COARSE WOODY DEBRIS IN INDUSTRIALLY MANAGED *PINUS TAEDA* PLANTATIONS OF THE SOUTHEASTERN UNITED STATES.

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(ABSTRACT)

Coarse woody debris (CWD) plays an influential role in forested ecosystems by adding organic matter to soils, stabilizing the soil environment, providing wildlife habitat, preventing soil erosion, providing seedling establishment habitat, and involvement in the nutrient cycle. Most CWD research has been conducted in old-growth and unmanaged, second-growth forests. However, less is understood about CWD in intensively managed ecosystems, such as industrialized southern pine plantations. The objectives of this study were to determine the climatic and ecological factors that affect the decomposition rate of CWD, to predict the decomposition rate, specific gravity, and time since death (TSD) using multiple linear regression in industrial loblolly pine (*Pinus taeda* L.) plantations in the southeastern United States. The study sites for this project were part of a long-term, loblolly pine thinning study maintained by the Loblolly Pine Growth and Yield Research Cooperative at Virginia Tech. Measurements included piece size, position, and decay class. Samples of CWD were collected and analyzed to determine their mass and density. Decomposition rate of CWD was significantly different across position classes and decay classes: disk decomposition rates were significantly negatively correlated with disk diameter, large and small end piece diameter, estimated disk height, and disk dry weight. Average annual precipitation and average annual temperature were not significantly correlated with CWD disk decomposition rate.

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Introduction

Coarse woody debris (CWD) is the residue of living trees in the forest ecosystem. Historically coarse woody debris was a component of the forest ecosystem that was poorly understood. However, as interest developed in forest nutrient cycles and global warming, scientists in the late 1970's began to study CWD in forested ecosystems. Forested ecosystems are the largest terrestrial storage area of carbon, which is intricately tied to processes of global warming; therefore there is interest in the increased forest productivity of intensively managed systems forests and the subsequent affect on carbon storage. Early research in the continental United States began in unmanaged old-growth coniferous forests of the Pacific Northwest, and the role of CWD in unmanaged stands has become better understood. The function of CWD within managed forested ecosystems has been a neglected realm of research. In the southeastern United States there are approximately 138,000 km^2 of industrially managed pine forestland (Prestemon and Abt 2001). This large amount of managed forest in the southeastern United States provides a unique opportunity for studying coarse woody debris dynamics.

Coarse woody debris is defined according to size and position or according to form and location (Harmon and Sexton 1996). Size and position will define CWD for this study. I will follow the definition for CWD used by Harmon and Sexton (1996), who defined CWD as snag or bole > 4 cm in diameter. Fine woody debris is smaller than 4 cm in diameter and is not considered in this study.

Coarse woody debris serves a variety of essential functions in the forest ecosystem. It provides habitat for microbes, fungi, bacteria, insects, earthworms, and birds (McMinn and Crossley 1993; Marra and Edmonds 1994; Harmon and Sexton 1996;

Goodburn and Lorimer 1998; Mackensen et al. 2003). Soil production is enhanced by the decomposition of CWD (Graham and Cromack 1982; McMinn and Crossley 1993; Marra and Edmonds 1994). Coarse woody debris in contact with the ground reduces surface erosion (McMinn and Crossley 1993; Marra and Edmonds 1994). Nutrients such as carbon, nitrogen, phosphorus, and potassium are stored and cycled through coarse woody debris. (Grier 1978; Graham and Cromack 1982; Barber and van Lear 1984; Pearson et al. 1987; Harmon et al. 1990; Marra and Edmonds 1994; Wei et al. 1997; Laiho and Prescott 1999; Holub et al. 2001; Janisch and Harmon 2001; Mackensen et al. 2003; Harmon et al. 2004). Finally, CWD affects the degree of disturbance in a forest ecosystem, acting as a fuel for fire or harboring pathogens that can be translocated to newly growing trees (Duvall and Grigal 1999).

In the forests of the Pacific Northwest, CWD plays an integral role in the phosphorus, nitrogen, and carbon cycles. Coarse woody debris in the Sitka spruce (*Picea sitchensis* Bong.) forests of the Pacific Northwest store 80.4 kg/ha of nitrogen and 6.6 kg/ha of phosphorus (Graham and Cromack 1982). Harmon et al. (1990) determined that coarse woody debris in old-growth Douglas fir (*Pseudotsuga menziesii* Mirbel)*)* forests store 97,000 kg/ha of carbon. In a more recent study of the Wind River Canopy Crane Research Facility, Harmon et al. (2004) found CWD to be the largest pool of carbon accounting for 95,500 kg C/ha. In the timberlands of the continental United States 10.0% of the carbon is stored in coarse woody debris (Turner et al. 1995). Coarse woody debris releases nitrogen, phosphorus, and carbon as it decomposes. Decomposition rates will help determine the resident time for CWD ultimately providing an understanding of the net CO_2 released from forested ecosystems. Knowledge of the decomposition rate of

CWD will provide information for the calculation of CO_2 emission from land-use change and forest management practices, and will also provide information on the nutrients released into the soil matrix (Mackensen 2003).

Thinning Study Site Description

In the 1980-1981 and 1981-1982 dormant seasons, long term research plots of planted loblolly pine *(Pinus taeda* L.*)* were established on cutover site-prepared land from eastern Maryland south to northern Florida and west to eastern Texas, encompassing loblolly pine natural range (Burkhart et al. 1985) (Figure 1). Each plantation site, to be included in the long term sample had to meet a variety of criteria: at least 8 years since planting, unthinned, free of heavy disturbance, free of interplanting, unpruned, not fertilized within four years of plot establishment, no genetically improved stock, 500 to 750 planted pine stems per hectare, and less than 25% of canopy composed of volunteer pines and hardwoods (Burkhart et al. 1985). Three separate density treatments were established at each site location, a control, a plot having < 50% of the original stems thinned, and a plot having > 50% of the stems thinned. After establishment each site was measured every three years until the stands were harvested. Remeasurement allowed for the time of death to be recorded for any dead trees within plot boundaries. Due to the continued remeasurement of the sites there is a valuable opportunity to understand decomposition rates of loblolly pine CWD at the piece level in industrially managed forest ecosystems.

Study Objectives

This study had three objectives:

1.) determine the individual CWD piece decomposition rate in the long-term loblolly pine thinning study plots located throughout much of the southeastern United States using the single exponential decay model ($X = X_0 e^{-kt}$) proposed by Olson (1963).

2.) explore whether different factors such as diameter, position class, average temperature, average precipitation, latitude, longitude, physiographic region, and heating degree days influence the decomposition rate of loblolly pine CWD via multiple linear regression techniques.

3.) develop multiple linear regression models across all physiographic regions and according to each physiographic region within the study area, for CWD disk decomposition rate, disk specific gravity, and time since death (TSD).

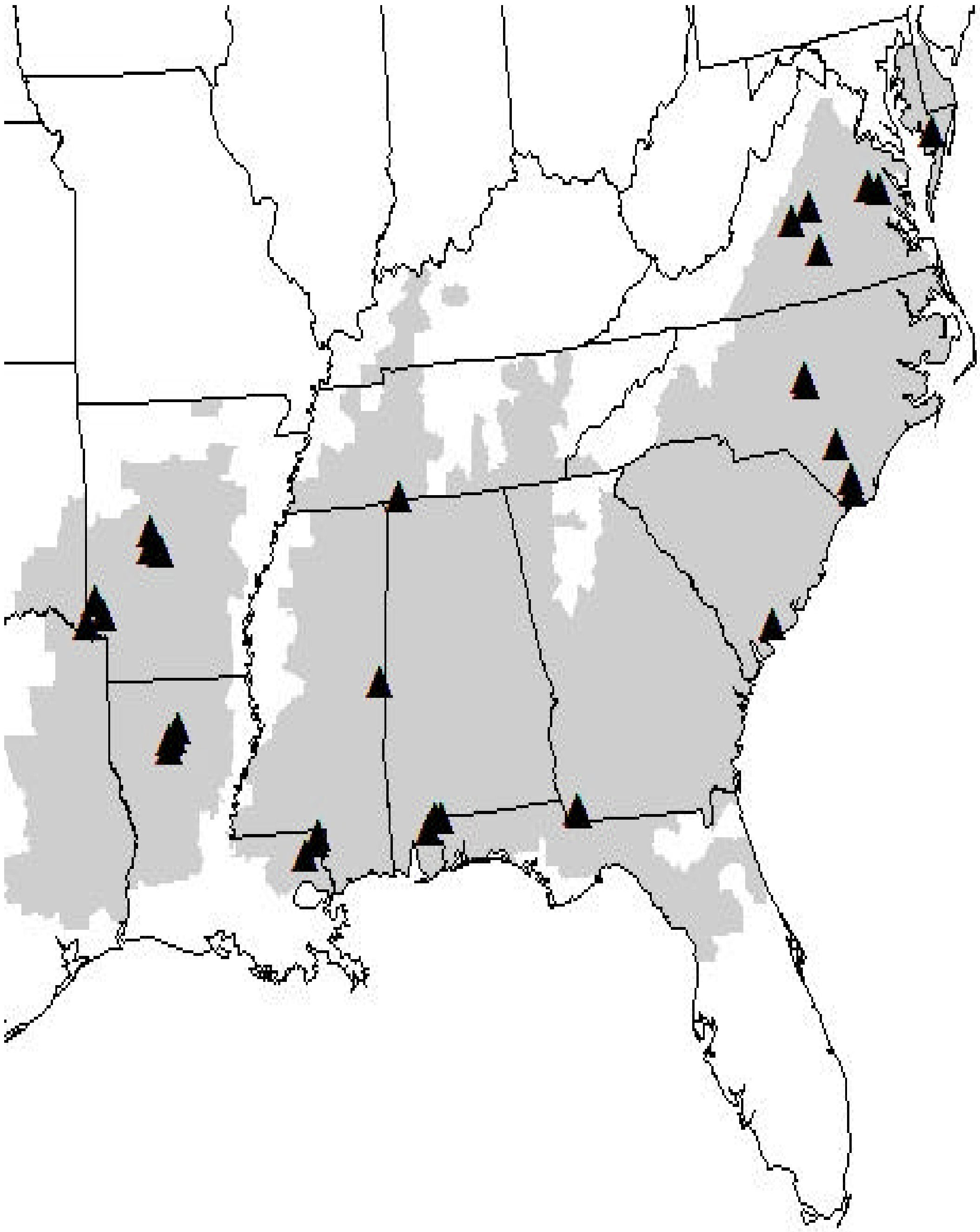

Figure 1: Location of the loblolly pine thinning study sites across the southeastern United States. One triangle in Mississippi but three sites 9173, 9174, and 9175 with same latitude and longitude. Two sites in Georgia with same latitude and longitude 6101 and 6103, appear as a single triangle. There were three sites in North Carolina with the same latitude and longitude 5112, 1417, and 5114. The gray area indicates the natural range of loblolly pine.

Literature Review

Definition and Forms of CWD

The definition of CWD has varied due to the different forms in the forest ecosystem. However, size and position are the most useful criteria for classifying CWD (Harmon and Sexton 1996). Coarse woody debris has been defined by a wide range of sizes. For example, several studies defined CWD as having a diameter ≥ 10.0 cm (Hale et al. 1999; Idol et al. 2001; Janisch and Harmon 2001; Krankina et al. 2002; Davis et al. 2003; Densmore et al. 2004; Harmon et al. 2004). Lee et al. (1997) used a diameter of ≥ 11 cm. A study assessing the carbon budgets of forests in the United States defined CWD as woody material with a diameter ≥ 2.00 cm (Turner et al. 1995). Barber and van Lear (1984), Ganjegunte et al. (2004), and McCarthy and Bailey (1994) defined CWD as woody material with a diameter of ≥ 2.5 cm. Dead boles in subalpine forests of the northeastern United States were defined as woody debris > 3.00 cm in diameter (Lambert et al. 1980). Woody material ≥ 5.00 cm in diameter was considered CWD by Lang (1985) and Harmon and Sexton (1996). I will use ≥ 4 cm large end diameter as the definition of CWD for this research study.

In combination with size, CWD can also be defined according to its position. Coarse woody debris at an angle < 45 ° off the ground is defined as a log (Harmon and Sexton 1996). A log can be in the form of an entire bole, sections of the bole, exposed roots, tree tops or fallen branches (Hely et al. 2000). Coarse woody debris off the ground and at an angle ≥ 45 ° is considered a snag (Harmon and Sexton 1996; Hagan and Grove 1999). A stump is another form of CWD found in the forest ecosystem. It is a standing cut tree bole ≥ 10 cm in diameter (Janisch and Harmon 2001). The combination of logs, snags, and stumps contributes to the total CWD load in the forest ecosystem.

Functions of CWD

Coarse woody debris is an important component of forested ecosystems serving a variety of functions. Coarse woody debris reduces soil erosion; affects the development of soil; impacts soil hydrology and soil biology; influences nutrient cycling; leaches nutrients, such as nitrogen, into the mineral soil; supplies energy and nutrients for a variety of organisms; acts as a seed bed for herbaceous plants; provides organic matter to the forest floor; and provides a habitat for microbes (Mattson et al. 1987; McMinn and Crossley 1993; Marra and Edmonds 1994; McCarthy and Bailey 1994; Harmon and Sexton 1996; Harmon et al. 2000). The organic matter provided by the fragmentation and decomposition or CWD helps to hold moisture in the soil matrix (Harvey et al. 1981). The variability and durability of CWD provides different niches for providing habitat for fungal and insect diversity thereby creating a healthy decomposer community within the forest ecosystem (Muller et al. 2002). Coarse woody debris acts as a barrier or protective structure facilitating seedling regeneration by decreasing browsing on the new sprouts (Ripple and Larson 2001). Coarse woody debris in direct contact with the ground serves as a reservoir of moisture, which maintains the productive capacity of the soil, and acts as a medium in the nutrient cycles (McMinn and Crossley 1993; Marra and Edmonds 1994). The presence of CWD in a forest ecosystem after a large natural disturbance helps stabilize the nutrient bank in the ecosystem. Surface soil temperatures are moderated by CWD (Marra and Edmonds 1994). Coarse woody debris is a natural albeit temporary carbon sink. Upon decomposition or burning, CWD releases carbon into the atmosphere, increasing the atmospheric carbon pool (Harmon et al. 1990; Marra and Edmonds 1994). Coarse woody debris also serves as a foraging and shelter area for birds and mammals (Lee et al. 1997).

The risk of fire, tree pathogens, and insect outbreaks are influenced by the volume/amount of CWD present in a forest ecosystem (Duvall and Grigal 1999). Coarse woody debris especially impacts fire. The volume of CWD in a forest ecosystem has little influence on spreading and intensity of the fire, but does control the size of fire, fire severity, fire persistence, resistance to control, and burnout time (Brown et al. 2003). These factors impact the degree of soil heating affecting subsequent forest regeneration and productivity (Brown et al. 2003). Soil temperature during fire is greater in areas where CWD covers the surface. For example, Brown et al. (2003) determined that increasing the CWD volume in a forest from 50.0 Mg/ha to 253 Mg/ha resulted in a 30° C increase in the first 2 cm of soil surface during a fire. Coarse woody debris on a harvested site can harbor pathogens that will be released upon decomposition during regeneration of the next forest stand.

Origin of CWD

The accumulation of CWD in a forest ecosystem depends upon the stand composition, stand age, disturbance, mortality, topography, species specific characteristics, and decomposition (Lang 1985; Spies et al. 1988; Duvall and Grigal 1999; McCarthy et al. 2001; Krankina et al. 2002). Topography in relation to site productivity influences CWD loads with more productive sites, which often have a northeastern aspect, having greater CWD loads (McCarthy et al. 2001). Species specific characteristics influence CWD load. For example, a species' susceptibility to pathogens, ice damage, or resistance to decay will affect CWD load (Rubino and McCarthy 2003). Coarse woody debris accumulation is related to the overstory forest composition. The CWD on the ground reflects the canopy species composition, but does not relate to the understory composition (Rubino and McCarthy 2003). For example, chestnut oak (*Quercus prinus* L.), beech (*Fagus gandifolia* Ehrh.), white oak (*Quercus alba* L.), and black oak (*Quercus velutina* Lam.) dominated a stand in Kentucky accounting for 56% of the total basal area, these same four species accounted for 61% of the CWD volume in the stand (Muller and Lui 1991). Rates of input both natural and anthropogenic depend upon tree mortality (Harmon and Sexton 1996; Clark et al. 1998). Natural disturbances that increase tree mortality can be broken into two distinct categories mechanical and biological. Mechanically caused inputs include wind, fire, rain, ice, and snow. Biological inputs include tree mortality caused by pathogens and insects (Harmon and Sexton 1996; Lee et al. 1997; Clark et al. 1998). Disease and insects such as chestnut fungus, beech bark disease, fusiform rust, and gypsy moth can greatly increase the load of CWD in a forest ecosystem by causing mass tree mortality. In old growth beech and maple forests of Adirondack Park, New York, beech bark disease increased the volume of CWD by 40.0% when compared with old growth forests not hit by the disease (McGee 2000).

