Interactions of temperature and moisture with respiration from coarse woody debris in experimental forest canopy gaps

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1. Introduction

Woody debris is a critical component of forest ecosystems since it retains essential nutrients, stores water, contributes to soil development and provides habitat for bacteria, insects, fungi, plants and animals. Coarse woody debris (CWD) influences the maintenance of local species diversity and contributes to the global carbon (C) cycle, yet despite its importance the dynamics of CWD are typically only included as a pool in most forest C models. Coarse woody debris (CWD) is a critical component of forest ecosystems since it retains essential nutrients, stores water, contributes to soil development, and provides habitat for bacteria, insects, fungi, plants, and animals. Coarse woody debris (CWD) influences the maintenance of local species diversity and contributes to the global carbon (C) cycle, yet despite its importance the dynamics of CWD are typically only included as a pool in most forest C models. Coarse woody debris (CWD) is typically only included as a pool in most forest C models. Estimates of fluxes from CWD are limited despite the significant pool size, though recently more flux estimates have been under-taken and methods are becoming further refined (Bond-Lamberty et al., 2002; Wang et al., 2002; Liu et al., 2006; Gough et al., 2007; Tang et al., 2008). The inclusion of estimates for each forest component making up ecosystem respiration is actually quite important, since the difference between the influx of CO2 during photosynthesis and efflux of CO2 during total ecosystem respiration is often small. However, these components, especially CWD, are not static and even within one forest ecosystem will vary seasonally, spatially, with wood age, and following disturbance (Bond-Lamberty et al., 2002; Law et al., 2003; Tang et al., 2008). Bond-Lamberty et al. (2002) estimated that over the course of a year, CWD respiration can be up to 50% of soil surface CO2 flux, indicating it can be a very important component of total detritus respiration.

Like CWD, canopy gaps are another structural characteristic more common to mature forests that affect biogeochemical cycles, productivity, and biodiversity of the forest stand (Mladenoff, 1987; Clebsch and Busing, 1989; Dahir and Lorimer, 1996; Scheller and Mladenoff, 2002; Latty et al., 2006). Estimates of the effects of canopy gaps on CWD respiration are lacking. Canopy openings are created through normal tree mortality, natural disturbance, or forest harvesting. The microclimate often differs between forest gaps...
and the surrounding intact canopy areas, with air and soil temperature, soil moisture and solar radiation generally increasing after canopy disturbance (Collins and Pickett, 1987; Denslow and Spies, 1990; Gray et al., 2002). Decay rates of CWD are related to microbial activity, air temperature, moisture availability and substrate quality (Edmonds et al., 1986; Harmon et al., 1995), several of which may be altered following canopy removal. If decomposition is occurring at a faster rate within canopy openings, this more rapid reduction of the pool is important since these rates would increase local resource heterogeneity and eventually affect the stand CWD pool and the C balance of the ecosystem.

Both microclimate effects and soil CO2 flux are better understood in large clearcut disturbances than that in small canopy openings. Warmer and moister conditions within openings created by clearcuts have been shown to increase the rates of decomposition of the residual organic matter (Bormann et al., 1974; Prescott, 2000). Janisch et al., (2005) predicted that the decomposition of CWD in regenerating clearcuts would be more rapid than under the closed canopy of proximate old growth Pacific Northwest forests. However, Marra and Edmonds (1996) reported annual respiration rates to be similar in clearcut versus closed-canopy environments though greater seasonal fluctuations occurred within the clearcut area. Likewise Liu et al., (2006) did not find woody debris respiration rates to differ significantly between a selectively logged site and an adjacent unlogged site. Most recently, Vanderwel et al., (2008) predicted slower decay rates in selectively managed versus unmanaged stands.

Contradicting results may be explained in part by the varied methodologies employed or by the different climates in which the studies were performed. In moisture-limited regions, respiration would be expected to increase with moisture. Whereas, in the relatively wet forests of the Pacific Northwest, dryer conditions promote higher respiration and decomposition rates (Progar et al., 2000). Nearly all studies show an interactive effect of temperature and moisture on decay dynamics. A number of other variables including wood characteristics such as density, nutrient content, decay resistance, and type (log, stump or root) may influence the decomposition as much as the environmental factors surrounding the wood, but few of these have been evaluated. Moreover, CWD dynamics in general are thought to be highly variable temporally and spatially, necessitating data from studies using multiple methods and repeated measurements to most accurately model decomposition and CWD pools and fluxes (Bond-Lamberty and Gower, 2008).

