Oecologia (2015) 179:889–900
DOI 10.1007/s00442-015-3393-4

ECOSYSTEM ECOLOGY - ORIGINAL RESEARCH

Temporal trends and sources of variation in carbon flux from coarse woody debris in experimental forest canopy openings

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Received: 12 January 2015 / Accepted: 7 July 2015 / Published online: 23 July 2015

Abstract Pulses of respiration from coarse woody debris (CWD) have been observed immediately following canopy disturbances, but it is unclear how long these pulses are sustained. Several factors are known to influence carbon flux rates from CWD, but few studies have evaluated more than temperature and moisture. We experimentally manipulated forest structure in a second-growth northern hardwood forest and measured CO_2 flux periodically for seven growing seasons following gap creation. We present an analysis of which factors, including the composition of the wood-decay fungal community influence CO_2 flux. CO_2 flux from CWD was strongly and positively related to wood temperature and varied significantly between substrate types (logs vs. stumps). For five growing seasons after treatment, the CO_2 flux of stumps reached rates up to seven times higher than that of logs. CO_2 flux of logs did not differ significantly between canopy-gap and closed-canopy conditions in the fourth through seventh post-treatment growing seasons. By the seventh season, the seasonal carbon flux of both logs and stumps had decreased significantly from prior years. Linear mixed models indicated the variation in the wood inhabiting fungal community composition explained a significant portion of variability in the CO_2 flux along with measures of substrate conditions. CO_2 flux rates were inversely related to fungal diversity, with logs hosting more species but emitting less CO_2 than stumps. Overall, our results suggest that the current treatment of CWD in dynamic forest carbon models may be oversimplified, thereby hampering our ability to predict realistic carbon fluxes associated with wood decomposition.

Keywords Canopy gap · Carbon flux · Coarse woody debris · Heterotrophic respiration · Stumps · Wood-decay fungi

Communicated by Hakan Wallander.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-015-3393-4) contains supplementary material, which is available to authorized users.

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Introduction

Coarse woody debris (CWD) is a critical component of forest biomass, and hence carbon storage representing up to 20 % of total aboveground biomass (Laiho and Prescott 1999; Bradford et al. 2009). This large store of carbon is beneficial to forested ecosystems because it is more slowly released to the atmosphere when compared to other ecosystem components. However, the rate of carbon flux from CWD fluctuates over time (Harmon 2011); in particular, following disturbance, it can be a major contributor to ecosystem carbon losses, via heterotrophic respiration.

Estimating the carbon flux of decomposing CWD remains an enormous challenge, simply because of the lengthy time scale of the process itself. One approach to quantifying CWD decomposition is the use of chronosequences, which can estimate decay rates based on density, volume, and/or biomass depletion through time (Janisch et al. 2005; Bond-Lamberty and Gower 2008; Fraver et al. 2013; Russell et al. 2014). This approach probably best captures leaching and fragmentation losses, two of the three primary mechanisms of decomposition (Harmon et al. 1986), but may not also represent losses from heterotrophic respiration. An alternative approach is to directly measure the heterotrophic respiration from CWD and use these measurements to estimate annual carbon fluxes. This approach may poorly represent fragmentation losses, depending on the phase of decomposition considered. Bond-Lamberty and Gower (2008) found that decomposition rates obtained by re-sampling pools in a chronosequence were relatively similar to those estimated from direct measurement of heterotrophic respiration. The quantification of CO_2 respired by the CWD pool is increasingly reported because it is an important component of the current and long-term carbon balance of the forest ecosystem, especially following disturbances (Bond-Lamberty 2002; Gough et al. 2007; Harmon 2011).

CO_2 flux from CWD is thought to primarily result from the activity of heterotrophic organisms, principally fungi, in early stages of decay (Carpenter et al. 1988; Marra and Edmonds 1994). With time, autotrophic respiration from the intrusion of roots may increase in importance (Carpenter et al. 1988). Air temperature and characteristics of the wood itself have proven to influence respiration rates and are therefore suggested as inputs for ecosystem carbon models. The direct role of moisture has been more difficult to explain in field settings, although laboratory studies clearly indicate its importance (Hermann and Bauhus 2013). Generally, respiration patterns follow the interactions of temperature and moisture through the growing season, with the highest rates in the moderately wet, warm late summer and lower rates when either temperature or moisture is extreme. Marra and Edmonds (1994, 1996) compared respiration rates from logs in an undisturbed closed canopy forest with logs in a recent clearcut and concluded that the increased temperatures of open conditions resulted in higher respiration rates from CWD throughout most of the season. The exception to this was during the winter when respiration rates and temperatures from the clearcut environment were lower than the forested environment. In addition to environmental parameters, biotic factors such as substrate species and their associated density and anatomical features, decay class, and previous growth rates and bryophyte cover have a strong influence on respiration and decomposition rates (Carpenter et al. 1988; Wang et al. 2002; Hermann and Bauhus 2013; Fraver et al. 2013). Additional measures such as ground contact and the presence/absence of fungal fruiting bodies have also been used for predicting respiration rates (Vanderhoof et al. 2013).