Stand Age and CWD

Time since last major disturbance, which relates to stand age, has an impact on the volume or load of CWD in a forest ecosystem. The accumulation of CWD in the forest ecosystem approximately follows a U – shaped pattern. Stands after a disturbance will initially have an elevated volume of CWD, however as a young forested ecosystem evolves into a mature forest the volume of CWD is reduced due to decomposition of the woody residue, but CWD accumulation again increases in old-growth stands (Table 1). Generally, as the stand ages, it undergoes a variety of disturbances causing a rise in tree mortality and therefore increased accumulation of CWD (Harmon et al. 1990; Muller and Lui 1991; McCarthy and Bailey 1994; Lee et al. 1997; Clark et al. 1998; Goodburn and Lorimer 1998; Krankina et al. 2002). For example, CWD composed up to 56% of total above ground detritus in the Changbai old-growth forest in Japan and between 71% and 81% of the above ground detritus in Andrew's old-growth forest in Oregon (Harmon and Hua 1991). In mature 60 – year old Douglas fir forests of the Pacific Northwest CWD accounted for 34% of the total above ground detritus (Harmon et al. 1990).

Anthropogenic Influences on CWD

Forest management practices such as controlled burns, thinning, salvaging, and harvesting are considered anthropogenic disturbances that can affect inputs, accumulation, and decomposition of CWD subsequently impacting the nutrient and carbon cycles within the forested ecosystem (Lee et al. 1997). Controlled burns have the capability of increasing the volume and biomass of CWD compared to non-disturbed early successional stands. For example, in the Northern Patagonian tropical forests of Chile there was 1111 m^3/ha of CWD in a controlled burned forested ecosystem compared to 65.0 m^3/ha of CWD in an unburned tropical forest ecosystem (Carmona et al. 2002). A high severity, post harvest, slash burn can be detrimental to subsequent forest health because large amounts of CWD are burned, which releases carbon and other nutrients (Harmon and Marks 2002). Timber harvesting or salvage logging a forest ecosystem after a major disturbance reduced the available pool of nutrients

Table 1: Forest composition and the volume of CWD at different successional stages throughout a variety of forested ecosystems.

Species Comp.	**Time Since Last Disturbance**	**CWD Accumulation**	**Source**
Douglas-Fir	< 80	423 m^3/ha	Spies et al. 1988
Douglas-Fir	80-199	250 m^3/ha	Spies et al. 1988
Douglas-Fir	> 200	534 m^3/ha	Spies et al. 1988
Boreal Forests	< 20	16 Mg/ha	Krankina et al. 2002
Boreal Forests	21-80	6 Mg/ha	Krankina et al. 2002
Boreal Forests	> 80	9 Mg/ha	Krankina et al. 2002
Beach	8-15	74.4 m^3/ha	Goodbum and Lorimer 1998
Sugar Maple	65-75	39.2 m^3/ha	Goodburn and Lorimer 1998
Chestnut-Oak	120+	126.9 m^3/ha	Goodburn and Lorimer 1998
Northern Hardwood	120+	151.4 m^3/ha	Goodburn and Lorimer 1998
Sub-boreal Spruce	0-50	110.0 m^3/ha	Clark et al. 1998
Sub-boreal Spruce	51-100	60.0 m^3/ha	Clark et al. 1998
Sub-boreal Spruce	201-250	100 m^3/ha	Clark et al. 1998
Sub-boreal Spruce	351-400	150 m^3/ha	Clark et al. 1998
Upland Hardwood	1	150.0 m^3/ha	Idol et al. 2001
Upland Hardwood	12-16	90.0 m^3/ha	Idol et al. 2001
Upland Hardwood	31	45.0 m^3/ha	Idol et al. 2001
Upland Hardwood	80-100	70.0 m^3/ha	Idol et al. 2001
Hardwood	< 50	592 m^3/ha	Carmona et al. 2002
Hardwood	< 120	215 m^3/ha	Carmona et al. 2002
Hardwood	>120	500 m^3/ha	Carmona et al. 2002

for ecosystem recovery (Harmon and Hua 1991) and decreased the amount of protection, provided by CWD, for new sprouting herbs, shrubs, and trees from browsing (Ripple and Larson 2001). Thinning a forest ecosystem reduced the total volume and number of snags in a forest ecosystem (Lee et al. 1997; Graves et al. 2000). However, if the thinned trees were left on site, total volume of CWD on the forest floor increased. Duvall and Grigal (1999) found that after 90 years, mature forests managed for timber production had 85% less CWD than unmanaged forests. Selective cutting increases the CWD in a forest ecosystem if the cut timber remained on site (Hale et al. 1999).

In clear-cut mixed boreal and mixed mesophytic forests the CWD was smaller in diameter, and less decayed then the CWD in pole and mature forest ecosystems (McCarthy and Bailey 1994; Lee et al. 1997). Clear-cutting impacted the decomposition rates of CWD by drastically changing the soil environment, removing the canopy, and exposing the soil surface to more direct radiation, which increased surface temperatures (Abbott and Crossley 1982; Childs and Flint 1987; Gordon et al. 1987; Chen et al. 1992; Marra and Edmonds 1996). Canopy removal affected internal CWD temperature, for example raising the daily temperature of the CWD from 17.5° C at the soil surface to between 23 ° and 35° C just beneath the CWD surface (Marra and Edmonds 1996). Clear-cutting also impacted soil moisture levels, for example Gordon et al. (1987) determined that moisture content was consistently elevated on the clear-cut sites (161.5%) compared to a full canopy forest ecosystem (142.5%). The higher soil temperature and moisture content increased decomposition rates by providing a more suitable habitat for fungi and bacteria to colonize (Gordon et al. 1987). Clear-cutting caused large seasonal fluctuations in CWD respiration rates, with lower rates in the winter and increased rates in the summer compared with respiration rates in a full canopy old-growth forest (Marra and Edmonds 1996). Without a forest canopy the ground surface is subject to extremely high temperatures causing all soft and hardwood species

CWD to be subject to case-hardening (Barber and van Lear 1984). Case-hardening is the drying or seasoning of the outer portions of the sapwood. Case-hardening caused a decreased in the respirations rate of CWD. Case-hardening disproportionately affected smaller diameter CWD. Larger CWD is less affected due to the greater surface area to volume ratio and more favorable conditions for decay (Barber and van Lear 1984).

Clear-cutting increased input of CWD volume into a forest ecosystem and affected the decomposition class of the CWD, however clear-cutting does not mimic the input of CWD caused by mortality, and/or natural disturbances such as wind or ice (Tinker and Knight 2001). Generally CWD in clear-cut stands will be disproportionately composed logs in the early stages of decay, and have fewer highly decayed logs (McCarthy and Baily 1994; Idol et al. 2001). McCarthy and Baily (1994) measured differences in volume of CWD inputs between clear-cuts, pole stage stands, mature stands, and old-growth forests. Coarse woody debris volume was significantly higher in the clear-cut stands compared with the other stands (McCarthy and Baily 1994). Clear-cuts had 90.0 m^3/ha of CWD, old growth stands had 65.0 m^3/ha, mature stands had 45.0 m^3 / ha, and pole-aged stands had 40.0 m^3 / ha (McCarthy and Baily, 1994). However if much of the bole wood is harvested during the clear-cut these larger pieces of CWD are disproportionately lost from the forest ecosystem, instead most of the CWD is composed of small woody debris and tree tops (Tinker and Knight 2001). After one rotation managed forests in British Columbia decreased to 30% of the original amount of CWD in natural stands (Densmore et al. 2004).

CWD Decomposition Process

The decomposition of CWD involves several different processes: microbial colonization, weathering, leaching, settling, and fragmentation. Microbial decomposition involves the colonization of the CWD by a variety of different species of fungi and bacteria (McMinn and Crossley 1993; Yin 1999). The invasion of fungi leads to an initial mass loss and break down of organic carbon leading to a release of carbon as CO_2 gas (Spies et al. 1988; Wei et al. 1997). The transformation of organic carbon into atmospheric carbon by fungi is called respiration. Fragmentation of CWD refers to the reduction of volume by environmental conditions and biological mechanisms (Harmon et al. 1986; McMinn and Crossley 1993; Marra and Edmonds 1994; Wei et al. 1997). For example, invertebrates rely on CWD as a food source. Invertebrates chew, ingest and excrete the digested CWD creating a dust that decays more rapidly due to the increased surface area to volume ratio (Harmon et al. 1986). Birds and mammals increased fragmentation by foraging for insects in the CWD and plant's roots burrowed through the woody material in search of nutrients (McMinn and Crossley 1993). Weathering or physical fragmentation is caused by gravity or water breaking the CWD into smaller pieces, which expose more surface area for microbial colonization (Harmon et al. 1986). Leaching, caused by the physical forces of water, temperature, and gravity, transport nutrients and soluble polymers from CWD into the soil matrix, breaks down wood structure and enhances decomposition (McMinn and Crossley 1993). The importance of leaching is enhanced by fragmentation and microbes. Microbes have the ability to change the polymeric material of CWD into soluble substances (Harmon et al. 1986). As CWD decays, the wood structure begins to deteriorate and the log is unable to support its own weight changing from circular in nature to elliptical. Settling increases the amount of log in contact with the ground and creates a more hospitable environment for invertebrates, bacteria, and fungi (Harmon et al. 1986). These processes all work synergistically to allow the decomposition of woody material.

Nutrient Cycling and CWD

Coarse woody debris acts as a medium for nutrients between the soil and the atmosphere. Coarse woody debris is composed of distinct substrates such as heartwood and sapwood; these substrates release nutrients at varying rates. Most nutrients are slowly released from CWD into the soil matrix through leaching, fragmentation and biological breakdown, however carbon can be released into the atmosphere by microbial respiration. Coarse woody debris is a significant sink for mineral nutrients such as nitrogen and phosphorus. For example between 80.4 kg/ha and 156.6 kg/ha of nitrogen and between 6.60 kg / ha to 8.80 kg / ha of phosphorus were stored in Sitka spruce forests of the Pacific Northwest (Graham and Cromack 1982; Edmonds 1987; Laiho and Prescott 1999; Idol et al. 2001). After a natural or anthropogenic forest disturbance, CWD stabilizes nutrients in the forested ecosystem because it slowly releases nutrients allowing forest production to recover (Harman and Hau 1991).

The importance of CWD in the forest nutrient cycle depends upon decay class (Pyle and Brown 1998). The definition for decay classes in the subsequent discussion is not the same as used for this study. For example, pine CWD in the Pacific Northwest had an increase in nitrogen content over a 14 year study period (Laiho and Prescott 1999). A direct relationship between increasing decay class and nutrient immobilization has been reported in forests of the western United States and British Columbia (Grier 1978;

Graham and Cromack 1982; Edmonds 1987; Pearson et al. 1987; Edmonds and Eglitis 1989; Wei et al. 1997; Preston et al. 1998; Holub et al. 2001). Patterns of calcium, phosphorus, and nitrogen immobilization (kg / ha) in association with decay class, were highest in decay classes IV (wood is spongy, bark is absent and becoming oval in shape) and V (bark is absent, wood has become a powder, and the bole is oval or has become flat), while in decay classes I-III calcium, phosphorus, and nitrogen remained at a steady concentration or were released slowly (Grier 1978; Lambert et al. 1980; Sollins et al. 1987; Preston et al. 1998; Pyle and Brown 1998; Holub et al. 2001; Idol et al. 2001; Hicks et al. 2003). Nitrogen can be a limiting factor for wood decomposing microbes; therefore nitrogen is especially immobilized, in later stages of decay. In balsam fir (*Abies balsamea* (L.) Miller.) CWD there was 1,800 μg N / g CWD in decay class III (loosening of the bark, decay of sapwood, heartwood intact), nitrogen content increased to 9000 μg N / g CWD in decay class IV, (Holub et al. 2001). The increased immobilization of nutrients in later stages of CWD decay could result from precipitation and throughfall, dry deposition, litter fall, root ingrowths, fungal translocation, animal inputs, and asymbiotic N^2 fixation (Lambert et al. 1980; Graham and Cromack 1982; Frey et al. 2000; Harmon et al. 1986; Sollins et al. 1987). One hypothesis for why nitrogen becomes immobilized in decay classes IV and V is the biology of decomposition. For microbes and bacteria to degrade carbon and obtain energy they must retain, import, or manufacture nitrogen to produce the decomposition enzymes (Holub et al. 2001). Potassium was the most mobile of the nutrients cycled through conifer CWD in forested ecosystem (Edmonds 1987). Potassium in western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) unlike nitrogen, calcium, and phosphorus, was released from CWD in decay classes I (freshly fallen) and III changing from a concentration of 1100 μg K / g CWD to 600 μg K / g. Coarse woody debris potassium concentration then remained steady throughout the rest of the decomposition process (Holub et al. 2001).

Coarse woody debris is also a significant carbon store accounting for 10% to 18% of the total carbon storage in the timberlands of the United States. The same relationship holds true when specifically looking at the timberlands of the southeastern United States (Turner et al. 1995; Laiho and Prescott 1999). Compared to all other terrestrial biomes, forests have the greatest capacity for storing and cycling carbon (Barford and Wofsy 2001; Harmon and Marks 2002; Hood et al. 2004). Old - growth forests normally have the greatest volume of CWD (Table 1) thus providing a significant carbon sink. For example, in old growth forests CWD carbon storage peaked and leveled off between 75.0 Mg C / ha and 127 Mg C / ha after 200 years of forest growth (Harmon et al 1990; Janisch and Harmon 2001). Coarse woody debris was the largest pool of stored carbon in the Wind River Canopy Crane Research Facility old growth Douglas fir forest storing 95.5 Mg C/ha (Harmon et al. 2004). A study conducted in New Zealand found that CWD in stands > 150 years in age stored the least amount of carbon (11.3 Mg/ha), while young stands still in the seedling stage stored up to 84.4 Mg / ha of carbon (Davis et al. 2003). Mature forests store less carbon than old-growth forests. Carbon storage in mature forests of the Pacific Northwest ranges from 3.80 Mg C / ha and 29.7 Mg C/ ha (Harmon et al. 1990; Turner et al. 1995; Idol et al. 2001).

Coarse woody debris decay stage influences the amount of carbon stored. For example, after 14 years of decomposition, pine CWD still contained 49.8% of its total carbon (Laiho and Prescott 1999). In Northern Patagonian forests of Chile carbon storage stayed relatively constant throughout decay classes I-V ranging from 49.5% to 44.7% dry weight (Carmona et al. 2002). Douglas fir logs in British Columbia had increased concentrations of carbon, with decay class I having 489 g C/kg and decay class V logs having 532 g C /kg (Preston et al. 1998).

Management influences a forested ecosystems capability of storing carbon. Forests managed using short rotation – high utilization techniques caused the greatest release of carbon from the landscape compared with longer rotation – low utilization management systems (Harmon et al. 1990; Harmon and Marks 2002). There are three management factors that have the greatest affect on a forest's potential for storing carbon: stand rotation length, amount of live mass harvested, and amount of detritus and/or CWD removed during slash burning and piling (Harmon and Marks 2002).

Coarse woody debris releases nutrients into the soil through net mineralization, performed by fungi or microbial bacteria (Barber and van Lear 1984; Holub et al 2001; Spears et al. 2003). In the early stages of decomposition, CWD released nutrients through leaching, as decomposition persisted and colonization of fungi was completed, the primary mechanism for nutrient release was mineralization (Barber and van Lear 1984; Harmon and Sexton 1996). Coarse woody debris is not the sole nutrient source for replenishing the soil. Non-woody debris such as leaf litter released more nitrogen and phosphorus than CWD into the soil (Barber and van Lear 1984; Harmon and Hua 1991; Harmon and Sexton 1996; Laiho and Prescott 1999). Coarse woody debris in Andrews old-growth forest in Oregon released < 10.0 kg / ha / yr of nitrogen and phosphorus, while the rest of the litter layer released > 20.0 kg / ha / yr of nitrogen and > 8 kg / ha / yr of phosphorus (Harmon and Hua 1991). However, CWD leachate provided a significant amount of dissolved organic carbon, over an 87-year period CWD was estimated to release 4.5 kg C / m^2 in forests of the Pacific Northwest (Spears et al. 2003). Non-woody debris released nutrients at a greater rate than CWD (Harmon and Hua 1991; Laiho and Prescott 1999; Spears et al. 2003).

