Oecologia (2006) 148: 108–117
DOI 10.1007/s00442-006-0356-9

ECOSYSTEM ECOLOGY

**Wendy H. Liu · David M. Bryant · Lucy R. Hutyra
Scott R. Saleska · Elizabeth Hammond-Pyle
Daniel Curran · Steven C. Wofsy**

Woody debris contribution to the carbon budget of selectively logged and maturing mid-latitude forests

Received: 5 May 2005 / Accepted: 4 January 2006 / Published online: 4 February 2006

Abstract Woody debris (WD) is an important component of forest C budgets, both as a C reservoir and source of CO_2 to the atmosphere. We used an infrared gas analyzer and closed dynamic chamber to measure CO_2 efflux from downed coarse WD (CWD; diameter≥7.5 cm) and fine WD (FWD; 7.5 cm > diameter≥2 cm) to assess respiration in a selectively logged forest and a maturing forest (control site) in the northeastern USA. We developed two linear regression models to predict WD respiration: one based on WD temperature, moisture, and size ($R^2 = 0.57$), and the other on decay class and air temperature ($R^2 = 0.32$). WD respiration (0.28 ± 0.09 Mg C ha^{-1} year^{-1}) contributed only ≈2% of total ecosystem respiration (12.3 ± 0.7 Mg C ha^{-1} year^{-1}, 1999–2003), but net C flux from CWD accounted for up to 30% of net ecosystem exchange in the maturing forest. C flux from CWD on the logged site increased modestly, from 0.61 ± 0.29 Mg C ha^{-1} year^{-1} prior to logging to 0.77 ± 0.23 Mg C ha^{-1} year^{-1} after logging, reflecting increased CWD stocks. FWD biomass and associated respiration flux were ≈7 times and ≈5 times greater, respectively, in the logged site than the control site. The net C flux associated with CWD, including inputs and respiratory outputs, was 0.35 ± 0.19 Mg C ha^{-1} year^{-1} (net C sink) in the control site and -0.30 ± 0.30 Mg C ha^{-1} year^{-1} (net C source) in the logged site. We infer that accumulation of WD may represent a small net C sink in maturing northern hardwood forests. Disturbance, such as selective logging, can enlarge the WD pool, increasing the net C flux from the WD pool to the atmosphere and potentially causing it to become a net C source.

Keywords Coarse woody debris · Fine woody debris · Infrared gas analyzer · Northern hardwood forest · Respiration

Introduction

The mid-latitude forests of North America may account for an important part of the terrestrial C sequestration thought to be largely responsible for the global “missing C sink” (Ciais et al. 1995; Fan et al. 1998; Curtis et al. 2002). Forest re-growth is a major driver for this C uptake, implying that forest management could be part of a strategy for mitigating anthropogenic emissions of CO_2 to the atmosphere (Houghton et al. 1999; Caspersen et al. 2000). Woody debris (WD) is often overlooked or roughly estimated in forest C budgets despite its role as a long-lived forest C pool; in temperate forests, it has been found to account for roughly 18% of total ecosystem C (Pregizter and Euskirchen 2004). Accurately estimating the fluxes into and out of WD may thus be important for assessing the current and long-term C balance of forest ecosystems.

Electronic Supplementary Material Supplementary material is available for this article at http://dx.doi.org/10.1007/s00442-006-0356-9 and is accessible for authorized users.

Communicated by Russell Monson

W. H. Liu · D. M. Bryant · L. R. Hutyra · S. R. Saleska
E. Hammond-Pyle · D. Curran · S. C. Wofsy
Department of Earth and Planetary Sciences, Harvard University, Cambridge, MA 02138, USA

Present address: W. H. Liu (✉)
Ecosystem Sciences Division, Department of Environmental Science, Policy and Management, University of California, 137 Mulford Hall #3114, Berkeley, CA 94720, USA
E-mail: wliu@nature.berkeley.edu
Tel.: +1-510-6433963
Fax: +1-510-6435098

Present address: D. M. Bryant
Environmental Education Program, University of New Hampshire, Durham, NH 03824, USA

Present address: S. R. Saleska
Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA

Most studies estimate WD turnover by measuring mass and density loss, from which total removal rates (including fragmentation, leaching, and respiration) may be inferred. These loss rates describe the ecological role of WD in forest nutrient cycling and as wildlife habitat but cannot be used to assess C dynamics because they overstate the transfer of C to the atmosphere (Harmon and Hua 1991; Mattson et al. 1987; Yin 1999). Moreover, these methods rely on chronosequences and therefore, cannot produce quantitative relationships between WD respiration rates and the driving variables (e.g., temperature, moisture, species, etc.). The ability to model WD respiration is needed to predict the response of WD dynamics to environmental changes caused by changing land use or climate.

Accurate WD respiration measurements are challenging because the decomposer communities may be highly sensitive to changes in temperature or wood moisture (Rayner and Boddy 1988), or other disturbance. Soda lime traps have been used for in situ measurements to avoid physically disturbing WD during the measurements process (e.g., Marra and Edmonds 1994; Progar et al. 2000). However, the traps are well known to underestimate respiration rates because the rate of CO_2 diffusion out of the WD decreases as the CO_2 concentration within the chamber increases (Ewel et al. 1987; Raich et al. 1990). Moreover, the soda lime method measures efflux only at the WD surface though decomposability of wood varies over the cross-section of a log (Harmon et al. 1986).

An alternative method is the direct measurement of coarse WD (CWD) respiration in a closed dynamic chamber using an infrared gas analyzer (IRGA; Chambers et al. 2001; Wang et al. 2002). The IRGA method provides precise respiration measurements from the entire cross-section of the WD but involves cutting a sample and removing it from its environment, with potential artifacts due to disturbance and to CO_2 outgassing from void spaces exposed by cutting. Chambers et al. (2001) showed that allowing samples to equilibrate for approximately 3 h controlled such outgassing artifacts while minimizing changes in sample temperature, wood moisture, and decomposer populations. Changes in the surface area to volume ratio of the sample caused by cutting may potentially induce changes in respiration rates that we investigated in this study.

We used the IRGA method to measure respiration rates from downed CWD (7.5 cm ≤ diameter) and fine WD (FWD; 2 cm ≤ diameter < 7.5 cm) at Harvard Forest (Petersham, Mass.) in a selectively logged stand and an adjacent maturing stand that served as a control. Our objectives were: (1) to investigate the driving variables of WD respiration and create a model to predict WD respiration rates, (2) to evaluate the importance of WD to the C budget at Harvard Forest, and (3) to assess the effect of selective logging on the C flux from WD.