Since environmental parameters typically explain less than half of the observed variation in decomposition rates (Liu et al. 2013), understanding how other factors including wood-decay fungal composition relate to decomposition dynamics is critical (Bradford et al. 2014). Earlier experimental investigations of CO_2 flux from CWD indicated that sheltered logs that had been inoculated with decay fungi had higher respiration than uninoculated logs, but the difference was temporally quite transient (Progar et al. 2000). Jacobs and Work (2012) found changes to forest structure following harvesting caused increased temperature and decreased wood moisture, which stimulated the activity and growth rates of the decomposer community, especially the wood-feeding beetle community. These studies indicate that disturbance-mediated changes to forest structure, the associated microclimate, and fungal composition can alter CWD decomposition rates and hence carbon pools in the post-disturbance stands. It is known that the interactions of temperature, moisture, nitrogen and oxygen concentrations have significant effects on the growth of wood decay fungi (Blanchette 1991). However, specific relationships between the wood-decay fungal community and CO_2 flux from CWD remain largely understudied.

We experimentally manipulated the forest structure in a second-growth northern hardwood forest to investigate the effects of these changes on ecosystem functioning (Forrester et al. 2013). Manipulations included the creation of variable sized canopy openings and the addition of woody debris. An earlier study reported that, for the first 2 years following gap creation, CO_2 flux from CWD was higher in canopy openings than in closed canopy conditions (Forrester et al. 2012). We found respiration had a more complex relationship with temperature and moisture in gap conditions than in closed canopy conditions where temperature explained a significant portion of the variability we observed. Noormets et al. (2012) found the pulse of respiration contributed by woody debris post-disturbance lasted only 2 years, yet Carpenter et al. (1988) found a strong increase in respiration rates of logs occurring the second year of decomposition, corresponding to the time it takes for colonization by decomposing organisms.

We also observed that the flux of CO_2 from stumps versus logs immediately after gap creation was quite different, but our low sample size limited the interpretation. The few studies comparing decomposition rates of stumps and logs have used a chronosequence approach and reported that these substrate types decomposed at the same rate (Janisch et al. 2005) or that stumps decomposed more quickly (Tobin et al. 2007; Shorohova et al. 2008; Shorohova and Kapitsa 2014). Because Janisch et al. (2005) found stump

and log wood density were not significantly different, they supported the substitution of log decay rates in carbon flux models when stump rates were unknown. We felt additional investigation was important because this simplification might lead to substantial underestimation of the carbon flux of an intensively managed landscape.

Here, our experimental design allowed us to simultaneously address post-disturbance temporal trends and multiple sources of variation in the CO_2 flux rate from CWD. We focused on three questions: (1) how long are higher respiration rates sustained in recent gaps versus closed canopy environments; (2) do CO_2 flux rates differ based on the type of debris, logs versus stumps; and (3) how does the composition of the wood-decay fungal community influence respiration rates of the substrate? Often, the CWD flux component of forest ecosystem carbon models is only roughly estimated (Gough et al. 2007), but, because of its large size and persistence, more comprehensive carbon budgets should include all components. Understanding the temporal patterns and factors controlling CO_2 flux rates for CWD will help to better estimate forest carbon dynamics.

Materials and methods

We measured CO_2 flux, temperature and moisture of logs and stumps from experimentally replicated plots which are part of an existing long-term field experiment investigating the effect of forest structural heterogeneity on ecosystem function. Canopy gaps were created and woody debris was added to a second-growth northern hardwood forest to test how these structural elements separately and in combination influence forest productivity (Dyer et al. 2010), carbon dynamics (Forrester et al. 2013), and diversity of wood-inhabiting fungi (Brazee et al. 2014). The 300-ha study site is within the Flambeau River State Forest, northern Wisconsin, USA (45°37.4′N, 90°47.8′W). *Acer saccharum*, *Tilia americana* and *Fraxinus americana* are the dominant overstory species in even-aged stands with most tree establishment between the 1920s and 1940s.

Experimental design of the larger study includes five replicate plots of seven treatments [control; woody debris (WD) addition; gap creation; gap + WD addition; deer exclusion; gap + deer exclusion; and mechanized control] randomly assigned to 35, 80 × 80 m (0.64-ha) plots. The WD treatment was a whole-plot treatment with the volume varying by plot depending on the pre-existing WD present. Plots receiving the WD addition treatment were brought to volumes comparable to typical old-growth northern hardwood stands in the region (i.e., 29 Mg ha^{-1}; Goodburn and Lorimer 1998). The material used for the WD additions was all from within the immediate study site. The gap creation treatment was a split-plot treatment with three circular canopy openings (50, 200 and 380 m^2) created in each whole plot assigned to this treatment. Sampling subplots of equal size were established in all non-gap treatment plots. Treatments were applied in late January 2007 on frozen ground conditions and snow cover with a PONSSE Ergo harvester and PONSSE Buffalo forwarder.

CO_2 flux of CWD and environmental parameters

CO_2 flux was later measured in the large subplots of the WD addition ($n = 5$), gap creation ($n = 5$), and gap + WD addition ($n = 5$) treatment plots. In May 2010, respiration collars (PVC pipe 20 cm diameter × 2.5 cm height) were custom-fit and attached to logs and stumps using silicone caulk. In all cases, we were careful that collars were tightly sealed to the substrate; in some cases, we molded duct seal compound to fill voids. The seal was checked before each round of measurements. In each WD addition plot, three logs were selected, and a respiration collar was attached to the side and cut end of each log. In each gap creation plot, three stumps were selected, and one collar was attached to the cut surface of the stump. In each gap + WD addition plot, three stumps and three logs were selected, and collars were attached to either the stump surface or the cut end and side of a log. Overall, 90 collars were attached to 60 individual pieces of debris.

