

CO₂ flux from *Acer saccharum* logs: sources of variation and the influence of silvicultural treatments

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Abstract

Several aspects of the forest carbon cycle have not been examined in detail, including sources of variation in carbon dioxide (CO₂) emissions from coarse woody material (CWM). To address this knowledge gap, we examined CO₂ emissions from *Acer saccharum* Marshall logs within four harvesting treatments, using closed chambers fitted to the logs. We found that CO₂ emissions were highest for logs in small ($31.8 \pm 20.4 \mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-3}\cdot\text{s}^{-1}$) and large gaps ($29.6 \pm 24.4 \mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-3}\cdot\text{s}^{-1}$) compared to those in control ($13.9 \pm 8.3 \mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-3}\cdot\text{s}^{-1}$) and thinned matrix ($13.6 \pm 8.0 \mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-3}\cdot\text{s}^{-1}$) treatments. CO₂ flux rates did not differ between gap sizes, but they increased with temperature, which was higher in the small gap treatment. In addition, two individual logs fitted with multiple closed chambers revealed significant within-log variability in CO₂ emissions. On a subset of logs repeatedly sampled throughout the day, we found that log surface temperature generally peaked at midday and was positively correlated with CO₂ emissions, although this relationship was weak in one log. This study provides insight into sources of variation in CO₂ emissions from CWM while improving our understanding of the forest carbon cycle.

Key words: carbon dioxide, carbon flux, forest carbon cycle, woody material, wood decomposition

Introduction

Forests are important contributors to the global carbon cycle, both as a sink of carbon dioxide (CO₂) through photosynthesis as well as an emitter of CO₂ as these carbon stocks decompose, combust, or transfer to other systems and pools (i.e., blue carbon). However, many components of the forest carbon cycle remain poorly understood. Decomposition of soil organic matter has been studied extensively and identified as a major contributor to carbon emissions (Kolari et al. 2009; Hollinger et al. 2021); however, the contribution of coarse woody material (CWM) decomposition to net forest carbon balances is less well understood (Harmon et al. 2011). Carbon is emitted via decomposing CWM primarily as CO₂, the result of heterotrophic respiration by fungi, bacteria, insects, and other decomposers. This comprises the majority of carbon loss from CWM in forested settings (Chambers et al. 2001), except perhaps in the case of wildfires (Hurteau and North 2009). Given the prevalence of this process, a better understanding of CO₂ emissions from CWM is needed to improve process-based models of forest carbon dynamics (Kurz et al. 2009), as well as anticipate the carbon dynamics following varying harvesting approaches and/or natural disturbances.

Forest harvesting modifies forest structure, which in turn may influence CO₂ fluxes from CWM. Previous studies have

investigated the effect of harvesting on soil carbon fluxes (Epron et al. 2006; Peng and Thomas 2006; Stoffel et al. 2010), but few have examined the effect on CWM fluxes. Forrester et al. (2012) found that canopy gap creation increased CWM carbon emissions and altered the relationship between CWM temperature and moisture, while Griffiths et al. (2021) found that canopy gaps can increase decomposition rates for CWM components left in gaps. These increases in decomposition rates (i.e., CO₂ emissions) likely result from alterations in forest structure that consequently affect local environmental variables such as temperature and moisture. As forest managers are increasingly considering the carbon consequences of their actions (Ontl et al. 2020), it becomes critically important to further examine the impact of canopy disturbance on environmental variables and subsequent CO₂ emissions from forest carbon pools.

Understanding the spatial and temporal variability of CO₂ from CWM is equally important for carbon modelling efforts and forest management. Field studies of CO₂ flux from decaying logs often rely on chambers placed at one location along the log's length (Forrester et al. 2015; Noh et al. 2019), assuming that chosen location is representative when scaling up. Boddy et al. (1989) tested this assumption and found variation in CO₂ emissions within a single log, suggesting that the variation was due to differences in fungal species

composition and moisture within the log. Further study is needed to understand the significance of this within-log variation. In addition, by convention, CO₂ flux rates are measured midday as this time period provides the least variation in moisture and temperature with the greatest flux values. However, when scaling such flux rates to a seasonal or annual rate, it is assumed that flux at other times of the day or year can be predicted by the relationship among temperature, moisture, and flux found at midday. Alternatively, daily flux rates can be estimated by multiplying by hours in the day. A comparison of continuous flux measurements against weekly flux measurements has been conducted for soils, suggesting that continuous flux measurements throughout the day improve predictions of flux from temperature and moisture and that a combination of both methods would be ideal to maximize coverage of both temporal and spatial variability (Savage and Davidson 2003). However, to the best of our knowledge, no previous studies have examined daily variation in CO₂ flux from CWM.

Our objectives were to (1) quantify the impact of silvicultural treatments and the resulting effects of temperature and moisture conditions on CO₂ emissions from decaying CWM and (2) characterize the small-scale spatial (within log) and short-term temporal (12-hr sequence) variability in CO₂ emissions from decaying wood. We focus our work on 12 instrumented *Acer saccharum* Marshall (sugar maple) logs placed in a replicated silvicultural study (part of the Adaptive Silviculture for Climate Change network) (Nagel et al. 2017; Jevon et al. 2019; Clark et al. 2021) in northern NH, USA. We expect these results to improve the understanding of variability in deadwood carbon fluxes and provide information to help refine forest carbon models.