Materials and methods

Site description

The study was conducted within the Prospect Hill Tract of Harvard Forest (380-ha control site) and the adjacent Simmes Trust land (43 ha) in Petersham, Massachusetts (42°32′N, 72°11′W, elevation 340 m). The control site is within the principal footprint of the Harvard Forest long-term eddy covariance tower (Goulden et al. 1996; Barford et al. 2001), whereas the Simmes tract lies southeast of the tower, a wind direction rarely sampled at the tower. The two sites are separated by a small dirt road and were similar in composition and stature in 1999 (Table 1). The Simmes tract was selectively logged from February 2001 to November 2001, reducing aboveground biomass, basal area, and stem density (Table 1). Removal volumes for saw timber and firewood were 15.6 and 27.3 m^3 ha^{-1}, respectively. The total amount of wood removed was typical for harvests in the Quabbin Reservoir region (44.7 m^3 ha^{-1}) where Harvard Forest is located (Kittredge et al. 2003).

WD respiration rate measurements

CWD sampling was stratified by site (Prospect Hill and the Simmes tract), taxonomic group (oak, maple, birch, conifer), decay class, and diameter (2 cm ≤ diameter < 7.5 cm, 7.5 cm ≤ diameter < 25 cm, 25 cm ≤ diameter). Decay state was categorized using a five-class system based on visual and physical characteristics following Harmon and Sexton (1996; cf. Rice et al. 2004). The most decayed classes (IV and V) were scarce at the logged site, and thus were combined to ensure a sufficient sample size. We tagged 500 pieces of downed CWD of the two larger diameter classes at each site. FWD, 2 cm ≤ diameter < 7.5 cm, could not be identified by taxonomic group and was stratified by decay class and site only.

Sampling for respiration measurements was conducted in four seasons: summer (12 July–8 October 2002), fall (9 November–2 December 2002), winter (12 January–19 January 2003), and spring (18 April–5 May 2003). Three replicate pieces of CWD per subcategory were randomly chosen from the tagged pool, except where infeasible. Samples of downed CWD≥25 cm diameter were rare. Replicates for fall sampling were reduced in some subcategories due to early snowfall, and snow cover in January impeded the location of WD, reducing sampling to six random samples from each site. Summer 2002 sampling showed no significant differences between respiration rates, wood density and wood moisture for decay classes I and II, so these were combined into one category for subsequent sampling.

A chainsaw was used to cut a cross-sectional disk, 10 cm thick, from downed CWD. If a tagged piece of downed CWD could not be relocated, the nearest

Table 1 Site characteristics (mean ± SE) for Prospect Hill and the Simmes tract pre- and post-logging

Site characteristic	Prospect Hill (1999, control)	Simmes tract	
		1999, Pre-logging	2002, Post-logging
Stand age (year)	60–80	60–80	No change
Aboveground biomass (Mg C ha^{-1})[a]	106.1 ± 5.7	84.1 ± 10.5	58.8 ± 6.8
Tree density (trees ha^{-1})	653.5 ± 40.5	632.6 ± 35.8	463.3 ± 44.6
Basal area (m^2 ha^{-1})	34.2 ± 1.9	27.4 ± 2.7	19.9 ± 1.9
Common tree species	*Quercus rubrum*, *Acer rubra*, *Tsuga canadensis*	*Quercus rubrum*, *Acer rubra*, *Tsuga canadensis*, *Fagus grandifolia*	No change

[a] This was determined using species-specific allometric equations applied to survey data from permanent plots in the sites

downed CWD of the same subcategory replaced it. Samples were allowed to equilibrate with the atmosphere for 3 h before measurement, following Chambers et al. (2001). Respiration rates for a subset of samples were measured immediately after cutting and followed in time to 10 h after cutting; after 3 h, respiration rate decreased very slowly, 1.2 ± 0.6% per hour, indicating adequate equilibration (Electronic Supplementary Material, S1).

Depending on the diameter of the sample disk, it was measured in either a 22.65-l bucket or a 5.9-l round plastic container to minimize the turnover time of headspace air. Samples with diameter > 30 cm were split into halves or quarters with a machete to fit them in the large chamber. Analysis of pilot data did not show a significant effect of surface area to volume ratio of samples disks on measured respiration rates (Electronic Supplementary Material, S2). Samples were placed on a wire rack at the bottom of the chamber to allow air circulation around them. Plexiglass lids fitted with silicon O-rings were custom-made for the chambers and sealed with 10-kg weights. Leak tests conducted by blowing CO_2 around the sealed lid showed no significant rise (< 1 p.p.m.) in CO_2 concentration in an empty chamber. The chambers were connected to a Li-Cor (Lincoln, Neb.) LI-6252 CO_2 analyzer fitted with an external in-line pump to circulate sample air through the closed loop at 1 l min^{-1}. Sample air was drawn from the top of the chamber and returned through a 1/4-inch brass tube extending below the wire rack at the bottom of the chamber. CO_2 concentration was measured every 5 s for either 5 min (in the small chamber) or 8 min (in the large chamber) as illustrated in Fig. 1. Prior to measurement, sample temperature was measured using a K-type thermocouple probe placed in a hole drilled in the sample, and air temperature was measured using a similar thermocouple in ambient air.

The wet weight of a sample was measured immediately after it was removed from the measurement chamber. The wood volume of the sample was measured within 3 weeks by water displacement (Næsset 1999), and the thickness and diameter of each sample were measured to calculate the bulk volume. The sample was then oven-dried at 105°C to constant weight. Wood density was calculated from dry weight and measured wood volume, and bulk density from dry weight and bulk volume. Wood moisture was calculated gravimetrically (g H_2O g^{-1} oven-dry wood).

Respiration rates [in μg C g^{-1}C s^{-1}, or equivalently, decay rates (k) in $year^{-1}$] were calculated from the rate of CO_2 increase in the chamber headspace air in the last 3 min of measurement (after the air was mixed well), accounting for the chamber volume, the dry weight of the sample, air temperature at the chamber, and pressure obtained from the nearby Fisher Meteorological Station. The rate of CO_2 accumulation was determined by regressing CO_2 concentration against time (Fig. 1). We carefully checked each WD respiration measurement to assess the possibility that CO_2 accumulation in the chamber could limit diffusion rates, but rarely saw this effect, even for the fast respiring samples. For the samples that did exhibit decreases in respiration rates (typically in the last 10–15 s of the measurement), we found that the inclusion or omission of the deviating data points did not greatly affect the slope of the regression line. Regressions with correlation coefficients < 0.90 were discarded for a total rejection rate of 5%. Extremely low respiration rates (< 1 p.p.m. min^{-1} rise in CO_2) were retained, even with low correlation, because of inherently high variability at low rates (≈8% total data exempted from rejection).