CO_2 flux of CWD was measured with a LI-8100 infrared gas analyzer and 20-cm survey chamber (Li-Cor, Lincoln, NE, USA) with a single 90-s measurement at each collar. CO_2 flux at all collars was measured within a 1- to 2-day period approximately every 4 weeks from May to November 2010, April to October 2011 and May to October 2013, the 4th, 5th and 7th growing seasons post-harvest. Plot measurement order was randomized each round of sampling. Wood temperature and moisture were measured immediately adjacent to respiration collars simultaneously with CO_2 flux. In May 2010, iButton Temperature Loggers (Maxim Integrated Products, Sunnyvale, CA, USA) were attached to the sample logs and stumps within 10 cm of each collar, recording bihourly temperatures through October 2013. The species and dimensions (diameter on either side of the collar, height, length of entire log) were recorded for all stumps and logs.

Survey of wood-decay fungi

Wood-inhabiting fungal species on all fine and CWD were inventoried in October 2011 as part of a companion study (see Brazee et al. 2014). Here, each respiration log/stump was assessed for the presence of polyporoid and corticoid fungal fruiting bodies. If a fruiting body was not readily identified to species in the field, a portion was collected, dried and identified in the laboratory using microscopic

analysis of morphological features or DNA sequencing of the internal transcribed spacer region.

Coarse woody debris pool

All CWD was inventoried in fall 2008; detailed methods are reported elsewhere (Forrester et al. 2013). Briefly, the species, decay class (using a 5-class system), length, diameter (at middle and ends), and hollow area were recorded for each CWD piece. Material 10 to <20 cm diameter of the large end was sampled on 380-m^2 fixed-area plots. Material >20 cm in diameter of the large end was sampled on 2290-m^2 fixed-area plots. Volume was calculated using Newton's formula (Harmon and Sexton 1996), and was converted to dry biomass using decay class specific densities estimated from the site and from published values (Supplementary Appendix 1). A carbon mass to dry biomass ratio of 0.48 was used, based on tissue analyses from the site.

Statistical analyses and scaling

We calculated the mean CO_2 flux, temperature and moisture per plot, measurement round and year. The relationship between CO_2 flux and wood temperature for substrate type and environment was determined using PROC REG in SAS v.9.3 (SAS Institute, 2010). Non-linear regression models relating wood temperature and CO_2 flux were used to model daily carbon flux from May through October (Julian days 128–301) using daily mean temperatures calculated from the iButton records for 2010–2013. Models were developed using collar-level measurements from all years and sampling rounds in PROC NLIN. Daily flux was summed for the period to produce an annual flux that was used in mixed model analysis of variance using PROC MIXED in SAS. The mixed model tested the main effects of treatment and year and assigned replicate plots within a treatment as random effects. Respiration rates were extrapolated to the treatment scale by multiplying annual respiration per kilogram of wood (g C kg^{-1} $season^{-1}$) to the CWD biomass measured in treatment plots (kg C ha^{-1}).

For illustrative purposes, we included previously collected data summarizing the mean CO_2 flux from CWD, temperature and moisture in 2007 and 2008. All data and associated methods are reported in Forrester et al. (2012); however, the CO_2 flux from stumps was not included in the earlier study due to a small sample size ($n = 6$ stumps). These measurements were made on different pieces of debris than those used from 2010 to 2013. Data from these 2 years (2007–2008) were not included in any analyses conducted here.

A Bray–Curtis ordination was performed to characterize the wood decay fungal communities on the respiration logs and stumps using PC-ORD (McCune and Mefford 2011). The primary matrix was composed of the presence–absence of fungal species (columns, $n = 20$) by host substrate (rows, $n = 20$). A secondary matrix composed of substrate parameters (large-end diameter, volume, surface area, substrate species), diversity metrics (richness, Simpson's, Shannon–Weaver), and annual CWD C flux was used in an overlay to examine relationships.

Linear mixed effects models with repeated measures were used to test the effects of overstory treatment, substrate type, wood-decay fungal community composition and substrate characteristics, as they influence CO_2 flux rates (using PROC MIXED in SAS). We used a global model with the instantaneous flux measurements from 2011. The full model included the same variables evaluated in our initial study (Forrester et al. 2012), as well as fungal ordination axes scores, treatment type (gap vs. closed canopy) and substrate type (stump vs. log). To control for the repeated flux measurements, we used a repeated statement with spatial power covariance structure due to the unequally spaced data. We performed backwards elimination using hierarchical principles and P values to guide model building. The significant variables from the global model were applied to the individual substrate and treatment types. The relative strength of the variables were evaluated using P values and AIC scores (Burnham and Anderson 2002); however, because both metrics led to nearly identical conclusions, we report only P values.

Results

Substrate type

The range of respiration rates measured from the bark side of downed logs (0.8–6.5 umol m^{-2} s^{-1}) was much narrower than those from the cut end of logs (3.5–46.4) or stumps (3.5–44.1). The range of wood temperatures recorded during our periodic measurements were less variable, with temperatures ranging from 2 to 31.2 °C for log sides, 2 to 29.6 °C for log ends, and 2 to 26.7 °C for stumps. For all wood types, respiration rates were strongly related to wood temperature (Fig. 1), and this relationship was thus used to extrapolate measurements to daily and seasonal time periods by developing non-linear models for each year (Supplementary Appendix 2).