Methods

Study site

This study was conducted at Dartmouth College's Second College Grant (SCG) (44°91'N, 71°10'W) in northern NH, USA. This forest is dominated by hardwood tree species, primarily *Acer saccharum* Marshall (sugar maple), *Betula alleghaniensis* Britton (yellow birch), and *Fagus grandifolia* Ehrh. (American beech), with *Acer rubrum* L. (red maple), *Picea rubens* Sarg. (red spruce), *Fraxinus americana* L. (white ash), *Populus grandidentata* Michx. (bigtooth aspen), *Prunus serotina* Ehrh. (black cherry), *Abies balsamea* (L.) Mill. (balsam fir), and *Acer pensylvanicum* L. (striped maple) in lesser amounts. Prior to project establishment in 2017, stand basal area averaged 24.9 m²·ha⁻¹ and tree density 559 trees·ha⁻¹. The site has spodosol soils (Petrenko and Friedland 2015) and has a mean annual temperature of 3.2 °C and mean annual precipitation of 1179 mm (30-year climatology 1981–2010; Jevon et al. 2019). Average site elevation is 550 m a.s.l., and snowpack generally develops in November and persists through March.

This research site is part of a larger network of forests that participate in the Adaptive Silviculture for Climate Change experimental network, or ASCC (Nagel et al. 2017). At the SCG, four 10 ha replicate blocks were established, and each block included stands with small gaps (approximately

0.1 ha, $N = 18$), large gaps (approximately 0.4 ha, $N = 3$), matrix (thinned areas between gaps), and control (no harvest of any kind) treatments. Further details of this ASCC study design can be found in Clark et al. (2021). The current study—an addition to the larger ASCC project—was conducted in one of these four blocks, where in the spring of 2019, three freshly cut 2.5 m long *Acer saccharum* logs were placed in each of the four treatments (i.e., 12 logs total, 3 replicate logs in each treatment). However, for the gap treatments, given site constraints, two logs were placed in one large gap, one log in another large gap, and likewise two logs were placed in one small gap and one log in another small gap. The average mid-point diameter of these logs was 30.0 cm (range 25.8–33.9). These logs form the basis of an ongoing study of CWM moisture dynamics in response to precipitation and drying events (e.g., Woodall et al. 2020). The current study of CO₂ flux was added two years later (2021), as new collaborators recognized that this design allowed us to examine the influence of harvesting treatments on CO₂ flux. However, the two-year delay was rather beneficial, given the well-reported initial lag in decay (i.e., negligible flux rates in the first years of decay) owing to delayed fungal colonization (Harmon et al. 1986) or low initial nitrogen content that limits fungal activity (Rinne-Garmston et al. 2019).

Carbon dioxide flux measurements

To measure and capture CO₂ emissions, a chamber was attached to the top-center of each log. This chamber was created by fitting a PVC pipe (10 cm diameter, average 7.1 cm height) to the log curvature and sealing it onto the bark with silicone caulk and clay, if needed. Within-log variability was assessed on a subset of logs, due to time and resource limitations. Thus, one log in the control treatment and one log in the large gap (both randomly chosen) were each fit with three collars spaced evenly along the log length. The control and gap treatments were selected because we anticipated the greatest differences between CO₂ flux rates in these more extreme treatments. CO₂ flux was sampled periodically from June to November 2021, for a total of seven sampling visits. During each sampling visit, a cap with a low-density polyethylene seal was placed over the open PVC collar and held tightly in place with a bungee cord. Air was pumped from the chamber through the Li-830 gas analyzer (Li-Cor, Lincoln, NE, USA) for three minutes. The “Flux Puppy” software application (Carbone et al. 2019) recorded the change in CO₂ concentration every second as it was emitted from the log and accumulated in the chamber.

The slope of the accumulation curve was used to determine the CO₂ flux rate ($\mu\text{mol}\cdot\text{CO}_2\cdot\text{mol}^{-1}\cdot\text{sec}^{-1}$) for each log at each sampling visit. An analysis of variance (ANOVA) found that log diameters were significantly greater in gap treatments; to account for this confounding variable, flux rates were expressed per volume (m³) of wood, assuming flux was emitted from a cylinder of wood below the collar whose height was the field-measured vertical diameter of the log (Forrester et al. 2012). For comparisons to other studies, we also calculated flux per mass (kg) of wood. To this end, large diameter (12 mm) increment cores were extracted from the logs

directly below the chambers and measured for volume and oven-dry mass to determine density ($\text{g}\cdot\text{cm}^{-3}$). These density values were used to convert cylinder volumes (wood below the collar) to mass. To examine the daily variability in CO_2 flux rates, we monitored flux, wood temperature, and soil moisture every hour (from 6:00 to 18:00) for one day (27 July 2022) on a subset of three logs representing small-gap, large-gap, and matrix conditions. These logs were chosen because their close proximity allowed a field crew to rotate among them on an hourly basis.

Environmental measurements

In July 2021, a hemispherical photo was taken at one meter height, centered above each log and processed using the Gap Light Analyzer software (Frazer et al. 1999) to estimate canopy openness (%). At each sampling visit, wood surface temperature was measured adjacent to the collar using a Dura 609001600 digital thermometer (Bel-Art-SP Scienceware, Wayne, NJ, USA) placed on the log surface north of the flux chamber. Volumetric soil moisture (%) was measured by averaging six measurements, three on each side of the log near the collar, using a TDR150 soil moisture meter (Spectrum Technologies, Aurora, IL, USA). We use soil moisture as a proxy for log moisture given the close relationship between the two (Green et al. 2022).

Statistical analyses

To address our first objective—to quantify the impact of silvicultural treatments on CO_2 emissions—we performed an ANOVA with CO_2 flux rate as the response variable and treatment as the predictor, followed by Tukey's post hoc comparisons among treatments. For the two logs fitted with multiple collars, we used only the center collar for analyses to remain consistent with the remaining 10 logs, each of which had one centrally placed collar. Data from one log in the large-gap treatment was excluded because the bark supporting the collar had sloughed off during the sampling season. Analyses were performed in R using the aov and TukeyHSD functions in the "stats" package (R Core Team 2020).

