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Coarse woody debris and the carbon balance of a north temperate forest

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Abstract

Comprehensive estimates of forest carbon (C) mass and respiration require measurements of all C pools, including coarse woody debris (CWD). We used inventory and chamber-based methods to quantify C mass and the annual respiratory C loss from CWD and other major ecosystem components for a deciduous forest in the upper Great Lakes region. Coarse woody debris mass (M_{CWD}, 2.2 Mg C ha^{-1}) was less than that of soils (104.1 Mg C ha^{-1}) and boles (71.7 Mg C ha^{-1}), but similar to that of leaves (1.8 Mg C ha^{-1}). Coarse woody debris respiration (R_{CWD}) increased with temperature and water content, with differences in R_{CWD} among decay classes due to variation in water content rather than to variable sensitivity to environmental conditions. Sensitivity of R_{CWD} to changing temperature, evaluated as Q_{10}, ranged from 2.20 to 2.57 and was variable among decay classes. Annual CWD respiration (F_{CWD}, 0.21 Mg C ha^{-1} year^{-1}) was 12% of bole respiration, 8% of leaf respiration, and 2% of soil respiration. The CWD decomposition rate-constant ($F_{\mathrm{CWD}}/M_{\mathrm{CWD}}$) in 2004 was 0.09 year^{-1}. When compared to the average annual ecosystem C storage of 1.53 Mg C ha^{-1} year^{-1}, F_{CWD} represents a small, but substantial flux that is expected to increase over the next several decades in this maturing forest.

Keywords: Coarse woody debris; Net ecosystem production; Net primary production; Carbon cycling; Carbon storage; Respiration; Aspen; Decomposition

1. Introduction

Comprehensive estimates of ecosystem C storage require full accounting of all C pools. However, CWD is often overlooked in forest C inventories, potentially resulting in an underestimation of ecosystem C storage by as much as 25% (Clark et al., 2001). In temperate North American forests CWD may comprise up to 12% of ecosystem C mass, but CWD quantities vary considerably across the continent (Turner et al., 1995; Bhatti et al., 2002). In some forests, tree mortality and corresponding increases in CWD determine whether an ecosystem is a C source or sink to the atmosphere (Sturtevant et al., 1997; Carmona et al., 2002; Janisch and Harmon, 2002).

The mass of CWD stored in forests varies due to succession and disturbance events such as senescence, wind, fire, disease, and insect infestation (Harmon et al., 1986; Chambers, 1998; Clark et al., 2001). The irregular distribution and frequency of these disturbances, together with the mosaic of forest succession across the landscape, contribute to high variability in CWD distribution within and across ecosystems (Harmon et al., 1986; Muller and Yan, 1991; Clark et al., 2001). Muller and Yan (1991) estimated CWD mass from 22 to 49 Mg ha^{-1} in North American temperate deciduous forests, depending on stand age and productivity. In a black spruce (*Picea mariana* P. Mill.) dominated boreal forest in northern Canada, CWD mass varied by over two orders of magnitude, from 1.4 to 177.6 Mg ha^{-1}, with higher values in stands recently disturbed by fire (Bond-Lamberty et al., 2003). Very high CWD pools of 500 Mg ha^{-1} are reported for senescing old-growth forests in the western Olympic Mountains (Agee and Huff, 1987).

The contribution of CWD respiration (R_{CWD}) to ecosystem respiration (R_{E}) has been rarely quantified despite these large stores of CWD in some forests. Hence, limited data are

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available for R_{CWD} in most forest types (Krankina and Harmon, 1995; Wang et al., 2002; Manies et al., 2005). In particular, analyses of CWD respiration in temperate deciduous forests are lacking. A few studies of R_{CWD} have been conducted in boreal forests (Krankina and Harmon, 1995; Harden et al., 2000; Wang et al., 2002; Bond-Lamberty et al., 2003), temperate coniferous forests (Marra and Edmonds, 1994), and tropical forests (Chambers et al., 2001). In boreal forests, R_{CWD} represented 50% of the C flux from the soil surface (Wang et al., 2002; Bond-Lamberty et al., 2003). Similarly, R_{CWD} was a large flux in central Amazonian forests, comparable in magnitude to fine litter respiration (Chambers et al., 2001). Physiologically based estimates of total ecosystem respiration (R_{E}) frequently do not incorporate R_{CWD} (e.g., Bolstad et al., 2004; Curtis et al., 2005), although in some forests R_{CWD} constitutes >30% of R_{E} (Knohl et al., 2002; Bond-Lamberty et al., 2003). Because the rate of annual forest C storage, or net ecosystem production (NEP), is the small difference between photosynthetic C uptake and respiratory C losses, incomplete accounting of R_{E} components could inflate NEP estimates (Ryan et al., 1996).

The importance of CWD to terrestrial C storage in the upper Great Lakes region likely is increasing, as 70% of the area's secondary deciduous forests approach or are past maturity (USDA, 2001). In this study, our objective was to quantify CWD mass and respiration in a typical secondary successional mixed-deciduous forest in northern lower Michigan and to compare the mass and annual respiratory C flux of CWD with that of leaves, boles, and soils. Our analysis provides one of the few comprehensive comparisons of C pools and fluxes for a temperate deciduous forest. This study is part of the University of Michigan Biological Station (UMBS) Forest Carbon Cycle Research Program and it operates within the AmeriFlux network of long-term carbon cycle research sites (Baldocchi et al., 2001).

