The Effect of Selective Cutting on the Carbon Budget of a Northern Hardwood Forest

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Introduction

1.1 The Carbon Cycle

The global carbon (C) cycle involves the exchange of C between the atmosphere, terrestrial biosphere and oceans. Since the Industrial Revolution, fossil fuel combustion, land-use changes and other human activities have disrupted the global C balance, causing a net accumulation of C in the atmosphere. In the last 200 years, CO_2 concentration in the atmosphere has risen from 280 parts per million (ppm) to 367 ppm, the sharpest increase in atmospheric CO_2 levels in 20,000 years (Prentice et al. 2001). As a greenhouse gas (GHG), CO_2 in the atmosphere can influence the radiative balance between incoming solar radiation absorbed by the Earth and infrared radiation re-emitted by the Earth. Increasing concentrations of CO_2 and other minor GHGs (e.g. methane and carbon monoxide) can potentially cause warming of the Earth's surface. Resulting changes in global climate could alter ecosystems and impact human health and activities (IPCC 2001).

Carbon Sequestration

In the 1990's, fossil fuel combustion released an average of 7.9 ± 1.2 Gt C yr^{-1} to the atmosphere (Prentice et al. 2001) while the atmospheric C pool increased by 2.8-3.3 Gt C yr^{-1} (Fan et al. 1998; Prentice et al. 2001). The remaining C balance is thought to be sequestered by the terrestrial biosphere and oceans but the magnitude and location of the terrestrial sink is uncertain (Malhi et al. 1999). By studying the $^{13}C/^{12}C$ ratio in atmospheric CO_2, Ciais et al. (1995) estimated that the temperate latitudes of the northern hemisphere accounted for half of the fossil-fuel emissions in 1992-1993. Fan et al. (1998) used an inverse model to estimate a large North American terrestrial sink, 1.7 ± 0.5 Gt yr^{-}

[1], largely in the mid-latitudes, south of 51˚. While these studies suggest that the temperate latitudes of North America are responsible for a significant portion of the global C uptake, these indirect methods of evaluating the terrestrial C sink are limited and cannot accurately assess the magnitude of the sink. More knowledge of the C cycle in North American mid-latitude forests is needed to determine their current contribution to the global C sink and predict how the role of these forests in the global C cycle will change over time. The terrestrial uptake in North America has been ascribed largely to land-use changes, with 20-30% of vegetation growth attributable to recovery from previous harvests and afforestation of abandoned agricultural land (Houghton et al. 1999). It is unknown how the global C balance will be impacted when most of these forests have fully recovered. A study in a North American mid-latitude forest suggests that forest management can manipulate long-term C sequestration (Barford et al. 2001).

Forest C Balance

Net ecosystem exchange (NEE) is the balance of photosynthesis by plants and respiration by plants, animals and microbes; it is one way to represent the relative C flux between the atmosphere and terrestrial biosphere. Eddy covariance towers are commonly used to measure net exchange of CO_2 between the atmosphere and ecosystems including forest, shrubland and grassland (Baldocchi et al. 1988). This technique allows for sensitive yet non-invasive measurements of NEE that can be scaled over long time periods. However, because NEE represents the difference between two large fluxes, small errors in estimates of either flux can result in proportionally large errors in estimated NEE. Biometric measurements, including tree growth, litter fall and soil respiration, can also be used to estimate NEE, and are often used to verify NEE estimates from eddy

covariance towers. Microbial respiration from the decomposition of dead wood, or coarse woody debris (CWD), is rarely included in the suite of biometric measurements, resulting in overestimates of NEE. Coarse woody debris has been found to represent 25% of the total aboveground wood biomass and 10% of total C in forests (Bobiec 2002; Turner et al. 1995). A model of the forests of the conterminous United States estimated that CWD is the only C pool to consistently show net emissions (0.062 Gt yr^{-1}).

1.2 Previous Coarse Woody Debris Studies

Coarse Woody Debris

For the purposes of this study, CWD is defined as snags, logs and stumps greater than 10cm in diameter. Snags are standing wood (45-90˚ relative to the ground) while logs are downed wood (<45˚ relative to the ground) that can be elevated above, lying on or partially buried in the forest floor. CWD has long been recognized for its important function as a plant and animal habitat in the forest ecosystem. In addition, the transfer of nutrients from CWD to the forest floor during the decay process can influence forest productivity (Harmon et al. 1986).

Previous studies have focused on understanding the ecological role of CWD in maintaining diversity and productivity in the forest rather than its role in biogeochemistry. Furthermore, the majority of these studies have been conducted in the coniferous forests of the Pacific Northwest, USA. As a result, CWD stocks, mass loss rates and density loss rates have been well-characterized for these forests while CWD dynamics in other regions of the United States and the world are poorly understood.

The understanding of CWD dynamics across forest ecosystems is complicated by inconsistencies in the parameters of the studies. The definition of CWD varies in the lower diameter limit, hindering comparisons of CWD stock estimates. In addition, few inventories include buried CWD due to sampling difficulties. Moreover, decay classifications are not standardized for across species or regions, so decay rates based on decay classes cannot necessarily be compared.

Effect of Forest Management

The effect of forest management on CWD stocks and dynamics has been the focus of many studies. However, many of these studies have been conducted at clear-cut sites, where the canopy has been removed (Abbott and Crossley 1982; Edmonds et al. 1986; McCarthy and Bailey 1994; Tinker and Knight 2001; Pedlar et al. 2002) while few have been conducted at thinned or selectively cut sites. Thinning is the removal of only trees that would have succumbed through competition in order to maintain the forest canopy. Selective, or shelterwood, cutting is more intense than thinning but leaves parts of the canopy intact and is most common in the Northeast region of the United States. It is difficult to compare the effect of forest management across sites not only because of these differences in impact on the canopy but also because of differences in the treatment of slash, the woody debris left from harvesting.

Mass Loss and Density Loss Studies

Coarse woody debris dynamics are often described by mass loss and density loss measurements. These rates are estimated by chronosequences, which involve dating pieces of wood that have been decomposing for varying lengths of time. However, mass loss and density loss rates cannot be directly compared because they measure different

processes in decomposition. Furthermore, these rates are not direct measures of CWD respiration. The decomposition of CWD occurs through three major processes: respiration, fragmentation and leaching (Harmon et al. 1986). Decay rates estimated by mass loss are based on volume loss and density loss, and thus estimate decomposition through respiration and fragmentation (Mattson et al. 1987; Yin 1999). Fragmentation has been estimated to account for 5-35% of mass loss, causing decomposition rates to be overestimated (Mattson et al. 1987; Harmon and Hua 1991; Yin 1999). Density loss, on the other hand, includes leaching and respiration (Yin 1999). It is estimated that 90% of density loss is attributable to respiration while only two-thirds of mass loss is due to respiration (Mattson et al. 1987).

Efflux Studies

Few researchers have attempted to measure CWD respiration rates because of the challenges in making accurate measurements. The microbial communities that decompose CWD are highly sensitive to changes in temperature and wood moisture content (Rayner and Boddy 1988). Soda lime traps have been used for *in situ* measurements to avoid disturbing the microclimate of the CWD in the measurement process (Yoneda 1985; Mattson et al. 1987; Marra and Edmonds 1994; Marra and Edmonds 1996; Progar et al. 2000). In this method, chambers are attached to the CWD and the amount of CO_2 absorbed by soda lime in the chamber is measured. Because the chambers are permanently attached to the CWD, measurements can be repeated on the same samples so that seasonal trends in respiration rates can be observed. Despite these advantages in the soda lime method, it may not accurately measure CWD respiration. Ewel et al. (1987) found that when compared to a flow-through chamber coupled with an

infrared gas analyzer (IRGA), the soda lime method underestimated soil CO_2 efflux at high efflux rates. Also, measuring surface area of CWD precisely is difficult, therefore integrating efflux measured from the surface of the CWD over the entire piece is challenging.

An alternative to the soda lime method is the direct measurement of CWD respiration with an IRGA (Chambers et al. 2001; Wang et al. 2002). In this method, a wedge or cross-section is removed from a CWD sample and placed inside a closed dynamic chamber. Air is circulated from the chamber through the IRGA, which measures the instantaneous CO_2 concentration. The respiration rate is determined by the rate of change in CO_2 concentration of the chamber headspace air. While the IRGA can provide precise respiration measurements, this method involves destructive sampling that removes the CWD sample from its original microclimate. Moreover, cutting a wedge or cross-section from a CWD sample changes the surface area to volume ratio of the sample, with an unknown effect on respiration rates. It is possible that the increased surface area exposes more microbes to oxygen rich air, stimulating microbial activity and increasing respiration rates (Rayner and Boddy 1988). Chambers et al. (2001) recognized that cutting a sample wedge also exposes the void spaces that had previously trapped CO_2 and that time is needed for the wedge to outgas and equilibrate with the atmosphere. If the respiration from sample wedges is measured before they have reached equilibration, respiration rates will be overestimated.

These respiration studies have contributed valuable data on seasonal trends in CWD respiration rates, and factors controlling CWD respiration such as temperature, moisture content, species, diameter and decay class. However, they have were conducted

in the Pacific Northwest and the tropics, leaving northern hardwood forests poorly understood. Variation in climate and species composition across regions preclude large-scale extrapolations.

1.3 Factors Controlling Coarse Woody Debris Respiration

Coarse woody debris is decomposed by communities of bacteria, fungi and invertebrates that utilize dead wood for energy, nutrients and habitat, releasing CO_2 into the atmosphere. Forest management and climate change alter the microclimatic conditions for these organisms. An understanding of the factors controlling CWD respiration is therefore critical to describing the turnover of CWD and its contribution to the C cycle at the regional and global scale.

Temperature and Moisture Content

Temperature and moisture content are dominant, and interacting, factors in CWD decomposition (Abbott and Crossley 1982; Edmonds et al. 1986; Marra and Edmonds 1994). The relative importance of temperature and moisture content in influencing microbial activity is not well-established. Marra and Edmonds (1996) and Edmonds (1987) concluded from studies at a clear-cut site and a closed canopy forest in the Pacific Northwest that temperature was more important than moisture. Knohl et al. (2002) found a strong correlation between average year temperature and decay rate on a global scale. However, while higher temperature can enhance microbial activity, it also increases evaporation. Conversely, Chambers et al. (2001) concluded that moisture content is the most important factor for CWD decomposition. Moisture is essential for fungal growth (Rayner and Boddy 1988). Moss-covered logs have higher moisture content and mass

loss rates than logs with little or no cover (Laiho and Prescott 1999). Elevated wood has lower moisture content and mass loss rates than buried wood while wood lying on the forest floor is intermediate (Edmonds et al. 1986). In addition, Mattson et al. (1987) found that density loss rates were 40% higher for logs on the ground than those off.

Substrate temperature may play a separate role from air temperature but few studies have investigated this relationship. Wang et al. (2002) observed that substrate temperature was correlated to air temperature but the strength of the correlation depended on the canopy cover. Marra and Edmonds (1996) found that canopy removal had a large impact on the surface temperature of CWD; substrate temperature was 10-15˚ cooler 10cm into the wood than on the surface.

Seasonal Effects

Few studies have examined seasonal trends in respiration rates, and those were conducted in the Pacific Northwest. Marra and Edmonds (1994) found that temperature and moisture content strongly influence seasonal respiration rates. CWD respiration rates in the Pacific Northwest are lowest in the winter and highest in the summer (Marra and Edmonds 1994; Progar et al. 2000). Marra and Edmonds (1996) found that seasonal fluctuations are greater in clear-cuts than old-growth forest. More studies are needed to understand seasonal effects in other regions and in open canopy sites relative to closed canopy sites.

Species Effect

Substrate quality (i.e. C chemistry, nutrient content and wood structure) of CWD differs widely between species. These differences can translate through to different decay rates because of the ability of microbes to decompose the wood. Wood that is high in

lignin decays slowly because lignin is more difficult for microbes to digest than labile C, such as sugars and starches (Rayner and Boddy 1988). Also, some species contain extractives that are toxic to microbes, thus inhibiting decay (Rayner and Boddy 1988). Furthermore, the structure of the wood influences the ability of decomposers to invade the wood. For instance, angiosperms have vessels larger and more continuous than the tracheids of gymnosperms that are connected by pits (Harmon et al. 1986).

Some studies in the Pacific Northwest have found a species effect in decay rates (Erickson et al. 1985; Edmonds et al. 1986; Marra and Edmonds et al. 1996). However, all of these studies involve the comparison of Douglas-fir, which decays slowly, to other conifer species. In contrast, in the White Mountains of New Hampshire, the decay rates of red spruce and balsam fir are not significantly different (Foster and Lang 1982). One of the few studies comparing species other than conifers found that species effects account for most of the variation in wood-density loss in hardwood-hemlock, oak-hickory and hardwood-pine stands (Mattson et al. 1987). More studies are needed to understand how decay rates are influenced by substrate quality in species found in northern hardwood forests.

Decay Class Effect

Wood density is strongly correlated to respiration rates (Chambers et al. 2001). This relationship is likely driven by the negative correlation between density and moisture content (Chambers et al. 2001). As wood decays, void spaces are created, increasing the water capacity of the wood. In addition, while higher moisture content in decayed wood encourages microbial activity, decayed wood with low moisture content can have higher respiration rates than sound wood with similar moisture content (Rayner

and Boddy 1988). The phenomenon occurs because water availability to microbes is better described by water potential than moisture content.

Wood density cannot easily be measured in the field or in a non-destructive manner. Therefore, CWD is often classified by decay state based on visual observations in order to estimate the density of the CWD (Sollins et al. 1982). Naesset et al. (1999) found a significant correlation between relative density (the ratio of current density to freshwood density) and decay classes assigned in Norwegian forests. However, the study also noted variability in density within the cross-sections of CWD. Harmon et al. (1986) states that decay resistant species have more variability in decomposition within the wood. This raises the question of whether decay classifications based on characteristics of the outer layer of CWD can capture differences in density in species found in ecosystems outside of Norway.

Diameter Effect

Microbes and other decomposers invade CWD through the wood surface, implying that colonization is related to the surface area to volume ratio of CWD (Harmon et al. 1986). Coarse woody debris diameter can influence decay rate because surface area to volume ratio decreases with increasing CWD diameter. Many studies have found that woody debris less than 16cm in diameter exhibits a strong negative correlation between diameter and decay rate (Abbott and Crossley 1982; Yoneda 1985; Edmonds et al. 1986; Harmon et al. 1995). However, this relationship is not consistent throughout published literature (Erickson et al. 1985). Furthermore, while studies in the Pacific Northwest, where CWD can exceed 100cm in diameter, observe a strong negative correlation between diameter and decay rate (Graham and Cromack 1982; Marra and Edmonds 1994;

Marra and Edmonds 1996; Stone et al. 1998), a study in a northern hardwood forest did not detect a diameter effect on decay rate (Foster and Lang 1982). This difference may arise because CWD in northern hardwood forests rarely exceed 25cm (Currie and Nadelhoffer 2002). Diameter effects in mid-range diameters require further study in order to understand this relationship between surface area to volume ratio and diameter, and its influence on CWD decomposition.

1.3. Objectives

The overall objective of this study is to determine the effect of selective cutting on the C budget of a northern hardwood forest. This study presents a rare opportunity to study adjacent harvested and unharvested sites within the footprint of an eddy covariance tower. In addition, aboveground woody growth, soil respiration and detrital litter input, have been measured in permanent plots at both sites since 1998. These biometric measurements can be compared with NEE estimates from the eddy covariance tower but currently do not include directly measured respiration from decaying wood. This study will account for the missing respiration term through the measurement of respiration rates from CWD logs, ≥7.5cm diameter, and fine woody debris (FWD), 2cm≤ diameter <7.5cm, using the chamber-IRGA method. This will be accomplished by the following:

(1) A pilot test will be conducted to determine the time needed for cut CWD samples to equilibrate with atmospheric CO_2 and the effect of surface area to volume ratio on measured respiration rates.

