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Previous research on coarse woody debris (CWD) indicated that moisture content and initial heterotrophic colonization of decaying wood can affect the decomposition process. Six heterotrophic treatments were created to simulate the effects of physical penetration of the bark and wood and the transmission of ascomycetes versus basidiomycetes into CWD. In 1995, 360 Douglas-fir (*Pseudotsuga menziesii*) were randomly placed at five replicate sites in old-growth stands. Each site had 6 heterotrophic (HET) x 2 moisture combinations (TENT). One set of logs representing the treatment combinations was used for sampling respiration and another set was used to measure volume affected by insect gallery excavations and fungal rot and to determine decay rates. Respiration was sampled three times during the summer of 2001. The results indicated that the HET treatments were no longer affecting respiration rates. Analysis of the average of the three sampling periods revealed no TENT effect but examinations of the individual sampling dates suggests that tented logs might have higher respiration rates than non-tented logs as summer

progresses. In the aggregate, the TENT treatment reduced moisture content from 45% to 36%, a 20 percent reduction in moisture levels. The HET and the TENT treatments did not affect decay rates. The mean density change for the logs was -0.072 g/cm^3 ± 0.03 and the mean decay constant was 0.026 ± 0.011. The TENT treatment did affect heterotrophic activity. The mean volume of wood borer excavation and extent of brown rot was higher in the tented logs (256 cm^3) than in the non-tented logs (59.9 cm^3). There was also a statistically significant interaction between the HET and TENT treatments. The largest differences in volume affected by wood borers and fungal rot were found in treatments that injected ascomycetes into the experimental logs. In sum, there was limited evidence that the differences in moisture content caused by the TENT treatment affected the decomposition process but the HET treatments appear to not be directly influencing decomposition after six years. The findings suggest differences in the initial community composition of heterotrophs have a decreasing impact on the decomposition process as it progresses.

The Effects of Moisture Content and Initial Heterotrophic Colonization on the Decomposition of Coarse Woody Debris

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Jason S. Barker, Author

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Chapter 1: Introduction

Coarse woody debris (CWD) plays a number of vital roles in maintaining the structural and functional integrity of forest ecosystems. Fallen trees can stabilize soils, provide substrate for reproduction, habitat for invertebrates and vertebrates, and can be an important pool of water and nutrients (Harmon et al. 1986). CWD ranges from snags and logs to large branches to coarse roots. Harmon et al. (1986) defined CWD as woody material that is larger than 2.5 cm in diameter. In North America, CWD is more often defined as material at least 7.5 cm in diameter.

In the Pacific Northwest, CWD is important in part because of its sheer mass. Researchers have found that CWD can account for as much as 60 percent of the litter in a stand (Maser and Trappe, 1984). The creation of CWD can vary seasonally, annually, and long-term. The major agents of mortality that produce CWD are wind, fire, insects, disease, and competition/suppression (Harmon et al., 1986). Each of these factors acting alone or in combination produces the spatial distribution and variation in substrate quality of CWD.

Schowalter (2000) defined decomposition as " ...the breakdown of dead organic matter that eventually results in release of CO_2, other organic trace gases, water, mineral nutrients, and energy." Rates of decomposition

are typically highest in warm tropical ecosystems and the slowest in desert, tundra, and boreal forests (Schowalter 2000). Harmon et al. (1986) outlined seven processes associated with the decomposition of CWD: leaching (removal of matter in solution), fragmentation (loss of volume), transport (the physical movement of CWD), collapse/settling (change in cross sectional profile shape due to loss of structural strength), seasoning (shrinkage and cracking that occurs in very dry environments), respiration (loss of mass from biological activity), and biological transformation (mass metabolized by microorganisms and invertebrates).

Decomposing CWD can be viewed in two ways: as part of a larger ecosystem or as distinct ecosystems. As a distinct ecosystem, it is possible to measure nutrient inputs, outputs, and internal cycling. Inputs include nitrogen fixation, interception of debris, water, and nutrients from the canopy, and the immigration of insects and decomposers. Outputs include fragmentation from insect gallery excavation, respiration, and leaching (Schowalter et al. 1992). The research presented here focuses primarily on the log as a distinct ecosystem.

The concentrations of nutrients can change as CWD decomposes as a result of inputs and outputs. N concentrations, for example, can increase relative to initial levels (Busse 1994; Krankina et al. 1999; Lambert 1980; Sollins et al. 1987). Chronosequence studies that have examined long - term N dynamics have found no consistent patterns as some studies report consistent net immobilization (Grier 1987) while others reported an

initially static period followed by either net mineralization (Lambert et al. 1980; Means et al. 1992) or net immobilization (Sollins et al. 1987).

Studying nutrient dynamics within CWD presents obstacles because CWD can persist for long periods and the accumulation or retention of nutrients over time can reduce the apparent turnover of nutrients. For example, studies that do not account for bark fragmentation may give misleading results regarding N dynamics because loss of nutrient-rich bark has a large influence on N levels of CWD and not accounting for its loss will underestimate release of nutrients (Harmon et al. 1994; Krankina et al. 1999).

The chemical composition of CWD has important implications for the heterotrophic organisms that decompose CWD and the overall decomposition process. Structural elements, such as lignin and cellulose, which serve to support the tree while alive, retard decomposition. Compounds, such as heartwood extractives, that protect the tree from microbial attack while alive continue to retard decay after the tree dies. Douglas-fir trees contain from 43-48% cellulose, 24-31% hemicellulose, and 26-28% lignin (Harmon et al. 1986). Substrates low in structural polymers, such as phloem, decay quite rapidly in comparison to heartwood, sapwood, and outerbark.

The decay of CWD is commonly modeled using exponential models. There are two common exponential models that are used to model losses from CWD via respiration and leaching but the exponential model also has been modified to incorporate fragmentation (Harmon et al. 1986).The most widely used model is the single exponential model that was developed by Olson (1963). It is based on the assumption that the decaying material is homogenous (Harmon et al. 1986).

Since wood is a heterogeneous substance with components that decompose at different rates , the single-exponential model can lead to misleading decay rates because prediction with this model depends on consistent and representative sampling of all the substrates in cross section (Harmon et al. 1986, Schowalter 2000). For example, two logs with the same diameter may decay very differently depending on amount of sapwood versus heartwood. As an alternative, decomposition can be modeled as a multiple negative exponential decay function over time. In this type of model, the decay constants are proportional to the qualitative components of the litter. In a typical system, an initially large decay constant results from the loss of labile materials. As time passes, the decay constants become progressively smaller due to the slower losses of more decay resistant materials, such as lignin (Schowalter 2000). Hence, phloem, with more labile material, decays more rapidly than does heartwood, with more decay resistant material.

Researchers have created a classification scheme to aid the study of wood decay (Maser and Trappe 1984). In the most commonly used schema, logs can be divided into five decay classes. In decay class one, tthe CWD is distinct from the soil layer, and the bark, heartwood, and sapwood are intact. By decay class five, the CWD is becoming indistinguishable from the soil and the heartwood is extensively decayed. This process can take tens to hundreds of years to complete (Maser and Trappe 1984).

Research on decomposing CWD is focused largely on dead trees but decay can occur while the tree is still living. Pathogenic fungi, such as heart rot fungi, colonize living trees, while animals can excavate the living or non-living portions of the tree. Furthermore, living trees often contain a large of amount of non-living mass before death, i.e. the heartwood. In fact, a dead tree can contain more living cells than a living tree. In a living conifer, only about 10 percent of the cells are alive, while in a tree in an advanced state of decay, living cells (primarily fungi) can account for as much as 35% of the total biomass (Franklin et al., 1987). Once dead, trees can remain standing for a number of years as a snag or fall to the forest floor. The focus of this literature review and research is on CWD on forest floors.

The rates and type of CWD decay have implications for forest nutrient cycling and importance of the role of CWD in nutrient cycles is the

subject of some debate. Because of the longevity of CWD compared to other litter types, nutrients stored or accumulated in CWD have potential to act as nutrient sources even in well decayed stages (Hart 1999). Studies have shown that CWD can be an important source of nutrients in forest ecosystems after a disturbance (Harmon and Chen 1991; Krankina et al. 1999; Schowalter et al. 1998). For example, Krankina et al. (1999) found evidence that nutrients from coarse woody debris can supply a large portion of N, Ca, and K after disturbances in Northwestern Russia. Although nutrient storage in woody biomass was low compared to overall biomass, they found that nutrients released from CWD could provide a large source of the N, Ca, and K that accumulates in living biomass in a forest ecosystem.

Other researchers have reported only a slight contribution of CWD to nutrient cycling, especially when CWD nutrient levels are compared to total pool sizes (Busse 1994; Laiho and Prescott 1999). Laiho and Prescott (1999) found that in three forest types (lodgepole pine, white spruce, and subalpinefir/Engelmann spruce) in the Rocky Mountains CWD contributed a maximum of 5.1% of the annual aboveground input of N and 2.2% of the annual aboveground input of P. Other studies have also pointed to a relatively minor role of log decay in nutrient cycling (Fahey et al. 1985). Since environmental conditions and wood composition vary

across time and space, it is not surprising that the role of log decomposition in nutrient cycling is variable.

Wood chemistry has a strong effect on the species composition of initial colonists. Trees release volatile chemical compounds that attract or repel insects. For instance, the chemical verbenone repels some bark beetles at high concentrations whereas ethanol attracts insects such as the ambrosia beetle and some bark beetles. Additionally, chemicals emitted by fungi also attract xylophagous insects (Witcosky et al. 1986). Microbial establishment and biodegradation activity are also determined by the bole environment, because terpenes and other inhibitory extracts limit fungal and bacterial growth. Since these compounds are broken down by a relatively few fungi, yeasts, and bacteria, the presence of these organisms is an important part of the decomposition process. Biodegradation activities by these organisms can pave the way for further colonization (Schowalter et al. 1992).

One of the most critical functions of the initial insect colonizers is the creation of pathways for fungi and micro-organisms to begin the biological decomposition of the wood. Because decomposer colonization is dependent to a large degree on penetration of the bark by insect colonizers, the interaction between the decomposers and insect colonizers is often characterized by life history synchronization (Schowalter et al.

1992). The transport of microbial organisms into CWD can be either through passive transport or through mutualistic associations with arthropods, such as ambrosia beetles (*Trypodendron* sp. e.g. (Schowalter 2000).

Fungi are the dominant decomposers in coniferous forest ecosystems. Fungal colonization of decaying litter can be characterized by three stages: initial colonization by spores or hyphae, expansion to exploit resource niches, and finally exhaustion of resources and exiting of the area to find new substrates (Boddy 1992). Early colonizers can either diminish the nutrients in a substrate or transform the substrate into a more suitable resource for subsequent colonization (Frankland 1992). The colonization by fungi of any given piece of CWD depends on factors such as substrate composition, temperature, pH, moisture levels, the physical structure, and interactions with other microorganisms (Kaarik 1974; Rayner and Boddy 1988).

Fungal succession can proceed from fungi that primarily consume simple sugars, such as primary molds, to fungi that can degrade cellulose, lignin, and cellulose, such as white or brown rot basidomycetes, that are in turn replaced by those that consume simple sugars (Frankland 1992). Whether or not this successional pathway occurs depends on the nature of the change in the substrate, resource availability, and success of colonization of a substrate by a species (Frankland 1992).

Wood colonized by brown rot versus white rot illustrates well the impact that differences in fungal decay can have on CWD decomposition. White rot fungi decompose lignin as well as cell wall polysaccharides and their action is confined largely to near the hyphae. In contrast, brown rot fungi decompose cellulose and hemicellulose but not lignin (Harmon et al. 1986). If only brown rot fungi are present then the ratio of C to lignin will decrease over time. There is even variation in decay patterns within these groups. Some white rot fungi simultaneously degrade lignin, cellulose, and hemicellulose while others degrade lignin first and degrade cellulose and hemicellulose later (Worrall et al. 1997).

Researchers have speculated that differences in the initial community composition of heterotrophs could affect CWD decomposition rates (Carpenter et al. 1988; Schowalter et al. 1992). Additionally, Progar et al. (2000) noted that research had shown that seasonal moisture patterns affected the activity of heterotrophic organisms, and therefore the decomposition of litter, but no study had experimentally manipulated moisture of CWD to determine the effect of decay.

Progar et al. (2000) designed a study that would experimentally test whether differing initial heterotrophic colonization conditions and moisture differences would affect CWD decomposition, measured as respiration rates and composition of the fungal community. The experiment had six heterotrophic treatments (HET). The first three

treatments were designed to simulate insect penetration of CWD by drilling sterile holes to different depths. The remaining three treatments were designed to simulate three different fungal colonization pathways by drilling holes and injecting the logs with macrofungi (decay fungi), microfungi (molds), and a mixture of the two. The moisture treatment (TENT) consisted of placing tents over half of the experimental logs to restrict moisture inputs (Progar et al. 2000).

The primary goal of this study was to increase knowledge of the role heterotrophs play in CWD decomposition. Based on respiration rates, Progar et al., (2000) suggested that the moisture treatment, and to a lesser degree, the HET treatments, had affected the decomposition process during the first two years.

The current research was an attempt to assess whether the TENT and HET treatments were affecting respiration rates, and therefore decomposition, six years after the beginning of the initial study, and to determine whether the patterns of treatments effects were the same as reported in Progar et al. (2000). Additionally, the logs were sampled to determine if the treatments had affected the colonization of the logs by wood borers.

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Chapter 2: Respiration Response to Experimental Treatments

Abstract: Previous research on coarse woody debris (CWD) indicated that moisture content and initial heterotrophic colonization of decaying wood can affect the decomposition process. In 1995, 72 Douglas-fir (*Pseudotsuga menziesii*) logs fitted with respiration chambers were randomly placed at five replicate sites in old-growth stands. Each site had 6 heterotrophic (HET) x 2 moisture combinations (TENT). In the aggregate, the TENT treatment reduced moisture content from 45% to 36%, a 20 percent reduction in moisture levels. Respiration was sampled three times during the summer of 2001. The results indicated that the HET treatments were no longer affecting respiration rates. Analysis of the average of the three sampling periods revealed no TENT effect but examinations of the individual sampling dates suggested that tented logs had higher respiration rates over the course of the summer of 2001 than non-tented logs.

Introduction: Researchers have commonly used CO_2 efflux to examine the functioning of forest ecosystems, such as carbon budgets, and to study mineralization in nutrient cycling (Edwards 1982). Forest floor respiration rates have been one of the most commonly measured parameters in forest ecosystem research (Harmon et al. 1986) and measuring respiration rates has been a common method for studying log decomposition (Harmon et al. 1986).

Respiration removes C from CWD and results primarily from the activity of microbes. As decay of CWD proceeds, the loss of C through respiration decreases the ratio of C to nutrients, such as N (Harmon et al.1986; Swift et al., 1979). The ratio of C to nutrients, especially N, is important because the availability of nutrients to decomposers is one of the factors that controls decay rates. Decomposers of CWD have lower ratios of C to nutrients than the resource, which is indicative of the high demand for nutrients (Swift et al. 1979). Low N and P levels are in part the reason for the relatively slower decay of CWD by fungi than other types of litter, such as leaf litter. Swift et al. (1979) concluded that wood decay provides "... perhaps the most extreme example of nutrient limitation due to the very low nutrient contents of wood."

The physical properties of wood affect the ability of organisms to decompose CWD and thus affect respiration rates. Studies that have examined CWD of different species reported differences in respiration

rates based upon differences in substrate quality (Carpenter et al, 1988; Marra and Edmonds 1994), such as amount of heartwood extractives or decay class. Respiration is typically highest in class 1 and/or class 2 logs and then declines (Marra and Edwards 1994; Sollins et al. 1987). Respiration can increase in later stages of decay, which is attributed in part to the colonization of CWD by roots (Marra and Edwards 1994).

A number of factors regulate the decomposition process: temperature, moisture, gas levels (O_2 and CO_2), substrate quality, the size of the CWD, and the community composition of the decomposer organisms (Harmon et al. 1986). Respiration reflects biotic activity in response to environmental conditions.

Some researchers have found a relationship between log diameter and respiration rates, but no consistent pattern has been found. In general, larger logs are believed to decay faster than smaller logs because the lower surface to volume ratios lead to a less suitable environment for microbial colonization (decreased gas diffusion e.g.) and thus slower decomposition of the smaller logs (Harmon et al. 1986). However, there are studies that found no significant diameter effect on the rate of decomposition (Graham 1982; Harmon et al. 1986) or reported diameter effects that varied by decay class (Marra and Edwards 1994). Marra and Edwards (1994) found that western hemlock logs in decay classes 1 and 2 had higher respiration rates with increasing diameter while class 3 logs had the opposite trends.

They speculated that the higher respiration in the larger diameter class 1-2 logs was due to increased insect colonization or a greater mass per unit surface area for the larger diameter logs.

Differences in substrate quality between tree species have been shown to affect respiration rates. As an example, Marra and Edmonds (1994) found that Class 1 and 2 logs had higher respiration rates than did class three logs and western hemlock had higher rates than did Douglas-fir. Western Hemlock (*Tsuga heterophylla*) is considered to be higher substrate quality than Douglas-fir, in part because Douglas-fir has more heartwood extractives than does western hemlock.

Hope and Li (1997) reported that respiration varied with depth in a log. Respiration rates in the study were found to be greater at 0-4 cm depth than at 4-20 cm depth. Since heartwood would comprise a large percentage of the 4-20 cm depth, the poorer quality substrate might be the cause of the lower respiration rates. Additionally, less oxygen diffusion to the greater depth should be a factor.

Moisture and temperature have been widely studied because variation in these factors affects decomposition processes over a wide range of spatial scales. In general, biological and chemical processes increase with increasing temperature up to a maximum point. The so-called Q_{10} equation reflects doubling of chemical and biological processes for each 10° C increase in temperature within a limited range. Yoneda (1975) reported

that CO_2 evolution rates in CWD rose exponentially with rising temperature, with Q_{10} values ranging from to 1.76 to 3.32.

A number of studies have indicated that moisture levels affect respiration rates (Hope and Li 1997; Progar et al. 2000; Yoneda 1975). Respiration rates are limited at very high and very low moisture levels. Yoneda (1975) found intermediate moisture levels in the logs produced the highest rates respiration rates. Progar et al. (2000) reported that moisture content can significantly affect carbon flux in the logs used in the current study with logs with low moisture due to experimental manipulation having higher respiration than logs receiving normal moisture inputs.

There has been some research that has indicates that differences in heterotrophic colonization can lead to differences in respiration (Marra and Edwards 1994; Progar et al. 2000). Progar et al. (2000) found evidence that logs inoculated with decay fungi had higher respiration rates in the first year of decomposition. Based upon their findings, they concluded that decay activity by basidiomycetes would be higher in the western Cascades under warmer and drier conditions predicted by global climate change models.

Regional climatic patterns together with site variations (north facing versus south facing slope e.g.) form the basis of decomposition dynamics at the stand level. In the Pacific Northwest, precipitation is highest from

late-fall to spring when temperatures are lowest, whereas the warmer summer months are typically the driest part of the year. These moisture and temperature patterns are the basis for seasonal variation in respiration rates with respiration highest in the late-summer early fall and the lowest rates in the winter (Carpenter et al. 1988; Marra and Edmonds 1994; Progar et al. 2000). Carpenter et al. (1988) and Marra and Edmonds (1994) found that respiration rates were highest in the fall and lowest in the winter. Hope and Li (1997) speculated that low mid-summer respiration rates were due to low moisture content and high temperatures. In contrast, Carpenter et al. (1988) found that high moisture levels that lasted until late summer restricted respiration rates.

