

Tipping the carbon balance?: Woody debris production and respiration following moderate disturbance

Abstract

Coarse woody debris (CWD) is a significant and growing component in forest ecosystems, especially those undergoing succession or withstanding disturbances. We combined CWD census data and *in situ* chamber respiration measurement to quantify the amount and carbon stored by CWD in an experimentally disturbed early successional aspen and birch forest. CWD was found to be 35.2 Mg C ha⁻¹ of which was 29.3 Mg C ha⁻¹ standing and 5.9 Mg C ha⁻¹ was downed. Downed CWD respiration averaged 1.1 μm CO₂ kg⁻¹ s⁻¹, but significant differences were found based on orientation, side or end. A statistical multi-variate linear combination model that related orientation, decay class, and CWD temperature to instantaneous efflux was used to model ecosystem level respiration for the month of July 2013. Total respiration was found to be 276.9 ± 223.1 kg C ha⁻¹ mo⁻¹. When compared to net ecosystem productivity and pre-disturbance CWD respiration rates, the our July 2013 respiration total represents a significant increase in respiration rates with the potential to limit the forest's ability to act as an effective carbon sink in the future.

1. Introduction

Forest succession, disturbance, and weather events attributed to climate change do and will have large-scale impacts on forest ecosystems. In the United States, forests sequester approximately 10% of total carbon emissions, making them integral in mitigating rising CO₂ levels (IPCC, 2007). Net Ecosystem Productivity (NEP), the difference between net CO₂ influx

from photosynthesis and loss via autotrophic and heterotrophic respiration, determines whether a forest is a carbon source or sink (Law et al, 1999). Downed coarse woody debris (CWD) is an important carbon store, constituting 1-45% of the above ground biomass (Harmon et al, 1986). The size of the CWD carbon store and the rate of its decomposition can determine whether a forest ecosystem acts as a net carbon source or sink (Janisch and Harmon, 2002).

In the upper Great Lakes region, CWD production and respiration should reach the higher end of this spectrum in coming decades. Many of the region's previously harvested forests are reaching maturity and progressing to later successional stages (Gough et al, 2007). Simultaneously, climate change is predicted to increase the likelihood of disturbance events (winds, fire, insect outbreaks, pathogens), increasing CWD production (Harmon et al, 2013). Major biome shifts, such as the decline of the middle boreal forest and replacement of the southern boreal forest, predicted by climate change models will increase CWD production. Increased temperature, growing season duration, and precipitation in the Great Lakes region will also increase cumulative annual respiration rates (NCA, 2013). The relationship between climate change and CWD production and respiration suggest an enhanced positive feedback loop in the future, in which increasing CO₂ levels alter climate and disturbance regimes in a way that enhances respiration rates and CWD production, releasing even more CO₂ into the atmosphere. Thus, as CWD carbon stores are projected to increase dramatically in some regions, further knowledge of how CWD respiration influences the forest C balance is necessary.

Accurate quantification of C fluxes, principally photosynthesis and respiration, is necessary to calculate NEP. Comparatively, photosynthesis has been more extensively studied (Law et al, 1999), even though respiration is equally important to Earth systems models that simulate C cycling (Tang et al, 2008). Fewer studies quantify the individual components of

forest respiration (Gough et al, 2007). Eddy covariance methods analyze ecosystem level fluxes, measuring aggregated respiration from multiple sources without distinguishing between soil, woody debris, stem, and leaf contributions (Tang et al, 2008). Furthermore, CWD has often been overlooked because of its spatial variation, slow decomposition time, stochastic production, and necessary knowledge of forest history (Jomura et al, 2007; Currie and Nadelhoffer, 2002). While some studies have tangentially touched on the spatial variation in respiration rates on a single CWD sample (Herrmann and Bauhus, 2008), this has not been adequately studied, especially for standing woody debris.

Multiple biotic and abiotic factors such as temperature, moisture, O₂, CO₂, substrate quality, woody debris size, and decomposers control CWD respiration rates (Harmon et al, 1986). At UMBS, previous experiments conducted both in the lab and field demonstrated a positive relationship between CWD respiration rates and temperature and moisture. Low moisture content is responsible for decreasing respiration rates while very high moisture levels could also limit CWD respiration as well; however this is unlikely in the well-drained UMBS soils. (Gough et al, 2007). Temperature increases soil respiration because of increased fungal and invertebrate activity within the approximate range of 0 °C and 40 °C (Harmon et al, 1986).

This study aims to quantify the contributions of standing and downed CWD to ecosystem respiration following a moderate disturbance. I will: (1) Quantify the amount of CWD following the moderate disturbance (girdling) in the Forest Accelerated Succession Experiment (FASET) site, (2) Measure downed and standing CWD respiration rates, (3) Test whether CWD respire at greater rates from their tops (standing) or ends (downed) as compared to sides because of the relative impermeability of the bark, which might create a “chimney effect,” and (4) Calculate the contribution of CWD respiration to total ecosystem respiration and to NEP.

2. Materials and methods

2.1 Study site

The study was carried out in the FASET site at the University of Michigan Biological Station in northern lower Michigan, USA (45° 35.5'N, 84° 43'W) (Figure 1). A 46m high meteorological tower continuously records net ecosystem CO₂ exchange between forest and atmosphere using an infrared gas analyzer. FASET is a 39 hectare section of forest in which over 6,700 aspen and birch were girdled in 2008, hastening the rate of senescence of the canopy dominants, bigtooth aspen (*Populus grandidentata*), trembling aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*). Girdling mimics a moderate species-specific disturbance and usually results in mortality within 1-2 years. Girdling also prevents suckering, in which the girdled plant generates new shoots and can survive. Other major tree species at the FASET site include red oak (*Quercus rubra*), sugar maple (*Acer saccharum*), white pine (*Pinus strobus*), American beech (*Fagus grandifolia*). Bracken fern (*Pteridium aquilinum*) dominates the understory. The average age of the overstory is 85 years, but there is much individual variation and substantial sapling growth. The forest withstood heavy logging into the late 19th century and fire disturbances until 1923 after which the forest has been relatively stable. FASET released approximately 30 Mg C ha⁻¹ in the forest before which pre-girdling NEP was 1.5-2 Mg C ha⁻¹ yr⁻¹ (Gough et al, 2007). The FASET site's elevation is 324m. The mean annual temperature is 5.5° C (1942-2003) and average precipitation is 817 mm (including 294 cm snowfall) (Nave et al, 2011).