(2) Respiration rates will be measured across seasons in order to observe the trend in respiration rates over a broad range of temperature and wood moisture content.

(3) The effects of air and sample temperatures, moisture content, density, site (i.e. canopy cover), genus (*Quercus, Acer, Betula* and conifers, which includes *Picea glauca, Tsuga canadensis, Pinus strobus,* and *Pinus resinosa*), decay class, and diameter will be investigated in order to create a model to predict respiration rates.

(4) Carbon flux per hectare and CWD decay rates will be compared between the harvest and unharvested sites in order to determine the effect of forest management on the CWD component of the C balance.

Methods

2.1 Study Sites

The study was conducted within the Prospect Hill Tract of the Harvard Forest and the Simmes Trust land, an adjacent privately-owned forest, near Petersham, Massachusetts (42º32' N, 72º11' W, elevation 340 m). The two sites are bisected by a dirt road and are within the measurement footprint of an eddy flux tower (Barford et al. 2001) near the southeast foot of Prospect Hill. The forest at Prospect Hill is 60-to-80 years old and dominated by red oak (*Quercus rubra*) and red maple (*Acer rubrum*), with scattered stands of hemlock (*Tsuga canadensis*), spruce (*Picea glauca*), and white and red pine (*Pinus strobus* and *Pinus resinosa*) (Goulden et al. 1996). The site contains 110.78 MgC ha^{-1} living biomass and 7.5 MgC ha^{-1} CWD biomass, with 2.0 MgC ha^{-1} in logs. The Simmes plot has a species composition similar to that of Prospect Hill but also includes a large beech component (18.9% total number of live trees after logging). The site was selectively logged from February 2001 to November 2001, with 42.8 m^3/ha of wood removed. The harvest decreased living biomass from 81 MgC ha^{-1} to 56.1 MgC ha^{-1} and increased CWD biomass from 10.52 MgC ha^{-1} to 21.98 MgC ha^{-1}. Specifically, log biomass increased from 3.55 MgC ha^{-1} to 10.22 MgC ha^{-1}.

2.2 Instrumentation

Two measurement chambers were used in this study to accommodate samples of different sizes and minimize turnover time of chamber headspace air. The chambers consisted of a 22.65L bucket and a 5.9L round Rubbermaid container with custom-made Plexiglass lids fitted with silicon o-rings to prevent leakage (Figure 2.1). The chamber

lids were sealed with 10kg weights. The chambers were connected to a LI-COR (Lincoln, NE) LI-6252 CO_2 Analyzer with 3 meters of PVC tubing attached to the lids with bulkhead fittings. An external in-line pump was used to circulate chamber headspace air through the closed loop at a rate of 1 L/min, regulated by a constant velocity flow meter. A wire rack was placed at the bottom of each chamber to allow air circulation around samples. To ensure that sample air was well-mixed, air was drawn out from the top of the chamber and pumped into the chamber through a ¼" brass tube extending from the lid to the bottom of the chamber. Output from the LI-COR was recorded every five seconds onto a laptop (Toshiba Portegé 300CT, Tokyo, Japan).

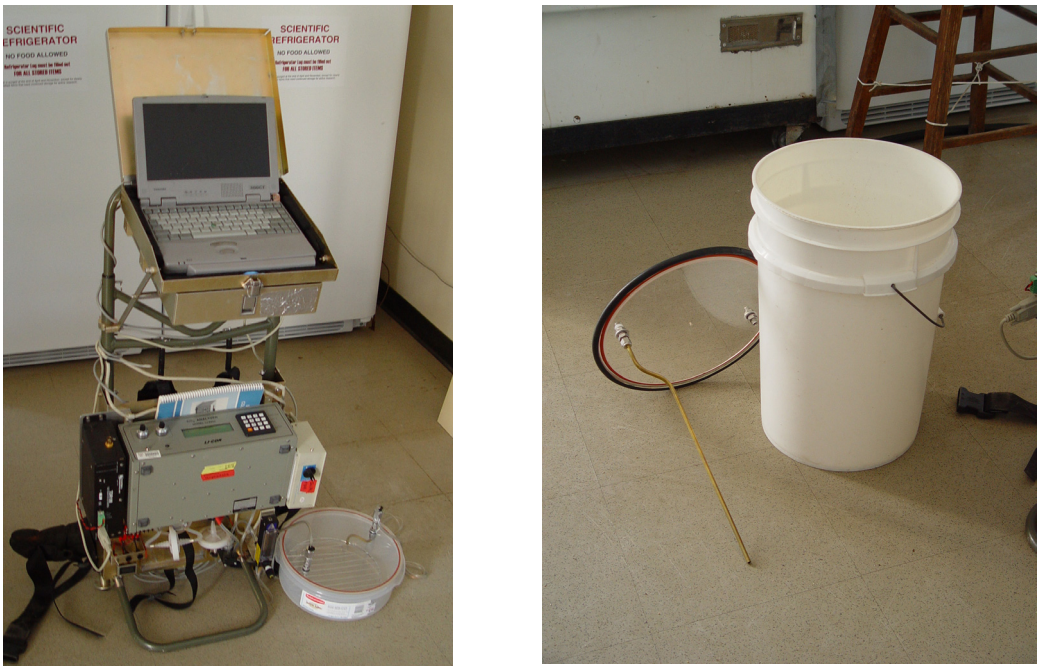

Figure 2.1. The small measurement chamber, IRGA-tubing system, and laptop (left). The large measurement chamber (right).

2.3 Field Methods

CWD Sample Pool

In July 2002, 500 logs, ≥10cm base diameter, at Prospect Hill and the Simmes plot were tagged and the location of each log was recorded with a handheld GPS unit (Garmin eTrex Legend, Romsey, Hampshire UK). Logs inside permanent research plots were not included because of the destructive sampling method of this study. Each sample log was tagged and categorized by genus, decay class and diameter (Figure 2.2). This CWD sample pool resulted in a distribution of samples throughout the two sites (Figure 2.3).

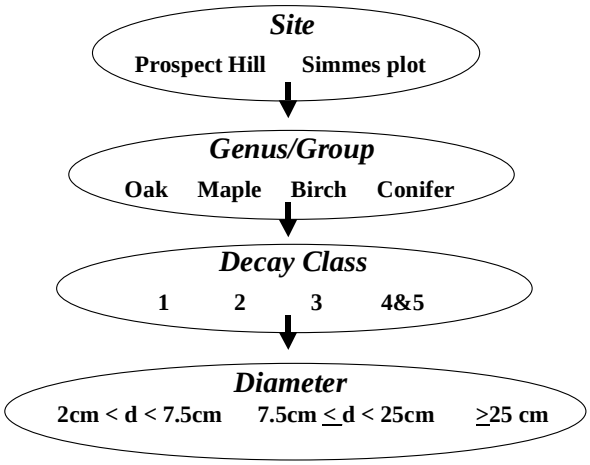

Figure 2.2. Sampling was stratified by Site x Genus x Decay Class x Diameter.

Decay state was determined by a five-decay-class system based on visual and physical characteristics (Harmon and Sexton 1996) (Table 2.1). Because logs of decay classes 4 and 5 were scarce at the Simmes plot (10.0% total number of logs), the two classes were combined to ensure a sufficient sample size for comparison with the Prospect Hill site.

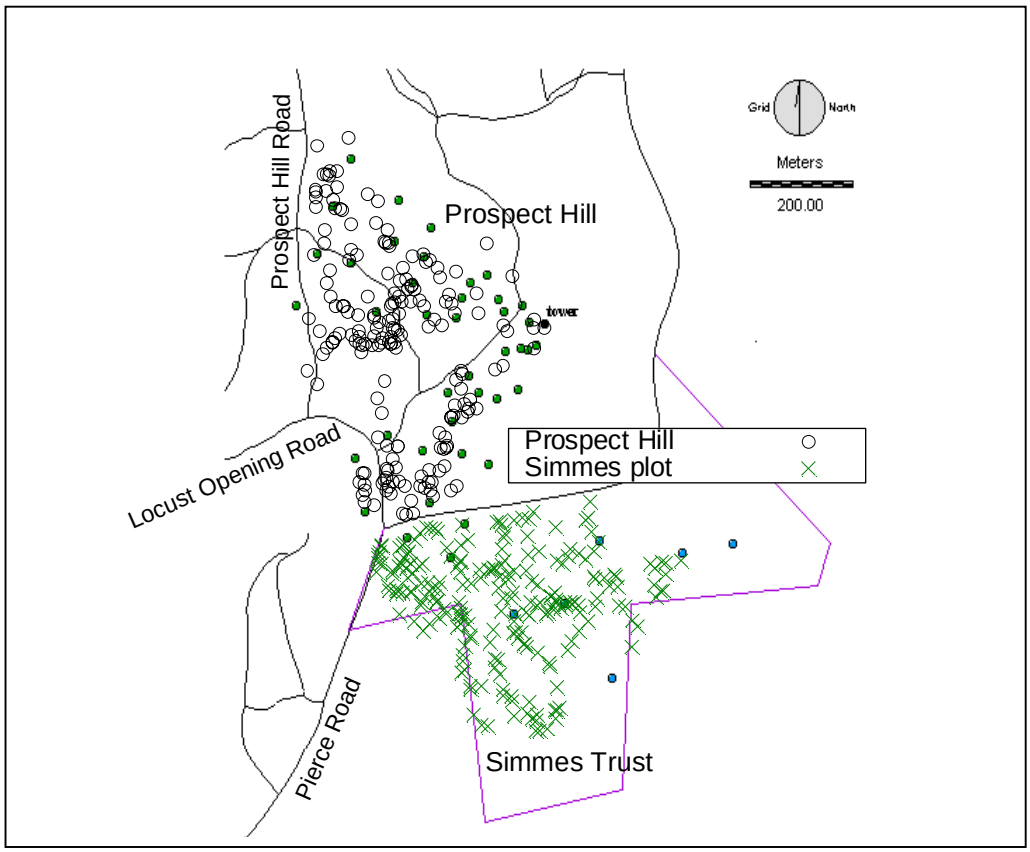

Figure 2.3. Map of Prospect Hill and the Simmes plot (NOTE: The boundary drawn around the Simmes plot was the planned boundary for harvesting and is not indicative of the actual harvest area which was 42 ha.). The solid green circles mark the location of permanent plots (radius=10m) in the EMS tower footprint on Prospect Hill. The solid blue circles mark the location of permanent plots (radius=15m) in the Simmes plot. Open circles mark tagged logs at Prospect Hill and green X's mark tagged logs at the Simmes plot.

Decay Class	**Physical Characteristics**
1	solid wood, recently fallen, bark and twigs present
2	solid wood, significant weathering, branches present
3	wood not solid, bark may be sloughing but nail still must be pounded into log
4	wood sloughing and/or friable, nail may be forcibly pushed into log
5	wood friable, barely holding shape, nail may be easily pushed into log

Table 2.1. Physical characteristics used to determine the decay class of logs according to a five-class system.

CWD was divided into three diameter classes—2cm ≤ d < 7.5cm, 7.5cm ≤ d < 25cm, and d ≥25cm. While only logs, ≥10cm base diameter, were tagged, often samples were not cut from the base of the logs, resulting in samples less than 10cm in diameter. The 7.5cm breakpoint was based on classifications used in the CWD inventories at both sites completed in 1999 and 2001 and used later in this study. The 25cm breakpoint for the large diameter logs is consistent with diameter classes used in other studies in northern hardwood forests (Foster and Lang 1982; Duvall and Grigal 1999; McGee et al. 1999). Fine woody debris was not tagged but was sampled from locations throughout both sites. Small diameter CWD is very difficult to identify to genus; therefore, it was only categorized by decay class.

Pilot Test

A pilot test was conducted in July 2002 to determine (1) the chamber mixing time, (2) the time needed for cut samples to outgas and re-equilibrate with the atmosphere, and (3) the effect of surface area to volume ratio on CWD respiration rates.

Pilot samples were randomly chosen from the tagged CWD pool. If a tagged log could not be relocated, it was replaced by a nearby log of the same subcategory. A chainsaw was used to cut 30-40cm wide samples either from the middle of the logs or others section of the logs, depending on the safest position for the chainsaw operator. If a sample was cut from the end of the log, two cuts were made so that the sample had two newly exposed surfaces. A 6mm hole was drilled into each sample so that a temperature probe could be inserted. Within 15 minutes after cutting, the sample and air temperatures were recorded, and the sample was placed inside the measurement chamber. Samples too large to fit into the large chamber were split into halves or quarters with a machete. CO_2

concentration in the chamber headspace was measured with the LI-COR and recorded every 5 seconds for 8 minutes. The sample was then transported to the laboratory approximately 1km away from the study sites, and the measurement procedure was repeated four more times, at approximately 45, 90, 120 and 180 minutes after cutting.

Measurements occurred outside or in a greenhouse to minimize sample temperature changes during measurement. Between measurements, samples were placed in the shade outside the laboratory to expose the samples to ambient CO_2 concentrations and temperature while preventing solar heating. In inclement weather, samples were moved to a greenhouse to prevent significant changes in moisture content. If IRGA battery failure or fuse problems prevented a sample from being measured for more than 12 hours, the sample was sealed in a plastic bag to prevent moisture loss and stored in the laboratory.

After the first set of flux measurements on a sample, it was cut in half with a handsaw to increase the surface area of the sample without significantly changing the volume or mass. The sample was weighed immediately before and after the cutting to account for the mass lost to sawdust. The three-hour measurement regime was then repeated for the sample. After the second set of measurements, the two halves of the sample were again cut in half with a handsaw, and the three-hour measurement regime was repeated.

This procedure was performed on nine pilot samples. For the remaining 39 pilot samples, the measurement regime was reduced to only one measurement at least three hours after each cut.

Summer Sampling

The summer sampling was performed July 12, 2002 through October 8, 2002, and included the pilot test samples. Samples were randomly chosen from the tagged pool so that there were three replicates per subcategory. However, some subcategories contained fewer than three replicates because of the sample distribution.

Three to ten centimeter thick cross-sectional disks were used in summer sampling and thereafter. Pilot test methods were used in the summer sampling except samples were measured once (at least three hours after cutting), and not subject to subsequent cuts.

Fall Sampling

The fall sampling was performed November 9, 2002 through December 2, 2002. Because summer sampling results showed no significant differences in respiration rates, density and moisture content between decay class 1 and 2 (respiration rates, df=97, p=0.32; density, df=97, p=0.19; moisture content, df=97, p=0.78), the two classes were combined for the fall sampling. Early snowfall required abbreviation of the fall sampling schedule, resulting in fewer than three samples being collected for many subcategories.

Winter Sampling

Winter sampling was performed January 12-19, 2003. Because snow cover impeded the location of logs and respiration rates were expected to be close to zero, the sampling objective was reduced to characterizing CWD respiration rates in the winter temperature regime without factors (i.e. genus, decay class, diameter). Six samples were collected from each study site to achieve this objective.

2.4 Calculations

Density and Moisture Content

The wet weight of a sample was measured immediately after the sample was removed from the measurement chamber. Within three weeks, the volume of the sample was measured by water displacement (Naesset 1999). The sample was then oven-dried at 105˚ C to constant weight. Density was calculated from the dry weight and volume. Moisture content was calculated gravimetrically (g H_2O g^{-1} oven dry wood).

Respiration Rates

Respiration rates (μg C g^{-1} C s^{-1}) were calculated from the chamber volume and the rate of CO_2 accumulation in the chamber headspace air. The respiration rates were standardized using measured air temperature and pressure obtained from the Shaler meteorological observation station at Harvard Forest.

CWD Biomass per Area

Biomass of CWD per hectare (MgC ha^{-1}) at each site was calculated by taking the product of volume per hectare and mean empirical densities by subcategory. Fifty percent carbon content in the wood was assumed. CWD inventories were used to determine the volume of CWD per hectare at both study sites.

