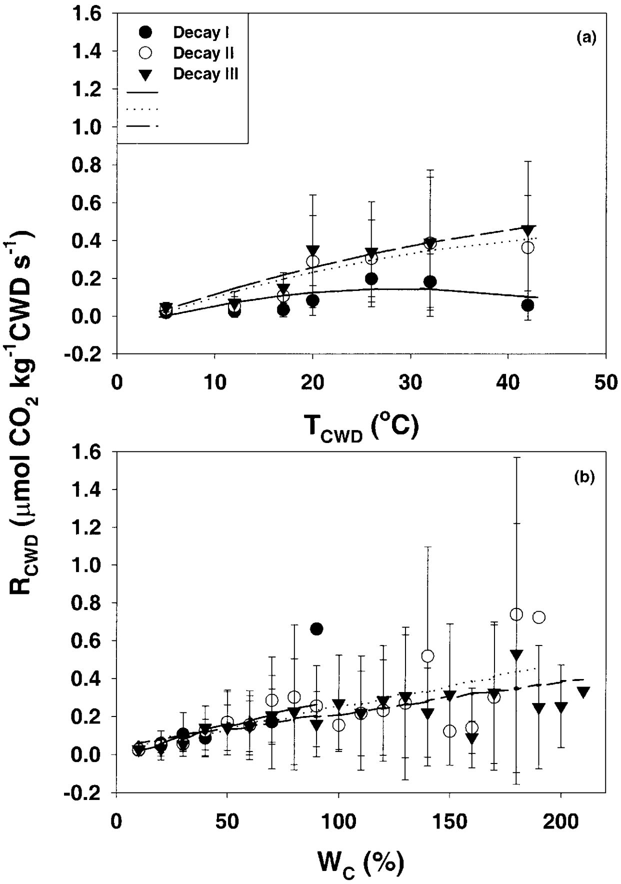

Fig. 1 Relationships between coarse woody debris (CWD) CO_2 flux (R_{CWD}, µmol CO_2 kg^{-1}CWD s^{-1}) and (**a**) temperature (T_{CWD}, °C), and (**b**) water content (W_C, %). The *bars* are standard deviations (n=2–88)

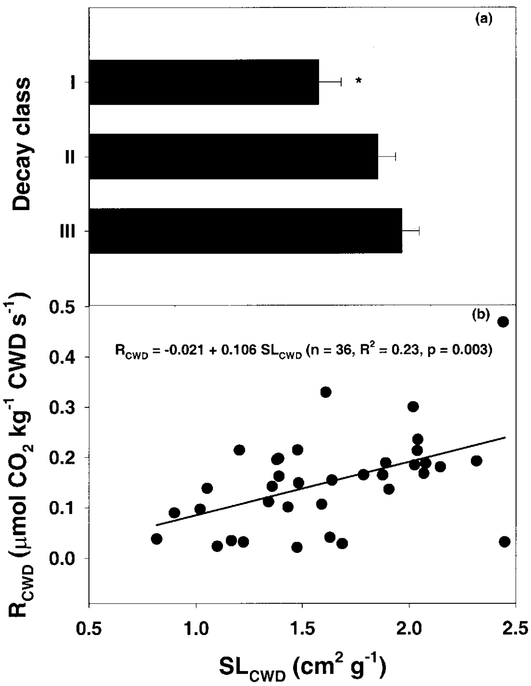

Fig. 2 (**a**) Specific CWD area (SL_{CWD}, cm^2 g^{-1}) by decay class. An *asterisk* denotes significant difference (α=0.05). *Error bars* are standard deviations (n=12). (**b**) Relationship between CWD CO_2 flux (R_{CWD}, µmol CO_2 kg^{-1}CWD s^{-1}) and SL_{CWD}

Table 2 Model relating CO_2 flux (R_{CWD}, µmol CO_2 kg^{-1} CWD s^{-1}) to temperature (T_{CWD},°C), water content (W_C), and specific CWD area (SL_{CWD}, cm^2 g^{-1}) for black spruce CWD. The model form is: $\ln(R_{CWD})$=a SL_{CWD} + b SL_{CWD} T_{CWD} + c T_{CWD}^2 + d W_C + e T_{CWD} W_C (n=636, R^2=0.73)

Coefficient	Estimate	SE	t-ratio	P
a	–3.272	0.117	–28.07	<0.001
b	0.097	0.008	12.54	<0.001
c	–0.003	0.000	–12.29	<0.001
d	1.214	0.198	6.13	<0.001
e	0.036	0.009	4.03	<0.001

Harmon et al. 1986; Käärik 1974; Progar et al. 2000; Rayner and Boddy 1988; Yoneda 1980).

