



Coarse woody debris and the carbon balance of a moderately disturbed forest



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ABSTRACT

Forested landscapes are shaped by disturbances varying in severity and source. Moderate disturbance from weather, pathogens, insects, and age-related senescence that kills only a subset of canopy trees may increase standing woody debris and alter the contribution of coarse woody debris (CWD) to total ecosystem respiration (R_E). However, woody debris carbon (C) dynamics are rarely examined following moderate disturbances that increase standing dead wood pools. We used an experimental manipulation of moderate disturbance in an upper Great Lakes forest to: (1) examine multi-year changes in CWD mass through a moderate disturbance; (2) quantify *in situ* CWD respiration during different stages of decay for downed and standing woody debris and; (3) estimate the annual contribution of CWD respiration to the ecosystem C balance through comparison with R_E and net ecosystem production (NEP). Six years following disturbance, we found that the standing dead wood mass of 24.5 Mg C ha⁻¹ was an order of magnitude greater than downed woody debris mass and a large source of ecosystem C flux. Instantaneous *in situ* respiration rates from standing and minimally decayed downed woody debris were not significantly different from one another. Separate estimates of ecosystem CWD respiration of 1.1–2.1 Mg C ha⁻¹ yr⁻¹ six years following disturbance were comparable in magnitude to NEP and 12.5–23.8% of R_E , representing a substantial increase relative to pre-disturbance levels. Ecosystem respiration and NEP were stable following moderate disturbance even though ecosystem CWD respiration increased substantially, suggesting a reduction in the respiratory C contribution from other sources. We conclude that standing and downed CWD can be essential components of the ecosystem C balance following moderate severity disturbance.

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1. Introduction

Forest disturbances alter the balance between ecosystem carbon (C) uptake and loss, and are primary determinants of the terrestrial C balance (Bond-Lamberty et al., 2007; Gough et al., 2007; Amiro et al., 2010; Pan et al., 2011). Tree mortality from disturbance may affect ecosystem C balance in two ways: by reducing the amount of C fixed via canopy photosynthesis (or gross primary production, GPP), and by altering the quantity of C lost through ecosystem respiration (R_E), particularly as detritus-fueled microbial respiration increases (Liu et al., 2006; Harmon et al., 2011). The difference between these two large opposing C fluxes determines ecosystem C balance, or net ecosystem production (NEP), with

a small post-disturbance change in either GPP or R_E potentially causing large alterations in NEP. Numerous studies show that tree mortality can considerably reduce NEP, with some forests becoming C sources immediately after severe, stand-replacing disturbance (Janisch and Harmon, 2002; Amiro et al., 2010; Harmon et al., 2011; Hicke et al., 2012). The effects of moderate disturbances that kill only a subset of canopy trees – such as those caused by insect pests, pathogens, and severe weather – on NEP are less certain even as lower severity disturbances increase in frequency and extent in many forested regions (Amiro et al., 2010). Coarse woody debris (CWD), defined here as standing and downed dead wood >10 cm diameter, is an important source of detritus following disturbance, but is often unaccounted for in estimates of R_E and, as a result, the extent to which CWD C cycling dynamics following disturbance alter ecosystem C balance is poorly understood (Amiro et al., 2010; Harmon et al., 2011; Renninger et al., 2014).

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Coarse woody debris C cycling dynamics are most thoroughly characterized for the extreme end-members on the disturbance severity continuum, with most prior work conducted in severely and minimally disturbed forests (Gough et al., 2007; Harmon et al., 2011); considerably less is known about CWD C cycling dynamics following moderate disturbances that kill a substantial fraction of, but not all, canopy trees within an ecosystem (Renninger et al., 2014). Studies conducted in recently undisturbed forests show that CWD is a relatively small C pool that contributes little to R_E and thus minimally affects NEP (Harmon et al., 2004; Janisch et al., 2005; Liu et al., 2006; Gough et al., 2007; Luysaert et al., 2008; Tang et al., 2008). Following severe, stand-replacing disturbance, CWD is a primary substrate for microbial decomposition and, therefore, a large component of R_E and a source of C losses that reduce NEP (Amiro et al., 2010; Harmon et al., 2011; Russell et al., 2014; Woodall et al., 2015). How CWD progresses through stages of decay and contributes to R_E following more moderate disturbance is less clear, though one recent study suggests that accounting for changes in CWD mass and respiration is essential to interpreting how and why NEP may shift following lower intensity disturbances (Renninger et al., 2014).