Decomposition Rates

Generally, studies determining the decomposition rate of CWD depend on chronoseqeuence data. Chronosequence is when sampling was performed over known ages and decay classes. It is rare to find a long-term CWD monitoring study where the time since death was determined for each piece of CWD through repeated site remeasurement (Mackensen et al 2003). Determining the decomposition rate of CWD has been attempted using different mathematical models that rely on changes in volume, biomass, and / or wood density overtime. The decomposition rate is generally expressed via a constant *k*, which is the percent mass, volume, or density loss over time (Harmon et al. 1986; Mackensen et al 2003). Four potential models for determining the decay rate constant or k-value of CWD were: single exponential model, multiple exponential model, lag-time model, and the linear model (Mackensen et al. 2003).

The single exponential model is the most common multiple linear regression model form used to determine CWD decomposition constants (Olson 1963; Graham and Cromack 1982; Barber and van Lear 1984; Lang 1985; Mattson et al. 1987; Edmonds and Eglitis 1989; Harmon and Hau 1991; Stone et al. 1998; Laiho and Prescott 1999; Harmon et al. 2000; Chen et al. 2001; Janisch and Harmon 2001; Klepzig et al. 2001; Mackensen and Bauhus 2003). The single exponential decay model assumes that all regressor variables remain constant throughout the decomposition process implying the proportion of wood lost over time remains constant (Olson 1963; Mackensen et al. 2003). Minderman (1968) argued against using the single exponential model because CWD is heterogeneous, with substances decomposing at different rates. The multiple exponential decay model assumes that CWD components decompose at varying

Table 2: Coarse woody debris decomposition rates by to species determined using the single exponential model according to Olson (1963).

Species	Decomposition Rate (k)	Source
Pinus spp.	0.024	Harmon et al. 2000
Picea spp.	0.027	Harmon et al. 2000
Eucalyptus regnans	0.041	Mackensen and Bauhus 2003
Eucalyptus maculata	0.049	Mackensen and Bauhus 2003
Pinus radiata	0.127	Mackensen and Bauhus 2003
Pinus rigida	0.063	Mattson et al. 1987
Acer rub rum L.	0.081	Mattson et al. 1987
Pinus taeda *	0.081	Barber and van Lear 1984
Pinus taeda ?	0.075	Barber and van Lear 1984
Tsuga heterophylla	0.0118	Grier 1978
Pinus spp.	0.052	Laiho and Prescott 1999
*Pseudotsuga menziesii**	0.050	Edmonds and Eglitis 1989
Pseudotsuga menziesii	0.028	Sollins 1982

Note: (*) indicates medium diameter logs ranging in size from 2.5 cm to 7.0 cm. (?) Indicates large diameter logs > 7.0 cm.

rates over time (Minderman 1968; Means et al. 1985). For example, a study of mountain ash (*Eucalyptus regnans* F. Muell*)* CWD determined that heartwood was more decay resistant than sapwood (Mackensen and Bauhus 2003). A short-coming of both the single and multiple exponential decay models is the assumption that as decomposition proceeds

CWD substrates do not transform into more or less decomposable substances (Harmon et al. 1986). The lag-time model takes into consideration the time required for fungi, bacteria, and macroinvertebrates to colonize CWD. This assumption leads to slower initial rates of decomposition in CWD (Harmon et al. 1986; Mackensen et al. 2003).The linear model assumes linear relationships between CWD decay and the variables influencing the decomposition process (Graham and Cromack 1982).

Factors Influencing CWD Decomposition

Coarse woody debris decomposition rates are influenced by diameter, decay stage, presence or absence of colonizing fungi and insects, climatic variables, surface to volume ratio, structural characteristics of wood, chemical characteristics of wood, and position. The relationship between CWD diameter and decomposition rate varies with site. For example, in the southern Appalachian forest, no significant relationship was determined between CWD diameter and decomposition rate (Mattson et al. 1987). Increased diameter of CWD boles leads to slower decomposition rates in the Pacific Northwest, and British Columbia (Graham and Cromack 1982; McMinn and Crossley 1993; Marra and Edmonds 1994; Stone et al. 1998). However, another study done in the Pacific Northwest indicated that large CWD boles had decomposition rates ranging from 0.044 – 0.05 while small CWD boles had decomposition rates ranging from 0.006-0.026 (Edmonds and Eglitis 1989). Increased log diameter results in a smaller surface to volume ratio exposing a minimal portion of exterior CWD to mechanical and biological weathering, colonization by fungi and insects, and ground contact (Abbott and Crossley 1982; Mackensen et al. 2003). Smaller diameter logs have an increased surface to volume ratio leading to increased fragmentation rates and surface contact between CWD and substrate (Abbott and Crossley 1982; Graham and Cromack 1982; Mackensen et al. 2003). Increased surface to volume ratio was the factor leading to elevated decomposition rates in smaller diameter Sitka spruce and western hemlock CWD of the Pacific Northwest (Graham and Cromack 1982). As diameter decreased in Douglas fir boles of the Pacific Northwest, decomposition rate increased, however the opposite trend was true for western hemlock (Marra and Edmonds 1994). Colonization by insects and fungi elevated large diameter CWD decomposition rates by increasing fragmentation (Edmonds and Eglitis 1989; Marra and Edmonds 1994; Laiho and Prescott 1999). Case hardening or seasoning, a phenomenon that occurs in small diameter CWD, significantly retards the decomposition process by decreasing moisture loss and fragmentation (Barber and van Lear 1984; Harmon et al. 1986).

Coarse woody debris position affects the decomposition rates. Coarse woody debris can be standing, leaning, in contact with the ground, and partially to completely covered by the forest floor. Contact with the ground increases decomposition rates of CWD due to elevated moisture content and increased fungal and insect colonization (Barber and van Lear 1984; Edmonds 1987; Mattson et al. 1987; Marra and Edmonds 1994; Wei et al. 1997; Mackensen et al. 2003). Coarse woody debris suspended in the air has decreased rates of decomposition compared to CWD in contact with the ground (Erickson et al 1985; Edmonds et al. 1986; Mattson et al. 1987). For example, loblolly pine CWD in contact with the ground decayed 50.0% faster than aerial loblolly pine CWD (Barber and van Lear 1984). Ground contact helps to stabilize the temperature and moisture content of CWD thereby making it a more suitable habitat for colonizing microbial organisms.

The decomposition rate of CWD fluctuates with changing decay stage. The accumulation of CWD in the forested ecosystem according to decay stage follows a bell shaped curve with a high number of boles in the middle stages of decay, and fewer in the early and late stages of decay (Graham and Cromack 1982). The highest decomposition rates occur during moderate stages of decay because resource quality, colonization by fungi, and moisture content are not limiting factors for decomposition (Hicks et al. 2003). In the early stages of decay colonizing fungi use all the easily decomposable compounds such as cellulose and hemicellulose (Preston et al. 1998). As decay proceeds, the remaining CWD is heavily laden with lignin containing compounds, which are more difficult for microbial breakdown (Preston et al. 1998). As the density of the CWD is reduced during decomposition, the moisture content is increased providing an explanation for the elevated decomposition rates at later stages of decomposition (Boddy 1983). Coarse woody debris in the initial stages of decomposition had a lower rate due to lack of colonizing fungi and a low moisture content, whereas CWD in the final stages of decomposition was limited by low resource quality and elevated moisture levels (Hicks et al. 2003).

Decomposition rates of CWD fluctuate according to changes in precipitation and temperature, and therefore are related to differences in longitude and latitude. Decomposition rates are highest in environments with elevated temperatures and sufficient precipitation allowing colonization of CWD by decomposing fungi and bacteria (Progar et al. 2000). Fluctuations in temperature and precipitation can increase or decrease the biological activity of fungi and bacteria. Most organisms have optimum temperature ranges for survival, for example the mesophilic fungi that colonize CWD have a temperature range of 0 ° C to 40 ° C (Harmon et al. 1986). Decay rates of CWD were enhanced following elevated temperatures during May, June, and July in old growth forests of the Pacific Northwest (Marra and Edmonds 1994; Marra and Edmonds 1996). For example, decay class I-II Douglas- fir logs had respiration rates during January of 1.0 g CO_2 / m^2 / day, but in the month of May had respiration rates of 7.50 g CO_2 / m^2 / day (Marra and Edmonds 1996). A temperature change exerts more influence on fluctuations in decomposition rates of CWD than any other climatic variables (Edmonds 1987; Gordon et al. 1987; Marra and Edmonds 1996; Trofymow et al. 2002). There was no consistent relationship between decomposition rate and temperature indicating that temperature may be confounded with other factors such as moisture content, species, and position (Harmon et al. 2000). For example, in Douglas fir CWD as the outside environmental temperature increased 7 ° C the decomposition rate increased 0.02 units, however over a similar increase in temperature the decomposition rates of western hemlock CWD stayed steady (Harmon et al. 2000).

Coarse woody debris is a heterogeneous substrate with a variety of structural, chemical, and anatomical features that influence the decomposition rate. Structurally, CWD is composed of bark, sapwood, and heartwood. Heartwood is the most resistant structural component to decay (Harmon et al. 1986). The amount of heartwood is positively correlated with size. As tree diameter increases, the greater proportion of heartwood should decrease the decomposition rate (Harmon et al. 1986). However, in Monterey pine (*Pinus radita* D.Don) logs the bark was determined to have significantly greater lignin concentrations and tannin concentration than the heartwood or sapwood, possibly explaining the slower decomposition rate of bark (Ganjegunte 2004).

Gymnosperm sapwood contains 5% to 10% living tissue by volume. The amount of living tissue affects the decomposition rate because it contains more readily decomposable substances e.g., for example sugars, starches, and proteins (Harmon et al. 1986). Another important characteristic of the living tissue are the water conducting elements. The size and orientation of these elements affect the ability of fungi, bacteria, and macroinvertebrates to colonize the substrate. Loblolly pine have longitudinally oriented, narrow trachieds for water transport compared to the larger vessels of angiosperms, this could explain the slower decomposition rates of gymnosperms (Harmon et al. 1986).

The chemical composition of CWD also affects the decomposition rate. Three different molecules make up the chemical composition of wood cell walls: cellulose, hemicellulose and lignin. Cellulose is a simple linear polymer, or a compound composed of several molecules, of linked glucose units. In gymnosperms the cell wall is around 44% cellulose (Wenzel 1970). Due to its simple chemical structure cellulose is the easiest molecule for fungi and other microbes to decompose. The next biggest component of the cell wall is hemicellulose, which compose 13% to 31% (Wenzel 1970). Hemicellulose is a branched molecule composed of several sugars, including glucose, galactose, mannose, arabinose, xylose, and glucuronic making it harder to decompose than cellulose (Harmon et al. 1986). The final component of the cell wall and the most complex molecule is lignin, which in gymnosperms is a guaiacyl-based compound, a more complex molecule than the syringly- based lignin compound in angiosperms. Gymnosperm lignin is a more decay resistant form of the molecule (Ganjegunte 2004). The difficulty of lignin decomposition is evident in the latter stages of CWD decay because CWD has elevated lignin concentration relative to the other carbon compounds in the total wood volume and a slower decomposition rate (Harmon et al. 1986; Ganjegunte 2004).

CWD Moisture Content

Another factor impacting CWD decomposition is moisture content, which is related to position, decay stage, and size. Moisture content can also be influenced by microbial respiration; for example, for every gram of cellulose respired 0.555 g of water is created (Griffin 1977). Log moisture content, on a dry-weight mass basis, below 30% limits biological activity because is not available to the wood colonizing organisms (Griffin 1977). Above the 30% log moisture content threshold, water within the decaying piece of CWD becomes available for uptake by fungi and other microbes. The optimal moisture content in CWD for decomposition ultimately depends on the organism, for example log moisture content between 30% and 160% supports growth of basidiomycetes, where as ascomycetes can tolerate up to 240% (Kaarik 1974; Griffin 1977).

Coarse woody debris in contact with the ground has an elevated moisture content and larger pieces of CWD retain a higher moisture content (Barber and van Lear 1984; Mattson et al. 1987; Laiho and Prescott 1999). Sitka spruce and western hemlock CWD in decay classes IV and V had higher moisture contents than CWD in earlier stages of decay (Graham and Cromack 1982). Elevated moisture content in decaying CWD increases microbiological activity creating a more suitable habitat for colonizing bacteria, fungi, and insects, thus increasing decomposition (Lambert et al. 1980; Gordon et al. 1987; Mattson et al. 1987; Marra and Edmonds 1994; Laiho and Prescott 1999; Progar et al. 2000). In the Pacific Northwest, decomposition was continued year-round due to the high amounts of precipitation and mild temperatures in the winter months (Marra and Edmonds 1994). Moisture content can limit decomposition. A reduced moisture level in CWD creates a hostile environment for fungi and bacterial activity and slows decomposition (Lambert et al. 1980; Carpenter et al. 1988; Progar et al. 2000). Coarse woody debris saturated with moisture also reduces decomposition rates by creating an anoxic environment (Lambert et al. 1980; Carpenter et al. 1988; Progar et al. 2000).

Aspect and CWD

Aspect is a site-specific factor affecting decomposition of CWD. An aspect creating an environment conducive to fungal and bacteria colonization would lead to an increase in the decomposition rate of CWD. In the northern hemisphere south and southwestern slopes are generally environments with harsh conditions because of high ground surface temperatures and low soil moisture content, which leads to a decrease in the decomposition rates of CWD, because of the inactivity of biological organisms (Barber and van Lear 1984; Mattson et al. 1987). However, in moist regions of the Pacific Northwest, southern-facing slopes increased the decomposition rates of CWD. In these regions, moisture was not a limiting factor affecting the decomposition rate of CWD (Progar et al. 2000).

Fungi and CWD

Coarse woody debris provides habitat for a variety of fungi. For example, a study in British Columbia determined a link between the presence of CWD and populations of mycorrhizal fungi (Stevens 1997). Coarse woody debris decomposition is influenced by soft rots (ascomycetes) and white and brown rot fungi (basidiomycetes). Soft rot fungi break down the cell wall by using and modifying cellulose, hemicellulose, and lignin (Harmon et al. 1986). Decomposition of wood in direct contact with the soil is affected by colonization of soft rot fungi. Soft rot fungi colonize the outer surface of the CWD and decompose inward layer by layer (Kaarik 1974). Soft rot fungi are most active in high moisture environments. Soft rot have a higher tolerance for moisture than basidiomycetes because of the ability to live in poorly aerated environments (Duncan 1961).

Two types of basidiomycetes, white rot and brown rot fungi are the major decomposers in the terrestrial environments. White rot and brown rot fungi are classified based on the different biological components of wood they decompose (McMinn and Crossley 1993). Brown rot fungi decompose simple carbon compounds, specifically cellulose and hemicellulose. The ability to decompose cellulose and hemicellulose during the decomposition process is analogous to the abilities of soft rot fungi (Harmon et al. 1986; Allen et al. 2000). White rot fungi decompose cellulose, hemicellulose, lignin, and cell wall polysaccharides (Harmon et al. 1986; Allen et al. 2000). Coarse woody debris fungal diversity and colonization were influenced by moisture content, temperature, degree of macroinvertebrate and earthworm infestation, contact with the ground, log volume, and individual tree species (Graham and Cromack 1982; Mattson et al. 1987; McMinn and Crossley 1993; Progar et al. 2000; Muller et al. 2002). In Sitka spruce and western hemlock brown-rot and white-rot fungi were colonized on the same piece of CWD within a 10.0 cm space indicating the importance of CWD size on fungal colonization and diversity (Graham and Cromack 1982). Fungal colonization increased the decomposition rate of CWD in the southern Appalachians (Mattson et al. 1987).

Fungal diversity was elevated with increased CWD volume (Allen et al. 2000). Fungal taxa richness decreased with CWD decomposition because the CWD looses total wood volume causing increased homogeneity of CWD (Allen et al. 2000). Basidiomycete colonization: increased CWD decomposition rate, immobilized nutrients such as nitrogen as decay proceeded, and mineralized nutrients, such as potassium, for release into the surrounding environment (Sollins et al. 1987; Harmon and Hau 1991; Allen et al. 2000; Progar et al. 2000).