Temporal trends

The CO_2 flux of stumps was higher than that of logs in all five measurement years (Fig. 2). In general, the magnitude of the differences expanded with increasing temperatures of each growing season. CO_2 flux rates of wood types began to differentiate early in the initial growing season following

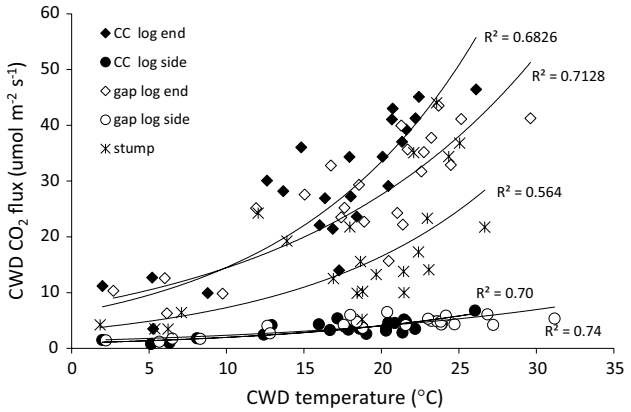

Fig. 1 Exponential relationships between coarse woody debris CO_2 flux and temperature for different substrate types (log end, log side, and stump) and environments (*CC* closed canopy, *G* gap)

gap creation. By the second, fourth and fifth seasons, CO_2 flux of stumps reached rates up to seven times that of the sampled logs. By the seventh season, the difference had declined, resulting in rates similar to the initial post-treatment season.

Few differences were observed between flux of logs in gaps and those in closed canopy conditions in the fourth through seventh years after gap creation (Figs. 2, 3). During this time, the seasonal carbon flux of logs did not differ significantly between canopy locations (gap log vs. closed canopy log, all $P > 0.7$). However, the annual carbon flux of stumps was significantly higher than the annual flux of logs in the fourth through sixth post-treatment growing seasons ($P < 0.02$), emitting more than three times the amount of carbon emitted annually by logs in year 4. By the seventh post-treatment growing season, the annual carbon flux of stumps and logs in both canopy conditions had significantly decreased from the rates measured in earlier years (all comparisons with $P < 0.01$) and no longer differed among substrate types ($P = 0.5$).

Wood temperature of the stumps was rarely higher than that of logs. Temperature patterns were related to canopy conditions, with logs in gap plots being warmer than logs in control plots during the majority of the leaf-on measurement periods (Fig. 4). Moisture patterns were more complex. Logs in closed canopy conditions typically had higher moisture content than logs in gap openings. Stump moisture varied year to year and was not consistently greater or less than substrates in closed canopy conditions.

CWD pool biomass and flux

Our survey of CWD in post-treatment plots was conducted as part of a larger experiment encompassing additional treatment types, including an undisturbed control treatment (Forrester et al. 2013). The CWD pool in the control (no manipulation) treatment is reported here (Table 1) for comparative purposes, although the carbon flux from CWD was not measured in this treatment. Woody debris mass ranged from 1.7 Mg C ha^{-1} on gap creation plots to 20.7 Mg C ha^{-1} on WD addition plots. In treatments with no gap creations, stump biomass contributed very little to the overall debris biomass pool. Where gaps were created, stump biomass was approximately 1 Mg C ha^{-1}.

When emission rates were extrapolated to the CWD biomass pools in experimental treatments, the average annual

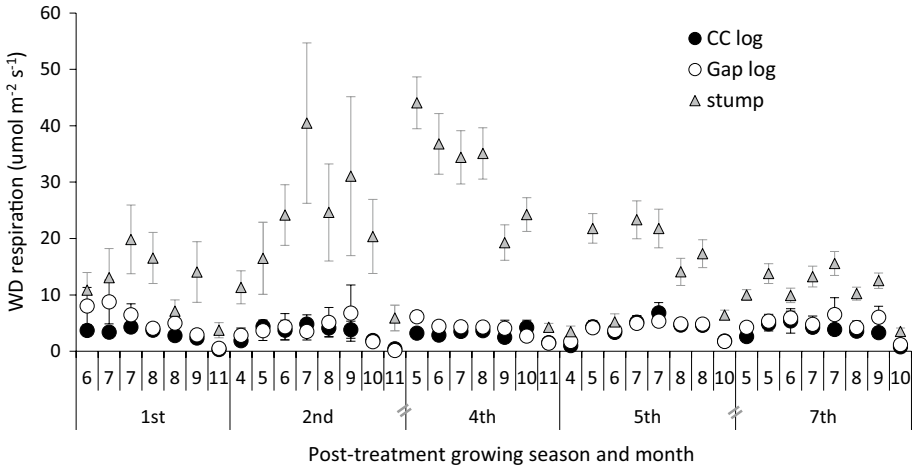

Fig. 2 The mean CO_2 flux of substrate types over the sampling period. In the first two growing seasons after gap creation, only 6 stumps were measured. In years 4–7, the sampling design was expanded and 3 stumps and/or 3 logs per plot were sampled and averaged by treatment plot ($n = 5$). The *horizontal axis* represents the sampling periods with year 1 beginning in June following gap creation in January of the same year. The number of measurement rounds vary by year. Log flux is an area weighted average of measurements from log end and side

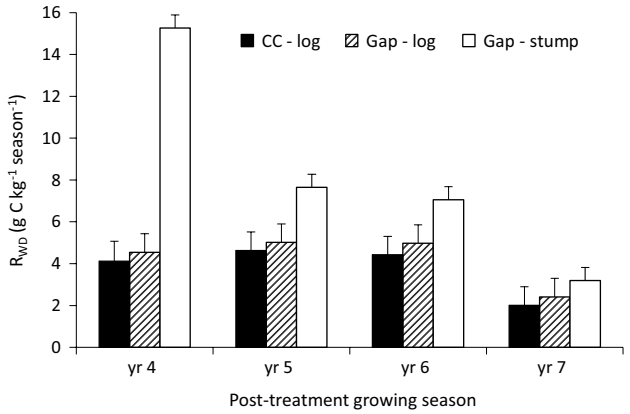

Fig. 3 Modeled annual growing season carbon flux of CWD by treatment and substrate type. Carbon flux of stumps occurring in gap addition treatments was significantly greater than logs in either gap addition or closed canopy (*CC*) plots in all growing seasons

flux of CWD logs ranged from 0.1 to 3.6 Mg C ha^{-1} and that of stumps ranged from 0.1 to 0.4 Mg C ha^{-1} (Table 1).