The motivation for studying forest C, including CWD, dynamics across a range of disturbance severities stems from observation and theory that suggests moderate disturbances modify ecosystem structure and function differently than severe disturbances (Nave et al., 2011), and these differences extend to CWD structure, mass and decomposition (Harmon et al., 2011). Some moderate disturbances initially leave more CWD standing than downed, with implications for woody debris microclimate and microbial colonization, and therefore microbial activity and CWD respiration (Pedlar et al., 2002; Forrester et al., 2012, 2013; Brazee et al., 2014; Lewandowski et al., 2015; White et al., 2015). For example, partial defoliation of forest canopies from insects increased standing dead wood mass, while severe disturbances such as clear-cut harvesting and fire felled, removed, or reduced standing wood (Pedlar et al., 2002; Renninger et al., 2014). Moreover, standing, but not downed, CWD has increased broadly in eastern US forests owing to patchy disturbance and natural tree senescence, with uncertain consequences for the C cycle (Woodall et al., 2015). Yet, C cycling studies tend to focus on downed rather than increasingly prevalent standing CWD, concluding the latter contributes nominally to detritus pools and decays slowly, therefore contributing little to R_E (Harmon et al., 1986; Yatskov et al., 2003; Liu et al., 2006; Jomura et al., 2008; Tang et al., 2008). However, a recent study reported similar *in situ* respiration rates for standing and downed CWD, with standing woody debris contributing substantially to R_E (Renninger et al., 2014).

We evaluated CWD dynamics following a moderate forest disturbance at the University of Michigan Biological Station (UMBS) in which all mature aspen (*Populus*) and birch (*Betula*) were killed via experimental stem girdling but not immediately felled. The treatment produced a forest structure and composition similar to that which is broadly emerging in the upper Great Lakes region as secondary forests reach the century mark in age (Gough et al., 2010). The experimental disturbance, which temporarily reduced live tree basal area by 39% and leaf area index by 44%, is similar in severity to increasingly prevalent naturally occurring disturbances in the region (Gough et al., 2013). Prior C cycling studies resulting from this experiment emphasized NEP, GPP and net primary production (NPP) following disturbance, demonstrating sustained production in the moderately disturbed forest despite the experimental disturbance-related transfer of 35 Mg ha⁻¹ of wood from live to dead pools (Nave et al., 2011; Gough et al., 2013; Stuart-Haentjens et al., 2015). Our prior emphasis on the unexpected resistance of forest production to moderate disturbance revealed mechanisms underlying sustained C uptake, notably

improved canopy resource-use efficiency and the rapid reallocation of limiting nitrogen and light resources in support of leaf area recovery. Here, we provide a first focus on C losses, asking whether a large pulse of CWD that followed moderate disturbance was a prominent contributor to R_E and, by extension, how this C lost by the ecosystem from CWD decomposition affects NEP. Specific objectives were to: (1) examine multi-year changes in CWD pools through moderate disturbance; (2) quantify *in situ* CWD respiration during different stages of decay for downed and standing woody debris and; (3) calculate the annual contribution of CWD respiration to the ecosystem C balance through comparison with R_E and NEP. We hypothesized that the large influx of CWD mass would constitute a substantial fraction of R_E and, because the disturbance did not cause the immediate felling of dead trees, standing woody debris would be the principle contributor to the respiratory flux from CWD.

2. Methods

2.1. Site description

The study was conducted at the University of Michigan Biological Station (UMBS) in northern, lower Michigan, USA (45°35'N 84°43'W). The site has a mean annual temperature of 5.5 °C and a mean annual precipitation of 817 mm (1942–2003) (Gough et al., 2013). The UMBS forest is a representative secondary broadleaf deciduous forest in the transition zone between temperate and boreal forests. The forest developed following a clear-cut and wildfire regime in the early 20th century and has since undergone only low severity, patchy disturbances. Early successional species such as bigtooth aspen (*Populus grandidentata*), trembling aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*) are nearing or past maturity and senescing naturally, or in response to experimental disturbance described below. Canopy dominance is shifting toward longer-lived, later successional species, including red oak (*Quercus rubra*), red maple (*Acer rubrum*), and to a lesser extent, sugar maple (*Acer saccharum*) and eastern white pine (*Pinus strobus*). The average overstory tree age is 100 years old (Gough et al., 2007). Downed woody debris represented a pool of 2.2 Mg C ha⁻¹ or 1.2% of total ecosystem C prior to the decline of mature aspen and birch (Gough et al., 2007).

The Forest Accelerated Succession Experiment (FASET) is an ecosystem-level manipulation that was initiated in May 2008 to quantify how forest C pools and fluxes are affected by moderate disturbance, ecological succession, and climate change. All early successional aspen and birch trees (~6700) were killed via stem girdling within a 39 ha area. Carbon dioxide exchange between the atmosphere and the forest is continuously measured using a meteorological tower established in 2007, with estimates of annual NEP and R_E through 2013 reported by Gough et al. (2013) and Bond-Lamberty et al. (2015). Coarse woody debris mass, respiration, and microclimate measurements, detailed below, occurred in the experimentally disturbed area positioned within the meteorological flux tower footprint and no more than 300 m away from the tower base.

