

Temporal trends in CO₂ emissions from *Picea rubens* stumps: A chronosequence approach

Zoe Read^{a,*}, Shawn Fraver^a, Jodi A. Forrester^b, Jay Wason^a, Christopher W. Woodall^c

^a School of Forest Resources, University of Maine, Orono, ME 04469, USA

^b Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695, USA

^c USDA Forest Service, Northern Research Station, Durham, NH 03824, USA

ARTICLE INFO

Keywords:

Carbon dioxide
Forest carbon cycle
Woody debris
Wood decomposition
Wood decay
Tree stumps

ABSTRACT

Understanding the forest carbon cycle has become increasingly important as carbon dioxide (CO₂) emissions contribute to the changing climate. Decomposition is a major component of the forest carbon cycle; however, aspects of wood decomposition remain poorly understood, especially for stumps. To fill this knowledge gap, we examined the change in CO₂ emissions over time from *Picea rubens* Sarg. (red spruce) stumps using a 32-year chronosequence (i.e., 0, 2, 4, 8, 23, and 32 years since harvest) derived from detailed harvesting records in a northern conifer forest in central Maine, USA, that has experienced repeated partial harvests. We found low initial CO₂ flux (3.2 μmol CO₂ m⁻² s⁻¹ at year 0) followed by a rapid increase, peaking 8 years post-harvest (24.3 μmol CO₂ m⁻² s⁻¹) followed in turn by a decrease to very low rates by years 23 and 32 (1.4 and 1.7 μmol CO₂ m⁻² s⁻¹, respectively). We found no clear relationship between CO₂ emissions and any of the environmental or stump variables tested (wood temperature, wood moisture, soil moisture, and/or stump volume), suggesting that time since harvest was the overriding influence on CO₂ flux rates. The large variability in CO₂ flux rates among stumps of the same time since harvest points to the need for future research that includes larger sample sizes and covers a wider range of environmental and stump variables to better capture potential sources of variation. Our results add to the growing body of research on carbon emissions from deadwood that can inform forest carbon-cycle models. In addition, forest managers, who are increasingly interested in carbon management, can use these results to assess harvesting impacts on forest carbon emissions.

1. Introduction

Global climate change has motivated the need to better understand the forest carbon cycle, particularly carbon emissions to the atmosphere (Bonan, 2008; Finzi et al., 2020). Although carbon emissions from forest soils have been relatively well studied (Bond-Lamberty and Thomson, 2010; Hashimoto et al., 2015), emissions from decomposing woody material have received much less attention (Russell et al., 2015). However, woody material represents ca. 8 % of total forest carbon stocks globally (Pan et al., 2011) and requires further study. Carbon is emitted from decomposing wood primarily as carbon dioxide (CO₂), the result of respiration by fungi and invertebrates that break down the various wood components. Quantifying these CO₂ emissions in forest experiments poses considerable challenges because of the many biotic and abiotic factors that interact to regulate detrital decomposition (Bradford et al., 2014; Zanne et al., 2015). Yet, a better understanding of the factors

governing woody debris CO₂ emission rates is needed to improve forest carbon-cycle models (Harmon et al., 2020).

One form of woody material that is particularly overlooked is that of stumps (Didion and Abegg, 2022). In fact, only 60 % of countries with national forest inventories of deadwood include stumps (Woodall et al., 2009), despite their prevalence in both managed forests (i.e., felled trees) and unmanaged forests (i.e., resulting from deadfalls). For example, the national forest inventory of Slovenia reports that stumps represent 22 % of total deadwood biomass (Dunger et al., 2012), and the Swiss national forest inventory indicates that stumps comprise 25 % of the total deadwood pool (Didion and Abegg, 2022). Stumps are also connected to the belowground coarse roots and have been found to be disproportionately important to soil carbon and nitrogen pools, relative to their volume (Sucre and Fox, 2009).

The few studies that have measured CO₂ emissions from cut stumps provide important baseline information, yet also point to the need for

* Corresponding author.

E-mail address: zoe.read@maine.edu (Z. Read).

<https://doi.org/10.1016/j.foreco.2022.120528>

Received 12 June 2022; Received in revised form 5 September 2022; Accepted 7 September 2022

Available online 18 September 2022

0378-1127/© 2022 Elsevier B.V. All rights reserved.

further study. Forrester et al. (2015) found that CO₂ flux from recently cut northern hardwood (*Acer saccharum* Marsh., *Fraxinus americana* L., *Tilia americana* L.) stumps increased two years post-harvest, peaked at four years, and then decreased significantly after five years. At the peak, these rates were up to seven times higher than those of logs of the same species and decay state. This difference may have been due to flux measurements capturing root decomposition and soil flux emerging through the stump, as well as differing fungal communities between stumps and logs. Noh et al. (2019) found similarly high flux rates from the cut surfaces of *Fraxinus nigra* Marsh. stumps in the fourth year post-harvest, and Martínez-García et al. (2015) found similar flux rates during the first three years post-harvest of fire-killed *Pinus nigra* Arnold stumps. However, none of these studies monitored changes in CO₂ flux through advanced stages of decay; CO₂ flux rates (and overall decay rates) likely fluctuate over the course of decomposition (Harmon et al., 2000), due to changes in wood structure and chemistry as well as concomitant changes in the fungal community (Stokland et al., 2012).

In addition to time since harvest, environmental factors influence CO₂ flux rates (Bond-Lamberty et al., 2002; Forrester et al., 2015). The CO₂ flux studies mentioned above consistently report a strong positive relationship between temperature (air or soil temperature) and stump CO₂ flux, as have studies of flux from coarse woody material (CWM) (Forrester et al., 2012; Gough et al., 2007; Olajuyigbe et al., 2012; Rinne-Garmston et al., 2019). Although moisture is often shown to have a positive relationship with CO₂ flux from CWM (Forrester et al., 2012; Gough et al., 2007; Olajuyigbe et al., 2012), excessive moisture may at times decrease CO₂ flux from CWM (Progar et al., 2000). Further knowledge regarding the influence of temperature and moisture on CO₂ flux rates is particularly important, as these variables are routinely used in predictive models of forest carbon dynamics (Harmon et al., 2011).

Our objectives were to (1) quantify temporal changes in CO₂ emissions (i.e., flux rates) using a 32-year chronosequence of cut *Picea rubens* stumps, and (2) determine the primary environmental factors governing CO₂ flux rates from stumps. Our study was conducted at the Penobscot Experimental Forest (Maine, USA), which provides the long-term record of harvested trees needed to construct the chronosequence. The results of this study will advance on-going research on woody material decomposition and CO₂ emissions and help inform process-based models of forest carbon dynamics.