Wood-decay fungal community

Wood decay fungal fruiting bodies occurred on 25 % of the experimental logs and stumps (overall present on 24 of 60 pieces of CWD) and only within gap creation treatment plots. Twenty fungal species occurred on 19 of the 30 stumps and 7 of the 30 logs. Fungal communities differed primarily by substrate type (Fig. 5). The ordination explained 72 % of the variance in fungal species composition. *Stereum ostrea* and *Trichaptum biforme* were strongly correlated with Axis 1 ($r^2 = 0.57$ and 0.55, respectively), and their occurrence was restricted to logs. *Trametes versicolor* and *Lenzites betulina* both occurred more often on stumps than logs and separated along Axis 2 ($r^2 = 0.65$ and

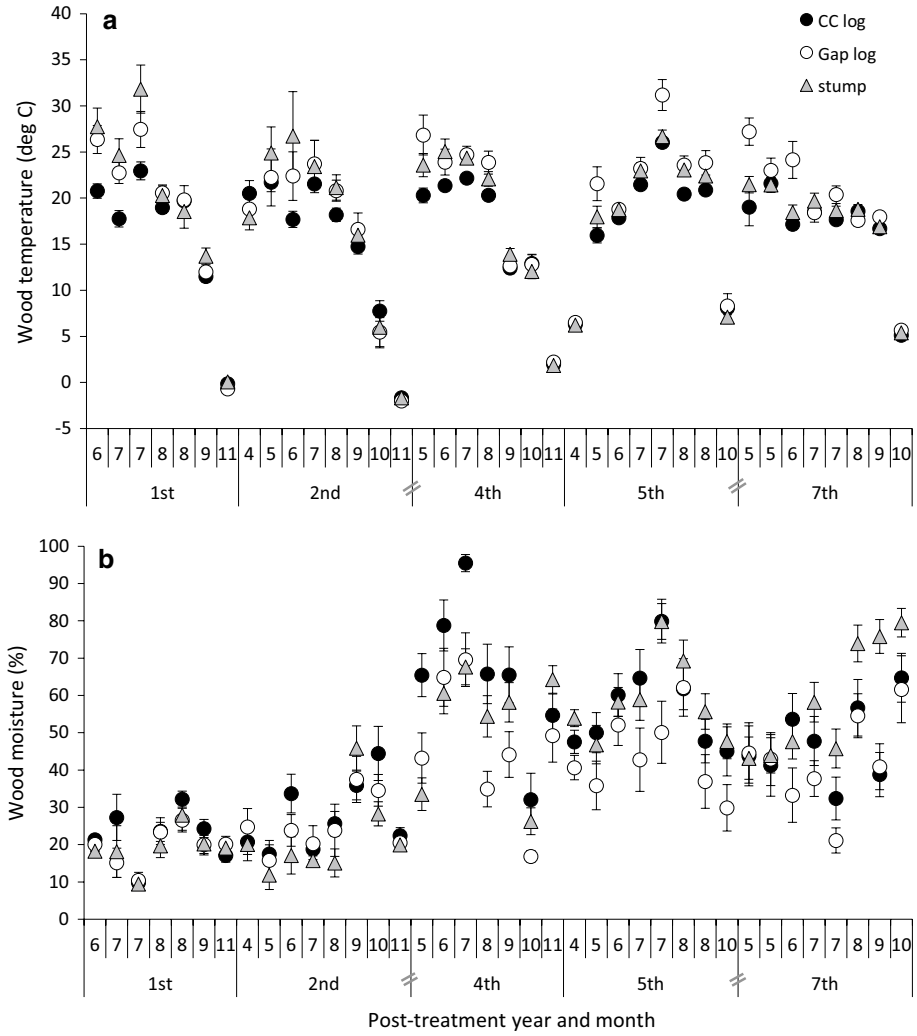

Fig. 4 The mean **a** temperature and **b** moisture of coarse woody debris at discrete sampling periods over 3 years

Table 1 Scaled biomass and annual carbon flux of coarse woody debris by experimental treatments

	Size class	Type	Closed canopy	WD addition	Gap addition	Gap + WD addition
Biomass	10–20 cm	Log	1.31 (0.32)	3.28 (0.74)	0 (0)	4.58 (1.59)
Mg C ha^{-1}		Stump	0.01 (0.01)	0.01 (0.01)	0.18 (0.16)	0.13 (0.04)
	20+ cm	Log	0.80 (0.76)	17.27 (2.96)	0.72 (1.50)	9.37 (3.22)
		Stump	0.12 (0.04)	0.19 (0.04)	0.87 (0.11)	0.98 (0.09)
C emissions	10+ cm	Log	0.37 (0.12)	3.62 (0.48)	0.13 (0.13)	2.48 (0.82)
Mg C ha^{-1} $year^{-1}$		Stump	0.06 (0.02)	0.09 (0.02)	0.47 (0.05)	0.51 (0.05)