2.2. Coarse woody debris carbon mass

In 2009, 2011, 2013, and 2014, downed coarse woody debris mass was inventoried by decay class in eight, 0.1 ha subplots within the experimentally manipulated area. In the first sampling year, all standing and downed CWD samples were tagged for repeated measures in subsequent years of volume and decay class; newly produced CWD identified for the first time in following sampling years was tagged and included in future inventories. Each

inventory year, all downed woody debris (>10 cm diameter, <45° from the forest floor) samples within a plot were individually classified into one of the following decay classes (Marra and Edmonds, 1994): (1) recently downed with bark and tissue fully intact, (2) sapwood is still present but beginning to show signs of decay and bark may be beginning to peel or crack, (3) heartwood is intact, sapwood is present but softening, (4) heartwood is beginning to decay, sapwood and bark are mostly gone, (5) heartwood shows signs of substantial decay, sapwood and bark are completely missing. Standing woody debris (>45° from the forest floor), which was identified as an additional category of woody debris, was inventoried in the same plots as downed wood in 2011 and 2014.

We measured the length and diameter, at the ends and middle, of each piece of downed CWD and measured total height, from sample base to top, and diameter at breast height of each piece of standing woody debris. The surface area and volume of each piece of CWD were calculated using the equation for the frustum of a cone (Harmon and Sexton, 1996). Site- and species-specific wood densities and C concentrations for each decay class were used to calculate C mass from CWD volume (Gough et al., 2007). In the case of standing CWD, which is difficult to representatively sample without felling, we used the wood density and C fraction of downed CWD, decay class 1 since values for these two categories are comparable (e.g., Koster et al., 2015).

2.3. Coarse woody debris respiration and microclimate

Instantaneous *in situ* respiration from the surface of aspen CWD (R_{CWD} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) was repeatedly measured on downed and standing aspen CWD in the field during July and August 2014. Though aspen and birch were both targeted in the disturbance experiment, aspen comprised over 80% of the biomass stem girdled (Gough et al., 2010) and has similar decay characteristics as birch (Russell et al., 2014); therefore, our analysis focused on aspen respiration. Five PVC respiration collars (2 cm high, 10 cm diameter) were permanently affixed with duct seal putty to each of three replicate CWD samples (>1.5 m long, >10 cm center diameter) per downed decay class and three standing CWD samples (>10 cm diameter at breast height). The five subsample collars were evenly spaced and positioned at random angles that did not interfere with measurements along each CWD replicate, including the ends of downed woody debris and the tops of standing woody debris when possible. For standing dead wood, collar heights above the ground ranged from 1.2 to 12.5 m. We measured R_{CWD} weekly beginning early July for downed CWD and mid-July for standing CWD through mid-August using a Li-Cor LI-6400 Portable Photosynthesis System (Li-Cor, Lincoln, NE, USA). Wood temperature (1 cm depth; T_{CWD}) and wood moisture (12 cm integrated depth; ϕ_{CWD}) were measured concurrently with R_{CWD} using a type-E thermocouple and a Campbell Scientific HydroSense II soil moisture sensor (Model HS2-12, Campbell Scientific, Logan, UT, USA), using a drill when necessary to produce holes for sensor placement in standing and downed CWD. Wood water content was converted from volumetric to gravimetric values using site-specific CWD densities (Gough et al., 2007).

2.4. Annual carbon flux estimates

We estimated the annual respiratory C flux from downed and standing CWD ($\text{Mg C ha}^{-1} \text{yr}^{-1}$), hereafter termed ecosystem CWD respiration, for 2014 using three different methods. We employed three different approaches because of the high uncertainty associated with estimates of heterotrophic respiration (Harmon et al., 2011), focusing on 2014 because this was the year in which we measured *in situ* CWD respiration. A mass balance estimate of ecosystem CWD respiration was calculated as the

change in total woody debris mass across all decay classes over one year, from 2013 to 2014. Standing dead wood was inventoried in 2011 and 2014 only, with mass values for 2013 estimated from linear interpolation between measurement years (Fig. 1). In this approach, ecosystem CWD respiration is the summed or aggregate change in CWD mass, including those that transitioned to a more advanced decay class. One limitation of this approach is that, similar to other cohort-based mass balance approaches (e.g., Johnson et al., 2001), it does not account for CWD production and losses occurring between inventories. The total annual loss of C mass from CWD was assumed to be equal to the flux to the atmosphere, as CWD-C leaching and export is considered negligible (Harmon et al., 1986; Laiho and Prescott, 1999). A second approach integrated measured R_{CWD} over time, with fluxes interpolated between measurement dates. To estimate R_{CWD} outside of the measurement period, we linearly extrapolated fluxes to zero on the dates in the Spring and Autumn when temperatures <0 °C; winter R_E (all sources) is <10% of the annual total at our site (Curtis et al., 2005). The integrated area under the R_{CWD} time series curve, shown in Fig. 2a (illustrated without extrapolated flux values), was calculated using SigmaPlot (SYSTAT Inc., San Jose, CA, USA). We scaled fluxes to the ecosystem by multiplying integrated R_{CWD} by the surface area of downed and standing dead wood. Lastly, we used a published site- and species-specific model to infer half-hourly R_{CWD} from T_{CWD} and ϕ_{CWD} ($R_{CWD} = 1.28 * e^{-0.034 * T_{CWD}} + 0.25 * \ln(\phi_{CWD})$); $r^2 = 0.64$, $P < 0.001$; Gough et al., 2007). Because continuous ϕ_{CWD} and T_{CWD} were required to model R_{CWD} but not available from direct measurements, regressions between (3–4 per sample) point measurements of ϕ_{CWD} and T_{CWD} and continuously (half-hourly) logged soil moisture and soil temperature, respectively, were developed following the approach of Gough et al. (2007) to derive continuous half-hourly estimates of ϕ_{CWD} and T_{CWD} for 2014. Respiration was assumed to be zero when T_{CWD} was <0 °C (Gough et al., 2007). Half-hourly estimates of R_{CWD} were summed and multiplied by decay class specific CWD mass to estimate ecosystem CWD respiration. Ecosystem CWD respiration was compared with published mean annual R_E and NEP (2009–2013) obtained from meteorological tower measurements of the exchange of CO_2 between the forest and atmosphere (Gough et al., 2013; Bond-Lamberty et al., 2015); we report mean, rather than single-year, R_E because this derived C flux, made with relatively high uncertainty, did not change significantly over time following disturbance (Gough et al., 2013), and therefore is a higher confidence estimate with which to compare ecosystem CWD respiration.