2. Materials and methods

2.1. Study site

Our study site is located at the University of Michigan Biological Station in northern lower Michigan, USA (45°35.5′N, 84°43′W), in the transition zone between the northern hardwood and boreal forests. The area is a gently sloping outwash plain at an elevation of 324 m with well-drained spodosols (92% sand, 7% silt, 1% clay, pH 4.8). The mean annual (1942–2003) temperature is 5.5 °C and the mean annual precipitation is 817 mm.

The study forest surrounds a 46 m high meteorological tower, which continuously measures net ecosystem CO_2 exchange between forest and atmosphere. Most of the secondary successional forest is comprised of bigtooth aspen (*Populus grandidentata* Michx.), northern red oak (*Quercus rubra* L.), sugar maple (*Acer saccharum* Marsh.), paper birch (*Betula papyrifera* Marsh.), and eastern white pine (*Pinus strobus* L.) (Gough et al., in press). The understory is dominated by bracken fern (*Pteridium aquilinum* L.). The forest was heavily logged in the late 1800s and disturbed by fire until 1923. Since then the area has been relatively free of major disturbances, but occasionally has experienced small patchy fires. Average overstory tree age is 85 years, but individual stands range in age from 30 to 90 years.

2.2. Coarse woody debris mass

We quantified the distribution of CWD mass in different decay classes across our site through inventories in twelve 0.1 ha plots during the summer of 2003. Plots were located along 1 km radial transects originating from the base of the meteorological tower. The degree of CWD decay was described using five classes (Marra and Edmonds, 1994): (1) recently downed material with tissue and bark intact throughout; (2) sapwood beginning to decay but completely present, bark beginning to crack; (3) sapwood and bark mostly present, heartwood tissue intact; (4) sapwood and bark mostly gone, heartwood beginning to decay; (5) sapwood and bark gone, heartwood with substantial decay. After assigning each sample to a decay class, we calculated the volume of all logs, snags, and stumps >10 cm diameter from measurements of length and the diameter of the base and top using the equation for the frustum of a cone (Harmon and Sexton, 1996). Partially or fully buried wood was not inventoried. These surveys showed that bigtooth aspen accounted for >95% of the CWD at our site. Hence, we restricted our analyses to this species.

We calculated CWD carbon mass (M_{CWD}, Mg C ha^{-1}) for each decay class from estimates of CWD volume, and from measurements of wood density and C content. Subsamples of wood were cut from the two distal ends and midpoint of two pieces of CWD per decay class. This was judged an adequate sample size because percent C did not differ among decay classes. Wood density was calculated from dry mass and volume estimated via water displacement, and the C content of dried CWD was determined using an elemental analyzer (Perkin-Elmer 2400, Perkin-Elmer Inc, Wellesley, MA, USA). Coarse woody debris C mass was calculated for each decay class as the product of CWD volume, decay class density, and decay class C content. Standard errors of M_{CWD} were calculated from the inter-plot variance ($n = 12$).

2.3. Coarse woody debris respiration: experimental design

Coarse woody debris respiration (R_{CWD}, μmol kg^{-1} s^{-1}) of the five decay classes was measured following laboratory and field incubations. Three replicate CWD samples from each decay class were collected in June 2006 and cut into four 20 cm long subsamples. The distal ends of CWD were sealed using paraffin to reduce CO_2 emissions (by >80%) from the newly cut surface. For the laboratory experiment, three subsamples originating from the same log were assigned to one of three moisture applications and grouped into blocks containing all five decay classes. Low moisture treated CWD was air dried at room temperature for 1 week. Medium and high moisture treated CWD was sprayed with 50 and 400 mL of distilled water, respectively, and stored in aerated plastic containers overnight to allow run-off to be absorbed by the wood. Coarse woody debris respiration was measured by block, containing one full replicate of the five decay classes each at the three moisture levels, and in sequence following 24–48 h incubations at the following target temperatures: 25, 6, 10, 15, 20, 25 °C [±2 °C] ($n = 3$/decay class). Measurements were conducted twice at ~25 °C to test for hysteresis and the effect of time on R_{CWD}. Water content of CWD (Φ_{CWD}) was determined by weighing each sample between R_{CWD} measurements. Sample Φ_{CWD} varied by <10% over the course of the study. Laboratory R_{CWD} measurements were completed within 10 days. To obtain field R_{CWD}, remaining CWD subsamples were incubated on the forest floor and R_{CWD} was measured under ambient conditions 14 times over a 3-week period.

Laboratory and field CWD respiration was measured using a portable photosynthesis system (Model LI-6400, Li-Cor, Lincoln, NE, USA) and a custom respiration chamber with internal volume ~7.5 L (Model 153C CAV4, Rubbermaid Inc., Fairlawn, OH, USA). Air was mixed in the chamber with an internal fan and the air flowed in a closed loop to the infrared gas analyzer of the LI-6400. Sample temperature (T_{CWD}) was recorded using a type E thermocouple inserted through the container and into the CWD. For laboratory R_{CWD} measurements, the respiration chamber was placed inside an incubator to maintain target temperature. Measurement protocol followed the standard operating procedure for the LI-6400 when fitted with a soil respiration cuvette. Daytime ambient CO_2 concentration ~0.05 m above the forest floor (C_a) was measured and an average value of 380 ppm was set for all respiration measurements. Respiration chamber CO_2 concentration was lowered 5–25 ppm below C_a and then allowed to rise the same amount above C_a. Laboratory and field CWD was weighed immediately following each respiration measurement and CWD was dried in an oven after completion of the experiment to determine moisture content at the time of measurement.

