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Coarse Woody Debris and the Carbon Balance of a Moderately Disturbed Forest

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COARSE WOODY DEBRIS AND THE CARBON BALANCE OF A MODERATELY DISTURBED FOREST

A Thesis submitted in partial fulfillment of the requirements for the degree of Master of Science

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ABSTRACT

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A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biology at Virginia Commonwealth University

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Landscapes are comprised of multiple ecosystems shaped by disturbances varying in severity and source. Moderate disturbance from weather, pathogens, insects, and age-related senescence, in contrast to severe disturbances that fell trees, may increase standing woody debris and alter the contribution of coarse woody debris (CWD) to total ecosystem respiration (R_E). However, woody debris dynamics are rarely examined following moderate disturbances that substantially increase standing dead wood stocks. We used an experimental manipulation of moderate disturbance in an upper Great Lakes forest to: 1) examine decadal changes in CWD stocks 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). 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 stocks and a large source of ecosystem C flux six years following disturbance. Instantaneous *in situ* respiration rates from standing and downed woody debris in the earliest stages of decay were not significantly different from one another. Independently derived estimates of ecosystem CWD respiration of 1.1 to 2.1 Mg C ha^{-1} yr^{-1} six years following disturbance were comparable in magnitude to NEP and 12.5 % to 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 CWD is an essential component of the ecosystem C balance following a moderate forest disturbance.

Keywords: Coarse woody debris; Disturbance; Mortality; Carbon cycling; Respiration; Wood decay; Standing woody debris

INTRODUCTION

Forest disturbances alter the balance between ecosystem carbon (C) uptake and loss, and are a primary determinant of the terrestrial C balance (Amiro et al., 2010; Bond-Lamberty et al., 2007; Gough et al., 2007; Pan et al., 2011). Tree mortality from disturbance may alter an ecosystem's C balance in two ways: by reducing the amount of C taken up and fixed by the forest canopy, and by increasing the amount of detritus available to fuel the respiratory release of CO_2 through microbial decomposition (Harmon et al., 2011; Liu et al., 2006). Coarse woody debris (CWD), defined here as standing and downed dead wood > 10 cm diameter, comprises an important input of detritus following disturbance (Amiro et al., 2010; Harmon et al., 2011; Renninger et al., 2014). Numerous studies show that the transfer of wood from live to dead stocks can considerably alter the ecosystem C balance, with some forests becoming C sources after severe, stand-replacing disturbance (Amiro et al., 2010; Harmon et al., 1986; Harmon et al., 2011; Hicke et al., 2012; Janisch & Harmon, 2002).

Coarse woody debris dynamics have been extensively characterized in mature forests with minimal recent disturbance and severely disturbed forests (Gough et al., 2007; Harmon et al., 2011; Hicke et al., 2012, Luyssaert et al., 2008); considerably less is known about CWD dynamics following moderate disturbances that kill only a subset of canopy trees (Gough et al., 2013; Harmon et al., 2011; Renninger et al., 2014). Studies conducted in mature forests show that CWD is a relatively small C pool that contributes little to total ecosystem respiration (R_E) or the overall C balance (net ecosystem production, NEP) (Gough et al., 2007; Harmon et al., 2004; Janisch et al., 2005 Liu et al., 2006; Luyssaert et al., 2008; Tang et al., 2008). In contrast, CWD, particularly downed, may be a primary substrate supporting respiratory C losses following high severity fire and clear-cut harvesting (Amiro et al., Harmon et al., 2011; Hicke et al., 2012;

Janisch & Harmon, 2002; Woodall et al., 2015). How CWD moves through stages of decay and contributes to R_E following more moderate disturbance is less clear, though a recent study suggests that accounting for changes in CWD stocks and respiration is essential to accurately estimating an ecosystem's C balance after lower intensity disturbances (Renninger et al., 2014). Understanding CWD dynamics following moderate disturbance is increasingly relevant as forest disturbances that kill only a subset of canopy trees – including insect or pathogen outbreaks, extreme weather events, or age-related senescence – increase in frequency and extent worldwide (Amiro et al., 2010).

Characterizing CWD dynamics at multiple levels of disturbance severity is important because the extent and nature of tree mortality has implications for ecosystem structure and consequently potential implications for the C balance (Pedlar et al., 2002; White et al., 2015). For example, moderate disturbances may substantially increase the amount of standing dead wood, while severe disturbances such as clear-cut harvesting and catastrophic fire may fell, remove, or reduce standing wood stocks (Pedlar et al., 2002; Renninger et al., 2014). Consequently, studies of CWD tend to focus on downed rather than standing woody debris, assuming the latter contributes nominally to detritus stocks and therefore R_E (Liu et al., 2006; Tang et al., 2008; Yatskov et al., 2003). Several studies show standing woody debris respires at a much lower rate than downed woody debris and therefore contributes little to R_E,,with microbial decomposers less prolific on recently senesced standing wood (Harmon et al., 1986; Jomura et al., 2008; Liu et al., 2006; Tang et al., 2008; Yatskov et al., 2003). However, a recent study in an oak (*Quercus*) forest disturbed by insect pests demonstrated that standing and downed wood sometimes respire at similar rates, with standing dead wood contributing substantially to R_E (Renninger et al., 2014).