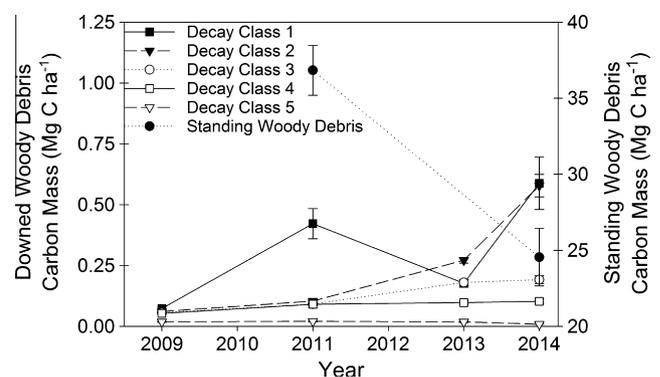


Fig. 1. Downed and standing woody debris carbon pools by decay class in a moderately disturbed upper Great Lakes forest in which all aspen and birch trees were stem girdled in 2008. Pool sizes reflect inputs from the experimental disturbance (35 Mg C ha^{-1}) plus those from naturally occurring tree senescence. Note the different y-axes and scales for downed (left) and standing (right) woody debris. Means $\pm 1/4$ S.E. for visual clarity.

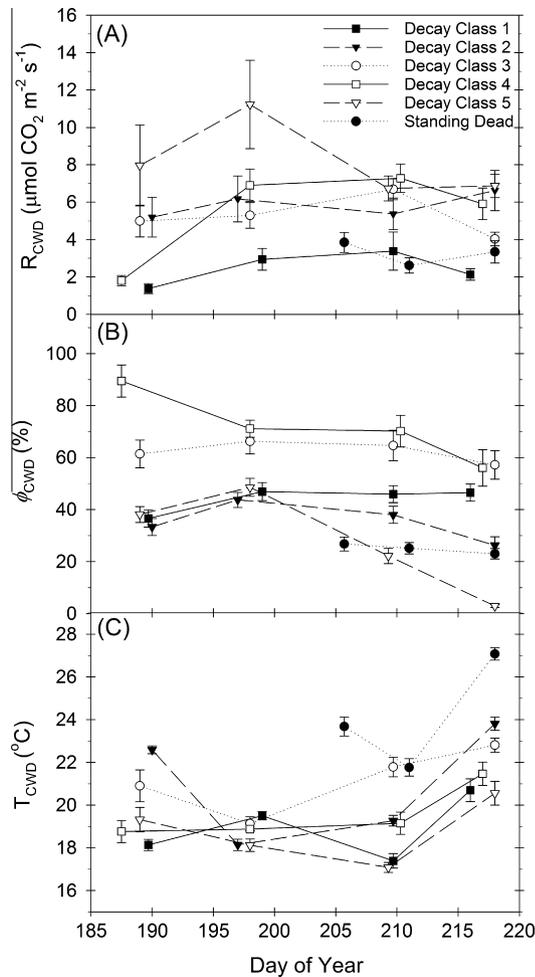


Fig. 2. Means \pm 1 S.E. of *in situ* coarse woody debris respiration (R_{CWD} ; A), wood gravimetric water content (ϕ_{CWD} ; B), and wood temperature (T_{CWD} ; C) of downed and standing woody debris by decay class during Summer 2014.