To test causal relationships for the treatment differences ultimately revealed in the ANOVA (above), we used a linear mixed-effects model with CO_2 flux as the response variable, the environmental variables (as above) as the predictors, and log ID as the random variable. The mixed-effects model was created using the lme function in the "nlme" package in R (Pinheiro et al. 2021). We used the vif function in the "stats" package in R to test for potential collinearity between wood temperature and canopy openness. We further tested this relationship using a linear model with the lm function in the "stats" package in R (R Core Team 2020), which confirmed collinearity. We thus removed canopy openness from the model. Our final mixed-effects model included CO_2 flux as the response variable and wood temperature, logit-transformed soil moisture, and the interaction between these variables as the predictors.

For our second objective—to characterize variability in CO_2 flux rates—we first examined differences in flux rates among the three collars placed on individual logs using an ANOVA

with CO_2 flux as the response variable, followed by Tukey's post hoc comparisons among collars. This test was conducted individually for the two logs with multiple collars. In addition, we tested for differences in temperature and soil moisture among collars using the same ANOVA and Tukey's post hoc tests. To assess the daily variability in CO_2 flux rates (6:00–18:00), we present the raw data in graphical form. In addition, we assessed the relationship between temperature and CO_2 flux rates for these data by linear regression (separately for each log), using the lm function in the "stats" package in R (R Core Team 2020).

Results

Treatment and environmental effects

Mean CO_2 emissions from *Acer saccharum* logs in small ($31.8 \pm 20.4 \mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-3}\cdot\text{s}^{-1}$) and large gaps ($29.6 \pm 24.4 \mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-3}\cdot\text{s}^{-1}$) were significantly higher than those in the control ($13.9 \pm 8.3 \mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-3}\cdot\text{s}^{-1}$) and matrix ($13.6 \pm 8.0 \mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-3}\cdot\text{s}^{-1}$) treatments (all P values < 0.05 ; Fig. 1). Our mixed-modelling approach for testing the influence of environmental variables revealed a significant positive relationship between flux rates and wood surface temperature ($P < 0.05$); these temperatures were significantly higher in small gaps than in the control and matrix treatments ($P < 0.05$; Fig. 1) but were not significantly different between large gaps and any of the treatments ($P > 0.05$; Fig. 1). CO_2 flux rates were unrelated to soil moisture ($P > 0.05$). Log attributes and associated environmental variables are presented in Table 1.

Within-log variation

In addition to differences among treatments, we also found significant within-log variation in CO_2 flux rates (Fig. 2). Flux rates were significantly higher in the center compared to off-center locations for log 6 ($P < 0.05$), while the center of log 11 had significantly lower flux compared to off-center locations ($P < 0.05$). Log 6 was located in a large gap; log 11 was located in a control treatment. Neither wood temperature nor soil moisture differed significantly among the three locations along either log (all P values > 0.05).

Temporal variation

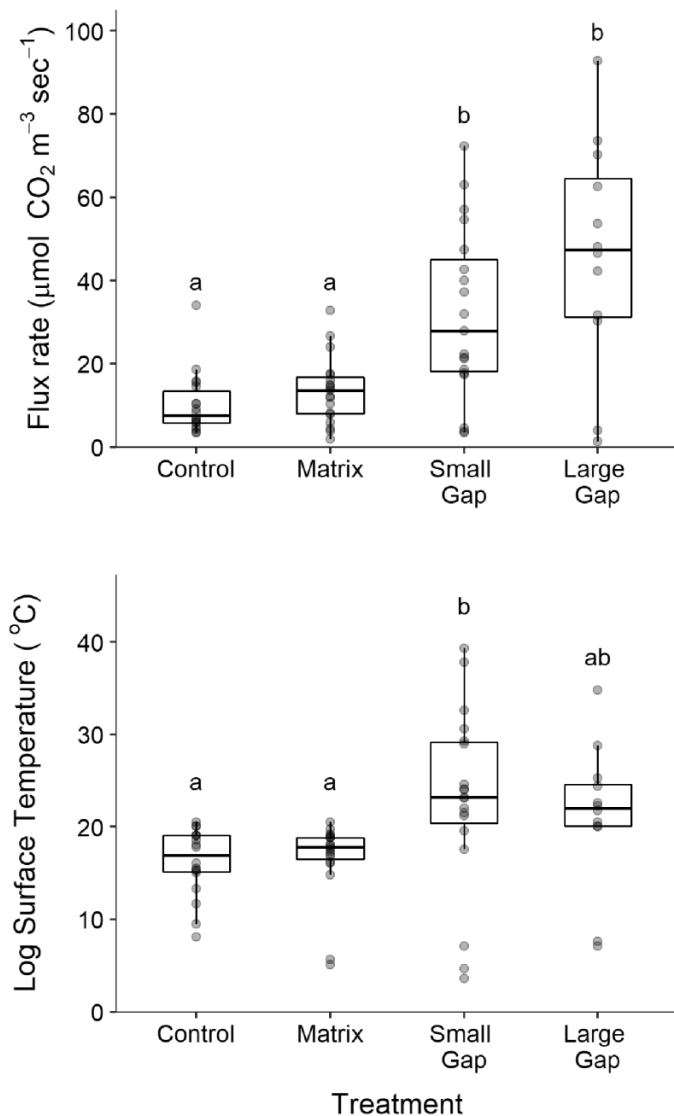
On the day of intensive sampling, CO_2 emissions increased from 6:00 to 13:00 and then decreased in two logs while continuing to increase in the third (Fig. 3). Temperature peaked in all three logs at 13:00 and then decreased to 18:00; however, soil moisture showed no obvious pattern throughout the day (Fig. 3). CO_2 flux was strongly and positively related to temperature throughout the day (P values < 0.05). The R^2 values for this linear relationship for logs 7, 8, and 9 were 0.88, 0.69, and 0.88, respectively (Fig. 3).