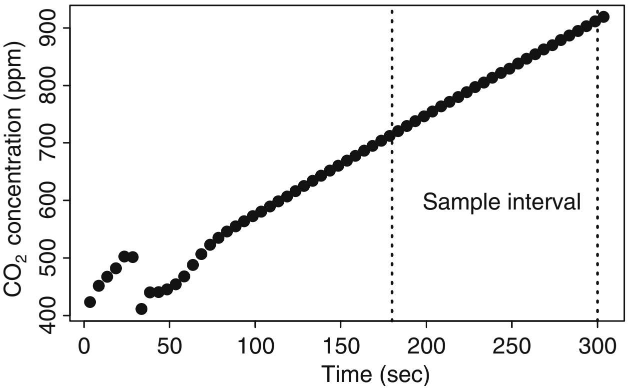

Fig. 1 Time series of CO_2 concentration in closed dynamic chamber containing a coarse woody debris (CWD) sample disk. Respiration rates were estimated using least-squares linear regression of CO_2 concentration versus time for the last 3 min of the measurement

Decay rate constants (year^{-1}) on an annual basis were estimated for downed CWD and FWD using linear regression models for each of three decay classes (Table 2). The models were created by regressing log-transformed respiration rates (μg C g^{-1}C s^{-1}) against air temperature. Annual average respiration rate was predicted using the mean annual temperature at Prospect Hill, 7.88°C, during the period 1992–2003 (Munger and Wofsy 2004). In this estimation, the predicted respiration rates were corrected for bias associated with the log-transform (see Eq. 1). Density loss rates for logs off the ground have been found to be 40% lower than those for logs on the ground (Erickson et al. 1985; Mattson et al. 1987), so we roughly estimated decay rate constants for standing CWD by reducing values by 40% from downed CWD.

WD biomass and C flux measurements

CWD volume was measured through surveys at both sites in 1999 and 2003, with an additional post-logging survey in the Simmes tract in 2001. Surveys accounted for all downed CWD and standing CWD (snags and stumps), ≥7.5 cm diameter, in permanent plots (radius = 10 m, $n = 27$ plots for 1999, $n = 15$ plots for 2003) at Prospect Hill and eight permanent plots (radius = 10 m in 1999, enlarged to 15 m for 2001, 2003) at the Simmes tract. Stumps were defined as rooted, standing CWD < 1.33 m tall. Volume of logs, log snags, and stumps (m^3) at each site were calculated using volume formulas from Harmon and Sexton (1996). Volumes for a few standing dead trees that were largely intact (retaining most branches) were calculated using species-specific allometric equations (Barford et al. 2001). The biomass of CWD (Mg C ha^{-1}) was calculated by multiplying CWD volume (m^3 ha^{-1}) and bulk density (kg dry wood m^{-3}) by subcategory (Table 3). We estimated C content to be 50% of the dry wood based on C content reported by Currie and Nadelhoffer (2002) for multiple species and decay classes at Harvard Forest.

Table 2 Woody debris (WD) respiration models[a]. *RSE* Residual SE

Variable	Coefficient estimate	SE	*P*-value	Partial R^2	RSE
Model 1[b]					0.391
Intercept	−33.466	0.047	< 0.001		
ln (M)	1.060	0.057	< 0.001	0.21	
T_s	0.096	0.002	< 0.001	0.33	
Size	0.725	0.051	< 0.001	0.04	
Model 2[c]					0.484
Intercept	−28.672	0.066	< 0.001		
T_a	0.078	0.003	< 0.001	0.22	
D_{III}	0.422	0.058	0.002	0.09[d]	
D_{IV}	0.976	0.059	< 0.001	0.09	

[a] Pooled coarse WD (CWD) and fine WD (FWD) data from both sites were used. Respiration rates were log transformed, so predicted rates must be back-transformed correctly (using Eq. 1). For example, the natural log of the respiration rate predicted by model 2 for a decay-class-III (D_{III}) log and an air temperature (T_a) of 281.03 K is $-28.672 + (281.03 \times 0.078) + 0.422 = -5.293$. The correctly back-transformed respiration rate is: $\exp(-6.3270 + 0.484^2/2) = 0.0020\,\mu\text{gC}\,\text{g}^{-1}\text{C}\,\text{s}^{-1}$

[b] The dependent variable is WD respiration rate (μg C g^{-1}C s^{-1}), and the independent variables are as follows: wood moisture (M; g H_2O g dry wood^{-1}), sample temperature (T_s; K), and size class (*Size*)(CWD, $S = 0$; FWD, $S = 1$). $R^2 = 0.57$ and the RSE is 0.391 on 381 *df*

[c] The dependent variable is WD respiration (μg C g^{-1}C s^{-1}), and the independent variables are as follows: T_a(K), $D_{III} = 1$, and D IV/V (D_{IV}) = 1. $R^2 = 0.32$ and RSE = 0.484 on 394 *df*

[d] The partial R^2 is for D as a categorical rather than continuous parameter in the model so that 9% of the variance in WD respiration rates is explained by all D categories together

In 2001, we measured FWD (2 cm ≤ diameter < 7.5 cm) by the line-intersect method (Brown 1974; Van Wagner 1968). We measured all pieces (2 cm ≤ diameter < 7.5 cm) that crossed twenty-six 10-m segments from two transect lines at Prospect Hill and four transect lines at the Simmes tract for a total of 260 m of transect at each site. The biomass of FWD (Mg C ha^{-1}) was calculated by multiplying FWD volume (m^3 ha^{-1}) and wood density (kg dry wood m^{-3}) by decay class.

C flux (Mg C ha^{-1} year^{-1}) was calculated by multiplying biomass (Mg C ha^{-1}) and annual decay rate constants (year^{-1}) by decay class. Decay rate constants to describe the entire CWD and FWD pools at each site were calculated by dividing the annual C fluxes by the total biomass. Average lifetimes of CWD and FWD were estimated by dividing the biomass by the C flux.

Continuous field measurements of environmental variables

To monitor site differences in temperature and moisture, air temperature and relative humidity were measured continuously at both sites from 16 May 2004 to 17 October 2004 using an YSI (Yellow Springs, Ohio) 44032 Precision Thermistor and a Vaisala (Woburn, Mass.) 50Y Humiter. Both were housed inside an aspirated Met One (Grant Pass, Oreg.) 076B-4 enclosure to minimize radiative biases, and placed 10–15 m apart and 1.5 m off the ground (two per site). The eddy covariance tower provided long-term continuous measurements of air temperature and relative humidity for Prospect Hill that correlated well with these measurements (air temperature, $r = 0.95$; relative humidity, $r = 0.88$).

