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Controls on the rate of CO_2 emission from woody debris in clearcut and coniferous forest environments

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Abstract The rate at which CO_2 is released from woody debris post-clearcut affects the long term carbon consequences of such disturbances. Changes in microclimate post-clearcut may alter the rate of woody debris decomposition from that in a mature forest. However, very few studies have explored post-disturbance rates of woody debris respiration and the possible influence of an altered microclimate, and even fewer have considered the role of log position in influencing rates of respiration. This study explored the effects of log position and microclimate variability on the rates of coarse woody debris (CWD) respiration. The rates of respiration of downed Norway spruce (*Picea abies*) logs were repeatedly measured in situ using an LI-6200 gas analyzer. Treatments included native logs in the clearcut site, native logs in a neighboring mature spruce stand, and logs transferred from the clearcut site to the mature spruce stand. The transfer logs showed the highest rates of respiration (0.44 ± 0.03 g CO_2 m^{-2} log surface h^{-1}), followed by the clearcut logs (0.36 ± 0.02 g CO_2 m^{-2} log surface h^{-1}), and spruce stand logs (0.30 ± 0.02 g CO_2 m^{-2} log surface h^{-1}) ($P < 0.01$). The boost in respiration found in the transfer treatment group was best explained by increases in log water content, while the slower rate of respiration in the spruce stand logs was best explained by the log's contact/non-contact with the ground prior to the start of the observational campaign. CWD respiration was found to represent 18 ± 3 % of total daytime ecosystem respiration (R_{eco}).

Keywords Woody debris respiration · Decomposition · Clearcut harvesting · Disturbance · Microclimate

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Introduction

Coarse woody debris (CWD) can store a large amount of gradually decomposing biomass and thus plays an important role in the biogeochemical cycling and carbon balance of forest ecosystems (Gough et al. 2007; Harmon et al. 1990). CWD was often overlooked in early regional and global carbon budgets (Houghton and Woodwell 1989; Post et al. 1990), but is now understood to be a critical component (Harmon et al. 1990; Janisch and Harmon 2002; Körner 2003). Its rate of decomposition and associated respiration contributes to the release of CO_2 from ecosystems to the atmosphere, acting as a sometimes-large carbon source particularly following stand-replacing disturbances (Janisch and Harmon 2002; Zhou et al. 2007; Williams et al. 2012).

Coarse woody debris (defined as dead wood greater than 7.5 cm in diameter) volume can be quantified using plot and line-intercept methods (Harmon and

Sexton 1996), but measuring its rate of decomposition can be challenging due to the slow nature of the process (Franklin et al. 1987). CWD volume typically peaks post-disturbance, initially declining over time due to decomposition and modest inputs before increasing as trees mature and thus shed larger branches, trunks, and roots (Brais et al. 2005; Janisch and Harmon 2002; Sturtevant et al. 1997). By measuring CWD volume at multiple sites with stands of different ages and arraying results as a chronosequence, decomposition rates can be derived from the slope of the net initial volume decline, where the colonization by decomposers causes a period of rapid exponential net mass loss, often followed by a period of slower decomposition as the net volume of CWD diminishes (Bond-Lamberty and Gower 2008; Duval and Grigal 1999; Harmon et al. 2000).

Measured changes in CWD volume do not provide a clear measure of CWD contributions to CO_2 emissions in part because the leaching and fragmentation of wood can reduce CWD volume without direct emission to the atmosphere, and conversely log density can change without a visible change in log volume. Fortunately, the rate of CO_2 emission from CWD can be directly measured using an infrared gas analyzer (IRGA) (Chambers et al. 2001; Bond-Lamberty et al. 2003). This approach allows detailed assessment of fine scale spatial and temporal patterns in CO_2 emission from CWD, something that cannot be readily derived from measured or inferred changes in CWD volume. Most studies utilizing this technique have focused on the rate of respiration of CWD within mature forests, such as the Amazon forest (Chambers et al. 2001), old-growth coniferous forests (Progar et al. 2000), secondary broad-leaved forests (Jomura et al. 2007) and mature northern temperate forests (Gough et al. 2007). Only a few studies have explicitly explored the rate of respiration for CWD following recent disturbance. These studies have documented CWD dynamics after fire in boreal forests (Bond-Lamberty et al. 2003; Wang et al. 2002), selective logging in temperate forests (Liu et al. 2006), and clearcut harvesting in the Pacific northwest and boreal forests (Marra and Edmonds 1996; Hagemann et al. 2010).