Here, 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 but not immediately felled via experimental stem girdling. The treatment produced a forest structure and composition similar to that which is broadly emerging in the upper Great Lakes region as secondary forests mature and as severe disturbances decline in frequency (Gough et al., 2010). Prior C cycling studies from this experiment emphasized C uptake following disturbance, demonstrating sustained NEP and primary production despite the mortality of more than a third of all canopy trees and corresponding transfer of 35 Mg ha^{-1} of wood from live to dead pools (Gough et al., 2013; Stuart-Haëntjens et al., *in press*; Nave et al., 2011). Our focus here is on C losses, asking whether this large pulse of CWD was a prominent contributor to R_E following moderate disturbance. Specific objectives were to: 1) examine decadal changes in CWD stocks through moderate disturbance; 2) quantify 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 woody debris 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.

METHODS

Site description

The study was conducted at the University of Michigan Biological Station (UMBS) in northern, lower Michigan, USA (45° 35N 84° 43W). 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. It developed following a clear-cut and wildfire regime in the early 20th century and has since undergone only moderate, patchy disturbances. Early successional 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 and woody debris represented a stock 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 (~6,700) 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 carbon stocks

Coarse woody debris mass was inventoried by decay class in 8, 0.1 ha subplots within the experimentally manipulated area in 2009, 2011, 2013, and 2014. Downed woody debris (> 10 cm diameter, < 45° from the forest floor) was classified into one of the following decay classes (Marra and Edmond, 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) was identified as a sixth class of woody debris.

Measurements of length and diameter at the distal ends and middle of each piece of downed CWD and measurements of height and diameter at breast height of each piece of standing woody debris were used to calculate the volume of each piece of woody debris using the equation for the frustum of a cone (Harmon & Sexton, 1996). Site- and species-specific carbon densities for each decay class were used to calculate C mass from CWD volume (Gough et al., 2007).

Coarse woody debris respiration and microclimate

Instantaneous *in situ* respiration from the surface of aspen CWD (R_{CWD}; μmol m^{-2} s^{-1}) was repeatedly measured on aspen logs 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). Five subsample PVC respiration collars (2 cm high, 10 cm diameter) were permanently affixed to each of three replicated CWD samples (1.5 m long) per decay class using duct seal putty. The five subsample collars were evenly spaced and positioned at random angles that did not interfere with measurements along each CWD replicate, including the distal ends of downed and the tops of standing woody debris when possible. We measured R_{CWD} weekly beginning early July for downed CWD and mid-July for standing woody debris 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). Wood water content was converted from volumetric to gravimetric values using decay-class specific CWD densities from our site (Gough et al. 2007).

Annual carbon flux estimates

We estimated the annual respiratory C flux from downed and standing CWD (Mg C ha^{-1} yr^{-1}), hereafter termed ecosystem CWD respiration, in 2014 using three different methods. A mass balance estimate of ecosystem CWD respiration was calculated as the change in total woody debris stocks summed across all decay classes over one year, from 2013 to 2014. The total loss of C mass was assumed to be equal to the flux to the atmosphere, as C retention in soils from the decomposition of woody debris is negligible (Harmon et al., 1986; Laiho & Prescott, 1999). A second approach integrated R_{CWD} over time, with fluxes interpolated between measurement dates, and used total surface area of downed and standing dead wood to scale to the ecosystem. We estimated R_{CWD} outside of the measurement period through linear extrapolation between first and last measurement dates and the dates in Spring and Autumn, respectively, assuming rates were zero when temperature was < 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 was calculated using SigmaPlot (SYSTAT Inc., San Jose, CA, USA). Lastly, a previously developed site- and species-specific model driven by ϕ_{CWD} and T_{CWD} was used to infer half-hourly R_{CWD} values, which were then integrated over time and scaled to the ecosystem using downed and standing CWD mass (Gough et al., 2007). Because continuous ϕ_{CWD} and T_{CWD} values were required to calculate R_{CWD} but not available from direct measurements, correlations between periodically measured ϕ_{CWD} and T_{CWD} and continuously logged soil moisture and soil temperature, respectively, were developed following the approach of Gough et al., 2007 to derive half-hourly estimates of ϕ_{CWD} and T_{CWD} for all of 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 across the year and multiplied by decay class specific CWD mass to estimate ecosystem CWD respiration per decay class. 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 the atmosphere (Bond-Lamberty et al., 2015; Gough et al., 2013).

Statistical analysis

Statistical differences over time and among decay classes in CWD stocks, R_{CWD}, ϕ_{CWD}, and T_{CWD} were assessed using a repeated measures analysis of variance (ANOVA). 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) approach and mass/area 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).

