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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.

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; Luyssaert 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°35N84°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. 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