Differences in the decomposition rate of CWD are broadly acknowledged to result from the physical environment, quantity and quality of the substrate, and characteristics of the microbial community (Swift et al. 1979). The decay rate of a given piece of woody debris or organic matter has been predominantly studied at the scale of a log, where substrate quality, size, species, microbial activity, decay class, temperature, and available moisture have all been found to affect the rate of decomposition (Harmon et al. 1986; Gholz and Clark 2002; Yin 1999; Zhou et al. 2007). On a regional basis, the decomposition rate is a function of species, temperature, latitude and elevation (Yin 1999). More specifically, the abundance, composition, and activity of the microbial community are all affected by stand age and species composition (Myers et al. 2001); nutrient availability (Högberg et al. 2007; Ingwersen et al. 2008); soil temperature and moisture (Kvaernø and Øygarden 2006; Mummey et al. 2010); substrate quality (Myers et al. 2001); and soil physical properties (Högberg et al. 2001; Kvaernø and Øygarden 2006). Whether rates of decomposition can be generalized to an ecosystem or site scale and related to disturbance history, is unclear. Of the relevant variables, temperature and moisture have consistently been found to be key drivers (Gough et al. 2007; Hagemann et al. 2010; Wang et al. 2002).

A clearcut event changes a site's microclimate and surface properties through modifications of the air temperature and humidity, wind speed, radiation, and soil temperature and moisture (Aussenac 2000; Chen et al. 1993; Parfitt et al. 2002). Many studies have also found a reduction of microbial biomass, lower fungi to bacteria ratio, and a shift in community composition in response to changes in microclimate and soil compaction common to clearcuts (Busse et al. 2006; Mummey et al. 2010; Siira-Pietikäinen et al. 2001; Tan et al. 2005). It could therefore be expected that differences in CWD characteristics (e.g. size, abundance, state of decay), as well as differences in microclimate and microbial community, would result in a change in decomposition rates between a mature forest and in a recent clearcut.

The effect of harvest on log-level rates of respiration appears to depend somewhat on harvest intensity, but total studies have been minimal (Harmon et al. 2011). While selective harvesting has not been found to affect the log-level rate of respiration for CWD (Liu et al. 2006), Forrester et al. (2012) found an increased rate of log-level respiration in forest gaps. In clearcut environments, meanwhile, Hagemann et al. (2010) and Marra and Edmonds (1996) both observed an increase in summer log-level rates of respiration, due

mainly to changes in air temperature. This study is one of the few that employs a paired site approach to address the effect of a disturbance on the site-level rate of CWD respiration, and one of the only studies that investigates both microclimate and stand structure related-parameters to explain site level differences.

This manuscript answers the following questions: do individual logs in a clearcut exhibit a different mean rate of respiration compared to that in a neighboring mature forest? And if so, what are the drivers of these site-level differences? The rate of respiration of Norway spruce (*Picea abies*) CWD was compared between a mature Norway spruce stand and a recently clearcut Norway spruce stand in Harvard Forest, Petersham, Massachusetts. We hypothesized that: (1) the clearcut site logs would have higher respiration rates than the mature forest logs because of a higher mean air temperature; and (2) the rate at which the spruce stand logs respire is the same as the rate for clearcut logs transplanted to the spruce environment because of their exposure to a similar decomposer community and microclimate. This study was methodologically unique in that the rate of CO_2 emissions from CWD was measured in situ, using the largest pieces of CWD (50 cm in length) of any study with which the authors are familiar, purposely selected to better represent CWD sizes common to forests. In addition, by measuring the rate of respiration in field conditions, results can be more appropriately extrapolated to the site-level than would be possible with lab-based techniques.

Materials and methods

Study sites

The clearcut site is located near the top of Prospect Hill (42.546N, 72.174W, elevation 403 m) within the Harvard Forest Long Term Ecological Research Site (Fig. 1). The clearcut site is a former Norway spruce (*Picea abies*) plantation (established in 1916) that was commercially harvested as a clearcut, except for a few seed trees, in August to September 2008 (Table 1). Soil at the clearcut site is a well-drained Typic Haplorthod (coarse-loamy, isotic, frigid) (NRCS 2010). The second site, a remnant mature Norway spruce stand (42.534N, 72.183W, elevation 360 m) is located approximately 1,500 m southwest of the clearcut site and in addition to Norway spruce, includes a lower abundance of red pine (*Pinus resinosa*), red oak (*Quercus rubra*), and red maple (*Acer rubrum*) (Fig. 1). The mature stand's soil consists of a well-drained Oxyaquic and Aquic Haplorthod (coarse-loamy, isotic, frigid) (NRCS 2010). The monthly mean temperature for Harvard Forest (2005–2010) in January was −4.5 °C (23.9 °F) and in July was 20.6 °C (69.1 °F). The mean annual rainfall, for 2005–2009, was 1,355 mm (Boose 2001). Norway spruce is one of the most common spruce species in North America and is an economically important species (Sullivan 1994). The primary fungus observed on spruce logs at both sites, was a resupinate wood decay fungus in the order Polyporales, and class Agaricomycetes.

Field measurements

Site level CWD abundance was quantified in the clearcut site in the summer of 2010 by measuring all CWD within nine 400 m^2 plots. CWD abundance was quantified in the spruce stand site in the summer of 2011 by measuring all CWD along two 75 m line intercept transects. The difference in method was necessary due to the narrowness of the spruce stand between adjacent forest types. Methodology followed that recommended by Harmon and Sexton (1996).