Discussion

Treatment and environmental effects

Harvesting treatments significantly influenced CO_2 emissions from logs, with higher flux rates in harvested canopy

Fig. 1. CO₂ flux rate by treatment (top panel) and log surface temperature by treatment (bottom panel). Logs in gap treatments had significantly higher flux rates than those in the unharvested control and thinned matrix treatments. Log surface temperatures were significantly higher in small gaps than in the control and matrix treatments. Boxes with different lower-case letters indicate significant differences at $P < 0.05$.



gaps than in the unharvested control and thinned matrix treatments. This finding supports previous studies that show increases in deadwood CO₂ flux (Hagemann et al. 2010; Forrester et al. 2012) and decomposition (Griffiths et al. 2021) in canopy gaps. In addition, midday temperatures were higher in the small gaps than in control and matrix treatments. Of the environmental variables tested, temperature best explained the treatment differences, given its positive relationship with CO₂ flux. This finding corroborates previous studies reporting that respiration rates of wood-decomposing fungi (A'Bear et al. 2014; Boddy 1983) and the activity of other decomposers increase with temperature (Pietikäinen et al. 2005).

However, within the harvested treatments, CO₂ flux rates did not differ between small (0.1 ha) and large (0.4 ha) gaps, which may be explained by the corresponding lack of temperature differences between these treatments. Nevertheless, and counter-intuitively, canopy openness above the logs was greater in the small than in the large gaps. During the three years between harvest and our sampling, the large gaps developed significant understory regrowth that overtopped the logs, producing lower canopy openness. Thus, even when canopy trees have been removed, other vegetation can shade CWM and alter temperature and thus CO₂ flux rates. For these reasons, larger gaps may not have consistently higher temperatures than control or matrix treatments, and gap size may not influence log CO₂ emissions three years post harvest. Future studies could examine year-to-year changes in flux rates under various harvesting treatments as post-harvest succession proceeds.

The range of flux rates for this study (0.003–0.166 µmol·CO₂·kg⁻¹·s⁻¹) was lower than that of a previous study of hardwood logs by Forrester et al. (2012) (0.1–1.1 µmol·CO₂·kg⁻¹·s⁻¹). The logs used in that study were recently harvested and of a variety of species. In addition, the gaps in Forrester et al. (2012) were created during the same year that sampling began, while the gaps in this study were created three years prior; regrowth of the understory may contribute to the differences in flux. Forrester et al. (2012) also found differences between CWM respiration in gaps and closed canopy forest, although these differences were non-significant at the log scale. For practitioners concerned about forest carbon management, we note that although logs in harvest gaps had higher CO₂ emissions (as shown herein), this potentially short-term effect is counterbalanced over time by the increase in carbon sequestration from rapid regrowth in gaps (Pregitzer and Euskirchen 2004), which is evidenced by the potential influence of overtopping vegetation in our current study's large gaps. Moreover, the ecological benefits of retained logs in gaps for biodiversity conservation (Sandström et al. 2019) should also be considered beyond solely focusing on CO₂ emissions or carbon management alone.

Within-log variation

In addition to variation in flux rates among treatments, flux rates differed among three locations within the two intensively sampled logs, with the log center emitting much higher (log 6) or lower (log 11) amounts of CO₂. Some individual collars also experienced large variation in flux rates, and the range of flux rates for log 6 (large gap) was greater than that for log 11 (control). Despite these other sources of variation, flux rates among collars on a log still differed significantly. This variation is noteworthy because most studies of CWM emissions measure and analyze CO₂ from only one location on the log (Progar et al. 2000; Forrester et al. 2012; our current study). Our results suggest that this sampling method overlooks variation in log emissions, potentially leading to measurement error when scaling up. Several factors may contribute to within-log CO₂ flux rate variability. First, fungal species vary greatly in their ability to decompose wood

Table 1. Attributes and environmental variables associated with the 11 *Acer saccharum* logs monitored for CO₂ flux.

Log ID	Collar ID	TRT	Open (%)	Diam (cm)	N	Temp (° C)	Soil VMC (%)	CO ₂ flux
1	1	Small gap	47.50	31.0	7	25 (11)	37 (4)	43.9 (21.5)
2	2	Small gap	43.91	29.8	5	20 (11)	50 (4)	34.7 (22.3)
3	3	Matrix	5.92	25.5	5	18 (1)	11 (2)	6.5 (2.8)
4	4	Matrix	8.42	29.8	7	16 (5)	22 (3)	17.7 (8.2)
7	7	Large gap	51.61	29.3	6	24 (10)	34 (5)	30.3 (26.6)
8	8	Matrix	6.15	28.5	7	16 (5)	20 (4)	14.6 (7.5)
9	9	Small gap	39.13	29.6	7	23 (9)	24 (4)	17.6 (6.1)
10	10	Control	5.68	30.0	7	16 (4)	31 (4)	16.5 (8.7)
12	12	Control	4.28	31.1	7	16 (4)	13 (3)	5.9 (2.3)
6	06A	Large gap	24.25	33.3	7	20 (7)	9 (3)	12.1 (3.4)
6	06B	Large gap	24.25	33.0	7	21 (7)	9 (3)	53.8 (27.8)
6	06C	Large gap	24.25	32.7	7	21 (7)	9 (3)	22.2 (10.3)
11	11A	Control	6.38	29.5	5	18 (2)	14 (3)	22.8 (6.4)
11	11B	Control	6.38	31.1	4	18 (2)	13 (5)	6.9 (2.4)
11	11C	Control	6.38	28.4	7	16 (4)	16 (4)	17.1 (5.3)

Note: Data for one log in the large-gap treatment is excluded because the bark supporting the collar had sloughed off during the sampling season. Log ID, identifier for individual log; collar ID, identifier for individual collar when there are multiple collars per log; TRT, harvesting treatment; open, % canopy openness above log; diam, horizontal diameter of the log at the collar in cm; N, number of sampling visits; temp, log surface temperature in °C; soil VMC, % soil volumetric moisture content adjacent to the log collar; CO₂ flux in $\mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-3}\cdot\text{s}^{-1}$. Values followed by standard deviations (in parentheses) represent means over the sampling season.