Annual carbon flux rates are an average of four growing seasons measured in the current study

Standard errors are in parentheses

0.43, respectively). Axis 3 was strongly correlated with the occurrence of *Trametes gibbosa* and *Ganoderma applanatum* ($r^2 = 0.52$ and 0.48, respectively). Results from analyses including the secondary matrix revealed that the volume and surface area of the host substrate correlated strongly with Axis 1 ($r^2 = 0.55$ for both). Though species richness ($r^2 = 0.36$) and diversity ($r^2 = 0.36$) had a strong positive correlation with Axis 1, annual CWD C flux was negatively related ($r^2 = 0.38$). Axis 2 had very weak linear relationships with any substrate-related metrics evaluated, but had a non-linear negative correlation with diversity metrics (tau = −0.196 for diversity and richness). The strongest relationship between Axis 3 and secondary variables was a positive, non-linear pattern with annual CWD C flux (tau = 0.18).

We found strong evidence that wood temperature, substrate type, treatment, and fungal composition influenced the variation in instantaneous flux measurements (Table 2). The global model indicated that the relationship was highly complex with several main effects and higher order interactions retained in the model that best fit the flux data. Substrate decay class and moisture dynamics were also influential predictors, each varying with substrate type. Separate models for each substrate type and treatment showed that CO_2 flux patterns for logs were strongly related to temperature, while those of stumps related most strongly to decay class. Fungal composition was weakly related to CO_2 flux of stumps ($P = 0.07$).

Discussion

We followed the CO_2 flux from CWD up to 7 years following experimental gap creation. Immediately after canopy gaps were created, CO_2 flux of logs was elevated when compared to logs in closed canopy (Forrester et al. 2012). Despite sustained differences in wood temperature (higher in gaps) and wood moisture (lower in gaps) between gap and closed canopy conditions, significant differences in flux rates of logs were no longer apparent at four growing seasons post-treatment. Microclimate characteristics did not explain the greater CO_2 flux rates recorded from stumps, when compared to logs either. Stumps released CO_2 at much higher rates than downed logs throughout the study period, peaking in the fourth year post-treatment and declining in subsequent years. The temperature of stumps was similar or often slightly lower than that of the logs in gaps, and stump moisture was often greater than that of

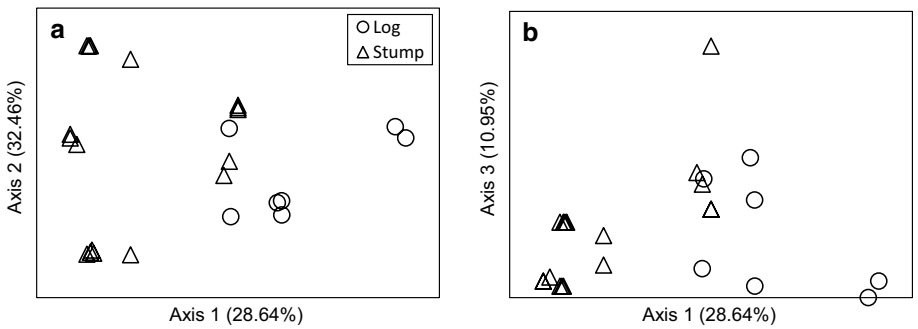

Fig. 5 Ordination plots of presence-absence of wood-inhabiting fungi on sampled logs and stumps for **a** Axes 1 and 2 and **b** Axes 1 and 3. Coarse woody debris was surveyed for the presence of wood-decay fungal fruiting bodies in October, 2011. Fruiting bodies were observed on 19 of the 30 experimental stumps and 7 of the 30 experimental logs; all within experimental gaps

Table 2 (A) Results from significance tests of variables retained in the global best model of instantaneous flux following a backwards selection procedure; (B) the global model was applied to individual substrate type and canopy treatment levels; *P* values from significance tests are reported by type

Effect	(A) Global model				(B) Individual models		
	Number *df*	Density *df*	*F* Value	Pr > *F*	Stumps	Logs in gap	Logs in closed canopy
Canopy treatment	1	46	12.24	0.0011	–	–	–
Substrate type	1	46	32.3	<0.0001	–	–	–
Temperature	1	387	38.69	<0.0001	0.1015	**0.0136**	**0.0066**
Moisture	1	387	5.81	0.0164	**0.0643**	0.5282	0.4157
Decay class	2	46	5.38	0.0079	**0.0077**	0.1914	0.9953
Fungal axis 1	1	46	4.72	0.0349	**0.0792**	0.9422	–
Fungal axis 2	1	46	11.06	0.0017	0.4665	0.1977	–
Temperature^2	1	387	10.18	0.0015	0.2467	0.5173	0.1475
Moisture^2	1	387	3.3	0.0699	0.2096	0.684	0.6282
Temp × gap	1	387	6.49	0.0112	–	–	–
Temp^2 × gap	1	387	4.99	0.0261	–	–	–
Decay class × gap	1	46	7.68	0.008	–	–	–
Moisture × type	1	387	6.13	0.0137	–	–	–
Moisture^2 × type	1	387	4.88	0.0278	–	–	–
Decay class × type	2	46	5.05	0.0104	–	–	–
Fungal axis2 × type	1	46	10.95	0.0018	–	–	–

Values in bold indicate significance using an alpha of 0.1. AIC scores were in agreement with *P* values