Sampled logs were Norway spruce, 50 cm in length, within two diameter size classes (8–13 and 15–20 cm), and two decay classes (decay class 2 and 3). Logs were cut to size in April 2011. Logs not in contact with the ground prior to cutting were placed on the ground at this point in time. In a mature forest, unlike in a clearcut environment, the density of standing trees results in many fallen trees lying at an angle, limiting ground contact. Log position (off-the-ground, on log or on-ground), discussed at a later point, refers to the log's position prior to April 2011. Decay classes ranged from 1 to 5 and followed the class definitions as specified by Harmon and Sexton (1996). The diameter size and decay classes were selected to be representative of the clearcut site. Log-level respiration and associated measurements for each log were measured seven times in varying environmental conditions between 26-May-2011 and 20-July-2011. Measurements were alternated between the sites on a daily basis, and within a given day of measurement, the order of log measurements was

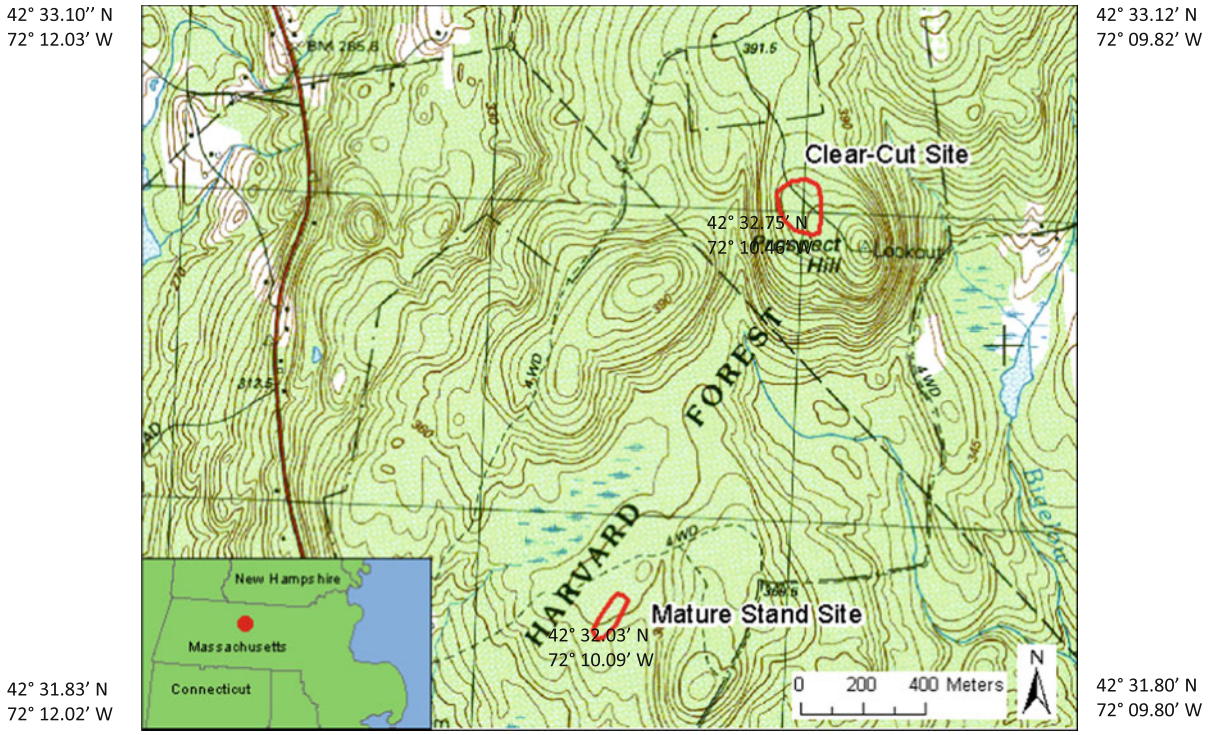

Fig. 1 The location of the mature stand site and clear-cut site (*circled in red*) from which sample logs were selected and measured. (Color figure online)

Table 1 Stand characteristics of the clearcut (CC) and mature spruce stand (SS) study sites

Parameter	CC	Spruce
Elevation (m)	403	360
Forest age (years)	3	85
CWD (m^3 ha^{-1})	244.3	64.7
Mean CWD diameter (cm)	17.9 ± 0.2	12.1 ± 0.6
Distribution of CWD decay classes (%)[a]	3/86/9/2/ < 1	24/37/24/ 11/4
Mean canopy height (m)	1–2	22
Tree density (ha^{-1})	NA	800
Total tree basal area (m^2 ha^{-1})	NA	39.7

[a] % in each decay class (1–5), where decay class is based on Harmon and Sexton (1996) classification method

rearranged to avoid temporal sampling bias. The sample consisted of 48 logs, comprising three treatment groups of 16 logs each (four logs of two size classes of two decay classes). The treatment groups consisted of, (1) mature spruce stand (SS), (2) transfer (CCT) (spruce logs transferred from clearcut to mature forest site), and (3) clearcut site (CC). Transferred logs were moved on 21-April-2011 and placed within a few feet of SS logs of identical size and decay class to minimize microclimate differences.