2.4. Coarse woody debris respiration: modeling

We modeled the relationship between R_{CWD} measured in the laboratory and field, and T_{CWD} and Φ_{CWD} using a non-linear function:

$$\bar{R}_{\mathrm{CWD}} = a\,\mathrm{e}^{b\bar{T}_{\mathrm{CWD}}} + c\ln(\bar{\phi}_{\mathrm{CWD}}) \tag{1}$$

where a, b, and c are fitted coefficients (SAS v. 8.2, Cary, NC, USA), and $\bar{R}_{\mathrm{CWD}}$, $\bar{T}_{\mathrm{CWD}}$, and $\bar{\phi}_{\mathrm{CWD}}$ are the means ($n = 3$) of R_{CWD}, T_{CWD}, and Φ_{CWD}, respectively, for each decay class. The temperature coefficient, $Q_{10} = \mathrm{e}^{b10}$. Using Eq. (1), respiration at a reference temperature of 15 °C was estimated at $\bar{\phi}_{\mathrm{CWD}}$ (R_{CWD15}) and when normalized for a $\bar{\phi}_{\mathrm{CWD}}$ of 150% ($R_{\mathrm{CWD15},\Phi150}$), and its standard error calculated as $\mathrm{S.E.} = \sigma/\sqrt{n}$, where σ is the standard deviation of mean R_{CWD15} or $R_{\mathrm{CWD15},\Phi150}$ and n is 3, the number of R_{CWD15} or $R_{\mathrm{CWD15},\Phi150}$ observations.

2.5. Annual coarse woody debris flux

Instantaneous R_{CWD} measurements were scaled to a land surface area basis to estimate the annual CWD flux (F_{CWD}, Mg C ha^{-1} year^{-1}) following the methods of Ryan et al. (1997). During 2004, in situ T_{CWD} was measured continuously in two CWD samples from each decay class using type E thermocouples inserted to the center of each sample. To estimate continuous Φ_{CWD}, we first developed an equation that relates Φ_{CWD} to volumetric soil moisture in the top 5 cm (Φ_{soil}) and CWD density (ρ):

$$\begin{aligned}\Phi_{\mathrm{CWD}} &= -71.2 + 36.3(\Phi_{\mathrm{soil}}) + 163.3(\bar{\rho}) \\ &\quad - 63.6(\Phi_{\mathrm{soil}}\bar{\rho}); \quad p < 0.001, n \\ &= 25, r^2 = 0.67\end{aligned} \tag{2}$$

where $\bar{\rho}$ is the mean for each decay class. This predictive model was developed from field observations in which five ~1 m long samples of CWD from each of the five decay classes were placed in a 25 m^2 plot in the forest understory and Φ_{CWD}, Φ_{soil}, and ρ were measured concurrently nine times over 3 weeks. Samples were weighed in the field and then dried and weighed at the end of the study to calculate Φ_{CWD}. Measurements of Φ_{soil} were made directly below each CWD sample using a Hydrosense Soil Water Content Measurement System (Campbell Scientific, Inc., Logan, UT, USA). Half-hourly Φ_{CWD} for 2004 was estimated using Eq. (2) from the average of four continuous onsite measurements of Φ_{soil} (CS616 soil moisture probe, Campbell Scientific, Inc.) and from field inventory estimates of $\bar{\rho}$.

Half-hourly hourly R_{CWD} ($T_{\mathrm{CWD}} > 0$ °C) throughout the year was calculated from mean half-hourly T_{CWD} and Φ_{CWD} using the function:

$$R_{\mathrm{CWD}} = a\,\mathrm{e}^{bT_{\mathrm{CWD}}} + c\ln(\phi_{\mathrm{CWD}}) \tag{3}$$

R_{CWD} was assumed to be zero when $T_{\mathrm{CWD}} < 0$ °C. A single model for all decay classes was used (Table 1) because parameter coefficients for individual decay class models had overlapping 95% confidence intervals, indicating a common quantitative response of R_{CWD} to T_{CWD} and Φ_{CWD}. The standard error interval for R_{CWD} was calculated as

$$\begin{aligned}&R_{\mathrm{CWD}} \pm \mathrm{S.E.} \\ &\quad = (a \pm a_{\mathrm{S.E.}})\,\mathrm{e}^{(b \pm b_{\mathrm{S.E.}})T_{\mathrm{CWD}}} + (c \pm c_{\mathrm{S.E.}})\ln(\phi_{\mathrm{CWD}})\end{aligned} \tag{4}$$

where $a_{\mathrm{S.E.}}$, $b_{\mathrm{S.E.}}$, and $c_{\mathrm{S.E.}}$, are standard errors of parameter coefficients a, b, and c (Table 1). Annual CWD flux is the sum of hourly R_{CWD} across 1 year multiplied by decay class M_{CWD} (Table 2). The standard error interval for annual R_{CWD} was estimated as the sum of hourly ($R_{\mathrm{CWD}} \pm$ S.E.)M_{CWD}.