2.2 Coarse woody debris census

Standing (above 45° from forest floor) and downed (below 45° from forest floor) aspen and birch CWD mass was quantified in 8, 0.1 ha plots within the FASET site. Four plots were located along transects originating from the base of the FASET meteorological tower and four others within a 1.1 ha large plot surrounding the tower (Figure 2). The volume of all downed CWD >10 cm in diameter were calculated from measurements of length and diameter at the base, middle, and top using the equation for the frustum of cone (Harmon and Sexton, 1996). A decay class (1-5) was next assigned to each piece of CWD using the parameters (Marra and Edmonds, 1994): (1) recently downed material with tissue and bark intact throughout; (2) sapwood beginning to decay but completely present, bark beginning to crack; (3) sapwood and bark mostly present, heartwood tissue intact; (4) sapwood and bark mostly gone, heartwood beginning to decay; (5) sapwood and bark gone, heartwood with substantial decay. Standing CWD was also assigned a decay class using the above parameters. The diameter at breast height (DBH) and height (using the Laser Technology Inc. TruPulse 200 hypsometer) were recorded for snags. The volume, surface area, and top diameter of snags were calculated using linear regressions that related the respective measurement to DBH and height. CWD carbon mass was calculated for each decay class using estimates of CWD volume and from site-specific C densities previously determined for each CWD decay class (Gough et al, 2007).

2.3 Instantaneous coarse woody debris respiration

Aspen and birch downed and standing CWD respiration rates were recorded in the field for each decay class using a custom built cuvettes. Downed CWD logs were randomly selected from a subset of four randomly selected plots of the original 8, .1 hectare census plots. For each log, instantaneous respiration rates were measured using a LiCor 6400 gas analyzer. Measurements were taken on 1-3 side locations and as many log ends (0-2) as the CWD structure

and state of decay permitted. Standing CWD instantaneous respiration rates for 5, ~1m standing bole samples were measured at 3 locations – ~50% of height, ~75% of height, and chimney (top parallel to ground) – along the snag. Multiple CWD surfaces were measured to account for surface variability. A transportable custom cuvette attached to each sample location enabled constant pressure and volume during measurements. Side measurements were done using a 340ml cuvette attached to the CWD surface by putty. If the topography of the log did not permit adhesion by putty, a foam gasket was used to prevent leakage. End CWD respiration measurements were conducted by enclosing the end with flashing to create an open cylinder and a flat chamber head that enclosed the open end. Standing CWD respiration was measured the same way for 5, ~1m trembling aspen snags. Temperatures were recorded for each measurement, using a type E thermocouple inserted into the CWD, neighboring soil, and chamber. Soil moisture was measured using Hydrosense Soil Water Content Measurement System (Campbell Scientific, Inc., Logan, UT, USA) directly adjacent to or below the downed and standing CWD. Moisture levels were recorded using a Lumber Moisture Meter DC-2000 calibrated using cookies taken from sample logs, which were dried to determine the water content by mass.

2.4 July coarse woody debris flux

Instantaneous standing and downed CWD respiration rates were scaled to estimate total July CWD respiration for the FASET forest. Total downed CWD surface area was calculated by modeling each log as a frustum. A model that predicted species-specific surface area and top diameter for standing snags was developed to calculate total standing surface area and top surface area. A site-specific statistical model relating the orientation on the log (side=0 or end=1), decay class (1-5), and CWD temperature ($^{\circ}\text{C}$) was created. Respiration rates were not

significantly different across different species so one model was used for all species. Downed CWD respiration was modeled using a multi-variate linear combination of the following parameters: downed CWD efflux (R_{CWD}) and orientation ($p=.0001$), decay class (D) with orientation (O) as an interaction term ($p=.0049$), and decay class with CWD temperature (T_{CWD}) as an interaction term ($p=.0704$).

$$R_{DCWD} = 0.869 + 20.978(O) - 6.046(D * O) + 0.137(D * T_{CWD}), \quad R^2 = .20$$

FASET tower 1m high 30 minute averaged air temperatures correlated with CWD temperature positively ($R^2=.54$), more strongly than instantaneous soil temperatures did with CWD temperature ($R^2=.12$), and thus were used to model continuous CWD temperature. This yielded total July respiration per unit surface area, which we then scaled to the ecosystem using an estimated total CWD surface area value. Standard error in cumulative July downed CWD respiration was calculated using the standard error in the parameter values from the statistical model. Standing CWD respiration rates were simply scaled from the instantaneous rates without accounting for July temperature variation or decay class variation. We compared our estimate CWD respiration with historical rates of ecosystem respiration and NEP and their component fluxes (Curtis et al. 2004).

3. Results

3.1 Coarse woody debris census

Five years following the 2008 moderate disturbance event, standing and down coarse woody debris mass within the experimentally disturbed site totaled 35.2 Mg C ha⁻¹. (Figure 3) Standing CWD constituted 29.3 Mg C ha⁻¹. Big tooth aspen comprised 95.5% of the Standing CWD mass while paper birch was 4.5%. Standing CWD was unevenly distributed across decay classes as 82.1% and 16.6% were in decay classes 1 and 2, respectively. Downed CWD

constituted 5.9 Mg C ha^{-1} , of which 80.3% was aspen and 5.3% paper birch. Red oak, sugar maple, and white pine made up the remaining small quantity of downed CWD. Downed CWD was also unevenly distributed across decay classes, heavily favoring less decayed classes, with 36.4% of all downed CWD in decay class 2. Decay class 1 and 3 was 23.7% and 24.1%, respectively, of total downed CWD. Cumulative downed CWD mass increased by 184% between 2009 and 2013 and 179% between 2011 and 2013. (Figure 4)

3.2 Instantaneous coarse woody debris respiration

Instantaneous downed CWD respiration varied considerably with spatial orientation and decay class. Downed CWD respired at an average rate of $13.4 \pm 1.7 \mu\text{m CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ from the ends and $7.5 \pm 1.5 \mu\text{m CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ from the sides. Standing CWD instantaneous respiration rates similarly varied strongly by orientation. The tops respired at a rate of $11.0 \mu\text{m CO}_2 \text{ m}^{-2} \text{ s}^{-1} \pm 3.77$ while sides respired at $0.6 \mu\text{m CO}_2 \text{ m}^{-2} \text{ s}^{-1} \pm 0.09$ respectively. (Figure 5) Sides made up 76.8% of total downed CWD surface area and 99.7% of total standing CWD surface area.