In situ temperature was measured for three pieces of downed CWD at each site, one from each decay class (I/II, III, IV/V). Three YSI thermistors hermetically sealed inside 1-cm-diameter stainless steel tubes were inserted into holes drilled into the center of each CWD sample. Temperature and relative humidity measurements were recorded every minute, then averaged and stored every 30 min, using a Campbell Scientific (Logan, Utah) CR10X datalogger and AM16/32 multiplexer.

Table 3 Mean (SE) bulk density (g dry wood cm^{-1}) and wood density (g dry wood cm^{-1}). For abbreviations, see Table 2

	D_{I}		D_{II}		D_{III}		D_{IV}	
	Bulk density (g cm^{-3})	Wood density (g cm^{-3})	Bulk density (g cm^{-3})	Wood density (g cm^{-3})	Bulk density (g cm^{-3})	Wood density (g cm^{-3})	Bulk density (g cm^{-3})	Wood density (g cm^{-3})
Birch	0.48 (0.02)	0.53 (0.02)	0.39 (0.02)	0.47 (0.02)	0.31 (0.02)	0.35 (0.02)	0.24 (0.02)	0.33 (0.02)
Maple	0.47 (0.02)	0.58 (0.04)	0.38 (0.02)	0.45 (0.02)	0.28 (0.02)	0.36 (0.02)	0.18 (0.02)	0.26 (0.02)
Oak	0.50 (0.04)	0.51 (0.03)	0.48 (0.02)	0.55 (0.01)	0.40 (0.02)	0.48 (0.02)	0.28 (0.04)	0.34 (0.03)
Conifer	0.40 (0.04)	0.44 (0.02)	0.33 (0.02)	0.36 (0.02)	0.24 (0.02)	0.29 (0.02)	0.20 (0.02)	0.28 (0.01)
Hardwood	0.48 (0.02)	0.53 (0.02)	0.43 (0.01)	0.50 (0.01)	0.33 (0.01)	0.40 (0.01)	0.24 (0.01)	0.31 (0.01)
All species	0.47 (0.02)	0.52 (0.01)	0.41 (0.01)	0.47 (0.01)	0.31 (0.01)	0.38 (0.01)	0.23 (0.01)	0.30 (0.01)
FWD		0.62 (0.05)		0.47 (0.02)		0.44 (0.02)		0.34 (0.01)

Statistical analyses

Statistical analyses were carried out using the Insightful (Seattle, Wash.) S-Plus 6.1 statistical software package. Ninety-five percent confidence intervals for CWD and FWD biomass or C flux were estimated using bootstraps with replacement of biomass or C flux on each plot and each 10-m transect section, respectively. Relationships between respiration rates and driving variables were evaluated using linear regressions ANOVA, with statistical significance determined at the $P < 0.05$ level. Respiration rates were log transformed to meet the homoscedasticity and normality assumptions of linear regressions and ANOVA. Tukey–Kramer multiple comparison tests were used for pairwise comparisons of respiration rates to follow up on significant main effects determined by ANOVA. All downed CWD and FWD data were combined to create two multiple linear regression models of respiration rates, one yielding the best fit possible and the other including only parameters most readily available in typical ecological studies.

Results and discussion

Driving variables of WD respiration rates

Air temperature and log-transformed wood moisture together accounted for the largest proportion of the variance in respiration rates (54%), suggesting that these were the most important driving variables controlling respiration rates. While moisture and temperature appear to be of comparable importance in general, the wide range of these variables in our study (0.10–6.80 g H_2O g^{-1} dry wood for moisture and −10 to +33°C for temperature) showed that the influence of one variable could outweigh the other at extreme values. For example, downed CWD respiration rates were 2 orders of magnitude higher in summer than in winter because respiration was inhibited at very low temperatures, regardless of wood moisture.

Respiration rates were correlated with air temperature ($r = 0.47$), sample temperature at time of measurement ($r = 0.43$), bulk density ($r = 0.39$), and wood moisture (log transformed, $r = 0.46$). The relationships between respiration rates and the individual variables of air temperature and wood moisture are shown in Fig. 2. Differences in respiration rates by decay class were significant for pooled CWD and FWD data ($F_{(378)} = 20.0$, $P < 0.001$]. Decay class was also a good proxy for both bulk density [$F_{(328)} = 85.1$, $P < 0.001$] and log-transformed wood moisture [$F_{(431)} = 43.2$, $P < 0.001$], reflecting the strong covariance of log-transformed wood moisture and bulk density ($R^2 = 0.46$). Wood density and bulk density by taxonomic group and decay class are presented in Table 3.

We expected respiration rates for downed birch and maple to be higher than for oak and conifer due to wood physiology and biochemistry (Edmonds et al. 1986; Harmon et al. 1986; Rayner and Boddy 1988; Schowalter 1992), but this difference was observed only for pieces in more advanced states of decay. Respiration rates were significantly higher for birch compared to oak and conifer, and for maple compared to oak for decay class III CWD [$F_{(90)} = 8.28$, $P < 0.001$]. Also, maple respiration rates were significantly higher than oak for decay class IV/V CWD [$F_{(74)} = 3.26$, $P = 0.03$]. The physical state of a piece of CWD reflects how much decomposition has occurred, and the lack of statistically significant differences in respiration rates among less decayed CWD may be an artifact of categorizing by physical decay state. Relatively decay resistant oak and conifer CWD would not reach advanced stages of decomposition unless microbes capable of breaking down lignin and tolerating extractives had successfully colonized the wood. In contrast, decay class I/II CWD are in the early stages of decomposition so not much microbial colonization has occurred, and labile C and nutrients are still relatively abundant in the wood regardless of genus. Though decay class categorization may mask taxonomic group effects on respiration rates, it is an important tool for estimating C flux from WD on an area basis because it is a good predictor of respiration rates and easy to measure in the field.