(Boddy 2001), with fungal community composition varying along the length of a log (Boddy 2001). In addition, competition among multiple fungal species can reduce respiration and decomposition (Progar et al. 2000; Pastorelli et al. 2017). Fungal community variation and activity within a log may also result from localized differences in moisture, temperature, N content, or C content (Progar et al. 2000; Pastorelli et al. 2017). Although wood temperature and soil moisture did not differ along our logs with multiple collars, other unmeasured microclimatic variables such as wood moisture, maximum or minimum daily wood temperature, or internal temperature may vary, causing differences in flux rates.

Daily variation

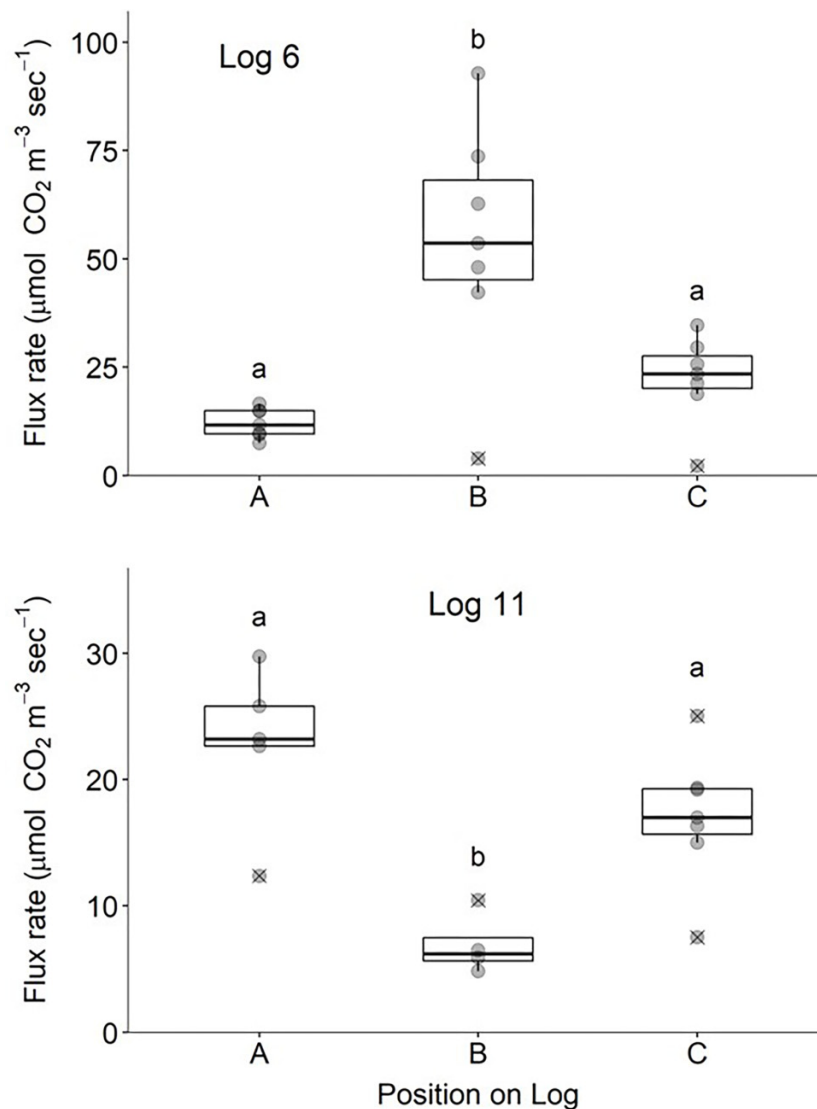
Both CO₂ flux rates and temperature varied throughout the 12 h measurement period (6:00–18:00), peaking around 13:00. The period between 10:00 and 14:00 tended to capture the highest flux rates, and rates doubled from 10:00 to 13:00 in two of the three intensively sampled logs, followed by a decline. CO₂ emissions from log 8 (within the thinned matrix) did not show such a peak; its flux continued to increase until measurements ended at 18:00, suggesting that other unmeasured factors may be driving hourly flux rates. However, we note that this log showed a narrow range of temperature and moisture values compared to the other logs, which may have contributed to this difference in flux patterns. Savage and Davidson (2003) found that weekly soil flux measurements taken once manually between 9:00 and 12:00 underestimated daily soil flux values when compared to automatic measurements taken hourly throughout the day. These same authors found that soil flux peaked in the late afternoon (17:00–19:00), in contrast to our finding of an early afternoon peak (for logs in gaps) or no peak achieved by 18:00 (matrix log).

Hourly flux rates were strongly and positively related to temperature but not to soil moisture, indicating a similar relationship to seasonal measurements (above). This result is reasonable given that soil moisture showed no strong pattern and exhibited minimal variation throughout the day. Soil moisture often changes over the time span of several days or longer (Green et al. 2022), while temperature may change more quickly. This result highlights the need for measuring log moisture directly (i.e., not using soil moisture as a proxy), given that log moisture has been shown to influence CO₂ flux rates (Gough et al. 2007; Forrester et al. 2012). However, recording log moisture repeatedly or continuously presents several methodological challenges (Woodall et al. 2020). Our study and that of Savage and Davidson (2003) found that sampling limitations made it feasible to measure hourly fluxes only from three chambers; thus, our measurements of hourly fluxes capture temporal variation but fail to fully capture spatial variation. Future studies could utilize automated chambers in a wide spatial distribution to capture both temporal and spatial variation and potentially identify stronger effects of environmental variables.