Downed CWD end respiration rates also varied by decay class. Decay class 1-3 end measurements were not statistically different and averaged $16.2 \mu\text{m CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, but decay class 4 and 5 end respiration rates were significantly lower at an average of $2.70 \mu\text{m CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Side respiration rates were variable by decay class, but did exhibit fluctuations within in decay classes. (Figure 6) When integrated across all surfaces, downed CWD respiration rates on a mass basis averaged $1.1 \mu\text{m CO}_2 \text{ kg}^{-1} \text{ s}^{-1}$. (Figure 6) Per log downed CWD respiration rates was found to positively correlate with increased decay class ($R^2=.89$). (Figure 7)

3.3 July coarse woody debris C flux

July CWD respiration was a substantial quantity of projected annual standing and downed CWD respiration. July 2013 CWD respiration totaled $276.9 \pm 223.1 \text{ kg C ha}^{-1} \text{ mo}^{-1}$, with downed CWD $232.3 \pm 216.4 \text{ kg C ha}^{-1} \text{ mo}^{-1}$. Bigtooth aspen and paper birch were the only contributors to standing CWD respiration at monthly rates of $39.5 \pm 6.0 \text{ kg C ha}^{-1} \text{ mo}^{-1}$ and $4.9 \pm .7 \text{ kg C ha}^{-1} \text{ mo}^{-1}$, respectively. July 2012 respiration was calculated to account for 23.4% of annual respiration. Applying the same proportion to July 2013 standing and downed CWD respiration, net CWD respiration is expected to be approximately $1.2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. (Figure 8, 9)

4. Discussion

Our coarse woody debris census totals, instantaneous respiration rates, and modeled July 2013 effluxes are both reasonable in context with other studies and demonstrate how CWD production and respiration has changed over time and in response to the moderate disturbance event. Our total coarse woody debris mass of $35.3 \text{ Mg C ha}^{-1}$ (75.1 kg ha^{-1}), is within the range of the pre-girdled projected pulse of 30 Mg C ha^{-1} . Harmon et al (1986) found *Acer-Betula* woody debris biomass to be 31.5 Mg ha^{-1} , similar in magnitude to our observations within a disturbed forest. Across different forest ecosystems woody debris biomass is highly variable as a chronosequence in boreal Manitoba, Canada found CWD biomass to range from 9.7 to 80.4 Mg ha^{-1} (Bond-Lambery and Gower, 2008) and Harmon et al, 1986 observed woody debris biomass in a Pacific Northwestern *Pseudotsuga-Tsuga* forest to be 490 Mg ha^{-1} . Cumulative downed CWD mass of $5.97 \text{ Mg C ha}^{-1}$ is comparable to the 2.2 Mg C ha^{-1} found in FASET pre-girdling by Gough et al, 2007. Although it represents a 184% increase, this is reasonable 5 years following the moderate disturbance event, especially as process of girdling does not cause instant tree mortality, but 97% of girdled trees were found to be dead in 2011 (Gough et al, 2013).

While cumulative downed CWD increased this much between 2009 and 2013, there was only a 2% between 2011 and 2013 indicating that the vast majority of CWD was produced in the two years following the 2009 census. Woodall, 2008 found in a national inventory that mean CWD carbon in the Great Lakes Region was $4.59 \text{ Mg C ha}^{-1}$, $4.89 \text{ Mg C ha}^{-1}$ in latitudes greater than 41° and less than 45° , and $7.35 \text{ Mg C ha}^{-1}$ in latitudes greater than 45° , all reasonable comparisons to our study. The National Greenhouse Gas Inventory (NGHGI) also reviewed in the study found downed dead wood (coarse and fine woody debris) in aspen/birch forests to be 3.9 Mg C ha^{-1} (Woodall et al, 2008). A study of an old growth hemlock-northern hardwood forest in the upper peninsula of Michigan found $.083 \text{ m}^2 \text{ m}^{-2}$ of CWD ($>7.5\text{cm}$ diameter), comparable to our findings of $.094 \text{ m}^2 \text{ m}^{-2}$ of CWD ($>10 \text{ cm}$ diameter) (Tang et al, 2008). Plot CWD variation was extremely high as CWD varied by as much as 1.2 Mg C between the 16m plots. Average per plot CWD increased 54% (kg C ha^{-1}). Mass CWD by plot increased for six of the eight sampled plots over the entire 2009-2013 period. One plot demonstrated unnatural CWD production as a considerable amount of standing CWD was cut down between the years 2009 and 2011.

The distribution of downed CWD across decay classes in the FASET forest is comparable to other findings of disturbed or mature, successional forest stands. CWD distribution in the FASET plots was found to be 24%, 36%, 24%, 13%, and 3% (decay class 1-5), mirroring a study that surveyed a similarly-aged Massachusetts Norway spruce stand with a decay class distribution of 24%, 37%, 24%, 11%, and 4% (Vanderhoof et al, 2012). Similarly, CWD distribution was found to be 31% decay class 1, 52% class 2-3, and 17% class 4-5 in a northern mature second-growth Wisconsin maple-basswood forest (Forrester, 2012). Our distribution, when grouped similarly follows a spread of 24%, 61%, and 16%. Between plots,

decay class distribution was highly heterogeneous. For example, two plots had 3 times as many decay class 5 CWD samples as the other six and one plot had no decay class 1 CWD samples.