2. Material and methods

2.1. Study site

This study was conducted in the U.S. Forest Service's Penobscot Experimental Forest in central Maine (44° 49' N, 68° 38' W). The portion of the forest in which this study was conducted (ca. 2 km²) is dominated by *Picea rubens* Sarg. (red spruce, representing 37 % of basal area), with *Tsuga canadensis* (L.) Carr. (eastern hemlock, 20 % of basal area) and *Thuja occidentalis* L. (northern white cedar, 20 % of basal area) as sub-dominants. *Larix laricina* (Du Roi) K. Koch (eastern larch), *Pinus strobus* L. (eastern white pine), and *Acer rubrum* L. (red maple) are present in lesser abundance. The forest supports 22 m² ha⁻¹ tree basal area and a density of 504 trees ha⁻¹ and has been actively managed under various partial-harvest systems since the 1950s. In the portion of the Penobscot Experimental Forest sampled, stumps occupy a mean of 18 m² surface area ha⁻¹ and number 377 stumps ha⁻¹. Mean annual temperature and precipitation from 1991 to 2020 are 6.6 °C and 1093 mm, respectively (PRISM Climate Group, Oregon State University, 2020), the growing season averages 160 days, spanning May into October (Nelson et al., 2014), and elevation at the site is 42 m a.s.l (PRISM Climate Group, Oregon State University, 2020). Soils in this portion of the Experimental Forest are derived from glacial till and range from somewhat poorly drained to poorly drained (Soil Survey Staff, 2022).

2.2. Stump selection

Silvicultural research at the Penobscot Experimental Forest provides a long-term record of individual tree removals, including mapped tree locations within 810 m² permanent plots. These records allowed us to relocate individual cut stumps of *P. rubens* for which we know the harvest dates. A list of stumps was compiled from harvests that occurred 0, 2, 4, 8, 23, and 32 years before our 2021 sampling (see Fig. 1 for examples). Stumps of 0 years since harvest resulted from a harvest that occurred in February to March 2021, that is, three months before our sampling began. Three stumps were randomly selected from each of these six times since harvest (N = 18 stumps), forming a chronosequence from fresh to well-decayed material. The selected stumps were ultimately located in 11 plots spanning 6 contiguous stands. For each stump, we recorded top diameter and height, and we obtained one hemispherical photograph to characterize canopy openness. Hemispherical photographs were processed using Gap Light Analyzer software (Frazer et al., 1999). Stump volume above ground was calculated as a conical frustrum, assuming a 1.15 cm/m taper from top diameter (Woodall and Westfall, 2008).

2.3. Carbon dioxide flux and environmental variables

Carbon dioxide (CO₂) flux from stumps was sampled from 10 am to 2 pm approximately every other week, except when raining, during the summer and fall for a total of 10 sampling visits between 25 May and 11 October 2021. For stumps 0 through 8 years since harvest, 10-cm-diameter PVC collars, 7.5 cm in height, were sealed to the cut surface of each selected stump using silicone caulk and clay if necessary (Forrester et al., 2015) (Fig. 1). For stumps 23 and 32 years since harvest, PVC collars (as above) of height 15 cm were driven half their height into the stump, thereby forming a seal. Collars on five stumps retained water after a rain, which required that we drill two drainage holes near the base of each collar. These holes were sealed during the flux measurements. At each sampling visit, any litter that had fallen inside the collar was removed. Then, a PVC cap was fit snugly over the collar, with inlet and outlet tubes connecting it to a LI-830 infrared gas analyzer (Li-Cor, Lincoln, NE, USA). As the CO₂ accumulated in the closed chamber, the concentration was measured every second for three minutes, using the 'Flux Puppy' software application (Carbone et al., 2019). We used data collected between 30 and 160 seconds because this period represented the most linear portion of CO₂ accumulation, thereby eliminating any fluctuations in concentration at the start of the measurement period and potential asymptotes near the end of the measurement period. A flux rate was calculated from the slope of the concentration increase within the chamber over time. Prior to each measurement, the cap was allowed to equilibrate to ambient CO₂ concentrations.

Stump surface temperature was automatically recorded every-two hours by Thermochron iButton DS1921G-F5 temperature loggers (Maxim Integrated Products, Sunnyvale, CA, USA), which were wrapped in plastic for moisture protection and placed directly on the stump surface on the north side of the PVC collar. The iButtons were then covered with a reflective solar cover elevated 4 cm above the iButton. In addition, during each sampling visit, wood surface temperature was measured using a Durac 60900-1600 digital thermometer (Bel-Art-SP Scienceware, Wayne, NJ, USA) placed on the stump surface, north of the flux collar. Wood moisture was measured using a wood moisture meter (Protimeter, St. Marys, PA, USA), averaging five measurements around the flux collar, and soil moisture (volumetric moisture content) was measured using a TDR150 soil moisture meter (Spectrum Technologies, Aurora, IL, USA), recording the average of six readings surrounding the stump base.

2.4. Statistical analyses

To address our first objective – quantify changes in CO₂ flux over the



Fig. 1. Examples of *Picea rubens* stumps used in a chronosequence of CO₂ flux, showing stumps 0, 8, 23, and 32 years since harvest. Images show PVC collars (A, 10 cm diameter) used for CO₂ flux measurements, as well as adjacent reflective solar covers (B) shielding the iButton temperature sensors.

chronosequence – we evaluated eight candidate models aimed at describing this temporal pattern. Models were selected to account for the mid-sequence peak evident in the raw data. Model selection was based on AICc scores, root mean square errors (RMSEs), and distributions of residuals, using the `nls` function in the ‘stats’ package (R Core Team, 2020) and the ‘AICcmodavg’ package (Mazerolle, 2020) in R software. In addition, we performed an ANOVA to test for differences in flux among the six times since harvest, using a Tukey’s one-way post-hoc test ($\alpha = 0.05$) with the `aov` and `TukeyHSD` functions in the ‘stats’ package in R (R Core Team, 2020).

Addressing our second objective – determine the primary environmental factors governing flux rates – involved two analytical steps (explained below). First, we aimed to summarize each stump’s repeated CO₂ flux measurements into a single value that could be attributed to that stump. Second, we used this summarized CO₂ flux as a response variable, testing the influence of stump characteristics and environmental variables.