The goal of this study was to investigate if temperature and moisture changes associated with treefall openings influenced the CO2 flux from CWD and how the differences in this flux affect estimates of C loss from the CWD pool. Because canopy cover influences temperature and moisture conditions that are often strongly correlated with respiration, it is reasonable to hypothesize that canopy removal will affect respiration rates of CWD within openings. Specifically, does the increased solar radiation in canopy openings (gaps) influence the surface temperature and evaporation of water from CWD; and does gap creation affect CWD respiration only through its influence on these two factors? We then examined the use of models based on wood temperature to estimate annual C emissions from woody debris in open and closed canopy conditions within a second-growth northern hardwood forest.

2. Methods

2.1. Site description

This study is part of a large-scale experiment established within the Flambeau River State Forest, an approximately-36,500 ha property located in north central Wisconsin, USA (Fig. 1). The 300 ha study site is located within the southernmost portion of the Flambeau (45° 37.4’ N, 90° 47.8’ W). Soils are predominantly well-drained silt loams (glossudalfs) of the Magnor and Freeon series overlaying dense glacial till. January and July air temperatures at the site (2005–2008) averaged −10 and 20 °C, respectively, with mean annual precipitation of 570 mm. The median length of the growing season is 105 days (1971–2000; Midwest Regional Climate Center). Annual precipitation was 618 mm in 2007 and 530 mm in 2008, based on a rain gauge in the center of the research area. The vegetation in this portion of the Flambeau is dominated by sugar maple (Acer saccharum), American basswood (Tilia americana) and white ash (Fraxinus americana). The plant communities of the study area are described in depth in Burton et al. (2011). The stand was logged in the early 20th century and is currently an even-aged, second-growth, mature forest with most stems originating between the 1920 and 1940s. Historically, the landscape of this part of the Flambeau was dominated by eastern hemlock (Tsuga canadensis), yellow birch (Betula alleghaniensis), and sugar maple (Schulte et al., 2002). The dominant historical disturbance regime was partial to infrequent complete canopy

Fig. 1. Location map of Flambeau River State Forest in northern Wisconsin, USA.
removal by windthrow (Frelich and Lorimer, 1991; Schulte and Mladenoff, 2005).

2.2. Experimental design

The goal of the larger experiment is to assess how restoring features more abundant in old-growth forests, namely, canopy gap openings and greater volumes of CWD, influence the productivity, diversity and C and nutrient cycling in a second-growth northern hardwood forest. Treatments including canopy gap creation, CWD additions, the combination of CWD and gap additions, and a series of controls to isolate the influence of logging machinery and white-tailed deer (Odocoileus virginianus) were randomly assigned to thirty-five 80 m × 80 m (0.64 ha) permanent plots. Three subplots were established in each plot and in gap addition treatments, a canopy opening was created in each subplot. The sizes of the openings (50, 200, and 380 m²) were selected to represent the range of gap sizes typical of old-growth northern hardwood forests in the region. The amount of CWD added to a main plot varied based on pre-existing amounts measured on that plot (unpublished data) prior to treatment. CWD was augmented to raise the mean CWD biomass to levels expected in typical old-growth northern hardwood stands of the region (mean 28.7 Mg ha⁻¹, Goodburn and Lorimer, 1998). Freshly cut trees were used so that all added CWD was of a uniform decay class (decay class 1). Logs were placed in contact with the ground with few exceptions. Treatments were applied to plots in late January 2007 with a Ponsse Ergo harvester and Ponsse Buffalo forwarder (both low-impact rubber-tired logging equipment) under frozen ground conditions and snow cover.

To investigate the effects of canopy gaps on CWD respiration, we focus primarily on only a subset of the experimental treatments: (1) CWD addition, under intact forest canopy (no-gap) and (2) CWD addition with gap creation. We used the control treatment (no manipulation) for comparison with Treatments 1 and 2 above to estimate the CWD pool and flux for the second-growth forest. We will follow the long-term decomposition of the CWD that was added, but here we focus on the short-term effects (2 years) of the canopy gap additions.

2.3. Estimating CO₂ flux from CWD

Coarse woody debris respiration was measured in the large (380 m²) subplots only in CWD addition (n = 5) and gap and CWD addition (n = 5) plots. Respiration was not measured in control plots. In early summer 2007, respiration collars (PVC pipe 15 cm diameter × 2.5 cm height) were attached to thirty-four logs and six stumps with a silicone sealant (four replicate logs/stumps per plot). Logs were selected to provide a range of size and decay classes in each plot whenever possible, so sampled logs included a mix of freshly added CWD and pre-existing, older CWD. Since only freshly cut stumps were used, these were confined to the combination of CWD and gap addition plots and were uniform in decay class. Decay classes were assigned based on attributes of bark and soundness of wood (Goodburn and Lorimer, 1998). The classification includes five categories for debris, but due to sample size constraints we combined classes 2 and 3, and 4 and 5 to create a modified three category system. Of the logs that could be identified to species (30 of 40 total), 56% were sugar maple (n = 17) with the remaining being white ash (n = 6), American basswood (n = 5), northern red oak (Quercus rubra, n = 1) and bittersweet hickory (Carya cordiformis, n = 1).