Macroinvertebrates and CWD

Coarse woody debris is inhabited by a plethora of invertebrates from centipedes to land snails. The proportion of macroinvertebrates colonizing CWD was directly related to CWD volume and length. Greater CWD volumes and lengths increase the number of colonizing macroinvertebrates (Barclay et al 2000). Macroinvertebrates enhance CWD decomposition in a variety of ways. Macroinvertebrates caused chemical and physical alterations in the CWD, which increased the decomposition rate. For example, wood boring macroinvertebrates provide a corridor for fungi to colonize the heartwood of CWD (Edmonds and Eglitis 1989; Muller et al. 2002; Hood et al. 2004). Pine logs in the Pacific Northwest, after ten years of decay, had significant colonization by carpenter ants, which increased the decomposition rate of CWD (Laiho and Prescott 1999). Macroinvertebrates added nutrients to the CWD by translocation and defecation, which establishes a more favorable environment for fungi (McMinn and Crossley 1993). Passive inoculation of fungi by macroinvertebrates in CWD was another method for increasing decomposition rates (Muller et al. 2002). Invertebrate dynamics regulate microbial succession and rates of microbial catabolism (McMinn and Crossley 1993).

Physical, chemical, and biological activity was enhanced by macroinvertebrates because increased fragmentation by chewing and tunneling through the CWD exposed more surface area to the environment (Edmonds and Eglitis 1989; McMinn and Crossley 1993; Muller et al. 2002).

Termites are wood feeding insects from the order Isoperta and usually enhance the CWD decomposition rate. There were two major families of termites found in the southeastern United States are Kalotermitadae (drywood) and Rhinotermitidae (subterranean) (McMinn and Crossley 1993). Most of the termite species in the southeast were cellulose-feeding insects (McMinn and Crossley 1993). As the decomposition of CWD progresses termite infestation steadily increased (Sollins et al. 1987). As the diameter of CWD, increased colonization of wood boring insects such as termites were enhanced, speeding up the rate of decomposition (Edmonds and Eglitis 1989).

Specific Gravity of Loblolly Pine

Specific gravity is the ratio of the density of a substance to the density of pure water at 4° C. Specific gravity is numerically equivalent to the density of the substance because in the metric system the density of water is 1.0 g/cm^3 (assuming the same basis of determination) (Megraw 1985). Often the terminology and values for density and specific gravity are used interchangeably due to their equivalence. The specific gravity of live loblolly pine has been extensively study throughout its natural range. Specific gravity has within tree variations. The specific gravity of loblolly pine is low near the pith and increases moving outward toward the bark. The specific gravity was reported to be highest at the base of the tree and decreased with increased height above the base (Megraw 1985; Tasissa and Burkhart 1998). Loblolly pine specific gravity changed from

0.500 at the butt to 0.395, 20 m up from the base (Megraw 1985; Tauer and Loo-Dinkins 1990; Tasissa and Burkhart 1998). These within tree variations in specific gravity are hypothesized to be physiological in origin.

According to a two studies, thinning does not influence the live wood specific gravity of loblolly pine (Taylor and Burton 1982; Tasissa and Burkhart 1998). This relationship should hold under the circumstances that thinning does not influence the proportion of late versus early wood in the bole. A regional study, using the same site locations as this study found no significant difference between the specific gravity of the control, lightly thinned, and heavily thinned plots for live loblolly pine (Tasissa and Burkhart 1998). A separate study in Arkansas found no thinning affects on loblolly pine live wood specific gravity (Taylor and Burton 1982).

Specific gravity has a narrow-sense heritability of at least (0.5), which is higher then the narrow-sense heritability of height growth or diameter growth suggesting the influence of genetics on specific gravity (Megraw 1985; Byrum and Lowe 1988; Groover et al. 1994). A seed source study in the Western Gulf region found that when seeds selected from south Arkansas, north Louisiana, southeast Texas, south Louisiana, and coastal plain of North Carolina were grown in the same environment there were significant differences in specific gravity between seed sources, suggesting genetics is a major component influencing specific gravity (Byrum and Lowe 1988).

Specific gravity of trees from the same seed source has displayed regional variation (Table 3). In a study of loblolly pine, specific gravity varied according to precipitation patterns. For example, the highest amount of summer rainfall occurred in the Mississippi gulf coast where the specific gravities ranged from 0.43 to 0.46, while the

Table 3: Regional average specific gravity of plantation grown loblolly pine.

Region	Specific Gravity	Variation	Reference
Atlantic Coastal Plain	0.515		Tasissa and Burkhart 1998
Gulf Coastal Plain	0.51		Tasissa and Burkhart 1998
Piedmont	0..475		Tasissa and Burkhart 1998
Highlands	0.47		Tasissa and Burkhart 1998
Southwest Arkansas	0.463	0.010	Tauer and Loo-Dinkins 1990
Southeast Arkansas	0.461	0.008	Tauer and Loo-Dinkins 1990
Lower Coastal Plain NC	0.456	0.005	Tauer and Loo-Dinkins 1990
South Eastern Virginia	0.454	0.007	Tauer and Loo-Dinkins 1990
East Shore Maryland	0.452	0.008	Tauer and Loo-Dinkins 1990
Central Louisiana	0.450	0.007	Tauer and Loo-Dinkins 1990
Lower Coastal Plain SC	0.448	0.007	Tauer and Loo-Dinkins 1990
Upper Coastal Plain SC	0.444	0.005	Tauer and Loo-Dinkins 1990
West Shore Maryland	0.444	0.006	Tauer and Loo-Dinkins 1990
Southern Mississippi	0.444	0.006	Tauer and Loo-Dinkins 1990
Piedmont North Carolina	0.443	0.006	Tauer and Loo-Dinkins 1990
Southern Alabama	0.441	0.007	Tauer and Loo-Dinkins 1990
Southeast Louisiana	0.441	0.008	Tauer and Loo-Dinkins 1990
South Central Georgia	0.437	0.005	Tauer and Loo-Dinkins 1990
Central Alabama	0.433	0.007	Tauer and Loo-Dinkins 1990
Piedmont South Carolina	0.428	0.010	Tauer and Loo-Dinkins 1990
South Central Georgia	0.427	0.006	Tauer and Loo-Dinkins 1990
Central Mississippi	0.424	0.007	Tauer and Loo-Dinkins 1990
East Central Alabama	0.423	0.008	Tauer and Loo-Dinkins 1990
Northwest, United States	0.460*		Tauer and Loo-Dinkins 1990
Northeast, United States	0.447*		Tauer and Loo-Dinkins 1990

Table 3 con't.: Plantation grown loblolly pine regional average specific gravity averages.

Region	**Specific Gravity**	**Variation**	**Reference**
Southwest, United States	0.447*		Tauer and Loo-Dinkins 1990
East Coast, United States	0.446*		Tauer and Loo-Dinkins 1990
Interior, United States	0.436*		Tauer and Loo-Dinkins 1990
Gulf Coast, United States	0.435*		Tauer and Loo-Dinkins 1990
Arkansas	0.53*		Taylor and Burton 1982
Arkansas	0.52*		Taylor and Burton 1982
South Arkansas	0.424	0.439–0.417'	Byrum and Lowe 1988
North Louisiana	0.405	0.414–0.393'	Byrum and Lowe 1988
South Louisiana	0.398	0.410–0.380'	Byrum and Lowe 1988
North Mississippi	0.408*		Byrum and Lowe 1988
South Mississippi	0.434*		Byrum and Lowe 1988
North Arkansas	0.403*		Byrum and Lowe 1988
North and South Carolina Coast	0.482		Talbert and Jett 1981
Lower Gulf Coastal Plain	0.47		Talbert and Jett 1981
Georgia / Florida Coast	0.468		Talbert and Jett 1981
GA / AL / TN Piedmont	0.4615		Talbert and Jett 1981
N. and S. Carolina Piedmont	0.459		Talbert and Jett 1981
Virginia and Maryland	0.4555		Talbert and Jett 1981
Upper Gulf Coastal Plain	0.454		Talbert and Jett 1981
North Carolina	0.410		Megraw 1985
Mississippi	0.435		Megraw 1985
Arkansas	0.44		Megraw 1985

Note: The (*) after a value corresponds to a reported average value

least amount of summer rainfall was recorded in northern Arkansas and Oklahoma where the specific gravities ranged from 0.39 to 0.42 (Talbert and Jett 1981). Regional differences were determined in a study comparing the loblolly pine specific gravity of North and South Carolina coastal plain, the Lower Gulf Coastal Plain, Georgia and Florida coastal plain, Georgia, Alabama, and Tennessee Piedmont, North and South Carolina piedmont, Upper Gulf Coastal Plain, and Virginia (Talbert and Jett 1981). The Upper Gulf Coastal plain had the lowest specific gravity (0.407), while the North and South Carolina coastal plain had the highest specific gravity (0.423) (Talbert and Jett 1981). Another regional study of loblolly pine also found the Atlantic Coastal Plain region to have the highest live wood loblolly pine specific gravity (0.515), followed by the Gulf Coastal Plain (0.51), the Piedmont (0.475), and finally the Highlands (0.47) (Tasissa and Burkhart 1998).

Study Area

The CWD study was conducted on plots established for the loblolly pine thinning study, maintained by the Loblolly Pine Growth and Yield Research Cooperative at Virginia Polytechnic Institute and State University (Burkhart et al. 1985; Radtke et al. 2004). The study sites were established between 1980 and 1982 on 186 industrially managed loblolly pine plantations in the southeastern United States. The distribution of the thinning study sites approximately follows a generalized randomized incomplete block design with physiographic region acting as the blocking factor (Burkhart et al. 1895; Tasissa and Burkhart 1998). Stand selection criteria consisted of eleven stand and site requirements (Table 4). After stand selection, management practices had to be consistent throughout

Table 4: Stand selection criteria for the Loblolly Growth and Yield Research Cooperative.

Stand Selection Criteria
1. Unthinned
2. Free of heavy disease or insect attack
3. Not heavily damaged by ice or wind
4. Free of interplanting
5. Unpruned
6. Not fertilized within the last 4 years
7. Not planted with genetically improved stock
8. At least 8 years in age
9. A minimum of 200-300 planted pine stems per acre which appear to be free to grow
10. Less than or equal to 25% of canopy composed of volunteer pines and hardwoods
11. Cutover site with typical site preparation treatment for site conditions and time of establishment

the study areas (Table 5). Study site characteristics are listed in Table 6. There were three treatments: treatment I (control), treatment II (lightly thinned), and treatment III

Table 5: Loblolly Pine Growth and Yield Research Cooperative stand preparation summary. The headings are defined as follows: Comp = Company and location number, ST = state, P = planting method, RLSE = release, DRN = drained, DSC = disced, WIN = windrows, CHP = chopped, BED = bedded, SHR = sheared, and O = any other activities

Study Site Preparation and Management											
Comp	**ST**	**P**	**RLSE**	**Burn**	**DRN**	**DSC**	**WIN**	**CHP**	**BED**	**SHR**	**O**
3104	LA	M	Y	Y	N	N	N	Y	N	N	N
3105	LA	H	Y	Y	N	N	N	Y	N	N	N
3122	LA	H	Y	N	N	N	Y	N	N	N	Y
3108	LA	HM	Y	Y	N	N	Y	N	N	N	Y
4107	LA	M	N	Y	N	N	N	Y	N	N	N
4108	LA	M	N	Y	N	N	N	Y	N	N	N
4111	LA	M	N	Y	N	N	N	Y	N	N	N
8111	VA	H	N	Y	N	N	N	Y	N	N	N
8112	VA	M	N	Y	N	Y	Y	N	N	Y	N
8114	VA	H	N	N	N	N	Y	N	N	N	Y
2110	VA	H	N	Y	N	N	N	N	N	N	N
2106	VA	H	N	Y	N	N	N	N	N	N	N
2101	VA	H	N	Y	N	N	N	Y	N	N	N
2118	MD	H	N	Y	N	Y	N	N	N	N	N
9134	ARK	M	Y	Y	N	Y	Y	N	N	N	N
9135	ARK	M	Y	Y	N	Y	Y	N	N	N	N
9144	ARK	M	Y	Y	N	Y	Y	N	N	N	N
9141	ARK	M	Y	Y	Y	N	Y	Y	Y	Y	N
9142	ARK	M	Y	Y	N	Y	Y	N	N	N	N
9131	ARK	M	Y	Y	N	Y	Y	Y	N	N	N

9173	MS	M	N	Y	N	N	Y	N	N	N	Y
9174	MS	H	N	Y	N	Y	Y	N	N	N	Y

Table 5con't.: Loblolly Pine Growth and Yield Research Cooperative stand preparation summary. The headings are defined as follows: Comp = Company and location number, ST = state, P = planting method, RLSE = release, DRN = drained, DSC = disced, WIN = windrows, CHP = chopped, BED = bedded, SHR = sheared, and O = any other activities.

Study Site Preparation and Management

Comp	ST	P	RLSE	Burn	DRN	DSC	WIN	CHP	Bed	SHR	O
9175	MS	H	N	Y	N	N	N	N	N	Y	N
6117	AL	M	N	N	N	N	Y	N	N	N	N
6106	AL	M	N	N	N	Y	N	N	N	N	N
6116	AL	M	N	N	N	Y	N	N	N	N	N
1120	TN	M	N	N	N	N	Y	N	N	Y	N
6101	GA	M	N	Y	N	N	N	N	N	N	N
6103	GA	M	N	Y	N	N	N	N	N	N	N
5112	NC	H	N	Y	N	N	N	N	N	N	Y
5104	NC	H	N	Y	Y	N	N	Y	N	N	N
5109	NC	H	N	Y	N	N	N	Y	Y	N	N
5114	NC	H	N	Y	N	N	N	N	N	N	Y
1405	NC	H	N	N	N	N	N	Y	Y	N	N
8101	SC	H	N	Y	N	Y	N	N	N	N	N

(heavily thinned). Treatment II was lightly thinned, cutting approximately 33% of basal area. Treatment III was the heavily thinned, cutting > 50% of the basal area (Burkhart et al. 1985). Each treatment had a standardized size: the control treatment was 0.04 ha; the lightly thinned treatment was 0.08 ha; and the heavily thinned treatment was 0.08 ha.

Table 6: Summary of the study site characteristics including the state location, county location, latitude, longitude, elevation, soil great group, and physiographic province. Column seven is providing the major soil family: Ult = Ultisol, Ent = Entisol, and Moll = Mollisol. Column eight is the physiographic provenance of each site: GCP = Gulf Coastal Plain, Pied = Piedmont, ACP = Atlantic Coastal Plain, O. Mt.= Ouachita, and ILP = Interior Low Plateau.

Company	**State**	**County**	**Latitude (° ‘)**	**Longitude (° ‘)**	**Elevation (meters)**	**Soil**	**Physiographic Region**
3104	LA	Jackson	32° 09’	92° 46	190	Ult	GCP
3105	LA	Jackson	32° 17	92° 42	185	Ult	GCP
3122	LA	Jackson	32° 25	92° 48	240	Ult	GCP
3108	LA	Bienville	32° 16	92° 37	180	Ult	GCP
4107	LA	Washington	30° 53	89° 54	250	Ult	GCP
4108	LA	Washington	30° 47	90° 07	180	Ult	GCP
4111	LA	Washington	30° 56	89° 11	220	Ult	GCP
8111	VA	Buckingham	37° 43	78° 30	490	Ult	Pied
8112	VA	Buckingham	37° 42	78° 54	500	Ult	Pied
8114	VA	Nelson	37° 35	78° 54	670	Ult	Pied
2110	VA	Pr. Ed.	37	78	400	Ult	Pied
2106	VA	K. Will.	37	77	190	Ult	ACP
2101	VA	K. Will.	37	76	50	Ult	ACP
2118	MD	Somerset	38° 16	75° 37	30	Ult	ACP
9134	ARK	Sevier	33° 51	94° 04	440	Ult	O. Mt.
9135	ARK	Sevier	34° 02	94° 16	410	Ult	O. Mt.
9144	ARK	Perry	34	93	620	Ult	O. Mt.
9141	ARK	Saline	34° 38	92° 52	560	Ult	O. Mt.
9142	ARK	Garland	34° 41	93° 06	920	Ult	O. Mt.
9131	ARK	Lit. Riv.	37° 46	94° 26	460	Moll	GCP
9173	MS	Kemper	32° 47	88° 28	180	Ult	GCP
9174	MS	Kemper	32° 44	88° 28	180	Ult	GCP

Table 6 con't.: Summary of the study site characteristics including the state location, county location, latitude, longitude, elevation, soil great group, and physiographic province. Column seven is providing the major soil family: Ult = Ultisol, Ent = Entisol, and Moll = Mollisol. Column eight is the physiographic provenance of each site: GCP = Gulf Coastal Plain, Pied = Piedmont, ACP = Atlantic Coastal Plain, O. Mt.= Ouachita, and ILP = Interior Low Plateau.