The use of multiple regression analysis to control for the effects of wood moisture and air temperature on respiration rates revealed that CWD respired more slowly than FWD ($P < 0.001$), but there was no effect of diameter for pieces >7.5 cm diameter. This result differs from other studies showing negative correlation of

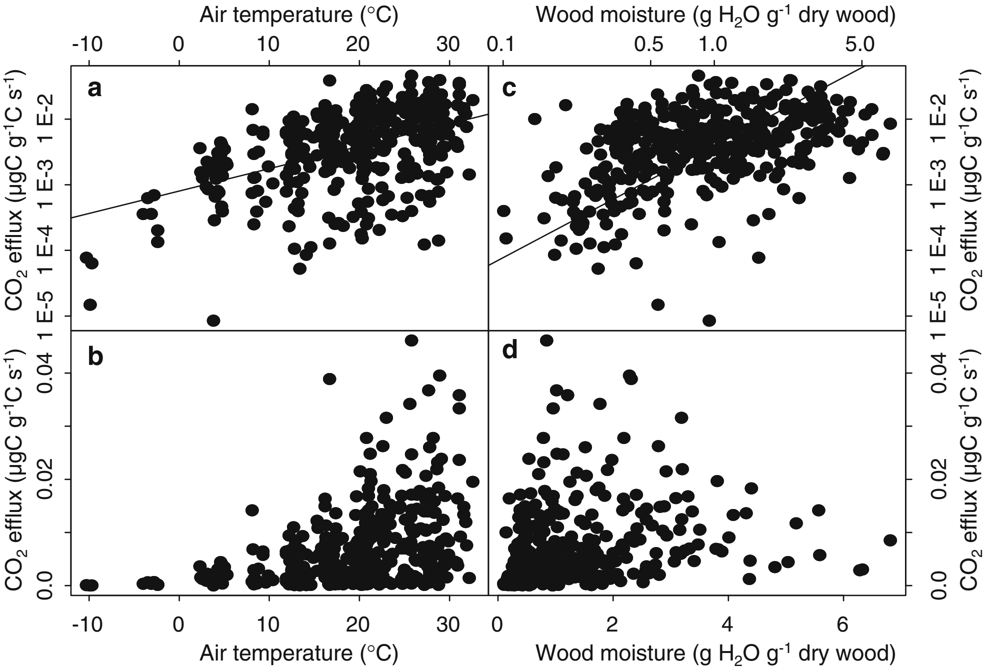

Fig. 2 **a** WD respiration rate (shown on $\log_{10}$ scale) versus air temperature. The *solid line* represents the least-squares linear regression, $\ln(y) = -7.127 + 0.079x$ ($n = 400$, $R^2 = 0.23$, $P < 0.001$). **b** WD respiration (shown on a linear scale) versus air temperature. **c** WD respiration (shown on base $\log_{10}$ scale) versus wood moisture (shown on $\log_{10}$ scale). The *solid line* represents the least-squares linear regression, $\ln(y) = -5.536 + 0.741 \times \ln(x)$ ($n = 395$, $R^2 = 0.21$, $P < 0.001$). **d** WD respiration (shown on a linear scale) versus wood moisture

CWD diameter and decay rate (Abbott and Crossley 1982; Edmonds et al. 1986; Harmon et al. 1995; Yoneda 1985). However, another study in a northern hardwood forest also did not detect a diameter effect for diameters of up to 16 cm (Foster and Lang 1982). CWD in northern hardwood forests is much smaller in diameter than CWD in the Pacific Northwest and the tropics where diameter effects were observed. Evidently, the dependence of decay dynamics on CWD diameter is not great enough in northern hardwood forests to significantly affect respiration rates.

Models to predict WD respiration rates and decay rate constants

The regression model providing the best fit for our WD respiration data included log-transformed wood moisture, sample temperature, and size class (CWD vs. FWD; $R^2 = 0.57$) is given in Table 2 (model 1). Notwithstanding the enormous range and variability of the respiration rates, this simple equation in model 1 explains almost 60% of the observed variance in log-transformed respiration rates. Unfortunately, wood moisture and sample temperature are often not available in WD data. We therefore also developed a model equation using air temperature and decay class only ($R^2 = 0.32$; Table 2, model 2).

In order to derive mean rates of respiration [$E(R)$] for a population of CWD, the following formulas should be used to back-transform the predicted respiration rates:

$$E(R) = \exp(\mu + \sigma^2/2), \qquad (1)$$

$$\mathrm{Var}(R) = \exp(2\mu)[\exp(2\sigma^2) - \exp(\sigma^2)]. \qquad (2)$$

Where R is respiration rate (in μg C g^{-1}C s^{-1}), $E(R)$ is the expected value of R, $\mathrm{Var}(R)$ is the variance of R, μ is the predicted value from the log-transform regression equation, and σ is the residual SE of the log-transform regression of our observations as given in Table 2 (see Gut 1995).

We derived annual decay rate constants for each decay class by averaging respiration rates over the year. We disaggregated the data by decay class and used model 2 to predict average annual respiration rates. This caused us to lose some predictive power because this model does not include the wood moisture parameter and thus, explains 21–30% of the large variance (e.g., 0.00014–0.0395 μg C g^{-1}C s^{-1} during the summer in Prospect Hill) in respiration rates (Table 4). We used this model because wood moisture is so variable within and between pieces of WD that we could not estimate annual average wood moisture values to predict respiration rates. Using decay class as a proxy for wood moisture, we estimated decay rate constants for decay classes I/II (combined), III, and IV/V (combined) of 0.06 ± 0.02, 0.10 ± 0.03, and 0.14 ± 0.07 year^{-1}, respectively.

The overall annual decay rate constants for downed WD, weighted by total C flux and biomass for each decay class at each site, were comparable with published rates (e.g., Mattson et al. 1987; Sollins et al. 1987; Schowalter 1992; Arthur et al. 1993; Stone et al. 1998). The annual downed CWD decay rates constants were 0.09 ± 0.04 year^{-1} in Prospect Hill and 0.08 ± 0.04 year^{-1} in the Simmes tract, corresponding to mean downed CWD lifetimes of approximately 11 years in Prospect Hill and 13 years in the Simmes tract. The annual decay rate constants for FWD estimated by total

Table 4 WD decay rate constants and linear regression models relating log-transformed respiration rates (μg C g^{-1}C s^{-1}) and T_a (K) by D[a]. For abbreviations, see Table 2

D	Intercept	T_a	R^2	RSE	*df*	Decay rate constant ($year^{-1}$)[b]
I–II	−31.695 ± 5.610	0.088 ± 0.019	0.30	1.367	170	0.06 ± 0.02
III	−25.157 ± 5.663	0.067 ± 0.018	0.21	1.262	116	0.10 ± 0.03
IV–V	−25.840 ± 12.175	0.071 ± 0.042	0.22	0.996	106	0.14 ± 0.07

[a] Mean values ± 95% confidence interval (CI) are shown. Pooled CWD and FWD data from both sites were used

[b] Decay rate constants were predicted using the annual mean air temperature (7.88°C) measured by the eddy flux tower at Prospect Hill from 1992 to 2003. Ninety-five percent CIs for decay rate constants were estimated using bootstraps with replacement of log-transformed respiration rates. The decay rate constants and 95% CI have been adjusted for the bias associated with the log-transformation (Gut 1995)

C flux and biomass were 0.09 ± 0.04 $year^{-1}$ in Prospect Hill and 0.07 ± 0.02 $year^{-1}$ in the Simmes tract, corresponding to mean lifetimes of approximately 11 years in Prospect Hill and 14 years in the Simmes tract. Despite the regression analyses that suggest FWD respires at higher rates than CWD, the estimated mean lifetimes of FWD and CWD appear similar, reflecting the decay class distributions at the sites. The overall decay rate constants given above pertain only to oxidation of WD, and therefore are lower than total decomposition loss rates that also include fragmentation and leaching losses.