CO₂ flux was measured with a Li-Cor 6200 infrared gas analyzer (Li-Cor Inc., Lincoln, NE) following Bond-Lamberty et al., (2002). The analyzer was calibrated daily with 400 ppm CO₂ and calibrated annually by Li-Cor. Respiration measurements were made in a 15 cm diameter clear acrylic chamber (flow rate 1100 cm³ s⁻¹, in 10 s intervals for 50 s). This allowed for rapid, accurate determination of CO₂ evolution (Norman et al., 1997). A dark towel was placed over the chamber head during every measurement period. In 2007, respiration was measured once in June, and twice in July, August, September and November. In 2008 measurements were conducted monthly from April to November. We randomly assigned the order in which the collars would be measured throughout each multi-day (8 am–6 pm) measurement period. Collars were checked monthly and resealed when needed.

Measured CO₂ flux was expressed per unit of wood mass. The diameter of each sampled log on either side of the collar was recorded and used to calculate the volume and surface area of the log beneath the PVC collar. In the case of stumps, height was substituted for diameter in the Newton formula (in Harmon and Sexton, 1996) to calculate the volume of wood. Density was estimated for the three decay classes of the tree mass species in the site (based on 20 pieces of CWD per class and species; unpublished data). Wood temperature, air temperature, and wood moisture content were measured simultaneously with CO₂ flux. Wood temperature was measured at approximately 2 cm depth using digital long stem thermometers (model No. 15–078 k, Fisher Scientific). Wood moisture at approximately 1 cm depth was measured with a GE Protimeter Timber Master. In May 2008, iButton Temperature Loggers (Maxim Integrated Products Inc., Sunnyvale, CA) were attached to each individual piece of woody debris within 50 cm of the collar and were protected with a solar shield. The data loggers recorded surface temperature at 60 min intervals.

We used a two-stage approach to analyze the effects of the experimental treatments on CWD respiration. First, we used a mixed model with random and fixed effects and repeated measures to test if and how the treatment influenced the moisture and temperature of the CWD. Next, we included these microclimatic variables as covariates in an analysis of covariance to test if the experimental treatment had any effect on the relationship between the response variable (CWD respiration) and covariates. This repeated measures mixed model included (1) treatment (gap or control), and (2) time (15 measurement rounds) as fixed class variables; (3) log mid-diameter, wood temperature and wood moisture as covariates; and (4) a random variable since logs within plots are not independent observations. A heterogeneous autoregressive covariance structure was used since measurements closer in time were likely to be more related than those with further separation in time (Littell et al., 2005). Beginning with a full model, an iterative approach was used to remove insignificant variable combinations with the final model selected based on the lowest Akaike’s Information Criterion (Burnham and Anderson, 2002).

Pearson’s correlation and least squares regression analyses were used to assess strength of the linear relationship among wood moisture, temperature and respiration. Full and partial models were compared to identify the significance of measured variables (temperature, moisture, the interaction of temperature and moisture, quadratic of temperature, decay class, and debris volume) on CWD respiration rates. Since fluxes exhibited positive exponential relationships with temperature and moisture, both correlations and regressions were performed on log transformed flux rates.

2.4. Estimating the CWD pool

Coarse woody debris mass was sampled in control (n = 10), woody debris addition (n = 5) and woody debris and gap creation plots (n = 5) in 2008. Although snags were also inventoried as part of the project, we included only downed CWD and stumps in this paper. All CWD ≥ 20 cm in diameter was measured within each 80 × 80 m plot. Debris between 10 and 20 cm diameter was sampled within each of the subplots (50, 200 and 380 m²); the created
gap area in the gap and CWD addition treatment). For each piece encountered within the fixed area, measurements included the species (when possible), decay class, length, and diameter at each end and in the middle. The length and diameter of any hollow areas were estimated using a diameter tape. We used a five class system to describe the decay class of CWD (Goodburn and Lorimer, 1998); the lowest class had the least decayed wood and the highest class contained the most decayed. Volume was calculated using Newton’s formula and hollow areas were subtracted (Harmon and Sexton, 1996). A C to dry biomass ratio of 0.48 was used, based on analyses of wood samples from the site (unpublished data).