The first step assumed a relationship between CO₂ flux rate (units $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and temperature. A strong relationship between flux and temperature at the time of sampling would allow us to estimate entire growing-season flux using the continuous temperatures recorded by the iButtons. Given the marked differences among individual stumps evident during exploratory analyses, we examined this relationship separately for each stump, testing linear, exponential, and power models. These models ultimately revealed no relationship between flux and temperature for the range of temperatures recorded. We also tested the relationship between flux and temperature using stump flux rates grouped by time since harvest and found similar results. For this reason we used a null (intercept only) model, which is simply the flux rate for each stump averaged across the 10 sampling periods. None of the other models tested (above) showed significant improvement in AICc, RMSE, or normality of residuals compared to the null model. The R package ‘AICcmodavg’ (Mazerolle, 2020) was used to calculate the corrected AICc for small samples sizes.

The second step involved testing this average flux as a function of mean wood temperature, mean wood moisture, mean soil moisture, and stump volume. Stump height and diameter were not included in the analyses because of strong collinearity with stump volume, and canopy openness was removed due to its collinearity with wood temperature. Moisture variables (percentages) were logit transformed prior to analysis. The effect of time since harvest, which was known from our first objective to strongly influence flux rates, was first removed in order to focus on the effect of these additional variables. To this end, we used the flux residuals as the response variable in a multiple linear regression. Residuals were calculated as the difference between mean flux per time since harvest and the mean flux per stump in that time class. The variance inflation factor (`vif`) function in the ‘rms’ package in R (Harrell Jr, 2021) was used to remove correlated predictor variables (above) that were least biologically significant. Next, backwards selection by AICc

was conducted using the AICc function in the ‘AICcmodavg’ package in R (Mazerolle, 2020). We also tested this model using the maximum stump flux rather than an average value, but doing so did not change the interpretation of results.

3. Results

3.1. Seasonal trends

Wood surface temperatures decreased slightly from May to October 2021, from a mean of 23.4 °C on May 25 to 15.3 °C on October 11 (Fig. 2a). Soil and wood moisture increased during the same time period, with soil moisture increasing from a mean of 9 % VMC on May 25 to 14 % VMC on October 11 (Fig. 2b, c). Stump CO₂ emissions generally increased to a peak in mid to late August, then decreased by October 11, although this pattern varied with time since harvest and by individual stump (Fig. 3). The large variability in all of these variables, especially in wood surface temperature and stump CO₂ emissions, may have obscured seasonal trends.

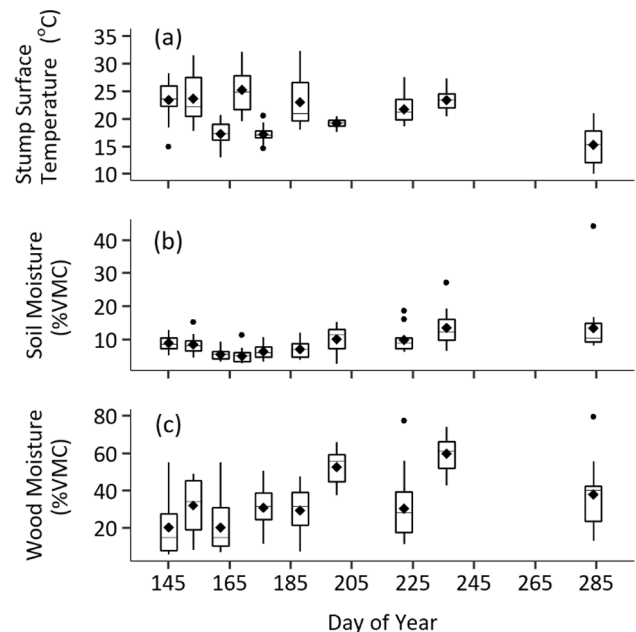


Fig. 2. Environmental variables measured on each sampling date throughout the sampling season. These include (a) stump surface temperature, (b) nearby soil moisture, and (c) stump wood moisture. Means at each sampling date are shown as a diamonds. Boxes enclose 50 % of the data, and whiskers cover the remaining 25 %. Outliers are shown as points above or below the whiskers. VMC = volumetric moisture content.

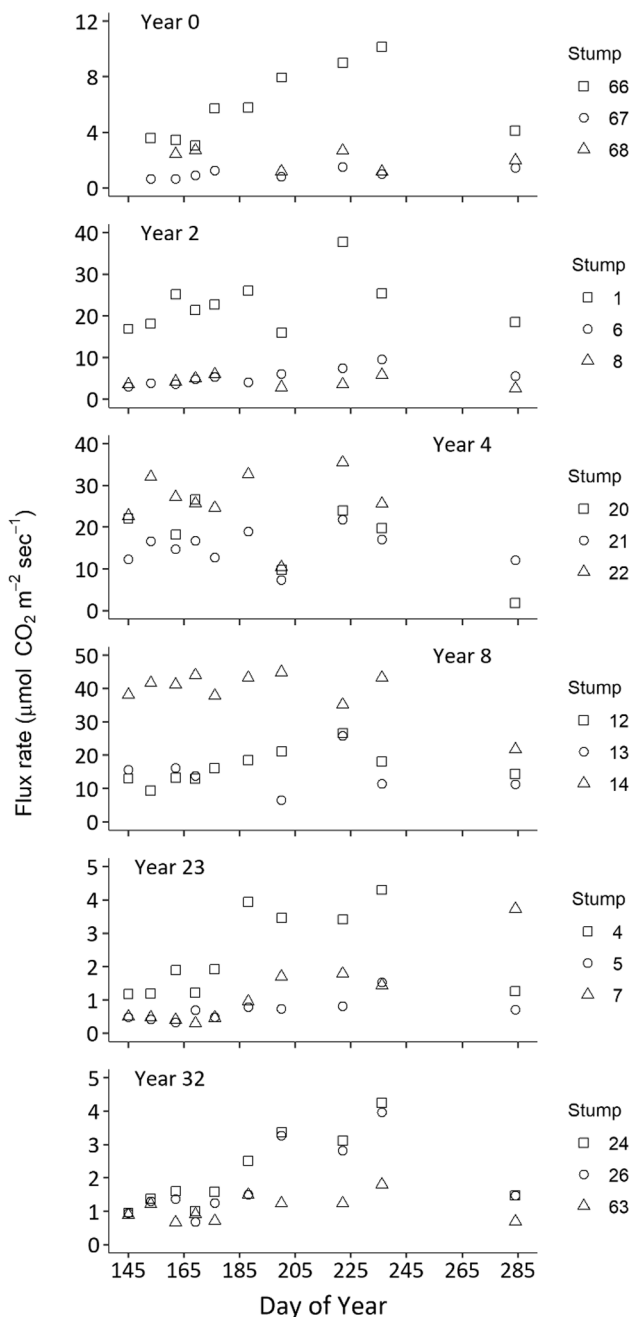


Fig. 3. Stump CO₂ flux rates throughout the growing season. Each panel shows stumps created in various years since harvest, from 0 to 32 years prior. Different symbols represent individual stumps. Note that vertical axes are on different scales.