The distribution of downed CWD across decay classes varied significantly over the years 2009 to 2013. Generally downed CWD totals fell as decay class increased. However, the spike in decay class 1 in year 2011 and decay classes 2 and 3 in year 2013 indicates the movement of CWD through decay classes in years following the moderate disturbance. This progression was roughly seen eight years following decay class designation in a boreal chronosequence (Bond-Lamberty and Gower, 2008). Approximately 1 Mg C ha^{-1} of new downed CWD was added to the ecosystem in 2013. As there was only a marginal increase of downed CWD mass between 2011 and 2013, this suggests that much CWD mass was respired or fragmented beyond classification. Production in 2009, the year immediately following the moderate disturbance event was low and consistent across decay classes, again most likely explained by the lag in tree mortality following girdling. Standing CWD ($29.3 \text{ Mg C ha}^{-1}$) is substantially higher than the average Northern Lake States region (4.3 Mg C ha^{-1}) and nearly double the Pacific Northwest (westside) region ($15.5 \text{ Mg C ha}^{-1}$) according to the NGHGI survey (Woodall, 2008). The FASET forest out produced high CWD production forest ecosystems, such as Hemlock/Sitka Spruce ($21.3 \text{ Mg C ha}^{-1}$) and Redwood ($16.1 \text{ Mg C ha}^{-1}$), which is expected as disturbance events are usually spatially and temporally variable, diminishing their large regional impacts. The balance between standing and downed CWD should tip in upcoming years as standing CWD falls to the forest floor at higher rates due to weather events and more decay.

Instantaneous CWD respiration rates at our site averaged $1.05 \mu\text{m CO}_2 \text{ kg}^{-1} \text{ s}^{-1}$ were similar to averaged previously reported at the FASET site. Over a comparable temperature range, Gough et al, 2007 found average efflux to be $\sim 0.4 \mu\text{m C kg}^{-1} \text{ s}^{-1}$. The potentially elevated

respiration rates between our study and Gough et al, 2007 could be explained by the difference in methodology. Gough et al, 2007 logs were placed in chambers with ends capped with wax. Because gas diffusion was prevented from the ends of logs, a higher resistance through log sides could have artificially reduced total respiration rates. This should be explicitly investigated both to compared the reliability of techniques and respiration rates. High variability suggests heterogeneity within decay classes and even one log. The strong statistically significant difference ($p=.0001$) between sides and ends of downed logs indicates that the wood structure may be important in determining how and where different fluxes occur. While sides constituted over three-quarters of downed CWD, the elevated respiration rates from the ends partially offsets this imbalance. End contribution to net respiration is crucial to consider as a study found that *in situ* chambers (not situated on cross-sectional areas) underestimated downed CWD respiration rates by as much as 74% as compared to full log segment incubations and wedges (Herrmann and Bauhus, 2008).

There was not a significantly different relationship between bark cover within a chamber and efflux. This suggests that CWD surface is independent of efflux; yet another physical structure of the log facilitates the channeling of effluxes to ends. In observations, it was noted that logs traditionally decay from the ends toward the center. Additionally, open ends have more access to circulating air and weather events, resulting in greater availability of oxygen and moisture. Colonization from microbes and fungi could be facilitated by the open end, also contributing to increased respiration rates from ends. While this study did look at bark coverage and orientation a more comprehensive assessment that focuses explicitly on the question of bark cover should be done to confirm our result that no relationship between bark cover and efflux exists. It is possible that cracks or other irregularities minimize a log's ability to channel

effluxes or the effect of bark's relative diffusional impermeability. Additionally, an insufficient number of chamber placed on one log might not accurately describe on-log spatial variability of effluxes as physical properties of a specific region of a log might direct effluxes away from where a specific chamber was placed (Herrmann and Bauhus, 2008). Additionally, no significant relationship between total log bark cover and efflux was found. This could be a result of high heterogeneity along logs, an insufficient number of chambers on one log to cover this heterogeneity, or lack of downed CWD sampled (n=26).

Instantaneous downed CWD respiration rates increased with increasing decay class, agreeing with trends in other studies (Harmon et al, 1986, Gough et al, 2007). The decreasing log density with increasing decay class is often an indicator of increased water absorption capabilities. Moisture has been proven to be a major driver of respiration (Gough et al, 2007, Vanderhoof et al, 2012, Chamber et al, 2001). Increased contact with the ground and longer contact periods both increase water content of logs and microbe activity and inoculation (Vanderhoof et al, 2012). Also, upon impact, standing CWD fragments, increasing the end to side ratio, which would suggest increased respiration rates of downed CWD. In our study, moisture measurements could not be collected accurately in non-invasive ways and did not respond to variations in moisture at higher moisture contents. Thus, we can instead follow the trend of increased moisture content with decreasing log density, and assume increased effluxes with increased moisture content. This result might have stronger correlation as measurement techniques were better suited to more intact wood as establishing a seal on wet or fragmented wood was difficult, which could have artificially lowered rates from lower decay classes. Respiration was only measured on a small number of decay class 5 CWD, which could have yielded an unrepresentative efflux; however because decay class 5 CWD represents such a small

portion of total CWD, the accuracy of our scaled predictions should not be affected. However, the random selection of logs reasonably matched (although disproportionately sampled decay class 4) the distribution of downed CWD across decay class as 15%, 38%, 19%, 23%, and 4%, were sampled across decay classes 1-5, respectively.

Decay class alone did not significantly correlate with instantaneous downed CWD respiration rates, but was a significant interacting variable with orientation (side or end, $p=.0049$). As decay class increases, the relative importance of the end efflux decreases, suggesting a structural change in downed CWD at higher decay classes in which the ends and sides become increasingly similar with advanced decay. Although no relationship to bark coverage was found, higher decay classes have substantially less overall and intact bark. Furthermore, splintering and fragmentation could deteriorate the lengthwise physical structure of logs that might facilitate diffusion out of the ends rather than sides.