Full model included main effects of canopy treatment, substrate type, temperature, temp^2 , moisture, moisture^2, decay class, fungal axis 1, fungal axis 2, fungal axis 3, species, diameter, and all interactions with substrate type and canopy treatment

logs in gaps, but similar to that of logs in closed canopies. One possible explanation could be that our flux measurements from stumps are capturing an additional root contribution. Typically, stumps survive only one growing season post-harvest (Bormann 1961); however, portions of stumps and associated roots grafted to living trees may survive for up to 15 years (Fraser et al. 2007). Published estimates of coarse root decomposition rates are very limited, but one study indicates that after 10 years more than half of the original root density had been lost (Fahey et al. 1988); an additional study indicates the majority of loss occurred between years 5–10 (Fahey and Arthur 1994). Chen et al. (2000) showed root respiration to be significantly influenced by species, temperature, moisture and decay class, with respiration rates higher in decay classes 1 and 3 than an intermediate class. Another possible explanation is the intrusion of living roots from other plants into the decaying stump and root complex, although this would be expected to occur much later as decay advances (Marra and Edmonds 1994).

Another plausible explanation for the higher respiration rates of stumps, when compared to logs, could be differences in the decomposer community. Similar to other early observational studies (Rayner 1977; Coates and Rayner 1985), we found that the wood decay fungal communities were distinct between logs and stumps. Certain species (*T. versicolor* and *L. betulina*) appear to rapidly colonize the substrate and produce abundant fruiting bodies. The volume of CWD is often the main driver of dead wood fungal species diversity (Lassauce et al. 2011), though substrate diversity, in terms of decay classes, tree species and sizes, is also important (Stokland et al. 2012; Blaser et al. 2013). Lindhe et al. (2004) observed significantly higher numbers of wood-decay fungi on downed logs than on stumps and noted that diversity peaked earlier on logs than on stumps following logging. When evaluating all debris in this experimental site, stumps, medium and large substrates and *A. saccharum* debris most strongly correlated to patterns of the wood-inhabiting fungal community composition (Brazee et al. 2014). Stumps were only 12 % of the observations, but supported 21 % of the fungal species surveyed. Most of these species were among those that were most frequently observed and those known to rapidly colonize fresh CWD after a disturbance.

A number of studies have examined the role of wood decay fungi in decomposition, but few have measured the respiration rates associated with specific fungal communities. Our models indicated that fungal community composition explained a significant portion of the variation in respiration rates. The global modeling we conducted could be performed at multiple scales. In addition to the data-rich modeling using the instantaneous flux measurements we

Table 3 (A) Results from significance tests of variables retained in the global best model of annualized flux following a backwards selection procedure; (B) the global model was applied to individual substrate types; *P* values from significance tests are reported by type

Effect	(A) Global model				(B) Individual models	
					Stumps	Logs
	Number *df*	Density *df*	*F* value	Pr > *F*	Pr > *F*	Pr > *F*
Decay class	2	45	5.12	0.0099	0.2731	**0.0112**
Canopy treatment	1	45	5.57	0.0227	–	0.1032
Substrate type	1	45	228.75	<0.0001	–	–
Temperature	1	45	12.72	0.0009	**0.0012**	0.1729
Species	5	45	5.9	0.0003	0.8606	**0.0004**
Diameter	1	45	41.57	<0.0001	**<0.0001**	**0.0079**
Substrate type × fungal axis 1	1	45	7.48	0.0089	–	–
Fungal axis 1	1	45	11.25	0.0016	**0.031**	0.373
Fungal axis 3	1	45	17.38	0.0001	**0.0098**	**0.0145**

Values in bold indicate significance using an alpha of 0.1. AIC scores were in agreement with *P* values

Full model included main effects of canopy treatment, substrate type, temperature, temperature^2 , decay class, fungal axis 1, fungal axis 2, fungal axis 3, species, diameter, and all interactions with substrate type and canopy treatment

present here, we used this approach with annualized flux data and found similar effects (Table 3). The substrate type, treatment, decay class, temperature and fungal axes scores all significantly influenced patterns in the annualized flux data. In addition, at this scale, the substrate species and diameter were also influential. When the best model was applied to substrate types individually, the fungal composition and substrate diameter were important for describing variation in both logs and stumps. While we found this modeling to be encouraging because of the congruence with other methods, we acknowledge that the foundation of the annualized modeling is not as firm due to the use of temperature to predict the daily carbon flux itself. At both scales, the fungal composition was significantly related to respiration patterns with at least two ordination axes retained in both models.

We found that respiration was negatively related to fungal diversity, with logs supporting more species but emitting less CO_2 than stumps. Within substrate types, diversity was again inversely related to respiration. Similarly, in a laboratory experiment, Fukami et al. (2010) found that fungal species composition explained 81 % and fungal species richness 70 % of the variation in decomposition rates and that high fungal diversity was associated with low decomposition and respiration. The negative relationship may be explained by competitive interactions occurring among wood-decay fungi (Boddy 2000; Liu et al. 2013), but certainly more research would be necessary to verify this pattern. *T. versicolor* was the most frequently encountered fungal species, observed on 6 (of 30) stumps and 4 (of 30) logs, and occurring on the substrate pieces with the highest CO_2 flux rates. *Bjerkandera adusta* and *T. gibbosa* were also associated with high CO_2 flux. In a survey of all the CWD, Brazee et al. (2014) found that *T. versicolor* had the highest number of occurrences and was significantly more abundant in gaps, suggesting that this species may play an important role in decomposition dynamics within this northern hardwood system. Interestingly, these species are all white-rot fungi that degrade lignin, hemicellulose and cellulose (brown-rot fungi degrade primarily hemicellulose and cellulose). One other study suggests that white-rot fungi can degrade wood faster than brown-rots (Harmon 1992), though this pattern may vary with temperature (Toljander et al. 2006), and brown-rot fungi may obtain energy from wood more efficiently (Worrall et al. 1997). This difference of respiration rates between white- and brown-rot functional groups warrants further work because of the important implications on CWD and forest carbon dynamics. During our model evaluation, we replaced the fungal ordination axes scores with a single binary term representing the presence or absence of a fruiting body. The presence—absence term was not retained in the model, indicating differences in species function.