RESULTS

Coarse woody debris carbon stock

The allocation of CWD stocks among decay classes as well as total woody debris mass changed over time following aspen and birch mortality. One year after the stem-girdling treatment, in 2009, and prior to peak mortality, downed CWD mass was evenly distributed among decay classes, totaling 0.3 ± 0.09 Mg C ha^{-1} yr^{-1}. By 2011, 97 % of stem-girdled aspen and birch were dead (Gough et al., 2013), resulting in a 35 Mg C ha^{-1} pulse of CWD in early stages of decomposition, including standing dead wood. In 2013 and 2014, following multiple years of decomposition, the stock of moderately decayed wood trended upward as standing CWD began to fall and gradually advanced to later stages of decay (Figure 1); this increase over time was not statistically significant, (time main effect, $p = 0.27$; time x decay class interaction, $p = 0.39$), however, because of the very high spatial variation among replicate plots in CWD mass, a signature of increased spatial heterogeneity of C pools and fluxes caused by disturbance (Gough et al., 2013). Six years following disturbance in 2014, standing dead wood was the largest stock of CWD ecosystem wide at 24.5 ± 7.6 S.E. Mg C ha^{-1}; downed dead wood comprised 1.5 ± 0.7 S.E. Mg C ha^{-1}.

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 (Figure 2A). Mean R_{CWD} varied by an order of magnitude among decay classes and across time, from 1.2 μmol CO_2 m^{-2} s^{-1} to 11.4 μmol CO_2 m^{-2} s^{-1}, with individual point measurements as high as 64.3 μmol CO_2 m^{-2} 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. Wood water content, ϕ_{CWD}, increased with increasing extent of decay, up to decay class 4 (decay class main effect, $p < 0.0001$) (Figure 2B); mean ϕ_{CWD} was from 3.5 g H_2O g^{-1} C to 47.1 g H_2O g^{-1} C. Wood temperature, T_{CWD}, increased with increasing extent of decay (decay class main effect, $p = 0.04$), and was highest in downed decay classes 4 and 5, and in standing dead wood (Figure 2C).

Although T_{CWD} and ϕ_{CWD} varied considerably over time and among decay classes (Figure 3A, 3B), microclimate was not a predictor of R_{CWD} in downed wood while moisture was a strong correlate of R_{CWD} in standing wood (Figure 4A). There was no significant relationship between downed R_{CWD} and ϕ_{CWD} ($p = 0.20$) (Figure 3A) or T_{CWD} ($p=0.16$) (Figure 3B) when regressions were fitted to data from all decay classes combined, even though ϕ_{CWD} was generally higher in more decomposed wood than less decomposed wood. Wood water content and T_{CWD} were significantly negatively correlated with each other ($p < 0.0001$, $r^2 = 0.03$) suggesting that with higher temperatures, less water was present in wood. In contrast to downed CWD, standing dead wood exhibited a significant decline in ϕ_{CWD} with increasing measurement height ($p < 0.0001$, $r^2 = 0.77$) (Figure 4A) and a significant relationship between mean ϕ_{CWD} and mean R_{CWD} ($p = 0.015$, $r^2 = 0.402$) (Figure 4B).

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 CWD respiration from changes in C stocks, a simple under the curve (Figure 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 ± 1.1 (95 % C.I.) Mg C ha^{-1} yr^{-1} for the mass balance approach, 2.1 ± 1.3 Mg C ha^{-1} yr^{-1} for the integration approach, and 1.2 ± 1.6 Mg C ha^{-1} yr^{-1} for the modeling approach. Standing dead wood was the largest contributor to ecosystem CWD respiration in all estimations (Figure 5), 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 (Figure 1) rather than high R_{CWD}. Decay class 2 downed woody debris was the second largest source of C flux 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.

Ecosystem CWD respiration (1.1 to 2.1 Mg C ha^{-1} yr^{-1}) following moderate disturbance was a substantial contributor to R_E and similar in magnitude to NEP. Mean R_E following disturbance (2009-2013) was 8.81 ± 0.23 (1 S.E.) Mg C ha^{-1} yr^{-1} (Bond-Lamberty et al., 2015) and did not differ significantly from a nearby undisturbed site (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 (Figure 5). Ecosystem CWD respiration was only slightly lower than mean NEP of 2.59 ± 0.18 Mg C ha^{-1} following disturbance (2009-2013) (Bond-Lamberty et al., 2015).

DISCUSSION

We have shown that ecosystem CWD respiration was a substantial contributor to R_E 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 CWD stock and respiration following moderate disturbance, with *in situ* standing woody debris respiration rates comparable to those of downed woody debris in early stages 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 other respiratory sources may have declined as ecosystem CWD respiration increased.