An inventory in 1999 accounted for all logs, snags and stumps, ≥7.5cm diameter, in 27 of the 34 permanent plots at Prospect Hill and all nine permanent plots at the Simmes plot. Species, decay class, base-, mid- and top-diameter, length and percentage bark cover were recorded for each piece of CWD. In 2001, following logging, the Simmes plot was resurveyed using the same size and decay classifications. An allometric equation from Harmon and Sexton (1996) was used to calculate the volume of logs (m^3) at each site (Equation 2.1).

$$\text{Volume} = \text{Length} * (\text{Base Area} + (4 * \text{Middle Area}) + \text{Top Area}) / 6 \qquad (2.1)$$

In 2001, the line-intersect method (Brown 1964, Van Wagner 1968) was used to inventory FWD, 2cm ≤ diameter < 7.5cm, at both sites. According to this method, FWD was inventoried if it crossed a randomly chosen section of a randomly placed transect line. The diameter and decay class at the exact point that the FWD crossed the line was recorded. If the FWD crossed the line twice, information from both intersection points was recorded as separate entries. Twenty-six 10m long sections from two transect lines at Prospect Hill and twenty-six 10m long sections from four transect lines at the Simmes plot were randomly chosen for the inventory, totaling 260m of transect line sampled at each site. The line-intersect expansion formula was used to calculate the volume of CWD per hectare (m^3 m^{-2}) (Van Wagner 1968) (Equation 2.2).

$$\text{Volume} = (\pi^2 \Sigma \text{diameter}^2) / (8 * \text{Length}) \qquad (2.2)$$

Carbon Flux per Hectare

Annual carbon flux per hectare (MgC ha^{-1} yr^{-1}) was calculated by taking the product of CWD biomass per hectare and mean respiration rates by subcategory, and then extrapolating to the annual time scale. Because spring season data was not available, this was done using two methods, one based on a two-season year and another based on a three-season year. The difference in the methods is in the subcategories used to calculate mean respiration rates and the weight of each season in the annual C flux. Because FWD was inventoried separately from CWD and was only categorized by decay class, C flux was calculated separately for FWD and CWD.

The two-season method is based on a six-month growing season, characterized by the summer data, and a six-month dormant season, characterized by the fall and winter

data. Because respiration rates were different between Prospect Hill and the Simmes plot during the summer ($p=0.02$), the mean respiration rates were calculated separately for the two sites. In the fall and winter, respiration rates were not different between the two sites ($p=0.17$) and early snowfall resulted in small sample sizes for each site (Prospect Hill, N=70; Simmes plot, N=43), so data from the two sites were pooled to calculate mean respiration rates. Subcategories by genus and decay class were used for both seasons. However, because decay class 1 and 2 were combined in the fall and winter samplings, a three-decay class system was used for the dormant season while a four-decay class system was used for the growing season. Because hardwood species other than those sampled in this study were included in the CWD inventory, maple, oak and birch data were pooled to produce mean respiration rates for hardwoods. In addition, the CWD inventory included CWD that could not be identified to species or genus. Mean respiration rates across all genera were used to characterize the unidentified CWD.

The three-season method is based on summer, fall and winter each accounting for one-third of the year. The calculation of mean respiration rates is similar to that for the two-season method except winter data is separated from fall data. Because the winter sample size was small (N=12) and the winter respiration rates were close to zero for a range of genera and decay classes at both sites, a single mean respiration rate was calculated from all winter data to characterize all CWD.

Fine woody debris was not sampled at the Simmes plot during the summer so two methods for estimation of respiration rates were applied. First, mean summer respiration rates from FWD at Prospect Hill were directly applied to Simmes plot biomass per hectare to calculate C flux per hectare. However, given that the respiration rates of larger

diameter CWD (≥7.5cm diameter) differed between the two sites during the summer (, it is likely that they also differed for FWD. This difference is accounted for in the second method which relies on a model created from a multiple linear regression to predict the summer respiration rates for FWD at the Simmes plot. This model was created from all summer data with site, diameter class and decay class as parameters.

The decay rate of CWD due to respiration was calculated for each site by dividing the total C flux per hectare by total biomass per hectare. This effectively weights the decay rates of each subcategory (genus x decay class) by their representation at each site.

Modeling C Flux

A multiple linear regression model was created from Prospect Hill data to predict respiration rates. Regressions were run with log-transformed respiration rates in order to determine the relative significance of the regression coefficients for various parameters. The parameters of the models were chosen to optimize the fit. A model including the optimal parameters was then created using un-transformed respiration rates because back-transformation of log-transformed predicted values involves subtleties that make the back-transformation prone to error. The model was tested using Simmes plot respiration rates and comparing the predicted values to observed rates.

Statistical Analyses

Statistical analyses were carried out using the MathSoft (Seattle, WA) S-Plus 6.2 statistical software package. Respiration rates were natural log-transformed for all analyses to meet normality assumptions for analysis of variance (ANOVA), student's t-test and linear regression. Orthogonal distance regressions were used to compare the respiration rates of the three cuts in the pilot test because error was associated with both

the independent and dependent variables. The errors for the orthogonal distance regression coefficients were obtained by bootstrapping the respiration rates for each cut with replacement. One-way ANOVAs were used to determine if genus, decay class and diameter class had effects on respiration rates, wood moisture content and wood density. F-statistic values greater than 4.0 were regarded as a significant. Student t-test's were used to perform pairwise comparisons of respiration rates, air temperature, wood moisture content and wood density between sites, genera, decay classes and diameter classes. P-values less than 0.05 were regarded as significant and p-values between 0.05 and 0.10 were marginally significant differences.

Error in volume per hectare were calculated by bootstrapping volume in each sample plot for the CWD inventory and volume per area in each line segment for the FWD inventory. Standard error calculations were used for wood density, wood moisture content and respiration rates. Error in biomass per hectare was estimated by taking the root mean square of the error in volume per hectare and the error in mean wood density by subcategory. Error in C flux per hectare was estimated by taking the root mean square of the error in biomass per hectare and the error in mean respiration rates.

Results

3.1 Pilot Test

Measurement Interval

Time series graphs of CO_2 concentration in the measurement chamber for each pilot sample show that chamber headspace air mixed within three minutes in the large chamber (Figure 3.1). The small measurement chamber was not used in the pilot test but similar graphs for samples measured in the small chamber later in the study show that three minutes is also an adequate mixing time for the small chamber (Figure 3.2).

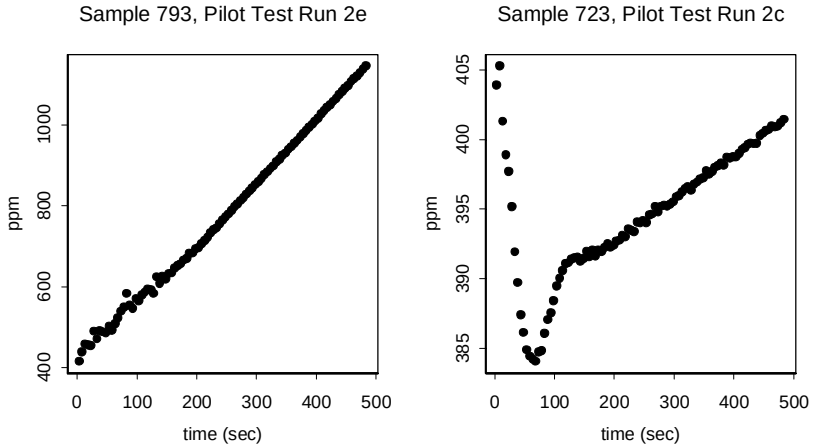

Figure 3.1. CO_2 concentration during the 8-minute measurement in the large chamber. Linear least squares regressions of the last two minutes of the measurements were used to calculate respiration rates.

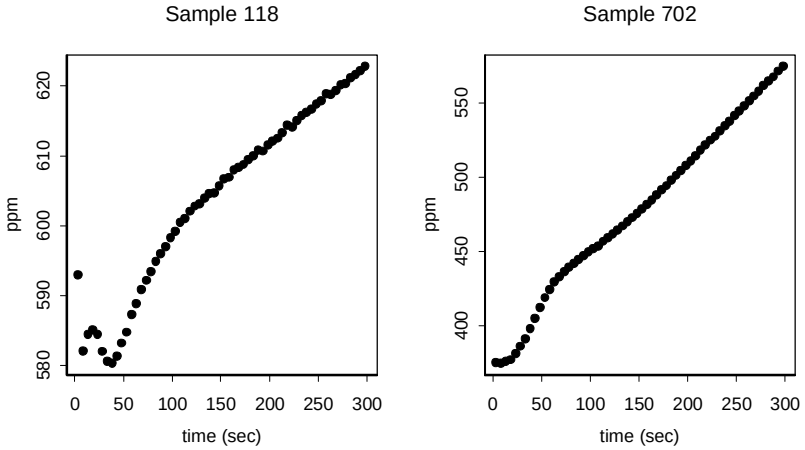

Figure 3.2. CO_2 concentration during the 5-minute measurement in the small chamber. Linear least squares regressions of the last two minutes of the measurements were used to calculate respiration rates.

Linear least squares regressions were used to determine the rate of CO_2 accumulation in the measurement chamber. Regression coefficients calculated from three measurement intervals—minutes 3-8, 6-8, and 6-7.5 within the 8-minute measurement for the large chamber—were compared to find the optimal measurement interval. Pairwise comparisons showed no difference between the regression coefficients derived from the three intervals (Table 3.1). Minutes 6-8 were selected as the measurement interval for samples measured in the large chamber to ensure adequate mixing. For measurements in the small chamber, regression coefficients calculated from minutes 3-5 and 3-4.5 were not significantly different (df=432, p=0.98). Minutes 3-5, the last two minutes of the measurement, were chosen as the measurement interval for samples measured in the small chamber for consistency with the large chamber measurement interval.

Large Chamber (df=352)	**Minutes 6-8**	**Minutes 6-7.5**
Minutes 3-8	p=0.85	p=0.83
Minutes 6-8	---	p=0.99

Table 3.1. Results from student's t-tests used to compare regression coefficients calculated from different measurement intervals from the 8-minute measurement in the large chamber.

Equilibration Time

The respiration rate of nine samples was measured four to five times within three hours after each of three cuts ("first cut"=whole log, "second cut"=two pieces, "third cut"=four pieces). Each respiration rate was calculated from an 8-minute measurement in the large measurement chamber after which the sample was removed from the chamber. The respiration rate calculated from the first measurement after a cut was excluded from analysis as an artifact of heating from the saw and rapid outgassing from newly exposed

pores. Figure 3.3 shows the respiration rates over the entire measurement series for each sample. Bootstrapping the set of measurements for each cut showed that respiration rates were not significantly different between sets for most samples (Figure 3.4). This suggests that the effects of cutting the samples were short-lived and samples equilibrated with the atmosphere within one hour.

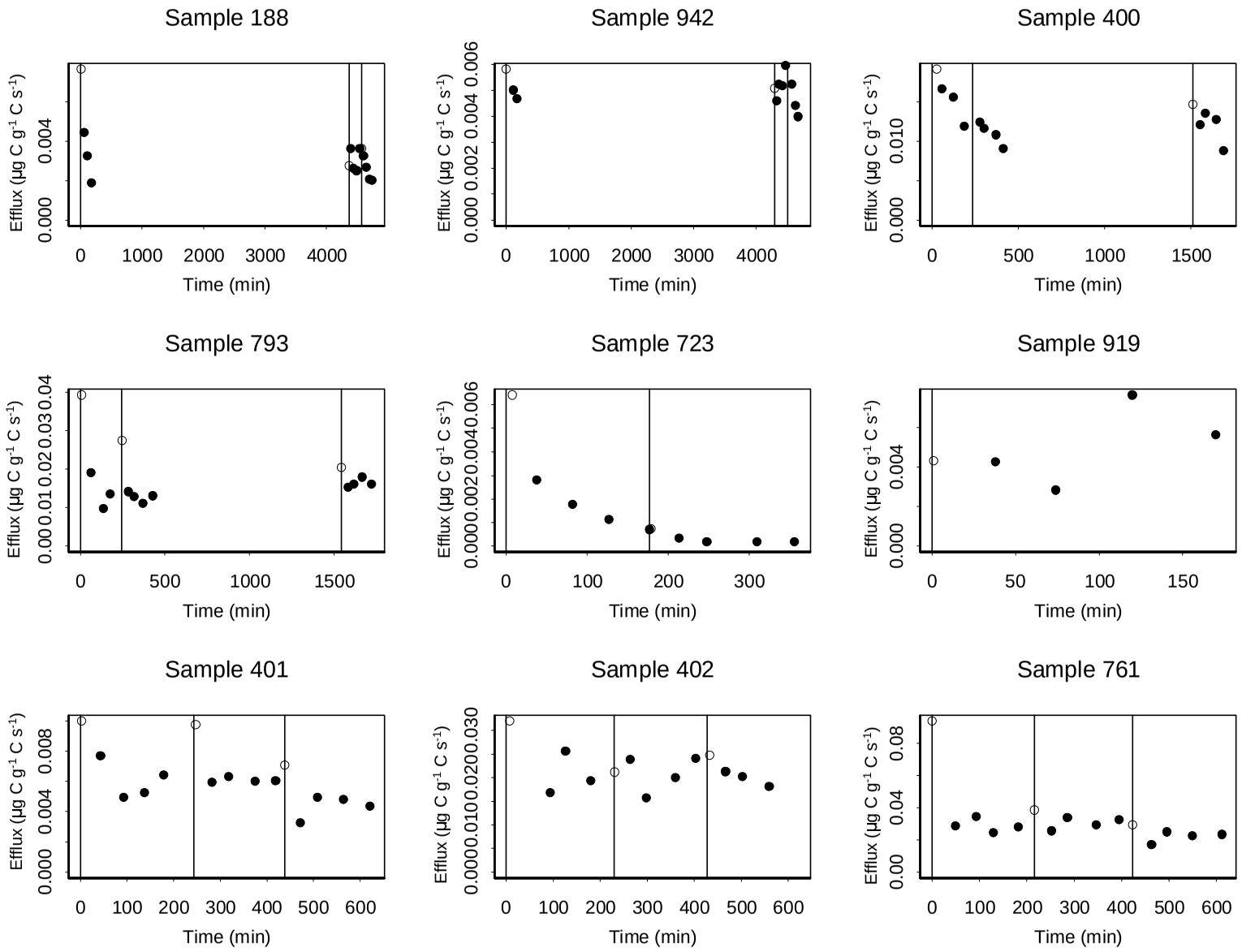

Figure 3.3. Respiration rate (µg C g^{-1} C s^{-1}) of nine pilot test samples over the entire measurement series. Each measurement point represents the respiration rate calculated from the last two minutes of an 8-minute measurement in the large chamber. Vertical lines mark the time that a sample was cut. Open circles denote the first measurement after a sample was cut. This measurement was excluded from analysis as an artifact from cutting. Closed circles denote measurements that were used in analysis. NOTE: Sample 919 was a high decay-class log so was cut only once.