Limitations

Several aspects of this study may limit the broad application of our conclusions. First, flux rates used for most analyses were measured at a single location on each log. Although this is common practice, our finding of significant within-log variation points to unaccounted variability in our analyses. In addition, we used only two logs to examine this within-log variation, and although we found significant variation, we did not attempt to identify its source. This topic could be more intensively studied in the future, ideally using a range of species and decay stages. Secondly, we measured flux rates between 10:00 and 14:00 during each sampling visit; this period was found to have the highest

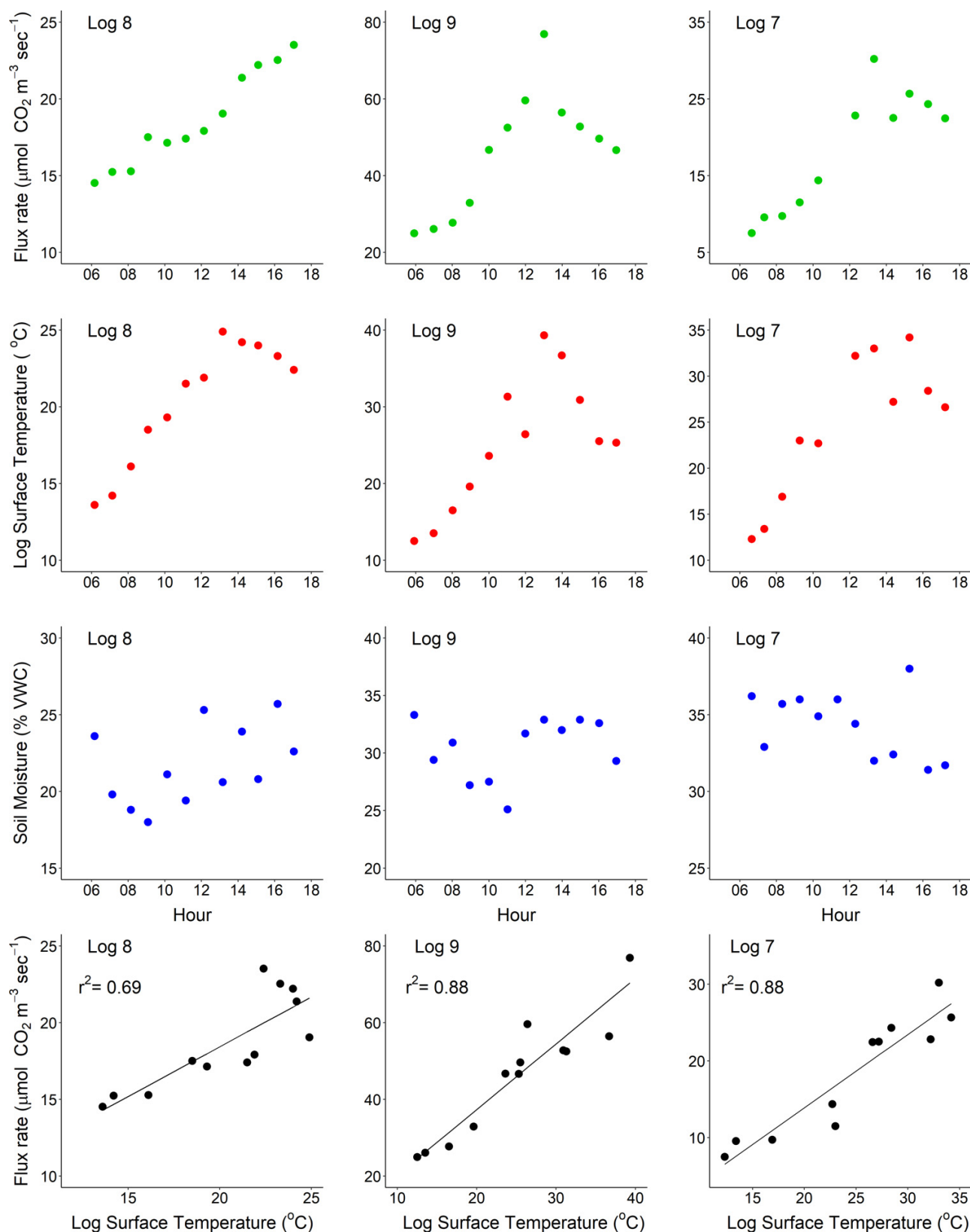
Fig. 2. Variation in CO₂ flux rate within two individual logs fitted with three chambers, showing significant within-log variation. Log 6 (pictured below) was in a 0.4 ha gap and log 11 was located in the control treatment. Note that vertical axes are on different scales. Boxes with different lower-case letters indicate significant differences at $P < 0.05$. Photo taken by Zoe Read.



variability in flux rates during our one day of intensive flux sampling. However, given our objective of comparing flux rates among treatments and our protocol of sampling logs in a different order on each sampling date, this sampling window may be valid for our purposes. Despite these sources of variation, we were able to detect meaningful differences in CO₂ flux rates among treatments consistent with expectations informed by previous work. Both sources of variation identified here—within-log and within-day—are perhaps

most problematic when scaling up spatially (e.g. fluxes per ha) or temporally (e.g. daily or annual fluxes). Finally, we sampled flux rates from logs three years post harvest, which precluded any assessment of shorter- or longer-term effects of harvesting treatments on flux rates. Previous studies have shown considerable year-to-year variability in deadwood flux, with rates reaching a peak 4 years post harvest for hardwood logs and stumps (Forrester et al. 2015) and 6–8 years for softwood stumps (Read et al. 2022).

Fig. 3. The first three rows of graphs show changes in CO₂ emissions, log surface temperature, and soil moisture from 6:00 to 18:00 in three logs. The bottom row shows the relationship between CO₂ flux rate and log surface temperature for each log, with the linear model fit to the data. Log 8 was in a matrix treatment, log 9 a small gap, and log 7 a large gap. Note that vertical axes are on different scales, particularly for CO₂ flux. VWC, volumetric water content.