CWD demonstrated a very significant relationship between orientation (side or ends) and instantaneous respiration rate. This relationship was more stratified between the tops (parallel to the ground, $11.51 \pm 3.50 \mu\text{m C m}^{-2}\text{s}^{-1}$) and sides (perpendicular to the ground and bark covered, $.62 \pm .09 \mu\text{m CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than downed CWD (ends, $13.39 \pm 1.73 \mu\text{m C m}^{-2}\text{s}^{-1}$ and sides, $7.52 \pm 1.49 \mu\text{m C m}^{-2}\text{s}^{-1}$). This might partially be due to the small number of snags sampled ($n_{\text{tops}}=5$, $n_{\text{side}}=10$) and their homogeneity ($\sim 1\text{m}$ high, decay class 2). However, standing CWD respiration reinforces the relationship between efflux and orientation and the interacting variable decay class. The standing CWD sampled had very intact bark and further study could reveal a relationship between chamber bark cover and efflux. Standing CWD respiration should be better quantified so that predictions about how respiration rates change as a standing CWD falls and

becomes downed CWD. Average instantaneous respiration rates are more than twice as high for downed CWD ($9.72 \mu\text{m CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) as compared to standing ($4.25 \mu\text{m CO}_2 \text{ m}^{-2} \text{ s}^{-1}$).

The contribution of CWD respiration to NEP is growing in significance after the moderate disturbance event. Month to year comparisons are crude because of seasonal variations in temperature and moisture, but they are informative and place into context our July finding. Pre-girdling, Gough et al, 2007 calculated that annual efflux was 21.3 g C m^{-2} , which roughly translates to $49.90 \text{ kg C ha}^{-1}$ during the month of July, as July net respiration is about 23.4% of yearly respiration. Our July net downed CWD efflux ($232.47 \text{ kg C ha}^{-1}$) represents an approximate 366% increase, which is a reasonable result following a disturbance event that increased downed CWD production by 184% and with our elevated instantaneous respiration rates compared to Gough et al, 2007.

The contribution of standing CWD, 16%, to July 2013 net respiration cannot be overlooked and standing CWD needs to be included in both mass and respiration estimates. When standing and downed CWD is considered, July 2013 represents a 455% increase in net CWD respiration as compared to pre-girdling July average. The standing CWD respiration estimates were calculated only from the 5 sample bigtooth aspen snags (~1m high, decay class 2). While this may have adequately measured the log variability on the samples, longer snags and/or different decay classes should demonstrate more variability, which could shift estimates. Because differences in species between downed CWD respiration rates was not statistically significant, the same standing CWD respiration rates measured from the 5 bigtooth aspen samples were used to estimate respiration rates from paper birch, but a more explicit comparison could yield significant relationship between respiration and species.

Cumulative July 2013 CWD respiration ($0.277 \text{ Mg C ha}^{-1}$) was 8.9% of total July 2012 NEP ($3.12 \text{ Mg C ha}^{-1}$) based on the FASET eddy covariance tower. For comparison, based on temperature dependent models created by Curtis et al, 2005, soil respiration during July 2013 should have been 1.9 Mg C ha^{-1} , or 6.9 times greater. Thus, CWD respiration is becoming a significant portion of ecosystem respiration. As NEP is a marginal difference between ecosystem photosynthesis and respiration, the increase production of CWD following the moderate disturbance event could have dramatic ramifications for the C balance. CWD respiration alone does not convert the FASET forest into a carbons source, but as more standing trees fall and respiration rates increase the marginal difference will decline. Regardless, increased CWD respiration reduces the capability of the FASET forest to provide the ecosystem service of carbon sequestration, crucial as atmospheric CO_2 increase and the impacts of climate change become more frequent and severe. As tree mortality of early successional aspen and birch increase in the Northern Great Lakes region, the increased importance of CWD respiration found at FASET should be mirrored elsewhere in the northern lake states.

Figure 1. UMBS forest site

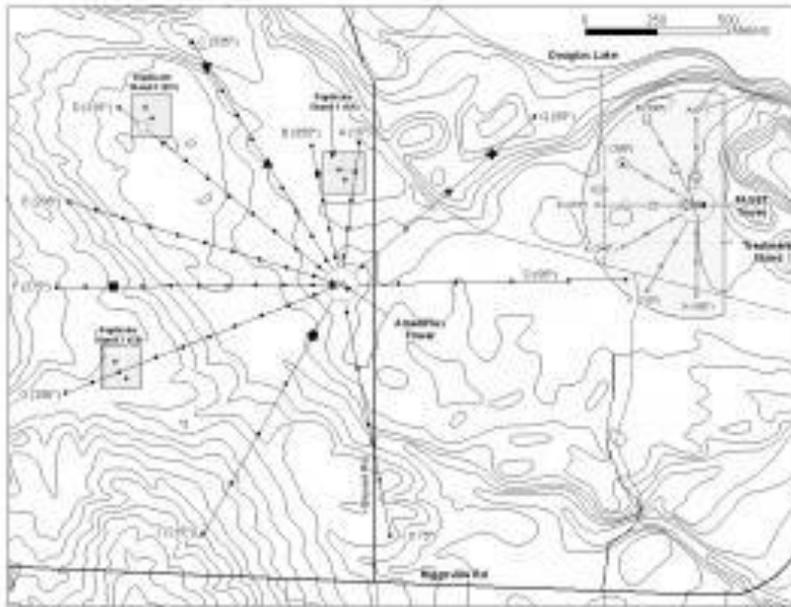


Figure 2. 8 Sample plots, 4 along transects, and 4 within 1.1 subplot surrounding FASET tower. Red dots indicate plots in which CWD respiration rates were measured.