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 stock 6 years following disturbance. This value is considerably higher than CWD stocks 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 stocks from 1.4 Mg C ha^{-1} to 33.9 Mg C ha^{-1} (Cobb et al., 2012). Gypsy moth defoliation increased CWD stocks 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 in magnitude to previously reported field measurements expressed on a surface area basis from our site and others (Forrester et al., 2012; Gough et al., 2007; 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 (Vanderhoof et al., 2012; Zhou et al., 2007) was associated with high variance in our field measurements, which were considerably more variable than controlled laboratory based measurements of whole CWD pieces conducted at our site (Gough et al. 2007). Poor correlations between R_{CWD} and microclimate in the field may occur because CO_2 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 weak relationship between R_{CWD} and 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 R_E or a decrease in NEP as expected, suggesting that respiration from other sources may have declined. 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. An increase in ecosystem CWD respiration without increasing R_E suggests that the contributions of other respiratory sources shifted by a similar amount but in the opposite direction, stabilizing the 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 shift in leaf level photosynthetic capacity and growth among vegetation within the ecosystem maintained C uptake (Bond-Lamberty et al., 2015; Gough et al., 2013; Stuart-Haëntjens et al., *in press*). 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 a near-term decrease in rhizosphere activity (Bhupinderpal-Singh et al., 2003; Högberg et al., 2001; Levy-Varon et al., 2012; Moore et al., 2013; Nave et al., 2011). Similarly, plant respiration decreased following a large-scale pine-beetle disturbance in a lodgepole pine forest because fewer live trees remained (Moore et al., 2013).

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 measurements. 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 low disturbance severity ecosystems (Gough et al., 2007; Tang et al., 2008). In our moderate experimental disturbance, however, standing wood was a large fraction of the total CWD stock. Respiratory C from standing woody debris was an important flux when present in large amounts following disturbances that left dead trees standing rather than felled (Jomura et al., 2007; Jomura et al., 2008; Renninger et al., 2014). Also, several previous studies, in contrast to our findings, report substantially lower rates of respiration for standing than for downed woody debris (Harmon et al., 1986; Jomura et al., 2008; Liu et al., 2006; Tang et al., 2008; Yatskov et al., 2003). We found instead that standing and downed wood in early stages of decay respire at similar rates. This result agrees with a recent study conducted in an oak forest following a gypsy moth invasion that showed standing dead wood may respire at rates even higher than downed CWD (Renninger et al., 2014).

The large remaining pool of CWD that originated following moderate disturbance indicates a 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 stocks (Gough et al. 2008). Aspen CWD can take > 70 years to fully decompose (Russell et al., 2014), suggesting that it could remain a persistent 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 a 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 increasing R_E is commonly observed, especially in disturbances 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 events (Handler et al., 2014).

We conclude that following a forest disturbance of moderate severity the accounting of downed and standing CWD stocks and fluxes is essential to accurately quantifying the ecosystem C budget. Our findings are in agreement with those for a moderately disturbed oak forest (Renninger et al., 2014) but contrast with others demonstrating that CWD was minimally important to the overall C budget during periods of low disturbance severity (Gough et al., 2007; Liu et al., 2006; Tang et al., 2008). Standing woody debris may be an especially important C stock to quantify following disturbances that do not immediately fell trees, such as insect defoliation, pathogen outbreaks, and age-related senescence. Finally, our work and that of others from our site shows that stability in the ecosystem C balance, NEP, following disturbance was tied not only to sustained C uptake (Gough 2013; Stuart-Haëntjens et al., *in press*) but also to stable R_E, despite a ≥ 5-fold increase in ecosystem CWD.