2.5. Estimating annual C flux

The instantaneous CO2 flux and wood temperature measurements were used to develop empirical equations. The continuous surface temperature data were used with the empirical models to scale instantaneous flux to annual time budget. Non-linear models were fitted using measurements of wood temperature and respiration from 2008. The daily C flux from each location was modeled using the surface temperature data from each individual collar location in 2008. The annual CWD flux from the site was estimated by summing the daily modeled flux for an extended growing season (196 days). The use of a shortened season is based on the assumption that no respiration takes place when the air temperature was <0 °C for four consecutive weeks (Bond-Lamberty et al., 2002). Decay rate constants were calculated for downed CWD based on the annual flux as a proportion of CWD C pool. Average lifetimes, or the time for loss of 95% of the CWD mass were estimated assuming a single-component, negative exponential decay model ($t_{0.95} = (-\ln 0.05)/k$; Mackensen and Bauhaus, 2003). All analyses were performed using SAS (SAS, 2008; System for Windows, Version 9.2, SAS Institute Inc., Cary, NC, USA).

3. Results

3.1. Gap influence on CWD temperature, moisture and respiration

Temperatures of CWD were greater in the gaps than beneath closed canopy, although the magnitude of these differences changed over time (treatment by time interaction, $p < 0.0001$), with significant differences especially at the peak of the growing seasons (Fig. 2). Differences in CWD temperatures ranged from 0.2 to 5.0 °C. Moisture content of CWD differed between gap and undisturbed canopy, but the differences varied between years. Debris moisture content was significantly greater for CWD in gaps than undisturbed canopy in the late fall of 2007, but moisture was lower in gaps than undisturbed canopy in 2008 (treatment by time interaction, $p = 0.0031$, Fig. 2). Debris in the most advanced decay stages

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Fig. 2. The mean CWD temperature (A) and moisture (B) (and SE) in gap and undisturbed (nongap) canopy conditions periodically measured throughout 2007–2008. Canopy gaps (380 m²) were created in January 2007. The line represents annual air temperature at the site across the measurement period. Asterisks (along the x-axis) indicate significant differences between the gap and non-gap treatments ($p < 0.1$).
was wetter and cooler than less decayed CWD in both growing seasons (Table 1).

Coarse woody debris CO2 flux exhibited a seasonal pattern similar to air and soil surface temperature (Stoffel et al., 2010), with means of sampling periods ranging from 0.1 to 1.1 µmol kg⁻¹ s⁻¹. Inspection of the raw respiration means per treatment and measurement period indicated that during the first growing season following gap creation, differences in respiration between treatments was consistently higher in gaps but not significantly so (Fig. 3). The ANCOVA was used to examine the regression relationship between temperature and moisture (covariates) and treatments. A significant interaction term indicated that the gap treatment altered the relationship between CWD respiration, temperature and moisture (p = 0.03, Table 2). Differences in CWD CO2 efflux between treatments depend on the interaction of temperature and moisture levels of the debris. Since the slopes of the response variable differed the means were not adjusted for the covariates and differences in relationships were examined further using regression analysis.

3.2. Relationships between CWD respiration and environmental conditions

Correlations between environmental variables and respiration rates were similar beneath gaps and undisturbed canopy, but stronger in the latter environment. Respiration rates were positively correlated with CWD moisture, air temperature and CWD temperature in undisturbed canopy plots (p < 0.0001; r² = 0.117, 0.271, and 0.176, respectively). In gap plots, respiration was positively correlated with air temperature and wood temperature (p < 0.0001; r² = 0.109 and 0.108, respectively) and weakly related to wood moisture (p = 0.02; r² = 0.02). Wood and air temperature were highly correlated (p < 0.0001; r² = 0.9) in both treatments. A significant, but weak negative relationship between wood moisture and temperature was measured within the gap treatment (p < 0.0001; r² = 0.1).

The best model explained 60% and 23% of variation in CWD respiration in gaps and undisturbed canopies respectively. Beneath the undisturbed canopy, respiration was best predicted by the decay class of the debris (0.36, partial r²), interaction of wood temperature and moisture (0.32), wood temperature (0.16) and wood moisture (0.12) (model Adj r² = 0.60). The best models for predicting respiration in the gap treatment included wood temperature and the quadratic temperature term (0.1, 0.04), CWD diameter (0.1), and decay class (.04) (Adj r² = 0.23). Restricting the analysis to logs only in the gap treatment plots (removing 6 stumps, leaving 14 logs), improved the model (Adj r² = 0.47) and incorporated variables similar to those model for the undisturbed canopy treatment (decay class-25%, temperature by moisture-23%, wood temperature-14%).