Measurements were taken in situ under ambient conditions to simulate existing conditions to the extent possible. Logs were placed one at a time inside an air tight plastic chamber with a wire rack at the bottom of the chamber to allow for air circulation around the log (Liu et al. 2006). An LI-6200 IRGA pumped air through the chamber in a closed loop at a set rate. A fan was installed inside the chamber to ensure adequate air circulation (Gough et al. 2007). The CO_2 concentration was recorded every 10 s until either a change of 50 ppm CO_2 or a cumulative 900 s occurred. To avoid the effects of air disturbance caused by opening the chamber cover, data for the first 45 s after the start of measurements was not used (Jomura et al. 2007). Log-level respiration was calculated as grams of CO_2 emitted per unit of wood surface per unit of time (Hagemann et al. 2010). Soil respiration was also measured with the chamber method. Eight PVC soil respiration collars (diameter = 25.4 cm) were installed at each site near a

subsample of the sample logs and a modified LI-6200 IRGA was used to record the rate of soil respiration.

At the time of each log respiration measurement the ambient air temperature, light level and relative humidity were recorded at log height. Soil temperature, moisture and pH were measured five cm below each sample log. Internal wood temperatures were recorded in pre-drilled 4 cm deep holes. Between measurements, the holes were sealed with wooden plugs to avoid equilibration with ambient air. At the time of each soil respiration measurement, soil temperature, soil moisture, and pH were measured 5 cm below the soil surface. Air temperature, relative humidity and light level were recorded at the ground surface. A soil survey meter (AMT-300, Amtech Industry, Quingdao, China) was used to measure the soil parameters, light levels, and internal log temperature, while an Oakton digital max/min thermohygrometer (Forestry Suppliers Inc, Jackson, MS), and LI-6200 IRGA (LI-COR Inc, Lincoln, NE) was used for air temperature and relative humidity measurements. In addition, logs were weighed immediately prior to each respiration measurement and oven dried at 105 °C post-experiment to obtain log density and log percent water content. Log density was assumed to be constant throughout the field season as it was calculated based on final dry weight after repeated measurements of each log. Cursory visual observations of microbial community abundance, temporal development, and type were made on the log surface at the beginning and end of the field season. Temporal development was defined as fungal fruiting bodies being absent or present throughout the data collection time period or developing within the data collection time period. Abundance of fungal fruiting bodies was categorized using both the percent of log covered with fungi as well as the size of shelf fungi, which extended off of logs. No assays or C-phospholipid fatty acid (PLFA) analysis was conducted, therefore references made to the microbial community in regards to diversity and abundance are assumed to be at best, proxies, for actual community dynamics.

Statistical analyses

The statistical analysis was conducted with SPSS Statistics (IBM Corporation, Armonk, NY). Statistical significance between groups was determined using repeated measures analysis of variance (ANOVA) test with a Greenhouse–Geisser correction applied. A *t* test was used to test for significance of pair-wise comparisons. To determine which variables may explain pair-wise differences, we performed a factorial ANOVA. The data was found to meet all test assumptions. The Levene's test for equality of error variances showed that the error variance of the dependent variable was equal across groups. Categorical variables tested included treatment (CC, SS, CCT), pre-April 2011 log position (off-the-ground, on log, on-ground), soil moisture (<5, 5–10, 10–20 %), time since last precipitation event (<8, 8–24, 24–48, >48 h), and local topography (slope, local high, local low). Continuous variables including log density (g cm^{-3}), air and soil temperature (°C), and log percent water content (%) were converted to low, low-moderate, moderate-high, and high categories with equal sample sizes per category. Akaike's Information Criteria (AIC) calculated using residual sum of squares was used to prevent model over-fitting. One-way analyses of variances (ANOVAs) were performed to explain independent variable inclusion/exclusion in the integrated ANOVA model. Differences in microclimate conditions between treatment groups were tested using Student's *t* test for continuous variables and Chi-square test for categorical variables.

Flux tower measurements

Daily site level rates of CWD and soil respiration at the clearcut site were related to daily site level rates of total ecosystem respiration using data collected from a flux tower located within the clearcut site. The tower is located three meters above the surface. Wind speed and direction, momentum and sensible heat fluxes were derived from data collected using a CSAT3 sonic anemometer (Campbell Scientific, Logan, UT) and water and carbon dioxide flux were measured with additional use of an open-path LI-7500 CO_2/H_2O analyzer (LI-COR Inc, Lincoln, NE). The eddy covariance technique employed at the towers was based on Goulden et al. (1996), Wofsy et al. (1993), Aubinet et al. (2000) and Lee et al. (2004). Heat and mass fluxes were calculated using conventional equations (Aubinet et al. 2000; Moncrieff et al. 1997). Data removal and corrections were applied as advised in Webb et al. (1980), Wilczak et al. (2001) and Moncrieff et al. (1997). For gaps of <3 h, rates of respiration prior and post-gap were averaged. For

consecutive gaps of more than 3 h, no relationship was calculated between the CWD, soil and flux tower rates of respiration. Ecosystem respiration (R_{eco}) was taken to be the night time net ecosystem exchange (NEE) and extrapolated to daytime conditions based on empirical functions of temperature (Reichstein et al. 2005). The percent of R_{eco} represented by CWD respiration and soil respiration was calculated for each measurement day using the mean R_{eco} for the specific hours during which CWD respiration measurements were made.