Table 1
Coarse woody debris respiration (R_{CWD}; μmol kg^{-1} s^{-1}) estimated from T_{CWD} (°C) and ϕ_{CWD} (%), where $R_{\mathrm{CWD}} = a\,\mathrm{e}^{bT_{\mathrm{CWD}}} + c\ln(\phi_{\mathrm{CWD}})$

Parameter	Coefficient	S.E.
a	−1.2773	0.1176
b	−0.0339	0.00592
c	0.2493	0.0209

$r^2 = 0.64$; $P < 0.0001$; S.E., standard error.

Table 2
Carbon mass distribution (M_{CWD}; $n = 12$), coarse woody debris density (ρ; $n = 12$), respiration normalized to 15 °C (R_{CWD15}; $n = 3$), respiration normalized to 15 °C and 150% CWD water content ($R_{\mathrm{CWD15},\Phi 150}$; $n = 3$); temperature response coefficients (Q_{10}; $n = 3$), and the annual C respiratory flux (F_{CWD}) for five decay classes

Decay class	M_{CWD} (g C m^{-2})	% M_{CWD}	ρ (g cm^{-3})	R_{CWD15} (μmol kg^{-1} s^{-1})	$R_{\mathrm{CWD15},\Phi 150}$ (μmol kg^{-1} s^{-1})	Q_{10}	F_{CWD} (g C m^{-2} $year^{-1}$)	% F_{CWD}
1	32 ab (24)	14.5	0.50 a (0.09)	0.14 (0.03) a	0.44 (0.05) a	2.20 (0.10) a	3.2 (0.7)	15
2	44 ab (28)	19.9	0.38 ab (0.06)	0.22 (0.07) ab	0.48 (0.19) a	2.46 (0.09) b	3.7 (0.9)	17
3	61 b (17)	27.6	0.31 bc (0.03)	0.13 (0.05) a	0.43 (0.06) a	2.57 (0.18) b	5.9 (1.3)	28
4	69 b (23)	31.2	0.29 bc (0.05)	0.45 (0.16) b	0.29 (0.14) a	2.37 (0.11) ab	6.9 (1.5)	32
5	15 a (4)	6.8	0.23 c (0.02)	0.36 (0.08) ab	0.46 (0.10) a	2.44 (0.12) ab	1.6 (0.3)	8
Total	221 (96)						21.3 (4.7)	

Standard errors are shown in parentheses and letters (a–c) indicate that values are significantly different ($\alpha = 0.10$).

2.6. Soil, bole, and leaf mass and fluxes

The C mass of soils, boles, and leaves at our site was measured for each of 5 years as described by Gough et al. (in press). They reported annual production for these pools, while here we provide new estimates of mean C mass. Briefly, aboveground wood mass was estimated from allometric equations relating bole diameter (D) to wood mass. Bole diameter was measured during the 2003 growing season on >700 trees ($D \geq 10$ cm). Leaf mass was calculated as the sum of understory and overstory litter mass collected in litter traps ($n = 26$). We estimated fine root mass (diameter ≤ 2 mm) from soil cores (1700 cm^3 $sample^{-1}$, $n = 30$) taken to a depth of 0.8 m. Fine roots were separated from soil using a 2 mm mesh sieve, and then washed, dried, weighed, and burned in a muffle furnace to determine ash-free mass. Coarse root (diameter >2 mm) mass was estimated from soil cores ($n = 90$) and allometric equations relating coarse root mass to aboveground wood mass. O-layer and the mineral soil were sampled using soil cores ($n = 30$). The percent C content of wood, fine roots, O-layer, and mineral soil was determined using an elemental analyzer (Perkin-Elmer 2400) and the C mass of each pool (M_i, Mg C ha^{-1}) was calculated by multiplying dry mass of each pool by its respective C percent. Soil C mass is the sum of coarse and fine root, O-layer, and mineral soil C mass. Standard errors of all C pools were estimated from inter-sample variances. We also compare estimates of F_{CWD} with the average annual respiratory flux of leaves, boles, and soil surface (F_i, Mg C ha^{-1} $year^{-1}$) for our site reported by Curtis et al. (2005).

2.7. Statistical analysis

The effect of decay class on M_{CWD} and ρ was tested using ANOVA followed by post hoc Tukey's tests to make comparisons between decay classes ($\alpha = 0.10$). The inverse of M_{CWD} was used in statistical analyses to correct a non-normal distribution. We used ANOVA followed by the LSD procedure to compare R_{CWD15}, $R_{\mathrm{CWD15},\Phi 150}$, and Q_{10} among decay classes, hypothesizing that respiration and sensitivity to temperature would increase with decay status of the wood ($\alpha = 0.10$). All analyses were performed using SAS statistical software (v. 8.2, Cary, NC, USA).