Moisture and temperature control gas diffusion rates. High moisture levels can lead to anaerobic conditions. Recent research by Hicks and Harmon (2002) indicate that anaerobic conditions in CWD in terrestrial ecosystems is relatively rare compared to water soaked logs; however, they noted that decayed CWD may be less prone to developing anaerobic conditions than sound wood.

Variation in environmental conditions also affects respiration rates because of the effects on decomposer organisms. For instance, most fungi are mesophilic (i.e. cannot grow above 40 Celsius) and have an optimum temperature 25 and 30 Celsius. In terms of moisture content, both high and low moisture content can limit the activity of decomposers. Kaarik (1976)

reported that moisture levels from 30% to 160 % were suitable for the growth of basidiomycetes, which are the primary decomposers of CWD in terrestrial ecosystems. Bacteria, and ascomycetes are more tolerant of higher moisture levels than basdiomycetes and thus dominate CWD decomposition in water-logged/aquatic environments (Harmon et al. 1986). Similarly, insect activity is constrained by extremes in environmental conditions. For example, thermophilic insects tend to inhabit the upper portion of a log (Harmon et al. 1986).

The underlying hypothesis that was tested in the current research was that the experimental treatments (TENT and HET) have altered the abiotic conditions and/or heterotrophic community to the point where differences in decomposition occurred and would be reflected through respiration. My hypothesis was that the reduced moisture levels in the tented logs would continue to lead to higher respiration rates than in the non-tented logs. I hypothesized that those logs injected with decay fungi (HET # 5 and 6) would have higher respiration rates than the other logs in 2001.

Methods: The study site was located at the H.J. Andrews Experimental Forest, a Long Term Ecological Research (LTER) site, located 80 km east of Eugene, Oregon in the central western Cascade Mountains (44° N, 122 W °). In 1995, 360 experimental Douglas-fir logs (25-35 cm diameter, 1.5 m long) were randomly assigned to five replicate sites. All the sites were in old-growth stands ranging in elevation from 700-1000 m. The logs at each site were randomly assigned to 12 treatments combinations (6 heterotrophic treatments) (HET) x 2 moisture contents (TENT) (Progar et al. 2000).

The moisture treatments consisted of half of the experimental logs being placed under elevated plastic tents and the other half exposed to normal levels of precipitation. HET treatments 1-3 were designed to simulate different levels of insect penetration: no penetration (1); drilled sterile 3mm diameter holes, 10 deep mm, at a density of $50m^{-2}$ of log surface area (2); and drilled sterile 3mm diameter holes, 37 mm deep, at a density of $50m^{-2}$ of log surface area. HET treatments 4-6 consisted of the experimental logs being drilled with sterile 3mm diameter holes, 37 mm deep, over $50m^{-2}$ of log with each one receiving a different injection of fungi: ascomycetes (4), basidiomycete decay fungi (5), and a mix of the fungi used in 4 and 5 (6). Further details are given in Progar et al. (2000).

Respiration was measured using the soda lime technique outlined by Edwards (1982). Respiration chambers (20 cm diameter x 20 cm high

PVC) were installed near the top center of the log. Respiration measurements were taken by placing an open jar (10cm diameter x 8cm high) containing 30g soda lime in each chamber and then capping and sealing the chamber for 24 hours to allow CO_2 movement. The soda lime was dried at 100 degrees C for 24 hrs before and after field collection. During 2001, respiration was measured June 2-3, July-20-21, and September 12-13th. In the June sampling, only sites 1-4 were accessed for sampling. Efflux of CO_2 during the 24 hour period was calculated by subtracting the 2nd weight measurement from the first.

To measure ambient CO_2 efflux, two control chambers (20 cm x 20cm high PVC) were placed at each site at opposite ends of the stands and measured using the methods described above. The two control efflux measurements were averaged to obtain a stand average. CO_2 efflux from heterotrophic activity was calculated by subtracting the average efflux of the two site controls from the effluxes from each of the chambers attached to the logs at that site.

Samples for moisture were taken with an increment borer. The cores were weighed, dried at 50 C° until weight was constant, and then reweighed. Moisture content was measured as the difference between the two weights. Percent moisture was calculated as (wet weight- dry weight)/dry weight. Moisture measurements were taken during the June, July, and September sampling periods. Temperature measurements were

taken with a mercury thermometer for the September measurement period. One measurement was taken before placing the soda lime jars in the chamber and after the soda lime jar was collected. The two temperatures were averaged for comparison.

Climate data from two weather stations at Andrews Experimental Forest was obtained from http://www.fsl.orst.edu/climhy/climdb/. Central Meteorological (CENMET) station is located in a regenerating clearcut (cut in 1967) at an elevation of 1018 meters. Primary Meteorological (PRIMET) station is located in an artificially maintained clearing at an elevation of 430 meters.

Carbon efflux was analyzed using two-way ANOVA with heterotrophic treatment, tent treatment as main factors and site as a block. Moisture content of the logs was also analyzed using two-way ANOVA with heterotrophic treatment, tent treatment, and site as factors. Each of the three sampling periods was analyzed using separate ANOVAs. The three sampling periods (sites 1 to 4) were then averaged and analyzed using the same manner as described above. Respiration rates were logged transformed using natural logarithm to better meet assumptions of normality. Significance level was set at $p=0.05$. Regression analysis was used on the combined data and the three individual sampling periods to determine if there was a correlation between moisture content of logs and respiration. All statistical analysis was conducted using S-PLUS.

Results: When the three sampling periods were averaged together, ANOVA indicated that site was significance (p=0.0013) and the tent treatment approached significance (p=0.073) (table 2.1) (Appendix table 4.1). Respiration of the tented logs had a mean efflux of 0.10 g CO_2 m^{-2} d^{-1} ± 0.06 and the non-tented logs 0.12 g CO_2 m^{-2} d^{-1} ± 0.04 (fig.2.1). Site 4 had the highest mean efflux (0.19 g CO_2 m^{-2} d^{-1} ± 0.05) and site 2 had the lowest 0.03 g CO_2 m^{-2} d^{-1} ± 0.03.

The mean respiration in the June sampling period was 0.1 g CO_2 m^{-2} d^{-1}. As figures 2.2 – 2.5 indicate, the respiration levels were very low, with a few exceptions, especially at sites 1 and 2. Respiration differences between sites were statistically significant (p = 0.05) but there was no evidence for a statistically significant difference in TENT or the HET treatment logs (p> 0.50) (Appendix table 4.2). Site 4 had the highest mean efflux of 0.23 ±0.05 g CO_2 m^{-2} d^{-1} and site 1 the lowest at 0.03± 0.05 g CO_2 m^{-2} d^{-1} Negative effluxes reflected a lower efflux than the control average.

In July, respiration differed significantly between sites (p< 0.001) (table 2.1) (Appendix table 4.3). Site 2 had the lowest mean efflux with 0.09 g CO_2 m^{-2} d^{-1} and site 5 had the highest efflux 0.37 g CO_2 m^{-2} d^{-1} (fig. 2.4). Additionally, the mean efflux of the non-tented 0.14 ± 0.05 g CO_2 m^{-2} d^{-1} and tented logs 0.20 ± 0.05 g CO_2 m^{-2} d^{-1} (fig. 2.2) was significantly different (p-value = 0.014).

In September, the mean efflux for the tented logs was 0.20 ± 0.05 g CO_2 m^{-2} d^{-} and non-tented 0.12 ± 0.06 g CO_2 m^{-2} d^{-1} (p-value=0.0014)(fig. 2.2) (Appendix table 4.4). Respiration differed significantly by site ($p<$ 0.0001) (table 2.1). Sites 3 and 4 had higher mean effluxes than 1, 2 and 5 (fig. 2.5).

Table 2.1. P values for respiration measured from Douglas-fir logs with heterotrophic (HET) and tent treatments (TENT) at the five replicate sites in the H.J. Andrews Experimental Forest during 2001.

C Efflux	June	July	Sept.	Combined
site	0.05	p< 0.0001	p< 0.0001	0.0013
HET	0.62	0.74	0.53	0.68
TENT	0.89	0.014	0.0014	0.073
HET x TENT	0.56	0.48	0.76	1.0

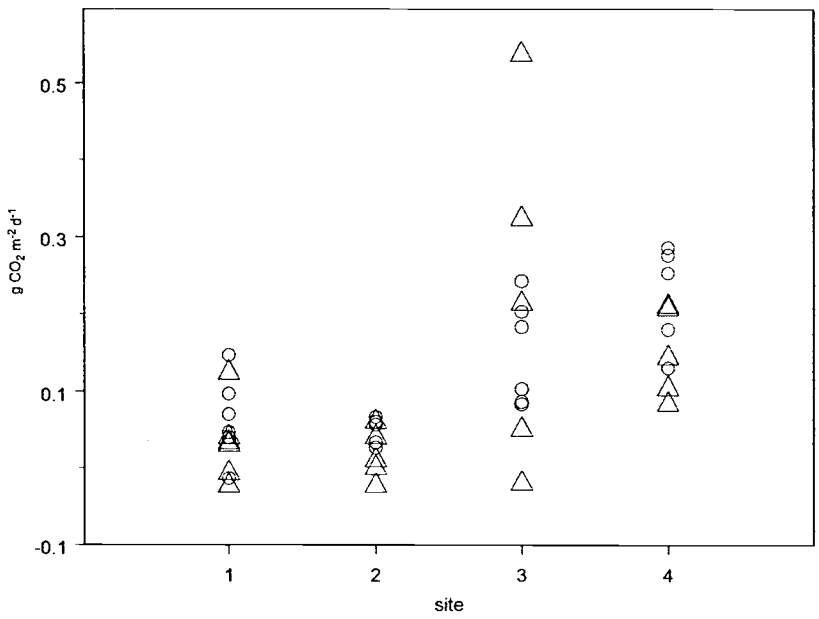

Figure 2.1. Respiration averages of the June, July, and September 2001 sampling periods from the experimental Douglas-fir logs at sites 1-4 in the H.J. Andrews Experimental Forest and by TENT treatment. Open circles represent non-tented logs and triangles represent tented logs.

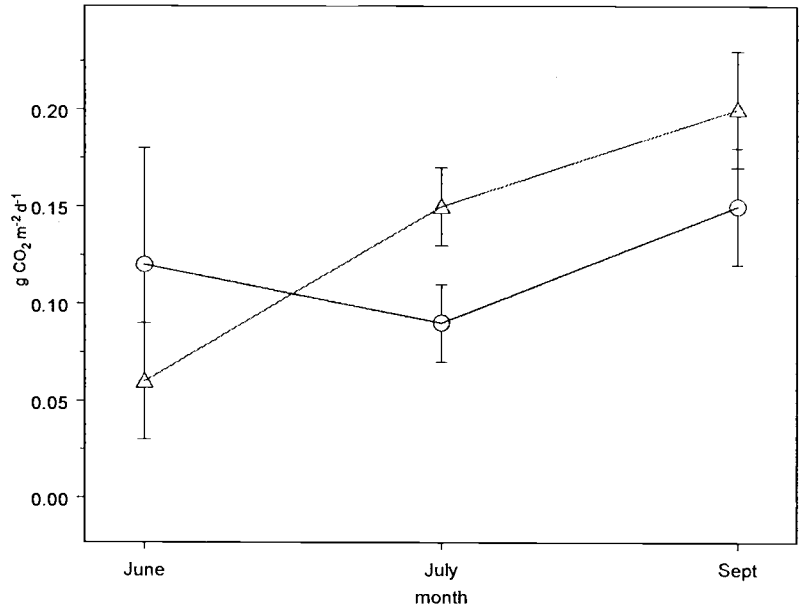

Figure 2.2. Mean respiration from experimental Douglas-fir logs by month of sampling in 2001 for the tented (triangles) and non-tented logs (open circles) at H.J. Andrews Experimental Forest. Bars represent one standard error of the mean.

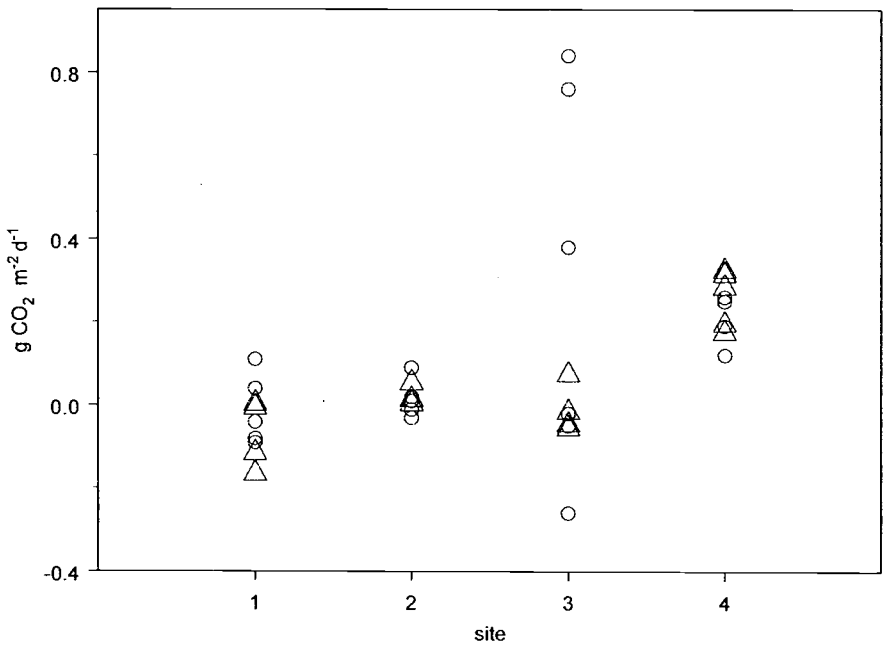

Figure 2.3. Respiration from experimental Douglas-fir logs for the June 2001 sampling period for sites 1-4 and the tented (triangles) and non-tented logs (open circles) at the H.J. Andrews Experimental Forest.

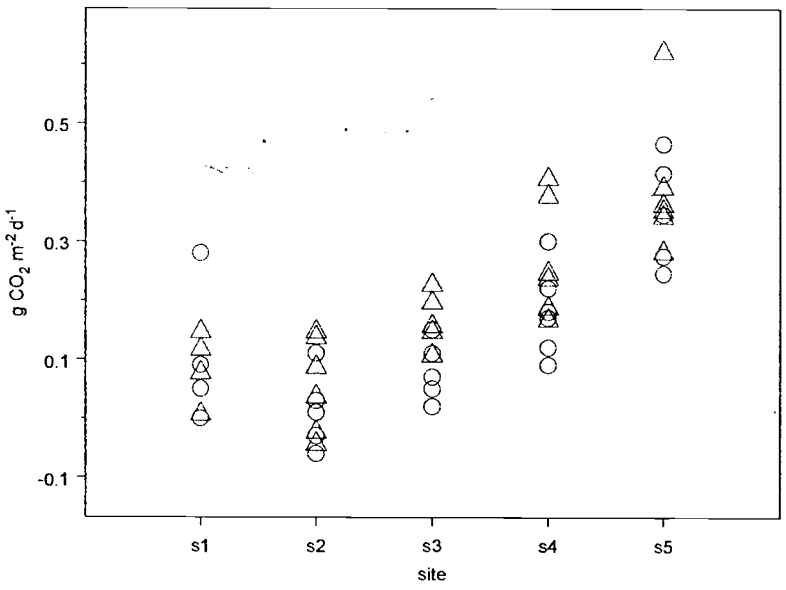

Figure 2.4. Respiration from experimental Douglas-fir logs for the July 2001 sampling period for sites 1-5 and the tented (triangles) and non-tented logs (open circles) at the H.J. Andrews Experimental Forest.

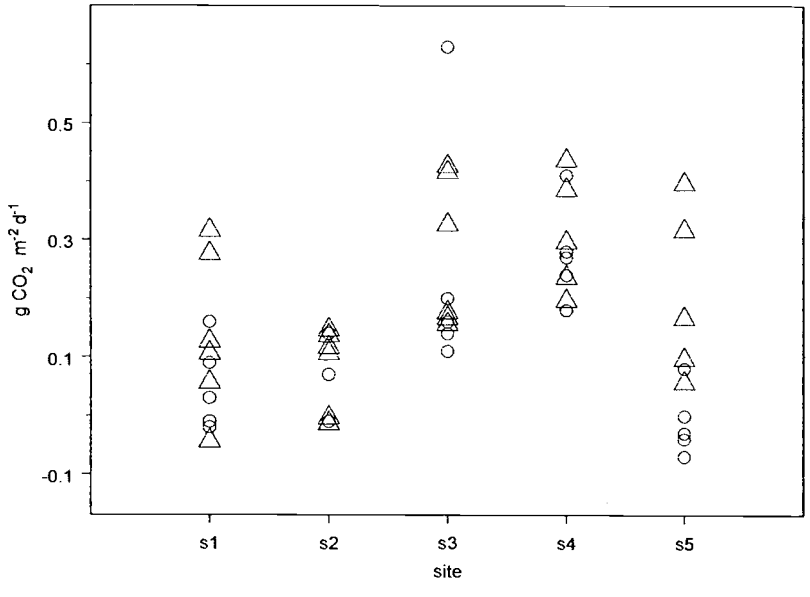

Figure 2.5. Respiration from experimental Douglas-fir logs for the September 2001 sampling for sites 1-5 and the tented (triangles) and non-tented logs (open circles) at H.J. Andrews Experimental Forest.

Examined on the whole, the tented logs contained less moisture than the non-tented logs ($p=0.0013$) (Table 2.2)(Appendix table 4.5). The mean moisture content of the tented logs was 36%±4 and non-tented 45%±5 (fig. 2.6). Site was also a significant factor ($p<0.001$) with site 1 having the highest mean moisture (51%±8) and site 4 had the lowest mean (33% ±5). There was no evidence of an interaction between HET and TENT.

When examined individually, the tent treatment was a significant factor ($p<0.05$) in June, July, and September (table 2.2). Site differences were significant ($p<0.05$) in June and September. In June, the tented logs had a mean moisture content of 40% ±8 and the non-tented logs 46% ±7 (fig. 2.7, fig. 2.8). In July, the tented logs had a mean moisture content of 35%±6 and the non-tented logs 43 ±6 (fig. 2.7, fig. 2.9). In September, the mean moisture content of the tented logs was 33% ±2 and the non-tented logs was 43%±6 (fig. 2.7, fig 2.10).

Table 2.2. P values for the percent moisture of the experimental Douglas-fir logs sampled in June, July, August and the average of the three at the H.J. Andrews Experimental Forest.