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FIGURES

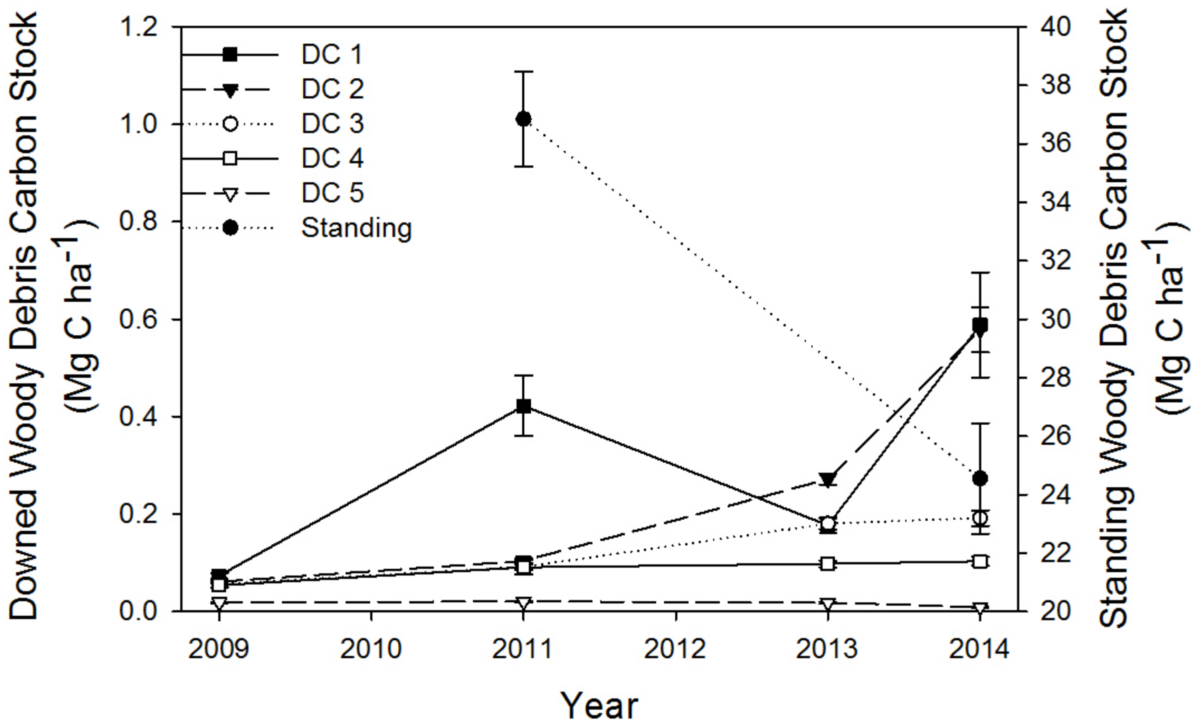

Figure 1. Downed and standing woody debris carbon stocks by decay class (DC) in a moderately disturbed upper Great Lakes forest in which all aspen and birch trees were stem girdled in 2008. Note the different y-axes and scales for downed (left) and standing (right) woody debris. Means ± ¼ S.E. for visual clarity.

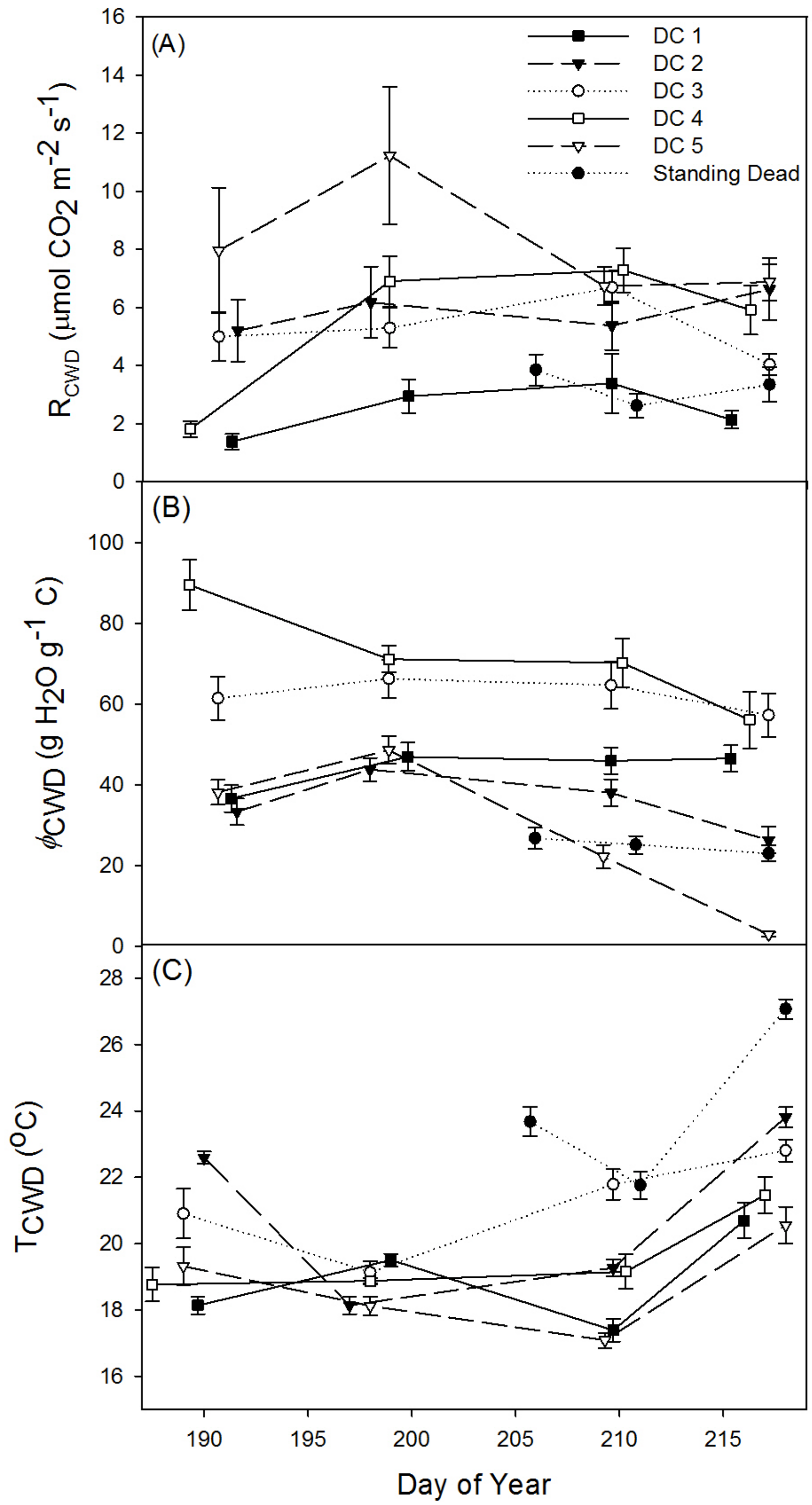

Figure 2. Means ± 1 S.E. of *in situ* coarse woody debris respiration (R_{CWD}; A), wood gravimetric water content (f_{CWD}; B), and wood temperature (T_{CWD}; C) of downed and standing woody debris by decay class (DC) during Summer 2014.