2.5. Statistical analysis

Statistical differences over time and among decay classes in CWD pools, R_{CWD} , ϕ_{CWD} , and T_{CWD} were assessed using a repeated measures analysis of variance (ANOVA), with values \pm 1 S.E. presented in the text. Multiple comparisons were made using post hoc Fisher's LSD analysis, selected because our hypotheses were based on *a priori* knowledge of differences among decay classes in CWD pools, fluxes, and microclimate from an earlier, more tightly controlled field and laboratory manipulation conducted at our site prior to disturbance (Gough et al., 2007). Linear and non-linear (2-parameter exponential function) regression analysis was used to examine decay class specific relationships between R_{CWD} , and both ϕ_{CWD} and T_{CWD} (Curtis et al., 2005; Gough et al., 2007) and standing woody debris measurement height, and ϕ_{CWD} and R_{CWD} . The uncertainty in each ecosystem CWD respiration estimate was expressed as a standard error (S.E.) derived from the cumulative error in model parameters (model approach only) and accounting for spatial variation in R_{CWD} (integration approach only) and CWD mass distribution (all approaches) (Gough et al., 2007). All statistical analyses used a significance level of $\alpha = 0.05$ and were performed in SAS (ANOVA; SAS 9.1, SAS Institute, Cary, NC, USA) or SPSS (regression; IBM SPSS Statistics, version 22, IBM Corp., Armonk, NY, USA).

3. Results

3.1. Coarse woody debris carbon pools

The allocation of CWD among decay classes and the total mass of woody debris changed over time following moderate disturbance. One year after the stem-girdling treatment, in 2009, and prior to peak tree mortality, downed CWD mass was evenly distributed among decay classes, totaling $0.3 \pm 0.09 \text{ Mg C ha}^{-1}$ for all decay classes combined (Fig. 1). By 2011, 97% of stem-girdled aspen and birch were defoliated and considered dead, resulting in a 35 Mg C ha^{-1} pulse of CWD from experimental disturbance (Gough et al., 2013) plus an additional 2.1 Mg C ha^{-1} of naturally senesced CWD in early stages of decomposition, including standing dead wood. In 2013 and 2014, following multiple years of decomposition, the mass of downed wood trended upward as standing CWD began to fall and advance through stages of decay (Fig. 1); this increase over time was not statistically significant, (time main effect, $p = 0.27$; time \times decay class interaction, $p = 0.39$), however, because of the very high spatial variation in CWD mass among replicate plots, a signature of disturbance-related increases in the spatial heterogeneity of C pools and fluxes (Gough et al., 2013). Six years following disturbance in 2014, standing dead wood remained the largest pool of CWD ecosystem-wide at $24.5 \pm 7.6 \text{ Mg C ha}^{-1}$; downed dead wood comprised $1.5 \pm 0.7 \text{ Mg C ha}^{-1}$.

3.2. Coarse woody debris respiration and microclimate

Instantaneous *in situ* respiration from the surface of CWD, R_{CWD} , was variable among decay classes and over time (Fig. 2A). Mean R_{CWD} varied by an order of magnitude among decay classes and across time, from $1.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ to $11.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, with individual point measurements as high as $64.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. In general, R_{CWD} increased with increasing extent of decay (decay class main effect, $p = 0.008$), but significant pairwise differences ($p < 0.05$) were only observed between decay class 1 and decay classes 2, 4, and 5, and decay class 5 and standing dead wood, decay class 1, and decay class 3. Notably, standing dead wood and downed decay class 1 CWD had comparable R_{CWD} (Fig. 2A). Wood water content, ϕ_{CWD} , increased with increasing extent of decay, up to decay class 4 (decay class main effect, $p < 0.0001$) (Fig. 2B). Wood temperature, T_{CWD} , increased with increasing extent of downed wood decay (decay class main effect, $p = 0.04$), and was highest in downed decay classes 4 and 5, and in standing dead wood (Fig. 2C).

Although T_{CWD} and ϕ_{CWD} varied considerably over time and among decay classes, temperature and moisture were not significant predictors of R_{CWD} in downed wood; contrastingly, mean moisture, which varied significantly by standing CWD height, was correlated with R_{CWD} in standing wood (Fig. 3A). There was no significant relationship between downed R_{CWD} , and either ϕ_{CWD} or T_{CWD} when each point measurement was treated as an independent observation or when averaged across measurement dates for any decay class individually or when all decay classes were combined ($p > 0.1$; data not shown). In contrast to downed CWD, standing dead wood exhibited a significant decline in mean ϕ_{CWD} , averaged across dates, with increasing measurement height ($p < 0.0001$, $r^2 = 0.77$) (Fig. 3A) and a significant relationship between mean ϕ_{CWD} and mean R_{CWD} ($p = 0.015$, $r^2 = 0.402$) (Fig. 3B).