Moisture	JUNE	JULY	SEPT.	Combined
Site	0.00025	0.56	0.007	p< 0.001
HET	0.204	0.76	0.55	0.63
TENT	0.037	0.03	p< 0.001	0.00013
HET x TENT	0.41	.40	0.46	0.20

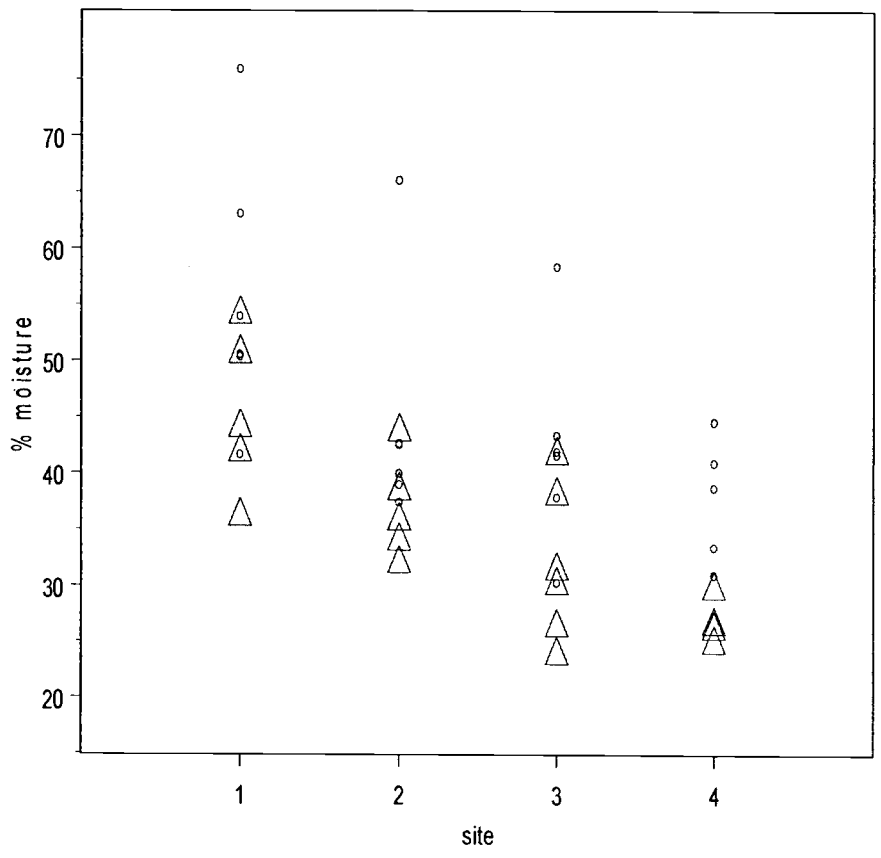

Figure 2.6. Average percent moisture of the June, July, and September sampling periods of the experimental Douglas-fir logs at sites 1-4. Triangles represent the tented logs and open circles represent non-tented logs.

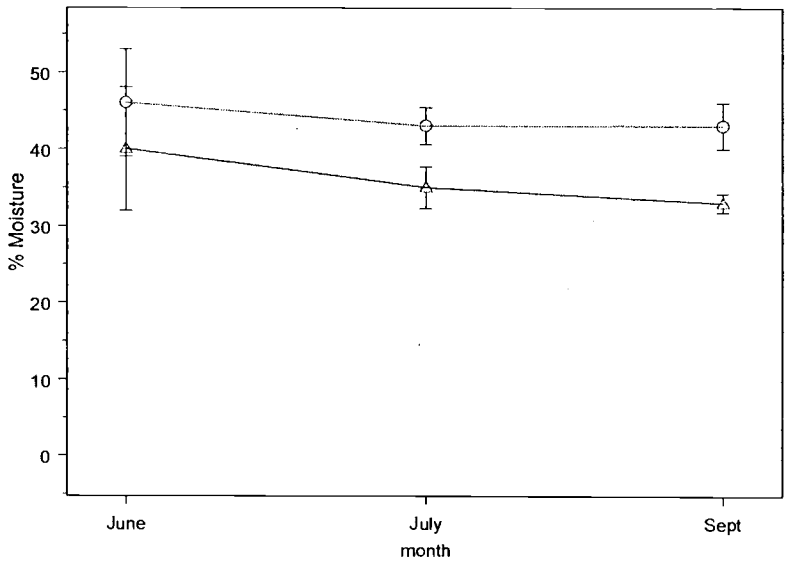

Figure 2.7. Percent moisture for June, July, and September 2001 samplings of the tented (triangles) and non-tented (open circles) experimental Douglas-fir logs. Bars represent standard error of mean.

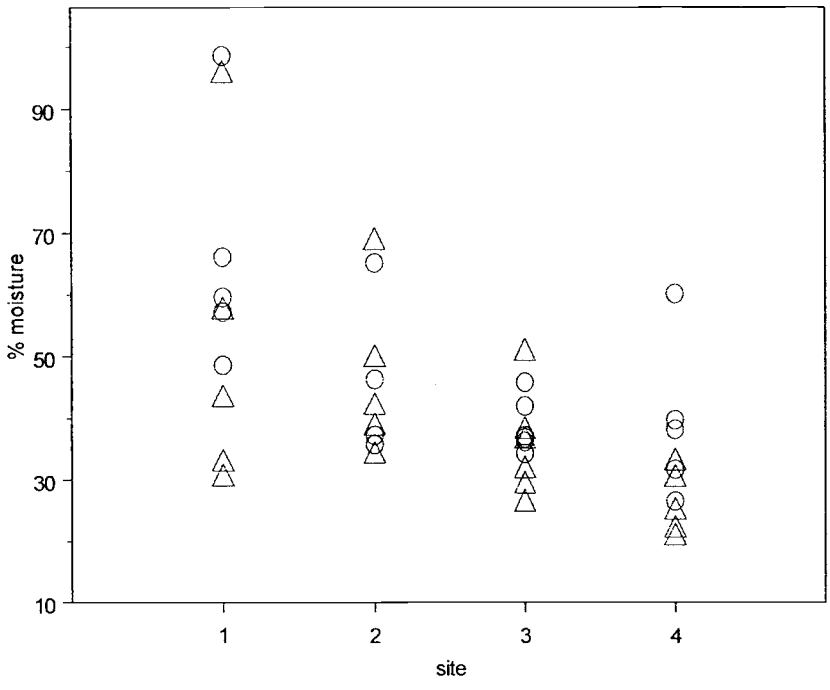

Figure 2.8. Percent moisture for the June 2001 sampling of the tented (triangles) and non-tented (open circles) experimental Douglas-fir logs in the H.J. Andrews Experimental Forest at sites 1-4.

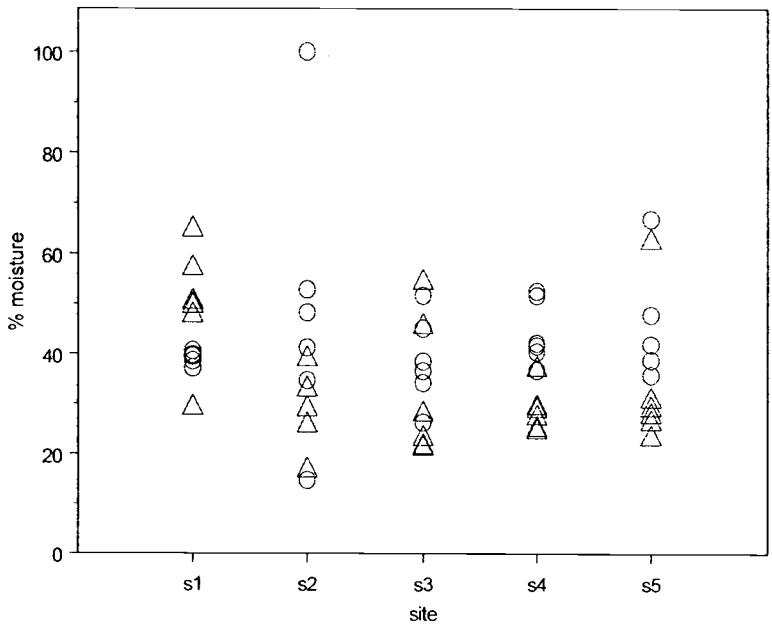

Figure 2.9. Percent moisture for the July 2001 sampling of the tented (triangles) and non-tented (open circles) experimental Douglas-fir logs in the H.J. Andrews Experimental Forest at sites 1-5.

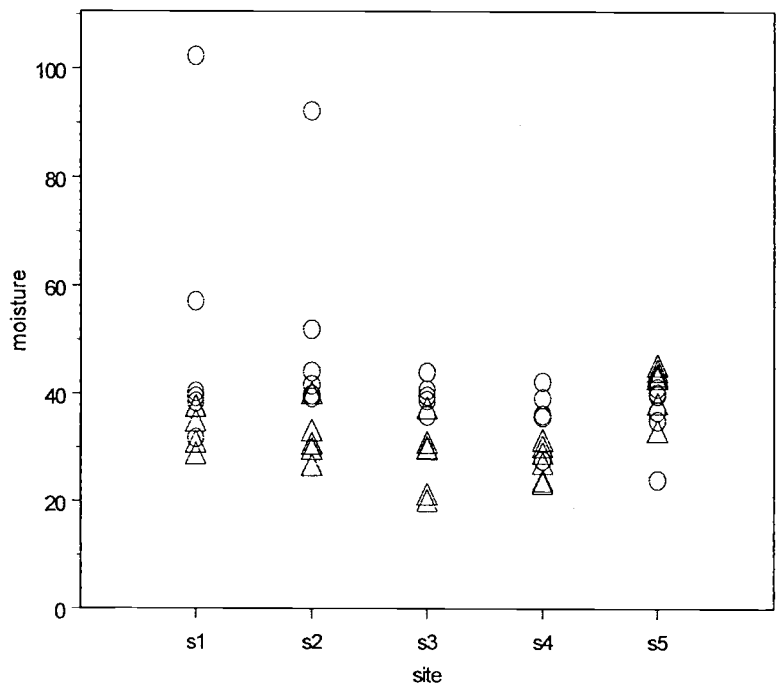

Figure 2.10. Percent moisture for the September 2001 sampling for the tented (triangles) and non-tented (open circles) experimental Douglas-fir logs in the H.J. Andrews Experimental Forest at sites 1-5.

There was no correlation between the % moisture and the C efflux for the combined measurements (R^2 =0.0065, p=0.61)(fig. 2.11). Individual regressions of the sampling periods provided support for a very weak correlation between % moisture level and respiration: June: R^2 =0.095, p= 0.047 (fig. 2.12); July: R^2 =0.058, p=0.013 (fig. 2.13); September: R^2 =0.097, p=0.018 (fig. 2.14).

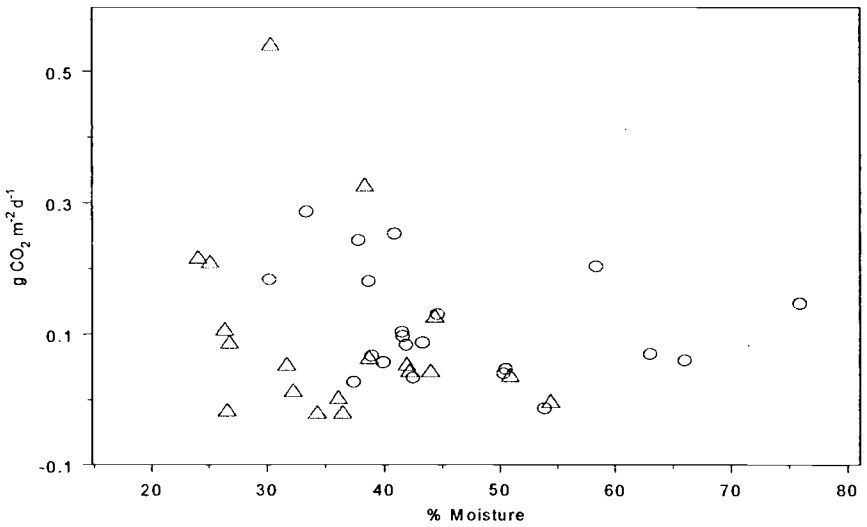

Figure 2.11. Percent moisture versus respiration from the tented (triangles) and non-tented (open circles) experimental Douglas-fir logs for the average of the June, July, and September 2001 sampling periods at the H.J. Andrews Experimental Forest.

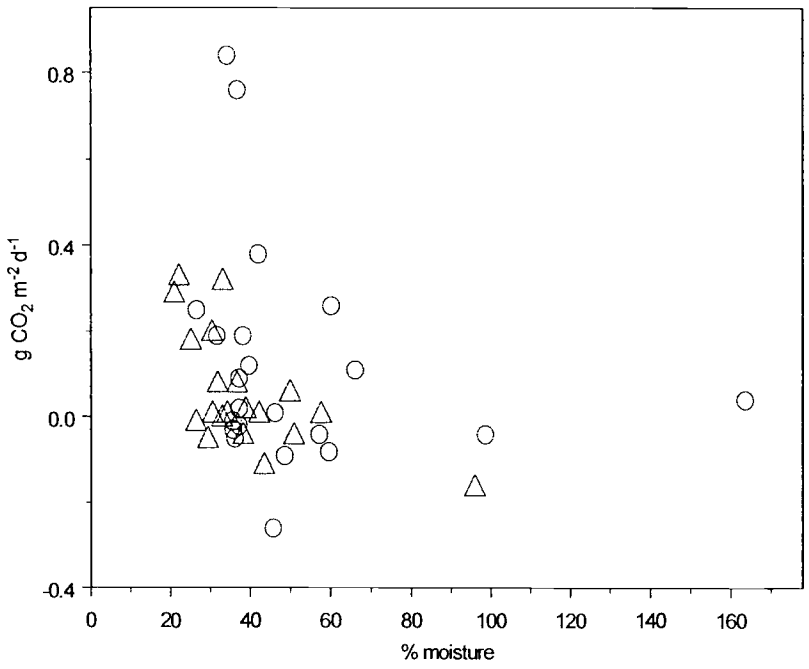

Figure 2.12. Percent moisture vs. respiration in the tented (triangles) and non-tented (open circles) experimental Douglas-fir logs for the June 2001 sampling period at the H.J. Andrews Experimental Forest.

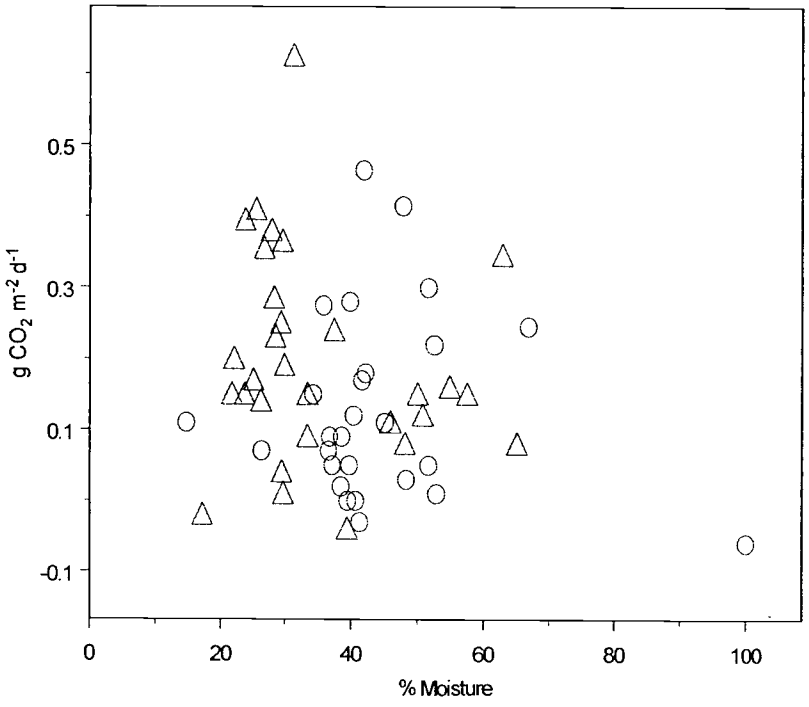

Figure 2.13. Percent moisture vs. respiration in the tented (triangles) and non-tented (open circles) experimental Douglas-fir logs for the July 2001 sampling period at the H.J. Andrews Experimental Forest.

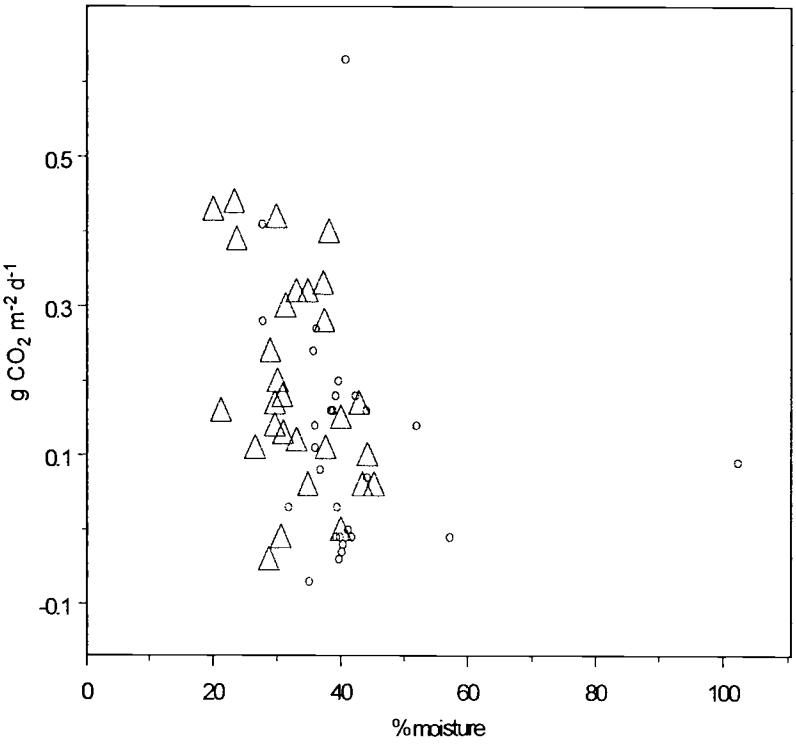

Figure 2.14. Percent moisture vs. respiration in the tented (triangles) and non-tented (open circles) experimental Douglas-fir logs for the September 2001 sampling period at the H.J. Andrews Experimental Forest. Circles represent non-tented logs and triangles represent tented logs.

Temperature measurements taken during the September sampling period indicate that overall the tents appear to have slightly higher temperatures in the chambers; however, the differences are quite small, and at site 1, the non-tented logs had a higher average than the tented logs (fig. 2.15). The largest difference occurred at site 5 where the tented logs had a mean temperature of 18.33 C° and non-tented a mean of 16.5 C° or a difference of 1.83 degrees.