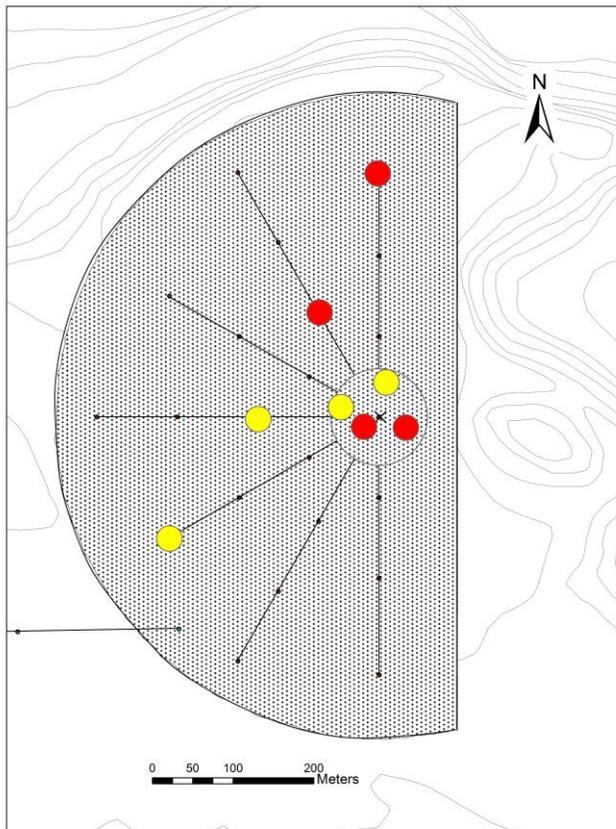


Figure 3. Total mass CWD (downed and standing) in 2013.

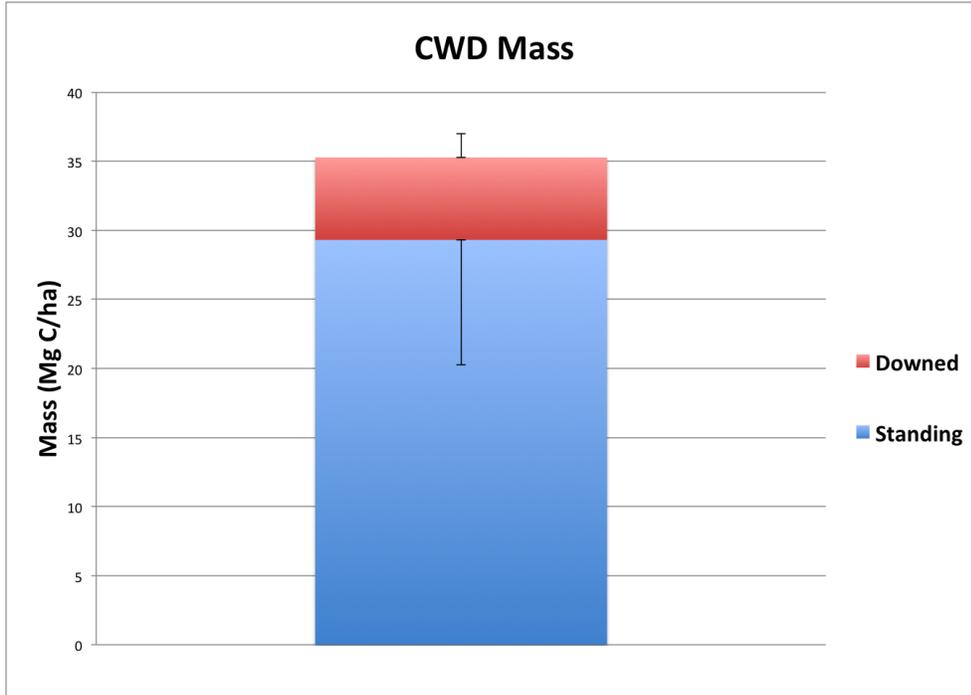


Figure 4. Annual change in downed CWD by mass and decay class (2009-2013).

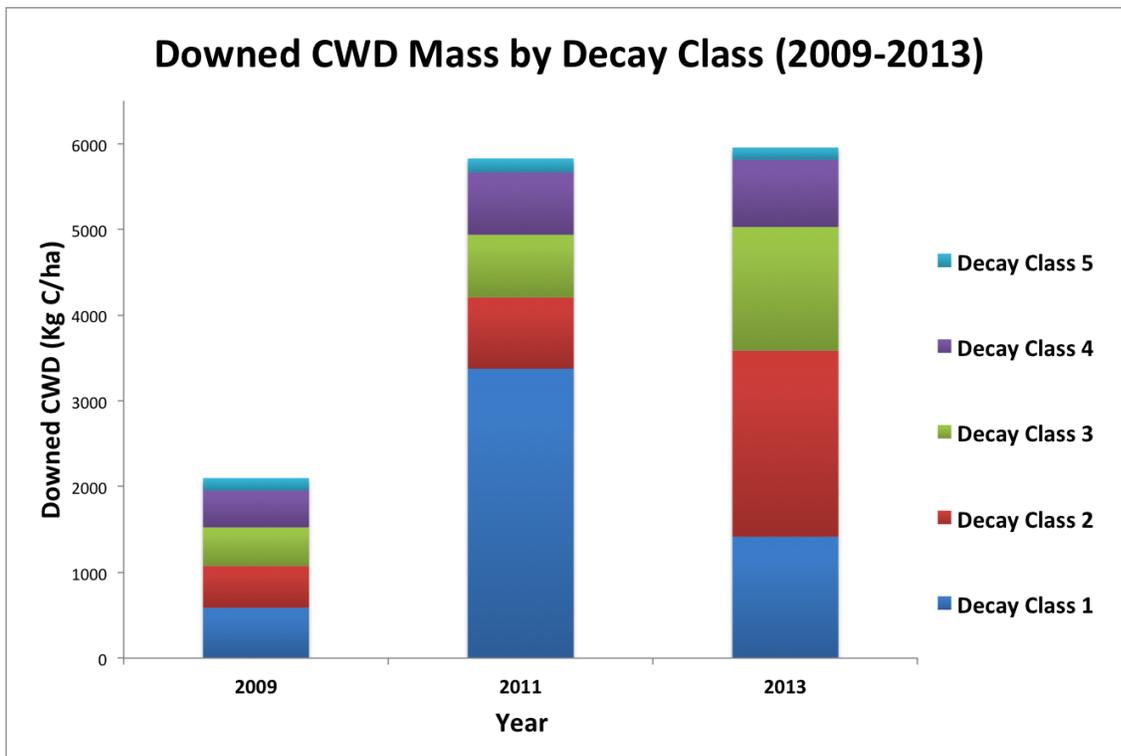


Figure 5. Instantaneous efflux by orientation, standing and downed CWD, ends (or top) and sides. Ends and tops have greater instantaneous efflux rates compared to sides; the difference is greater for standing CWD than downed.