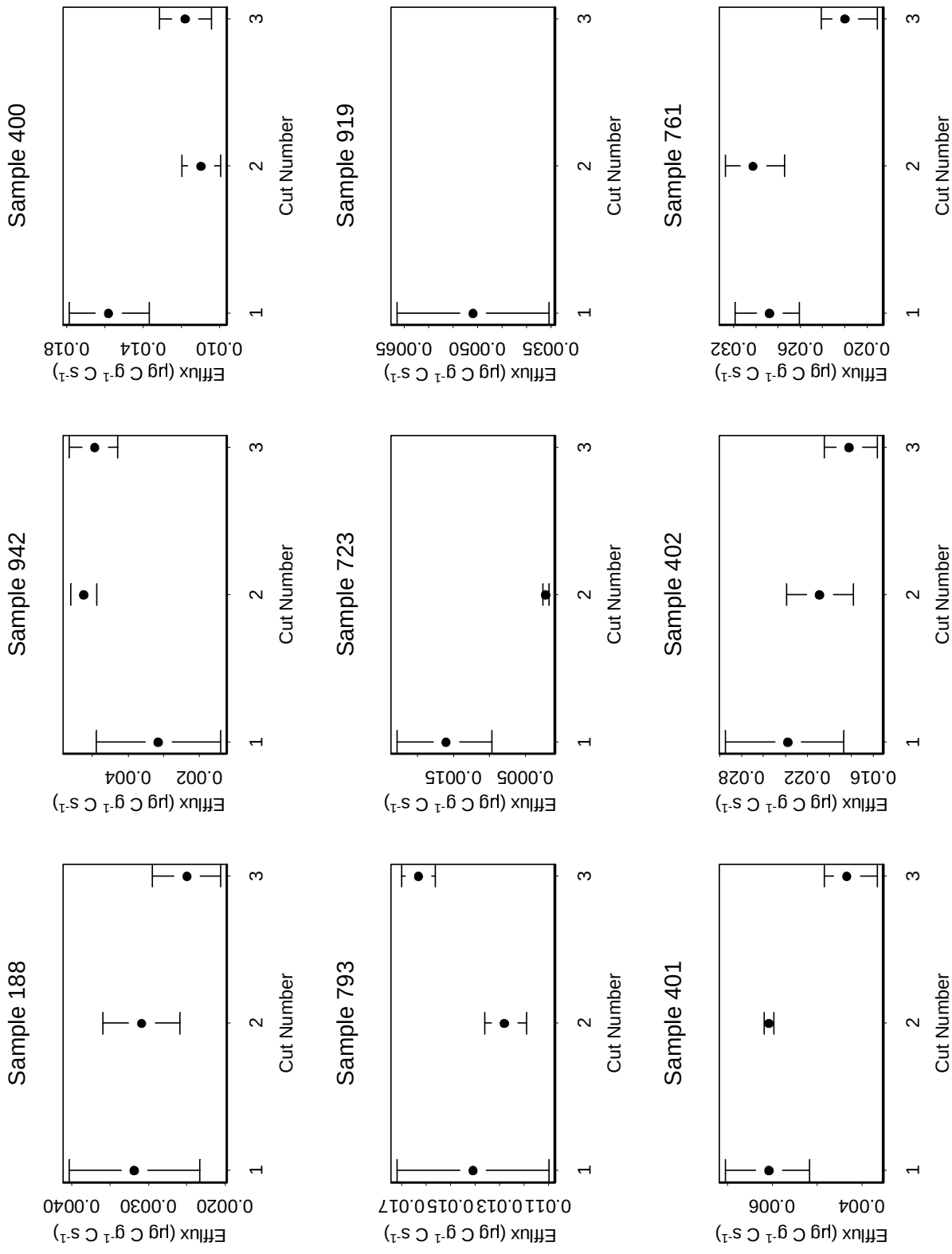

Figure 3.4. Results of bootstrapping respiration rates within each cut series for each sample. Error bars show 90% confidence intervals. NOTE: Sample 919 was a high decay-class log so was cut only once.

Surface Area to Volume Ratio

Respiration rates for each cut were affected by changes in air temperature and wood moisture content over the course of the day, and mass lost to sawdust from cutting. Samples were cut and measured at similar times of day so that air temperature was similar within each of the three cuts. Table 3.2 shows the mean and standard deviation of air temperature during each cut.

	Mean Air Temperature (°C)
First Cut	27.4 (0.31)
Second Cut	25.6 (0.35)
Third Cut	22.3 (0.22)

Table 3.2. Mean (SE) air temperature (°C) for each of the three cuts in the pilot test.

Pilot samples lost an average of 3.8 ± 0.6% of wood moisture content in the time between the first cut and second cut measurements, and an average of 9.1 ± 0.7% between first cut and third cut measurements. In addition, an average of 26 ± 3 g (wet wood) was lost as sawdust from the samples when the second cut was performed, and an additional 43 ± 4 g (wet wood) was lost when the third cut was performed. This was taken into account when calculating respiration rates by estimating dry mass lost to sawdust from the wet mass and the moisture content at the time of cutting. A multiple linear regression of log-transformed respiration rates on air temperature, moisture content and the interaction of air temperature and moisture content, weighted by the inverse of the standard error in the respiration rates, was used to create a model to correct for the differences in air temperature and moisture content. Table 3.3 shows the regression coefficients of the model.

Variable	Regression coefficient	Standard Error of Coefficient	P-value of Coefficient
(Intercept)	-7.7633	0.1968	~0
T	0.0605	0.0105	~0
M	0.3447	0.1165	0.0033
T x M	0.0154	0.0069	0.0257

Table 3.3. Regression coefficients, and standard error and p-value of coefficients from a multiple linear regression model of log-transformed respiration rates (μg C g^{-1} C s^{-1}) used to correct the pilot test respiration rates. T is air temperature (°C), M is moisture content (g H_2O g^{-1} dry wood) and T x M is the interaction of air temperature and moisture content.

Orthogonal distance regressions were used to perform pairwise comparisons of the residuals from the model for each of the three cuts (Figure 3.5. The results of bootstrapping the residuals for each cut show that the respiration rates of the second cut are not significantly different from the first cut (Table 3.4). However, the respiration rates of the third cut are significantly lower than those of the first and second cuts (Table 3.4). This 4-33% decrease in respiration rates is likely an artifact from cutting the samples.

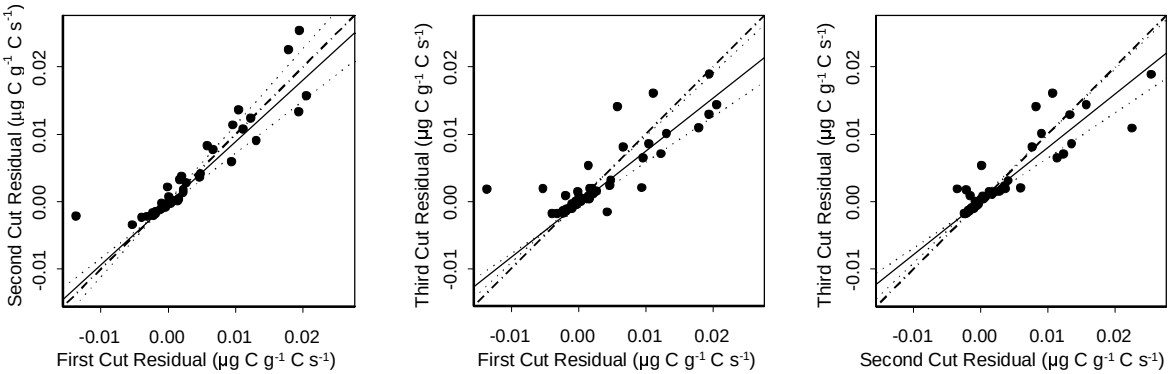

Figure 3.5 Comparison of residuals from a multiple linear regression model correcting for air temperature and moisture content differences of the three cuts in the pilot test. Solid lines represent regression lines calculated from orthogonal distance regressions. Dotted lines represent the 90% confidence bounds. Segmented lines are 1:1 lines. (a) An orthogonal distance regression of corrected second cut respiration rates on corrected first cut respiration rates predicts Log (Y) = 0.92 x – 0.0002. (b) An orthogonal distance regression of corrected third cut respiration rates on corrected first cut respiration rates predicts Log (Y) = 0.79 x – 0.0004. (c) An orthogonal distance regression of corrected third cut respiration rates on corrected second cut respiration rates predicts Log (Y) = 0.79 x + 0.0001.

	90% Confidence Interval
Second Cut v. First Cut	0.78 – 1.13
Third Cut v. First Cut	0.68 – 0.94
Third Cut v. Second Cut	0.67 – 0.96

Table 3.4. Ninety-percent confidence intervals for regression coefficient estimated by bootstraps of respiration rates for each cut.

3.2. Factors Controlling CWD Respiration

Moisture Content, Temperature and Density

Sample temperature was strongly correlated to air temperature (R^2=0.97, p~0) so air temperature was used in analysis. Respiration rates increased with air temperature (R^2=0.16, p~0) (Figure 3.6). Because the relationship appears logarithmic, respiration rates were log-transformed to meet the linear relationship assumption of linear least squares regressions (R^2=0.22, p~0) (Figure 3.7). Figure 3.6 shows that above 20° C, higher decay classes have higher respiration rates than lower decay classes. In addition, Figure 3.7 suggests that, in general, respiration rates were higher for decay classes 4 and 5 than for the lower decay classes.

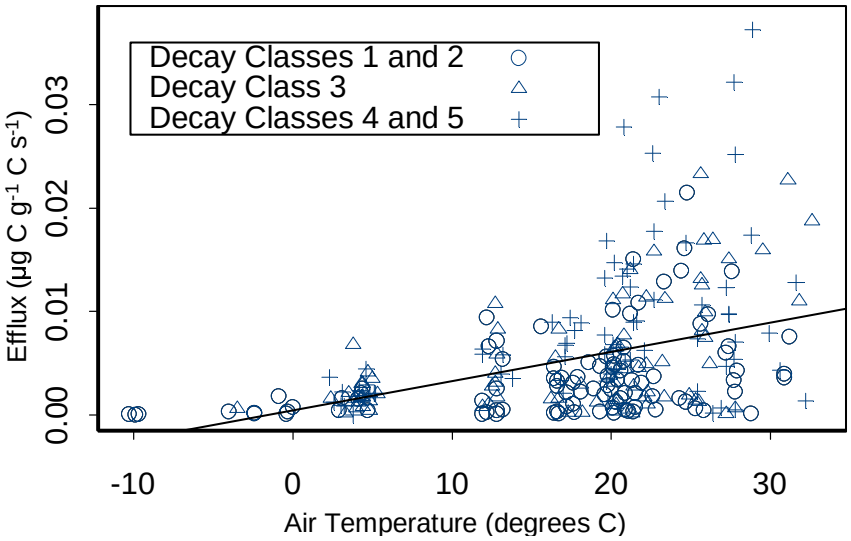

Figure 3.6. A linear least squares regression of respiration rates (µg C g^{-1} C s^{-1}) on air temperature (°C) predicts y = 0.0003 x + 0.0004 (N=308, R^2=0.16, p~0). Symbols represent CWD of different decay classes in a three-class system.

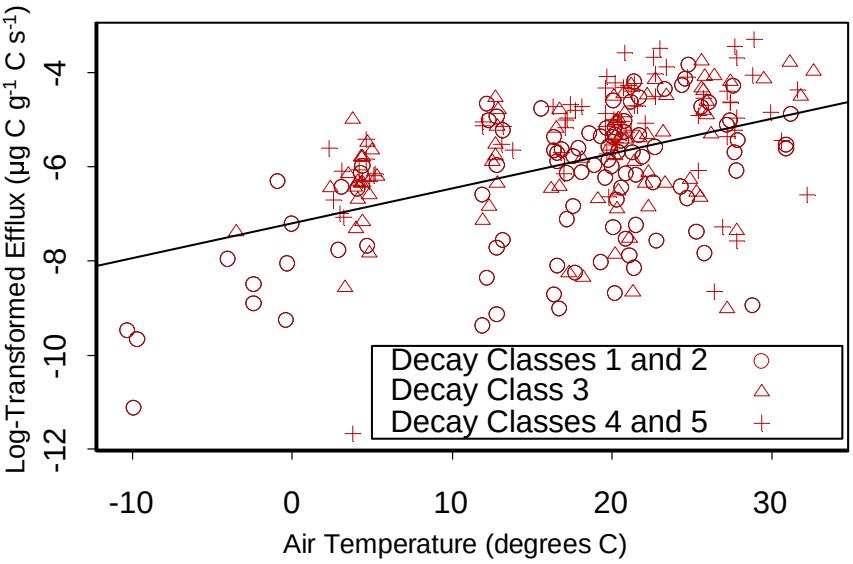

Figure 3.7. A linear least squares regression of log-transformed respiration rates (µg C g^{-1} C s^{-1}) on air temperature (°C) predicts y = 0.074 x – 7.19 (N=308, R^2=0.22, p~0). Symbols represent CWD of different decay classes in a three-class system.

Respiration rates increased with moisture content (R^2=0.09, p~0) (Figure 3.8a), but because the relationship was logarithmic, a linear least squares regression was also performed with log-transformed respiration rates (R^2=0.12, p~0) (Figure 3.8b).

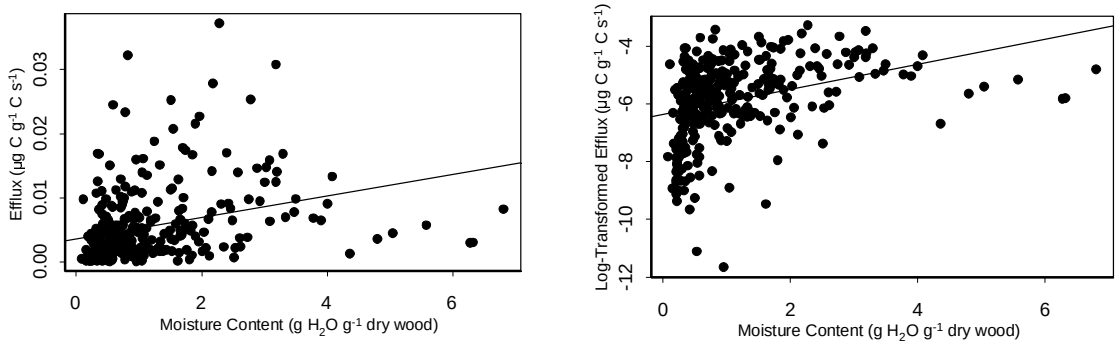

Figure 3.8. (a) A linear least squares regression of respiration rates (µg C g^{-1} C s^{-1}) on wood moisture content (g H_2O g^{-1} dry wood) predicts y = 0.0035 x + 0.0017 (N=304, R^2=0.09, p~0). (b) A linear least squares regression of log-transformed respiration rates (µg C g^{-1} C s^{-1}) on wood moisture content (g H_2O g^{-1} dry wood) predicts Log (Y) = 0.43x – 6.37 (N=304, R^2=0.12, p~0).

A linear least squares regression indicates that respiration rates decreased with wood density (R^2=0.19, p~0) (Figure 3.9a). The regression was also performed with log-

transformed respiration rates in order to create a linear relationship between the two variables (R^2=0.17, p~0) (Figure 3.9b). Wood moisture content and density were negatively correlated (R^2=0.41, p~0) (Figure 3.10).

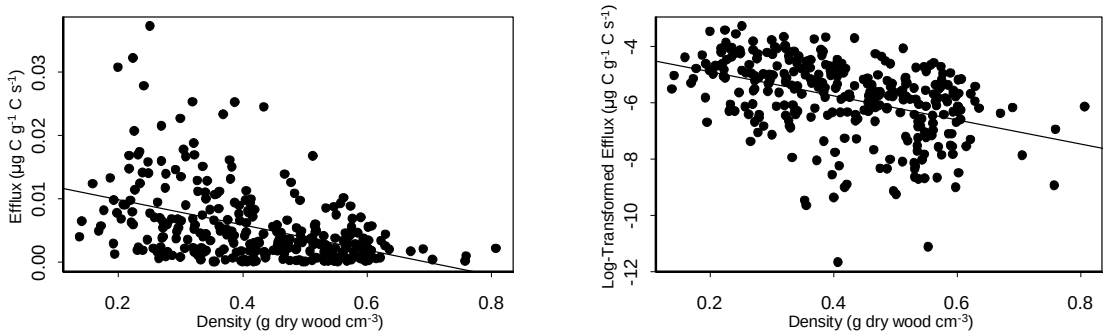

Figure 3.9. (a) A linear least squares regression of respiration rates (µg C g^{-1} C s^{-1}) on wood density (g dry wood cm^{-3}) predicts y = -0.0199 x + 0.0139 (N=307, R^2=0.19, p~0). (b) A linear least squares regression of log-transformed respiration rates (µg C g^{-1} C s^{-1}) on wood density (g dry wood cm^{-3}) predicts Log (Y) = -4.27x – 4.06 (N=307, R^2=0.17, p~0).