SL_{CWD} was a good indicator of CWD decay status, and hence R_{CWD} (Fig. 2b). SL_{CWD} increased as decomposition proceeded because of carbon losses through CO_2 fluxes and dissolved organic carbon (Yavitt and Fahey 1985), and increased fragmentation (Harmon et al. 1986) (Fig. 2a). Increased specific area increased water holding capacity and water potential because of greater internal surface and pore space (Boddy 1983b; Bond-Lamberty et al. 2002a; Chambers et al. 2001; Harmon and Sexton 1995). We speculate that the lower water holding capacity of decay class I CWD may restrict the R_{CWD}, especially when T_{CWD} and W_C are high (Fig. 1a).

R_{CWD} model

A polynomial model including SL_{CWD}, T_{CWD}, W_C, and their interactions provided a good fit for the laboratory R_{CWD} measurements (n=636, R^2=0.73) (Table 2). The Q_{10} for R_{CWD} averaged 2.5±1.6 across the environmental conditions and decay classes examined in this study. Q_{10} was significantly affected by temperature range (df=1, 36, F=57.2, P<0.001) and averaged 4.1 for 5–20°C and 1.7 for 20–42°C. CWD decay class (df=2, 36, F=1.5, P=0.249) and W_C gradient (df=16, 36, F=0.8, P=0.729) did not significantly affect Q_{10} (Fig. 3).

Carbon dioxide flux from organic matter is commonly modeled using a simplified Q_{10} function (Lloyd and Taylor 1994) or using an environment-driven model (Raich and Schlesinger 1992). The Q_{10} model oversimplifies the respiration process by assuming a constant response of respiration rate to temperature within a certain temperature range, and thus is easy for general application. However, a single Q_{10} is not appropriate to quantify R_{CWD} because Q_{10} changes with temperature (Fig. 3). Such a Q_{10} temperature dependence has also been reported for soil surface CO_2 flux (Nadelhoffer et al. 1991; Rayment and Jarvis 2000; Stromgren 2001; Wang et al. 2002) and decaying root respiration (Chen et al. 2000). It is important

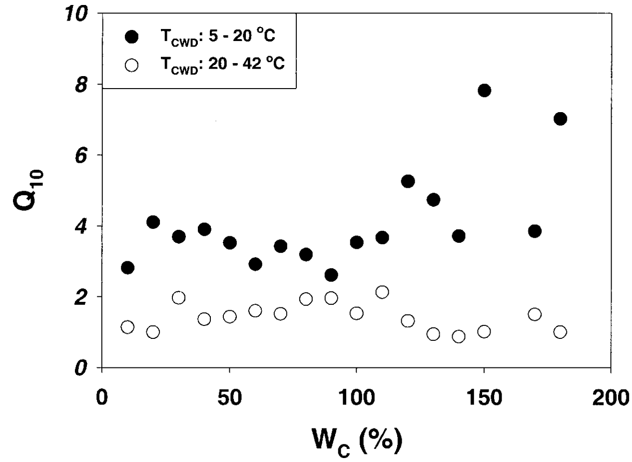

Fig. 3 Temperature coefficient (Q_{10}) dynamics along water content (W_C, %) gradient for two temperature (T_{CWD}, °C) ranges

to notice that using variable Q_{10} values for various temperature ranges also failed to characterize the significant effect of CWD decay status on R_{CWD} (Table 2) and introduced appreciable errors in annual R_{CWD} estimates (discussed below).

Accurately modeling R_{CWD} requires a process-based understanding of the factors that influence CWD decomposition, and continuous data for each variable. In tropical regions, where temperature is favorable for microbial activity year-round, substrate W_C is the major environmental factor influencing R_{CWD} (Chambers et al. 2001). In boreal forests, temperature restricts R_{CWD} in winter, and the limiting effect of W_C on R_{CWD} increases with increasing temperature in the growing season (Bond-Lamberty et al. 2002a). These data suggest that a comprehensive model should be used to simulate R_{CWD} in boreal forest ecosystems, a finding corroborated by decomposition studies in various ecosystems (Boddy 1983b; Chen et al. 2000; Flanagan and Veum 1974; Marra and Edmonds 1994; O'Connell 1990). The incubation study also demonstrated the importance of quantifying the interactive effect of CWD decay status, temperature, and W_C on R_{CWD}.