3. Results

3.1. Coarse woody debris mass and production

Coarse woody debris mass averaged 221 g C m^{-2} across our site, with M_{CWD} distributed unevenly among decay classes (Table 2). Moderately decomposed wood, classes 3 and 4, comprised 59% of total M_{CWD} while less decayed wood, classes 1 and 2, contributed 34% to ecosystem M_{CWD}. Highly decayed CWD, class 5, was only 7% of total M_{CWD}. The distribution of CWD across our site was more variable for lower decay classes. The among-plot coefficient of variation (CV) of M_{CWD} was highest for least decayed CWD, decay class 1 (CV = 75%).

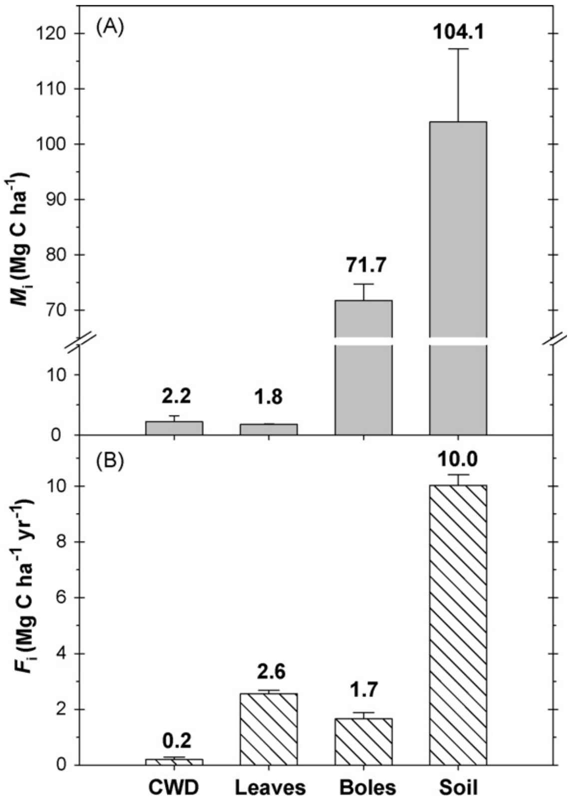

Fig. 1. Mass and annual respiratory flux of coarse woody debris (CWD) compared with other ecosystem components. Carbon mass (M_i) stored in each pool (A), and annual respiratory carbon flux (F_i) of CWD, leaves, boles, and soil (B). Vertical bars illustrate one standard error.

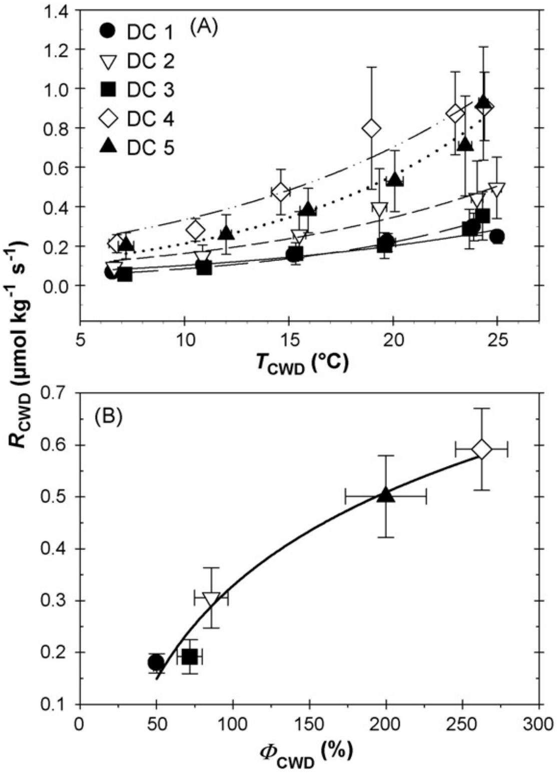

Fig. 2. The response of coarse woody debris (CWD) respiration (R_{CWD}) to CWD temperature (T_{CWD}) averaged across moisture treatments (A), and to CWD water content (Φ_{CWD}) averaged across moisture and temperature treatments (B). Vertical and horizontal bars illustrate one standard error.

Moderately to highly decayed wood, classes 3–5, was distributed more evenly (CV < 35%).

Coarse woody debris was a small fraction of ecosystem C mass, comprising 1% of stored C (Fig. 1A). This contribution was similar to that of leaves, while C storage in boles and soils was 40% and 58%, respectively, of the 179.8 Mg C ha^{-1} stored in our forest.

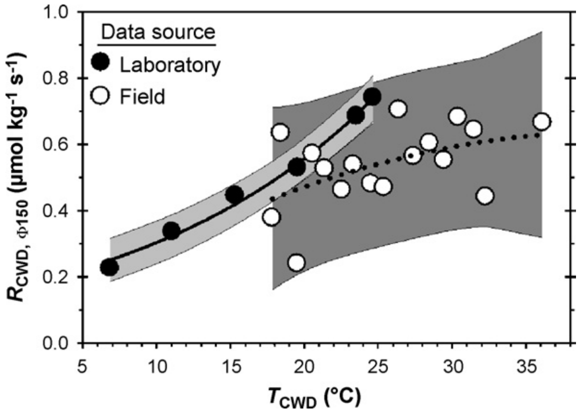

Fig. 3. The response of laboratory and field coarse woody debris respiration normalized for (150%) water content ($R_{\mathrm{CWD},\Phi 150}$) to coarse woody debris temperature (T_{CWD}). R_{CWD} was averaged across decay classes because differences among decay classes are not significant when normalized for water content. Data from field observations were pooled into 1 °C intervals. Grey shaded areas illustrate 95% confidence intervals.