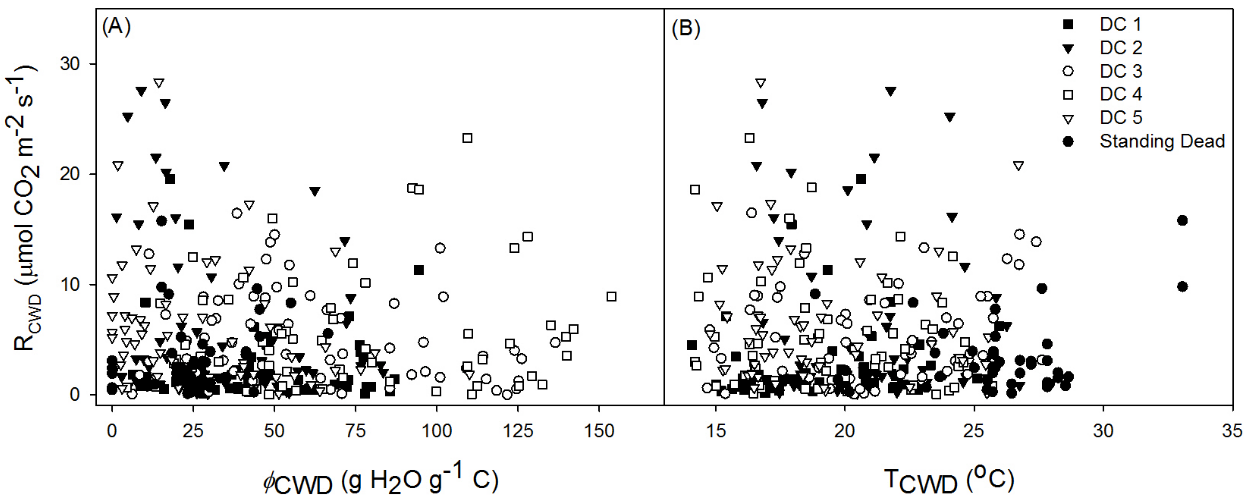

Figure 3. *In situ* coarse woody debris respiration (R_{CWD}) in relation to wood gravimetric water content (f_{CWD}; A) and wood temperature (T_{CWD}; B) by decay class (DC).