Company	**State**	**County**	**Latitude (° ‘)**	**Longitude (° ‘)**	**Elevation (meters)**	**Soil**	**Physiographic Region**
9175	MS	Kemper	32° 47	88° 28	180	Ult	GCP
6117	AL	Escambia	87° 42	30° 50	11	Ult	GCP
6106	AL	Escambia	87° 36	31° 08	9	Ult	GCP
6116	AL	Baldwin	30°	87°	190	Ult	GCP
1120	TN	Wayne	35°	87°	900	Ult	ILP
6101	GA	Decatur	30°	84°	15	Ent	GCP
6103	GA	Decatur	30°	84°	15	Ent	GCP
5112	NC	Lee	35°	79°	200	Ult	ACP
5104	NC	Columbus	34°	78°	64	Ult	ACP
1417	NC	Lee	35	79	200	Ult	ACP
5109	NC	Brunswick	34°	78°	49	Ult	ACP
5114	NC	Chatham	35°	79°	250	Ult	ACP
1405	NC	Baldwin	34°	78°	40	Ult	ACP
8101	SC	Charleston	32°	80°	20	Ult	ACP

There was one thinning operation at the time of plot establishment and one thinning approximately 10 years after plot establishment (Burkhart et al. 1985; Tasissa and Burkhart 1998). Thinning selection was primarily based on stem quality. Once thinned, the tree tag was removed from the bole and nailed into the stump. A 6.0-m buffer was established surrounding the perimeter of each treatment for the younger stands, but for the older stands in the study the buffer was variable.

Immediately following treatment establishment and during every subsequent remeasurement were recorded on each live loblolly pine: DBH (cm); total height (m); and height to the base of the live crown (m); crown class. Mortality records were collected during each remeasurement phase, noting the tag number and year of death.

The climate varied in the study area due to the vast geographic distance between site locations (Table 6). The study area included five physiographic provinces: Atlantic Coastal Plain (ACP), Gulf Coastal Plain (GCP), Ouachita Mountains (O. Mt.), Piedmont, and Interior Low Plateau (ILP). The physiographic region surrounding the southeastern edge of the North American continent bordering the Gulf of Mexico and Atlantic Ocean is the Coastal Plain. The Coastal Plain is divided into the ACP and the GCP. In the United States the ACP runs from Cape Code, Massachusetts to northern Florida, while the GCP extends from central Georgia to eastern Texas (Fenneman 1938). Both sections of the Coastal Plain have sediments originating from deposits of alluvial gravel, sand, and clay (Fenneman 1938). There were a total 26 sites in the Coastal Plain region: 10 sites in the ACP and 16 sites in the GCP (Table 6). The sites visited in the Coastal Plain ranged in elevation, but never exceeded 250 m above sea level (Table 6). Annual average daily minimum and maximum temperatures in the ACP ranged from 24 C $^{?}$ to 7 C $^{?}$ with an average daily temperature for the 10 site locations of 15.8 C $^{?}$ (Table 7). Annual average daily minimum and maximum temperatures in the GCP ranged from 26 C $^{?}$ to 11 C $^{?}$, with an average temperature across the 16 site locations of 17.7 C $^{?}$ (Table 7). The ACP had annual precipitation averages ranging from 148 cm in Virginia to 122 cm in North Carolina, and the GCP had precipitation averages ranging from 168 cm in Alabama to 115 cm in Arkansas (Table 7).

Table 7: Average temperate and precipitation from the nearest weather monitoring station. Source was Southern Regional Climate Center and Southeast Regional Climate Center. (P) = physiographic region, (Max) = maximum average temperature, (Min) = minimum average temperature, (Avg) = average annual temperature.

Study Site Climatic Conditions

Site	State	P	Max (C ?)	Min (C ?)	Avg (C ?)	Rainfall (cm)	Snowfall (cm)
3104, 05 ,22	LA	GCP	24.0	12.0	18.0	131	3.0
3108	LA	GCP	25.0	14.0	20.0	158	5.0
4107,08, 11	LA	GCP	25.0	14.0	20.0	158	0
8111, 12, 14	VA	Pied	19.0	8.0	13.0	104	54.0
2110	VA	Pied	21.0	7.0	14.0	113	36.0
2101, 06	VA	ACP	20.0	7.0	14.0	109	39.0
2118	MD	ACP	20.0	8.0	14.0	113	24.0
9134, 35	ARK	O. Mt.	24.0	12.0	18.0	110	5.1
9142,44	ARK	O. Mt.	23.0	16.0	16.0	128	0
9141	ARK	O. Mt.	23.8	16.0	16.5	120	0
9131	ARK	GCP	24.0	12.0	18.0	111	5.0
9173, 74, 75	MS	GCP	23.0	11.0	17.0	135	3.0
6106,17	AL	GCP	25.0	13.0	19.0	168	0
6116	AL	GCP	25.0	13.0	20.0	160	0
1120	TN	ILP	21.0	7.0	12.0	158	16.0
6101, 03	GA	GCP	26.0	12.0	19.0	140	0
5112	NC	ACP	23.0	8.0	16.0	120	9.14
5104	NC	ACP	23.0	10.0	16.0	126	6.0
5109	NC	ACP	23.0	10.0	17.0	139	4.0
5114	NC	ACP	21.0	8.0	15.0	118	13.0
1417	NC	ACP	22.7	8.3	15.5	120	9.1
1405	NC	ACP	23.0	10.0	17.0	119	3.0
8101	SC	ACP	24.0	13.0	19.0	127	1.0

The O. Mt. province extends north of the GCP extending through Arkansas and into Oklahoma. Five research sites were visited in the O. Mt. region of Arkansas, with elevations ranging from 440 to 920 m above sea level, the highest elevation range of all sites (Table 6). Mountains in the region have a complex bedrock structure and generally have east to west trends separated by topographical basins (Fenneman 1938). The five different site locations had annual average daily minimum and maximum temperatures ranging from 12 C ? to 24 C ? with an average temperature of 17.1 C ? (Table 7).

Located in portions of Tennessee, Kentucky, and northern Alabama east of the O. Mt. physiographic province is the ILP (Buol 1973). One research site was visited in the ILP (Table 6). The site had an elevation of 900 m above sea level (Table 6). The temperature at the site in the ILP ranged from 21 C ? to 12 C ? with an average of 7 C ? (Table 7). There was a total of 174 cm of precipitation (Table 7).

Stretching from Virginia to Georgia, the Piedmont is the east sloping non-mountainous portion of the Appalachian Highlands (Fenneman 1938). The Piedmont province is bordered by the ACP, the Blue Ridge Mountains, and the Ridge and Valley physiographic provinces. The geology in the Piedmont covers almost all-metamorphic and igneous type rocks, creating a diverse soil composition (Fenneman 1938, and Buol 1973). There were a total of four sites visited within the Piedmont physiographic province ranging in elevation from 400 to 670 m above sea level (Table 6). Average annual daily minimum and maximum temperatures at the sites in the Piedmont ranged from 7 C ? to 21 C ? with an average temperature of 13.2 C ? (Table 7). The annual precipitation in the Piedmont ranged from 158.0 cm to 149.0 cm (Table 7).

Field Methods

Inventory Data Collection

Live and dead tree lists in combination with stem maps for each treatment were used to locate CWD at each site. The stem maps had each tagged loblolly pine tree within the plot boundaries labeled with an X, Y coordinate to describe the position of stems in the plot. Once a dead tree was located, inventory data were collected for each CWD piece. The inventory data recorded for each sample was: tree number (tag), plot number, position, decay class, piece number, large end diameter, small end diameter, and piece length.

Position and decay class were two categorical variables collected during the inventory phase. I defined four position classes: Position 1 (standing), Position 2 (leaning $> 45^{?}$ above ground), Position 3 ($< 45^{?}$ angle and having ground contact), and Position 4 (partially or completely covered by the litter layer). Physical characteristics of the five decay classes were defined based on the criteria developed by Pyle and Brown (1998) for identifying CWD decay classes I through V. In decay class I the bark is firmly attached and any exposed, wood has a fresh color. In decay class II the bark may or may not be present, wood is generally solid, the primary surface substrate is hard wood with decayed bark and if the log is kicked the surface does not flake. In decay class III the bark is generally absent, log is firm when kicked but surface of dry wood will flake, wet surface of wood will compact like a wet sponge. In decay class IV the CWD is not intact, log will crush or cleave when kicked, and the shape has changed from cylindrical to oval or flattened. Decay class V logs are > 85% powder with a relatively flat shape and the primary surface is loosely aggregated powder wood appearing to be part of the soil substrate.

Sampling CWD

After recording the inventory data, representative specimens of CWD from pieces with the different decay classes and positions were collected. Standing or leaning CWD was felled before disks could be extracted from the bole. Pieces covered by the litter were exposed for sampling. Disks specimens were extracted with a chainsaw or knife. The number of samples collected was based on piece length. If the piece was < 1 m then one disk was sampled from the midpoint of the log. If the piece length was > 1 m but < 5 m one disk was sampled 1 m from the large end and one disk was sampled 1 m from the small end. If the piece was > 5 m three disks were sampled, the first disk 1 m from the large end, the second disk, from the midpoint of the log, and the third disk 1 m from the small end.

Coarse woody debris samples were labeled by piece. If a tagged dead loblolly pine could be labeled as two different position classes, or decay classes then the sample would be labeled as two separate pieces and additional measurements were recorded. For example, if one stem section was in contact with the forest floor, and another stem section was leaning against a tree at a > 45.0 degree angle, then the sample was labeled as two separate pieces each having samples collected based on piece length, but having the same ID number, treatment number, and tag number.

Each CWD disk had three measurements recorded: thickness, diameter one (dd1) and diameter two (dd2). The second disk diameter measurement was taken at a 90-degree angle to the first diameter measurement. Once the disk was measured for diameter and thickness, it was stored in a plastic bag and identified with a tag denoting: site number, tree or tag number, plot number, disk number, thickness of disk (cm), disk diameter (cm), height along stem (m), and piece number.

Laboratory methods

Once in the lab the CWD samples were placed in paper bags in preparation for three stages of drying. First, the bags were placed in a walk-in drying room ranging from 32-38° C. Second, the samples were moved into a standing convection drying oven at 60° C for several days. The final stage of drying was in one of two different convection ovens: Yamato Mechanical Convection Oven DNN 810, or Fisher Isotemp Oven Deluxe Model. The CWD samples remained in the oven until there was less then a 1% change in dry weight from the previous measurement. Next, each sample was removed from the bag, observed for any deformities such as branch knots, excessive mud or dirt incorporation into the sample, and/or insect/macroinvertebrate activity. Physical observations were recorded and each specimen was weighed to the nearest 0.01 g using an Ohaus Adventurer Pro AV4101 scale. After the weight was recorded the samples were archived and placed in box storage in the lab.

Data Analysis

There were 1,154 dead loblolly pine trees inventoried. The CWD data set had a total of 2,308 disks removed from 1,112 inventoried specimens. Several disks were entered into the data set numerous times once these samples were removed that data set was reduced to 2,288 samples. The observations that were exclusively inventoried but no disks were sampled were removed from the data set before further analysis. An additional 217 samples were removed during the analysis because there was no year of death recorded during the treatment remeasurements reducing the final data set to 2,071 samples. During the analysis the sample size varied because some observations were lacking information on position class, decay class, or other remeasurement variables.

Three variables were used to determine decomposition rate: initial live density, final density and time since death (TSD). The TSD was determined from the remeasurement data, subtracting the year a tree was observed dead from the year in which CWD measurements were recorded. The volume for each CWD disk was a function of three field measurements: thickness, diameter one (dd1) and diameter two (dd2) all measured in centimeters. The volume of each disk was determined using the equation for volume of a cylinder, similar to the technique by Chen et al. (2001) for coarse root decomposition:

$$V = c * dd^2 * h$$

where

c = a constant 0.7854

$dd^2 = dd1 * dd2$ (cm)

h = thickness of disk (cm)

The dry weight mass (grams) was determined in the lab for each CWD disk. Density was calculated by dividing the dry weight mass of each disk by the calculated volume. Density and specific gravity are interchangeable measurements, therefore for this study all density measurements were converted to specific gravity. Decomposition rate could be determined using four separate models: single exponential, multiple exponential, lag-time, and linear (Table 8) (Olson 1963; Lambert et al. 1980; Means et al. 1985; Harmon et al. 1986; Mackensen and Bauhus 2003). The single exponential model is the most common model for determining the decomposition rate of biological substances (Olson 1963; Harmon et al. 1986; Mackensen et al 2001), and the one I selected for this study.

Table 8: Model forms for determining biological decomposition rates. For the single exponential model and linear model X = final density, X_0 = initial density. For the multiple exponential model X_{1-3} are partitioned parameters such as change in bark, sapwood, and heartwood. For the lag-time model X_a is the proportion of initial mass remaining.

Decomposition Models		
Model	**Expression**	**Reference**
Single-exp	$X = X_0 e^{-kt}$	Olson 1963
Multiple-exp	$X = X_{0,1} e^{-k_1 t} + X_{0,2} e^{-k_2 t} + X_{0,3} e^{-k_3 t}$	Means et al. 1985
Lag-time	$X_a = 1 - (1 - \exp[-kt])^N$	Harmon et al. 1986
Linear	$X = X_0 - kt$	Lambert et al. 1980

After the initial refinement of the data set, the single exponential model was used to determine the CWD disk decomposition rate (Table 8). The decomposition rate can be determined by a change in volume, mass, or density or specific gravity. For this study, a change in specific gravity over time was used for determining the CWD disk decomposition rate. Cores were not sampled from live loblolly pine trees at each site to determine the live specific gravity therefore, the initial specific gravity had to be estimated. Specific gravity is a function of relative height, latitude, and physiological age (Ralph Amateis, personal communication). The relative height of each CWD disk was determined using a taper equation that was developed from data collected as part of the Loblolly Pine Growth and Yield Research Cooperative (Tasissa et al. 1997). The taper equation developed by Tasissa et al. (1997) had the following form:

$$hd = th\ B_1 * (d^{B_2} / dbh^{B_3}) * th^{B_4}$$

where

hd = height of disk along bole (m)

th = total height of tree as of last live remeasurement (m)

d = disk diameter, which was an average between dd1 (cm) and dd2 (cm)

dbh = dbh of tree as of last live remeasurement (in).

The definition of (d) in the taper equation reduced the sample size for determining the decomposition rate of CWD, because there were 85 samples without a diameter (dd2) measurement recorded in the field. The estimated parameters were different because loblolly pine taper displays a thinning effect (Table 9). The two thinning treatments were not significantly different from one another but the two thinning treatments were significantly different from the control or unthinned treatment (Tasissa et al. 1997).

Table 9: Estimated parameters according to treatment for the taper equation developed by Tasissa et al. 1997 for loblolly pine on cut-over site prepared plantations throughout five different physiographic regions of the Southeastern United States.

Taper Model Parameter Estimates				
	B_1	B_2	B_3	B_4
Thinned	0.862	1.50	1.43	0.984
Unthinned	0.969	1.43	1.32	0.936

To get the initial specific gravity of each individual disk one applied the specific gravity model developed by Amateis (personnel communication), which had the following form:

$$isg = B_1 + B_2 * (1 / age) + B_3 * (rh) + B_4 * (lat)$$

where

isg = live initial specific gravity of each CWD disk

age = age in years of tree as of last remeasurement before death

rh = estimated disk height (H) (m) / total tree height (TH) (m)

lat = latitude in degrees.

The specific gravity equation and taper equation were developed from the same data set, collected from site locations in the Loblolly Pine Growth and Yield Research Cooperative (Tasissa et al. 1997). The parameter estimates for the specific gravity equation are in Table 10.

Table 10: Parameter estimates for the specific gravity model for data recorded by Tasissa et al. (1997).

Model Parameter Estimates					
	B_1	B_2	B_3	B_4	R^2 = 0.544
Specific Gravity Model	0.565	-1.52	-0.123	-0.006	**RMSE** = 0.035

Note: Equations were developed by (Amateis 2005 unpublished) from Tasissa et al. 1997 data set for cut-over site prepared plantation loblolly pine.