3.2. CO₂ flux over the chronosequence

Our chronosequence results show low initial CO₂ flux, a strong and consistent increase through year 4, an apparent peak at years 6–8, followed by a decrease to very low rates by years 23 and 32 (Fig. 4). Mean overall flux (μmol CO₂ m⁻² s⁻¹) and standard deviations (in parentheses) for each time since harvest are as follows: 0 years = 3.2 (2.8), 2 years = 11.3 (9.6), 4 years = 19.6 (8.2), 8 years = 24.3 (13.0), 23 years = 1.4 (1.2), and 32 years = 1.7 (1.0). ANOVA revealed significant differences among the times since harvest, and the Tukey's post-hoc test showed that CO₂ fluxes from years 0, 23, and 32 were significantly lower than those of years 2, 4, and 8 (Fig. 4). A four-parameter Gaussian model provided the best characterization of CO₂ flux over time, in the form:

$$CO_2 \text{ flux} = 1.38 + 25.60 * \exp(-0.5 * ((\text{time} - 6.51)/3.13)^2) \quad (\text{Equation 1}).$$

where *time* is the years since harvest; RMSE = 7.38 μmol CO₂ m⁻² sec⁻¹. Table S1 (Supplementary Materials) provides rankings and diagnostics for the eight candidate models.

3.3. Environmental factors governing CO₂ flux

The full model used to test the relationship between mean CO₂ flux and environmental variables included mean wood temperature, mean wood moisture, mean soil moisture, and stump volume as predictors and the residuals of the flux (by time since harvest) as the response variable. Backwards model selection by AICc revealed the null model to be the most parsimonious; that is, the relationships were not significant (Table 1) for any of the models. Thus, none of these environmental or stump variables were significant predictors, meaning that time since harvest was the only significant predictor for CO₂ flux in this study. Stump attributes and associated environmental variables are presented in Table 2 and Fig. 2.

4. Discussion

4.1. CO₂ flux over the chronosequence

Our first objective was to quantify temporal trends in stump CO₂ flux over time. Detailed harvesting records available for the Penobscot Experimental Forest allowed us to create a 32-year chronosequence of *P. rubens* stumps for this purpose. Our results show low initial CO₂ flux (year 0), followed by an increase to a peak at years 6–8, in turn followed by a decrease to very low rates by years 23 and 32. The low initial flux rate supports previous work suggesting a lag in decomposition due to delayed fungal colonization of fresh woody material (Harmon et al., 1986) and low initial nitrogen content that limits fungal activity (Rinne-Garmston et al., 2019). However, the flux evident at year 0 (albeit at a low rate) might suggest fungi were present in the lower stem prior to harvest (Parfitt et al., 2010). The increase in CO₂ emissions to the peak ca. 6–8 years post-harvest likely represents the phase of greatest fungal activity (i.e., respiration) and abundance. After 8 years, CO₂ emissions decrease, likely because the decomposers have exhausted the most easily accessible carbon compounds and can no longer maintain high respiration rates (Rinne-Garmston et al., 2019), as well as a concomitant shift in fungal community composition (Stokland et al., 2012). The large variability evident in CO₂ flux, even among stumps of the same time since harvest, may be due to differing fungal communities among stumps, as fungal community composition has been shown to strongly influence wood decay rates (Lindner et al., 2011; van der Wal et al., 2015).

The range of CO₂ flux (0.7 to 44.9 μmol CO₂ m⁻² s⁻¹) from more recently cut *P. rubens* stumps (those up to 8 years since harvest) is quite similar to that of hardwood stumps in the initial years following harvest (3.5 to 44.1 μmol CO₂ m⁻² s⁻¹) (Forrester et al., 2015). However, the peak flux for hardwood stumps occurred ca. 2–4 years, while the peak flux for our *P. rubens* stumps occurred ca. 6–8 years. Similarly, Noh et al. (2019) report relatively low flux (6.7 μmol CO₂ m⁻² s⁻¹ at 20 °C) from *Fraxinus nigra* stumps measured for the first time 5 years after harvest, that is, presumably after peak flux had occurred. We acknowledge that peak CO₂ flux for our stumps may occur after 8 years. Unfortunately, *P. rubens* stumps harvested between 8 and 23 years prior were not available for our study. The earlier peak for hardwood stumps (above) could be explained by the more rapid decay for these taxa, when compared to conifers (Russell et al., 2014; Weedon et al., 2009). With this in mind, our peak flux at ca. 6–8 years for a conifer species seems reasonable; however, this should be explored in future studies.

Average stump flux rates ranged from a low of 1.4 ± 1.2 μmol CO₂ m⁻² s⁻¹ in year 23 to a high of 24.3 ± 13.0 μmol CO₂ m⁻² s⁻¹ in year 8. The Howland Research Forest provides soil CO₂ flux for comparison.

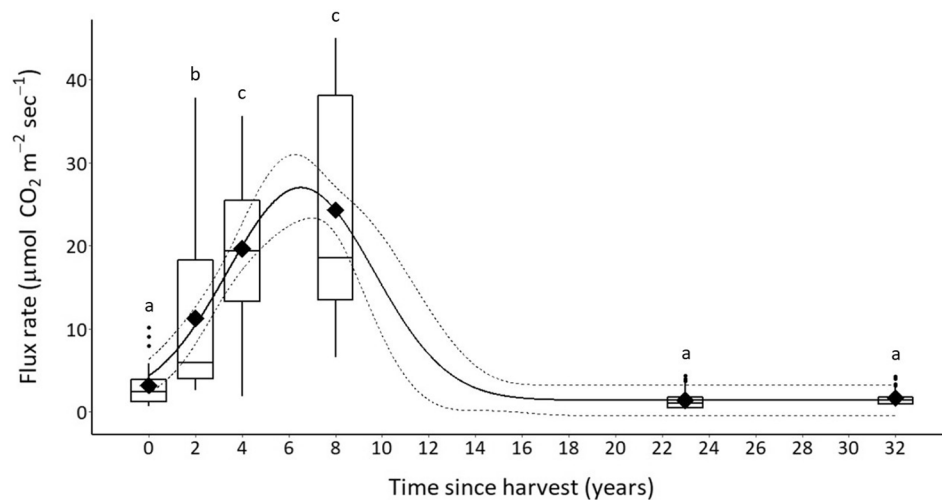


Fig. 4. CO₂ flux rates from a chronosequence of *Picea rubens* stumps. The mean flux rate at each time since harvest is shown as a diamond. Boxes encompasses 50 % of the data; the central line represents the median, and whiskers represent the remaining 25 % above and below the box. Outliers are shown as points above or below the whiskers. Boxes with different lowercase letters are significantly different at $p < 0.05$. The predictive model is shown as a solid line, with the 95 % confidence intervals shown as dashed lines.