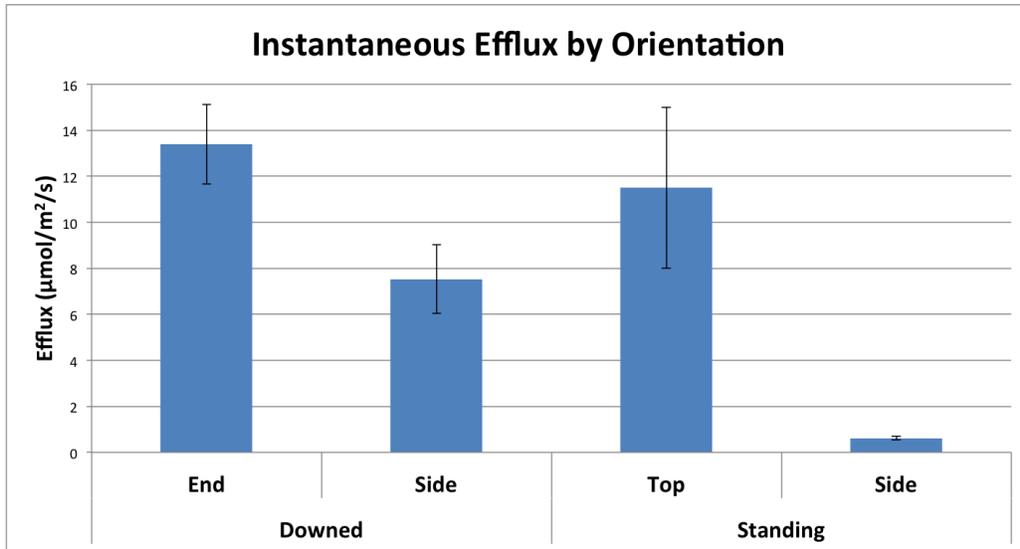


Figure 6. Downed CWD instantaneous efflux by decay class. Side versus end orientation decreases as decay class increases and does average efflux.

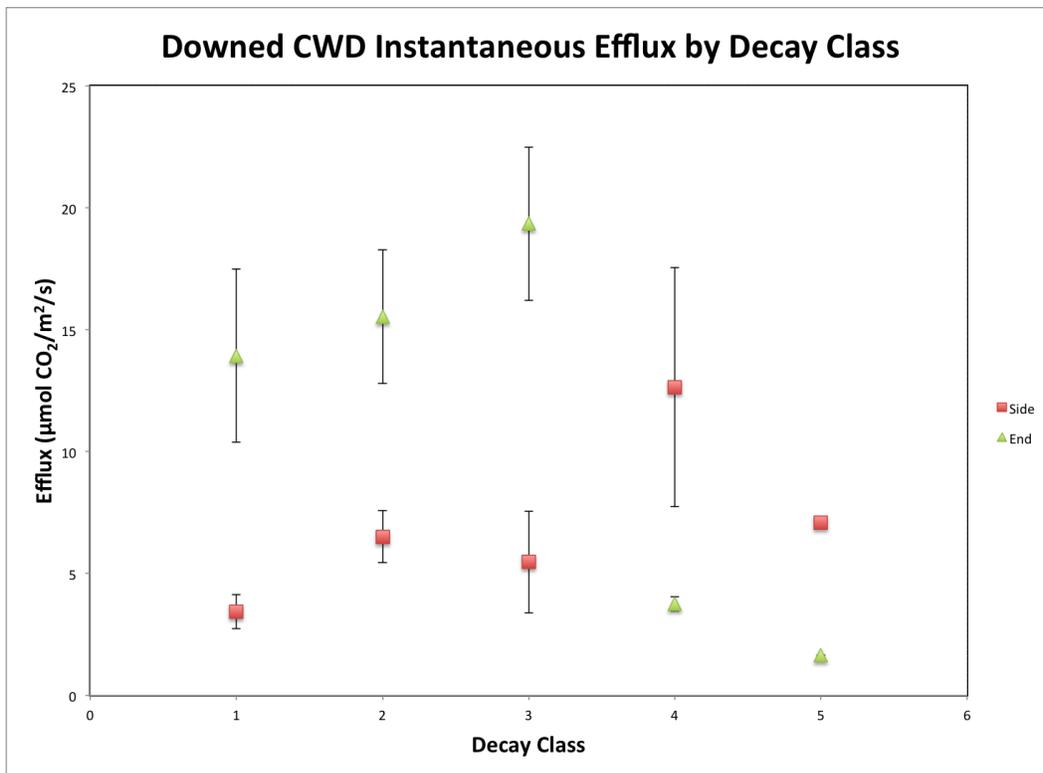


Figure 7. Per log average efflux by decay class.