Role of WD in the Harvard Forest C budget

Changes in the CWD pool and CWD respiration accounted for non-trivial portions of net ecosystem exchange (NEE). The difference between the tree mortality rate (inputs to WD) and annual C flux from WD is the annual net rate of C storage (if positive) or release (if negative) from WD. Using the mortality rate reported for Prospect Hill, 0.64 Mg C ha^{-1} $year^{-1}$ (Barford et al. 2001; assuming 25% uncertainty in the estimate), we estimate that the CWD pool is currently increasing, representing net C storage (a sink) of 0.35 ± 0.19 Mg C ha^{-1} $year^{-1}$, up to 30% of NEE at Prospect Hill (−2.0 ± 0.4 Mg C ha^{-1}; Barford et al. 2001). This rate is comparable to the rate of belowground C storage in soils at Harvard Forest, 0.1–0.3 Mg C ha^{-1} $year^{-1}$ (Gaudinski et al. 2000). However, the C storage in CWD is likely to vary annually because CWD inputs through mortality are episodic (ranging from 0.27 to 1.34 Mg C ha^{-1} $year^{-1}$) in Prospect Hill from 1993 to 2003, while C losses through respiration are likely more consistent year to year. This potential for large annual imbalances in inputs and outputs to the CWD pool makes CWD dynamics important for overall C balance despite their small magnitude relative to other fluxes in the ecosystem.

It is easy to overlook the importance of CWD in the long-term C balance of the site, because WD contributed only a small percentage of total stand respiration. WD released an average of 0.28 ± 0.09 Mg C ha^{-1} $year^{-1}$ in Prospect Hill (Table 4) compared to 12.3 ± 0.7 Mg C ha^{-1} $year^{-1}$ total stand respiration (Munger and Wofsy 2004). WD respiration was also low compared soil respiration, which was reported at 6.47–7.48 Mg C ha^{-1} $year^{-1}$ in Prospect Hill (Davidson et al. 2002). However, most of the ecosystem and soil C fluxes reflect metabolism of short-lived carbohydrates whereas fluxes to or from CWD represent changes in a long-lived pool of organic matter.

Effect of selective logging on C flux from WD

Partial canopy removal (≈30%) at the logged site did not have a statistically significant effect on WD respiration rates. Continuous environmental measurements in both sites from May to October 2004 showed that CWD temperature was significantly higher ($P < 0.001$) and relative humidity significantly lower ($P < 0.001$) in the Simmes tract (Fig. 3). Respiration rates were inherently variable, and the differences in temperature and moisture may have compensated, so that site differences in respiration rates per unit biomass were not detectable.

Despite the similar decay rate constants for logged and unlogged sites, the C flux from WD was higher in the Simmes tract following logging because of the larger measured volume of WD at the logged site (Table 5). The increase in CWD biomass at the Simmes tract was not statistically significant ($P = 0.14$), but considering the negligible change in CWD biomass at Prospect Hill during the same period, the lack of significance was likely due to the high spatial variability in CWD rather than no change in the CWD stock (Table 5).

For the period of this study, CWD may be a net C source in the selectively logged site compared to a net sink in the control site. Following logging, the estimated losses from the CWD pool though respiration (0.77 ± 0.23 Mg C ha^{-1} $year^{-1}$) outweighed the inputs into the CWD through mortality (0.47 ± 0.20 Mg C ha^{-1} $year^{-1}$), leading to an estimated net flux of −0.30 ± 0.30 Mg C ha^{-1} $year^{-1}$. The greater C flux from CWD at the Simmes tract is due not only to greater CWD biomass, but also a post-logging shift in the composition of the CWD pool from comparable amounts of downed and standing CWD to a greater proportion of downed CWD, which decomposes more quickly. This increase in C flux was moderated by a notable shift in CWD biomass towards less decayed CWD. McGee et al. (1999) reported the same change in the CWD pool in another selectively logged northern

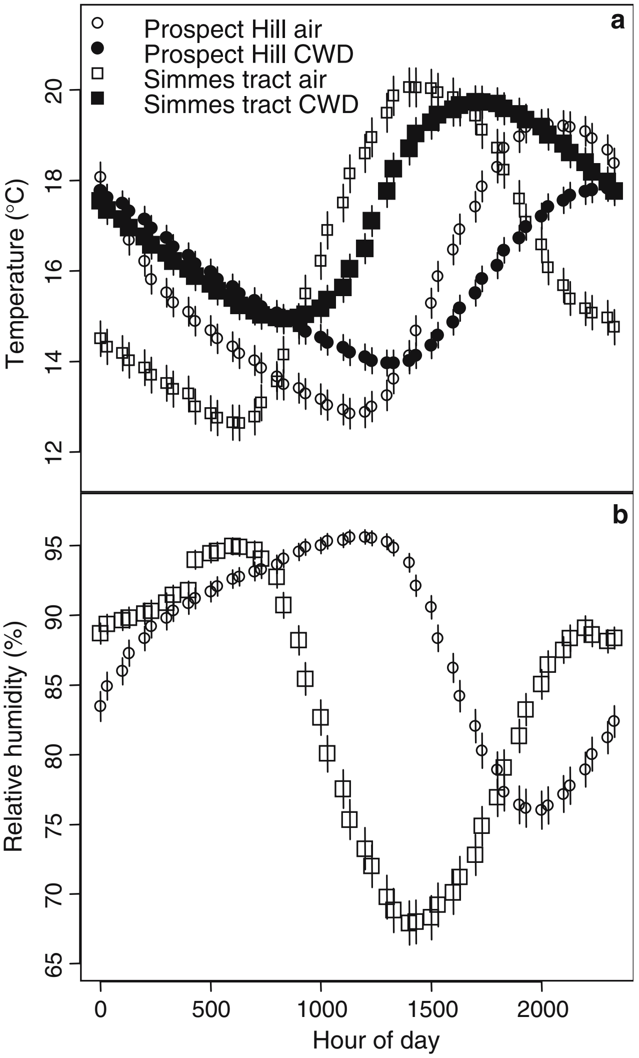

Fig. 3 **a** Half-hourly air temperature and temperature of decay-class-III downed CWD in Prospect Hill and the Simmes tract averaged over the period, 16 May–17 October 2004. **b** Half-hourly relative humidity in Prospect Hill and the Simmes tract averaged over the same period. *Error bars* represent SEs

hardwood forest and attributed it to the fragmentation of more decayed CWD by logging equipment in addition to new inputs of less decayed CWD.