Once a specific gravity value was determined for each individual CWD disk I used the single exponential model equation developed by Olson (1963) to determine the decomposition rate (k). The single exponential model (Table 8) had to be transformed and took the following form:

$$k = - [\ln (fsg) – \ln (isg)] / t$$

where

k = decomposition rate

Final (fsg) = final specific gravity determined by finding the density of each CWD disk

Initial (isg) = initial specific gravity estimated using the taper function (Tasissa et al. 1997) and the specific gravity model.

t = time since death (TSD) measured in years.

Exploration of the relationships between decomposition rate, specific gravity, and the 107 different variables was done using collinearity diagnostics. Twenty-five of the variables in the data set were added to the suite of variables recorded during site establishment and plot remeasurements (Table 11). A total of 28 variables were initially selected for multiple linear regression model development (Table 11). To determine the level of collinearity between independent variables the Pearson and Spearman collinearity diagnostics were used. The Pearson test was used to test for collinearity between all variable types. The Spearman's rank order correlation test is a nonparametric statistic used to analyze rank variables. For example, position and decay class were two rank order variables measured in the study. The correlation analysis provided information on the suite of variables in the data set and their interrelationships. These variables were chosen for analysis because approximately all the samples had information recorded for these variables. The variables were examined at different resolutions from plot to region.

After statistical examination of the variables further assessment of each variable was preformed looking for variables that provided sampling artifacts, or were not reproducible or meaningful to by subsequent researches. Nine variables were not used during the specific gravity, decomposition rate, and TSD model development were: ISG, GDD, cause, piece, ht, disk, thick, soil, and mud (Table 11). Once this step was complete the hypothesized full model for predicting the decomposition rate, specific gravity, and TSD contained the following variables: decay, pos, thin, eleve, physio, len, plot, hdisk, avetemp, avepre, HDD, longdeg, latdeg, dd1, dd2, d1, d2, maxtemp, and mintemp (Table 11).

Table 11: Definition and abbreviations for variables added to the data set and used in model development.

Variable Definitions	
Tree Level Variables	Stand Level Variables
decay – decay class I - V	eleve – site elevation (m)
pos – position class I - IV	maxtemp – max annual temperature (C°)
mud – 0 = mud present, 1 = mud absent	mintemp – minimum annual temperature (C°)
dd1 – disk diameter (cm)	avgtemp – average annual temperature (C°)
dd2 – disk diameter (cm)	avgpre – average annual precipitation (cm)
thick – disk thickness (cm)	HDD – heating degree days
len – piece length (m)	GDD – growing degree days
D1 – large end piece diameter (cm)	longdeg – longitude (degrees)
D2 – small end piece diameter (cm)	latdeg – latitude (degrees)
disk – number corresponds to disk along bole from large end	soil – soil type Ultisol, Mollisol, or Entisol
piece – number 1, 2, etc from large end	state – location within the United States
ht – disk height along piece (m)	physio – physiographic region
hdisk – estimated disk height (m)	
thin– type of death natural or thinned	
ISG – initial specific gravity	
cause – mortality type: lightning insect, disease, and/or suppression	

For this study, the stepwise selection procedure, at a significance level of 0.05, was used to develop decomposition rate, specific gravity, and TSD models across all physiographic regions and for each physiographic region (Ott and Longnecker 2001). Before developing multiple linear regression models for each of the physiographic regions an overall model was developed across all regions incorporating interaction variables (personnel communication Dr. Harold Burkhart). The importance of the interaction variables was to determine if the estimated coefficients for each variable (Table 11) were different across physiographic region. This procedure was performed for all three prediction variables: decomposition rate, specific gravity, and TSD.

Other diagnostics were used in combination with the stepwise selection method to determined the reduced model form. The variance inflation factor (VIF) indicates the inflation in variance of the parameter estimates due to collinearities that exist between each of the independent variables in the model (Ott and Longnecker 2001). A large VIF for a particular independent variable identified collinearity, nominating that variable for removal. The condition index (CI) is the ratio of the square root of the largest eigenvalue to each individual eigenvalue (Ott and Longnecker 2001). A CI between 10 and 100 indicates that there are dependencies developing between variables, and a CI > 100 indicates there are dependencies between independent variables.

Three other diagnostics were considered before variable removal from the model for example, the contribution of the variable to the total model R^2. Each of the model variables had a p – value associated with the parameter estimate. If the p – value was above 0.04 then the variable was considered for elimination from the model. Finally, the C_p diagnostic was considered before variable removal. The C_p is related to the total mean squared error and the total number of parameters in the model (Ott and Longnecker 2001). If the C_p value is low it indicates the model has a low total mean squared error and if C_p is close to the total number of variables in the model it indicates the model contains no bias (Ott and Longnecker 2001). Once a variable was removed, another iteration of the regression was performed until the model was reduced to the simplest form. Once a model form was chosen the estimated variable coefficients were used to predict the "Y" variable in the validation data set. The predicted "Y" variable was then examined for similar trends with the stand level and tree level variables that the observed value displayed.

The SAS 9.0 statistics package was also used to analyze for significance between different variable averages. For example, to test for differences in dry weight specific gravity of the five different decay classes or differences in the four position classes. The *proc glm* command in combination with significance tests such as Tukey's W test or Fisher's LSD were used to perform this type of analysis (Ott and Longnecker 2001).

Results

Estimated Specific Gravity (isg)

The estimated initial specific gravity was highest for the GCP and significantly different than the mean estimated initial specific gravities (isg) of the ACP, GCP, and O. Mt. (Table 11). The mean estimated initial specific gravity for the GCP was not significantly different from the mean (isg) for the ILP (Table 11). The control plot had the highest estimated mean specific gravity, but it was not significantly different from the lightly thinned or heavily thinned treatments (Table 12).

Table 12: Estimated initial specific gravity (isg) by physiographic region. (N) is the total number of samples

Mean Estimated Initial Specific Gravity			
Physiographic Region	**N**	**Mean (isg)**	**Standard Error**
ACP	595	0.429 [a]	0.050
GCP	832	0.459 [b]	0.050
Piedmont	316	0.417 [a]	0.046
O. Mt.	176	0.416 [a]	0.066
ILP	54	0.452 [b]	0.024

Note: Averages were determined to be significant using Tukey's test at an alpha level of 0.05. The letters superscripted above the mean decomposition rates indicate significance.

Table 13: Estimated initial specific gravity (isg) by treatment. (N) indicates number of samples.

Mean Estimated Initial Specific Gravity			
Treatment	**N**	**Mean (isg)**	**Standard Error**
Control	833	0.443 [a]	0.046
Lightly Thinned	757	0.436 [a]	0.055
Heavily Thinned	387	0.438 [a]	0.063

Note: Averages were determined to be significant using Tukey's test at an alpha level of 0.05. The letters superscripted above the mean decomposition rates indicate significance.

Data Distribution Summary

A summary of the sample distribution across physiographic region and treatment by tree level variables and stand level variables is presented in Tables 14 - 15. The difference in total sample size between tree level variables is due to inconsistencies in recording for each sample (Table 14). Eighty-four percent of the samples died within the last 10 years (Table 14). Approximately 12% of the samples were from trees that had been commercially thinned during plot establishment with a TSD of 10 years, while the samples recorded as not thinned had an average TSD of 7.6 years (Table 14). Coarse woody debris sampled from a ground contact position accounted for 76% of the samples (Table 14).

Table 14: Sample distribution according to decay class, position class, cause of death (thin), and time since death (TSD) across physiographic region and treatment. (N) indicates the number of samples in each category.

Sample Distribution							
Decay	**N**	**Position**	**N**	**Thin**	**N**	**TSD**	**N**
I	82	I	306	Natural	1825	1 – 5	548
II	490	II	153	Thinned	246	6 – 10	1191
III	707	III	1133			11 – 15	249
IV	451	IV	449			16 – 20	62
V	318					21 - 25	21
Total	2048		2041		2071		2071

Virginia and Louisiana had a total of 13 sites accounting for approximately 51% of the samples collected compared to Maryland and Tennessee which accounted for approximately 4% (Table 15). Approximately 40% of the samples were collected from the GCP compared to only 3% from the ILP (Table 15). The most samples were collected from the control plot with an average TSD of 7.7 years, followed by the lightly thinned plot with an average TSD of 8.2 years, and the heavily thinned plot with an average TSD of 7.7 years (Table 15).

Table 15: Sample distribution according to state, physiographic region, treatment, and latitude. (N) indicates the number of samples in each category.

Sample Distribution							
State	**N**	**Physiographic R.**	**N**	**Treatment**	**N**	**Latitude**	**N**
AL	111	ACP	637	Control	879	30	420
AK	199	GCP	833	Light Thin	780	31	71
GA	96	Piedmont	362	Heavy Thin	412	32	462
LA	505	O. Mt.	185			33	56
MS	107	ILP	54			34	269
NC	295					35	223
SC	134					37	546
TN	54					38	24
VA	546						
MD	24						
Total	2071		2071		2071		2071

Approximately 32%, 38%, and 32% of the samples collected in the control, light, and heavy thinned plots were documented as decay class III (Table 16). Across treatment decay classes II – IV had the most samples (Table 16). The GCP had the most samples collected across all five decay classes (Table 17). Decay class III had the most samples except for in the Piedmont (Table 17). For the control, light, and heavy thinned treatments the largest number of samples were collected from position class III and the least from position class II (Table 18). Across physiographic region position class III had

Table 16: Sample distribution for the control, light thinned, and heavy thinned plots by decay class. (N) indicates the number of samples.

	Sample Distribution		
	Control	**Light Thin**	**Heavy Thin**
Decay Class	**N**	**N**	**N**
I	43	21	18
II	252	129	109
III	280	298	129
IV	169	192	90
V	131	134	53
Total	875	774	399

Table 17: Distribution of samples in decay class by physiographic region.

	Physiographic Region				
Decay Class	**ACP**	**GCP**	**Piedmont**	**O. Mt.**	**ILP**
I	14	23	20	25	0
II	137	156	109	78	10
III	241	338	72	32	24
IV	136	172	101	24	18
V	106	132	57	22	1
Total	634	821	359	181	53

the most samples (Table 19). Position class II CWD was had the fewest samples across physiographic regions (Table 19). Less than 23% of the all the samples collected were thinned trees (Table 20) in the lightly thinned treatment. In the heavily thinned treatment approximately 18% of the samples collected were from trees that were thinned (Table 20).

Table 18: Sample distribution for the control, light thinned, and heavy thinned plots by position class. (N) indicates the number of samples.

	Sample Distribution		
	Control	**Light Thin**	**Heavy Thin**
Position Class	**N**	**N**	**N**
I	147	86	73
II	83	41	29
III	475	432	230
IV	167	215	67
Total	872	774	399

Table 19: Distribution of CWD samples in position class I – IV across physiographic region.

	Physiographic Region				
Position Class	**ACP**	**GCP**	**Piedmont**	**O. Mt.**	**ILP**
I	74	139	44	42	7
II	67	42	25	9	10
III	196	546	174	107	14
IV	197	91	116	23	22
Total	534	818	359	181	53

Table 20: Sample distribution for the control, light thinned, and heavy thinned by vigor code natural death or thinned. (N) indicates the number of samples.

	Sample Distribution		
	Control	**Lightly Thinned**	**Heavily Thinned**
Vigor	**N**	**N**	**N**
Natural	879	607	339
Thinned	0	173	73
Total	879	780	412

Across All Treatment Analysis

The decomposition rate (k), time since death (TSD), and specific gravity at time of death (SG_t) of loblolly pine CWD disks were examined across different populations. Coarse woody debris specific gravity and decomposition rate were examined across all physiographic regions: ACP, GCP, Piedmont, O. Mt., and ILP, searching for relationships with stand level and tree level variables such as latitude, decay classes, and position classes. Similar analysis of CWD decomposition rates and specific gravities were examined for physiographic regions. Finally decomposition rate and specific gravity were analyzed across the three treatments: control, light thin, and heavy thin.

The mean SG_t was significantly different for each decay class across all physiographic regions and treatments (Table 21). From decay class I to decay class V there was approximately a 43% change in the mean CWD SG_t (Table 21). There was a significant linear correlation between CWD decay class and CWD disk SG_t (Table 22). The intercept (0.456), of the regression between SG_t and time since death (TSD) corresponds with the estimated average live specific gravity of a CWD disk.

Table 21: Coarse woody debris average disk (SG_t) and average disk (k) according to decay class.

Decay Class	N	Mean (SG_t)	N	Mean (k)
I	79	0.393 [a]	78	0.023 [c]
II	479	0.335 [b]	456	0.055 [b]
III	691	0.288 [c]	671	0.070 [b]
IV	439	0.204 [d]	439	0.096 [a]
V	316	0.171 [e]	312	0.098 [a]

Note: Different letters above each mean specific gravity value represent significantly different values according to the Tukey's W Test at an alpha significance level = 0.05. The letters indicating significant differences apply to each column separately.

Decay class IV and V disk decomposition rates were significantly different from decay classes I, II, and III (Table 21). Decay classes IV and V disk decomposition rates were not significantly different from one another and neither were the disk decomposition rates of decay classes II and III CWD (Table 21). The mean CWD disk decomposition rate (k) across all physiographic regions and treatments had a significant linear correlation ($r = 0.287$, $p < 0.0001$) with decay class (Table 22).

The relationships between tree level variables and CWD disk specific gravity at time of sampling (SG_t) and decomposition rate are presented in Table 22. All relationships were significant between tree level variables and SG_t except for large end

Table 22: Relationships between SG_t and decomposition rate (k) with recorded tree level variables. For variable definition refer to table (11). (R) is the linear correlation coefficient.

	Specific Gravity (SG_t)		**Decomposition Rate (k)**	
	R	**P – Value**	**R**	**P - Value**
SG_t			- 0.700	< 0.0001
decomposition rate (k)	- 0.708	< 0.0001		
len	0.220	< 0.0001	0.111	< 0.0001
hdisk	0.073	0.0012	0.403	< 0.0001
dd1	0.098	< 0.0001	- 0.280	< 0.0001
dd2	not significant		- 0.328	< 0.0001
d1	not significant		- 0.194	< 0.0001
d2	0.192	< 0.0001	- 0.095	< 0.0001
decay	- 0.557	< 0.0001	0.287	< 0.0001
pos	- 0.525	< 0.0001	0.317	< 0.0001

diameter (d1) and one of the disk diameter measurements (dd2) (Table 22). All the linear correlations between disk decomposition rate (k) and the recorded tree level variables were significant (Table 22).

The ACP and the Piedmont disk specific gravities were not significantly different from one another, but were significantly different from the GCP and the ILP CWD disk specific gravities (SG_t) at the time of sampling (Table 23). The O. Mt. mean CWD disk SG_t was not significantly different from the other physiographic regions (Table 23).

Table 23: Coarse woody debris average observed disk specific gravity and observed average decomposition rate according to physiographic region.

Physiographic Region	N	Mean (SG_t)	N	Mean (k)
ACP	623	0.244 [b]	595	0.070 [ab]
GCP	813	0.295 [a]	831	0.080 [ab]
Piedmont	353	0.242 [b]	310	0.068 [b]
O. Mt.	176	0.266 [ab]	176	0.088 [a]
ILP	52	0.268 [a]	54	0.082 [ab]

Note: Different letters above each mean specific gravity value represent significantly different values according to the Tukey's W Test at alpha = 0.05. The letters indicating significant differences apply to each column separately.

The Piedmont and O. Mt. had significantly different disk decomposition rates (k) (Table 23). The decomposition rate for the ACP, GCP, and ILP were not significantly different from one another and were not significantly different from either the Piedmont or O. Mt. (Table 23).

The mean CWD disk SG_t was significantly different for each position class (Table 24). There was a 44% change in the mean disk specific gravity at time of sampling from standing CWD to covered CWD (Table 24). The largest change in mean SG_t was between position classes III and IV (Table 24). A significant linear correlation was determined between CWD disk SG_t and position class (Table 22).

The CWD disk decomposition rate (k) was significantly different across position class (Table 24). Standing CWD had the slowest mean disk decomposition rate, which was significantly different from the other position classes. Coarse woody debris in position class IV had the fastest decomposition rate, which was significantly different from the other position classes (Table 24). Position class and disk decomposition rate had a significant linear correlation (Table 22).

Table 24: Average CWD disk SG_t and average CWD disk (k) according to position class across treatment and physiographic region disregarding the difference between thinned samples and naturally dead samples.