Results

The logs transferred from the clearcut to the spruce stand (CCT) showed the highest mean rate of respiration (0.44 ± 0.03 g CO_2 m^{-2} log surface h^{-1}), followed by the clearcut logs (0.36 ± 0.02 g CO_2 m^{-2} log surface h^{-1}), and spruce stand logs (0.30 ± 0.02 g CO_2 m^{-2} log surface h^{-1}) (Fig. 2). There was a statistically significant difference between log treatment groups as determined by a repeated measures ANOVA, with a Greenhouse–Geisser correction applied [$F(1.20, 193.43) = 10.92$, $P < 0.0005$]. Pair-wise comparisons showed that the transfer group (CCT) respired at a significantly faster rate than the clearcut group (CC) ($P = 0.0096$) and the spruce stand group ($P < 0.005$), while the clearcut group respired significantly faster than the spruce stand group ($P = 0.014$).

Respiration rate did not differ between logs of decay classes 2 and 3 ($P = 0.30$). However, respiration rate did depend on log size, with a lower rate for the small log size class (diameter = 8–13 cm) (0.36 ± 0.02 g CO_2 m^{-2} log surface h^{-1}) compared to the large log size class (diameter = 15−20 cm) (0.48 ± 0.02 g CO_2 m^{-2} log surface h^{-1}) ($P < 0.01$), consistent with expectations based on surface area to volume ratios. When expressed on a log-volume basis (g CO_2 m^{-3} log volume h^{-1}) instead of log-surface area (g CO_2 m^{-2} log surface h^{-1}), the small log size class (15.46 ± 0.78 g CO_2 m^{-2} log surface h^{-1}) respired 11 % faster than the large log size class (13.92 ± 0.72 g CO_2 m^{-2} log surface h^{-1}), although the difference was not significant at the $\alpha = 0.05$ level ($P = 0.07$).

The rate of log respiration, pooled across the three treatment groups, was found to be significantly explained by one-at-a-time effects of the following factors: treatment, log position (off-the-ground, on log, on-ground), air temperature, soil temperature, log density, log percent water content, soil moisture, local topography, and time since last rain (Table 2). The rate of respiration was consistently higher for logs in contact with the ground, and with lower log density, higher moisture availability and higher temperatures. When all independent variables were included in a factorial analysis that tested both main effects and interactions, the rate of respiration was best explained by treatment, log density, and the interaction between log density and log water content ($r^2 = 0.83$) (Table 3). As log density decreases with increased decay, log water holding capacity increases, hence a significant ANOVA interaction between these two variables. The lack of significant interactions within the factorial ANOVA between microclimate parameters allows for their across-site comparison. The microclimate of the clearcut site relative to the spruce stand site was consistently and significantly different ($P < 0.01$) (Table 4). Logs in the clearcut (CC) were exposed to significantly higher air temperatures, shown to increase respiration rate, but lower log percent water content and soil moisture, each shown to decrease respiration rate. No significant differences in microclimate were found between the transferred logs (CCT) and the native counterparts (SS) (Table 4).

In addition to the effects of microclimate, microbial community composition and abundance could also be

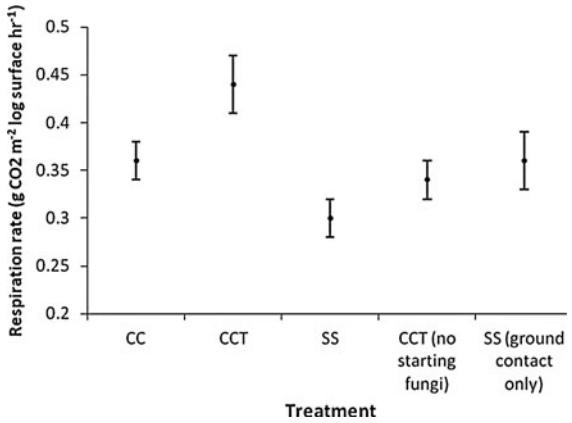

Fig. 2 Mean rates of coarse woody debris respiration for the clearcut (CC), transfer (CCT) and spruce stand (SS) treatment groups. The CCT (no starting fungi) refers to the presence/absence of fungal fruiting bodies at the start of the field season being controlled for. The SS (ground contact only) refers to a sub-group of the SS treatment group consisting only of logs that were in contact with the ground prior to the start of April 2011. *Lines* indicate ± log-to-log standard error

Table 2 Results of the one way analysis of variance (ANOVA) tested the ability of individual independent variables to explain the rate of CWD respiration with data pooled across treatments