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Conclusions

We found that CO₂ emissions from *Acer saccharum* logs located in canopy gaps were significantly higher than those under intact or thinned canopies; however, gap size did not influence emissions. The effect of silvicultural treatment on CO₂ emissions was likely caused by higher midday temperature in gaps, which can increase the respiration of fungi and other decomposers. In addition, CO₂ flux rates varied within individual logs, calling into question the common practice of using one measurement location to represent the entire log. Lastly, flux rates and wood surface temperature increased from morning to midday, in some cases doubling in value, and then continued to increase or decrease toward the afternoon, depending on the individual log. Taken together, these sources of variation in CO₂ flux rates represent important knowledge gaps to be addressed in future studies.

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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Competing interests

The authors declare there are no competing interests.

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References

- A'Bear, A.D., Jones, T.H., Kandler, E., and Boddy, L. 2014. Interactive effects of temperature and soil moisture on fungal-mediated wood decomposition and extracellular enzyme activity. *Soil Biol. Biochem.* **70**: 151–158. doi:[10.1016/j.soilbio.2013.12.017](https://doi.org/10.1016/j.soilbio.2013.12.017).
- Boddy, L. 1983. Effect of temperature and water potential on growth rate of wood-rotting basidiomycetes. *Trans. Br. Mycol. Soc.* **80**: 141–149. doi:[10.1016/S0007-1536\(83\)80175-2](https://doi.org/10.1016/S0007-1536(83)80175-2).
- Boddy, L. 2001. Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. *Ecol. Bull.* 43–56.
- Boddy, L., Owens, E.M., and Chapela, I.H. 1989. Small scale variation in decay rate within logs one year after felling: effect of fungal community structure and moisture content. *FEMS Microbiol. Ecol.* **5**: 173–183. doi:[10.1111/j.1574-6968.1989.tb03691.x](https://doi.org/10.1111/j.1574-6968.1989.tb03691.x).
- Carbone, M.S., Seyednasrollah, B., Rademacher, T.T., Basler, D., Le Moine, J.M., Beals, S., et al. 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. doi:[10.1016/j.agrformet.2019.04.012](https://doi.org/10.1016/j.agrformet.2019.04.012).
- Chambers, J.Q., Schimel, J.P., and Nobre, A.D. 2001. Respiration from coarse wood litter in central Amazon forests. *Biogeochemistry*, **52**: 115–131. doi:[10.1023/A:1006473530673](https://doi.org/10.1023/A:1006473530673).
- Clark, P.W., D'Amato, A.W., Evans, K.S., Schaberg, P.G., and Woodall, C.W. 2021. Ecological memory and regional context influence performance of adaptation plantings in northeastern US temperate forests. *J. Appl. Ecol.* **59**: 314–329. doi:[10.1111/1365-2664.14056](https://doi.org/10.1111/1365-2664.14056).
- Epron, D., Nouvellon, Y., Deleporte, P., Ifo, S., Kazotti, G., Thongo M'bou, A., et al. 2006. Soil carbon balance in a clonal eucalyptus plantation in Congo: effects of logging on carbon inputs and soil CO₂ efflux. *Global Change Biol.* **12**: 1021–1031. doi:[10.1111/j.1365-2486.2006.01146.x](https://doi.org/10.1111/j.1365-2486.2006.01146.x).
- Forrester, J.A., Mladenoff, D.J., Gower, S.T., and Stoffel, J.L. 2012. Interactions of temperature and moisture with respiration from coarse woody debris in experimental forest canopy gaps. *For. Ecol. Manage.* **265**: 124–132. doi:[10.1016/j.foreco.2011.10.038](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., et al. 2015. Temporal trends and sources of variation in carbon flux from coarse woody debris in experimental forest canopy openings. *Oecologia*, **179**: 889–900. doi:[10.1007/s00442-015-3393-4](https://doi.org/10.1007/s00442-015-3393-4). PMID: [26201261](https://pubmed.ncbi.nlm.nih.gov/26201261/).
- Frazier, G.W., Canham, C.D., and 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 fisheye photographs, users manual and program documentation.
- Gough, C.M., Vogel, C.S., Kazanski, C., Nagel, L., Flower, C.E., and Curtis, P.S. 2007. Coarse woody debris and the carbon balance of a north temperate forest. *For. Ecol. Manage.* **244**: 60–67. doi:[10.1016/j.foreco.2007.03.039](https://doi.org/10.1016/j.foreco.2007.03.039).