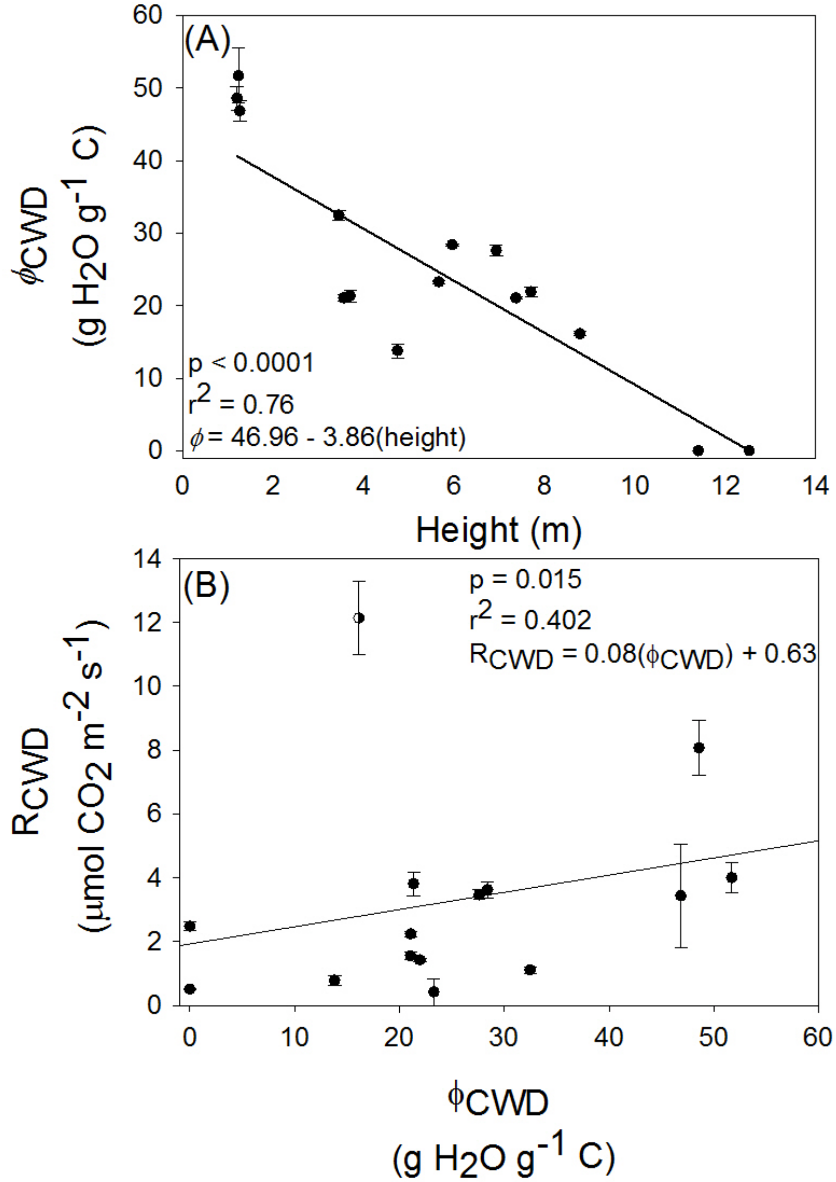

Figure 4. Standing dead wood sample height in relation to mean wood water content (ϕ_{CWD}; A) and mean *in situ* coarse woody debris respiration (R_{CWD}) in relation to mean wood water content (ϕ_{CWD}; B). An outlier (half-filled circle), greater than two standard deviations from the mean, was excluded from the regression analysis of mean R_{CWD} and mean ϕ_{CWD}. Means across sample dates ± 1 S.E.

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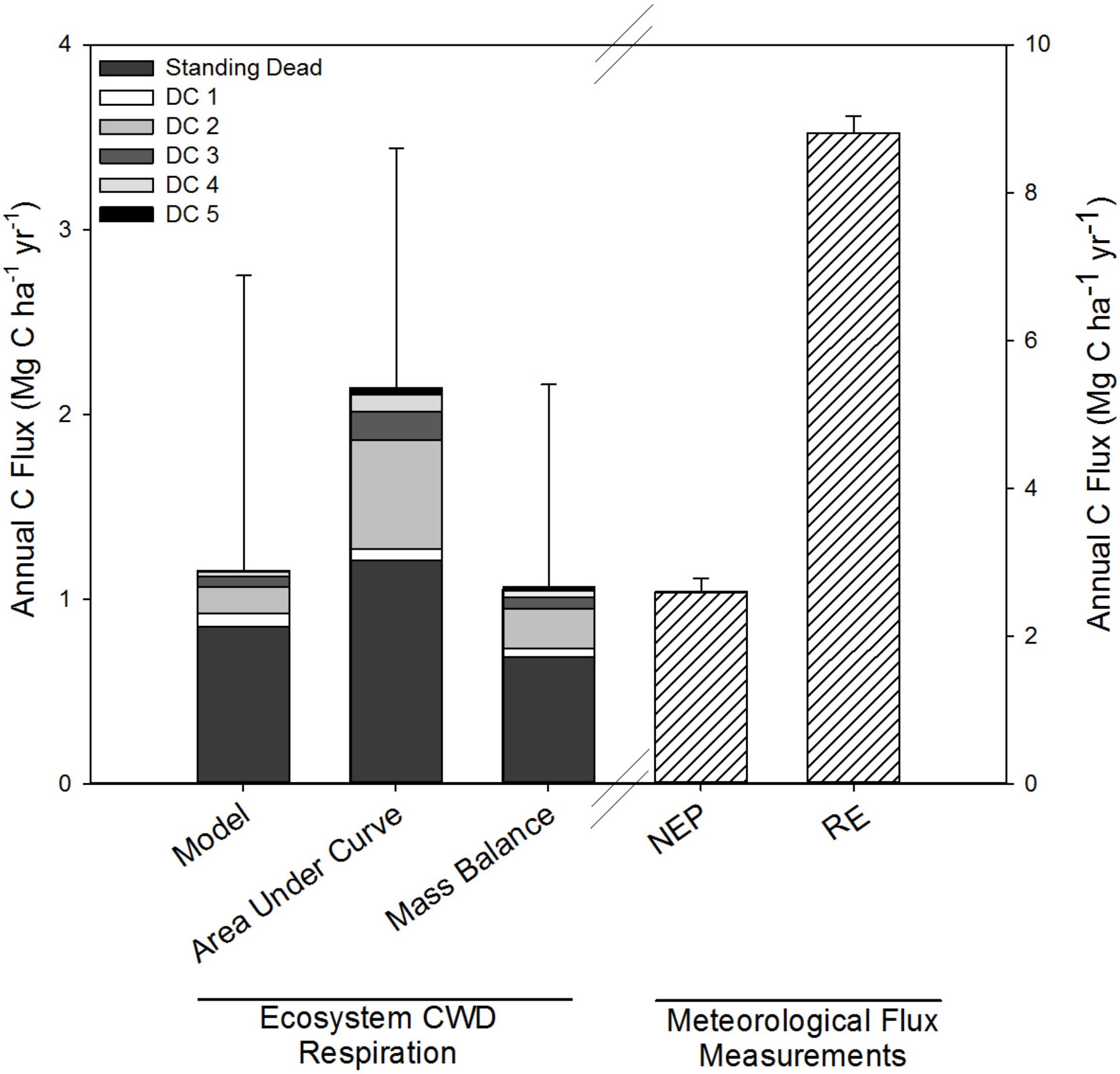

Figure 5. Annual ecosystem CWD respiration, 2014, estimated using three different approaches in comparison to mean net ecosystem production (NEP) and ecosystem respiration (R_E) for a Great Lakes forest, 2009-2013 by CWD decay class (DC). Note that NEP and R_E are expressed on a separate y-axis and scale. 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).