3.3. Carbon pool in CWD

Coarse woody debris mass averaged 4.9 ± 1.8 Mg ha⁻¹ in control and 22.1 ± 5.3 Mg ha⁻¹ in plots receiving CWD additions (Table 3). Before CWD additions, fifty-two percent of the CWD was in decay classes 2 and 3, while 31% was in decay class I and the remaining 17% in the most advanced decay classes.

Table 1

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Air Temp. (°C)</th>
<th>Decay Class</th>
<th>% Moisture</th>
<th>Wood Temp. (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2007</td>
<td>2008</td>
<td>2007</td>
<td>2008</td>
</tr>
<tr>
<td>Gap</td>
<td>17.8 ± 1.1</td>
<td>16.0 ± 1.0</td>
<td>20.0 ± 1.0</td>
<td>24.0 ± 1.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>18.0 ± 1.2</td>
<td>18.0 ± 1.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>I (n = 10)</td>
<td>20.0 ± 1.0</td>
<td>24.0 ± 1.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>II/III (n = 3)</td>
<td>18.9 ± 2.1</td>
<td>25.0 ± 3.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>IV/V (n = 6)</td>
<td>40.5 ± 2.8</td>
<td>42.5 ± 3.2</td>
</tr>
<tr>
<td>Non-gap</td>
<td>16.4 ± 1.1</td>
<td>15.5 ± 1.1</td>
<td>20.8 ± 1.3</td>
<td>29.0 ± 2.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>I (n = 7)</td>
<td>23.0 ± 1.9</td>
<td>25.7 ± 2.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>II/III (n = 7)</td>
<td>40.2 ± 3.4</td>
<td>45.9 ± 2.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>IV/V (n = 6)</td>
<td>40.2 ± 3.4</td>
<td>45.9 ± 2.9</td>
</tr>
</tbody>
</table>

Fig. 3. The mean CWD respiration (and SE) in canopy gaps and in undisturbed (non-gap) canopy conditions. CO2 flux was measured on selected dates the first two seasons (2007 and 2008) following gap creation (January 2007). The line represents annual air temperature at the Flambeau across the measurement period.
table 2
Results from ANCOVA testing for differences in CWD respiration between treatments using discrete measurements of CWD temperature and moisture as covariates. Measurement rounds for both growing years were combined in the analysis.

<table>
<thead>
<tr>
<th>Effect</th>
<th>DF</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Measurement round</td>
<td>14,146</td>
<td>1.70</td>
<td>0.0616</td>
</tr>
<tr>
<td>Temp.</td>
<td>2319</td>
<td>6.83</td>
<td>0.0094</td>
</tr>
<tr>
<td>Moisture²</td>
<td>1309</td>
<td>0.16</td>
<td>0.6891</td>
</tr>
<tr>
<td>Treatment</td>
<td>1111</td>
<td>1.12</td>
<td>0.2918</td>
</tr>
<tr>
<td>Temp × Temp</td>
<td>1285</td>
<td>22.27</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Moisture² × time</td>
<td>14,135</td>
<td>2.49</td>
<td>0.0036</td>
</tr>
<tr>
<td>Temp × time</td>
<td>14,146</td>
<td>2.25</td>
<td>0.0086</td>
</tr>
<tr>
<td>Temp × moisture²</td>
<td>1290</td>
<td>0.01</td>
<td>0.9041</td>
</tr>
<tr>
<td>Moisture² × treatment</td>
<td>1110</td>
<td>1.96</td>
<td>0.1647</td>
</tr>
<tr>
<td>Temp × treatment</td>
<td>1187</td>
<td>3.95</td>
<td>0.0482</td>
</tr>
<tr>
<td>Temp × moisture² × treatment</td>
<td>1178</td>
<td>4.48</td>
<td>0.0357</td>
</tr>
</tbody>
</table>

* Data were log transformed.

Table 3
Decay class distribution of CWD (> 10 cm diameter) biomass (Mg ha⁻¹) in control (no manipulation) and CWD addition plots. Values are means with standard errors (n = 20).

<table>
<thead>
<tr>
<th>Decay class</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>1.5 ± 0.9</td>
<td>1.6 ± 0.6</td>
<td>1.0 ± 0.2</td>
<td>0.6 ± 0.1</td>
<td>0.3 ± 0.1</td>
</tr>
<tr>
<td>CWD addition</td>
<td>18.6 ± 4.2</td>
<td>14.4 ± 0.4</td>
<td>13.0 ± 0.4</td>
<td>0.4 ± 0.1</td>
<td>0.4 ± 0.2</td>
</tr>
</tbody>
</table>

3.4. Upscaling of daily and annual flux

Daily C flux was predicted using surface temperature data from 2008 and equations derived from discrete field measurements of CWD temperature and respiration (Table 4). The modeled daily CWD respiration varied from 0.38 to 0.84 g C kg⁻¹ day⁻¹ in the growing season of 2008 (Fig. 4). The annual C flux was 128.2 g C kg⁻¹ year⁻¹ in canopy openings and 108.5 g C kg⁻¹ year⁻¹ in the undisturbed canopy locations.