Table 1

Result of backward-selection analyses of environmental and stump variables, using residuals of CO₂ flux (from each time since harvest) as the response variable (see text). mean_temp = mean of the wood surface temperature measured by thermometer, logit_soil_mc = logit-transformed volumetric soil moisture content, logit_wood_mc = logit-transformed volumetric wood moisture content, stump_volume = calculated volume of the entire stump. AICc is the Akaike information criterion adjusted for small sample sizes, and ΔAICc is the difference in AICc from the null model. Adj. R² is the adjusted R squared value. Root mean square error (RMSE) is in units of $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

Model Predictors	AICc	ΔAICc	Adj. R ²	RMSE	p-value
Null model	121.3	0	–	6.16	–
logit_soil_mc	122.1	0.8	0.056	5.81	0.18
logit_soil_mc + stump_volume	124.6	3.3	0.042	5.66	0.28
logit_wood_mc + logit_soil_mc + stump_volume	128.5	7.2	–0.023	5.66	0.48
mean_temp + logit_wood_mc + logit_soil_mc + stump_volume	133.1	11.8	–0.100	5.65	0.66

Howland Forest is ca. 45 km north of the PEF; it has similar soils and the same three dominant tree species with relative basal areas similar to those of the PEF: *P. rubens* at 46 %, *T. canadensis* 26 %, and *T. occidentalis* 10 % (Fien et al., 2019) (compared to 37 %, 20 %, and 20 %, respectively

at the PEF). There, soil flux is $2.2 \pm 0.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Hollinger et al., 2021) meaning that flux from well-decayed stumps is roughly 64 percent of that from soils, when compared at this scale. However, flux from stumps 8 years post-harvest is roughly 11 times higher than that from soils. As such, in the years following harvest, stumps function as CO₂ flux ‘hot spots’ (Noh et al., 2019). Nevertheless, when scaled to a per-ha basis, growing-season soil flux likely greatly exceeds growing-season stump flux simply because of the much greater area of soils.

The carbon loss by CO₂ emissions, as shown here, does not directly translate to a mass-loss decay rate because other carbon losses, such as volatile organic compounds lost to emissions or DOC lost to leaching, as well as the loss of non-carbon compounds that comprise wood tissue, are not accounted for (Harmon et al., 1986; Mali et al., 2019). Nevertheless, the form of the flux-rate curve fit to the chronosequence (low–high–low over time), which as above suggests an initial lag of 6–8 years before peak flux rate (mass loss), calls into question the pervasive use of negative exponential loss to model decay. Numerous previous studies have demonstrated an initial lag in CWM mass loss, supporting results reported here (e.g., Cornwell and Weedon, 2014; Rinne-Garmston et al., 2019; Yatskov et al., 2003).

4.2. Environmental and stump factors governing CO₂ flux

Our second objective was to determine the environmental and stump

Table 2

Attributes and environmental variables associated with the 18 *Picea rubens* stumps monitored for CO₂ flux. Time = time since harvest (years), Diam = stump top diameter in cm, Ht = stump height in cm, Temp = stump surface temperature in °C, VMC = volumetric moisture content, Open = percent canopy openness above stump, CO₂ flux in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ sec}^{-1}$. Values followed by standard deviations (in parentheses) represent means over the sampling season (n = 10).

Time	Stump ID	Diam (cm)	Ht (cm)	Temp (°C)	Soil VMC (%)	Wood VMC (%)	Open (%)	CO ₂ flux
0	66	36.5	60	24 (6)	16 (12)	34 (7)	29	5.9 (2.6)
0	67	36.5	42	22 (5)	7 (4)	24 (14)	20	1.0 (0.3)
0	68	17.5	23	21 (5)	10 (4)	67 (11)	17	2.0 (0.7)
2	1	41.0	58	19 (5)	8 (3)	28 (19)	18	22.8 (6.4)
2	6	30.0	36	19 (4)	6 (2)	38 (18)	11	5.4 (2.0)
2	8	36.5	45	20 (5)	7 (3)	24 (13)	13	4.2 (1.3)
4	20	41.5	40	23 (4)	11 (4)	33 (25)	18	17.5 (8.7)
4	21	40.0	57	24 (5)	7 (3)	19 (16)	28	15.1 (4.1)
4	22	42.0	42	24 (4)	9 (2)	21 (21)	35	26.3 (7.3)
8	12	42.0	27	21 (4)	7 (2)	40 (20)	19	16.4 (5.0)
8	13	25.5	29	21 (2)	10 (4)	33 (23)	24	14.4 (6.0)
8	14	32.5	30	24 (5)	11 (5)	26 (23)	28	39.1 (6.8)
23	4	30.0	33	18 (3)	8 (3)	44 (10)	10	2.4 (1.3)
23	5	33.5	30	21 (4)	12 (4)	41 (11)	18	0.7 (0.3)
23	7	33.0	40	19 (4)	9 (4)	44 (17)	12	1.2 (1.1)
32	24	34.0	20	17 (3)	11 (5)	46 (9)	7	2.1 (1.1)
32	26	37.5	35	20 (4)	7 (3)	33 (13)	10	1.9 (1.1)
32	63	20.5	20	20 (3)	7 (2)	49 (14)	8	1.1 (0.4)

factors that govern CO₂ flux rates from stumps. However, results revealed that time since harvest was the only significant predictor of CO₂ flux rate in this study. The lack of a relationship between CO₂ flux rate and temperature and/or moisture may have resulted from sampling within a small range of temperature and moisture values, especially as CO₂ fluxes were primarily measured mid-day and from May to October. We note that Herrmann et al. (2015) found that temperature explained very little variation (2 %) in CWM mass loss when tested in a global model that included decomposition time (analogous to our time since harvest), CWM species, CWM diameter, and site (random factor). However, most previous studies report a strong relationship between temperature, moisture, and stump flux (Forrester et al., 2015) or deadwood flux (GitarSKIY et al., 2017; Rinne-Garmston et al., 2019; Wang et al., 2002), suggesting that this relationship may be revealed if flux were measured across a wider range of temperatures and moisture, starting measurements earlier in the season, and taking measurements at times other than midday. In contrast to Forrester et al. (2012), we did not detect an influence of canopy openness, likely because our stumps occurred within a small range of canopy openness values (7–35 %), and although stumps spanned a range of diameters (18–42 cm) and volumes (0.006–0.078 m³), stump size did not influence flux rates.