Source	SS	df	MS	F	Sig
Log position (off-the-ground, on log, on-ground)	1.07	2	0.54	8.92	0.000
Air temperature (°C)[a]	0.98	4	0.25	4.05	0.003
Treatment (CC, CCT, SS)	1.20	2	0.60	10.06	0.000
Log density (g cm^{-3})[a]	2.62	4	0.65	11.66	0.000
Log water content (%)[a]	2.39	4	0.60	10.53	0.000
Soil moisture (%)	1.26	2	0.63	10.54	0.000
Local topography (high, low, slope)	0.43	3	0.14	2.32	0.075
Soil temperature (°C)[a]	0.88	3	0.29	4.84	0.003
Time since last rain (h)	0.29	3	0.10	1.54	0.203

SS sum of squares, *df* degrees of freedom, *MS* mean squares *F* F-statistic

[a] Continuous variables have been categorized into four categories (low, low-moderate, moderate-high, high) with equal sample sizes in each category

Table 3 Results of the factorial analysis of variance (ANOVA) tested the combined main effects and interactions of microclimate and log condition on the rate of CWD respiration

Source	SS	df	MS	F	Sig
Treatment (CC, CCT, SS)	0.19	2	0.10	2.98	0.06
Log density (g cm^{-3})[a]	0.32	4	0.08	2.49	0.05
Log density (g cm^{-3})[a] × log water content (%)[a]	0.53	8	0.07	2.04	0.05
Error	3.95	122	0.03		
Total sum of squares[b]	22.78	363			

Only significant variables have been included in the final model

SS sum of squares, *df* degrees of freedom, *MS* mean squares, *F* F-statistic

[a] Continuous variables have been categorized into four categories (low, low-moderate, moderate-high, high) with equal sample sizes in each category

[b] $r^2 = 0.83$

expected to contribute to treatment group differences in the rate of respiration. Relying on visual observations, both the CCT and SS treatment groups showed extensive development of fungal fruiting bodies on log surfaces throughout the data collection period and a higher end of season fungal fruiting body abundance compared to the CC group ($P < 0.01$). The SS treatment group also showed a significant difference in log ground contact ($P < 0.01$) (Table 3). Eight of the 16 SS treatment logs were originally not in contact with the ground [differentiated from snags by exhibiting an angle of <45° from the ground (Harmon and Sexton 1996)]. These eight logs, when cut to size (50 cm) in April 2011, fell to the ground for the first time. In contrast, all sample logs in the CC or CCT treatment groups were in contact with the ground prior to the field measurements.

When comparing the SS logs that were consistently in contact with the ground to CC logs, their between treatment difference disappeared and the CC and SS logs were found to have similar respiration rates ($P = 0.37$) (Fig. 2). Further, when explaining pairwise differences between CCT and SS treatments, controlling for log ground contact did not eliminate their difference ($P = 0.037$). However, additionally controlling for starting fungi by comparing the SS logs in contact with the ground and absent of fungi at the season start to the CCT logs with no fungi at season start eliminated the difference in respiration rates between these populations ($P = 0.36$) (Fig. 2). SS non-ground-contact logs showed significantly higher dry log density than SS logs consistently in contact with the ground ($P < 0.01$) indicative of differences in microbial community establishment. In addition,

Table 4 Mean microclimate and log-specific conditions at sample logs, by clearcut (CC), transfer (CCT) and spruce stand (SS) treatments

Treatment	Mean air temp (°C) (S.E.)	Mean log temp (°C) (S.E.)	Mean soil temp (°C) (S.E.)	Log water content (%) (S.E.)	Soil moisture[A] <5 %	Soil moisture 5-10 %	Soil moisture 10-20 %
CC[E]	26.1 (0.5)[a]	26.0 (0.5)[a]	21.2 (0.3)[a]	27.9 (1.1)[a]	78.5[a]	20.0	1.5
CCT[E]	20.9 (0.4)[b]	20.5 (0.3)[b]	17.9 (0.3)[b]	36.6 (1.1)[b]	52.1[b]	44.4	3.4
SS[E]	20.8 (0.4)[b]	20.4 (0.4)[b]	17.7 (0.3)[b]	33.0 (2.5)[b]	53.0[b]	47.0	0

	Log ground contact[B]				Fungi temporal development[C]			Fungi visual abundance[D]			
Treatment	On ground (% of total)	On log (% of total)	Off ground (% of total)	Log density (g cm^3)	Fungi N/N (%)	Fungi N/Y (%)	Fungi Y/Y (%)	F. absent (%)	F. low (%)	F. mod (%)	F. high (%)
CC	87.5[a]	12.5	0	0.42 (0.01)[a]	43.1[a]	19.2	37.7	43.1[a]	24.6	12.3	20.0
CCT	87.5[a]	12.5	0	0.38 (0.01)[a]	6.0[b]	57.3	36.8	6.0[b]	63.2	17.9	12.8
SS	43.7[b]	6.3	50.0	0.33 (0.01)[b]	6.8[c]	93.2	0	6.8[c]	48.7	32.5	12.0

Superscript letters indicate results significance testing among treatment groups, where significant differences are evaluated at the level $\alpha = 0.05$

[A] Significance for categorical variable comparison listed on first category

[B] Log ground contact prior to cutting to size (50 cm) in spring 2011

[C] *N/N* no fungal fruiting bodies throughout the data collection, *N/Y* fungal fruiting bodies developed within data collection time period, *Y/Y* fungal fruiting bodies present throughout data collection time period

[D] Abundance of fungal fruiting bodies as of the end of the data collection period, as observed visually, where low = <1 % cover, mod = 1–5 % cover and high = >5 % cover

[E] *CC* clearcut, *CCT* clearcut transfer to spruce stand, *SS* spruce stand

although temperature conditions were similar, soil moisture and log percent water content were significantly lower in SS non-ground-contact logs compared to SS logs consistently in contact with the ground ($P < 0.05$). The significant difference between the CC and CCT treatment groups was not explained by differences in ground contact.