3.3. Annual carbon flux estimates

We used three different approaches to estimate the contribution of standing and downed CWD respiration to ecosystem respiration, R_{E} , in 2014: a mass balance approach calculating ecosystem

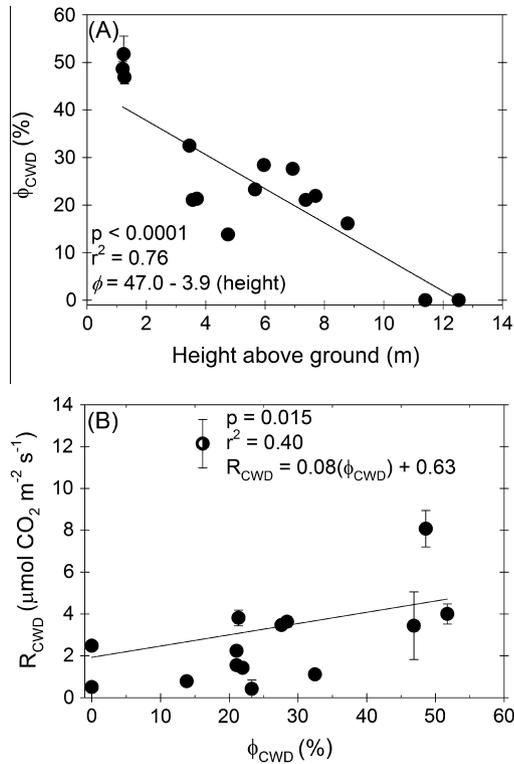


Fig. 3. Standing dead wood sample height in relation to mean wood water content (ϕ_{CWD} ; A), and mean *in situ* coarse woody debris respiration (R_{CWD}) in relation to mean wood water content (ϕ_{CWD} ; B). An outlier (half-filled circle), greater than two standard deviations from the mean, was excluded from the regression analysis of mean R_{CWD} and mean ϕ_{CWD} . Means across sample dates ± 1 S.E.

CWD respiration from changes in C pools, a simple under the curve (Fig. 2A) integration and scaling of mean *in situ* instantaneous CWD respiration from point measurements, R_{CWD} , and a previously developed site-specific model driven by continuous ϕ_{CWD} and T_{CWD} estimations. Estimates of ecosystem CWD respiration from downed and standing dead wood combined did not differ significantly among approaches, totaling $1.1 \pm 1.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for the mass balance approach, $2.1 \pm 1.3 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for the integration approach, and $1.2 \pm 1.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for the modeling approach. Standing dead wood was the largest contributor to ecosystem CWD respiration in all estimations (Fig. 4), comprising 65%, 57%, and 74% of the total annual CWD respiration from the mass balance, integration, and model estimates, respectively. This large contribution from standing dead wood was a function of its high surface area relative to downed wood (Fig. 1) rather than high R_{CWD} . Decay class 2 downed woody debris was the second largest source of respired C from CWD in all estimations. Total C flux from downed woody debris classes 1, 3, 4, and 5 contributed <20% of the total ecosystem CWD respiration in all estimations. Given total CWD mass (26 Mg C ha^{-1}) and ecosystem CWD respiration values ($1.1\text{--}2.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) six years following disturbance, the CWD decomposition rate-constant (ecosystem CWD mass/ecosystem CWD respiration) was between 0.4 and 0.8 yr^{-1} .

Ecosystem CWD respiration ($1.1\text{--}2.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) following moderate disturbance was a substantial contributor to R_{E} and similar in magnitude, but opposite in sign, to NEP. Mean R_{E} following disturbance (2009–2013) was an $8.81 \pm 0.23 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ flux to the atmosphere (Bond-Lamberty et al., 2015) and did not differ significantly over time or from a nearby undisturbed, control forest (Gough et al., 2013). The different estimation approaches suggest that ecosystem CWD respiration comprised 12.0–24.3% of the total respiratory C flux ecosystem-wide 6 years following disturbance

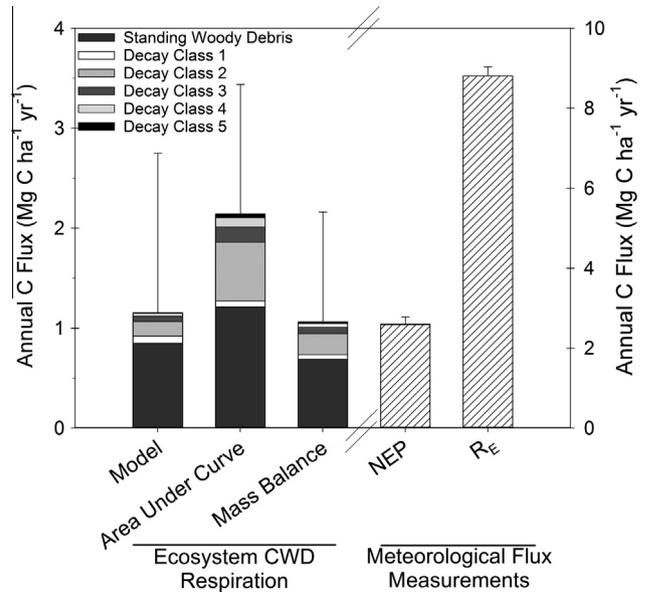


Fig. 4. Annual ecosystem CWD respiration, 2014, estimated using three different approaches, in comparison to mean net ecosystem production (NEP) and ecosystem respiration (R_{E}) for a Great Lakes forest, 2009–2013 by CWD decay class. Note that NEP and R_{E} are expressed on a separate y-axis and scale. Error bars are ± 1 S.E. and represent cumulative uncertainty from model error and spatial variation in the case of ecosystem CWD respiration, or meteorological flux estimation for NEP and R_{E} (see Gough et al., 2013).