Standing woody debris decomposes extremely slowly (Harmon et al. 1986; Bond-Lamberty et al. 2002a), but decomposition accelerates once the woody debris falls and establishes contact with forest floor. The CWD samples in the incubation experiment were not in contact with the soil, although they were in full contact with the ground before being collected. This might restrict the inference of our laboratory study to field application. However, validation of the R_{CWD} model with field data showed that the difference between the model predictions and measurements of R_{CWD} averaged ±2% for decay I and II, and 18% for decay III CWD. The greater error for decay III may be attributed to the fragmentation effect on R_{CWD} (Harmon et al. 1986). The different decomposition rates are probably attributed to greater microbial colonization and water content of downed than standing CWD.

We compared annual R_{CWD} estimates between the environment-driven models (this study) and a Q_{10} model (Bond-Lamberty et al. 2002a). The annual R_{CWD} using the former approach was over two-fold greater than using the later approach. We speculate that the differences were due to effects of T_{CWD} hysteresis, different modeling time steps, and, more importantly, the R_{CWD} models used. The annual R_{CWD} by Bond-Lamberty et al. (2002a) was estimated from separate Q_{10} and W_C models, but the revised estimates were from a model that included the interactions between SLCWD, T_{CWD}, and W_C, all of which contributed significantly the R_{CWD} models (Table 2). We conclude that CWD decay status in various environmental conditions must be considered when estimating R_{CWD}.

Modeling R_{CWD}: temporal-spatial considerations

In the field, T_{CWD} was positively correlated to T_A (n=2,424, R^2=0.79, P<0.001), but the relationship significantly differed among stands (df=3, 2,070, F=13.1, P<0.001) and CWD decay classes (df=2, 2,070, F=4.2, P=0.015). The slope of the relationship between T_{CWD} and T_A increased from old to young stands, except for decay class III at the 20-year-old stand; the slope was less for decay class III than decay class I and II except, for the 37-year-old stand (Table 3). The T_{CWD} at old stands with closed canopies responded to T_A changes

Table 3 Models relating CWD temperature (T_{CWD},°C) to air temperature (T_A,°C) for the black spruce fire chronosequence. The model form is: T_{CWD}=a + b T_A. The models are based on daily mean values of T_{CWD} and T_A

Stand age (years)	Coefficient	Decay I					Decay II					Decay III				
		Estimate	SE	*df*	*t*-ratio	*P*	Estimate	SE	*df*	*t*-ratio	*P*	Estimate	SE	*df*	*t*-ratio	*P*
12	a	2.672	0.35	2,387	7.62	<0.001	2.310	0.35	2,352	6.55	<0.001	2.773	0.35	2,385	7.90	<0.001
	b	0.846	0.02	2,386	37.35	<0.001	0.850	0.02	2,352	37.29	<0.001	0.794	0.02	2,383	35.00	<0.001
20	a	3.505	0.53	2,360	6.57	<0.001	3.323	0.53	2,379	6.21	<0.001	4.665	0.53	2,360	8.74	<0.001
	b	0.805	0.03	2,356	23.89	<0.001	0.811	0.03	2,374	24.02	<0.001	0.596	0.03	2,356	17.68	<0.001
37	a	4.068	1.55	2,017	2.63	0.009	3.495	1.55	1,998	2.26	0.024	3.918	1.55	1,998	2.54	0.011
	b	0.608	0.10	1,954	5.98	<0.001	0.720	0.10	1,933	7.09	<0.001	0.622	0.10	1,933	6.13	<0.001
131	a	5.860	0.98	1,514	6.00	<0.001	5.484	0.98	1,548	5.60	<0.001	5.958	0.98	1,514	6.10	<0.001
	b	0.443	0.07	1,437	6.50	<0.001	0.389	0.07	1,466	5.69	<0.001	0.381	0.07	1,437	5.59	<0.001