Annual flux per unit area (scaled using CWD pool estimates) was 0.53 Mg C ha⁻¹ year⁻¹, in undisturbed canopy plots. When the respiration rate is scaled to the experimental plots where CWD was added, the annual C flux increases to 2.45 Mg C ha⁻¹ year⁻¹ due to the higher CWD biomass.

The annual decay rate (k) for CWD was 0.07 to 0.08 year⁻¹ for the two post-treatment growing seasons. The average lifetime of the logs based on an exponential model of decay ranged from 37 to 43 years for CWD under undisturbed canopies, while the lifetime was 35–40 years within canopy gaps.

4. Discussion

4.1. Treatment and microclimate influence

Our central question focused on whether the changes in microclimate within canopy openings would influence the rate of CO₂ flux from CWD. Since respiration is often strongly correlated with temperature and moisture, and these factors are strongly influenced by canopy cover, we hypothesized that canopy removal would have a stimulatory effect on respiration rates. We found the gap treatment increased the CWD respiration rates, but altered the relationship between the temperature and moisture of CWD. The higher air temperature in gaps likely both dried and heated the debris, despite the higher soil moisture availability within the openings (Stoffel et al., 2010). In general, during the growing season the CWD beneath the undisturbed canopy was both moister and cooler than debris in the gaps (Table 1; Fig. 2). However, during spring and fall, periods of high precipitation and cooler temperatures, CWD in gaps retained more moisture than CWD beneath undisturbed canopy, which was in contrast to the general pattern of drier and warmer debris in the gaps.

Differences in CWD temperature between gaps and undisturbed canopies declined in significance in the second year. We speculate that this may be due to changing vegetation patterns and shading within the gaps in the two seasons. In the first growing season following treatment, understory plant biomass and productivity were significantly lower than the surrounding undisturbed canopy areas; however, in the second post-treatment growing season understory biomass was over three times greater than the previous year and two times that of the undisturbed canopy (Dyer et al., 2010). The increased plant cover resulted in a more shaded environment for the CWD and soil surface and caused a reduction in temperature, evaporation, throughfall, and nutrient availability. Yet, CWD experienced higher daily maximum temperatures within the canopy gaps (20.9 °C ± 0.2) versus non-gap locations (18.3 °C ± 0.1). Alternatively, differences in annual air temperature could also explain the pattern, though overall the mean air temperature in gaps was greater than in non-gaps in both years (Table 1).

The moisture content of CWD has previously been identified as a key variable affecting decomposition (Progar et al., 2000) with the strongest effects exhibited at low and high moisture extremes (Chambers et al., 2001; Wang et al., 2002). High moisture inhibits decay by obstructing fungal growth and/or limiting available oxygen, both of which result in lower respiration rates (Rayner and Boddy, 1988; Progar et al., 2000). Although differences in moisture

Table 4
Parameters from the empirical model, \( R_{\text{CWD}} = a e^{bT} \), used to scale instantaneous flux to an annual time budget, where \( R_{\text{CWD}} \) is daily coarse woody debris respiration (µmol kg⁻¹ s⁻¹) and T is wood surface temperature (°C).

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>Treatment</th>
<th>Parameters</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wood temperature</td>
<td>Gap</td>
<td>( a = 0.4338 ± 0.0626 )</td>
<td>( b = 0.0268 ± 0.0080 )</td>
<td>128.2</td>
</tr>
<tr>
<td></td>
<td>Non-gap</td>
<td>( a = 0.2709 ± 0.2095 )</td>
<td>( b = 0.0491 ± 0.0149 )</td>
<td>126.10</td>
</tr>
</tbody>
</table>

Fig. 4. Measured and modeled daily CWD carbon flux by gap and non-gap (undisturbed canopy) treatment in the northern hardwood forest for 2008. Symbols represent measured field data (gaps = circles, non-gaps = squares, bars = SE) and lines represent modeled daily data.
were apparent between gap and non-gap canopy conditions, these differences were relative and neither canopy treatment condition experienced extremes in moisture conditions. The regression analyses confirmed that while respiration was positively related with temperature and moisture in both gap and undisturbed canopy treatments, temperature most strongly influenced patterns of CWD respiration.