- Green, M.B., Fraver, S., Lutz, D.A., Woodall, C.W., D'Amato, A.W., and Evans, D.M. 2022. Does deadwood moisture vary jointly with surface soil water content? *Soil Sci. Soc. Am. J.* **86**: 1113–1121. doi:10.1002/saj2.20413
- Griffiths, H.M., Eggleton, P., Hemming-Schroeder, N., Swinfield, T., Woon, J.S., Allison, S.D., et al. 2021. Carbon flux and forest dynamics: increased deadwood decomposition in tropical rainforest tree-fall canopy gaps. *Global Change Biol.* **27**: 1601–1613. doi:10.1111/gcb.15488.
- Hagemann, U., Moroni, M.T., Gleißner, J., and Makeschin, F. 2010. Disturbance history influences downed woody debris and soil respiration. *For. Ecol. Manage.* **260**: 1762–1772. doi:10.1016/j.foreco.2010.08.018.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., et al. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* **15**: 133–302. doi:10.1016/S0065-2504(08)60121-X.
- Harmon, M.E., Bond-Lamberty, B., Tang, J., and Vargas, R. 2011. Heterotrophic respiration in disturbed forests: a review with examples from North America. *J. Geophys. Res. Biogeosci.* **116**. doi:10.1029/2010JG001495.
- Hollinger, D.Y., Davidson, E.A., Fraver, S., Hughes, H., Lee, J.T., Richardson, A.D., et al. 2021. Multi-decadal carbon cycle measurements indicate resistance to external drivers of change at the Howland Forest AmeriFlux site. *J. Geophys. Res. Biogeosci.* **126**: e2021JG006276. doi:10.1029/2021JG006276.
- Hurteau, M., and North, M. 2009. Fuel treatment effects on tree-based forest carbon storage and emissions under modeled wildfire scenarios. *Front. Ecol. Environ.* **7**: 409–414. doi:10.1890/080049.
- Jevon, F.V., D'Amato, A.W., Woodall, C.W., Evans, K., Ayres, M.P., and Matthes, J.H. 2019. Tree basal area and conifer abundance predict soil carbon stocks and concentrations in an actively managed forest of northern New Hampshire, U.S.A. *For. Ecol. Manage.* **451**: 117534. doi:10.1016/j.foreco.2019.117534.
- Kolari, P., Kulmala, L., Pumpanen, J., Launiainen, S., Ilvesniemi, H., Hari, P., and Nikinmaa, E. 2009. CO₂ exchange and component CO₂ fluxes of a boreal Scots pine forest. *Boreal Environ. Res.* **14**: 761–783.
- Kurz, W.A., Dymond, C.C., White, T.M., Stinson, G., Shaw, C.H., Rampley, G.J., et al. 2009. CBM-CFS3: a model of carbon-dynamics in forestry and land-use change implementing IPCC standards. *Ecol. Model.* **220**: 480–504. doi:10.1016/j.ecolmodel.2008.10.018.
- Nagel, L.M., Palik, B.J., Battaglia, M.A., D'Amato, A.W., Guldin, J.M., Swanston, C.W., et al. 2017. Adaptive silviculture for climate change: a national experiment in manager–scientist partnerships to apply an adaptation framework. *J. For.* **115**: 167–178. doi:10.5849/jof.16-039.
- Noh, N.J., Shannon, J.P., Bolton, N.W., Davis, J.C., Van Grinsven, M.J., Pypker, T.G., et al. 2019. Temperature responses of carbon dioxide fluxes from coarse dead wood in a black ash wetland. *Wetlands Ecol. Manage.* **27**: 157–170. doi:10.1007/s11273-018-9649-0.
- Ontl, T.A., Janowiak, M.K., Swanston, C.W., Daley, J., Handler, S., Cornett, M., et al. 2020. Forest management for carbon sequestration and climate adaptation. *J. For.* **118**: 86–101. doi:10.1093/jofore/fvz062.
- Pastorelli, R., Agnelli, A.E., De Meo, I., Graziani, A., Paletto, A., and Lagomarsino, A. 2017. Analysis of microbial diversity and greenhouse gas production of decaying pine logs. *Forests*, **8**: 224. doi:10.3390/f8070224.
- Peng, Y., and Thomas, S.C. 2006. Soil CO₂ efflux in uneven-aged managed forests: temporal patterns following harvest and effects of edaphic heterogeneity. *Plant Soil*, **289**: 253–264. doi:10.1007/s11104-006-9133-0.
- Petrenko, C.L., and Friedland, A.J. 2015. Mineral soil carbon pool responses to forest clearing in northeastern hardwood forests. *GCB Bioenergy*, **7**: 1283–1293. doi:10.1111/gcbb.12221.
- Pietikäinen, J., Pettersson, M., and Bååth, E. 2005. Comparison of temperature effects on soil respiration and bacterial and fungal growth rates. *FEMS Microbiol. Ecol.* **52**: 49–58. doi:10.1016/j.femsec.2004.10.002. PMID: 16329892.
- Pinheiro, J., Bates, D., DebRoy, S., and Sarkar, D., R Core Team. 2021. nlme: linear and nonlinear mixed effects models.
- Pregitzer, K.S., and Euskirchen, E.S. 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. *Global Change Biol.* **10**: 2052–2077. doi:10.1111/j.1365-2486.2004.00866.x.
- Progar, R.A., Schowalter, T.D., Freitag, C.M., and Morrell, J.J. 2000. Respiration from coarse woody debris as affected by moisture and saprotroph functional diversity in Western Oregon. *Oecologia*, **124**: 426–431. doi:10.1007/PL00008868. PMID: 28308782.
- R Core Team. 2020. R: the R project for statistical computing.
- Read, Z., Fraver, S., Forrester, J.A., Wason, J., and Woodall, C.W. 2022. Temporal trends in CO₂ emissions from *Picea rubens* stumps: a chronosequence approach. *For. Ecol. Manage.* **524**: 120528. doi:10.1016/j.foreco.2022.120528.
- Rinne-Garmston, K.T., Peltoniemi, K., Chen, J., Peltoniemi, M., Fritze, H., and 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. *Global Change Biol.* **25**: 1852–1867. doi:10.1111/gcb.14594.
- Sandström, J., Bernes, C., Junninen, K., Löhmus, A., Macdonald, E., Müller, J., and Jonsson, B.G. 2019. Impacts of dead wood manipulation on the biodiversity of temperate and boreal forests. A systematic review. *J. Appl. Ecol.* **56**: 1770–1781. doi:10.1111/1365-2664.13395.
- Savage, K.E., and Davidson, E.A. 2003. A comparison of manual and automated systems for soil CO₂ flux measurements: trade-offs between spatial and temporal resolution. *J. Exp. Bot.* **54**: 891–899. doi:10.1093/jxb/erg121. PMID: 12598560.
- Stoffel, J.L., Gower, S.T., Forrester, J.A., and Mladenoff, D.J. 2010. Effects of winter selective tree harvest on soil microclimate and surface CO₂ flux of a northern hardwood forest. *For. Ecol. Manage.* **259**: 257–265. doi:10.1016/j.foreco.2009.10.004.
- Woodall, C.W., Evans, D.M., Fraver, S., Green, M.B., Lutz, D.A., and D'Amato, A.W. 2020. Real-time monitoring of deadwood moisture in forests: lessons learned from an intensive case study. *Can. J. For. Res.* **50**: 1244–1252. doi:10.1139/cjfr-2020-0110.