Our characterization of the fungal communities was based only on direct observation of fruiting bodies at a single point in time; we likely underestimated the species presence and relative abundance (Rayner 1977). Additional monitoring of the communities and their function would provide insight into fungal successional dynamics, and species-level monitoring would be even more beneficial in identifying important indicator species for assessments of ecosystem function. Further substantiation of the differences in functional roles of white- and brown-rot fungi is critical to understanding and predicting heterotrophic respiration and hence ecosystem carbon dynamics.

Both the spatial distribution and abundance of the substrate types is an important part of the equation when considering the implications of the differences in substrate rates that we quantified. Although CO_2 flux rates from cut ends of logs exceeded even those of stumps, cut ends accounted for a minimal amount of the CWD surface area. Stumps too typically comprise only a small portion of the total ground surface area or biomass, with the exception of more intensively managed stands. In mature managed Sitka spruce forests of Ireland, Olajuyigbe et al. (2011) reported stumps contributed up to 69 % of the aboveground volume of woody debris. In the experimental treatments evaluated here, stumps comprise 60 % of the CWD biomass in the gap creation treatment and contribute 76 % of the carbon emitted from the total CWD pool. The proportions in the control treatment indicate that in typical second-growth stands, stumps would contribute 6 % of the biomass and 13 % of total carbon emissions. Overall, the emissions of the gap creation treatment were lower than any other treatment because of the small size of the CWD pool (Table 1). The largest emissions occurred in the WD addition treatment plots, where the flux rate was 3–4 Mg C ha^{-1}, an amount reflecting the larger than average CWD pool sizes. The contribution of the stump component in the gap + WD addition treatment is somewhat masked due to the unequal pool sizes between the two WD addition treatments (WD addition and gap + WD addition treatments). The variation between these treatments as presented to this point has focused on a subplot area, yet the WD additions occurred at a whole-plot level. When evaluated at the whole-plot level, the CWD pool is equivalent between these two treatments. Therefore, the gap + WD addition treatment would more likely have the higher annual carbon emission (see Forrester et al. 2013), given the presence of stumps and their higher attendant CO_2 flux rates.

Current forest carbon models that contain only a single WD pool or separate pools based on chemical features may not adequately represent WD dynamics. Harmon (2011) suggested a model structure that segregates heterotrophic respiration into components characterized by substrate quality and environment. Here, we provide further evidence that this type of model structure will be necessary for properly modeling carbon dynamics, especially following disturbance. By overlooking differences in CO_2 flux rates by substrate type, current carbon models potentially underestimate the differences in carbon flux between managed areas and no-harvest baseline scenarios. That initial pulse in CO_2 flux from stumps and their roots is especially important to consider when modeling forest carbon dynamics. Assuming stumps and logs to have the same decomposition rates would lead to an overestimation of stump residence time and obscure a pulse of heterotrophic respiration. Harmon (2011) discussed examples of disturbances that may produce temporal patterns that differ from that suggested by classical theory, namely a single monotonic pulse of heterotrophic respiration (Odum 1969). Our data suggest that harvest events can produce multiple pulses, with an initial peak of respiration from stump material that will likely be followed by a secondary peak associated with peak respiration from logs in later decay stages.

Conclusions

We have demonstrated how changes in forest structure influence CWD decomposition rates in the initial years following a disturbance. The CO_2 flux of logs in canopy gaps was indistinguishable from fluxes of logs beneath undisturbed canopy, despite sustained differences in substrate temperature and moisture within canopy gaps. We have also shown that the quantity of CO_2 emissions and the duration of the response to a disturbance vary substantially depending on the type of substrate; as such, in an intensively harvested landscape, stumps will contribute a disproportionately large amount of the total carbon emitted from the CWD pool in the short term. Our results also highlight the role of wood-decay fungal community composition in explaining the variation of CWD respiration in a forest ecosystem, with higher fungal richness showing a decrease in decomposition rates. Since the main determinant of fungal diversity is often the volume of woody debris, silvicultural strategies that create structural heterogeneity in regards to woody debris are critical for developing functional diversity. Overall, our results add to a growing concern that the current treatment of WD in forest carbon models may be oversimplified, thereby hampering our ability to predict realistic patterns associated with wood decomposition.

Acknowledgments This study was supported by the US Department of Agriculture Biomass Research and Development Initiative. The Wisconsin DNR Division of Forestry and WI DNR Bureau of Integrated Science Services, Pittman-Robertson Funds provided support for establishing the Flambeau Experiment. We greatly appreciated assistance from field crews, especially Tera Lewandowski, Emily Lannoye, Jason Schatz, and Amy Milo. Thanks to the staff at the Flambeau River State Forest, especially Heidi Brunkow.

Author contribution statement JAF, DJM, STG, SF, AWD, DLL and MKC conceived and designed the experiment; JAF, DLL, and NJB performed the experiment; JAF and MKC analyzed the data; JAF wrote the manuscript, other authors provided editorial advice.

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