3.2. Coarse woody debris respiration

Laboratory R_{CWD} increased in response to rising T_{CWD} and Φ_{CWD}, with differences in R_{CWD} among decay classes due to variation in Φ_{CWD} (Fig. 2). Measurements of R_{CWD} were positively correlated with T_{CWD} in all decay classes, but the magnitude of the temperature response was not uniform among decay classes (Fig. 2A). Temperature normalized respiration rates (R_{CWD15}) generally increased with decay class (Table 2). However, elevated R_{CWD} in more decayed wood was due to higher Φ_{CWD} rather than to greater sensitivity to T_{CWD} as indicated by Q_{10} (Fig. 2B). Water absorption and, consequently, Φ_{CWD} was greater by less dense wood, decay classes 4 and 5, than by denser decay classes. Respiration did not differ among decay classes when normalized for water content (Table 2). The sensitivity of R_{CWD} to changes in T_{CWD}, or Q_{10}, was variable across decay classes, ranging from 2.20 to 2.57 (Table 2).

We compared laboratory and field R_{CWD} normalized for water content ($\Phi_{\mathrm{CWD}} = 150$) to determine if laboratory

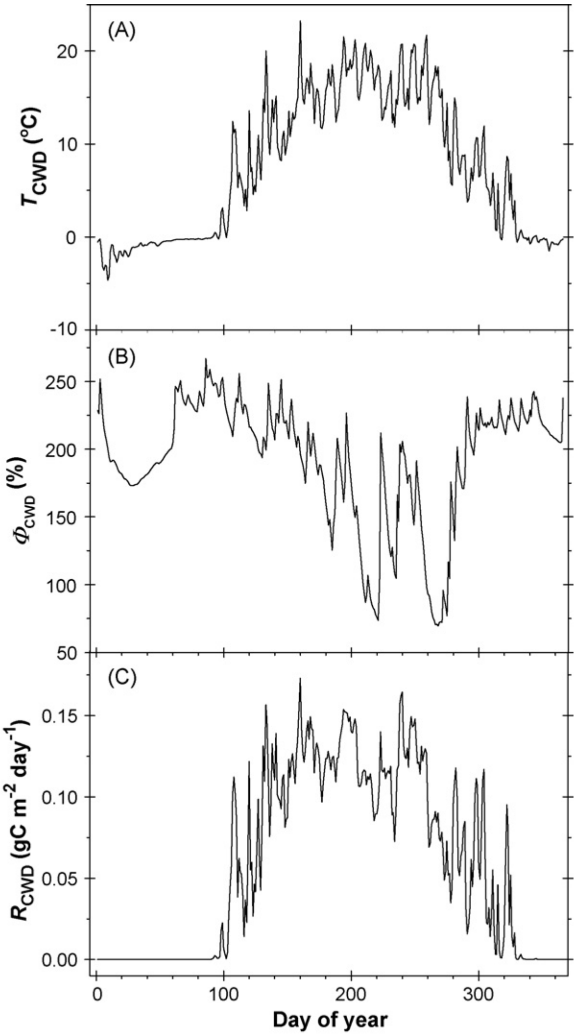

Fig. 4. Mean daily coarse woody debris (CWD) temperatures (T_{CWD}) averaged over five decay classes of wood ($n = 10$) (A), modeled mean daily CWD water content (Φ_{CWD}) averaged over five decay classes ($n = 25$) (B), and modeled daily CWD respiration (R_{CWD}) (C) in 2004.

incubations affected the response of R_{CWD} to T_{CWD}. Laboratory and field R_{CWD} were not significantly different, with the two methods of incubation displaying overlapping 95% confidence intervals at common temperatures (Fig. 3). However, field R_{CWD} had a more variable and attenuated response to T_{CWD} than did laboratory R_{CWD}. Field R_{CWD} exhibited a curvilinear rather than exponential response to temperature, approaching a maximum at high temperatures.

Modeled daily R_{CWD} varied seasonally in response to T_{CWD} and Φ_{CWD}, increasing rapidly following snow melt in early April and peaking at 0.17 g C m^{-2} day^{-1} in early June (Fig. 4). Daily R_{CWD} was greatest in late spring and early summer when Φ_{CWD} was high. Daily R_{CWD} in the early growing season (days 130–200) averaged 13% greater than that during the late growing season (days 201–279) when Φ_{CWD} was 69% higher, even though T_{CWD} was 1.5 °C cooler. Although daily R_{CWD} fluctuated rapidly in response to T_{CWD}, two prolonged droughts during late summer had marked effects on R_{CWD}, reducing respiration rates by >50% relative to adjacent periods with comparable T_{CWD} and high Φ_{CWD} (>150%).

The annual flux from CWD was 21.3 g C m^{-2} year^{-1} in 2004, with contributions from each decay class varying with M_{CWD} (Table 2). Moderately decomposed wood, decay classes 3 and 4, contributed 60% to total F_{CWD}. The CWD decomposition rate-constant ($F_{\mathrm{CWD}}/M_{\mathrm{CWD}}$) in 2004 was 0.09 year^{-1}. Annual C losses from CWD respiration were lower than those from other ecosystem components. The annual CWD flux was 1.4% of annual ecosystem respiration (R_{E}, 14.5 Mg C ha^{-1} year^{-1}), with soil contributing 69%, leaves 18%, and stems 12% to R_{E} (Fig. 1B).