(Fig. 4). Despite the mortality of more than one-third of all canopy trees, the ecosystem remained a modest C sink following disturbance, with mean NEP (= GPP – R_{E}) comparable to that of the control forest (Gough et al., 2013). Ecosystem CWD respiration was only slightly lower in magnitude than mean NEP of $2.59 \pm 0.18 \text{ Mg C ha}^{-1}$ following disturbance (2009–2013) (Bond-Lamberty et al., 2015).

4. Discussion

We have shown that ecosystem CWD respiration was a substantial contributor to R_{E} , and therefore a large C loss from the ecosystem, following a moderate forest disturbance, approaching NEP in magnitude. Our results indicate that standing woody debris mass, though spatially variable, was a particularly important contributor to the ecosystem's total CWD pool and respiration following moderate disturbance, with *in situ* standing woody debris respiration rates comparable to those of downed woody debris in the earliest stage of decay. Despite an increase in ecosystem CWD respiration following tree mortality, comparable levels of R_{E} before and after disturbance, and relative to a nearby undisturbed control site suggest that the respiratory contribution from other sources may have declined as ecosystem CWD respiration increased, helping to stabilize NEP.

Our experimental disturbance was similar in severity to moderate disturbances caused by insect defoliation, pathogen outbreaks, and extreme weather, resulting in a comparable input of CWD. Our experiment gradually transferred 35 Mg C ha^{-1} from live to dead wood pools, with standing woody debris accounting for >90% of the total CWD mass 6 years following disturbance. This value is considerably higher than CWD pools of 2.2 Mg C ha^{-1} in a nearby undisturbed forest (Gough et al., 2007) and of 0.3 Mg C ha^{-1} one year following the disturbance treatment. Sudden oak death similarly increased standing woody debris and total CWD mass from 1.4 Mg C ha^{-1} to $33.9 \text{ Mg C ha}^{-1}$ (Cobb et al., 2012). Gypsy moth defoliation increased CWD mass to a lesser extent, from

2.5 Mg C ha⁻¹ to 11 Mg C ha⁻¹ three years post-disturbance, with standing woody debris making up 75% of dead wood mass (Renninger et al., 2014).

Although measurements of *in situ* CWD respiration, R_{CWD} , were highly variable within and among decay classes, and across time, our measured values are similar to previously reported field measurements expressed on a surface area basis from our site and others (Gough et al., 2007; Forrester et al., 2012; Renninger et al., 2014). Our observation of increasing R_{CWD} with increasing extent of decay was previously observed at our site (Gough et al., 2007) and others (Forrester et al., 2012; Renninger et al., 2014). In contrast, less decayed CWD respired at a higher rate than more moderately decayed wood following pest-related mortality in an oak forest (Renninger et al., 2014). Our inability to detect significant relationships between downed R_{CWD} and known microclimatic drivers (Zhou et al., 2007; Vanderhoof et al., 2013) was associated with high variance in our field measurements, which are considerably more variable than controlled laboratory based measurements of whole CWD pieces (Gough et al., 2007). Poor correlations between R_{CWD} and microclimate in the field may occur because CO₂ emitted from the CWD surface may originate far from the location of measurement and, therefore, be decoupled from the local microclimate (Teskey et al., 2008). Nevertheless, we did detect a relationship between R_{CWD} and respiration collar height in standing dead wood, which corresponded with differences in ϕ_{CWD} .

Moderate disturbance caused a considerable increase in ecosystem CWD respiration without a corresponding increase in total R_E or a decrease in NEP, suggesting that the quantity of respired C from other sources may have declined and, in doing so, stabilized ecosystem C losses. Though ecosystem CWD respiration estimates varied nearly 2-fold among the three approaches, this level of variation among methods is typical of heterotrophic C fluxes, which are made with high uncertainty (Gough et al., 2008b; Harmon et al., 2011). Our estimates of ecosystem CWD respiration before and after moderate disturbance suggest an increase from 0.2 Mg C ha⁻¹ yr⁻¹ (Gough et al., 2007) to a conservative estimate of 1.1 Mg C ha⁻¹ yr⁻¹, or from 2% to 12.5% of R_E six years after disturbance chiefly because of the increase in total downed and standing CWD mass. An increase in ecosystem CWD respiration without a concomitant increase in R_E suggests that the contributions of other respiratory sources shifted by a similar amount but in the opposite direction, stabilizing the total ecosystem respiratory C flux. Interestingly, this shift in the relative contributions of different respiratory C fluxes parallels findings from our site demonstrating that, following disturbance, a rapid compensatory increase in leaf photosynthesis and new growth by undisturbed vegetation maintained ecosystem C uptake, thereby sustaining GPP and NPP despite the mortality of more than a third of all canopy trees (Gough et al., 2013; Bond-Lamberty et al., 2015; Stuart-Haentjens et al., 2015). Though we did not quantify respiration from other sources in the current study, soil respiration, the primary contributor to R_E in most ecosystems, temporarily declined at our site and others following disturbance perhaps due to an initial decrease in rhizosphere activity (Hogberg et al., 2001; Bhupinderpal et al., 2003; Nave et al., 2011; Levy-Varon et al., 2012; Moore et al., 2013). Similarly, total plant respiration decreased following pine-beetle disturbance because fewer live trees remained (Moore et al., 2013). Placed within the broader context of prior results from our experimental disturbance, sustained NEP in the first several years following moderate disturbance may be attributed to the maintenance of C uptake and primary production (Gough et al., 2013) and, given the present findings, stability in C losses owing to compensatory shifts in respiratory sources that maintained, rather than increased, R_E .