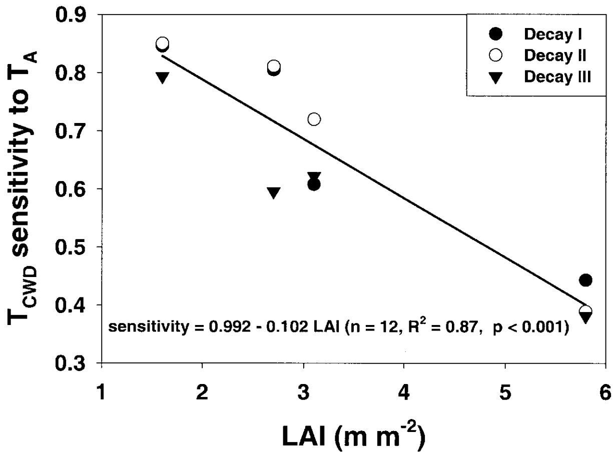

Fig. 4 Relationship between CWD temperature sensitivity to air temperature (regression slope between T_{CWD} and T_A in Table 3) and stand leaf area index (*LAI*) (adapted from Bond-Lamberty et al. 2002b) in the chronosequence

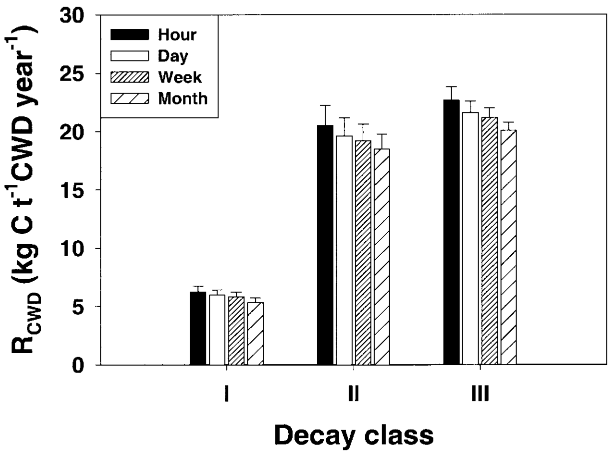

Fig. 6 Modeled CWD CO_2 flux (R_{CWD}, kg C t^{-1} CWD year^{-1}) at hourly, daily, weekly, and monthly time steps for the three decay classes. *Error bars* are standard errors (*n*=4)

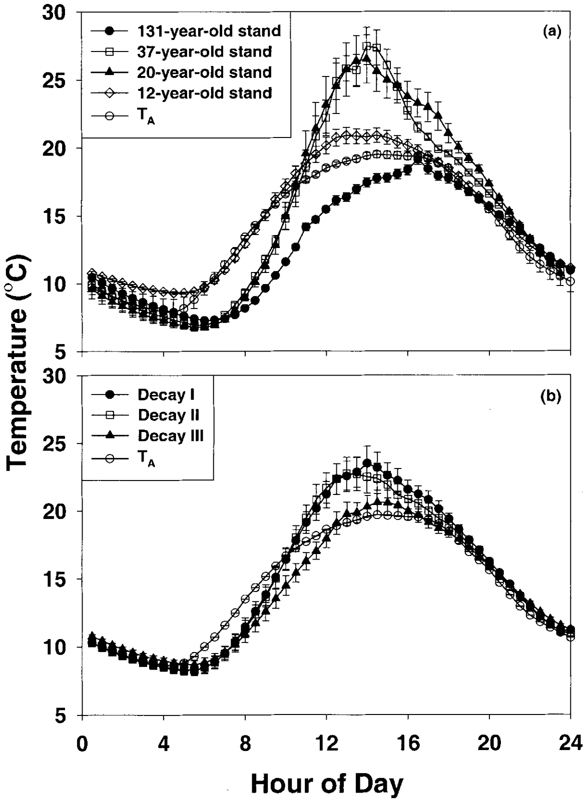

Fig. 5 Diurnal patterns of CWD temperature (T_{CWD}, °C) during the growing season by **a** stands, and **b** decay classes. *Error bars* are the standard deviations (*n*=3 or 4). T_A is air temperature

more slowly than at young stands with open canopies, because the greater leaf area index (LAI) influenced the energy balance near the soil surface (Fig. 4). These results indicated that the T_{CWD} for decay class III at the older stand with the greatest LAI experienced the greatest hysteresis to T_A.