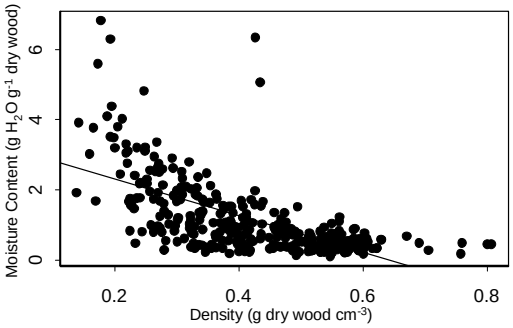

Figure 3.10. A linear least squares regression of moisture content (g H_2O g^{-1} dry wood) on density (g dry wood cm^{-3}) predicts y = -5.54 x + 3.36 (N=315, R^2=0.41, p~0).

Seasonal Effects

Respiration rates and air temperature decreased from summer through winter (Figures 3.11 and 3.12). Moisture content increased between summer and fall at Prospect Hill but was not different between seasons at the Simmes plot (Prospect Hill, p=0.03; Simmes Plot, p=0.89) (Figure 3.13). Moisture content did not differ between fall and winter at either site (Prospect Hill, p=0.76; Simmes Plot, p=0.29).

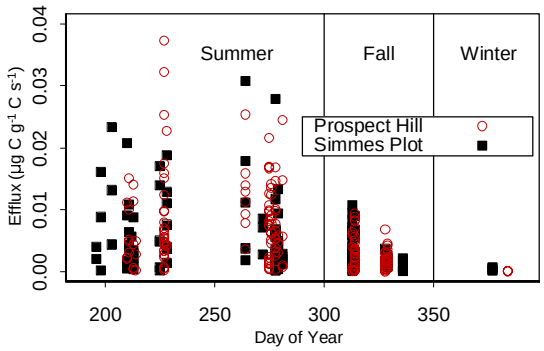

Figure 3.11. Respiration rates at Prospect Hill and the Simmes Plot from July through January.

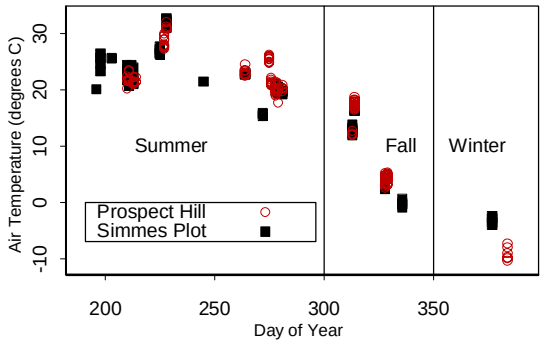

Figure 3.12. Air temperature at time of measurement for samples from Prospect Hill and the Simmes Plot from July through January.

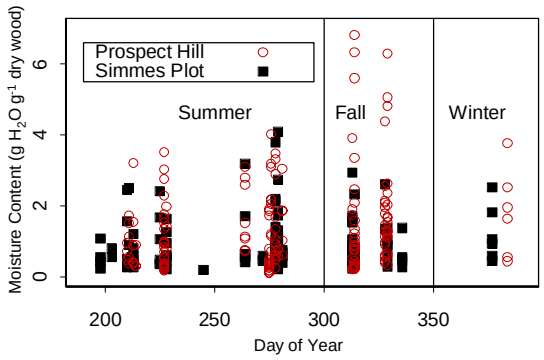

Figure 3.13. Moisture content at Prospect Hill and the Simmes Plot from July through January.

Site Effect

During the summer, air temperature, sample temperature and wood moisture content were significantly different between the two sites (air temperature, p=0.002; sample

temperature, p=0.03; moisture content, p=0.05) (Table 3.5a). Because air and sample temperatures were measured immediately before the respiration measurement, which occurred by the laboratory, they are not representative of temperatures at the two sites but are representative only of temperatures at the time of measurement. During the fall, wood moisture content was significantly different between the two sites while air temperature and sample temperature were not different (moisture content, p=0.01; air temperature, p=0.60; sample temperature, p=0.82) (Table 3.5b).

(a)

Summer	**df**	**Prospect Hill, $\bar{x}$**	**Simmes Plot, $\bar{y}$**	**t-test p-value**
Air temperature	198	24.0 (0.32)	22.4 (0.37)	0.0015
Sample temperature	193	22.7 (0.36)	21.4 (0.46)	0.027
Moisture content	192	1.16 (0.09)	0.90 (0.08)	0.0461

(b)

Fall	**df**	**Prospect Hill, $\bar{x}$**	**Simmes Plot, $\bar{y}$**	**t-test p-value**
Air temperature	111	10.7 (0.75)	10.1 (0.83)	0.5999
Sample temperature	111	9.4 (0.79)	9.2 (0.81)	0.8217
Moisture content	109	1.59 (0.19)	0.92 (0.10)	0.01

Table 3.5. Results of student's t-tests used to compare air temperature (°C), sample temperature (°C) and moisture content (g H_2O g^{-1} dry wood) between Prospect Hill and the Simmes plot for summer and fall. The standard error is given in parentheses.

Respiration rates were significantly different between Prospect Hill and the Simmes plot during the summer (t=2.49, df=192, p=0.02), but Prospect Hill samples were measured at higher air temperatures than Simmes Plot samples (p=0.0015). A multiple regression of log-transformed respiration rates on site (as a factor) and air temperature shows that site remains a significant factor when air temperature is taken into account (site, p=0.04; air temperature, p=0.19). A multiple regression of log-transformed respiration rates on site (as a factor), moisture content and temperature shows that, in the summer, moisture content and temperature were significantly correlated to respiration rates but site was not (moisture content, p~0; temperature, p=0.02; site, p=0.27). In the

fall, respiration rates were not different between the sites (t= -1.39, df=105, p=0.17). The comparison was not made for the winter sampling because the small sample size (N=12) precluded a meaningful analysis.

Summer CWD respiration rates at the two sites were compared by genus, decay class and diameter class (Table 3.6). Within these categories, air temperature was significantly different between the two sites for birch (p=0.02), conifer (p=0.0001), decay class 1 (p~0), and the middle diameter class, (p=0.05). Maple CWD respiration rates were marginally different between the two sites (p=0.07). Respiration rates from decay class 1 and decay class 4 and 5 were also marginally different between the two sites (class 1, p=0.06; class 4 and 5, p=0.09). No FWD was sampled from the Simmes plot during the summer so no comparison was made for that diameter class. There was no significant difference in respiration rates of the middle and large diameter CWD between the two sites (middle diameter, p=0.12; large diameter, p=0.32).

Summer Respiration Rates	**df**	**Prospect Hill, $\bar{x}$** ($\mu g\ C\ g^{-1}\ C\ s^{-1}$)	**Simmes Plot, $\bar{y}$** ($\mu g\ C\ g^{-1}\ C\ s^{-1}$)	**95% Confidence Interval**	**t-test p-value**
Genus					
Birch*	55	0.0094 (0.0016)	0.0080 (0.0011)	0.57 - 1.98	0.83
Maple	39	0.0105 (0.0016)	0.0063 (0.0023)	0.95 - 4.79	0.07
Oak	55	0.0054 (0.0078)	0.0040 (0.0008)	0.80 - 2.68	0.21
Conifer*	31	0.0071 (0.0013)	0.0042 (0.0009)	0.65 - 2.92	0.40
Decay Class					
1*	40	0.0071 (0.0015)	0.0037 (0.0044)	0.98 - 2.96	0.06
2	55	0.0056 (0.0010)	0.0044 (0.0007)	0.56 - 2.04	0.84
3	45	0.0075 (0.0011)	0.0074 (0.0017)	0.57 - 2.80	0.55
4 & 5	46	0.0120 (0.0015)	0.0098 (0.0021)	0.91 - 3.27	0.09
Diameter Class					
2cm < d <7.5cm	8	0.0094 (0.0016)	---	---	---
7.5cm≤ d <25cm*	161	0.0083 (0.0008)	0.0065 (0.0008)	0.92 - 1.95	0.12
d ≥25cm	19	0.0043 (0.0006)	0.0032 (0.0005)	0.54 - 5.93	0.32

Table 3.6. Results of student's t-tests used to compare log-transformed summer respiration rates ($\mu g\ C\ g^{-1}\ C\ s^{-1}$) between Prospect Hill and the Simmes plot by genus, decay class and diameter. Un-transformed mean (SE) respiration rates are displayed in the table. *Air temperature at the time of measurement was significantly different between the two sites for this category.

The fall sampling was separated into two temperature regimes, with 10°C as the breakpoint, because the simple comparison of respiration rates between the two sites does not account for major differences in temperature within a season (Table 3.7a, T>10°C; Table 3.7b, T<10°C). During both fall temperature regimes, respiration rates showed no significant difference between the two sites for any category.

(a)

Fall (T > 10°C) **Respiration Rates**	**df**	**Prospect Hill, $\bar{x}$** (μg C g^{-1} C s^{-1})	**Simmes Plot, $\bar{y}$** (μg C g^{-1} C s^{-1})	**95% Confidence Interval**	**t-test p-value**
Genus					
Birch	16	0.0040 (0.0006)	0.0058 (0.0007)	0.44 – 1.22	0.21
Maple	5	0.0059 (0.0012)	0.0026 (0.0012)	0.54 - 19.90	0.15
Oak	17	0.0033 (0.0012)	0.0033 (0.0009)	0.15 - 1.92	0.32
Conifer	13	0.0024 (0.0007)	0.0026 (0.0018)	0.11 - 11.22	0.91
Decay Class					
1 & 2	30	0.0020 (0.0004)	0.0035 (0.0008)	0.19 - 1.40	0.19
3	14	0.0026 (0.0011)	0.0042 (0.0011)	0.12 - 1.24	0.10
4 & 5	12	0.0068 (0.0006)	0.0052 (0.0009)	0.86 - 2.29	0.16
Diameter Class					
2cm < d <7.5cm	9	0.0059 (0.0021)	0.0055 (0.0013)	0.13 - 3.95	0.68
7.5cm≤ d <25cm	36	0.0026 (0.0005)	0.0040 (0.0007)	0.21 - 1.26	0.14
d ≥25cm	11	0.0041 (0.0009)	0.0030 (0.0009)	0.37 - 4.38	0.68

(b)

Fall (T < 10°C) Respiration Rates	**df**	**Prospect Hill, $\bar{x}$** (μg C g^{-1} C s^{-1})	**Simmes Plot, $\bar{y}$** (μg C g^{-1} C s^{-1})	**95% Confidence Interval**	**t-test p-value**
Genus					
Birch	6	0.0027 (0.0011)	0.0021 (0.0011)	0.21 - 23.58	0.45
Maple	13	0.0021 (0.0002)	---*	---	---
Oak	10	0.0018 (0.0005)	0.0013 (0.0003)	0.49 - 3.80	0.52
Conifer	6	0.0009 (0.0003)	---	---	---
Decay Class					
1 & 2	12	0.0011 (0.0003)	0.0014 (0.0003)	0.31 - 3.36	0.98
3	16	0.0022 (0.0004)	0.0012 (0.0004)	0.37 - 6.00	0.55
4 & 5	11	0.0019 (0.0004)	0.0028 (0.0009)	0.03 - 6.85	0.52
Diameter Class					
2cm < d <7.5cm	10	0.0011 (0.0004)	0.0010 (0.0004)	0.07 - 7.30	0.77
7.5cm≤ d <25cm	16	0.0025 (0.0004)	0.0015 (0.0002)	0.85 - 2.99	0.13
d ≥25cm	10	0.0014 (0.0002)	0.0018 (0.0005)	0.33 - 1.84	0.53

Table 3.7. Results of student's t-tests used to compare log-transformed fall respiration rates (μg C g^{-1} C s^{-1}) between Prospect Hill and the Simmes plot by genus, decay class and diameter. Un-transformed mean (SE) respiration rates are displayed in the table. *No mean value listed because only one sample in this subcategory.

Student's t-tests were used to compare wood moisture content between the two study sites by genus, decay class and diameter class (Table 3.8). Moisture content was significantly higher for birch and marginally higher for maple in Prospect Hill than in the Simmes plot (birch, p=0.004; maple, p=0.09). Decay class 3 and decay class 4 and 5 CWD from Prospect Hill had marginally significantly higher moisture content than from the Simmes plot (class 3, p=0.06; class 4 and 5, p=0.06). The moisture content of middle and large diameter CWD was also higher in Prospect Hill than in the Simmes plot (middle size, p=0.003; large size, p=0.009).

Moisture Content	**df**	**Prospect Hill, $\bar{x}$** ($g\ H_2O\ g^{-1}$ dry wood)	**Simmes Plot, $\bar{y}$** ($g\ H_2O\ g^{-1}$ dry wood)	**95% Confidence Interval**	**t-test p-value**
Genus					
Birch	82	1.59 (0.13)	1.04 (0.09)	0.18 - 0.93	0.004
Maple	67	1.35 (0.30)	0.79 (0.27)	-0.08 - 1.20	0.09
Oak	90	0.89 (0.48)	0.74 (0.10)	-0.20 - 0.51	0.38
Conifer	59	1.38 (0.35)	1.17 (0.24)	-0.52 - 0.95	0.56
Decay Class					
1	53	0.77 (0.28)	0.71 (0.09)	-0.21 - 0.34	0.63
2	100	0.69 (0.14)	0.73 (0.09)	-0.27 - 0.18	0.71
3	80	1.35 (0.35)	0.91 (0.11)	-0.02 - 0.91	0.06
4 & 5	76	2.21 (0.50)	1.58 (0.26)	-0.03 - 1.30	0.06
Diameter Class					
2cm < d <7.5cm	35	0.59 (0.14)	0.67 (0.12)	-0.39 - 0.24	0.62
7.5cm≤ d <25cm	223	1.33 (0.21)	0.93 (0.10)	0.14 - 0.66	0.003
d ≥25cm	50	1.99 (0.54)	0.96 (0.14)	0.27 - 1.80	0.009

Table 3.8. Results of student's t-tests used to compare moisture content ($g\ H_2O\ g^{-1}$ dry wood) between Prospect Hill and the Simmes plot by genus, decay class and diameter class. The standard error is given in parentheses.

Genus Effect

A one-way ANOVA showed a significant effect of genus on log-transformed respiration rates (F=5.67, df= 3, p=0.0008). Pairwise comparisons revealed significant differences in respiration rates between oak and birch (p=0.0005), oak and maple (p=0.04), conifer and birch (p=0.001), and conifer and maple (p=0.03) (Table 3.9). Air temperature was compared between genera to ensure that differences in respiration rates

were not due to differences in the air temperature when the samples were measured (Table 3.9).

Table 3.10 shows the mean respiration rate, density and moisture content for each genus. Differences in wood density and moisture content between genera may explain the differences in respiration rates (density, F=17.4, df=3, p~0; moisture content, F=4.32, df=3, p=0.005). Table 3.9 summarizes the results of pairwise comparisons of density and moisture content between genera. All genera, except birch and maple, differed significantly from each other in wood density. Oak had a significantly higher density and lower moisture content than birch, maple and conifer.