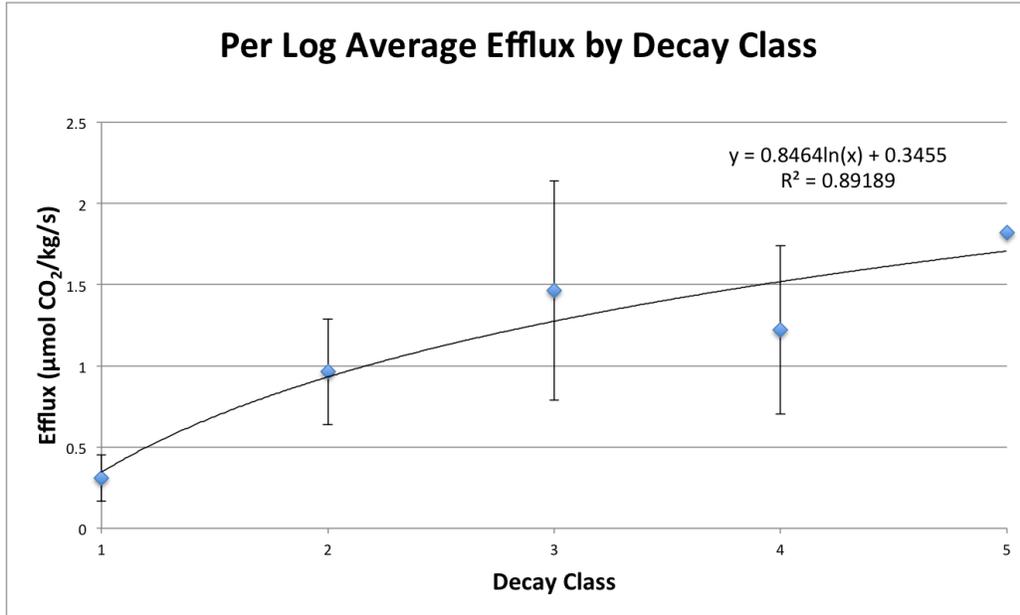


Figure 8. Modeled July 2013 CWD temperature, soil respiration, and downed CWD respiration. CWD temperature is derived from half-hourly averaged air temperatures at 1m high on the FASET tower. Half hour CWD temperatures were averaged for six hour periods and soil and downed CWD respiration rates were summed by the same six hour intervals.

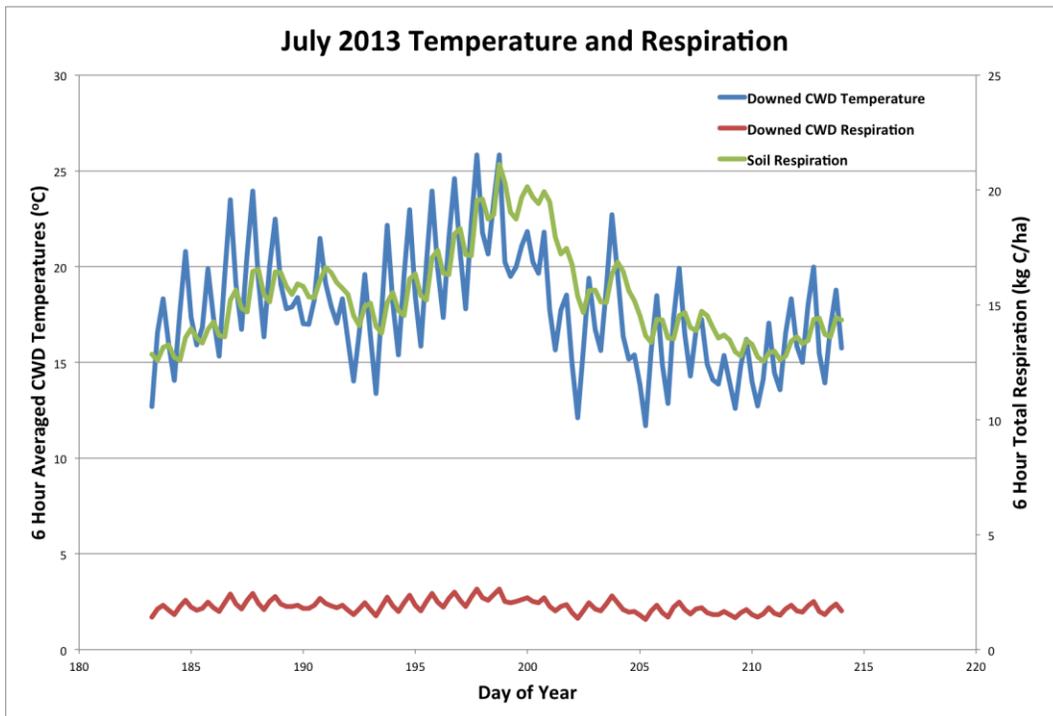
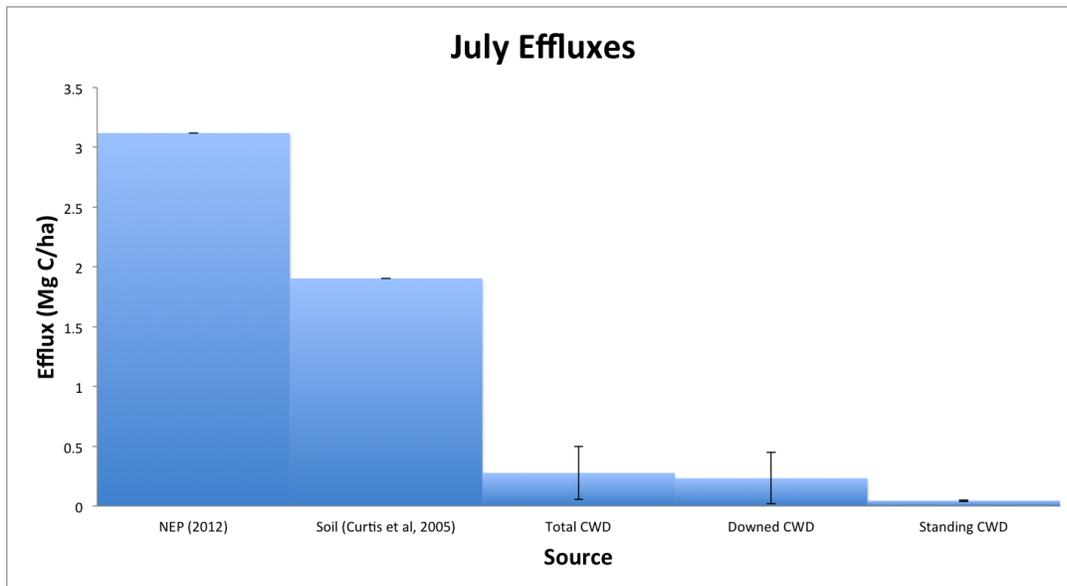


Figure 9. Cumulative July 2013 effluxes. NEP is calculated from 2012 data and not adjusted for differences in weather between years. Soil respiration is modeled from Curtis et al, 2005. There are no error bars for these effluxes as the uncertainty in the NEP calculation and soil model is unknown.



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