For FWD, net C flux is not estimated, because inputs to the FWD pool were not measured. However, FWD respiration accounted for C fluxes of 0.45 ± 0.15 Mg C ha^{-1} year^{-1} at the Simmes tract and 0.08 ± 0.04 Mg C ha^{-1} year^{-1} at Prospect Hill, a fivefold difference between sites (Table 5). This reflects the sevenfold difference in FWD biomass between sites (Table 5). Whereas the FWD in Prospect Hill was fairly evenly divided between decay classes, almost 80% of the FWD in the Simmes tract was decay class I/II, likely due to slash piles created from logging. This suggests that slash piles left at logging sites can greatly influence the size of the FWD pool and its contribution to whole ecosystem respiration.

Conclusions

We have presented a simple, uniform methodology for measuring WD respiration rates and applied this chamber-based IRGA method to determine rates per unit biomass in a New England forest. Though highly variable, WD respiration rates were well predicted by WD temperature and moisture. We also presented two simple models for estimating WD respiration rates based on only air temperature and decay class or using WD sample moisture, temperature, and size. The resulting empirical equations should be applicable to mixed northeastern forests with typical assemblages of northern species.

We showed that both CWD and FWD lifetimes associated with respiration are moderately long, ranging from 6 to 16 years, likely much longer than overall turnover rates that include additional C losses from fragmentation and leaching. Rates of input and oxidation of WD can significantly affect net C balance in northeastern forests, even though the associated C fluxes

Table 5 Mean biomass (Mg C ha^{-1}) by *D* and annual C flux (Mg C ha^{-1} year^{-1}) (±95% CI) for CWD and FWD at Prospect Hill (control) and the Simmes tract (selectively logged in 2001). For abbreviations, see Tables 2 and 4

Year	Biomass (Mg C ha^{-1})						C flux (Mg C ha^{-1} year^{-1})[a]	
	$D_{I/II}$		D_{III}		$D_{IV/V}$		Total	
	Prospect Hill	Simmes tract	Prospect Hill	Simmes tract	Prospect Hill	Simmes tract	Prospect Hill	Simmes tract
Downed CWD								
1999	0.79 ± 0.46	0.10 ± 0.20	0.98 ± 0.55	1.16 ± 1.05	0.65 ± 0.26	3.32 ± 2.45	0.20 ± 0.06	0.49 ± 0.29
2001	–	6.66 ± 3.14	–	1.06 ± 0.61	–	2.61 ± 1.68	–	0.71 ± 0.23
2003	1.06 ± 0.58	6.27 ± 2.99	0.75 ± 0.32	1.45 ± 0.46	0.81 ± 0.60	2.22 ± 1.53	0.21 ± 0.08	0.68 ± 0.22
Standing CWD								
1999	1.59 ± 0.96	1.06 ± 0.84	0.86 ± 0.92	1.27 ± 1.80	0.18 ± 0.09	1.15 ± 0.76	0.07 ± 0.03	0.11 ± 0.06
2001	–	1.91 ± 0.81	–	0.34 ± 0.26	–	0.30 ± 0.33	–	0.06 ± 0.01
2003	0.99 ± 0.60	2.79 ± 1.18	1.25 ± 1.62	0.69 ± 0.50	0.30 ± 0.23	0.30 ± 0.19	0.08 ± 0.06	0.09 ± 0.03
FWD								
2001	0.29 ± 0.18	6.10 ± 3.08	0.50 ± 0.29	1.13 ± 0.41	0.25 ± 0.20	0.56 ± 0.22	0.08 ± 0.04	0.45 ± 0.15

[a] C flux was estimated using biomass from 1999, 2001 and 2003 and downed CWD decay rate constants (see Table 4) from 2002 to 2003 respiration measurements. Standing CWD decay rates were assumed to be 40% lower than downed CWD decay rates

are small relative to total annual ecosystem respiration. Fluxes in and out of WD pools represent changes in long-lived organic matter, and therefore must be compared to *net* ecosystem C fluxes. Net C fluxes from WD accounted for up to 30% of NEE in this forest. Selective logging can potentially change WD from a net C sink to a net C source to substantially impact NEE. Though partial canopy removal from selective logging did not have a detectable effect on WD respiration rates, logging induced substantial inputs to the WD pool that increased the C flux from the WD pool to the atmosphere. WD dynamics should thus be included in assessments of factors that control long-term net C balance, particularly following disturbance.

Acknowledgements We thank C. Barford, B. Curry, C. Jones, Z. Liscow, K. McKain, D. Patterson, and J. Silvis for conducting the CWD and FWD inventories. Thanks to S. Pears, G. Santoni, J. Wofsy, and G. Yang for field assistance with the WD respiration measurements. We also thank J. W. Munger whose dedication makes our Harvard Forest research possible. This work was supported by grants to Harvard University from the National Science Foundation LTER program (NSF DEB-0080592) and by the Office of Science (BER), U.S. Department of Energy, through the Northeast Regional Center of the National Institute for Global Environmental Change under Cooperative Agreement no. DE-FC02-03ER63613 and the Terrestrial Carbon Program (DE-FG02-95ER62002). Financial support does not constitute an endorsement by DOE of the views expressed in the report.