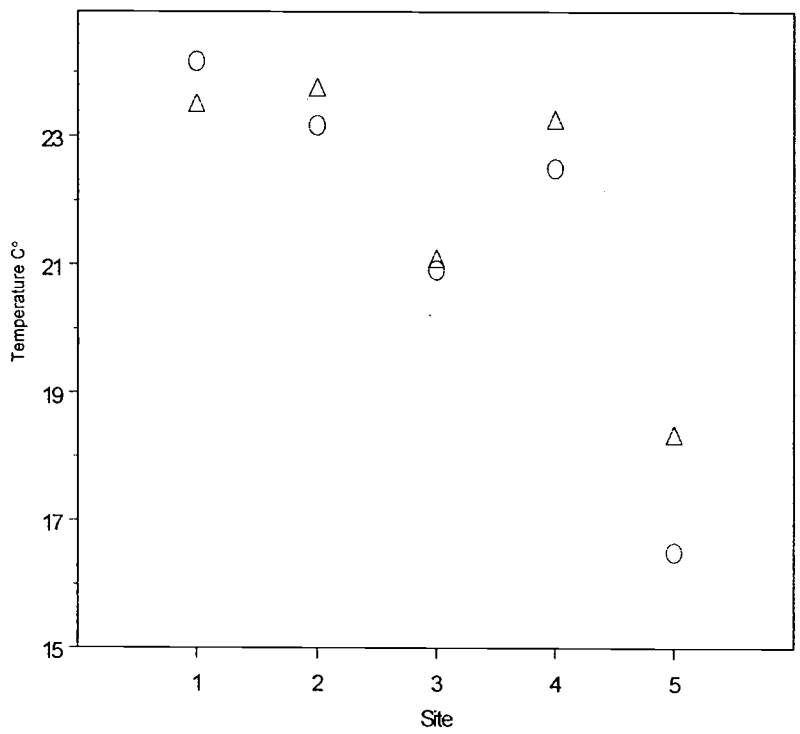

Figure 2.15. Combined temperature averages taken during the September sampling period for sites 1-5 at the H.J. Andrews Experimental Forest for the measurements taken in the respiration chamber shortly before the jar was placed into the chamber and shortly after the jar was taken out of the chamber.

The mean temperature at PRIMET in 2001 was 10.6 C°, which was higher than any of the original sampling years: 1995 (9.6 C°), 1996 (9.1 C°), 1997 (9.9C°) (fig. 2.18). The general weather patterns from the meteorological data indicate that 2001 was warmer and drier than the period of 1995-1997. The driest conditions in September were associated with the highest respiration rates.

While annual temperatures rose from 1995 to 2001, annual precipitation dropped dramatically. Based on data from the primary meteorological station (PRIMET) and central meteorological station (CENMET) 2, precipitation in 1996 were very high (over 3000 mm) and precipitation dropped to near 2000 mm in 2000 and moisture continued to decline in 2001 (figs. 2.16 and 2.17). The 20 % reduction in wood moisture was the same value reported in Progar et al. (2000), but the decline in precipitation probably contributed to the decrease in the overall moisture in the logs from 54% in 1996 to 45% in 2001 in the non-tented logs.

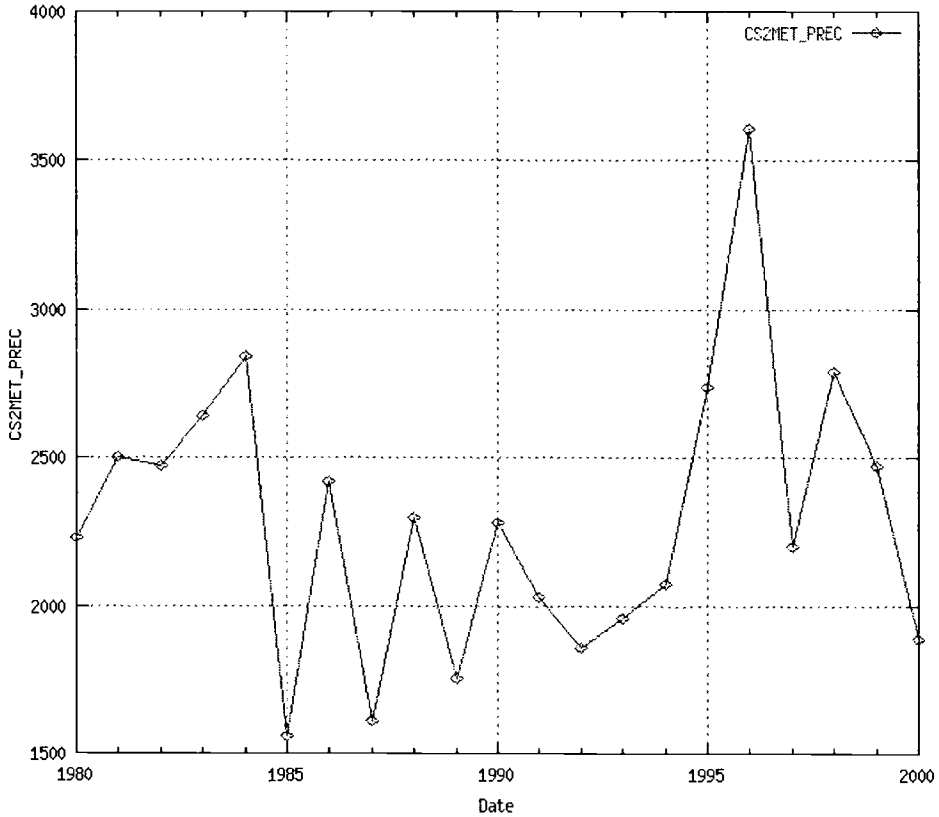

Figure 2.16. Precipitation (mm) from 1980 to 2000 at Central Metrological Station 2 located in the HJ Andrew Experimental Forest. Data source: Andrews Experimental Forest: Meteorological stations: Corvallis, OR: Forest Science Data Bank: MS001. [Database]. Graph source: http://www.fsl.orst.edu/climhy/climdb/ (2-01-03).

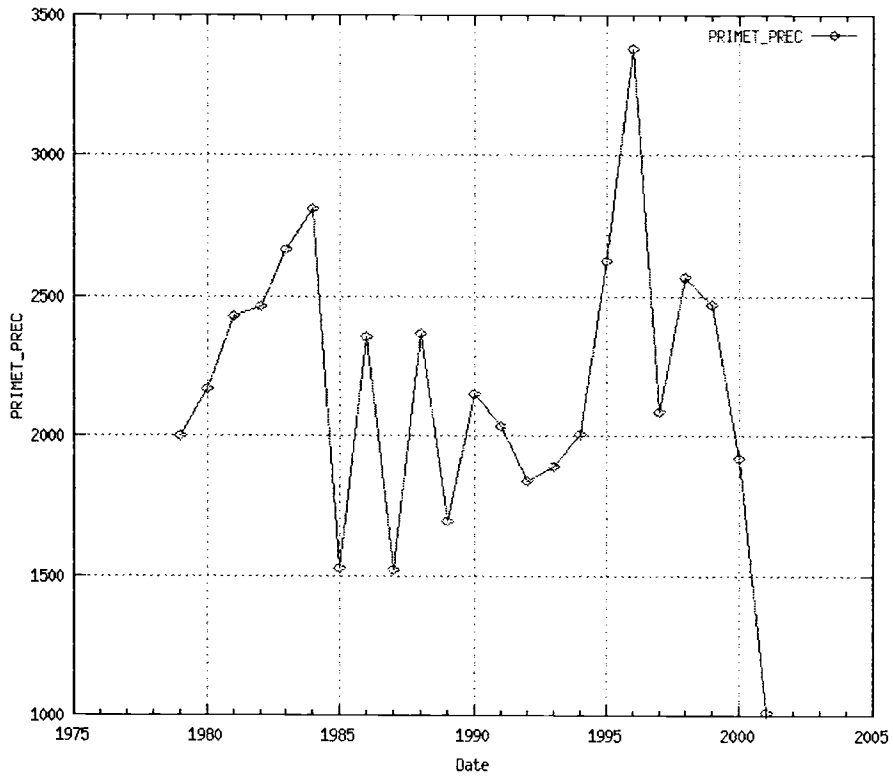

Fig. 2.17 Precipitation (mm) from 1979 to 2001 at the Primary Metrological Station located in the HJ Andrews Experimental Forest. Data source: Andrews Experimental Forest: Meteorological stations: Corvallis, OR: Forest Science Data Bank: MS001. [Database]. http://www.fsl.orst.edu/climhy/climdb/ (2-01-03).

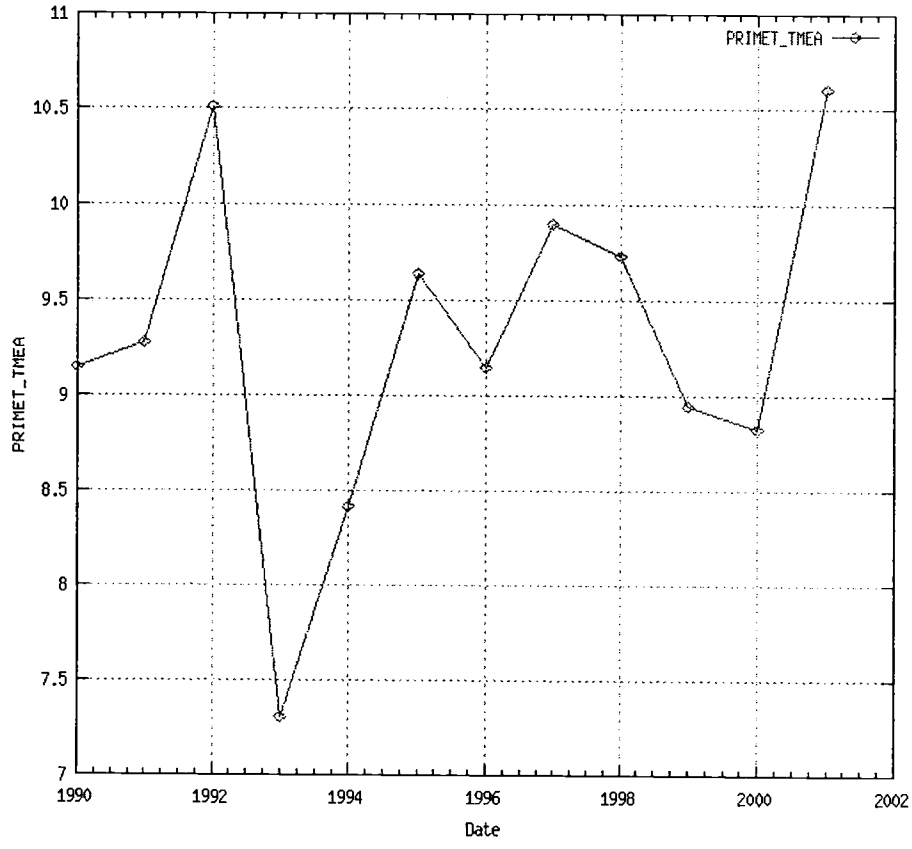

Figure 2.18. Yearly temperature (C°) averages for the Primary Meteorological Station. Data source: Andrews Experimental Forest: Meteorological stations: Corvallis, OR: Forest Science Data Bank: MS001. [Database]. http://www.fsl.orst.edu/climhy/climdb/ (2-01-03).

Discussion: Progar et al. (2000) reported that the logs inoculated with decay fungi appeared to have the highest respiration rates, but this was not statistically significant ($p=0.08$). In subsequent measurements, Progar et al. (2000) found that the logs inoculated with decay fungi had some of the highest respiration rates of the HET treatments but this trend was also not significant. Based on their data, I hypothesized that only the logs injected with basidiomycetes (HET treatment # 5 and # 6) would be likely to still influencing decomposition, but there was no evidence for any HET treatment effect.

The lack of evidence for an effect of the HET treatments on respiration rates in this study was not entirely unexpected given earlier results. Progar et al. (2000) found evidence that HET treatments had an effect on respiration. Logs inoculated with decay fungi and those that were not penetrated had the highest respiration rates in the first year. In general, logs inoculated with decay fungi generally had the highest respiration rates. In the current study, statistical analysis of the averages of the three sampling periods showed no HET treatment effects. Fungal isolations after the study began indicated that differences in the microbial communities due to the HET treatments disappeared after one year (Progar et al. 2000).

Examination of the respiration of the three sampling periods averaged together did not support the hypothesis that the tented logs would have higher respiration rates than the non-tented logs. The non-tented logs

actually had a slightly higher mean respiration than the tented logs but the difference was not significant. Regression analysis indicated that there was no correlation between the % moisture and C efflux. The combined mean % moisture of the non-tented logs was 20 % higher than in the tented logs.

The respiration data suggested a seasonal respiration trend with respiration higher in late-summer than in late-spring. Other research on respiration from CWD conducted in the western Cascades and Olympic Peninsula has found similar seasonal trend that respiration rates were highest in the drier part of the year (Carpenter et al. 1988; Marra and Edmonds 1994; Progar et al. 2000). The pattern of moisture content and respiration rates over the course of the three sample dates differed between the tented and non-tented logs (fig. 2.19).

Since the tented logs had significantly higher respiration in July and September, it follows that respiration would show a correlation with moisture levels but no such correlation was found. Because the moisture measurements integrate the moisture content of all the substrates, it is possible that testing for a relationship between sapwood moisture levels and respiration would produce a higher correlation, because sapwood is the most favorable substrate for heterotrophs available after the inner bark has been decayed. Additionally, spatial heterogeneity in moisture levels can exist in wood (Boddy 1983) and research has indicated that the heartwood and sapwood can vary significantly in moisture content (Carpenter et al. 1988).

Carpenter et al. (1988) suggested the generally dry conditions in autumn in the Pacific Northwest favor activity by basidiomycetes. Decay fungi are able to grow at moisture levels as low as 20% to 30% (Kaarik 1976; Progar et al. 2000). The range of moisture levels (25% to 76%) for the average of the three sampling periods fell within the above mentioned range, and as figures 2.11-2.14 illustrate, logs with moisture levels below 30% did not necessarily have the lowest respiration rates.

Variations in fungal colonization might explain part of the differences in respiration rates. Progar et al. (2000) found evidence for antagonistic interactions between decay and mold fungi reduced as respiration rates when they were injected into the logs together (HET # 6). If these types of interactions (whether or not related to the HET treatments) slowed colonization of the sapwood by basidiomycetes, then these interactions could have contributed to lower respiration rates by reducing colonization of sapwood. Additionally, decay fungi vary in the amount of activity by species; e.g., brown rot fungi differ at the rate at which they decay wood (Kaarik 1974).

Overall, respiration rates declined from the 1995-1996 to 2001. Progar et al. (2000) reported the highest mean respiration of approximately 9 g CO_2 m^{-2} d^{-1} and a low of approximately 0.5 g CO_2 m^{-2} d^{-1}, which was much higher the range of values in this study. A decline in respiration rates was expected given the utilization of easily degradable components

of the inner bark during the first years of colonization (Harmon et al. 1986).

By 2001, bark beetles, wood-borers and microorganisms had consumed nearly all the inner bark thereby leaving only the more recalcitrant substrates available for consumption. After six years of decomposition, any variations in nutrient content and amount of structural components in the sapwood have the potential to affect respiration rates. For example, Edmonds (1987) found that the decomposition of small diameter woody litter (branches, twigs and cones) was highly correlated with the ratio of initial lignin/initial N. However, there is no single factor that controls respiration (Carpenter et al. 1988), and thus, decomposition.

In terms of the tents affecting microclimate, fig. 2.15 provides evidence that the tents for the most part did not cause a difference in temperature between the tented and non-tented logs. Only at site five, where the average temperature under the tents was 1.83 degrees higher than under the non-tented logs was there evidence of a temperature effect from the tents.

The study was not designed primarily to assess the effect of stand location, but the results of the current study (together with past results) indicate site location influences respiration rates. In the combined analysis, both the % moisture and respiration varied significantly ($p<0.05$) by site (tables 2.1 and 2.2). Progar et al. (2002) reported significantly

higher respiration rates in logs sites 4 and 5 (south facing) than the three north-facing sites, but in contrast to this study, they did not find a significant difference in moisture content between the sites. Progar et al. (2000) speculated that respiration at the two south facing sites (4+ 5) was higher because of increased temperatures but no temperature data were available for analysis in the current or past study. Site moisture levels did significantly vary but moisture differences alone cannot explain differences in respiration because there was little correlation between % moisture and respiration.

In sum, the results suggest drier conditions, on a seasonal basis, are associated with higher levels of heterotrophic activity, which is expressed through higher respiration rates. The lack of correlation between moisture levels and respiration rates implies that in mid- to late-summer, when respiration was higher in the tented logs, moisture levels are interacting with other factor(s) that are more directly controlling respiration. The initial differences in moisture may have resulted in different heterotrophic communities, with the communities in the tented logs being seasonally more active than in the non-tented logs, and the differences in respiration in 2001 being more closely tied to substrate quality rather than moisture differences. Moisture content might have had a better correlation with respiration from 1995-1997 when at least some of the inner bark was still available for consumption. The lack of HET treatment effects provides

further evidence that differences in decomposition due to differing initial heterotrophic communities, as represented by the HET treatments, are short-lived and confined to the inner bark.

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Chapter 3: The Effects of Heterotrophic Colonization on the Decay of Coarse Woody Debris

Abstract: Previous research on coarse woody debris (CWD) indicates that the moisture content and initial heterotrophic colonization can affect the decomposition process. Six heterotrophic treatments were created to simulate the effects of physical penetration of the bark and wood and the transmission of ascomycetes versus basidiomycetes into CWD. In 1995, 72 Douglas-fir (*Pseudotsuga menziesii*) logs (60 fitted with respiration chambers) were randomly placed at five replicate sites in old-growth stands to assess, with each site having 6 heterotrophic x 2 moisture combinations. Half of the logs were exposed to normal precipitation and the other half were placed under elevated plastic tents. Density measurements were taken in 1995 and 2001 to determine the effect of the treatments on density change and decay rates. Volume of insect gallery excavations and fungal rot were recorded to assess the extent to which the treatments affected heterotrophic activity. Based on density change and decay rates, the HET and TENT treatments did not affect decay rates. The mean density change for the logs was -0.072 g/cm^3 ± 0.03 and the mean decay constant was 0.026 ± 0.011. The TENT treatment, influenced by a significant interaction with the HET treatment, affected heterotrophic activity with the tented logs in HET treatments 2-6 having higher levels of heterotrophic activity than the non-tented logs. Tented logs in HET treatment 6 had the greatest difference with 3 times more heterotrophic

activity that the non-tented logs. The mean volume of wood borer excavation and extent of brown rot was significantly higher in the tented logs (256 cm^3) than in the non-tented logs (59.9 cm^3).

Introduction: The process of coarse woody debris (CWD) decomposition is started in part by xylophagous insects. There is evidence to support that differing initial conditions and colonization patterns can lead to differences in decomposition rates (Progar et al. 2000). Initial colonization of CWD by insects is strongly influenced by wood chemistry. Trees release volatile chemical compounds that attract or repel insects. For instance, the chemical verbenone repels bark beetles at high concentrations whereas ethanol attracts insects such as ambrosia beetle and some bark beetles (Carpenter et al. 1988).

Microbial establishment and biodegradation activity are also determined by the bole environment, because terpenes and other inhibitory extracts limit fungal and bacterial growth. Since these compounds are broken down by a limited number of fungi, yeasts, and bacteria, the presence of these organisms is an important part of the decomposition process. Biodegradation activities by these organisms can pave the way for further colonization (Schowalter et al. 1992).

One of the most critical functions of the initial colonizers is the creation of entry points for fungi and micro-organisms to begin the biological decomposition of the wood. Schowalter et al. (1992) found that fungi and bacteria were confined to the outer bark until the outer bark was breached by insects. Because decomposer colonization is dependent to a large degree on penetration of the bark by insect colonizers, the interaction

between the decomposers and colonizers is often characterized by life history synchronization (Schowalter et al. 1992). Since different kinds of fungi decompose different components of wood, the community composition of fungi and other microorganisms can impact the decomposition process.