	Genus	**Maple**	**Oak**	**Conifer**
Respiration Rate	**Birch**	p=0.33	p=0.0005	p=0.001
	Maple	---	p=0.04	p=0.03
	Oak	---	---	p=0.54
Density	**Birch**	p=0.73	p=0.0006	p~0
	Maple	---	p=0.0008	p=0.0008
	Oak	---	---	p~0
Moisture Content	**Birch**	p=0.65	p=0.0004	p=0.80
	Maple	---	p=0.01	p=0.58
	Oak	---	---	p=0.003
Air Temperature	**Birch**	p=0.31	p=0.76	p=0.13
	Maple	---	p=0.45	p=0.77
	Oak	---	---	p=0.24

Table 3.9. Results of student's t-tests used to perform pairwise comparisons of log-transformed respiration rates (μg C g^{-1} C s^{-1}), density (g dry wood cm^{-3}), moisture content (g H_2O g^{-1} dry wood), and air temperature (°C).

Genus	**Mean Respiration Rate** (μg C g^{-1} C s^{-1})	**Mean Density** (g dry wood cm^{-3})	**Mean Moisture Content** (g H_2O g^{-1} dry wood)
Birch	0.0035 (0.0007)	0.42 (0.01)	1.27 (0.09)
Maple	0.0034 (0.0009)	0.41 (0.02)	1.32 (0.14)
Oak	0.0019 (0.0004)	0.48 (0.01)	0.80 (0.09)
Conifer	0.0021 (0.0006)	0.33 (0.01)	1.20 (0.17)

Table 3.10. Mean (SE) respiration rate, density and moisture content for each genus.

Decay Class Effect

Respiration rates, density, and moisture content were significantly different between decay classes (respiration rates, F=11.6, df=3, p~0; density, F=55.4, df=3, p~0; moisture content, F=31.2, df=3, p~0). Respiration rates and moisture content generally increased while density decreased with decay class (Table 3.11). Because summer data indicated no significant difference between decay classes 1 and 2 in log-transformed respiration rates, density, and moisture content (respiration rates, df=97, p=0.32; density, df=97, p=0.19; moisture content, df=97, p=0.78), the two decay classes were combined for reduced fall and winter samplings.

Decay Class	**Mean Respiration Rate** ($\mu g\ C\ g^{-1}\ C\ s^{-1}$)	**Mean Density** ($g\ dry\ wood\ cm^{-3}$)	**Mean Moisture Content** ($g\ H_2O\ g^{-1}\ dry\ wood$)
1	0.0044 (0.0005)	0.52 (0.02)	0.73 (0.06)
2	0.0037 (0.0004)	0.47 (0.01)	0.71 (0.06)
1 & 2	0.0039 (0.0003)	0.49 (0.01)	0.72 (0.04)
3	0.0055 (0.0006)	0.38 (0.01)	1.19 (0.11)
4 & 5	0.0087 (0.0009)	0.31 (0.01)	2.00 (0.16)

Table 3.11. Mean (SE) respiration rate, density and moisture content for each decay class calculated from summer, fall and winter data. Values for the combination of decay classes 1 and 2 are also included.

Because of this change in sampling procedure, analysis involving decay class was completed based on both the four-class system and the three-class system. In the four-class system, log-transformed respiration rates, density and moisture content were significantly different between all decay class except in two cases (Table 3.12). The respiration rates of decay classes 1 and 3 and the moisture content of decay classes 1 and 2 were not significantly different. In the three-class system, all decay classes differed significantly in log-transformed respiration rates, density and moisture content (Table 3.13). Air temperature was compared between decay classes in both systems to ensure that differences in respiration rates were not due to differences in the air temperature when the samples were measured (Tables 3.12 and 3.13).

	Decay Class	2	3	4 & 5
Respiration Rate	**1**	p=0.006	p=0.78	p=0.01
	2	---	p=0.006	p~0
	3	---	---	p=0.005
Density	**1**	p=0.003	p~0	p~0
	2	---	p~0	p~0
	3	---	---	p~0
Moisture Content	**1**	p=0.83	p=0.003	p~0
	2	---	p=0.0001	p~0
	3	---	---	p=0.0001
Air Temperature	**1**	p=0.10	p=0.14	p=0.64
	2	---	p=0.89	p=0.20
	3	---	---	p=0.28

Table 3.12. Results of student's t-tests used to perform pairwise comparisons of log-transformed respiration rates (μg C g^{-1} C s^{-1}), density (g dry wood cm^{-3}), moisture content (g H_2O g^{-1} dry wood), and air temperature (°C) based on the four-decay-class system.

	Decay Class	3	4 & 5
Respiration Rate	**1 & 2**	p=0.05	p~0
	3	---	p=0.005
Density	**1 & 2**	p~0	p~0
	3	---	p~0
Moisture Content	**1 & 2**	p~0	p~0
	3	---	p=0.0001
Air Temperature	**1 & 2**	p=0.59	p=0.47
	3	---	p=0.28

Table 3.13. Results of student's t-tests used to perform pairwise comparisons of log-transformed respiration rates (μg C g^{-1} C s^{-1}), density (g dry wood cm^{-3}), moisture content (g H_2O g^{-1} dry wood), and air temperature (°C) based on the three-decay-class system.

Diameter Effect

One-way ANOVA analysis showed a significant effect of diameter classes on log-transformed respiration rates, density, and moisture content (respiration rate, F=6.83, df=2, p=0.001; density, F=4.01, df=2, p=0.02; moisture content, F=5.79, df=2, p=0.003). The middle diameter class (7.5cm ≤ diameter < 25cm) had significantly higher respiration rates than the small (2.5cm ≤ diameter <7.5cm) and large (≥25cm diameter) diameter classes (Tables 3.14 and 3.15). However, the air temperature during the middle diameter class measurements was significantly higher than during small and large diameter class measurements (small, p~0; large, p~0). A multiple regression of log-

transformed respiration rates on air temperature and diameter class showed no significant difference in the respiration rates of the medium and small diameter classes (p=0.56) and the medium and large diameter classes (p=0.84). The moisture content of the middle diameter class was significantly higher than the small diameter class and the density was significantly lower (moisture content, p=0.001; density, p=0.02). The moisture content of the large diameter class was significantly higher than that of the small diameter class (p=0.003).

	Diameter Class	**7.5cm≤ d <25cm**	**d ≥25cm**
Respiration Rate	**2cm ≤ d <7.5cm**	p=0.004*	p=0.53
	7.5cm≤ d <25cm	---	p=0.007*
Density	**2cm ≤ d <7.5cm**	p=0.02	p=0.40
	7.5cm≤ d <25cm	---	p=0.08
Moisture Content	**2cm ≤ d <7.5cm**	p=0.001	p=0.003
	7.5cm≤ d <25cm	---	p=0.25
Air Temperature	**2cm ≤ d <7.5cm**	p~0	p=0.52
	7.5cm≤ d <25cm	---	p~0

Table 3.14. Results of student's t-tests used to perform pairwise comparisons of log-transformed respiration rates (μg C g^{-1} C s^{-1}), density (g dry wood cm^{-3}), moisture content (g H_2O g^{-1} dry wood), and air temperature (°C) by diameter class. *This relationship was no longer significant when air temperature was taken into account.

Diameter Class	**Mean Respiration Rate** (μg C g^{-1} C s^{-1})	**Mean Density** (g dry wood cm^{-3})	**Mean Moisture Content** (g H_2O g^{-1} dry wood)
2cm ≤ d <7.5cm	0.0047 (0.0008)	0.46 (0.02)	0.62 (0.07)
7.5cm≤ d <25cm	0.0062 (0.0004)	0.41 (0.01)	1.16 (0.07)
d ≥25cm	0.0028 (0.0003)	0.44 (0.02)	1.35 (0.19)

Table 3.15. Mean (SE) respiration rate, density and moisture content for each diameter class.

3.3. Carbon Flux Estimates

Prospect Hill contained 20.3 ± 2.0 m^3 ha^{-1} of CWD in logs while the Simmes plot contained 80.9 ± 5.6 m^3 ha^{-1}. Figure 3.14 shows the relative contribution of CWD logs and FWD at each study site.

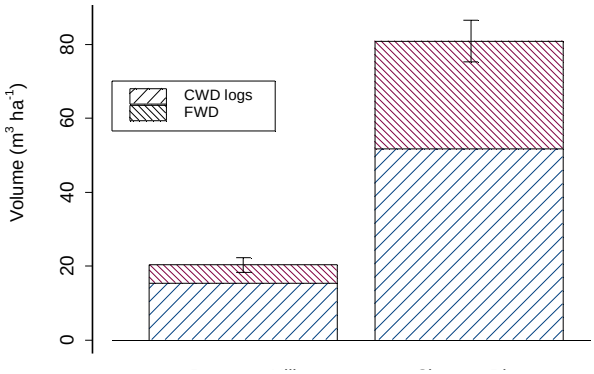

Figure 3.14. Logs, ≥7.5cm diameter, contributed 15.3 ± 1.8 m^3 ha^{-1} at Prospect Hill and 51.7 ± 2.5 m^3 ha^{-1} at the Simmes plot. FWD contributed 5.0 ± 1.0 m^3 ha^{-1} at Prospect Hill and 29.2 ± 5.0 m^3 ha^{-1} at the Simmes plot.

Mean empirical densities were calculated by site, genus and decay class using samples from all seasons (N=321) (Table 3.16). Biomass per area was calculated by summing the products of volume per area and mean empirical density by subcategory. Prospect Hill contained 3.9 ± 1.8 MgC ha^{-1} and the Simmes plot contained 20.2 ± 5.6 MgC ha^{-1} (Figure 3.15).

PROSPECT HILL Density (g cm^{-3})	***Decay Class***			
CWD logs	**1**	**2**	**3**	**4 & 5**
Birch	0.45 (0.05)	0.44 (0.04)	0.37 (0.03)	0.34 (0.04)
Maple	0.52 (0.06)	0.41 (0.03)	0.36 (0.03)	0.26 (0.02)
Oak	0.51 (0.03)	0.51 (0.02)	0.45 (0.04)	0.33 (0.06)
Conifer	0.50 (0.04)	0.37 (0.02)	0.29 (0.03)	0.26 (0.02)
Hardwood	0.53 (0.02)	0.47 (0.01)	0.39 (0.01)	0.31 (0.01)
All Genera	0.47 (0.02)	0.45 (0.01)	0.37 (0.02)	0.29 (0.01)
FWD	0.56 (0.04)	0.48 (0.03)	0.43 (0.02)	0.35 (0.02)

SIMMES PLOT Density (g cm^{-3})	***Decay Class***			
CWD logs	**1**	**2**	**3**	**4 & 5**
Birch	0.56 (0.03)	0.50 (0.02)	0.36 (0.03)	0.32 (0.02)
Maple	0.63 (0.06)	0.53 (0.01)	0.36 (0.03)*	0.19 (0.01)
Oak	0.52 (0.04)	0.57 (0.02)	0.44 (0.04)	0.44 (0.04)
Conifer	0.50 (0.02)	0.36 (0.03)	0.31 (0.02)	0.33 (0.05)
Hardwood	0.53 (0.02)	0.47 (0.01)	0.39 (0.01)	0.31 (0.01)
All Genera	0.54 (0.02)	0.50 (0.01)	0.40 (0.02)	0.34 (0.02)
FWD	0.68 (0.07)	0.46 (0.04)	0.43 (0.05)	0.37 (0.02)*

Table 3.16. Mean (SE) empirical densities (g dry wood cm^{-3}) by subcategory (site x genus x decay class). *There was only one sample in this subcategory so samples from the two sites were pooled to calculate the mean for the category.

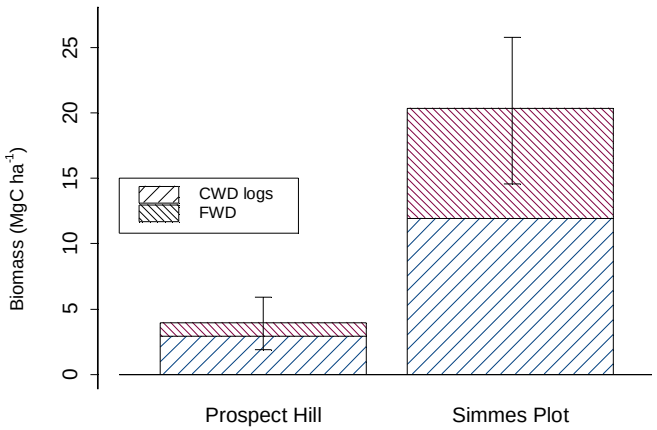

Figure 3.15. CWD logs contributed 2.9 ± 1.0 MgC ha^{-1} at Prospect Hill and 11.9 ± 2.5 MgC ha^{-1} at the Simmes plot. FWD contributed 1.0 ± 1.0 MgC ha^{-1} at Prospect Hill and 8.3 ± 5.0 MgC ha^{-1} at the Simmes plot.

Carbon flux per hectare (MgC ha^{-1} yr^{-1}) was calculated by taking the product of CWD biomass per hectare and mean respiration rates by subcategory. In the two-season method, summer respiration rates were used to characterize the six-month long growing season, and fall and winter respiration rates were used to characterize the six-month long dormant season. The C flux estimated by this method is 0.67 MgC ha^{-1} yr^{-1} at Prospect Hill and 2.16-2.91 MgC ha^{-1} yr^{-1} at the Simmes plot, which translates into decay rates of 0.17 yr^{-1} and 0.12-0.14 yr^{-1}. Table 3.17 shows the breakdown of carbon flux by season and diameter class. The large uncertainty in C flux at the Simmes plot is a result of uncertainty in the summer respiration rates of FWD at the site. The upper limit of the range was calculated by using mean summer respiration rates from FWD at Prospect Hill. However, wood moisture content of FWD at the Simmes plot should be lower than at Prospect Hill because the high surface area to volume ratio of the woody debris makes it vulnerable to rapid moisture loss under an open canopy (Marra and Edmonds 1996). This suggests that the respiration rates should be lower at the Simmes plot, and therefore, that the upper limit of C flux at the Simmes plot is an overestimate. The lower limit was

calculated from a multiple regression model of log-transformed summer respiration rates on site, diameter class and decay class as factors (Equation 3.2).

$$\text{Log}(Y) = -5.9458 + 0.2481\,(\text{site} = \text{Prospect Hill}) + 0.2325\,(\text{diameter class} = \text{medium}) + 0.6247\,(\text{diameter class} = \text{small}) - 0.2150\,(\text{decay class} = 1) + 0.0555\,(\text{decay class} = 3) + 0.6688\,(\text{decay class} = 4 \text{ and } 5) \quad (3.1)$$

	Growing Season Flux ($MgC\ ha^{-1}\ yr^{-1}$)	**Dormant Season Flux** ($MgC\ ha^{-1}\ yr^{-1}$)	**Annual Flux** ($MgC\ ha^{-1}\ yr^{-1}$)
CWD logs			
Prospect Hill	0.33 (0.24)	0.13 (0.20)	0.46 (0.31)
Simmes Plot	0.93 (0.32)	0.48 (0.31)	1.41 (0.45)
FWD			
Prospect Hill	0.16 (0.01)	0.05 (0.01)	0.21 (0.01)
Simmes Plot	0.68* (0.01)	0.30 (0.01)	0.98 (0.01)
Total			
Prospect Hill	0.49 (0.24)	0.18 (0.20)	0.67 (0.31)
Simmes Plot	1.61 (0.32)	0.78 (0.31)	2.39 (0.45)

Table 3.17. Carbon flux ($MgC\ ha^{-1}\ yr^{-1}$) (SE) based on a six-month growing season. * The estimate calculated from mean respiration rates at Prospect Hill is 1.20 $MgC\ ha^{-1}\ yr^{-1}$.

The three-season method is based on summer, fall and winter each accounting for one-third of the year. This method yields an estimate of 0.481 $MgC\ ha^{-1}\ yr^{-1}$ at Prospect Hill and 1.787-2.137 $MgC\ ha^{-1}\ yr^{-1}$ at the Simmes plot (Table 3.18). This converts to decay rates of 0.12 yr^{-1} for Prospect Hill and 0.09-0.11 yr^{-1} for the Simmes plot.