References

Abbott DT, Crossley DA (1982) Woody litter decomposition following clear-cutting. Ecology 63:35–42

Arthur MA, Tritton LM, Fahey TJ (1993) Dead bole mass and nutrients remaining 23 years after clear-felling of a northern hardwood forest. Can J For Res 23:1298–1305

Barford CC, Wofsy SC, Goulden ML, Munger JW, Hammond-Pyle E, Urbanski SP, Hutyra L, Saleska SR, Fitzjarrald D, Moore K (2001) Factors controlling long- and short-term sequestration of atmospheric CO_2 in a mid-latitude forest. Science 294:1688–1691

Brown J (1974) Handbook for inventorying downed woody material. General technical report. USDA Forest Service, Ogden, Utah

Caspersen JP, Pacala SW, Jenkins JC, Hurtt GC, Moorcroft PR, Birdsey RA (2000) Contributions of land-use history to carbon accumulation in U.S. forests. Science 290:1148–1151

Chambers JQ, Schimel JP, Nobre AD (2001) Respiration from coarse wood litter in central Amazon forests. Biogeochemistry 52:115–131

Ciais P, Tans PP, Trolier M, White JWC, Francey RJ (1995) A large northern hemisphere terrestrial CO_2 sink indicated by the $^{13}C/^{12}C$ ratio of atmospheric CO_2. Science 269:1098–1102

Currie WS, Nadelhoffer KJ (2002) The imprint of land-use history: patterns of carbon and nitrogen in downed woody debris at the Harvard Forest. Ecosystems 5:446–460

Curtis PS, Hanson PJ, Bolstad P, Barford C, Randolph JC, Schmid HP, Wilson KB (2002) Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. Agric For Meteorol 113:3–19

Davidson EA, Savage K, Bolstad P, Clark DA, Curtis PS, Ellsworth DS, Hanson PJ, Law BE, Luo Y, Pregitzer KS, Randolph JC, Zak D (2002) Belowground carbon allocation in forests estimated from litterfall and IRGA-based soil respiration measurements. Agric For Meteorol 113:39–51

Edmonds RL, Vogt DJ, Sandberg DH, Driver CH (1986) Decomposition of Douglas-fir and red alder wood in clear-cuttings. Can J For Res 16:822–831

Erickson HE, Edmonds RL, Peterson CE (1985) Decomposition of logging residues in Douglas-fir, western hemlock, Pacific silver fir, and Ponderosa pine ecosystems. Can J For Res 15:914–921

Ewel KC, Cropper WP, Gholz HL (1987) Soil CO_2 evolution in Florida slash pine plantations. 1. Changes through time. Can J For Res 17:325–329

Fan S, Gloor M, Mahlman J, Pacala S, Sarmiento J, Takahashi T, Tans P (1998) A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. Science 282:442–446

Foster JR, Lang GE (1982) Decomposition of red spruce and balsam fir boles in the White Mountains of New Hampshire. Can J For Res 12:617–626

Gaudinski JB, Trumbore SE, Davidson EA, Zheng SH (2000) Soil carbon cycling in a temperate forest: radiocarbon-based estimates of residence times, sequestration rates and partitioning of fluxes. Biogeochemistry 51:33–69

Goulden ML, Munger JW, Fan S, Daube BC, Wofsy SC (1996) Measurements of carbon sequestration by long-term eddy-covariance: methods and a critical evaluation of accuracy. Global Change Biol 2:169–182

Gut A (1995) An intermediate course in probability. Spring, Berlin Heidelberg New York

Harmon ME, Hua C (1991) Coarse woody debris dynamics in two old-growth ecosystems. BioScience 41:604–610

Harmon ME, Sexton J (1996) Guidelines for measurements of woody detritus in forest ecosystems. LTER Network Office, Seattle, Wash.

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K Jr, Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. Adv Ecol Res 15:133–302

Harmon ME, Whigham DF, Sexton J, Olmsted I (1995) Decomposition and mass of woody detritus in the dry tropical forests of the northeastern Yucatan peninsula, Mexico. Biotropica 27:305–316

Houghton RA, Hackler JL, Lawrence KT (1999) The US carbon budget: contributions from land-use change. Science 285:574–578

Kittredge DB, Finley AO, Foster DR (2003) Timber harvesting as ongoing disturbance in a landscape of diverse ownership. For Ecol Manage 180:425–442

Marra JL, Edmonds RL (1994) Coarse woody debris and forest floor respiration in an old-growth coniferous forest on the Olympic Peninsula, Washington, USA. Can J For Res 24:1811–1817

Mattson KG, Swank WT, Waide JB (1987) Decomposition of woody debris in a regenerating, clear-cut forest in the southern Appalachians. Can J For Res 17:712–721

McGee GG, Leopold DJ, Nyland RD (1999) Structural characteristics of old-growth, maturing, and partially cut northern hardwood forests. Ecol Appl 9:1316–1329

Munger WJ, Wofsy SC (2004) Harvard Forest CO_2 flux data. Earth and Planetary Sciences, Harvard University, Cambridge, Mass.

Næsset E (1999) Relationship between relative wood density of *Picea abies* logs and simple classification systems of decayed coarse woody debris. Scand J For Res 14:454–461

Pregizter KS, Euskirchen ES (2004) Carbon cycling and storage in world forests: biome patterns related to forest age. Global Change Biol 10: 2052–2077

Progar RA, Schowalter TD, Freitag CM, Morrell JJ (2000) Respiration from coarse woody debris as affected by moisture and saprotroph functional diversity in Western Oregon. Oecologia 124:426–431

Raich JW, Bowden RD, Steudler PA (1990) Comparison of two static chamber techniques for determining carbon dioxide efflux from forest soils. Soil Sci Soc Am J 54:1754–1757

Rayner A, Boddy L (1988) Fungal decomposition of wood: its biology and ecology. Wiley, New York

Rice AH, Hammond-Pyle E, Saleska SR, Hutyra L, Palace M, Keller M, de Camargo PB, Portilho K, Marques DF, Wofsy SC (2004) Carbon balance and vegetation dynamics in an old-growth Amazonian forest. Ecol Appl 14:S55–S71

Schowalter TD (1992) Heterogeneity of decomposition and nutrient dynamics of oak (*Quercus*) logs during the first 2 years of decomposition. Can J For Res 22:161–166

Sollins P, Cline SP, Verhoeven T, Sachs D, Spycher G (1987) Patterns of log decay in old-growth Douglas-fir forests. Can J For Res 17:1585–1595

Stone JN, MacKinnon A, Parminter JV, Lertzman KP (1998) Coarse woody debris decomposition documented over 65 years on southern Vancouver Island. Can J For Res 28:788–793

Van Wagner CE (1968) The line intersect method for forest fuel sampling. For Sci 14:20–26

Wang C, Bond-Lamberty B, Gower ST (2002) Environmental controls on carbon dioxide flux from black spruce coarse woody debris. Oecologia 132:374–381

Yin XW (1999) The decay of forest woody debris: numerical modeling and implications based on some 300 data cases from North America. Oecologia 121:81–98

Yoneda T (1985) Relation of wood diameter to the rates of dry weight loss and CO_2 evolution of wood litter in evergreen oak forests (studies on the rate of decay of wood litter on the forest floor, V). Jpn J Ecol 35:57–66