There was no significant difference between diurnal T_{CWD} at the 12-year-old stand and T_A (*df*=1, 46, *F*=1.15, *P*=0.289). The T_{CWD} amplitude was greater than T_A from late morning to early evening in the other stands, except for the oldest stand, where the T_{CWD} was significantly lower during daytime (Fig. 5a). The diurnal T_{CWD} of decay class III followed that of T_A (*df*=1, 46, *F*=3.3, *P*=0.075), but the T_{CWD} for decay class I (*df*=1, 46, *F*=115.6, *P*<0.001) and II (*df*=1, 46, *F*=84.8, *P*<0.001) were significantly higher than T_A during the daytime (Fig. 5b).

Stand (*df*=3, 738, *F*=11.9, *P*<0.001) and decay class (*df*=2, 738, *F*=3.1, *P*=0.045) significantly affected weekly-based seasonal dynamics in T_{CWD}. The mean T_{CWD} during the growing season (from 1 June to 30 September 2001) were 15.0, 14.4, 13.6, and 12.1°C for 20-, 12-, 37-, and 131-year-old stands, respectively. The seasonal average T_{CWD} was lower than T_A in all the stands except the 20-year-old stand where T_{CWD} and T_A were similar (*df*=1, 15, *F*=0.9, *P*=0.351). Mean T_{CWD} in the growing season decreased as CWD became more decomposed. There was no significant difference in T_{CWD} diurnal (*df*=1, 1163, *F*=1.0, *P*=0.309) or seasonal (*df*=1, 443, *F*=0.7, *P*=0.406) patterns within a specific CWD sample.

Modeling long-term CWD decomposition is challenging (Stone et al. 1998), because biophysical and chemical properties of CWD change as decomposition proceeds in forest ecosystems. Examples of such properties include CWD fragmentation, substrate heterogeneity (Harmon et al. 1986; Rayner and Boddy 1988; Schowalter 1992), density, surface area, charred CWD in fire-prone ecosystems, and nutrient losses (Yavitt and Fahey 1985). For simplicity, we restricted our study to examining the effects of temperature, W_C, and decay class on R_{CWD}. The empirical models developed in this study may not provide accurate estimates of R_{CWD} if other abiotic or biotic variables are more limiting to microbial activity.

Temperature is a major environmental factor influencing R_{CWD}. Spatial dynamics of T_{CWD} at various decomposition stages under different canopy conditions must be considered in estimating annual R_{CWD}. T_{CWD} generally follows T_A (Boddy 1983b), but substrates with such a high thermal capacity as CWD exhibit hysteresis (Campbell and Norman 1998). Ignoring T_{CWD} hysteresis in different stands can introduce large errors in annual R_{CWD} estimates. If T_A, instead of T_{CWD}, was used in the R_{CWD} models with an hourly time step, the annual R_{CWD} for the 12-, 20-, 37-, and 131-year-old stands varied by –2, –1, +14, and +32%, respectively. These differences were –4, –5, +9, and +20% when a weekly time step was used.

Modeled annual R_{CWD} across the chronosequence on daily, weekly, and monthly time steps averaged 5%, 7%, and 11%, respectively, less than that on an hourly time step (Fig. 6). The use of large time steps in R_{CWD} models underestimates annual R_{CWD} because of the nonlinear relationship among R_{CWD}, T_{CWD}, and W_C (Table 2). Nonlinear relationships between temperature, autotrophic and heterotrophic respiration have been widely reported (Kozlowski and Pallardy 1997; Landsberg and Gower 1997; Raich and Schlesinger 1992). Thus, the respiration nonlinearity feature should be taken into account in all CO_2 flux modeling.

In conclusion, CO_2 flux from CWD was an important CO_2 input to the atmosphere in the fire-prone boreal forest that we studied. The importance of CO_2 flux from CWD in most forest ecosystems is unknown because of the paucity of CWD CO_2 flux data; however, R_{CWD} should not be ignored in any forest ecosystem that contains large amount of CWD. Annual estimates of CWD CO_2 flux can be improved if the spatial-temporal dynamics in decay status, temperature, and W_C are included in R_{CWD} models.

Acknowledgements This research was supported by grants from the National Science Foundation (DEB-0077881) and NASA (NAG5–8069) to S.T. Gower Wang was supported by a 2001 Vilas Travel Fellowship at University of Wisconsin–Madison. We are grateful for the assistance of Yunrong Sang with the CWD CO_2 flux measurements, and thank Dr. H. Chen and one anonymous reviewer for their valuable comments.

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