For the purpose of understanding the magnitude of CO_2 release from CWD respiration compared to the broader context of soil and ecosystem respiration rates in a mature forest and post-disturbance, rates of CWD CO_2 efflux were up-scaled to the ecosystem scale using site-level differences in CWD quantities. Mean log respiration (g CO_2 log volume^{-1} h^{-1}) was converted to mean CWD site respiration (g CO_2 m^{-2} ground surface h^{-1}) using site level CWD abundance. CWD abundance at the two sites, clearcut and spruce stand, was 0.024 ± 0.0025 and 0.0065 m^3 log volume m^{-2} ground surface, respectively. Once CWD abundance was accounted for, the site-level rate of CWD respiration at the clearcut site (the up-scaled CC treatment group) far exceeded that at the mature spruce stand (the up-scaled SS treatment group) ($P < 0.01$). Mean CWD respiration at clearcut and spruce stand site-levels, when calculated per measurement day, were 0.32 ± 0.01 g CO_2 m^{-2} ground surface h^{-1} and 0.09 ± 0.004 g CO_2 m^{-2} ground surface h^{-1}, respectively. The soil respiration rate, where "soil" included leaf litter and small fine woody debris, was found to be almost three times greater at the clearcut site (0.84 ± 0.05 g CO_2 m^{-2} surface area h^{-1}) compared to the spruce stand (0.29 ± 0.01 g CO_2 m^{-2} surface area h^{-1}) ($P < 0.01$). CWD respiration represented $\sim$28 % of daily combined CWD and soil respiration at the clearcut site and $\sim$24 % of daily combined CWD and soil respiration at the spruce stand site. We also compared the per day rate of clearcut CWD respiration to total ecosystem respiration (R_{eco}) estimated from an eddy covariance flux tower located within the clearcut site. CWD respiration was found to represent 18 ± 3 % of ecosystem respiration (R_{eco}). In comparison, clearcut soil respiration was found to represent, on average, 44 ± 3 % of R_{eco}.

Discussion

Our study was unique in relating rates of CWD respiration to log ground contact. Although all sample logs in the CC and CCT treatment groups were located in contact with the ground or on another log, half of the SS treatment logs were not in contact with the ground prior to measurements. Log position prior to cutting to size was found to be important in explaining pair-wise differences. Contact with the ground is reportedly important for the establishment of microbial communities on logs (Mäkinen et al. 2006; Naesset 1999). Additionally, a significantly higher log density and lower log percent water content was observed in the spruce stand logs not in contact with the ground prior to April 2011. Lower log water content suggests a potential difference in pore volume or water holding capacity possibly a consequence of a higher dry log density (Harmon and Sexton 1995). It remains unclear if the significantly lower rate of respiration in the SS logs not in contact with the ground is the result of a reduced microbial establishment or decreased moisture availability or both.

Log decay class was initially defined using Harmon and Sexton's (1996) technique which relies on characteristics such as the presence/absence of bark and "hardness" of the log. Harmon and Sexton (1996) argue that biological indicators such as fungal fruiting bodies or the presence of insect galleries vary widely even in a limited area, and are therefore of limited value in separating decay classes. Observations of a correlation between visible fungi abundance and higher rates of log respiration, however, necessitated the inclusion of additional definitions of "decay" that relied on visual abundance of fungal fruiting bodies. Controlling for presence/absence of fungal fruiting bodies at the start of the field season, in addition to controlling for ground contact, both being transfer related parameters, explained the significant difference observed between the CCT and SS treatment groups (Fig. 2). An exploration of how post-disturbance changes in microbial community composition may be correlated with variation in rates of log respiration would be a logical next step for continued research.

Despite similar initial ground contact and starting microbial community, the CCT logs showed a significantly higher rate of respiration compared to the CC logs. Air temperature was a significant variable in explaining daily variation in rates of CWD respiration, however a significantly warmer air temperature in the clearcut did not result in an increased rate of respiration for the CC logs relative to the CCT logs. In

contrast, increased moisture content in the CCT logs, as evidenced by significantly higher soil moisture and log percent water content, did appear to elevate respiration for the CCT logs, suggesting that effects of elevated moisture outweighed lower temperatures. The greater importance of moisture may be a consequence of stricter moisture requirements than temperature requirements for microbial activity (Kvaernø and Øygarden 2006; Mummey et al. 2010). A log percent water content of 30–40 % has been found to be necessary for uninhibited microbial community activity (Griffin 1977; Haynes 1986; Stark and Fireston 1995). Across treatment groups, the percent of respiration measurements where logs met the 30 % moisture content ranged from 48 to 65 %, while the percent of measurements where logs met the 40 % moisture content ranged from 23 to 39 %, suggesting that log moisture was frequently inhibiting microbial respiration. Furthermore, the increased moisture availability for the CCT logs likely fostered increased microbial community development, as evidenced by the large number of the CCT logs that developed fungal fruiting bodies throughout the field season.