Position Class	N	Mean (SG_t)	N	Mean (k)
I – Standing	296	0.370 [a]	280	0.030 [a]
II - Leaning	151	0.306 [b]	145	0.063 [b]
III – Ground	1114	0.275 [c]	1094	0.078 [c]
IV – Covered	442	0.163 [d]	434	0.099 [d]

Note: Position Class IV – Covered is defined as CWD partially or completely covered by the litter layer. Different letters above each mean specific gravity value represent significantly different values according to the Tukey's W Test at alpha = 0.05. The letters indicating significant differences apply to each column separately.

The linear correlations between elevation (eleve), average annual precipitation (avgpre), and SG_t were not significant (Table 25). However, specific gravity at the time of sampling (SG_t) was significantly correlated with all other stand level variables (Table 25). Decomposition rate did not have a significant correlation with average annual precipitation (avgpre) or site elevation (eleve) (Table 25). However, CWD disk decomposition rate was significantly correlated with minimum temperature, maximum temperature, average temperature, latitude, longitude, and heating degree days (Table 25).

Table 25: Relationship between SG t and decomposition rate (k) with stand level variables. Variable definitions are in table (11). (R) is the linear correlation coefficient.

	SG_t		Decomposition Rate (k)	
	R	**P - Value**	**R**	**P - Value**
avgtemp	0.051	=0.024	0.131	< 0.0001
mintemp	0.075	=0.0008	0.103	< 0.0001
maxtemp	0.071	= 0.002	0.147	< 0.0001
avgpre	not significant	= 0.137	not significant	= 0.304
latdeg	0.071	= 0.002	0.151	< 0.0001
longdeg	0.053	= 0.018	0.178	< 0.0001
hdd	0.062	= 0.006	- 0.115	< 0.0001
eleve	not significant	= 0.559	not significant	= 0.577

Each of the five different decay classes had significantly different TSD (Table 26). The minimum TSD was the same for decay classes I through III and decay classes IV through V, while the maximum TSD was the same for decay classes II through IV (Table 26). Decay class and TSD had a significant linear correlation ($r = 0.607$, $p < 0.0001$).

Table 26: Combined treatment averages of CWD disk time since death (TSD) according to decay class and position class.

Decay	N	Mean TSD	Range	Position	N	Mean TSD	Range
I	79	4.34 [a]	2.00 – 12.0	Stand-I	296	6.20 [c]	2.00 – 21.0
II	479	5.64 [b]	2.00 – 21.0	Leaning-II	151	6.76 [bc]	3.00 – 21.0
III	691	7.14 [c]	2.00 – 21.0	Ground-III	1114	7.12 [b]	2.00 – 21.0
IV	439	9.70 [d]	5.00 – 21.0	Covered - IV	442	11.6 [a]	5.00 – 22.0
V	316	11.6 [e]	5.00 – 22.0				

Note: Averages were determined to be significant using Tukey's test at an alpha level of 0.05. The letters superscripted above the average time since death values (TSD) indicate significance. Position class IV is CWD that was partially to completely covered by the litter layer. The letters indicating significant differences apply to each column separately.

The average TSD for partially to completely covered CWD was significantly different from all other position classes (Table 26). Covered CWD disks significantly had the highest average TSD 11.6 (Table 26). There was a significant linear correlation ($r = 0.422$, $p < 0.0001$) between CWD position class and TSD.

Position Analysis

The thinning treatments provided an opportunity to examine the importance of ground position versus aerial position on loblolly pine CWD disk decomposition rates (Table 27). The lightly thinned and heavily thinned treatments, had loblolly pine felled directly onto the forest floor, providing immediate ground contact decomposition. The CWD classified as standing or leaning provided examples of only aerial decomposition. The decomposition rate of aerial CWD was significantly different from the decomposition rate of ground contact CWD. The samples in position classes III – IV could be separated into samples dying from natural death or samples that died from thinning. The mean decomposition rates of natural versus thinned ground contact CWD were not significantly different (Table 28).

Table 27: Coarse woody debris disk decomposition rate for aerial versus ground contact samples. The aerial CWD was a combination of position class I and II, and the ground contact CWD samples were trees that were thinned, immediately having ground contact classified as either position class III or IV.

Position class	N	Mean Decomposition Rate	SD	Range
Aerial	425	0.041 [a]	0.075	- 0.629 – 0.353
Ground (thinned)	242	0.084 [b]	0.044	- 0.092 – 0.211

Note: Averages were determined to be significant using Tukey's test at an alpha level of 0.05. The letters superscripted above the mean decomposition rates indicate significance.

The average CWD disk specific gravities were significantly different between aerial and ground contract positions (Table 29). The aerial CWD had a wider range of disk specific gravities than the ground contact CWD. The relationship between CWD disk specific gravity and position class was significant ($r = -0.525$, $p < 0.0001$) (Table 22).

Table 28: Coarse woody debris disk decomposition rate for naturally dying ground contact CWD versus thinned ground contact samples. The ground contact CWD samples were a combination of position class III or IV.

Position class	N	Mean Decomposition Rate (k)	SD	Range
Ground (natural)	1303	0.086 [a]	0.062	- 0.178 – 0.727
Ground (thinned)	242	0.084 [a]	0.043	- 0.092 – 0.211

Note: Averages were determined to be significant using Tukey's test at an alpha level of 0.05. The letters superscripted above the mean decomposition rate indicate significance.

Table 29: Coarse woody debris SG_t for aerial versus ground contact samples. The aerial CWD was a combination of position class I and II, and the ground contact CWD samples were trees that were thinned, immediately having ground contact classified as either position class III or IV.

Position Class	N	Mean SG_t	SD	Range
Aerial	459	0.348 [a]	0.108	0.0249 – 1.05
Ground (thinned)	245	0.201 [b]	0.095	0.054 – 0.553

Note: Averages were determined to be significant using Tukey's test at an alpha level of 0.05. The letters superscripted above the mean SG_t indicate significance.

Treatment Analysis

The control treatment and the heavily thinned treatment did not have significantly different average CWD disk SG_t (Table 30). The average CWD disk SG_t for the lightly thinned treatment was significantly different from the heavily thinned and control treatments (Table 30). The average CWD disk decomposition rate for the control, lightly, and heavily thinned treatments were not significantly different (Table 30). The decomposition rates for the three treatments were separated by 0.001 (Table 30).

The control treatment had the narrowest range of average CWD disk specific gravities (SG_t) (Table 31). There was a 47% change in the average disk specific gravity from decay class I to V. The control treatment had average CWD disk specific gravities significantly different among all five decay classes (Table 31). The disk specific gravity

Table 30: Coarse woody debris average disk specific gravity and average disk decomposition rate according to treatment.

Treatment	N	Mean SG_t	N	Mean Decomposition Rate
1-Control	858	0.276 [a]	833	0.075 [a]
2-Light	767	0.251 [b]	757	0.077 [a]
3- Heavy	402	0.271 [a]	387	0.075 [a]

Notes: The superscripted letters designate plots that have average disk decomposition rates and average CWD disk specific gravities that are significantly different according to a Tukey's test at alpha = 0.5. The letters indicating significant differences apply to each column separately.

for the control treatment had a significant correlation (r = - 0.533, p < 0.0001) with decay class. There was a significant correlation (r = - 0.339, p < 0.0001) between disk specific gravity and TSD for the control treatment. The intercept for the "y" axis that resulted from the linear regression between disk specific gravity and TSD was 0.44.

Table 31: Coarse woody debris average disk specific gravity by decay class for the control, lightly thinned, and heavily thinned treatments.

	Plot 1 – Control		Plot 2 – Light Thin		Plot 3 – Heavy Thin	
Decay Class	**N**	**Mean SG_t**	**N**	**Mean SG_t**	**N**	**Mean SG_t**
I	43	0.375 [a]	21	0.373 [a]	18	0.453 [a]
II	252	0.336 [b]	129	0.341 [a]	109	0.329 [b]
III	280	0.293 [c]	298	0.285 [b]	129	0.283 [b]
IV	169	0.215 [d]	192	0.191 [c]	90	0.202 [c]
V	131	0.174 [e]	134	0.159 [c]	53	0.195 [c]

Note: Different letters above each mean specific gravity value represent significantly different values according to the Tukey's W Test at alpha = 0.05. The letters indicating significant differences apply to each column separately.

There was a 43% change in the average CWD disk specific gravity from decay class I to decay class V in the lightly thinned treatment (Table 31). Decay class IV and V disk specific gravities in the lightly thinned treatment were not significantly different (Table 31). The disk specific gravities for decay classes I and II were not significantly different (Table 31). There was a significant correlation ($r = -0.581$, $p < 0.0001$) between disk specific gravity and decay class for the lightly thinned treatment. Specific gravity and TSD had a significant correlation ($r = -0.513$, $p < 0.0001$). The intercept for linear regression of disk specific gravity versus TSD was 0.384.

The heavily thinned treatment had the widest range of mean CWD disk specific gravities across the five decay classes (Table 31). There was a 43% change in the average disk specific gravity from decay class I to decay class V. Decay class II and III SG_t were not significantly different from one another, but were significantly different from all other decay classes. Decay class IV and V were not significantly different, but were significantly different from all other decay classes (Table 31). There was a significant correlation ($r = -0.544$, $p < 0.0001$) between CWD disk SG_t and decay class. There was a significant correlation ($r = -0.386$, $p < 0.0001$) between CWD disk specific gravity and TSD. The intercept for disk specific gravity (SG_t) versus TSD was 0.3794.

Coarse woody debris average disk specific gravity was not significantly different across physiographic regions for the control treatment (Table 32). For the lightly thinned treatment the mean specific gravity of CWD disks for the GCP and the ACP were not significantly different (Table 32). The CWD mean specific gravity for the Piedmont and O. Mt were not significantly different, but were significantly different from the ILP, and GCP (Table 32). The heavily thinned treatment had no samples collected from the ILP because the treatment had been harvested before sampling (Table 32). The mean CWD disk specific gravity was not significantly different across the four different physiographic regions for the heavily thinned treatment (Table 32). The intercept for the linear regression between CWD disk specific gravity at the time of sampling and TSD was 0.367.

Table 32: Coarse woody debris average disk specific gravity according to physiographic region for the control, lightly thinned, and heavily thinned treatment.

	Plot 1 - Control		**Plot 2 – Light Thin**		**Plot 3 – Heavy Thin**	
P Region.	**N**	**Mean SG $_t$**	**N**	**Mean SG $_t$**	**N**	**Mean SG $_t$**
ACP	282	0.245 [a]	246	0.234 [ab]	106	0.262 [ab]
GCP	333	0.300 [a]	300	0.284 [a]	199	0.299 [a]
Piedmont	141	0.280 [a]	157	0.220 [b]	61	0.221 [b]
O. Mt.	102	0.287 [a]	34	0.221 [b]	46	0.239 [b]
ILP	17	0.244 [a]	37	0.273 [a]		

Note:. Different letters above each mean specific gravity value represent significantly different values according to the Tukey's W Test at alpha = 0.05. The letters indicating significant differences apply to each column separately.

For the control, the mean specific gravity of standing CWD was significantly different from leaning, ground contract, and partially to completely covered CWD, however the specific gravities for leaning and ground contact CWD were not significantly different (Table 33). Coarse woody debris disk specific gravity had a significant correlation with position (r = - 0.440, p < 0.0001). There was a 43% change in the mean CWD specific gravity from standing to covered CWD.

The mean disk specific gravity for standing and leaning CWD in the lightly thinned plot were not significantly different, but were significantly different from ground contact or covered CWD. Coarse woody debris disk specific gravity was significantly different between position classes III and IV (Table 33). For the lightly thinned treatment, there was a 46% change in mean CWD disk specific gravity from position class I to IV. There was a significant correlation between CWD disk specific gravity and position class (r = - 0.560, p < 0.0001).

Table 33: Coarse woody debris average disk specific gravity according to position class for the control, lightly thinned, and heavily thinned treatments.

	Control		Lightly Thinned		Heavily Thinned	
Position	**N**	**Mean SG $_t$**	**N**	**Mean SG $_t$**	**N**	**Mean SG $_t$**
I - Standing	147	0.379 [a]	86	0.350 [a]	73	0.375 [a]
II - Leaning	83	0.299 [b]	41	0.322 [a]	29	0.291 [b]
III - Ground Contact	475	0.282 [b]	432	0.271 [b]	230	0.271 [b]
IV – Covered	167	0.163 [c]	215	0.161 [c]	67	0.164 [c]

Note: Different letters above each mean specific gravity value represent significantly different values according to the Tukey's W Test at alpha = 0.05. Position class IV is CWD that was partially to completely covered by the litter layer. The letters indicating significant differences apply to each column separately.

Leaning CWD and ground contact CWD were not significantly different for the heavily thinned treatment (Table 33). Coarse woody debris partially or completely covered was significantly different from standing, leaning, and ground contact CWD (Table 33). Standing mean CWD disk specific gravity was significantly different from all other position classes. Disk specific gravity displayed a significant correlation between CWD disk specific gravity and position class (r = - 0.576, p < 0.0001). There was a 43% change in average CWD disk specific gravity from position class I to position class IV.

Individual Treatment Analysis of CWD Disk Decomposition Rate

Decay class I CWD decomposition rate was significantly different from decay class IV and V in the control treatment (Table 34). In the control treatment the decomposition rate of decay class III CWD was significantly different from decay class

IV and V (Table 34). There was a significant correlation ($r = 0.295$, $p < 0.0001$) between CWD disk decomposition rate and decay class for the control treatment.

Decay class IV and V CWD decomposition rates were not significantly different from one another but were significantly different from the average CWD disk decomposition rates of decay classes I and II CWD in the lightly thinned plot (Table 34). Decay class I and decay class II CWD disk decomposition rates were significantly different in the lightly thinned treatment (Table 34). Coarse woody debris decomposition rate and decay class had a significant correlation ($r = 0.311$, $p < 0.0001$). The mean decomposition rate of decay class II CWD from the heavily thinned plot was significantly different from the decomposition rate of decay class II CWD sampled from the lightly thinned treatment (Table 35).

Table 34: Coarse woody debris average disk decomposition rate according to decay class for the control, lightly thinned, and heavily thinned treatments.

	Control		Lightly Thinned		Heavily Thinned	
Decay Class	**N**	**Mean (k)**	**N**	**Mean (k)**	**N**	**Mean (k)**
I	41	0.046 [c]	21	0.004 [c]	16	-0.008 [a]
II	232	0.052 [bc]	124	0.049 [b]	100	0.068 [b]
III	260	0.072 [b]	298	0.072 [ba]	123	0.066 [b]
IV	169	0.099 [a]	184	0.095 [a]	86	0.093 [b]
V	127	0.098 [a]	133	0.097 [a]	52	0.098 [b]

Note: Different letters above each mean specific gravity value represent significantly different values according to the Tukey's W Test at alpha = 0.05. The letters indicating significant differences apply to each column separately.

Decay class I CWD in the heavily thinned treatment had a negative mean decomposition rate (Table 30). Decay class I CWD disk decomposition rate was significantly different from the decomposition rate of CWD across all other decay classes in the heavily thinned treatment (Table 34). Decomposition rate and decay class had a significant correlation (r = 0.270, p < 0.0001) in the heavily thinned treatment.

Table 35: Decay class decomposition rate (k) by treatment: control, lightly thinned, and heavily thinned.

	Decay Class				
Treatment	**I**	**II**	**III**	**IV**	**V**
Control	0.046 [a]	0.052 [ab]	0.072 [a]	0.099 [a]	0.98 [a]
Light Thin	0.004 [a]	0.049 [b]	0.072 [a]	0.095 [a]	0.097 [a]
Heavy Thin	- 0.008 [a]	0.068 [a]	0.066 [a]	0.093 [a]	0.098 [a]

Note: Different letters above each mean decomposition rate represent significantly different values according to the Tukey's W Test at alpha = 0.05. The values are mean decomposition rate for each decay class. The letters indicating significant differences apply to each column separately.

The CWD mean decomposition rate in the Piedmont was significantly different from the mean CWD disk decomposition rate in the ILP (Table 36). The CWD disk decomposition rate in the ACP was significantly different from all other physiographic regions (Table 36). The O. Mt. mean CWD decomposition rate for the heavily thinned plot was significantly different from the ACP, GCP, and the Piedmont (Table 36).

Table 36: Coarse woody debris mean disk decomposition rate by physiographic region for the control, lightly thinned, and heavily thinned treatments.