4.3. Study limitations

We acknowledge several assumptions and shortcomings in this study that limit the generalizability of our conclusions. First, our small sample size (three stumps per time since harvest and ten sampling visits between May and October) may have limited the ability to detect the influence of environmental and stump variables; future studies could examine these relationships using larger sample sizes. Second, CO₂ emissions were only measured in a 10-cm diameter PVC collar placed roughly in the center of the stump's cut surface. This placement assumes the location to be representative, although it does not account for CO₂ emissions from the sides of the stump. Previous studies suggest that CO₂ emissions through bark are significantly reduced compared to cut areas (Noh et al., 2019; Shorohova et al., 2020), indicating that the majority of the CO₂ is emitted from the stump surface. In addition, we primarily captured heartwood flux rates by measuring in the center of the stump. Heartwood and sapwood may have distinct fungal and bacterial species and diversity (Mieszkin et al., 2021; Zhang et al., 2008), and may decompose at different rates (Taylor et al., 2002). This potential difference could also be addressed in future research. Finally, flux values may be spatially autocorrelated, because harvests of particular stands created clusters of stumps with similar times since harvest. For example, stumps with times since harvest of 0 were located in the same recently harvested stand. The influence of this potential autocorrelation remains unknown; however, given the large flux-rate variability within a time-since-harvest class, we suspect it had little influence on our interpretation of results.

5. Conclusions

To the best of our knowledge, ours is the first study to assess CO₂ emissions from cut stumps over an extended time period. Our results clearly show changes in CO₂ emissions from stumps with time since harvest. Emissions follow a peaked (low–high–low), right-skewed relationship over time, with stumps harvested 8 years prior producing the greatest emissions. Surprisingly, we found no clear relationship between CO₂ emissions and environmental or stump variables within the range of values captured in our study. The large variability evident in CO₂ flux, even among stumps of the same time since harvest, points to the need to examine the role of the fungal community, given that fungal species composition has been shown to influence decay rates (Lindner et al., 2011; van der Wal et al., 2015), and that fungal species composition changes dramatically through the decay process (Stokland et al., 2012). Our study examined CO₂ flux rates from one species and one deadwood

substrate using admittedly small sample sizes; future studies could expand this approach to determine if the temporal trends seen here are evident across a range of species and other deadwood types (e.g., downed woody debris, snags). For practitioners interested in including carbon management as one of their objectives, we point out that although harvesting leads to pulses in CO₂ emissions from stumps (as shown herein), this negative aspect must be weighed against the increase in carbon sequestration from rapid tree growth during the post-harvest recovery period.

CRedit authorship contribution statement

Zoe Read: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft. **Shawn Fraver:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Supervision, Funding acquisition. **Jodi A. Forrester:** Methodology, Writing – review & editing. **Jay Wason:** Formal analysis, Writing – review & editing. **Christopher W. Woodall:** Formal analysis, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We thank Jeanette Allogio, Alley Barry, Elyse Daub, Kasey Grass, Holly Hughes, Keith Kanoti, Laura Kenefic, John Lee, and Christopher London for assistance in the field and/or laboratory. We thank the current and past Penobscot Experimental Forest staff for maintaining the long-term research that made this work possible. This study was improved through discussions with Ivan Fernandez, Dave Hollinger, and Kathleen Savage. We thank two anonymous reviewers for insightful comments that have improved the paper.

Funding

This research was supported in part by the U.S.D.A. Forest Service, Northern Research Station (JVA 17-JV-11242307-018), the Maine Agricultural and Forest Experiment Station (#ME042118 and #ME042121), the Penobscot Experimental Forest Research Operations Fund, the Office of the Vice President for Research (University of Maine), and the University of Maine Graduate Student Government.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120528>.

References

- Bonan, G., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests 320, 1444–1449. <https://doi.org/10.1126/science.1155121>.
- Bond-Lamberty, B., Wang, C., Gower, S.T., 2002. Annual carbon flux from woody debris for a boreal black spruce fire chronosequence. *J. Geophys. Res. Atmospheres* 107, WFX 1-1-WFX 1-10. 10.1029/2001JD000839.
- Bond-Lamberty, B., Thomson, A., 2010. A global database of soil respiration data. *Biogeosciences* 7, 1915–1926. <https://doi.org/10.5194/bg-7-1915-2010>.
- Bradford, M.A., Warren, R.J., Baldrian, P., Crowther, T.W., Maynard, D.S., Oldfield, E.E., Wieder, W.R., Wood, S.A., King, J.R., 2014. Climate fails to predict wood decomposition at regional scales. *Nat. Clim. Change* 4, 625–630.