4.2. Other important factors

Based on our regression models, other factors that remain to be measured are likely important for interpreting the variability of the CWD respiration rates, especially within the canopy gaps. Our modeling of annual respiration based on surface temperature alone is consistent with instantaneous measurements for closed canopy conditions (Fig. 4), but departs widely from measurements from gap conditions at different times of the season. Clearly, other factors need to be monitored and included in predicting annual estimates for heterogeneous forest conditions.

We speculate that differences in microbial activity in CWD within the gaps may help to explain more of the observed variation. Studies examining patterns of epixylic species composition have found the decay state and species of the CWD to be the primary influences of microbial community composition, with the greatest microbial species richness occurring on CWD in intermediate stages of decay (Lindblad, 1998; Heilmann-Clausen, 2001). Structural features at the log scale, such as the percentage of bark cover and amount of decayed areas present have been found to be important for ectomycorrhizal fungi (Rubino and McCarthy, 2003), while moisture patterns at both the log and plot scale correlate with the presence of myxomycetes (slime molds) (Heilmann-Clausen, 2001; Rubino and McCarthy, 2003). Debris size and the amount of CWD per unit area have also been found to correlate with epixylic species richness (Rayner and Boddy, 1988; Humphrey et al., 2002). It is possible that the higher CWD load and more variable microhabitat conditions within canopy gaps host a more diverse and possibly more abundant group of wood-inhabiting biota. We speculate that with time, either more colonization will occur and patterns between treatments may become even more different; or microclimate may differentially moderate the treatment effect.

This study contributes to the mixed results reported for the influence of diameter on CWD respiration rates. Our range of diameters available in the 100 year old northern hardwood stand is substantially smaller than that available in Pacific Northwest forests in which diameter has been shown to be an important factor (Harmon et al., 1986). The diameter range of our experimental logs was 19–65 cm, with a median diameter of 30 cm in the undis turbed forest and 35 cm in the gaps. Several recent discussions indicate the inconsistencies of the diameter effect on decomposition rates (Mackensen et al., 2003; Shorohova et al., 2008), though when focusing on just two coniferous species a meta-analysis indicated a strong negative correlation between decay rate and log diameter (Mackensen et al., 2003).

We did not seek to separate the effect of tree species on CWD respiration in this study since the Flambeau is dominated by angiosperm species that are all relatively non-resistant to decay. However, Marra and Edmonds (1996) found rates differed significantly between species when sampling western hemlock (Tsuga heterophylla) and Douglas-fir (Pseudotsuga menziesii), both gymnosperms, but Liu et al., (2006) found only a few differences in a select number of decay classes when focusing on eastern North America species (hardwoods and eastern hemlock). Arthur et al. (1992) found bole decay rates among species to differ mostly between conifers and hardwoods, but of the species common to our studies, maple was found to decompose faster than ash. Differences in physiology, anatomical structure, lignin and other secondary compounds, and nutrient content of wood among species may help to explain decay resistance and our reported variation in CWD respiration.

4.3. C loss in context

Elsewhere we detail the effects of canopy openings on soil respiration (Stoffel et al., 2010) and aboveground productivity (Dyer et al., 2010). Stoffel et al., (2010) estimated annual soil respiration to range from 9.6 to 10.1 Mg C ha$^{-1}$ year$^{-1}$ among treatments. Using the equation for the heterotrophic component of soil respiration derived by Bond-Lamberty et al., (2004), we estimated the heterotrophic portion of soil respiration to range from 5.1 to 5.3 Mg C ha$^{-1}$ year$^{-1}$, Respiration occurring from CWD in this second-growth northern hardwood forest contributes 10% as much C to the atmosphere as does the soil. In experimental plots where we have added additional woody debris, CWD respiration is 46–48% of the heterotrophic soil flux.

Our estimate of annual CWD C flux from a second growth northern hardwood forest is within the range of other studies reporting such measures (Table 5). These estimates are products of a variety of methodologies, ranging from chronosequences to direct measures of gas flux. Recently, Herrmann and Bauhus (2008) estimated that attaching collars to the CWD bark could potentially underestimate real CO$_2$ flux by up to 74%, however, creating chambers to enclose the large logs and stumps was not feasible. An advantage to our method was that the samples were left intact in the field to experience natural climatic conditions. By not using a chamber method, we avoided both a diameter constraint and the necessity to cut samples. We opted to adhere collars to the bark surface, rather than to the ends of logs since this reflects the majority of

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**Table 5**

Annual coarse woody debris (CWD) carbon flux (FCWD) and pools reported from this study and compared to others.