4. Discussion

Coarse woody debris mass at our site is within the range reported for temperate (Muller and Yan, 1991) and boreal forests (Fleming and Freedman, 1998; Nalder and Wein, 1999; Bond-Lamberty et al., 2003). Our M_{CWD} value of 2.2 Mg C ha^{-1} is very similar to the estimate for a temperate deciduous forest in the mid-Atlantic region of North America (2.1 Mg C ha^{-1}, Vogt, 1991). Although M_{CWD} in a temperate Chilean forest was higher than our site (9–194 Mg C ha^{-1}), the relative distribution of M_{CWD} among decay classes was comparable, with moderately decayed wood, classes 3 and 4, representing a majority of total M_{CWD} (Carmona et al., 2002).

The relative contribution of CWD to ecosystem C mass at our site is generally lower than other forests. In a survey of six forest ecosystems, M_{CWD} was 4–10% of ecosystem C mass (Vogt, 1991), compared with our estimate of 1.2%. Similarly, other surveys suggest that CWD stocks comprise 4–12% of C stored in Canadian and US forests (Turner et al., 1995; Bhatti et al., 2002). We expect relative contribution of M_{CWD} to total ecosystem C mass to increase in our maturing forest. Sturtevant et al. (1997) showed a u-shaped trend in CWD mass over time that was dominated by two phases, one of CWD decay following stand initiation and another by CWD accumulation as mortality increases with forest maturation.

Precise estimates of M_{CWD} are difficult to obtain because CWD distribution generally is very heterogeneous (Clark et al., 2001; Ehman et al., 2002; Bond-Lamberty et al., 2003). For example, decay class distribution changed with stand age and M_{CWD} varied by >100-fold across a boreal forest chronosequence (Bond-Lamberty et al., 2003). Coarse woody distribution in our study forest was highly variable for the least decayed class, which was present in only 4 of 12 plots. The patchy distribution of decay class 1 reflects the current low tree mortality. However, this should change relatively soon as the 85-year-old forest matures and increased mortality adds to the pool of least decayed CWD (Sturtevant et al., 1997; Carmona et al., 2002).

Coarse woody debris respiration is a small, but important component of the ecosystem carbon balance at our site. Although the current annual flux of 0.21 Mg C ha^{-1} year^{-1} is low when compared with other respiratory sources, annual C storage or net ecosystem production (NEP) is the small difference between net primary production (NPP) and heterotrophic respiration (R_{h}). Thus, a small increase in F_{CWD}, a component of R_{h}, could significantly reduce NEP. Currently, NPP at our forest averages 6.54 Mg C ha^{-1} year^{-1} and annual R_{h} is 5.02 Mg C ha^{-1} year^{-1}, resulting in an NEP of 1.53 Mg C ha^{-1} year^{-1} (Gough et al., in press). Because our study forest is approaching maturity, we expect that CWD will become an increasingly important determinant of the ecosystem C balance. For example, a doubling of present F_{CWD} would reduce current average NEP by ~14%. Janisch and Harmon (2002) stressed the importance of CWD to the C balance of a forest, showing that F_{CWD} in aging forests can drive NEP to zero as C losses from tree mortality become the dominant C flux.

Although our estimate of F_{CWD} (0.21 Mg C ha^{-1} year^{-1}) is the first reported for a temperate deciduous forest, the annual respiratory flux from CWD at our site falls within the range estimated for a boreal forest in northern Canada (0.11–1.92 Mg C ha^{-1} year^{-1}) and is close to that for an old-growth coniferous forest in the western US (0.3–0.9 Mg C ha^{-1} year^{-1}) (Bond-Lamberty et al., 2003; Janisch et al., 2005). In contrast, F_{CWD} in a central Amazon forest was 12× greater than that for our site (Chambers et al., 2001). These differences in F_{CWD} are due primarily to greater amounts of CWD in tropical and boreal forests, and also to more rapid decay in the warm, moist conditions of tropical forests (Krankina and Harmon, 1995; Chambers et al., 2001). Variability in F_{CWD} across ecosystems also results from large fluctuations in M_{CWD} that occur from stand initiation to maturation (Carmona et al., 2002; Davis et al., 2003) and because of variable sampling strategies. Our estimate of F_{CWD} only includes woody debris with a midpoint diameter >10 cm. Small diameter debris is included in our soil surface respiration measurements and is not represented in our estimate of F_{CWD}.

The CWD decomposition rate-constant at our site in 2004 of 0.09 year^{-1} compares well with long-term estimates of 0.08 and 0.06 year^{-1} reported for aspen in northern Minnesota (Miller, 1983; Alban and Pastor, 1993). Our single-year estimate was derived from modeled C fluxes, while those reported for sites in Minnesota were calculated from mass decay functions following ≥5 years of repeated measures on decomposing logs. Lower annual CWD decomposition rate-constants at the Minnesota sites may be explained by cooler mean annual air temperatures, which average ~4 °C less than the 6.4 °C observed at our site in 2004.