- Carbone, M.S., Seyednasrollah, B., Rademacher, T.T., Basler, D., Le Moine, J.M., Beals, S., Beasley, J., Greene, A., Kelroy, J., Richardson, A.D., 2019. Flux Puppy – An open-source software application and portable system design for low-cost manual measurements of CO₂ and H₂O fluxes. *Agric. For. Meteorol.* 274, 1–6. <https://doi.org/10.1016/j.agrformet.2019.04.012>.
- Cornwell, W.K., Weedon, J.T., 2014. Decomposition trajectories of diverse litter types: a model selection analysis. *Methods Ecol. Evol.* 5, 173–182. <https://doi.org/10.1111/2041-210X.12138>.
- Didion, M., Abegg, M., 2022. Tree stumps — an important but undervalued dead wood pool. *Ann. For. Sci.* 79, 34. <https://doi.org/10.1186/s13595-022-01155-7>.
- Dunger, K., Petersson, S.-H.-O., Barreiro, S., Cienciala, E., Colin, A., Hylen, G., Kusar, G., Oehmichen, K., Tomppo, E., Tuomainen, T., Ståhl, G., 2012. Harmonizing Greenhouse Gas Reporting from European Forests: Case Examples and Implications for European Union Level Reporting. *For. Sci.* 58, 248–256. <https://doi.org/10.5849/forsci.10-064>.
- Fien, E.K.P., Fraver, S., Teets, A., Weiskittel, A.R., Hollinger, D.Y., 2019. Drivers of individual tree growth and mortality in an uneven-aged, mixed-species conifer forest. *For. Ecol. Manag.* 449, 117446. <https://doi.org/10.1016/j.foreco.2019.06.043>.
- Finzi, A.C., Giasson, M.-A., Barker Plotkin, A.A., Aber, J.D., Boose, E.R., Davidson, E.A., Dietze, M.C., Ellison, A.M., Frey, S.D., Goldman, E., Keenan, T.F., Melillo, J.M., Munger, J.W., Nadelhoffer, K.J., Ollinger, S.V., Orwig, D.A., Pederson, N., Richardson, A.D., Savage, K., Tang, J., Thompson, J.R., Williams, C.A., Wofsy, S.C., Zhou, Z., Foster, D.R., 2020. Carbon budget of the Harvard Forest Long-Term Ecological Research site: pattern, process, and response to global change. *Ecol. Monogr.* 90, e01423. <https://doi.org/10.1002/ecm.1423>.
- Forrester, J.A., Mladenoff, D.J., Gower, S.T., Stoffel, J.L., 2012. Interactions of temperature and moisture with respiration from coarse woody debris in experimental forest canopy gaps. *For. Ecol. Manag.* 265, 124–132. <https://doi.org/10.1016/j.foreco.2011.10.038>.
- Forrester, J.A., Mladenoff, D.J., D'Amato, A.W., Fraver, S., Lindner, D.L., Brazee, N.J., Clayton, M.K., Gower, S.T., 2015. Temporal trends and sources of variation in carbon flux from coarse woody debris in experimental forest canopy openings. *Oecologia* 179, 889–900. <https://doi.org/10.1007/s00442-015-3393-4>.
- Frazer, G.W., Canham, C.D., Lertzman, K.P., 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fish-eye photographs, users manual and program documentation.
- Gitariski, M.L., Zmolodchikov, D.G., Mukhin, V.A., Grabar, V.A., Diyarova, D.K., Ivashchenko, A.I., 2017. Carbon fluxes from coarse woody debris in southern taiga forests of the Valdai Upland. *Russ. J. Ecol.* 48, 539–544. <https://doi.org/10.1134/S1067413617060030>.
- Gough, C.M., Vogel, C.S., Kazanski, C., Nagel, L., Flower, C.E., Curtis, P.S., 2007. Coarse woody debris and the carbon balance of a north temperate forest. *For. Ecol. Manag.* 244, 60–67. <https://doi.org/10.1016/j.foreco.2007.03.039>.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15, 133–302. [https://doi.org/10.1016/S0065-2504\(08\)60121-X](https://doi.org/10.1016/S0065-2504(08)60121-X).
- Harmon, M.E., Krankina, O.N., Sexton, J., 2000. Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. *Can. J. For. Res.* 30, 76–84. <https://doi.org/10.1139/x99-187>.
- Harmon, M.E., Bond-Lamberty, B., Tang, J., Vargas, R., 2011. Heterotrophic respiration in disturbed forests: A review with examples from North America. *J. Geophys. Res. Biogeosciences* 116. <https://doi.org/10.1029/2010JG001495>.
- Harmon, M.E., Fasth, B.G., Yatskov, M., Kastendick, D., Rock, J., Woodall, C.W., 2020. Release of coarse woody detritus-related carbon: a synthesis across forest biomes. *Carbon Balance Manag.* 15, 1. <https://doi.org/10.1186/s13021-019-0136-6>.
- Harrell Jr, F.E., 2021. rms: Regression Modeling Strategies.
- Hashimoto, S., Carvalhais, N., Ito, A., Migliavacca, M., Nishina, K., Reichstein, M., 2015. Global spatiotemporal distribution of soil respiration modeled using a global database. *Biogeosciences* 12, 4121–4132. <https://doi.org/10.5194/bg-12-4121-2015>.
- Herrmann, S., Kahl, T., Bauhus, J., 2015. Decomposition dynamics of coarse woody debris of three important central European tree species. *Forest Ecosyst.* 2, 27. <https://doi.org/10.1186/s40663-015-0052-5>.
- Hollinger, D.Y., Davidson, E.A., Fraver, S., Hughes, H., Lee, J.T., Richardson, A.D., Savage, K., Sihi, D., Teets, A., 2021. Multi-decadal carbon cycle measurements indicate resistance to external drivers of change at the Howland forest AmeriFlux site. *J. Geophys. Res. Biogeosciences* 126, e2021JG006276. <https://doi.org/10.1029/2021JG006276>.
- Lindner, D.L., Vasaitis, R., Kubartová, A., Allmér, J., Johannesson, H., Banik, M.T., Stenlid, J., 2011. Initial fungal colonizer affects mass loss and fungal community development in Picea abies logs 6yr after inoculation. *Fungal Ecol. Decompos. Forest Ecosyst.* 4, 449–460. <https://doi.org/10.1016/j.funeco.2011.07.001>.
- Mali, T., Mäki, M., Hellén, H., Heinonsalo, J., Bäck, J., Lundell, T., 2019. Decomposition of spruce wood and release of volatile organic compounds depend on decay type, fungal interactions and enzyme production patterns. *FEMS Microbiol. Ecol.* 95, f135. <https://doi.org/10.1093/femsec/f135>.
- Martínez-García, E., López-Serrano, F.R., Dadi, T., García-Morote, F.A., Andrés-Abellán, M., Rubio, E., 2015. Carbon loss during the early decomposition stages of tree stumps in a post-wildfire Spanish black pine forest. *For. Ecol. Manag.* 358, 321–334. <https://doi.org/10.1016/j.foreco.2015.09.022>.
- Mazerolle, M.J., 2020. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c).