Fragmentation is the process of breaking CWD into smaller subcomponents. Physical fragmentation is caused by gravity and flowing water that is hastened by decay organisms. Insects are also responsible for fragmenting CWD by the creation of galleries. Fragmentation increases the area for microbial organisms to colonize and ultimately decompose because the process of chewing, ingesting, and excavating creates a fine powdered dust that creates more surface area for the decay processes to work on (Harmon et al. 1986). Log fragmentation, defined here as loss of volume, is used to measure decay rates and has lag times (delay of measurable effects) that are typically 25 years or more (Harmon et al. 1986). Early in the decomposition process insect feeding typically does not reduce the volume of the entire log, i.e. the log largely retains its shape.

The transport of microbial organisms into CWD can be either through passive transport or through mutualistic associations with arthropods, such as ambrosia beetles (*Trypodendron* sp.) (Schowalter 2000). Ambrosia beetles have a dependent relationship with some of the fungi they vector.

In other cases, such as the buprestid *Buprestis aurulenta*, there is no consistent vectoring of wood decay and basdiomycetes constituted only 2.8% of all the isolates (Garcia and Morrell 1999).

Insect colonization varies between tree species, and consequently, the amount and type of fragmentation caused by insects can vary as well. For instance, in a study of Douglas- fir, Pacific silver fir, western hemlock, and western redcedar, Zhong and Schowalter (1989) reported that ambrosia beetles only colonized Douglas and western hemlock. In Douglas fir, ambrosia beetles excavated 0.2% of the sapwood volume during the first year. Bark beetles excavated 7.6 % of the phloem surface area of Douglas-fir logs versus 0.13% for western hemlock during the first year.

Bark beetles, which are largely confined to recently dead trees, and wood borers colonize CWD during first year (Schowalter et al. 1998). As wood decays, wood feeders are replaced by fungal feeders (Haack and Slansky 1987). Turnover of colonizing insects can be rapid. In a study of beetles colonizing CWD in aspen stands in Canada, Hammond et al. (2001) found a 65% turnover of taxa over a two year period.

The presence of insect galleries can affect the overall substrate quality of CWD. Maser and Trappe (1984) reported that substrate samples taken from CWD with insect galleries were softer and wetter, had a lower density, more plants roots, higher microbial activity, higher nitrogen

fixation activity, higher microarthropod populations, and higher exchangeable and mineralizable nitrogen than did samples from the same substrate without galleries.

Insect colonization of CWD is affected by substrate composition. One method to assess nutrient availability is to compare C: nutrient ratios of decomposers with their food resources. Swift et al. (1979) concluded that wood decay provides "... perhaps the most extreme example of nutrient limitation due to the very low nutrient contents of wood." Evidence of this deficiency comes from the fact that decomposers have much lower C:N ratios than the resource, which is indicative of a high demand for the nutrients. Deficiencies in nitrogen and phosphorus levels can retard the decay of wood by fungi. The process of decomposition eventually results in a decline in the C: nutrient ratio (Swift et al. 1979).

Insects have adapted to cope with low nutrient values in CWD. Bark beetles concentrate on the inner bark where nutrient levels are higher than in other areas of the log. Many cerambycids feed on the inner bark before moving into the sapwood and heartwood, which are relatively poor growth substrates. Other invertebrates feed on fungi and insects that have concentrated nutrients. Another adaptation is extended life cycles (Haack and Slansky 1987; Harmon et al. 1986). Wood feeders, and xylem feeders in particular, have very low growth rates and very long development times. The survival and growth of wood feeding larvae is positively

correlated with wood N content. Interestingly, the efficiency of nitrogen utilization by cerambycid beetles is low (Haack and Slansky 1987; Ikeda 1979).

The ability of wood feeding insects to consume the constituent components of wood varies widely. Those insects that feed in the heartwood have greater ability to degrade structural polysaccharides than those that feed in the sapwood and both of those have greater ability than do those feeding in the phloem. Some wood borers produce their own wood degrading enzymes, have gut microorganisms capable of enzyme production, obtain the enzymes by ingesting fungi, or a combination of these (Haack and Slansky 1987; Kukor and Martin 1986).

There is experimental evidence which indicates that wood borer colonization can increase the rate of CWD decomposition. Edmonds and Eglitis (1989) conducted an experiment using screens to exclude insects from logs of two size classes: large (average diameter 37.4 cm) and small (average diameter 24.1 cm). They observed that the unscreened large logs had extensive decay in both the sapwood and heartwood whereas the large screened logs had more limited decay in the sapwood. They found that large unscreened logs, which had wood borers present, decayed faster than did the smaller unscreened logs, which had no wood borers. They also found the same pattern in the screened logs; wood borers were able to colonize the large screened logs. They attributed the increased decay in the

central portion of the logs and wood borers vectoring wood decay fungi as cause.

After ten years, Edmonds and Eglitis (1989) found that the percentage of original total mass remaining was 79.5% (11.8 sd) for the pooled large logs and 92.3 % (6.3 sd) for the pooled small diameter logs. The greatest reported percentage mass loss was 22.4% and the least was approximately 3.3%. As these numbers indicate, there were large variances in both the screened and unscreened logs.

Termites are a good example of how insect colonization can affect decomposition rates, because termites are capable of more rapidly fragmenting CWD than wood borers. Termites form colonies only when certain acids and aldehydes are produced by certain fungi (Maser and Trappe 1984). These substances attract the termites to the log and to areas where the wood is suitable for termite consumption. Termites are able to digest wood due to symbiosis with two other organisms: cellulose digesting Protozoa and nitrogen-fixing bacteria that live in their gut. (Maser and Trappe 1984).

In the Pacific Northwest, the Pacific dampwood termite (*Zootmermopsis angusticollis*) can be commonly found in moderately decayed wood. Evidence suggests that the population numbers and type of Protozoans associated with the termites can be affected by the substrate quality, due either to fungal activity or to the wood itself. Mankowski et

al. (1998) found that prior colonization by fungi had an effect on termite feeding, which of course is influenced by gut fauna. For instance, they found that Douglas-fir wood exposed to fungi prior to feeding increased consumption by termites. Fungi can improve the nutritional quality or soften the wood and thus allow for easier decay by the gut protozoa.

Differences in fungal colonization also have implications for the rate and nature of decomposition of CWD. Two of most common types of decay fungi are white rot and brown rot. White rot fungi decompose lignin as well as cell wall polysaccharides and there action is confined largely to near the hyphae. In contrast, brown rot fungi decompose cellulose and hemicellulose but not lignin (Harmon et al. 1986). There is also evidence that antagonistic relationships between decay fungi and other microorganisms in CWD can affect decomposition by promoting or retarding decay (Kaarik 1974).

Mass, density, and volume loss are often used to assess decay. As CWD decomposes, it loses mass, and as decay progresses from decay class 1 to 5, the general trend is for wood density to decrease (Means et al., 1985; Sollins et al., 1987). Means et al. (1985) reported that logs with a mean residence time of 7(±2) years had a density of 416 (±18) (mg/cm^3). The logs in decay class 2 with a mean residence time of 16.7 (±2.6) had a mean density of 317 (±20) (mg/cm^3). After an estimated residence of 218.7± 17.9 years, the density had been reduced to 80± 7 (mg/cm^3).

Researchers have also recorded mass gains in the first years of decay (Edmonds and Egilits 1989), which is presumably due to influx of heterotrophs. The decay of CWD is commonly modeled using exponential models. There are two common exponential models that are used to model losses from CWD via respiration and leaching (Harmon et al. 1986). The most widely used model is the single exponential model that was developed by Olson (1963). It is based on the assumption that the decaying material is homogenous (Harmon et al. 1986). The exponential model also has been modified to incorporate fragmentation (Harmon 1985).

Since wood is a heterogeneous substance with components that decompose at different rates, the single-exponential model can lead to misleading decay rates because prediction with this model depends on consistent and representative sampling of all the substrates in cross section (Harmon et al. 1986, Schowalter 2000). For example, two logs with the same diameter may decay very differently depending on amount of sapwood versus heartwood. As an alternative, decomposition can be modeled as a multiple negative exponential decay function over time. In this type of model, the decay constants are proportional to the qualitative components of the litter. In a typical system, an initially large decay constant results from the loss of labile materials. As time passes, the decay constants become progressively smaller due to the slower losses of more

decay resistant materials, such as lignin (Schowalter 2000). Hence, phloem, with more labile material, decays more rapidly than does heartwood, with more decay resistant material.

Decay processes in CWD, such as fragmentation, mineralization, and leaching, do not occur at the same rates and can be analyzed individually or integrated. Fragmentation and mineralization decay constant are commonly reported in CWD studies (Harmon et al. 1986). Log fragmentation, defined as loss of volume, has lag times that are typically 25 years or more. Early in the decomposition process, insect feeding typically does not reduce the volume of the entire log, i.e. the log largely retains its shape. There is wide range of variation between tree species. *Abies concolor*, a tree species which decomposes quickly, has a bole fragmentation constant of 0.019 yr^{-1} and a bark fragmentation constant of 0.125 yr^{-1} (Harmon et al. 1986). In contrast, Douglas-fir, which decomposes slower, has a bole fragmentation constant of 0.0008 yr^{-1} and a bark fragmentation constant of between 0.018 yr^{-1} and 0.039 yr^{-1} (Graham 1982). Using mass loss over a ten year period, Edmonds and Eglitis (1989) reported k-values ranging from 0.006 yr^{-1} to 0.044 yr^{-1} for Douglas-fir.

Log mineralization constants, based on respiration, ranged from 0.004 yr^{-1} to 0.007 yr^{-1} in Douglas-fir (Graham 1982). For *Abies concolor*, Harmon et al. (1982) reported a k-value of 0.05. Not surprisingly, studies

which have integrated respiration and fragmentation in Douglas-fir have reported higher k-values than when the two are analyzed separately: 0.028 yr^{-1} (Sollins 1982).

Progar et al. (2000) reported that initial respiration rates were higher in the logs sheltered to reduce moisture content and in logs that had been inoculated with decay fungi. The aim of the current research was to determine if those differences had translated after six years of decomposition into faster decay rates and increased heterotrophic activity in the tented logs and logs inoculated with decay fungi (HET # 5 and #6) over a longer time period. Decay rates constants were determined using density change from 1995 to 2001. Heterotrophic activity was assessed by measuring the excavation of the sapwood and heartwood by wood borers and the extent of visible fungal rot.

Methodology: The study site is located at the H.J. Andrews Experimental Forest, a Long Term Ecological Research (LTER) site, located 80 km east of Eugene, Oregon in the central western Cascade Mountains (44° N, 122 W°). In 1995, 360 experimental Douglas-fir logs (25-35 cm diameter, 1.5 m long) were randomly assigned to five replicate sites. All the sites were in old-growth stands ranging in elevation from 700-1000 m. The 72 logs at each site were randomly assigned to 12 treatments combinations (6 heterotrophic treatments, HET x 2 moisture contents, TENT (Progar et al. 2000). Sixty of these logs were fitted with respiration chambers. The remaining 12 were sampled for heterotrophic activity in 2001.

The moisture treatments consisted of half of the experimental logs being placed under elevated plastic tents. HET treatments 1-3 were designed to simulate different levels of insect penetration: no penetration (1); drilled sterile 3mm diameter holes, 10 deep mm, over $50m^{-2}$ of log surface area (2); and drilled sterile 3mm diameter holes, 37 mm deep, over $50m^{-2}$ of log surface area. HET treatments 4-6 consisted of the experimental logs being drilled with sterile 3mm diameter holes, 37 mm deep, over $50m^{-2}$ of log with each one receiving a different injection of fungi: ascomycetes (4), basidiomycete decay fungi (5), and a mix of the fungi used in 4 and 5 (6). Further details are given in Progar et al. (2000).

In the summer of 2000, logs were cut into 4 sections, approximately 37 cm long, to determine the extent of fungal colonization. In September

2001, one 37 cm section from each of these logs were collected and transported to the Forest Insect lab at Oregon State University. Initial density measurements were taken by Schowalter and Morrell (2002). Volume of the logs in the study from 1995 was determined by water displacement (Schowalter and Morrell 2002)

The procedures for measuring insect activity and decay were modified from Zhong and Schowalter (1989) and Schowalter (1992).The radius of the entire cookie and the heartwood, and the thickness of the sapwood, were measured at three points and averaged. Three 3 cm sections were cut with a chainsaw from the slice: 3 cm from the two ends and 3 cm from the middle. These sections were then cut into approximately 1 cm slices for measurement of the galleries. The three sections were then separated with a band saw into three substrates based on physical characteristics: bark, sapwood and heartwood. Gallery measurements consisted of the height, length, and width of the gallery. Whenever irregular edges of galleries were encountered, the gallery was measured to the nearest regular edge.

Insect galleries were encountered in areas affected by rot. In some cases, the gallery dimensions were distinguishable from the rot and in other cases they were not. To classify the damage, two categories were created for the sapwood and heartwood: insect galleries and insect galleries and rot combined. The latter category contains insect galleries not included in the insect galleries category because the dimensions could

not be determined because of rot. The excavation of the inner bark was not included in any of the gallery measurements because it was mostly consumed by heterotrophic activity.

Brown rot was the only visible decay present in the sampled portion of the logs. The affected volume was determined by measuring the height, length, and width of the impacted area. Irregular edges were excluded from the measurements as were areas where the rot was not visible on both sides of the sections.

To determine moisture content, the three substrates were weighed individually and then dried at 50C° until weight loss was no longer detected. The moisture content of the log was obtained by averaging the moisture content of the three substrates. Volume of the bark was estimated by water displacement and the volume of the sapwood and heartwood by using the volume calculations for a cylinder (Harmon et al. 1999). The dry weight and volumes of the three substrates were added together respectively to determine the density for the log as whole. Decay constants, using density measurements from 1995 and 2001, were modeled using the single exponent equation: $X/X_o = e^{-kt}$ where X=density in 2001, X_o =density in 1995, k=decay constants, t=time elapsed. Decay constants were calculated for the total log and for the bark, sapwood, and heartwood individually.

ANOVA of density changes, decay constants, and total decay was used to detect statistically significant treatment differences. The measurements of total decay were natural log transformed to better meet assumptions of normality and results are reported in the log scale. Linear regression was used to determine correlation between dependent variables (density changes, decay constants) and manipulated moisture levels and initial substrate density. Logs that lost bark in transit to the lab were excluded from the total log category.

Results: The mean density of the logs was 0.42±0.03 g/cm^3 (table 3.1). The mean density of the substrates in 2001 was as follows: bark density was 0.55±0.07 g/cm^3, sapwood density of 0.35±0.03 g/cm^3, and heartwood density was 0.42±.03. From 1995 to 2001, the mean decline in density of the total log was -0.072 g/cm^3 ± 0.03 (figure 3.1). ANOVA of the density change (2001 -1995) of the total log from did not reveal a statically significant difference for the HET (p-value 0.42) or TENT (p-value 0.30) treatment (figure 3.3)(Appendix table 4.6).

Examination of the density change of the substrate components of the log and of the log as a whole (fig. 3.2) yields no apparent trends in the treatment effects and ANOVA did not reveal statically significant differences (p-values > 0.1)(Appendix tables 4.6-4.9). The mean density change (2001-1995) in the sapwood was the highest of the three substrates at -0.18 g/cm^3± 0.04. The mean heartwood difference was -.065 ±0.03, and in the bark, -0.05 g/cm^3 ±0.05.

Table 3.1. Mean density and standard error of the sapwood, heartwood, and bark, and total log of the experimental Douglas-fir logs sampled in 2001 for insect and fungal activity.

Substrate	Density (g/ cm^3)
Bark n= 47	0.55±.07
Sapwood n=54	0.35±.03
Heartwood n=54	0.42±.03
Total n=47	0.42±.03

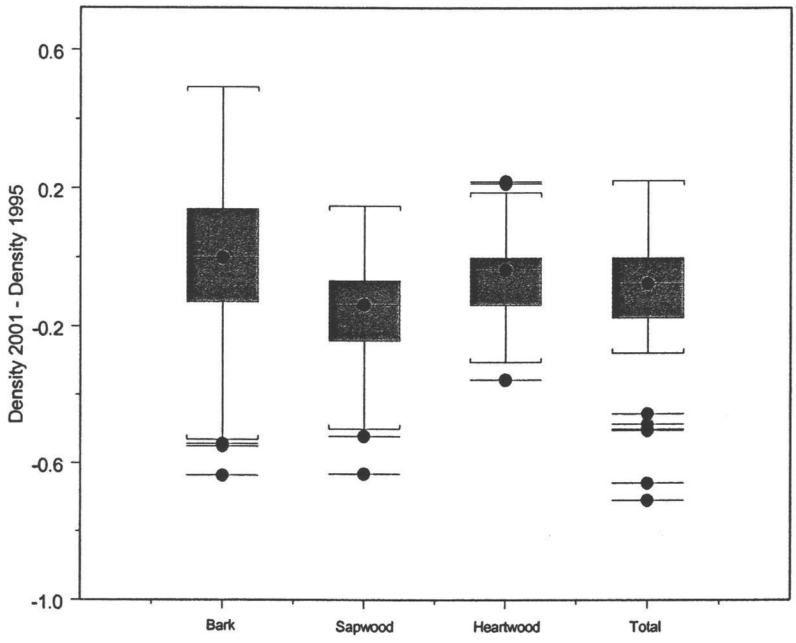

Figure 3.1. Box plots of density change (2001 -1995) for the experimental Douglas-fir logs at the H.J. Andrews Experimental Forest sampled for insect and fungal activity in the bark, sapwood, heartwood, and total log.

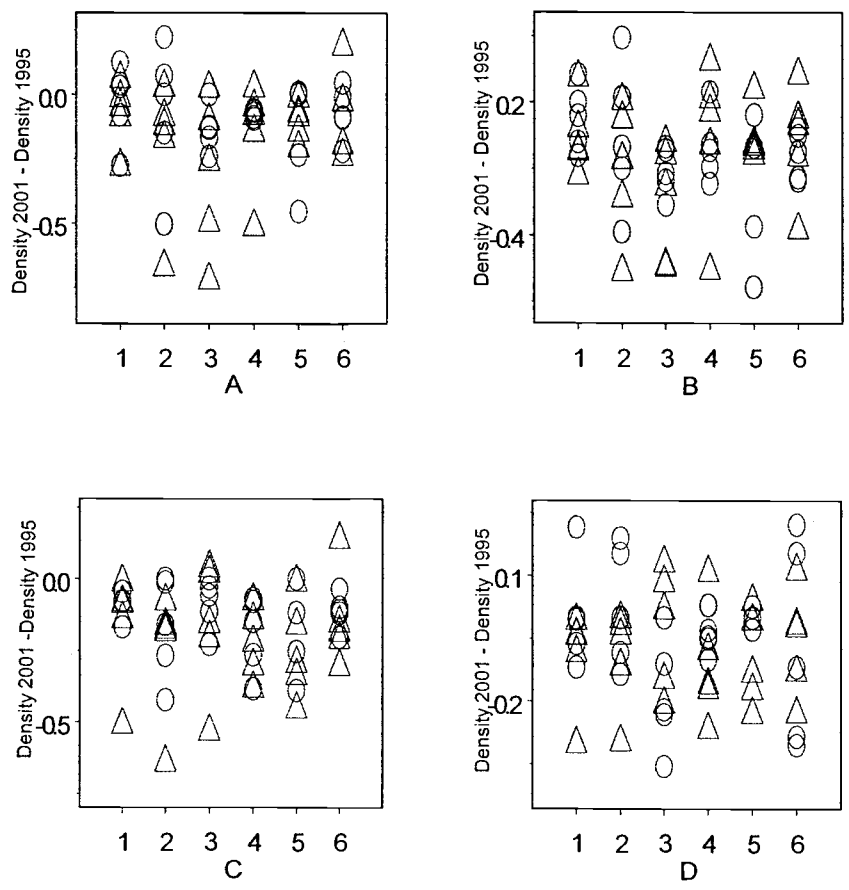

Figure 3.2. Density change (2001-1995) in the experimental tented Douglas-fir logs sampled for insect and fungal activity in 2001 for the total log (A), bark (B), sapwood (C), and heartwood (D) by HET and TENT treatments. 1. No penetration. 2. Sterile hole through phloem. 3. Sterile holes through sapwood. 4. Inoculated with ascomycetes 5. Inoculated with basidiomycetes. 6. Inoculated with both types of fungi. The tented logs are represented by triangles and non-logs by open circles.