APPENDIX I: ANOVA Tables

Table 1. ANOVA summary table for the comparison of coarse woody debris mass (Mg C ha^{-1}) among decay classes (DC) and across time (2009-2014).

Source	DF	Type III SS	Mean Square	F	p-value
Replicate	7	415787778	59398254	1.59	0.1430
Date	3	89753473.40	29917824.47	1.41	0.2680
DC	5	12383416503	2476683301	66.47	<0.0001
Date x DC	13	517795408	39830416	1.07	0.3919
Replicate x Date	21	445827543	21229883	0.57	0.9319
Error	126	4694715827	37259649		

Table 2. ANOVA summary table for the comparison of mean instantaneous *in* situ respiration from the surface of coarse woody debris rates (R_{CWD}; μmol CO_2 m^{-2} s^{-2}) among decay classes (DC) and across time (2009-2014).

Source	DF	Type III SS	Mean Square	F	p-value
Replicate	2	53.83	26.91	2.13	0.1337
Date	4	42.60	10.65	0.66	0.6359
DC	5	234.1	46.82	3.70	0.0083
Date x DC	13	77.30	5.946	0.47	0.9273
Replicate x Date	8	128.8	16.10	1.27	0.2879
Error	36	455.2	12.64		

Table 3. ANOVA summary table for the comparison of mean gravimetric wood water content (ϕ_{CWD}; g H_2O g^{-1} C) among decay classes (DC) and across time (2009-2014).

Source	DF	Type III SS	Mean Square	F	p-value
Replicate	2	3464	1732	5.60	0.0076
Date	4	2512	628.0	6.26	0.0138
DC	5	17847	3589	11.61	<0.0001
Date x DC	13	3625	278.9	0.90	0.5595
Replicate x Date	8	802.4	100.3	0.32	0.9513
Error	36	11133	309.2		

Table 4. ANOVA summary table for the comparison of wood temperature (T_{CWD}; °C) among decay classes (DC) and across time (2009-2014).

Source	DF	Type III SS	Mean Square	F	p-value
Replicate	2	26.07	13.04	1.19	0.3155
Date	4	128.0	31.99	14.39	0.0010
DC	5	140.7	28.1	2.57	0.0434
Date x DC	13	56.34	4.33	0.40	0.9619
Replicate x Date	8	17.78	2.22	0.20	0.9885
Error	36	393.9	10.94		

APPENDIX II: Coarse Woody Debris Enzyme Analysis

Methods

Coarse woody debris samples were collected in mid-July 2014 from the FASET experimental area in the UMBS forest. Cross-sections approximately 5-13 cm thick were cut from random locations along the length of downed bigtooth aspen (*Populus grandidentata*) logs of all decay classes (1-5) using a chain saw. These cross sections were frozen at -20° C until further processing. Two triangular wedges, each 1/6 of the total sample, were randomly selected and then cut from each approximately circular cross section. These wedges were then manually splintered with a wedge and ground in a Wiley mill.

Assays were proposed to be completed by first extracting enzymes by shaking ground wood samples in distilled water for 2h on an orbital shaker, centrifuging the enzyme extraction at 4000 rpm for 30 minutes, and filtering the supernatant (Vetrovsky et al., 2010). Decay class 4 and 5 samples were extracted and frozen at -20° C. Manganese peroxidase activity was proposed to be measured with phenol red following Vares et al., 1995. Laccase activity was proposed to be measured through the oxidation of the dye 2,2'-azino-bis(3-ethylbenzothiazoline-6-sulfonate) (ABTS) following Bourbonnais and Paice, 1990. β-Glucosidase activity was proposed to be measured using β-NPG substrate and following supplier protocol (Abnova, Taiwan). Xylanase and β-Glucanase activity were proposed to be measured using azo-dyed carbohydrate substrates following supplier protocol (Megazyme, Ireland).

Discussion

Assays for enzyme activity were not completed as proposed for a number of reasons. Principally, there were multiple factors that would have resulted in measures of enzyme activity that would not have accurately reflected the enzymes present in the wood samples collected. For example, extracted enzyme solutions from decay classes 4 and 5 were frozen for > 6 months; decay class 1, 2, and 3 wood samples were also frozen for > 6 months and additionally went through multiple freeze/thaw cycles in the process of further breaking them down. Detectable enzyme activity has previously been reported in European beech (*Fagus sylvatica*) and silver birch (*Betula pendula*) wood in early stages of decay (Vetrovsky et al., 2010); however, the amount of time samples remained frozen in between sample collection, processing, and analysis could have also affected enzyme activity because enzymes could have been denatured from the formation and subsequent thawing of ice crystals (Cao et al., 2003). In future studies of extracellular enzyme activity in coarse woody debris, field samples should be collected, processed, and analyzed within the shortest amount of time to minimize the effects of enzyme degradation on enzyme activity. Additionally, it may be useful to collect samples of fungal fruiting bodies from logs, as in Vetrovsky et al. (2010) to compare the activity of enzymes in the fruiting body to that of activity in the wood itself.

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VITA

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