- Mieszkis, S., Richet, P., Bach, C., Lambrot, C., Augusto, L., Buée, M., Uroz, S., 2021. Oak decaying wood harbors taxonomically and functionally different bacterial communities in sapwood and heartwood. *Soil Biol. Biochem.* 155, 108160. <https://doi.org/10.1016/j.soilbio.2021.108160>.
- Nelson, A.S., Wagner, R.G., Saunders, M.R., 2014. Silvicultural options for early-successional stands in Maine: 6-year results of the Silvicultural Intensity and Species Composition Experiment, in: In: Kenefic, Laura S.; Brisette, John C., Comps. Penobscot Experimental Forest: 60 Years of Research and Demonstration in Maine, 1950–2010. Gen. Tech. Rep. NRS-P-123. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. pp. 91–102.
- Noh, N.J., Shannon, J.P., Bolton, N.W., Davis, J.C., Van Grinsven, M.J., Pypker, T.G., Kolka, R.K., Wagenbrenner, J.W., 2019. Temperature responses of carbon dioxide fluxes from coarse dead wood in a black ash wetland. *Wetl. Ecol. Manag.* 27, 157–170. <https://doi.org/10.1007/s11273-018-9649-0>.
- Olajuyigbe, S., Tobin, B., Nieuwenhuis, M., 2012. Temperature and moisture effects on respiration rate of decomposing logs in a Sitka spruce plantation in Ireland. *For. Int. J. For. Res.* 85, 485–496. <https://doi.org/10.1093/forestry/CPS045>.
- Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. *Science* 333, 988–993. <https://doi.org/10.1126/science.1201609>.
- Parfitt, D., Hunt, J., Dockrell, D., Rogers, H.J., Boddy, L., 2010. Do all trees carry the seeds of their own destruction? PCR reveals numerous wood decay fungi latently present in sapwood of a wide range of angiosperm trees. *Fungal Ecol.* 3, 338–346. <https://doi.org/10.1016/j.funeco.2010.02.001>.
- PRISM Climate Group, Oregon State University, <https://prism.oregonstate.edu>, data created 2020, accessed 24 Aug 2022.
- Progar, R.A., Schowalter, T.D., Freitag, C.M., Morrell, J.J., 2000. Respiration from coarse woody debris as affected by moisture and saprotroph functional diversity in Western Oregon. *Oecologia* 124, 426–431. <https://doi.org/10.1007/PL00008868>.
- R Core Team, 2020. R: The R Project for Statistical Computing.
- Rinne-Garmston, K.T., Peltoniemi, K., Chen, J., Peltoniemi, M., Fritze, H., Mäkipää, R., 2019. Carbon flux from decomposing wood and its dependency on temperature, wood N₂ fixation rate, moisture and fungal composition in a Norway spruce forest. *Glob. Change Biol.* 25, 1852–1867. <https://doi.org/10.1111/gcb.14594>.
- Russell, M.B., Woodall, C.W., Fraver, S., D'Amato, A.W., Domke, G.M., Skog, K.E., 2014. Residence Times and Decay Rates of Downed Woody Debris Biomass/Carbon in Eastern US Forests. *Ecosystems* 17, 765–777. <https://doi.org/10.1007/s10021-014-9757-5>.
- Russell, M.B., Fraver, S., Aakala, T., Gove, J.H., Woodall, C.W., D'Amato, A.W., Ducey, M.J., 2015. Quantifying carbon stores and decomposition in dead wood: A review. *For. Ecol. Manag.* 350, 107–128. <https://doi.org/10.1016/j.foreco.2015.04.033>.
- Shorohova, E.V., Mamai, A.V., Moshkina, E.V., Romashkin, I.V., Lopes de Gerenyu, V.O., Kurganova, I.N., 2020. Comparing measurement approaches for quantifying CO₂ flux from downed woody debris with a dynamic chamber method. *Russ. J. Ecol.* 51, 351–362. <https://doi.org/10.1134/S1067413620040116>.
- Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture, 2022. Web Soil Survey [WWW Document]. URL <https://websoilsurvey.sc.egov.usda.gov/App/HomePage.htm> (accessed 5.19.22).
- Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in Dead Wood, Ecology, Biodiversity and Conservation. Cambridge University Press, Cambridge. 10.1017/CBO9781139025843.
- Sucre, E.B., Fox, T.R., 2009. Decomposing stumps influence carbon and nitrogen pools and fine-root distribution in soils. *For. Ecol. Manag., Forest Soil Science: Celebrating 50 Years of Research on Properties, Processes and Management of Forest Soils* 258, 2242–2248. <https://doi.org/10.1016/j.foreco.2009.05.012>.
- Taylor, A.M., Gartner, B.L., Morrell, J.J., 2002. Heartwood Formation and Natural Durability—A Review. *Wood Fiber Sci.* 587–611.
- van der Wal, A., Ottosson, E., de Boer, W., 2015. Neglected role of fungal community composition in explaining variation in wood decay rates. *Ecology* 96, 124–133. <https://doi.org/10.1890/14-0242.1>.
- Wang, C., Bond-Lamberty, B., Gower, S.T., 2002. Environmental controls on carbon dioxide flux from black spruce coarse woody debris. *Oecologia* 132, 374–381. <https://doi.org/10.1007/s00442-002-0987-4>.
- Weedon, J.T., Cornwell, W.K., Cornelissen, J.H.C., Zanne, A.E., Wirth, C., Coomes, D.A., 2009. Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? *Ecol. Lett.* 12, 45–56. <https://doi.org/10.1111/j.1461-0248.2008.01259.x>.
- Woodall, C.W., Rondeux, J., Verker, P.J., Ståhl, G., 2009. Estimating Dead Wood During National Forest Inventories: A Review of Inventory Methodologies and Suggestions for Harmonization. *Environ. Manage.* 44, 624–631. <https://doi.org/10.1007/s00267-009-9358-9>.
- Woodall, C.W., Westfall, J.A., 2008. Controlling coarse woody debris inventory quality: taper and relative size methods. *Can. J. For. Res.* 38, 631–636. <https://doi.org/10.1139/X07-171>.
- Yatskov, M., Harmon, M.E., Krankina, O.N., 2003. A chronosequence of wood decomposition in the boreal forests of Russia. *Can. J. For. Res.* 33, 1211–1226. <https://doi.org/10.1139/x03-033>.
- Zanne, A.E., Oberle, B., Dunham, K.M., Milo, A.M., Walton, M.L., Young, D.F., 2015. A deteriorating state of affairs: how endogenous and exogenous factors determine plant decay rates. *J. Ecol.* 103, 1421–1431.
- Zhang, H.-B., Yang, M.-X., Tu, R., Gao, L., Zhao, Z.-W., 2008. Fungal Communities in Decaying Sapwood and Heartwood of a Conifer Keteleeria evelyniana. *Curr. Microbiol.* 56, 358–362. <https://doi.org/10.1007/s00284-007-9092-6>.