	Summer Flux ($MgC\ ha^{-1}\ yr^{-1}$)	**Fall Flux** ($MgC\ ha^{-1}\ yr^{-1}$)	**Winter Flux** ($MgC\ ha^{-1}\ yr^{-1}$)	**Annual Flux** ($MgC\ ha^{-1}\ yr^{-1}$)
CWD logs				
Prospect Hill	0.22 (0.14)	0.10 (0.12)	0.03 (0.12)	0.35 (0.22)
Simmes Plot	0.62 (0.19)	0.33 (0.19)	0.14 (0.18)	1.09 (0.32)
FWD				
Prospect Hill	0.10 (0.01)	0.03 (0.01)	0.001 (0.005)	0.131 (0.01)
Simmes Plot	0.45* (0.01)	0.23 (0.01)	0.007 (0.01)	0.687 (0.02)
Total				
Prospect Hill	0.32 (0.14)	0.13 (0.14)	0.031 (0.12)	0.481 (0.22)
Simmes Plot	1.07 (0.19)	0.56 (0.19)	0.147 (0.18)	1.787 (0.32)

Table 3.18. Carbon flux ($MgC\ ha^{-1}\ yr^{-1}$) (SE) based on a three-season year. * The estimate calculated from mean respiration rates at Prospect Hill is 0.80 $MgC\ ha^{-1}\ yr^{-1}$.

Decay rates by genus and species for CWD logs are displayed in Table 3.19 to allow for comparison with other studies. These rates are based on year-long summer respiration rates.

PROSPECT HILL Decay rate (yr^{-1})	***Decay Class***			
CWD logs	**1**	**2**	**3**	**4 & 5**
Birch	0.37 (0.009)	0.09 (0.002)	0.34 (0.008)	0.38 (0.006)
Maple	0.14 (0.001)	0.30 (0.003)	0.26 (0.004)	0.57 (0.010)
Oak	0.15 (0.002)	0.11 (0.002)	0.15 (0.002)	0.14 (0.003)
Conifer	0.16 (0.005)	0.25 (0.014)	0.11 (0.002)	0.30 (0.003)
Hardwood	0.14 (0.001)	0.12 (0.001)	0.17 (0.001)	0.27 (0.002)
All Genera	0.21 (0.003)	0.18 (0.02)	0.21 (0.002)	0.38 (0.003)

SIMMES PLOT Decay rate (yr^{-1})	***Decay Class***			
CWD logs	**1**	**2**	**3**	**4 & 5**
Birch	0.15 (0.002)	0.20 (0.003)	0.31 (0.006)	0.37 (0.006)
Maple	0.07 (0.001)	0.07 (0.001)	0.26 (---)	0.69 (0.014)
Oak	0.12 (0.001)	0.10 (0.003)	0.16 (0.006)	0.16 (0.006)
Conifer	0.07 (0.001)	0.13 (0.002)	0.21 (0.006)	0.13 (0.005)
Hardwood	0.14 (0.001)	0.12 (0.001)	0.18 (0.001)	0.28 (0.002)
All Genera	0.12 (0.001)	0.14 (0.001)	0.23 (0.003)	0.31 (0.004)

Table 3.19. Mean decay rates (SE) by genus and decay class based on year-long summer respiration rates.

Modeling C Flux

A simple model predicting respiration rates from Prospect Hill data was created using a multiple linear regression. Log-transformed respiration rates were used in choosing the parameters of the model in order to properly evaluate the significance of the parameters. Size class and diameter as a continuous variable did not improve the fit of the model and did not have significant regression coefficients. Although decay class, in the three-class system, was significant in the model, density was a better predictor. Genus was not significant in the model until birch, maple and oak were grouped together as hardwoods. The following parameters optimized the fit of the model: air temperature,

wood moisture content, wood density, the interaction of moisture content and density, genus grouped as hardwoods and conifer (as factor), and season (as factor).

The model was created based on un-transformed Prospect Hill respiration rates with the aforementioned parameters (N=175, R^2=0.42). Table 3.20 displays the regression coefficients of the model.

Variables	Regression Coefficient	Standard Error of Coefficient	P-value of Coefficient*
(Intercept)	-0.0572	0.0249	0.0228
T	0.0002	0.0001	0.0040
M	-0.0010	0.0009	0.2456
D	-0.0252	0.0047	0.0000
M x D	0.0050	0.0030	0.1037
Hardwood	0.0027	0.0010	0.0039
Fall	-0.0023	0.0014	0.0954
Winter	0.0002	0.0041	0.9640

Table 3.20. A simple multiple linear regression model predicting respiration rate (μg C g^{-1} C s^{-1}) based on Prospect Hill data where T is air temperature (K), M is wood moisture content (g H_2O g^{-1} dry wood), D is wood density (g cm^{-3}), M x D is the interaction of moisture content and density, Hardwood is a factor including birch, maple and oak, Fall is a factor for the fall season and Winter is a factor for the winter season. *The regression coefficient was significant for all parameters in a multiple regression of log-transformed respiration rates, which is more appropriate for assessing significance.

To test the goodness of the model fit, respiration rates at the Simmes plot were predicted using the model and compared to observed respiration rates. The predicted respiration rates for the Simmes plot were fairly strongly correlated to observed rates (R^2=0.36) (Figure 3.17). However, predicted respiration rates were upper-limited, suggesting that a log-transformed model would predict better. Figure 3.18 displays observed versus predicted log-transformed respiration rates from a log-transformed model with the same parameters as the un-transformed model. The fit improves for this model (R^2=0.42) but the back-transformation of predicted values is complicated and prone to error.

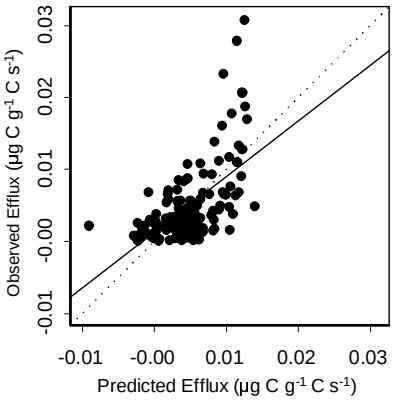

Figure 3.17. Comparison of predicted and observed respiration rates at the Simmes plot using the multiple regression model based on un-transformed Prospect Hill data. The dotted line indicates the 1:1 line. The solid line represents the regression line (y= 0.77 x + 0.001, R^2=0.36).

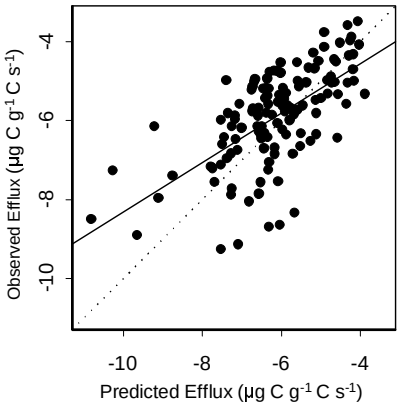

Figure 3.18. Comparison of predicted and observed log-transformed respiration rates at the Simmes plot using the multiple regression model based on log-transformed Prospect Hill data. The dotted line indicates the 1:1 line. The solid line represents the regression line (y= 0.62 x – 2.06, R^2=0.42).

Discussion

4.1 Pilot Test

Equilibration Time

The pilot test results show that respiration rates were initially high after cross-sectional sample disks were cut, and leveled off within one hour (Figure 3.3). In using the chamber-IRGA method to measure CWD respiration rates, it is critical to measure the respiration rates after the cut CWD samples have equilibrated with atmospheric CO_2 in order to capture actual microbial respiration rates. During cutting, friction from the saws heat the surface of the sample disks, potentially increasing microbial activity for a period of time. More importantly, when samples are cut, the surface area is exposed to the atmosphere is increased, changing the gradients for CO_2 diffusion (Chambers et al. 2001). In addition, void spaces in the dead wood could be opened, releasing previously trapped CO_2. This effect of cutting was observed when the samples were originally cut from the parent logs and when the samples were subsequently cut two more times (Figure 3.3). Chambers et al. (2001) also observed this effect when measuring sample wedges cut from dead boles in an Amazonian old-growth forest, and determined a three-hour equilibration time. The difference in one-hour equilibration time determined by this study and the three-hour equilibration time estimated by Chambers et al (2001) could be due to differences in the pore structures of decaying northern hardwood species and central Amazonian species.

Surface Area to Volume Ratio Effect

When a cross-sectional sample is cut from a log, the surface area to volume ratio of the sample is increased. This gives microbes more access to oxygen rich air and

thereby potentially increases microbial activity (Harmon et al. 1986). In order to test the validity of the chamber-IRGA method in describing respiration rates in uncut CWD, it is important to determine if increasing the surface area to volume ratio by cutting significantly changes microbial respiration rates. The pilot test shows that respiration rates did not increase but decreased when surface area to volume ratio was increased after allowing an equilibration period (Figure 3.5). When samples were cut in half, no change in respiration rates was observed. However, an additional cut resulted in lowered rates (4-36% reduction) even when air temperature and wood moisture content changes over the course of the day, and sampling regime, was taken into account (Figure 3.5). Respiration rates could not be corrected for mass loss to sawdust causing an overestimate of first cut and second cut respiration rates because the dry mass after all three cuts was used in calculating the respiration rates. Nevertheless, the mass lost was small compared to the remaining mass (<1%) and most likely cannot account for the 4-32% decrease in respiration rates between the first cut and third cut.

There could be a threshold of surface area to volume ratio in altering microbial respiration that was not crossed until the samples were cut into four pieces. Nonetheless, an increase in respiration rates was expected. The decrease in respiration rates is, therefore, likely an artifact of the pilot test methodology. The model used to correct for air temperature and wood moisture content differences between the three cuts could have been inadequate because of the confounding effects of other variables, such as density and genus, inherent in the data used to create it. An incubation experiment is needed to create a model that describes the relationship between respiration rates and air temperature and moisture content without the confounding effects of other variables.

Alternatively, the pilot test could be re-designed to control for air temperature and moisture content changes over the course of the sampling regime. For instance, different width samples could be cut from random points along the same log, allowing the respiration rates of different sized samples to be measured at approximately the same time.

4.2. Factors Controlling CWD Respiration

Temperature, Moisture Content and Density

Respiration rates were positively correlated to air temperature and moisture content (Figures 3.7 and 3.8b), and negatively correlated to density (Figure 3.9b). These relationships are consistent with those found in other CWD respiration studies (Marra and Edmonds 1994; Chambers et al. 2001; Wang et al. 2002). The relative importance of temperature and moisture content in controlling the respiration rates is difficult to determine because of the interaction between the two factors (Harmon et al. 1986). However, some studies have concluded that temperature is the most important factor (Edmonds 1987; Marra and Edmonds 1996; Knohl et al. 2002) while others cite wood moisture content as the most important factor (Chambers et al. 2001). This study suggests that temperature dominates over moisture content in controlling respiration rates at temperatures under 20˚C. Figure 3.6 shows that the respiration rates of decay class 4 and 5 samples, which had higher wood moisture content on average than lower decay class samples, were in the same range as those of lower decay classes at air temperatures under 20˚C. However, above 20˚C, decay class 4 and 5 samples were able to achieve higher respiration rates than lower decay class samples. Seasonal comparisons show that the

variation in respiration rates decreases dramatically from summer, when air temperature ranged from 13˚ to 34˚C, to fall, when air temperature never reached 20˚C (Figures 3.11 and 3.12). This variation was reduced further in winter when air temperature remained below 0˚C on sampling days (Figures 3.11 and 3.12). Air temperature appears to be driving the decrease in variation because wood moisture content increased at Prospect Hill and did not change significantly at the Simmes plot from summer to fall, and did not change significantly between fall and winter at either site (Figure 3.13). Evidence from an incubation experiment in which moisture content and temperature were manipulated supports this observation that respiration rates are restricted under 20˚C regardless of wood moisture content (Wang et al. 2002).

Consistent with Chambers et al. (2001), this study found that wood moisture content and density were negatively correlated (Figure 3.10). As wood decays, void spaces are created, increasing the water capacity of the wood, and thus the water-holding capability, of the wood (Rayner and Boddy 1988). This negatively correlated relationship between respiration rates and density (Figure 3.9) is driven largely by this relationship between moisture content and density (Chambers et al. 2001).

Wood moisture content can restrict respiration rates when excessively low because fungal growth relies on moisture (Rayner and Boody 1988). The threshold moisture content is not agreed upon in published literature. Kaarik (1974) states that moisture content below 30% of dry weight severely restricts microbial activity while Chambers et al. (2001) concluded that 50% moisture content is the threshold. Figure 3.8b shows that at 50% moisture content, the full range of respiration rates is still observed, and suggests that the threshold in this temperate forest is around 30%. The high

respiration rates associated with low moisture content can be explained by the concept of water potential, which is a measure of water availability to microbes in the wood. Microbes do not respond directly to wood moisture content but to water potential, which can be higher in decayed wood than sound wood at the same moisture content (Rayner and Boddy 1988).

Wood moisture content can also restrict respiration rates when excessively high because water-filled pores limit aerobic activity in the wood (Harmon et al. 1986). Figure 3.8b provides evidence that moisture content above 400% restricts microbial activity. This is consistent with Chambers et al. (2001) who concluded that optimum respiratory activity occurs around 250% moisture content and Wang et al. (2002) who found that respiration rates increased through 200% moisture content (the upper limit tested in the incubation experiment) with temperature held constant.

Seasonal Effects

Most CWD studies rely on chronosequences to determine CWD decay rates, and thus cannot explicitly discriminate seasonal effects on the decay rates. The Prospect Hill and Simmes plot respiration rates decreased significantly from summer through winter (Figure 3.11), following the trend in air temperature (Figure 3.12). This supports the findings of a study in the Pacific Northwest that respiration rates follow the seasonal changes in air temperature and moisture content (Marra and Edmonds 1994). Moisture content at Prospect Hill increased from summer to fall, and did not change significantly between fall and winter (Figure 3.13). This trend is consistent with the trend in a Pacific Northwest old-growth forest (Sollins et al. 1987). Moisture content did not change significantly between seasons at the Simmes plot (Figure 3.13). Respiration rates during

the spring may be higher than during the fall despite a similar temperature range because the moisture re-charge in the fall and winter encourages microbial activity as temperatures increase in the spring (Harmon et al. 1986).

Site Effect

During the summer, respiration rates were higher at Prospect Hill than at the Simmes plot even when sampling bias in air temperature was taken into account ($p=0.04$). This difference is inconsistent with a Pacific Northwest study comparing adjacent open and closed canopy sites (Marra and Edmonds 1996). In this study, when moisture content is taken into account, the site effect on respiration rates is no longer significant, suggesting that moisture content is the driving force in the site difference in respiration rates. Unfortunately, the three-hour equilibration time required prior to measurement obscures the role of site temperature. Wang et al. (2002) found that, in a closed canopy forest, greater leaf area index shades CWD from solar radiation, making sample temperature less sensitive to air temperature. This implies that moisture loss is reduced because CWD is protected from the high temperatures that induce evaporation. Marra and Edmonds (1996) found a dramatic positive effect of an open canopy on CWD surface temperature, implying that moisture loss is more rapid due to evaporation in the high temperatures. In the context of these two studies, this study provides evidence that the interaction between temperature and moisture content is important in determining differences in respiration rates between open and closed canopy forests.

Genus Effect

Published literature is marked by conflicting evidence of a species or genus effect on decomposition rates. In this study, a strong genus effect on respiration rates was

observed, with oak and conifer respiration rates significantly lower than birch and maple respiration rates (Table 3.9). Most CWD studies have focused on conifer species so there are few studies with which to compare these results. However, the difference between maple and oak decay rates is supported by a study in an Indiana old-growth forest (MacMillan et al. 1988). The low oak respiration rates are also supported by other evidence from this study. Oak wood density was significantly higher and wood moisture content significantly lower than that of birch, maple and conifers (Tables 3.9 and 3.10). Oak respiration rates should be lower than those of the other genera because respiration rates are negatively correlated with density and positively correlated with moisture content. In addition, MacMillan et al. (1988) found that oak immobilizes N slowly relative to maple, thereby hindering rapid colonization by fungi and subsequent decomposition. Furthermore, oak contains high concentrations of phenolic compounds which inhibit decay (Rayner and Boddy 1988).