ANOVA of the decay constants did not reveal any statistical differences for the HET or TENT treatments (Appendix tables 4.10-4.13). However, in the analysis of decay constant of sapwood, the HET treatment approached significance ($p=0.058$)(figure 3.2). Table 3.2 shows the mean decay constants for each of the three substrates and the log as a whole.

Table 3.2. Decay constants for bark, sapwood, heartwood, and whole log (total) of the experimental Douglas-fir logs sampled in 2001 for insect and fungal activity at the H.J. Andrews Experimental Forest.

Substrate	k	n
Bark	-0.015 ± .016	47
Sapwood	0.076 ± .018	54
Heartwood	0.03 ±.016	54
Total	0.026±.011	47

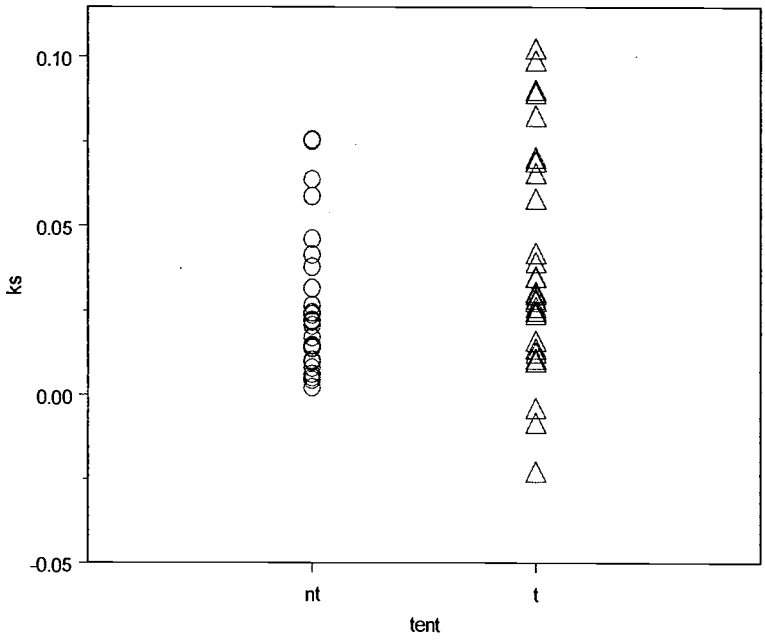

Figure 3.3. Sapwood decay constant (ks) (yr^{-1}) for tented (t) and non-tented (nt) experimental Douglas-fir logs sampled for insect and fungal activity in 2001 at the H.J. Andrews Experimental Forest. The tented logs are represented by triangles and non-logs by open circles.

Total density in 1995 was significantly, but weakly, correlated with density change (figure 3.4) and the total decay constant (R^2=0.21). Sapwood density in 1995 was very weakly correlated (figure 3.5) with density change in the sapwood. There was no correlation between sapwood density in 1995 and the sapwood decay constant (figure 3.6).

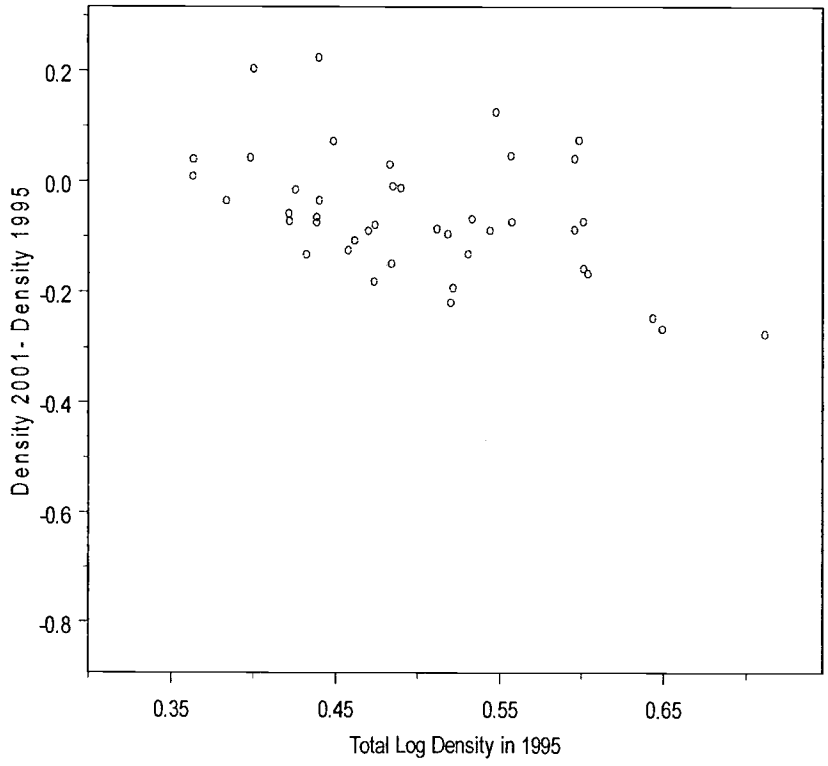

Figure 3.4. Correlation between total density in 1995 and density change (2001-1995) in the experimental Douglas-fir logs sampled for insect and fungal activity in 2001 at the H.J. Andrews Experimental Forest (R^2=0.29. $p < 0.001$. n=47).

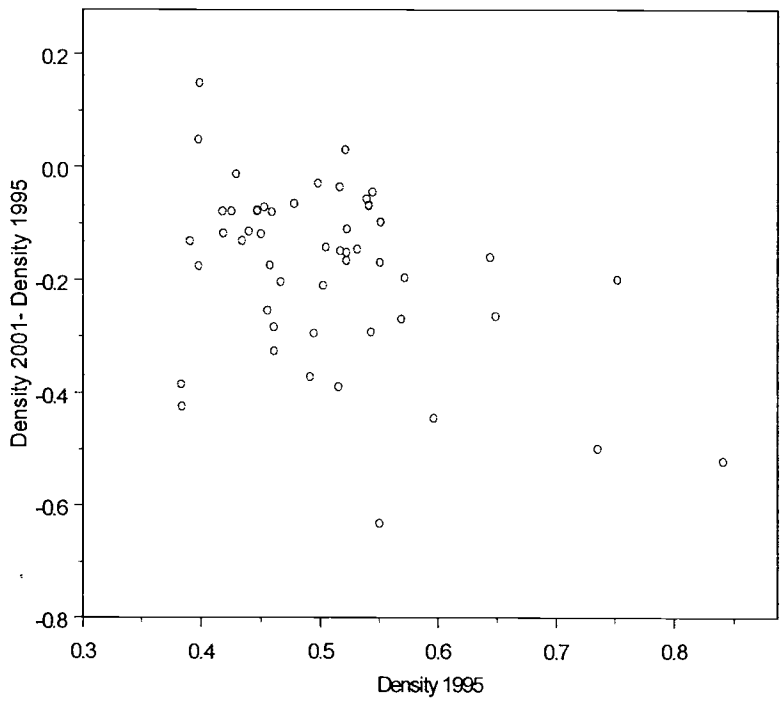

Figure 3.5. Correlation between sapwood density in 1995 and density change (2001-1995) in the experimental Douglas-fir logs sampled for insect and fungal activity in 2001 at the H.J. Andrews Experimental Forest (R^2=0.166. p< 0.003. n=52).

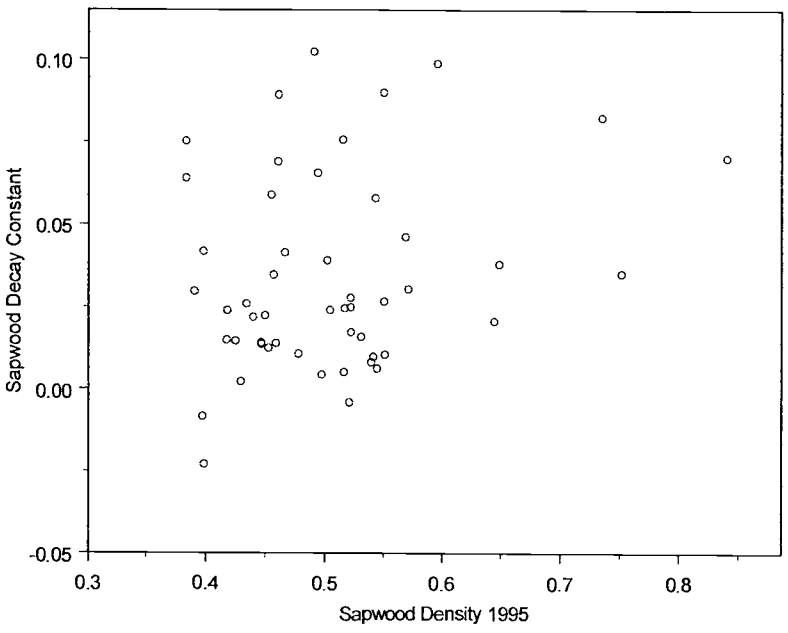

Figure 3.6. Correlation between sapwood density in 1995 and decay rate constant (k) in the experimental Douglas-fir logs sampled for insect and fungal activity in 2001 at the H.J. Andrews Experimental Forest (R^2= 0.06. p=0.08. n= 53).

As figures 3.7 and 3.8 illustrate, the tented logs had more insect galleries and brown rot than the non-tented logs. The mean volume affected by total decay of the non-tented logs was 59.9 cm^3 and the mean of the tented logs was 305.3 cm^3. The mean total sapwood decay in the tented logs was 256 cm^3, and in the non-tented logs, 49 cm^3. ANOVA indicated that the TENT treatment was significant ($p< 0.001$), but the HET treatment was not ($p= 0.16$); however, there was a significant interaction between the HET and TENT treatments ($p=0.0024$) (Appendix Table 4.15). In the sapwood and total log, the tented logs with HET treatments 2-6 had a greater volume affected by total decay. For the total log, the lowest difference for HET treatments 2-6 was in HET treatment 3 and HET treatment 6 (Table 3.3). In the sapwood, the lowest difference was in HET 3 and the greatest difference in HET 4. In both the sapwood and total log, the non-tented logs with HET 1 had 1.3 times more decay than the tented logs with the same treatment. The differences in the extent of treatment effect between the total log and the sapwood were attributable to decay in the heartwood (fig. 3.11).

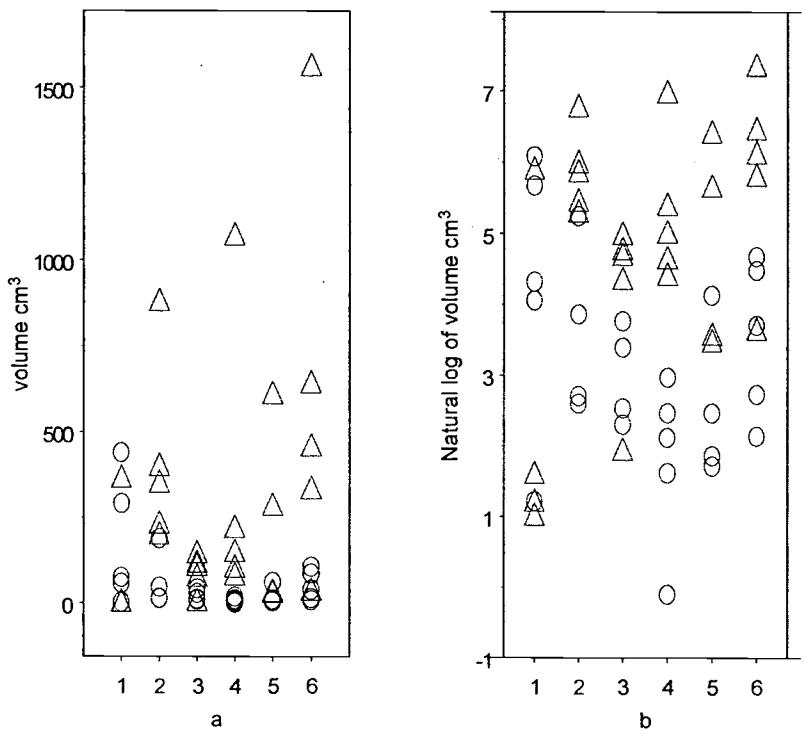

Figure 3.7. Volume (cm^3) affected in the experimental logs at the H.J. Andrews Experimental forests by insect galleries and fungal rot from 1995 to 2001 in the logs sampled in 2001 for insect and fungal activity on the original scale (a) and on natural log scale (b). X-axis represents HET treatments 1-6. The triangles are represented by tented logs and the open circles by non-tented logs.

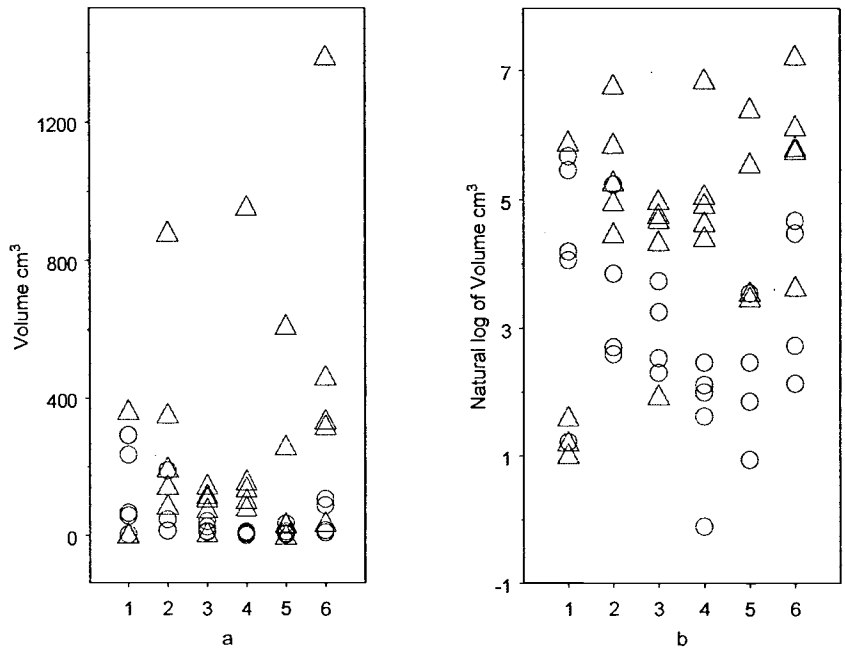

Figure 3.8. Sapwood volume (cm^3) affected by wood borers and fungal decay from 1995 to 2001 in the Douglas-fir experimental logs sampled in 2001 for insect and fungal activity at the H.J. Andrews Experimental Forest. X-axis represents HET treatments 1-6 on the original scale (a) and on the natural log scale (b). The triangles represent tented logs and the open circles represent non-tented logs.

Table 3.3. Volume of the tented logs affected by total decay minus the volume affected by total decay in non-tented logs for each HET treatment for the total log and sapwood in the experimental logs at the H.J. Andrews Experimental Forest in the logs sampled in 2001 for insect and fungal activity on the natural log scale. Back-transformed values are given in parentheses.

Treatment	Total log	Sapwood	n
1	-1.3 (3.7)±1.5	-1.3 (3.7)±1.5	4
2	2.3 (10.0)±1.5	2.3(10.0)±1.5	4
3	1.0 (2.7)±1.5	1.02 (2.8)±1.5	4
4	3.03 (21.0)±1.1	3.03(21.0)±1.3	5
5	1.8 (6.04)±1.8	2.5±(12.0)1.7	3
6	3.04 (21.0)±1.5	2.8±(16.0)1.5	4

As figs. 3.7 and 3.8 demonstrate, sapwood decay accounts for the vast majority of the measured decay. However, linear regression revealed no correlations between total sapwood decay sapwood and density change (fig.3.9) or sapwood k (fig. 3.10), which suggests that the measured indicators (galleries and brown rot) of decay are not sufficient by themselves to explain the decay patterns in the logs.

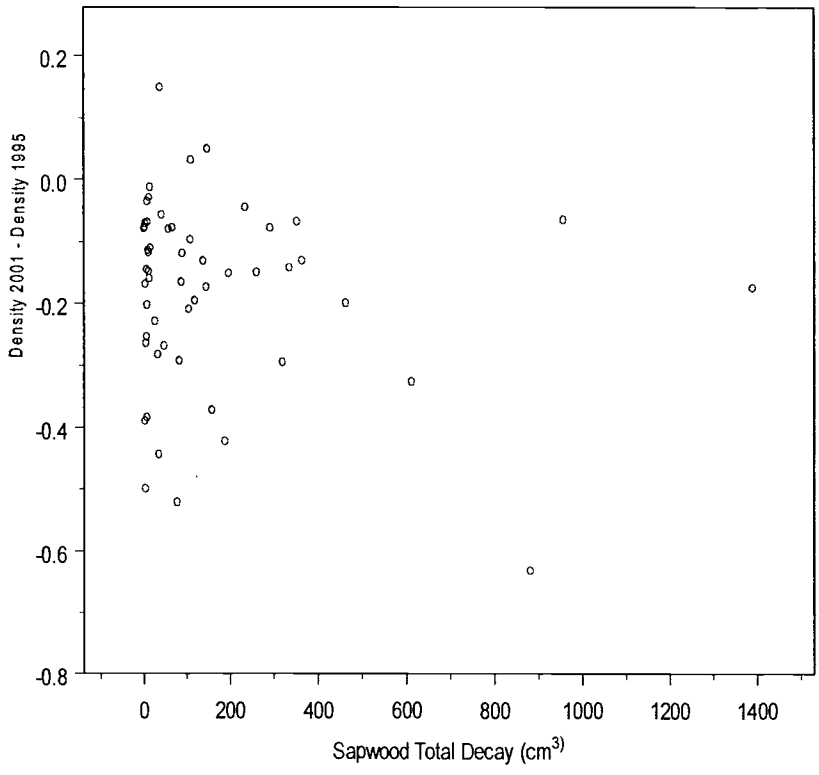

Figure 3.9. Correlation between total sapwood decay and density change (2001 – 1995) in the experimental logs sampled in 2001 for insect and fungal activity at the H.J. Andrews Experimental Forest (R^2= 0.019. p= 0.32. n= 53).