<table>
<thead>
<tr>
<th>Annual FCWD (Mg C ha$^{-1}$ year$^{-1}$)</th>
<th>CWD Pool (Mg C ha$^{-1}$)</th>
<th>Forest type (dominant species of CWD)</th>
<th>Latitude</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.11–1.92</td>
<td>1.4–177.6</td>
<td>Boreal, Manitoba, Canada, Picea mariana fire chronosequence</td>
<td>55°53’</td>
<td>Bond-Lamberty et al. (2002)</td>
</tr>
<tr>
<td>0.42–0.45</td>
<td>NA</td>
<td>Old-growth northern hardwood, Michigan, Acer - Tsuga</td>
<td>46°14’</td>
<td>Tang et al. (2008)</td>
</tr>
<tr>
<td>0.3–2.3</td>
<td>35.5–198.5</td>
<td>Old-growth coniferous, Washington, Tsuga heterophylla and Pseudotsuga menziesii</td>
<td>45°49’</td>
<td>Janisch et al. (2005)</td>
</tr>
<tr>
<td>0.5</td>
<td>4.9</td>
<td>100 year old northern hardwood, Wisconsin Acer, Tilia, Prunus</td>
<td>45°35’</td>
<td>This study</td>
</tr>
<tr>
<td>0.21</td>
<td>2.2</td>
<td>90 year old aspen, Michigan, Populus grandidentata</td>
<td>45°35’</td>
<td>Gough et al. (2007)</td>
</tr>
<tr>
<td>0.30–0.35</td>
<td>2.6–9.9</td>
<td>Maturing northern hardwood, Massachusetts, Quercus, Acer, Betula, Tsuga</td>
<td>42°32’</td>
<td>Liu et al. (2006)</td>
</tr>
<tr>
<td>1.6</td>
<td>32.7</td>
<td>Old-growth spruce-fir, GSMNP, North Carolina/Tennessee, Picea, Abies, Betula</td>
<td>35°34’</td>
<td>Van Miegroet et al. (2007)</td>
</tr>
<tr>
<td>0.5</td>
<td>3.7</td>
<td>2nd-growth temperate deciduous, Kyoto, Japan, Quercus serrata, Ilex pedunculosa, Pinus densiflora</td>
<td>34°47’</td>
<td>Jomura et al. (2007)</td>
</tr>
</tbody>
</table>
the surface area of CWD in the site. Our estimates are similar to other studies using a chamber method and reflect the trends that a higher wood CO2 flux would be prevalent in sites that have either (1) warm, moist conditions or (2) higher biomass of CWD. In time, we can revisit the CWD and compare decomposition rates estimated from inventories with these based on instantaneous measures, such as Bond-Lamberty and Gower (2008) have done to assess boreal CWD dynamics.

The overall annual decomposition rate constant (k) of 0.07–0.08 year−1 for CWD at our site is comparable with other published rates of 0.09 year−1 for northern hardwood forest in New Hampshire and Massachusetts (Arthur et al., 1993; Liu et al., 2006, respectively). The k is also similar to aspen in northern Michigan and Minnesota that ranges from 0.08 to 0.09 year−1 (Alban and Pastor, 1993; Gough et al., 2007) and to Japanese red pine logs in a secondary broad-leaved temperate forest in Japan (Jomura et al., 2008), but higher than many other published values based on either coniferous species or colder climates.

Although we included the major controlling factors for woody debris respiration, we still have models that describe just over half of the variation. With future efforts we hope to examine the influence of tissue chemistry and density on the decay process as well as re-sampling CWD to further test and refine our models. Modeling annual CWD respiration with wood temperature alone is currently underestimating the differences between the two studied canopy conditions. Future studies should include continuous measurements of wood moisture at a minimum. Ultimately long-term field experiments are critical to the calculation of CO2 emissions from land-use change and forest management (Mackensen et al., 2003).

5. Conclusions

This study demonstrates how changing environmental conditions may alter decomposition rates and influence ecosystem C balance. We showed that CWD in canopy gaps experiences greater surface temperatures and decreased moisture conditions throughout most of the growing season. In undisturbed canopy areas, CWD respiration was related to the interaction of moisture and temperature of the CWD. The addition of experimental canopy gaps altered the relationships among CWD respiration, moisture and temperature. CWD respiration in these small gaps exceeds rates under intact canopy by 18%. Because gaps typically occupy only a minimal percentage of the forest, C flux from CWD in gaps at a landscape scale may be modest at times. However, in experimental treatments where CWD was added, the annual C flux increased over four times the rate from undisturbed conditions. Following a major disturbance event with larger transfers of wood to the forest floor, or in forests where microclimatic changes are more pronounced in gaps, these pulses of CWD respiration from gaps deserve more attention. Ultimately, the quantification of decomposition and accumulation of CWD in forests from a variety of climate, age, disturbance history and species types is important and will be useful for inclusion into models of global forest C cycling.

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References