The mean decay rate for conifers, 0.07 ± 0.02 yr^{-1}, is within the range of published values for conifers in the Pacific Northwest and northeastern forests (Table 4.1). In contrast to oak, low conifer respiration rates cannot be explained by density and moisture content. Conifer wood moisture content was not significantly different from that of birch and maple, and was significantly higher than that of oak. In addition, conifer density was significantly lower than those of the other genera. The low respiration rates of conifers may be attributable to the wood structure and nutrient content differences between hardwoods and conifers.

Location	Forest Type	Methodology	Diameter	Species/Genus	Decay Rate (yr^{-1})	*Study*
North Carolina	Hardwood	Mass loss	0-1 cm 1-3 cm 3-5 cm	*Quercus prinus*	0.1524 0.1728 0.0912	Abbot and Crossley 1982
North Carolina	Mixed hardwood	Mass loss	≤5 cm >5 cm	Mixed hardwood	0.185 0.083	Mattson et al. 1987
Oregon/Minnesota/Kansas /North Carolina	Hardwood	Mass loss	25-35 cm	*Quercus* spp	0.28 ± 0.04	Schowalter et al. 1992
Hubbard Brook, New Hampshire	Northern hardwood	Mass loss	>3 cm	Hardwoods	0.096	Arthur et al. 1993
New Hampshire	Northern hardwood	Density loss	≥10 cm	*Picea rubens* and *Abies balsamea*	0.033 0.029	Foster and Lang 1982
Indiana	Mesophytic deciduous	Density loss	>5 cm	*Quercus* spp *Carya* spp *Fagus grandifolia* *Acer spp*	0.018 0.035 0.019 0.045	MacMillan et al. 1988
National Sequoia Park, CA	Mixed conif.	Density loss	>20 cm	*Abies concolor*	0.05	Harmon et al. 1987
Washington State	Mixed conif.	Mass loss	8-12 cm	Conifer	0.03-0.11	Edmonds 1987
Washington State	Mixed conifer	Mass loss	1-12 cm	*Alnus rubra* *Pseudotsuga menziesii*	0.035-0.517 0.006-0.205	Edmonds et al. 1986
Washington State	Mixed conifer	Mass loss	1-2, 8-12 cm	*Pseudotsuga menziesii* *Tsuga heterophylla* *Abies amabilis* *Pinus ponderosa*	0.004-0.037 0.01-0.3 0.005 0.01	Erickson et al. 1985
Vancouver Island	Mixed conifer	Volume loss	≤20 cm 21-40 cm 41-80 cm >80 cm	*Pseudotsuga menziesii*	0.067 0.056 0.021 0.012	Stone et al. 1998
Oregon & Washington	Mixed conifer	Density loss	<15 cm	*Pseudotsuga menziesii* *Tsuga heterophylla* *Thuja plicata*	0.10 0.016 0.009	Sollins et al. 1987
Northeastern Yucatan peninsula	Dry tropical	Mass loss	<10 cm ≥10 cm	---	0.151-1.019 0.008-0.615	Harmon et al. 1995
Central Amazon	Rain forest	Mass loss	<10 cm	---	0.19 ± 0.026	Chambers et al.2000
Central Amazon	Rain forest	Mass loss	>10cm	---	0.13	Chambers 2001
Russia	Boreal forest	Mass loss	<5 cm	*Picea, Betula, Populus*	0.04	Knohl et al. 2002

Table 4.1. Comparison of decay rates found in across diameter classes, species and regions.

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First, the vessels of angiosperms, such as birch, maple and oak, are larger in diameter and more continuous than the tracheids of gymnosperms, such as spruce, hemlock and pine, which are connected by pits, creating easier access routes for decay organisms (Harmon et al. 1986). Gymnosperms also have less living tissue (i.e. sapwood), which has higher concentrations of sugars, starches and proteins that can be readily decomposed, than angiosperms (Harmon et al. 1986). Moreover, decaying hardwood logs contain higher concentrations of nutrients than softwood logs, thus enhancing microbial activity in hardwood logs (Arthur et al. 1993).

Decay Class Effect

Respiration rate, density and moisture content were significantly different between decay classes in the four-class system and the condensed three-class system (Tables 3.12 and 3.13). Decay classes 1 and 2 were combined to create the three-class system for the fall and winter samplings because summer data showed no differences in the three variables between the two classes ($p=0.32$). In the three-decay class system, respiration rates and moisture content increased significantly, and density decreased significantly with increasing decay class (Tables 3.11 and 3.13). This trend in wood moisture content is corroborated by evidence from an old-growth Douglas-fir forest (Sollins et al. 1987). However, the trend in respiration rates conflicts with findings from Pacific Northwest studies (Marra and Edmonds 1994; Marra and Edmonds 1996; Sollins et al. 1987). Marra and Edmonds (1994) and Marra and Edmonds (1996) found that decay class 1 and 2 logs had higher respiration rates than decay class 3 logs in an old-growth and a clear-cut forest. In contrast, the effect of decay class on respiration rates varied with conifer species in another old-growth Pacific Northwest forest (Sollins et al.

1987). These contradictions in decay class effects may be clarified by acknowledging that decay class is not only an indicator of wood density but also an indicator of nutrient content (Idol et al. 2001). Idol et al. (2001) found that in the inner woody tissue of oak and hickory, N, sulfur and phosphorus concentration increase and C:N and lignin:N decrease with increasing decay class. Differing nutrient dynamics during decomposition may be driving the differences in decay class effect between species.

While the three-decay class system captured differences in respiration rate, density and moisture content, variation of wood density over the sample cross-sections was observed. This variation was also noted by Naesset (1999) and has implications for integrating fluxes over entire logs from relatively small samples cut from them.

Diameter Effect

Diameter class did not have a significant effect on respiration rates (Table 3.14). This is consistent with another northern hardwood study using similar diameter classes (Foster and Lang 1982) but conflicts with Pacific Northwest studies involving a broader range of CWD diameter (Graham and Cromack 1982; Marra and Edmonds 1994; Marra and Edmonds 1996; Stone et al. 1998). This supports the theory that surface area to volume ratio changes are not significant enough to affect microbial activity in the range of CWD diameters found in northern hardwood forests.

Fine woody debris was expected to have higher respiration rates based on observations from other studies (Mattson et al. 1987; Harmon et al. 1995; Stone et al. 1998). However, respiration rates did not differ significantly from those of larger diameter CWD (Table 3.14). This could be a result of significantly lower wood moisture content found in FWD. Marra and Edmonds (1996) suggest that moisture loss is rapid

from FWD in clear-cuts because the high surface area to volume ratio makes it vulnerable to evaporation. Wood moisture content in FWD was not significantly different between Prospect Hill and the Simmes plot, but was low at both sites. This implies that moisture loss is rapid from FWD regardless of the canopy cover.

4.3 Carbon Flux

The amount of log biomass per hectare in Prospect Hill and the Simmes plot were comparable before harvesting at the Simmes plot (Section 2.1). However, after harvesting, the Simmes plot contained 20.4 MgC ha^{-1} compared to 3.9 MgC ha^{-1} at Prospect Hill. Fine woody debris accounted for 42% of the downed woody debris at the Simmes plot and 26% at Prospect Hill. The log biomass per hectare used to calculate the total carbon flux per hectare differs slightly from the figures cited in the site description (Section 2.1) because different wood densities were used to determine biomass. Wood densities used for the biomass estimates in the site description were taken from a study of a northern hardwood forest, and was based on a six-decay class system (McGee et al. 1999). Biomass estimates used to calculate carbon flux were derived from empirical wood densities determined from samples that were collected for respiration measurements.

While the respiration rate of CWD was higher at Prospect Hill than the Simmes plot during the summer, when much of the annual C flux occurs, the total C flux per hectare is three times higher at the Simmes plot (Tables 3.17 and 3.18). This difference is due to the over five-fold difference in log biomass between the two sites.

Because this study was not able to include a spring sampling to cover the annual range of temperature and wood moisture content, annual C flux per hectare was calculated using several methods in order to bound the estimates. Annual C flux per hectare based on a two-season year is 0.67 MgC ha^{-1} yr^{-1} at Prospect Hill and 2.16 MgC ha^{-1} yr^{-1} at the Simmes plot. This is an overestimate for two reasons. First, summer sampling occurred in July through mid-October, encompassing the peak in the annual trend in air temperature at Harvard Forest. Assuming that the summer data from this study characterizes the entire six-month growing season will thus give too much weight to the high respiration rates associated with higher air temperature in late summer. Second, mean respiration rates used to calculate the total C flux per hectare for the non-growing season were determined by pooling the fall and winter data. Because of the small sampling size in the winter, the means are over-influenced by fall respiration rates, which are higher than the near-zero respiration rates measured during the winter (Figure 3.11).

Annual C flux per hectare based on a three-season year is 0.45 MgC ha^{-1} yr^{-1} at Prospect Hill and 1.43 MgC ha^{-1} yr^{-1} at the Simmes plot. This is a better estimate than the two-season estimate because it effectively separates fall and winter respiration rates which were found to be significantly different, and gives less weight to the high summer respiration rates. However, it may be a conservative estimate because fall and winter respiration rates are lower than spring respiration rates (Progar et al. 2000). Spring sampling in 2003 will allow an even more accurate estimate, based on a four-season year, to be determined.

The C flux per hectare from FWD in the Simmes plot during the summer season is uncertain because no small diameter samples were collected from the site in the summer sampling. The two-season C flux estimate gives the range of 0.45-1.21 MgC ha^{-1} yr^{-1} from FWD in the summer, and the three-season C flux estimate gives the range of 0.30-0.81 MgC ha^{-1} yr^{-1}. The upper limit of these estimates was calculated by directly applying mean summer respiration rates from FWD at Prospect Hill to calculate the C flux from FWD at the Simmes plot. However, this is a gross overestimate because Prospect Hill respiration rates were significantly higher than Simmes plot respiration rates across all diameters. In addition, moisture loss is rapid from FWD because of its high surface area to volume ratio makes. Erickson et al. (1986) found that moisture plays a large role in determining respiration rates of FWD in clear-cuts. Similarly, the Simmes plot is mostly open canopy, and the FWD is likely drier and thus respiring less than FWD at Prospect Hill. To account for the differences in the two sites, a simple model was created based on the factors, stand, diameter class and decay class.

The lower limit given in the C flux estimates was calculated from mean respiration rates predicted from this model. Because the contribution of FWD to the summer C flux at the Simmes plot is potentially 32-57% of the total summer C flux, it is vital to directly measure the respiration rates in the summer of 2003.

The decay rates for individual genera are within the range of published values (Tables 3.19 and 4.1). Furthermore, many of the other studies relied on density loss and mass loss to determine decay rates, and thus should overestimate of decay rates from respiration only. While this comparison implies some error in C flux calculations in this study, no errors in data entry or computer coding were found. Chambers et al. (2001) is

the only study found that employed the same methodology used in this study; it determined that the carbon loss rate due to respiration was 0.13 yr^{-1} in a central Amazonian forest where the growing season is year-round. As a comparison, the summer C flux estimated from this study was used to characterize a year-long C flux. Carbon loss rates of 0.25 yr^{-1} and 0.14 yr^{-1} were determined for Prospect Hill and the Simmes plot. While such high decay rates seem unlikely for a temperate forest compared to a tropical forest, wood moisture content was higher at Harvard Forest than at the Amazonian forest (Figure 3.8) (Figure 2c in Chambers et al. 2001). A model developed by Chambers et al. (2001) from data collected at the Amazonian forest was used to predict respiration rates based on wood moisture content data from this study in order to determine if the high respiration rates found at Harvard Forest are due to high wood moisture content. Equation 4.1 shows the model where k_r is the respiration rate (μg C g^{-1} wood C min^{-1}) and M is wood moisture (g H_2O g^{-1} dry wood).

$$\text{Log}_{10}(k_r) = -0.65 + 1.592 \text{ Log (M)} \qquad (4.1)$$

This model predicts that the carbon loss rate is 0.26 yr^{-1} at Prospect Hill and 0.13 yr^{-1} at the Simmes plot, suggesting that the calculated C flux per hectare for Harvard Forest is accurate. It also implies that moisture content is a dominant factor in determining respiration rates.

Barford et al. (2001) estimated that CWD respiration, from logs, snags and dead woody roots, was 0.3 ± 0.3 MgC ha^{-1} yr^{-1} at the Prospect Hill site. This estimate was based on a 6% mass loss rate taken from other studies of northern hardwood forests. The C flux per hectare from logs at Prospect Hill was calculated to be 0.45 MgC ha^{-1} yr^{-1} in this study, and is within the 95% confidence interval of the Barford et al. (2001) estimate.

Using the mortality (0.64 MgC ha^{-1} yr^{-1}) given in Barford et al. (2001), this suggests that the CWD pool at Prospect Hill is a sink of about 0.19 MgC ha^{-1} yr^{-1}. In comparison, Gaudinski et al. (2002) determined that below-ground storage of C in well-drained soils at Harvard Forest is increasing by 0.1-0.3 MgC ha^{-1} yr^{-1}, which is 5-15% of the total ecosystem sink measured using eddy covariance. The accumulation of C in CWD at Prospect Hill is thus similar to the accumulation in soils. In contrast, logs at the Simmes plot site are releasing 1.43 MgC ha^{-1} yr^{-1}. Given the 0.64 MgC ha^{-1} yr^{-1} mortality, the CWD pool at the Simmes plot is a source of 0.79 MgC ha^{-1} yr^{-1}. Davidson et al. (2002) reported 6.47-7.48 MgC ha^{-1} yr^{-1} from soil respiration at Harvard Forest. The large C flux from the Simmes plot is due to the reverse-J curve phenomenon seen in harvested sites (Spies et al. 1988). In the years immediately following harvest, large amounts of C are released as the high input of CWD from harvesting decomposes. After a period of time, the CWD stock reaches steady state. Because the Simmes plot was logged in 2001, the CWD stock is still in the steep portion of the reverse-J curve. This study site will present an opportunity to observe CWD dynamics throughout the curve.

Modeling C Flux

The model suggests that air temperature, moisture content, density, season and genera group (as hardwood and conifers) are the most influential factors in controlling respiration rates. Diameter and decay class had no effect on the fit of the model. More investigation into the relative influence of each parameter is needed to build an accurate model.

Conclusions

(1) Periodic measurements of cross-section CWD disks showed that a one hour equilibration with ambient air is required to achieve a constant flux measurement.

(2) A pilot test showed that respiration rates did not increase but rather decreased with increasing surface area to volume ratio, following the equilibration period. The reduction was not significantly different from whole log flux but suggests further study is required to identify the cause of the reduction.

(3) Respiration rates were positively correlated to air temperature and sample moisture content, and negatively correlated to sample density. However, wood moisture content and density were negatively correlated. Therefore changes in temperature and moisture account for seasonal differences in CWD respiration rate

(4) Respiration rates of samples taken at the Prospect Hill site were significantly higher than those from the Simmes site. These differences were attributed to reduced canopy coverage, following selective logging of the Simmes site in year 2000. Reduced canopy coverage translates to greater solar radiation and reduced moisture content of CWD.

(5) Relative differences in respiration among CWD genera in the Prospect Hill site followed the pattern: birch = maple > conifer > oak. The pattern on the Simmes site was similar except that conifer did not differ significantly from oak. These differences were attributed to variation in wood density which translate to wood moisture content.

(6) Decay classes of CWD differed only when the four class system was modified by combining classes 1 and 2. The relative pattern of respiration was: decay class 1 > 2 > 3, which reflects decreasing density and increasing moisture content among classes.

(7) Sample diameter had no significant effect on respiration rates.

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