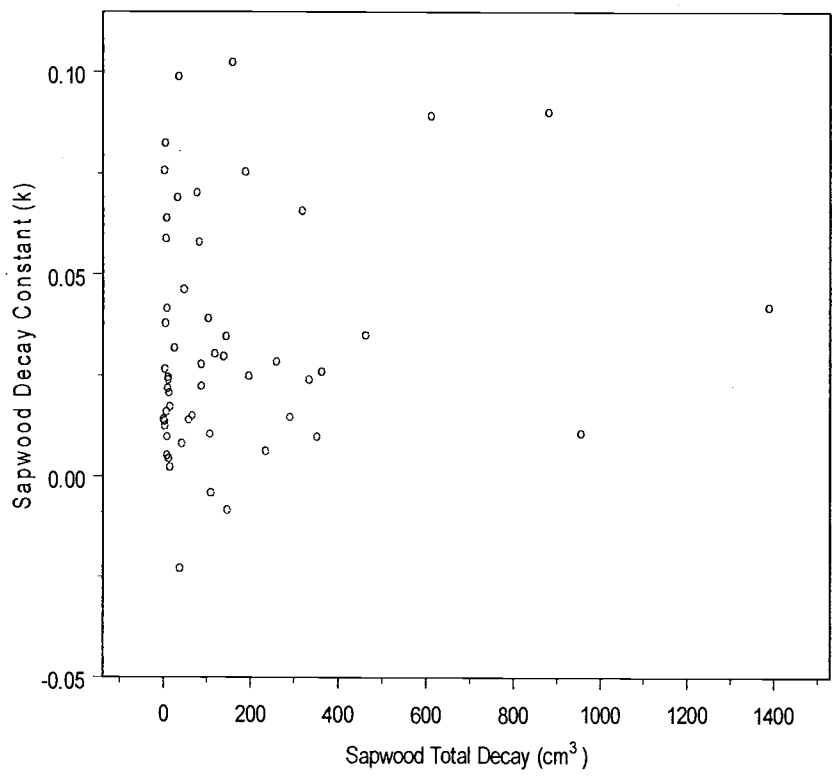

Figure 3.10. Correlation between sapwood total decay and sapwood decay constant in the experimental Douglas-fir logs sampled in 2001 for insect and fungal activity at the H.J. Andrews Experimental Forest (R^2= 0.026. p=0.24. n= 53).

There was some decay activity in the heartwood by both brown rot fungi and wood borers, but it amounted to only a small fraction of measured decay (fig. 3.11). The addition of heartwood amplifies the TENT treatment effect because nearly all the decay measured in the heartwood was in tented logs.

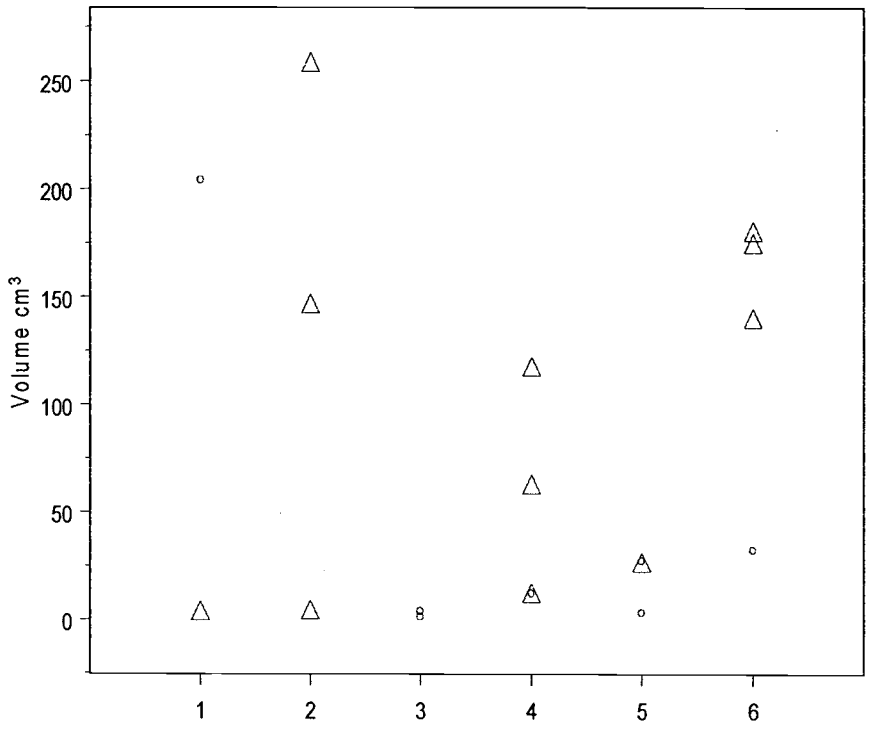

Figure 3.11. Volume of heartwood affected from 1995 to 2001 by total decay in the experimental Douglas-fir logs sampled in 2001 for insect and fungal activity at the H.J. Andrews Experimental Forest. X-axis represents HET treatments 1-6. Triangles represent tented logs and open circles represent non-tented logs.

Many of the wood borer galleries were not associated with observable brown rot. Fig. 3.12 shows the extent of gallery excavation in the sapwood that was clearly distinguishable from brown rot. It illustrates that tented logs had a greater extent of borer activity than did the non-tented logs. The highest volume falling into this category excavated by insects was 613 cm^3.

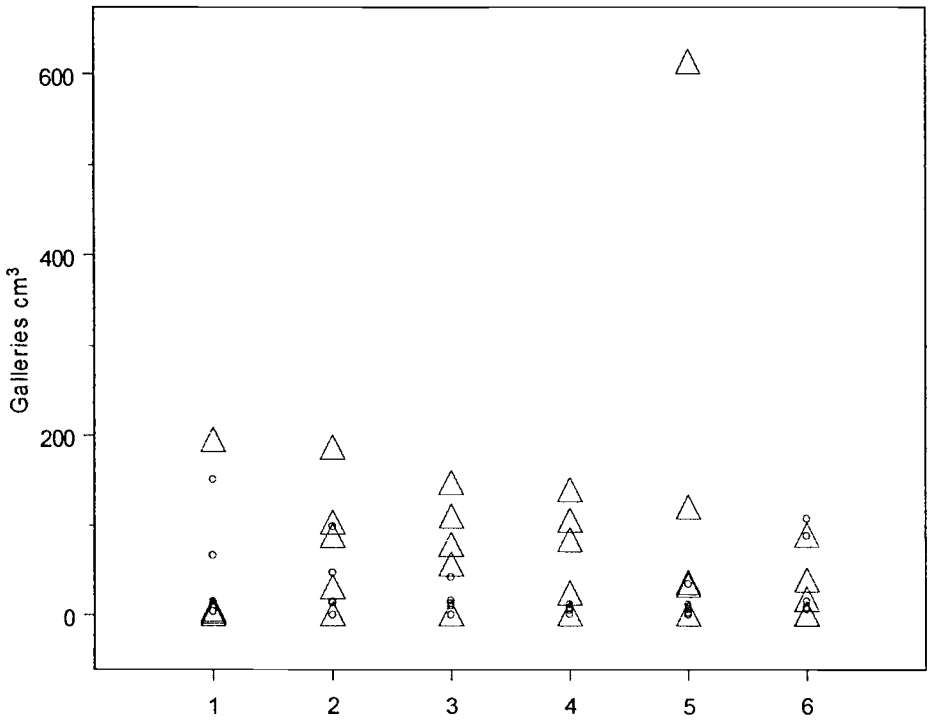

Figure 3.12. Sapwood gallery volume (cm^3) excavated from 1995 to 2001 not associated with visible brown rot by insects in the experimental Douglas-fir logs sampled in 2001 for insect and fungal activity at the H.J. Andrews Experimental Forest. X-axis represents HET treatments 1-6. Triangles represent tented logs and open circles represent non-tented logs.

The percentage of total volume affected by measured fungal rot and wood borer galleries in relation to the entire volume of the log was very small: a mean of 3.9 % for all the logs (fig. 3.13). The highest affected volume of the total log was 36% and lowest was 0.024%. The tented logs had a mean of 11% volume affected by total decay and non-tented a mean of 1.1%. The percentage of the fresh volume excavated by wood borers was small (fig. 3.14). In the tented logs, the mean excavation was 3.3% with a high of 21.7%. In the sapwood, the mean percentage of volume affected by total sapwood decay was 6.6% (fig. 3.15). The range of volume affected was 0.045% to 69%. The mean volume affected was 6.5% in the tented logs and 1.9 % for non-tend logs.

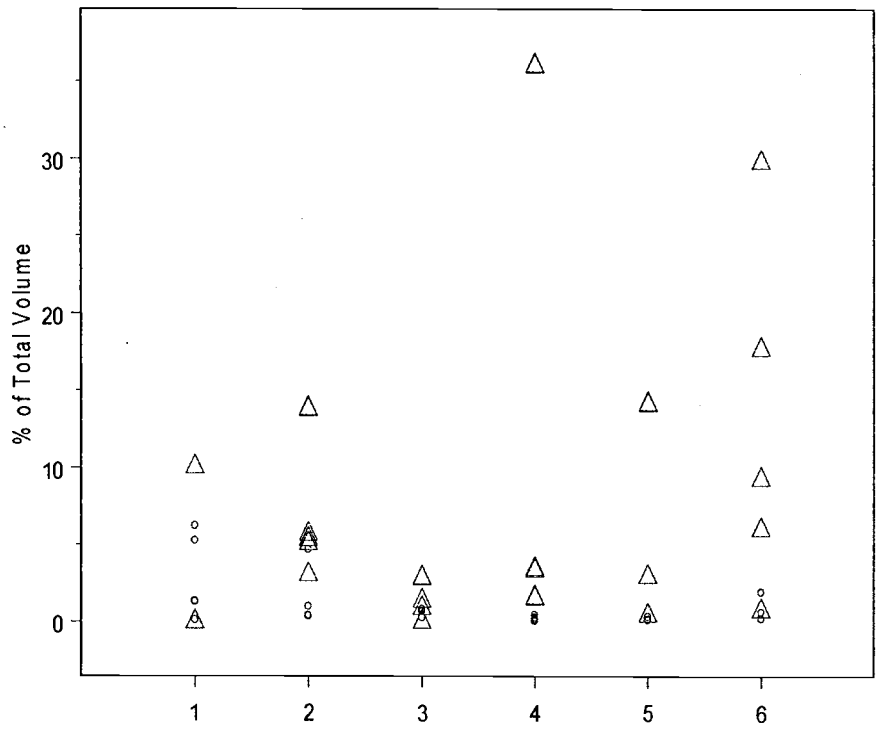

Figure 3.13. Percentage of total log volume affected from 1995 to 2001 by fungal rot and insect galleries by treatment in the Douglas-fir experimental logs sampled in 2001 for insect and fungal activity at the H.J. Andrews Experimental Forest. X-axis represents HET treatments 1-6. Triangles represent tented logs and open circles represent non-tented logs.

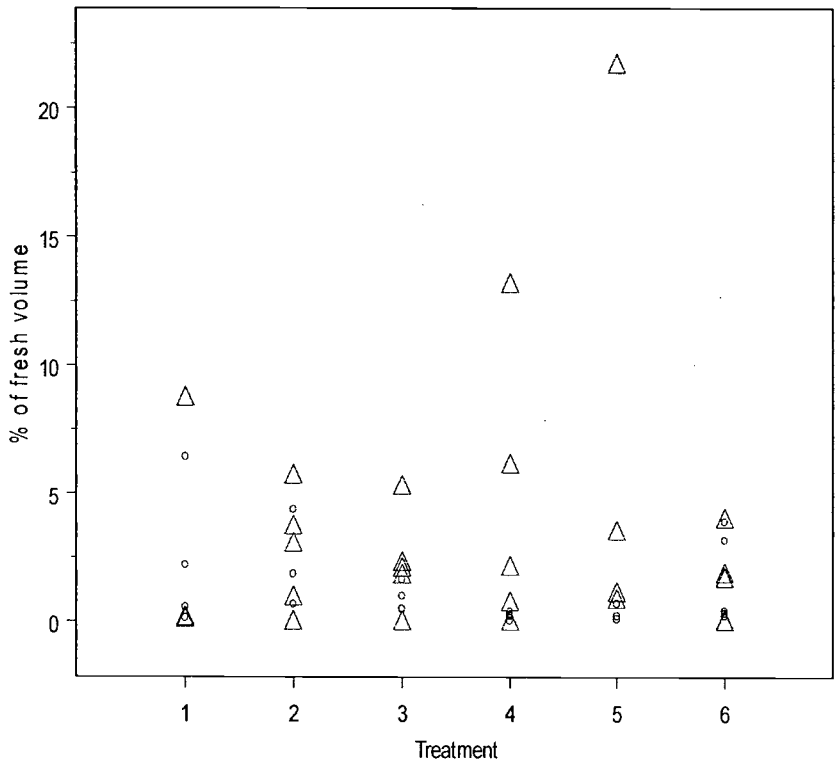

Figure 3.14. Percentage of total log volume affected by wood borer galleries by treatment in the experimental Douglas-fir logs sampled in 2001 for insect and fungal activity at the H.J. Andrews Experimental Forest. X-axis represents HET treatments 1-6. Triangles represent tented logs and open circles represent non-tented logs.

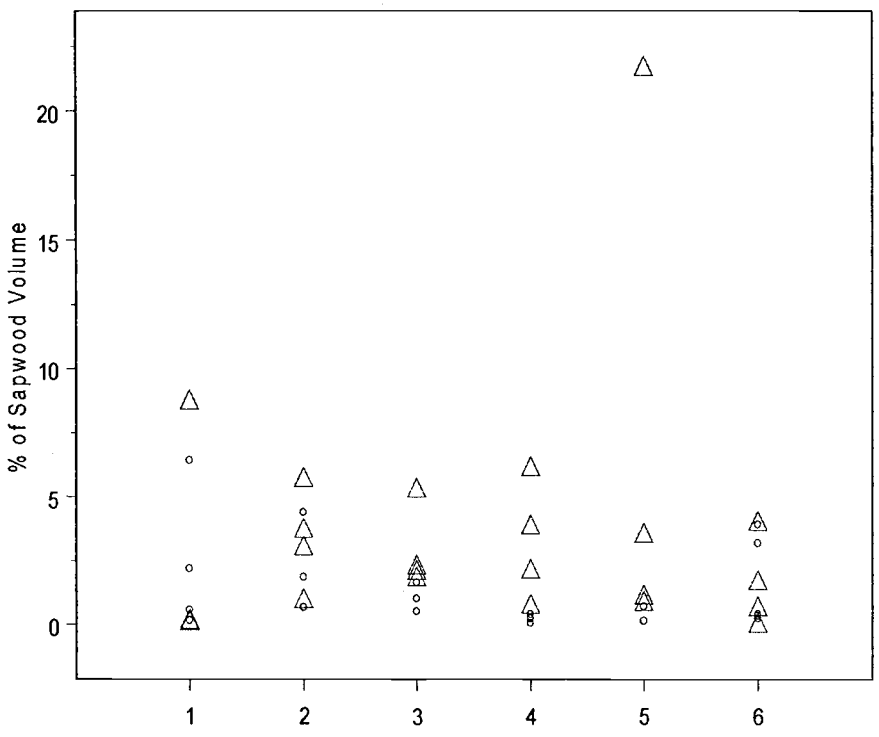

Figure 3.15. Percentage of sapwood volume affected by fungal rot and insect galleries by treatment in the experimental Douglas-fir logs sampled in 2001 for insect and fungal activity at the H.J. Andrews Experimental Forest. X-axis represents HET treatments 1-6. Triangles represent tented logs and open circles represent non-tented logs.

Examination of frass indicated that both buprestidae and cerambycidae were feeding in the inner bark of some of the logs. Wood boring beetles feeding in the sapwood before sampling had exited prior to sampling date. Feeding by wood borers in the phloem eliminated evidence of bark beetle colonization. There were 33 larval cerambycids recovered in 11 tented logs and 18 in 7 non-tented logs (fig. 3.17).

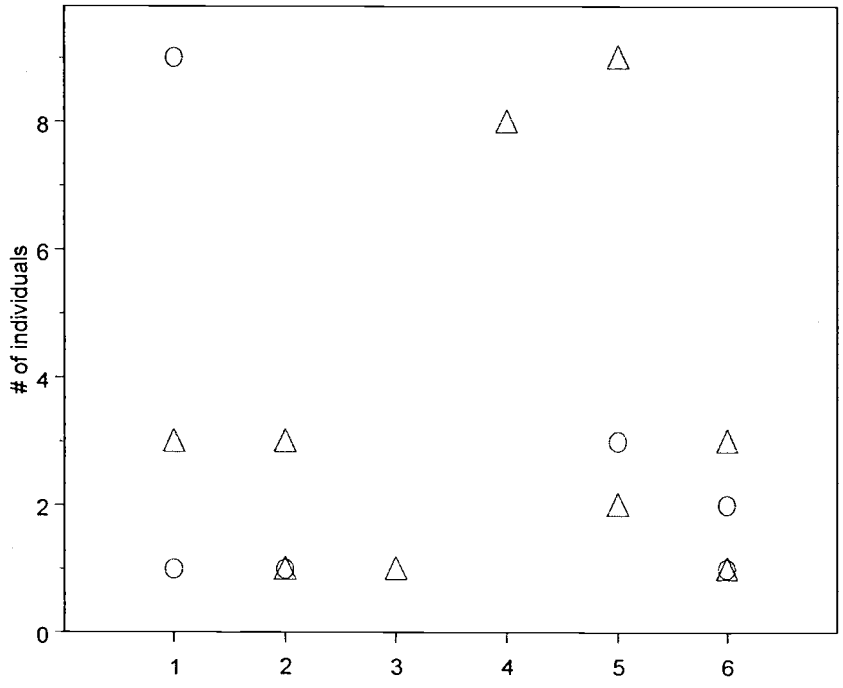

Figure 3.16. Number of cerambycids recovered from the experimental Douglas-fir logs sampled for insect and fungal activity in 2001. X-axis represents HET treatments 1-6. Triangles represent tented logs and open circles represent non-tented logs.

Discussion: This study was designed to test the hypothesis that differences in initial heterotrophic conditions lead to differences in decomposition. Based on the results of Progar et al. (2000), I predicted that the tented logs and logs inoculated with decay fungi (HET treatments 5 and 6) would have the greatest decline in density, largest decay constants, and the highest levels of insect galleries and fungal rot compared to the other experimental logs.

Analysis of the data indicates that TENT treatment had an impact on the extent of colonization of the logs by wood borers and the extent of brown rot but the magnitude and direction of the effect depended on the HET treatment. However, the hypothesis that the inoculation of basidiomycetes in HET treatments 5 and 6 would lead to greater levels of decay was not supported. The two treatments that included inoculation with ascomycetes (HET 4 and 6) had the greatest magnitude in treatment affect, which indicate that the inoculations non-decay fungi did not slow down the decomposition process and may have contributed to increased heterotrophic activity. However, as HET treatments 2 and 5 had comparable levels of affected volume (figures 3.7 and 3.8) the other treatments were also affecting the heterotrophic colonization to a similar degree.

The obvious inference from TENT treatment effect on gallery excavation and brown rot is that lower moisture levels in the tented logs of

HET 2-6 favored higher levels of wood borer activity Based on the moisture measurements taken in 1995-1996 and 2001 (Chapter 2) from experimental logs still in the field, there was a 20% functional reduction in moisture in the tented logs. In HET treatment 1, the non-tented logs had the higher levels of decay which indicates that the bark penetration and/or the inoculations used in the HET treatments helped to increase heterotrophic colonization in the tented logs. In the absence of the treatments the drier conditions in the tented logs appears to have lessened the amount of volume affected by wood borers and advances stages of brown rot.