Hypothesis 1 stated that clearcut logs would have a higher mean log-level rate of respiration than mature forest spruce stand logs because of a higher mean air temperature. This hypothesis was proposed given the findings of Hagemann et al. (2010) and Marra and Edmonds (1996) both of whom found clearcut logs to have higher summer rates of respiration compared to logs in nearby mature forest stands. The CC logs were found to have a slightly higher rate of respiration than the SS logs but after controlling for ground contact, differences in moisture, temperature, and fungal community canceled the between site differences that were initially apparent. Hypothesis 2 stated that spruce stand logs would respire at the same rate as the clearcut transfer logs. The SS and CCT logs were found to have similar rates of respiration when we compared logs with a common condition of ground contact and early-season presence of fungi. Since the SS and CCT logs experienced the same microclimate conditions, these conditions could not explain the initial significant difference in rate of respiration between the treatment groups. Lastly, because the CC and CCT treatment groups experienced initially similar ground contact and fungal development, the significantly higher respiration of CCT logs is attributed to effects of elevated wetness that outstripped effects of reduced temperature.

Several additional factors must be considered in interpreting the results. First, differences inherent between the sites or due to measurement timing could have affected recorded parameters despite efforts to minimize such sources of error. Differences in substrate quality and quantity could also have affected a site comparison as both factors have been shown to affect the rate of decomposition (Harmon et al. 1986; Zhou et al. 2007). Substrate quality was controlled for through the usage of transfer logs (CCT). The CCT logs were used to eliminate any unforeseen differences in substrate quality between the clearcut and spruce stand. The difference in substrate quantity between the two sites was seen to be an inherent difference between a clearcut and mature spruce stand and thus indirectly tested through the site level comparison. Finally, categorizing continuous variables to submit to ANOVA testing may have resulted in a reduction in their ability to explain variance, but was seen as necessary to simultaneously test for effects of categorical and continuous independent variables.

In conclusion, ground contact and log water content were found to best explain treatment level differences. While temperature helped to explain within-treatment variation in respiration rate, it did not explain site level differences between clearcut and mature forest respiration rates though this factor may have compensated by opposite effects based on wetness (clearcut was warmer and drier). Correspondingly, the effect of increased log water content was found to overwhelm the effect of lower temperature in explaining boosted respiration for clearcut transfer logs. It is suggested that this is a consequence of stricter moisture than temperature requirements for microbial activity as logs frequently exhibited wetness conditions reported to be limiting to microbial activity.

Rates of log-level respiration measured in this study were comparable to rates documented in similar studies. Jomura et al. (2007) found rates of CWD respiration in a mature, secondary, temperate forest ranging from 0.1 to 148.6 mg CO_2 kg^{-1} h^{-1}, with a mean rate of $\sim$30–40 mg CO_2 kg^{-1} h^{-1} at the air temperature, 24 °C (the mean air temperature documented at the time of measurement across our two sites). In comparison, the CC, CCT and SS treatment groups had a mean rate of respiration of 39.98, 41.91, and 28.46 mg CO_2 kg^{-1} h^{-1}, respectively. The Hagemann et al. (2010) study, meanwhile, documented a rate of 0.16–0.34 g CO_2 m^{-2} h^{-1} in a boreal harvested

site and 0.09–0.19 g CO_2 m^{-2} h^{-1} in a boreal old growth site, comparable to our findings of the CC, CCT and SS treatment groups respiring 0.36 ± 0.02, 0.44 ± 0.03, and 0.30 ± 0.02 g CO_2 m^{-2} log surface h^{-1}, respectively. When rates of log respiration were scaled to the site level at our clearcut and spruce stand, it was evident that the higher quantity of CWD in the clearcut site outweighed site-level differences in the rate of log respiration. However, this study demonstrated that emissions of CO_2 from CWD in a clearcut site may differ from that in a mature forest not just because of differences in the volume of CWD, but additionally because of disturbance-related differences in log ground contact, log water content and resulting microbial community characteristics. Regardless, CWD respiration was found to represent a substantial portion of ecosystem respiration, representing ~ 28 % of combined CWD and soil respiration and ~ 18 % of total ecosystem respiration at the clearcut site. Direct measurements of CWD respiration are valuable for partitioning flux-tower based measurements, but are rarely included in this partitioning, despite potentially significant fractional contributions towards ecosystem respiration post-disturbance (Griffis et al. 2004; Flanagan et al. 2005; Davidson et al. 2006). Future work should continue to expand upon in situ measurements of CWD respiration, particularly in post-disturbance conditions where such debris may represent a higher portion of respiration than in mature forest conditions.

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