We found that standing woody debris, an often unmeasured source of respiratory C, was the largest component of ecosystem CWD respiration, with relatively high *in situ* CWD respiration rates. Respiration from standing dead wood is infrequently measured or accounted for in ecosystem C budgets because it is assumed to be a small fraction of total CWD in recently undisturbed ecosystems (Harmon et al., 2011), and is thought to have very low *in situ* respiration rates (Harmon et al., 1986; Yatskov et al., 2003; Liu et al., 2006; Jomura et al., 2008; Tang et al., 2008). However, recent region-wide forest inventories suggest standing dead wood pool size, in contrast to downed CWD, is broadly increasing in aging forests of the Eastern US (Woodall et al., 2015). In our moderate experimental disturbance standing wood was a large fraction of the total CWD pool, with *in situ* CWD respiration rates comparable to those for downed wood in decay class 1. Similarly, respiratory C losses from standing woody debris were substantial following disturbances that initially left dead trees standing rather than felled and when *in situ* standing CWD respiration rates were comparable to those of downed wood (Jomura et al., 2008; Renninger et al., 2014).

The large remaining pool of CWD that originated following moderate disturbance demonstrates the lasting, but presently uncertain, effect of disturbance on the forest's future C cycle. Six years following disturbance, 26.0 Mg C ha⁻¹ of mostly legacy woody debris remained in the ecosystem, a large C pool approaching 15% of the ecosystem's total carbon stores (Gough et al., 2008a). At present, the CWD decomposition rate-constant of 0.4–0.8 yr⁻¹ is slightly lower than the 0.9 yr⁻¹ reported for our undisturbed, control forest (Gough et al., 2007) because of the dominance of slowly decaying standing CWD in the disturbed forest. However, CWD decomposition rate-constants, as the term implies, assume unchanged environmental conditions and decomposer activity, an assumption that is violated by disturbance and which suggests the rate-constants we report here are likely to change in the future (Harmon et al., 2011; Russell et al., 2014, 2015; Woodall et al., 2015). Nonetheless, aspen CWD can take >70 years to fully decompose (Russell et al., 2014), suggesting that dead wood could remain a source of C until the end of this century. Although respiration from decomposing CWD may continue for decades, the contribution of ecosystem CWD respiration to R_E is likely to change. For example, respiration from other sources returned to pre-disturbance levels within several years of an ecosystem perturbation (Levy-Varon et al., 2014; Trahan et al., 2015). However, uncertainty exists in precisely when ecosystem CWD respiration will peak following disturbance. A lag in time between disturbance and peak R_E is commonly observed following perturbations that do not immediately kill or fell trees (Harmon et al., 2011; Renninger et al., 2014). In our system, the abrupt felling of standing CWD from wind or ice, for example, could accelerate decomposition and consequently increase ecosystem CWD respiration. Rates of dead wood decomposition could also be affected by climate change, as the climate in northern lower Michigan becomes warmer and drier with more variable precipitation (Duveneck et al., 2014; Peterson et al., 2014).

We conclude that following a moderate severity forest disturbance the accounting of downed and standing CWD pools and fluxes was essential to accurately quantifying the ecosystem C budget, and interpreting the relative stability in R_E and NEP following tree mortality. Our findings are in agreement with those for a moderately disturbed oak forest (Renninger et al., 2014), but contrast with many other studies demonstrating that CWD was minimally important to the overall C budget during periods of low disturbance (Liu et al., 2006; Gough et al., 2007; Tang et al., 2008). Standing woody debris, which our study suggests may respire more than often assumed, may be an especially important C pool and flux to quantify following disturbances that do not

immediately fell trees, such as insect defoliation, pathogen outbreaks, and age-related senescence. Finally, our work here and that of others from our site show that stability in the ecosystem C balance, NEP, during the first several years following disturbance was tied not only to sustained C uptake and primary production (Gough et al., 2013; Stuart-Haentjens et al., 2015) but also to unexpectedly stable R_E , despite a ≥ 5 -fold increase in ecosystem CWD.

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