There was no evidence that the drier conditions in the tented logs or any of the HET treatments resulted in a faster rate of decay (fig. 3.2). In the sapwood, the tented logs had a slightly higher mean decay rate constant than non-tented logs, but as fig. 3.3 illustrates, most of the decay constants were clustered together and the difference was not significant. There is a possibility that the TENT treatment affected the decomposition of the inner bark drier conditions favoring more rapid decay by basidiomycetes, which generally favor drier conditions (Kaarik 1974). Since the inner bark is the fastest substrate to decompose, it is possible that there were treatment effects in the inner bark that was not detected by the timing and methods of this study. In the initial study, the tented logs that were inoculated with basdiomycetes (HET treatment # 5) were associated with

increased respiration rates and this could have been partially associated with insect activity.

A more rapid decay of the inner bark could be the reason for the overall increased excavation in the tented logs because for wood borers, the ability to feed in inner bark has implications for the amount to time spent in the log since the remaining substrates are relatively poor substrates for growth. Bark beetles typically only colonize recently dead CWD and the remainder of the inner bark is consumed in part by wood borers. The activity of wood borers in the inner bark eliminated evidence of bark beetle activity. Zhong and Schowalter (1989) reported that bark beetles had excavated 7.6 % of the phloem and cerambycids had excavated 0.05% in the first two years of decomposition of Douglas-fir logs. If this remaining inner bark was consumed by wood borers at a faster rate in the tented logs then they could colonize the sapwood faster.

An examination of figure 3.1 and tables 3.2 and 3.3, indicate that the sapwood is decreasing in density faster than the other components (except the inner bark) and the log as a whole. In Douglas-fir, the sapwood begins to decay shortly after tree death (Sollins et al. 1987; Wright and Harvey 1967). In a study of decomposition of Douglas-fir killed by bark beetles in the Western Cascades of Washington and Oregon, Wright and Harvey (1967) reported that 5 years after the death of the tree most of the sapwood had decayed in snags.

The extent of decay by brown rot fungi has the potential to affect colonization by wood borers because in general, they do not feed in rotten wood (Linsley 1958). Based on characteristic gallery patterns, both buprestids and cerambycids excavated the inner bark, but only cerambycids were recovered from the sapwood and heartwood. Since cerambycids, such as *Leptura* sp., feed in the inner bark before feeding in the sapwood (Kimmey and Furniss 1943), rapidly decaying logs will become largely unsuitable for most wood borers. Based on density change and total decay, the experimental logs sampled in 2001 had moderate levels of decay and so probably remain suitable substrates for wood borers.

More generally, the presence or absence of fungi in CWD has the potential to impact wood borer colonization because research suggests cerambycids are not able to produce all the enzymes needed to degrade wood and instead obtain the enzymes from ingesting fungi (Haack and Slansky 1987; Kukor and Martin 1986). Fungal colonization can aid cerambycids that need the fungal enzymes to feed, but advanced decay caused by fungi could potentially curtail the extent of CWD colonization. Despite the significant interaction between the HET and TENT treatments, levels of wood borer galleries did not appear to be affected by the HET treatments (figure 3.12).

Edmonds and Eglitis (1989) reported that the presence of wood borers can increase decomposition rates. They used screens to exclude insects from logs in two size class: large (average diameter 37.4 cm) and small (average diameter 24.1 cm). The diameter of logs used in the current study (25-35 cm) fall into both categories. They calculated decay rates based on mass loss. They did not quantify wood borer activity but assessed the impact of wood borers on decomposition by comparing the decay rates of the logs based on the presence or absence of wood borers. They reported that wood borer activity was associated with faster decomposition of the larger diameter logs compared to smaller diameter logs. The fastest decomposition was in the large unscreened logs (77.6 % of mass remaining after ten year) and slowest was the small diameter logs (97.6 % mass remaining after ten years). The pooled (screened and unscreened logs) decay constant for the larger diameter logs was 0.05 and 0.026 for the pooled smaller diameter logs. They attributed the higher rate of decay in the larger diameter logs to the presence of *Monochamus scutellatus* in those logs.

Edmonds and Eglitis (1989) observed that the unscreened large logs had extensive decay in both the sapwood and heartwood. The extensive decay was attributed to wood borers vectoring decay fungi. In contrast, I found only a few logs with visible heartwood decay (fig. 3.11) and the mean heartwood density change (2001-1995) was small (-0.065) (fig. 3.1).

Additionally, most of the heartwood with wood borers did not have visible evidence of rot.

The mean decay constant for the logs from the logs in this study was 0.026 ± 0.011. The decay rate constant reported in Edmonds and Eglitis (1989) was 0.026 for small diameter unscreened logs and 0.05 for the large diameter unscreened logs. The decay rate constant for large screened logs decay constant was 0.044 and 0.006 for the small screened diameter logs.

Although decay can proceed right after the death of sound CWD, the results of early heterotrophic activity can be difficult to detect using mass loss or density change as indicators. Edmonds and Eglitis (1989) found no detectable mass loss after five years in small diameter logs. The colonization of the inner bark certainly leads to some mass loss, as reflected in respiration measurements, in addition to the production of frass but it may not be detectable.

A number of factors that are not related to the treatments can potentially explain the variation in decay. Research indicates a general trend that wood of tree species with higher density decay slower than wood from tree species of lighter density but considerable variability exists in the decay rates within trees with a particular density (Chambers et al. 2000). Within a given log, higher density substrates can decompose faster than lower density substrates if the higher density substrate is of a higher

quality (inner bark versus sapwood e.g.) (Schowalter 1992). Initial wood density of the total log was moderately correlated with density change (figure 3.5). The correlation between the sapwood density change and the density of the sapwood in 1995 was also significant (figure 3.6). This may be due to some of the denser log having higher nutrient concentrations.

Since no direct measurements of the chemical composition of the logs were taken in this study the effects of the nutrient content and relative proportion of structural components, such as lignin, cannot be assessed. Ausmus (1977) argued that wood decay rates directly reflect nitrogen concentration of wood substrates. Research indicates that the N increases in decomposing Douglas-fir wood as decomposition progress from class 1 and class 5 (Sollins et al. 1987). However, in the first years of decomposition of Douglas-fir wood N levels probably do not increase. Edmonds and Eglitis (1989) found that a net release of N and other nutrients after ten years but overall the N concentration of the logs was similar to levels at the start of the study, indicating that changes in N may be negligible during this period. Insects emerging from the logs would be exporting nutrients, but the impact of this on nutrient cycling on larger scales is not known.

After six years of decomposition, the TENT treatment, influenced by the HET treatments, had affected heterotrophic colonization. The hypothesis that TENT treatment would affect processes has been

supported by the overall higher levels of wood borer galleries and brown rot in the tented logs. The results indicate that drier conditions in the tented logs were only correlated with increased heterotrophic activity when bark barrier was penetrated experimentally at the beginning of the decomposition process. However, regardless of the treatment, the higher levels of wood borer activity have not resulted in the tented logs decaying faster than the non-tented logs. If this trend continues, then it would indicate that initial differences in wood borer colonization do not influence long-term decomposition of CWD. Alternatively, it is possible that the logs with highest levels of gallery excavation will decay faster if gallery excavation facilitates faster spread of decay fungi throughout the log, especially in the heartwood.

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Conclusion

Still tied to this world

I cool off and lose

My form

Ozui (1783)

The results of the current study provide evidence that after six years of decomposition TENT treatment, influenced by the HET treatments, has affected the decomposition process. The tented logs in HET treatments 2-6 had a greater extent of volume affected by wood borers and brown rot than the non-tented logs. In contrast, the combined respiration measurements indicate that the tented logs have only slightly higher mean respiration rate but the difference was not significant. The evidence of increased heterotrophic activity in the tented logs did not translate into greater density change or decay rates. There were no treatment effects found in the examination in the average respiration rates of the three sampling periods and this is consistent with the lack of treatment effects found in density changes and decay rates. Additionally, there was no evidence of a HET treatment effect in analysis of respiration rates in contrast to the gallery and rot measurements. Examination of the July and September respiration measurements indicate that tented logs may have the highest

respiration rates in late summer but more measurements are needed to confirm the existence of any seasonal trend.

The lack of a correlation between respiration and moisture raises some interesting questions concerning the higher respiration rates in the tented logs in the July and September sampling periods. A possible explanation for the TENT treatment effect is that moisture levels had previously caused a change in heterotrophic community that was expressed seasonally. Additionally because of spatial heterogeneity in moisture content, the moisture measurements may underestimate the moisture content of the logs.

The TENT treatment effect on wood borer activity may in the future produce a more pronounced effect on the decomposition process. Wood borers have the potential to affect the decomposition process in two major ways: through fragmentation resulting in volume loss and vectoring decay fungi. Since the experimental logs had their original cylinder shape and bark attached, the logs in this study have not yet experienced major fragmentation. In the long term, the increased gallery excavations could lead to increased decay rates in the tented logs due to fragmentation.

The current study did not assess fungal community present in the log or the composition of the fungal community vectored by insects. However, the seasonal change in respiration rates and higher volume affected by brown rot in the tented logs suggests a greater level of activity by decay

fungi, even if there is no difference between the fungal communities in the tented and non-tented logs. The wood borers probably carried fungi and other microorganisms into sapwood as they fed but the importance of this method of colonization versus decay fungi spreading through growth is not clear. Edmonds and Eglitis (1989) presented circumstantial evidence, based on an insect exclusion experiment, that wood borers do vector decay fungi by excavating into the heartwood, which resulted in faster decay rates. The type of brown rot vectored into a log by insects can also have an impact on the extent decay in the initial stages of decomposition because brown rot fungi can vary in the rate of wood decay they cause (Kaarik 1974), but the importance of the differences in CWD that decomposes over an extended period of time (over decades) is unknown.

Over the course of six years, the tented logs, on the whole, have shown evidence of increased levels of heterotrophic activity over the non-tented logs. Respiration rates were higher in the tented logs than the non-tented logs from 1995-1997 (Progar et al. 2000), a period of time in which the inner bark was probably not entirely decomposed. It is possible that faster consumption of the phloem by insects and fungi resulted in the wood borers feeding in the sapwood and heartwood earlier, and thus contributing to a quicker spread of decay fungi. The lack of a treatment effect when the sampling periods were aggregated likely reflects the fact that sapwood is a much poorer substrate for fungi regardless of the

treatment and only when temperatures seasonally increase were the decay fungi able to become more active than in the non-tented logs.

Climate plays a major role in determining the parameters of the rates decomposition, and as such, climate related variables such as temperature, might explain more of the variation in decay rates than do moisture levels. Chambers et al. (2000) used results from CWD decomposition studies around the globe to compare the relative of importance of moisture and temperature in determining decay rates. They found that mean annual temperature serves as a better indicator of decay rate than moisture for CWD. They reported a Q_{10} of 2.4 (10° C^{-1}) whereas they found no correlation between moisture and decomposition rates. However, on the stand level, temperature likely interacts with other factors, such as substrate quality, to produce the variation in decomposition rates found in the current research.

Previous researchers have found indications that the differences in the initial heterotrophic community can affect seasonal and long term decomposition processes (Carpenter et al. 1988; Progar et al. 2000; Schowalter et al. 1992). The current research provides limited support for the hypothesis that differences in initial community composition, as represented by the HET treatments, lead to differences in decomposition processes. Stronger support was found for the hypothesis that moisture differences, both initial and continuing, can affect decomposition

processes seasonally, and over longer time frames, as witnessed by the extent of insect galleries and brown rot. Whether differences in heterotrophic activity in the tented logs translate into faster decay rates as decomposition progresses remains to be seen.

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APPENDIX

Table 4.1. ANOVA table for the respiration averages of the June, July, and September 2001 sampling periods from the experimental Douglas-fir logs at sites 1-4 in the H.J. Andrews Experimental Forest.

	df	Sum. of Sq.	Mean Sq.	F	P
Site	3	13.6	4.6	6.8	.0013
Het	5	2.1	0.42	0.63	0.68
Tent	1	2.3	2.3	3.5	0.073
Het x tent	5	0.41	.081	0.12	1.0
Resid-uals	29	19.3	.67		

Table 4.2. ANOVA table for respiration measurements from experimental Douglas-fir logs for the June 2001 sampling period for sites 1-4 at H.J. Andrews Experimental Forest.

	df	Sum. of Sq.	Mean Sq.	F	P
Site	3	3.3	1.1	2.9	0.05
Het	5	1.3	0.27	0.71	0.62
Tent	1	0.0077	0.020	0.021	0.89
Het x tent	5	1.5	0.30	0.81	0.56
Residuals	27	10.9	0.37		

Table 4.3. ANOVA table for respiration measurements from experimental Douglas-fir logs for the July 2001 sampling period for sites 1-5 at H.J. Andrews Experimental Forest.

	df	Sum. of Sq.	Mean Sq.	F	P
Site	4	19	4.7	18	P<.0001
Het	5	0.74	0.15	0.55	0.74
Tent	1	1.8	1.8	6.7	0.014
Het x tent	5	1.2	0.25	0.91	0.48
Residuals	42	11.2	0.27		

Table 4.4. ANOVA table for respiration from experimental Douglas-fir logs for the September 2001 sampling for sites 1-5 at H.J. Andrews Experimental Forest.

	df	Sum. of Sq.	Mean Sq.	F	P
Site	4	10.4	2.6	9.9	p<.0001
Het	5	1.1	0.22	.84	0.53
Tent	1	3.1	3.1	11.7	0.0014
Het x tent	5	0.68	0.14	0.52	0.76
Residuals	41	10.7	0.26		

Table 4.5. ANOVA table for the average moisture content of the experimental Douglas-fir logs sampled in June, July, August at H.J. Andrews Experimental Forest.

	df	Sum. of Sq.	Mean Sq.	F	P
Site	3	0.94	0.31	10.7	0.00007
Het	5	0.101	0.0202	0.69	0.63
Tent	1	0.58	0.58	19.0	0.00013
Het x tent	5	0.23	0.047	1.6	0.20
Residu-als	28	0.82	0.029		

Table 4.6. ANOVA table for density change (2001 -1995) for the experimental Douglas-fir logs at the H.J. Andrews Experimental Forest sampled for insect and fungal activity for the total log.

	df	Sum. of Sq.	Mean Sq.	F	P
Site	4	0.084	0.021	0.58	0.68
Het	5	0.18	0.037	1.01	0.42
Tent	1	0.039	0.039	1.07	0.30
Het x tent	5	0.084	0.017	0.46	0.80
Residuals	44	1.6	0.036		

Table 4.7. ANOVA table for density change (2001 -1995) for the experimental Douglas-fir logs at the H.J. Andrews Experimental Forest sampled for insect and fungal activity for the sapwood.

	df	Sum. of Sq.	Mean Sq.	F	P
Site	4	0.17	0.042	1.7	0.15
Het	5	0.094	0.018	0.78	0.57
Tent	1	0.047	0.047	1.9	0.17
Het x tent	5	0.0093	0.0019	0.078	1.0
Residuals	44	1.1	0.024		

Table 4.8. ANOVA table for density change (2001 -1995) for the experimental Douglas-fir logs at the H.J. Andrews Experimental Forest sampled for insect and fungal activity for the heartwood.

	df	Sum. of Sq.	Mean Sq.	F	P
Site	4	0.074	0.018	1.03	0.40
Het	5	0.031	0.0062	0.34	0.88
Tent	1	0.014	0.014	0.76	0.38
Het x tent	5	0.14	0.029	1.6	0.18
Residuals	44	0.79	0.018		

Table 4.9. ANOVA table for density change (2001 -1995) for the bark for the experimental Douglas-fir logs at the H.J. Andrews Experimental Forest sampled for insect and fungal activity.

	df	Sum. of Sq.	Mean Sq.	F	P
Site	4	0.26	0.064	1.1	0.36
Het	5	0.41	0.083	1.5	0.22
Tent	1	0.0005	0.0005	0.0080	0.93
Het x tent	5	0.26	0.052	0.91	0.49
Resid-uals	44	2.5	0.057		

Table 4.10. ANOVA table for decay constants for the total log of the experimental Douglas-fir logs sampled in 2001 for insect and fungal activity at the H.J. Andrews Experimental Forest.

	df	Sum. of Sq.	Mean Sq.	F	P
Site	4	0.0010	0.00024	0.72	0.58
Het	5	0.0014	0.00028	0.85	0.53
Tent	1	0.0001	0.00011	0.33	0.57
Het x tent	5	0.0010	0.00020	0.59	0.71
Resid-uals	32	0.011	0.00033		

Table 4.11. ANOVA table for the sapwood decay constants of the experimental Douglas-fir logs sampled in 2001 for insect and fungal activity at the H.J. Andrews Experimental Forest.

	df	Sum. of Sq.	Mean Sq.	F	P
Site	4	0.0020	0.0005	0.65	0.63
Het	5	0.009	0.0018	2.4	0.058
Tent	1	0.0022	0.0022	2.9	0.10
Het x tent	5	0.00055	0.00011	0.14	0.98
Resid-uals	38	0.029	0.00076		

Table 4.12. ANOVA table for the heartwood decay constants of the experimental Douglas-fir logs sampled in 2001 for insect and fungal activity at the H.J. Andrews Experimental Forest.

	df	Sum. of Sq.	Mean Sq.	F	P
Site	4	0.0025	0.00063	0.98	0.43
Het	5	0.00099	0.00020	0.31	0.90
Tent	1	0.00051	0.00051	0.79	0.38
Het x tent	5	0.0060	0. 0012	1.9	0.12
Resid-uals	38	0.024	0.00064		

Table 4.13. ANOVA table for the bark decay constants of the experimental Douglas-fir logs sampled in 2001 for insect and fungal activity at the H.J. Andrews Experimental Forest.

	df	Sum. of Sq.	Mean Sq.	F	P
Site	4	0.0033	0.00083	1.66	0.18
Het	5	0.0058	0.0012	2.3	0.067
Tent	1	0.00002 6	0.00002 6	0.052	0.82
Het x tent	5	0.0049	0.00097	2.0	0.11
Residuals	31	0.015	0.00050		

Table 4.14. ANOVA table for total volume (cm^3) affected in the experimental logs at the H.J. Andrews Experimental Forest by insect galleries and fungal rot from 1995 to 2001 in the logs sampled in 2001 for insect and fungal activity.

	df	Sum. of Sq.	Mean Sq.	F	P
Site	4	1.6	11.0	2.8	0.19
Het	5	2.0	17.1	3.4	0.10
Tent	1	36.2	36.2	21.4	0.00 0040
Het x tent	5	37.0	7.4	4.4	0.00 3
Residual -s	39	65.8	1.7		

Table 4.15. ANOVA table for sapwood volume (cm^3) affected in the experimental logs at the H.J. Andrews Experimental Forest by insect galleries and fungal rot from 1995 to 2001.

	df	Sum. of Sq.	Mean Sq.	F	P
Site	4	11.9	3.0	1.8	0.14
Het	5	13.7	2.7	1.7	0.16
Tent	1	40.7	40.7	25.1	0.00 0012
Het x tent	5	36.5	7.3	4.5	0.00 24
Residuals	39	63.2	1.6		