The contribution of F_{CWD} to soil surface respiration at our site (2%) is included in the range for a Saskatchewan jack pine (*Pinus banksiana* Lamb.) forest (1.7–8.3%; Howard et al., 2004), but is lower than that for a deciduous forest in Indiana (7.6%; Curtis et al., 2002). The relative contribution of F_{CWD} to total ecosystem respiration has not been reported for a predominately deciduous forest. However, F_{CWD} comprised 30% of total ecosystem respiration in a Russian spruce boreal forest following severe wind throw (Knohl et al., 2002) and was 7% of ecosystem respiration in an old-growth mixed coniferous forest in the western US (Harmon et al., 2004). Although the contribution of F_{CWD} to ecosystem respiration at our site currently is much lower (1.4%), age-related mortality in our maturing forest is expected to increase fluxes from CWD and other heterotrophic sources while decreasing those from autotrophic sources. The degree to which F_{CWD} will increase following successional maturity depends on climate change and also atmospheric nitrogen deposition, which has been shown to affect decomposition rates of fine litter (Knorr et al., 2005).

Coarse woody debris temperature and Φ_{CWD} were important predictors of R_{CWD} at our site. We generally observed an increase in R_{CWD15} with decreasing CWD density. However, this increase was due to greater water absorption and, consequently, higher Φ_{CWD} in more decayed wood rather than because of greater T_{CWD} sensitivity in the higher decay classes. Coarse woody debris respiration generally increases as wood density decreases (Boddy, 1983a; Chambers et al., 2001; Wang et al., 2002; Bond-Lamberty et al., 2003). However, Marra and Edmonds (1994) report the opposite trend for CWD in a coniferous forest of the Pacific Northwest, suggesting that less decayed wood had elevated R_{CWD} because of high labile C content. Consistent with numerous other reports, we observed a positive correlation between T_{CWD} and Φ_{CWD}, and respiration (Boddy, 1983b; Marra and Edmonds, 1994; Chen et al., 2000; Wang et al., 2002; Bond-Lamberty et al., 2003). Our Q_{10} values of 2.20–2.57 fall within the range reported for decaying *Pinaceae* CWD, which varied from <1 to 8 (Chen et al., 2000; Bond-Lamberty et al., 2003). The response of R_{CWD} to Φ_{CWD} at our study site was similar to that for other ecosystems, with decreasing water content increasingly limiting respiration (Chen et al., 2000; Wang et al., 2002; Bond-Lamberty et al., 2003). High Φ_{CWD} may limit R_{CWD} in some ecosystems (Chen et al., 2000), but well-drained sandy soils at our site likely minimize anoxic conditions that decrease microbial activity.

Although F_{CWD} at our site is comparable to that in other forests, the accuracy of this annual flux cannot be readily assessed. However, we undertook several measures to avoid biasing this estimate. To test for T_{CWD} hysteresis and temporal effects on R_{CWD}, we incubated and measured R_{CWD} twice at ~25 °C and found no significant difference between these two measurement periods. Temperature hysteresis did not occur from 0 to 40 °C in laboratory measurements of R_{CWD} conducted by Chen et al. (2000). Because laboratory incubations create an artificial environment that may alter gas (CO_2, O_2, H_2O) exchange between CWD and the atmosphere, we measured R_{CWD} after both field and laboratory incubations. Laboratory R_{CWD} normalized for Φ_{CWD} was not significantly different from that observed in the field, indicating that laboratory measurements adequately simulated field conditions. However, field measurements of R_{CWD} were more variable and did not span the range of temperatures observed in the laboratory. In addition, we sealed the cut ends of CWD with paraffin to minimize R_{CWD} from this surface (Bond-Lamberty et al., 2003). We were constrained by the size of the cuvette used to measure R_{CWD}, sampling CWD that was 20 cm long and <13 cm in diameter. Although a negative correlation between CWD mass and decay rate has been proposed (Rayner and Boddy, 1988), this relationship is not consistently observed in the field (Harmon et al., 1986; Marra and Edmonds, 1996). We observed no correlation between sample diameter or volume and R_{CWD}, but we did not sample the upper diameter limit (~30 cm) of CWD found in our study forest. One principal assumption made in our scaling procedure is that R_{CWD} is zero when T_{CWD} is <0 °C. Respiration of decomposing woody roots approached zero at 0 °C in a mixed coniferous forest (Chen et al., 2000). In our study, F_{CWD} only increased by <10% when we assumed that R_{CWD} occurred below 0 °C and exhibited the same functional response to temperature as fluxes occurring >0 °C.

5. Conclusions

Coarse woody debris currently is a relatively minor component of the total C pool and ecosystem respiratory C losses in this northern deciduous forest. However, both CWD mass and respiration are expected to increase over the next several decades as age-related mortality of canopy trees becomes a primary factor in the production of CWD. Observed annual CWD respiration (0.21 Mg C ha^{-1} $year^{-1}$) already is a significant C flux compared to the recorded range in annual NEP at this site of 0.80–1.98 Mg C ha^{-1} $year^{-1}$ (Gough et al., in press). Increasing woody debris production will increase the relative contribution of CWD to ecosystem respiration and therefore could substantially reduce the rate of annual forest C storage. These findings underscore the growing importance of CWD to the C balance of this late successional forest.

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