	Control		Lightly Thinned		Heavily Thinned	
Physiographic Region	**N**	**Mean (k)**	**N**	**Mean (k)**	**N**	**Mean (k)**
ACP	277	0.075 [ab]	231	0.069 [b]	87	0.055 [b]
GCP	333	0.080 [ab]	300	0.081 [a]	199	0.076 [b]
Piedmont	100	0.055 [b]	149	0.074 [a]	61	0.069 [b]
O. Mt.	102	0.072 [ab]	34	0.099 [a]	40	0.120 [a]
ILP	17	0.091 [a]	37	0.077 [a]		

Note: Different letters above each mean specific gravity value represent significantly different values according to the Tukey's W Test at alpha = 0.05. The letters indicating significant differences apply to each column separately.

For the control treatment standing CWD had a significantly different mean decomposition rate from CWD classified as leaning, ground contact, or covered (Table 37). The decomposition rate of leaning and ground contact CWD was not significantly different for the control (Table 37). The decomposition rate of covered CWD was significantly different from all other position classes (Table 37). There was a significant correlation ($r = 0.348$, $p < 0.0001$) between CWD disk decomposition rate and position class for the control treatment. According to position class there were no significant differences in the CWD disk decomposition rates across treatments (Table 38).

Table 37: Coarse woody debris mean decomposition rate by position class for the control, lightly thinned, and heavily thinned treatments.

	Control		Lightly Thinned		Heavily Thinned	
Position Class	**N**	**Mean (k)**	**N**	**Mean (k)**	**N**	**Mean (k)**
I - Standing	132	0.030 [c]	84	0.026 [c]	64	0.033 [b]
II - Leaning	77	0.062 [b]	40	0.059 [b]	28	0.069 [a]
III - Ground	454	0.079 [b]	418	0.078 [ab]	222	0.080 [a]
IV - Covered	163	0.101 [a]	208	0.097 [a]	63	0.096 [a]

Note: Different letters above each mean specific gravity value represent significantly different values according to the Tukey's W Test at alpha = 0.05. Position class IV is CWD that was partially to completely covered by the litter layer. The letters indicating significant differences apply to each column separately.

For the lightly thinned treatment mean CWD disk decomposition rate was significantly different between standing and covered position classes (Table 37). The decomposition rate of standing CWD was significantly different from the decomposition rate of leaning CWD (Table 37). There was a significant correlation ($r = 0.318$, $p< 0.0001$) between CWD disk decomposition rate and position class for the lightly thinned treatment.

The mean CWD disk decomposition rate for standing CWD was significantly different leaning, ground contact, and covered CWD (Table 37). The CWD disk decomposition rates were not significantly different among leaning, ground contact, or covered CWD position classes (Table 37). There was a significant correlation ($r = 0.294$, $p < 0.0001$) between CWD disk decomposition rate and position class for the heavily thinned treatment.

Table 38: Coarse woody debris mean decomposition rate for each position class by treatment: control, lightly thinned, and heavily thinned.

	Position Class			
Treatment	**Standing**	**Leaning**	**Ground**	**Covered**
Control	0.030 [a]	0.062 [a]	0.079 [a]	0.101 [a]
Light thin	0.026 [a]	0.059 [a]	0.078 [a]	0.097 [a]
Heavy thin	0.033 [a]	0.069 [a]	0.080 [a]	0.096 [a]

Note: Different letters above each mean decomposition rate represent significantly different values according to the Tukey's W Test at alpha = 0.05. The letters indicating significant differences apply to each column separately.

CWD TSD Position Class and Decay Class

The average TSD had a different relationship with decay class for each of the three treatments (Table 39). For the control treatment each decay class had a significantly different average TSD (Table 39). The average TSD had a significant correlation ($r = 0.581$, $p < 0.0001$) with decay class for the control treatment.

The lightly thinned treatment had significantly different average CWD TSD for each of the five decay classes (Table 39). Time since death displayed a significant correlation ($r = 0.643$, $p < 0.0001$) with decay class for the lightly thinned treatment. The TSD for decay class I and II were not significantly different, but were significantly different from decay classes III, IV, and V (Table 39). The TSD values corresponding to decay classes III, IV, and V were significantly different in the heavily thinned treatment (Table 39). In the heavily thinned plot decay class II had a lower mean CWD TSD value than decay class I (Table 39). Time since death and decay class displayed a significant correlation ($r = 0.606$, $p < 0.0001$) for the heavily thinned treatment.

Table 39: Coarse woody debris mean time since death (TSD) by decay class for the control, lightly thinned, and the heavily thinned treatments.

	Control Treatment		Lightly Thinned		Heavily Thinned	
Decay Class	**N**	**Mean TSD**	**N**	**Mean TSD**	**N**	**Mean TSD**
I	43	4.5 [a]	21	2.95 [a]	18	5.44 [a]
II	252	5.93 [b]	129	5.60 [b]	109	4.82 [a]
III	280	7.03 [c]	298	6.93 [c]	129	7.48 [b]
IV	169	9.14 [d]	192	10.1 [d]	90	9.39 [c]
V	131	11.5 [e]	134	11.8 [e]	53	11.4 [d]

Note: Different letters above each mean specific gravity value represent significantly different values according to the Tukey's W Test at alpha = 0.05. The letters indicating significant differences apply to each column separately.

The mean TSD for covered CWD was significantly different from the mean TSD for standing, leaning, or ground contact CWD in the control treatment (Table 40). There was a significant correlation ($r = 0.341$, $p < 0.0001$) between average TSD and position for the control treatment.

The mean TSD for standing CWD was significantly different from the average TSD for covered CWD (Table 40) in the lightly thinned plot. Covered CWD and grounded CWD had significantly different average TSD values (Table 40). The average TSD for covered CWD was significantly different from the average TSD for leaning CWD in the lightly thinned treatment (Table 40). There was a significant correlation ($r = 0.496$, $p < 0.0001$) between TSD and position class.

Table 40: Coarse woody debris mean TSD by position classes for the control, lightly thinned, and the heavily thinned treatments.

	Control Treatment		Lightly Thinned		Heavily Thinned	
Position	**N**	**Mean TSD**	**N**	**Mean TSD**	**N**	**Mean TSD**
I - Standing	147	6.73 [b]	86	5.62 [c]	73	5.51 [c]
II - Leaning	83	6.66 [b]	41	6.71 [bc]	29	7.00 [b]
III - Grounded	475	6.82 [b]	432	7.25 [b]	230	7.18 [b]
IV - Covered	167	11.4 [a]	215	11.5 [a]	67	11.6 [a]

Note: Different letters above each mean specific gravity value represent significantly different values according to the Tukey's W Test at alpha = 0.05. Position IV was CWD that partially to completely covered by the litter layer.

The average standing TSD was significantly different from the average TSD for leaning, grounded, and covered CWD for the heavily thinned treatment (Table 40). Leaning and grounded CWD did not significantly different mean TSD values (Table 40). There was a significant correlation ($r = 0.436$, $p < 0.0001$) between TSD and CWD position class for the heavily thinned treatment.

CWD Decomposition Rate Models

Multiple linear regression models for predicting loblolly pine CWD disk decomposition rate in industrialized cut – over plantations were developed across all physiographic regions and individually for the ACP, GCP, Piedmont, O. Mt., and ILP. The models were developed from a randomly generated model building data set, which was a subset of the entire data set. A building data set was created for the all regions model (Table 41) and separate building data sets were developed for each physiographic region (Tables 41 – 46). The randomly generated validation data set was the other portion of the entire data set that was not used in the model building data set. The validation data set was used to examine relationships among the predicted value and observed variables. The validation data sets were created for the all regions model and for each physiographic region model.

The model developed across all regions incorporates interaction variables to examine for differences in the estimated parameter coefficients among physiographic regions. In the final model there were eight regressor variables; decay class (decay), position class (pos), estimated height of disk (hdisk), longitude (longdeg), and two interaction variables (z2pos) and (z4plot), which indicate differences in the estimated parameter coefficient for position class in the GCP and the importance of plot in the and O. Mt (Table 41). The model was significant with an R^2 of 0.315 (Table 41).

Table 41: Coarse woody debris disk decomposition rate (k) model and parameter estimate statistics across all physiographic regions.

Physiographic Region	**Decomposition Rate Model**	**R^2**	**P-Value**
		0.315	< 0.0001
All Regions	$B_0 + B_1$ (decay) + B_2 (pos) + B_3 (hdisk)+ B_4 (longdeg) + B_5 (z2pos) + B_6 (z4plot)	**RSME**	**Cp**
		0.056	7.01

Coefficient	**Estimate**	**Standard Error**	**Partial R Square**	**P – Value**
B_0	0.188	0.047		< 0.0001
B_1	0.009	0.002	0.012	< 0.0001
B_2	0.011	0.003	0.077	< 0.0001
B_3	- 0.003	0.0002	0.182	< 0.0001
B_4	- 0.002	0.0006	0.009	0.0003
B_5	0.012	0.002	0.017	< 0.0001
B_6	0.036	0.005	0.019	< 0.0001

Variable	**N**	**Mean (k)**	**Standard Error**	**Range**
Observed (k)	995	0.075	0.061	- 0.178 – 0.343
Predicted (k)	984	0.074	0.037	- 0.164 – 0.194

Note: The mean statistics are derived from the model validation data set.

The observed CWD disk decomposition rate had a significant correlation ($r = 0.540$, $p < 0.0001$) with predicted decomposition rate. The predicted decomposition rate and observed specific gravity (SG_t) had a significant correlation ($r = -0.350$, $p < 0.0001$). The observed TSD and predicted decomposition rate had a significant correlation ($r = 0.251$, $p < 0.0001$).

The model developed for the ACP had seven regressor variables; position class (pos), estimated disk height (hdisk), and treatment, control, light, or heavy thinned (plot), (Table 42). The decomposition rate model developed for the ACP was significant ($R^2 = 0.361$, $p < 0.0001$). Coarse woody debris position class (pos) comprised the largest portion of the total model R^2 and plot comprised the smallest portion (Table 42).

Table 42: Coarse woody debris disk decomposition rate (k) model and parameter estimate statistics for the ACP.

Physiographic Region	**Decomposition Rate Model**	**R^2**	**P-Value**
		0.361	< 0.0001
ACP	$B_0 + B_1$ (hdisk) + B_2 (pos) + B_3 (plot)	**RSME**	**Cp**
		0.041	4.0

Coefficient	**Estimate**	**Standard Error**	**Partial R Square**	**P – Value**
B_0	0.043	0.011		0.0001
B_1	- 0.002	0.0003	0.122	< 0.0001
B_2	0.021	0.003	0.212	< 0.0001
B_3	- 0.012	0.003	0.027	0.0009

Variable	**N**	**Mean (k)**	**Standard Error**	**Range**
Observed (k)	325	0.069	0.055	- 0.156 – 0.214
Predicted (k)	325	0.069	0.029	- 0.0478 – 0.133

Note: The mean statistics are derived from the model validation data set.

There was a significant correlation ($r = 0.573$, $p < 0.0001$) between the predicted CWD disk decomposition rate and the observed CWD disk decomposition. Coarse woody debris observed SG_t and predicted decomposition rate had a significant correlation ($r = -0.448$, $p < 0.0001$). There was a significant correlation ($r = 0.298$, $p < 0.0001$) between predicted CWD disk decomposition rate and TSD.

The model developed for the GCP had four different regressor variables; position class (pos), estimated disk height (hdisk), thinned or natural death (thin) and longitude (longdeg) (Table 43). The decomposition rate model was significant (R^2 0.236, $p < 0.0001$) (Table 43). Coarse woody debris position class comprised the largest portion of the total model R^2 (Table 43).

Table 43: Coarse woody debris disk decomposition rate (k) model and parameter estimate statistics for the GCP.

Physiographic Region	**Decomposition Rate Model**	**R^2**	**P-Value**
		0.236	< 0.0001
GCP	$B_0 + B_1$ (pos) $+ B_2$ (thin) $+ B_3$ (hdisk) $+ B_4$ (longdeg)	**RMSE**	**Cp**
		0.057	5.0

Coefficient	**Estimate**	**Standard Error**	**Partial R Square**	**P – Value**
B_0	0.585	0.106		< 0.0001
B_1	0.022	0.003	0.092	< 0.0001
B_2	- 0.036	0.011	0.019	0.002
B_3	- 0.002	0.0003	0.083	< 0.0001
B 4	- 0.005	0.001	0.042	< 0.0001

Variable	**N**	**Mean (k)**	**Standard Error**	**Range**
Observed (k)	414	0.080	0.071	- 0.166– 0.554
Predicted (k)	407	0.075	0.056	- 0.87 - 0.143

Note: The mean statistics are derived from the model validation data set.

There was a significant correlation ($r = 0.456$, $p < 0.0001$) between the predicted CWD disk decomposition rate and the observed decomposition rate. A significant correlation ($r = 0.182$, $p < 0.0001$) was determined between predicted decomposition rate and TSD. Observed disk SG_t and predicted disk decomposition rate had a significant correlation ($r = -0.372$, $p < 0.0001$).

The model developed for the Piedmont region had two different regressor variables; decay class (decay), and estimated disk height (hdisk) with decay class comprising the largest portion of the total model R^2 (Table 44). The decomposition rate model was significant ($R^2 = 0.540$, $p < 0.0001$) (Table 44).

Table 44: Coarse woody debris disk decomposition rate (k) model and parameter estimate statistics for the Piedmont.

Physiographic Region	**Decomposition Rate Model**	**R^2**	**P-Value**
		0.372	< 0.0001
Piedmont	$B_0 + B_1$ (decay) + B_2 (hdisk)	**RSME**	**Cp**
		0.050	3.0

Coefficient	**Estimate**	**Standard Error**	**Partial R Square**	**P – Value**
B_0	0.041	0.01		= 0.001
B_1	0.019	0.003	0.241	< 0.0001
B_2	- 0.005	0.0005	0.132	< 0.0001

Variable	**N**	**Mean (k)**	**Standard Error**	**Range**
Observed (k)	140	0.075	0.055	- 0.155 – 0.353
Predicted (k)	140	0.071	0.043	- 0.099 – 0.135

Note: The mean statistics are derived from the model validation data set.

There was a significant correlation ($r = 0.656$, $p < 0.0001$) between predicted CWD disk decomposition rate and observed CWD disk decomposition rate. A significant correlation ($r = 0.565$, $p < 0.0001$) between predicted CWD disk decomposition rate and TSD. There was a significant correlation ($r = -0.611$, $p < 0.0001$) between the predicted decomposition rate and the observed SG_t.

The model developed for the O. Mt. had two regressor variables treatment (plot) and estimated disk height (hdisk) (Table 45). The decomposition rate model was significant ($R^2 = 0.498$, $p < 0.0001$) for the O. Mt. (Table 45). Observed decomposition rate and predicted decomposition rate had a significant correlation ($r = 0.701$, $p < 0.0001$). Observed CWD disk SG_t did not have a significant correlation ($p = 0.620$) with predicted CWD disk decomposition rate. Observed TSD did not have a significant correlation ($p = 0.582$) with predicted disk decomposition rate for the O. Mt.

Table 45: Coarse woody debris disk decomposition rate (k) model and parameter statistics for the O. Mt.

Physiographic Region	**Decomposition Rate Model**		**R^2**	**P-Value**
			0.498	< 0.0001
O. Mt.	$B_0 + B_1$ (plot) $+ B_2$ (hdisk)		**RMSE**	**Cp**
			0.058	3.0

Coefficient	**Estimate**	**Standard Error**	**Partial R Square**	**P – Value**
B_0	0.075	0.014		< 0.0001
B_1	0.036	0.008	0.369	< 0.0001
B_2	- 0.004	0.0005	0.129	< 0.0001

Variable	**N**	**Mean (k)**	**Standard Error**	**Range**
Observed (k)	122	0.064	0.070	- 0.270 – 0.215
Predicted (k)	122	0.075	0.054	- 0.164 – 0.175

Note: The mean statistics are derived from the model validation data set.

The decomposition rate model developed for the ILP had one regressor variable; decay class (decay) (Table 46). The decomposition rate model was significant for the ILP ($R^2 = 0.499$, $p < 0.0001$). The parameter estimates were all significant (Table 46).

There was a significant correlation ($r = 0.713$, $p < 0.0001$) between observed decomposition rate and predicted decomposition. Observed CWD disk SG_t had a significant correlation ($r = -0.801$, $p < 0.0001$) with predicted CWD disk decomposition rate. Observed TSD had a significant correlation with predicted CWD disk decomposition rate ($r = 0.762$, $p < 0.0001$).

Table 46: Coarse woody debris disk decomposition rate model and parameter statistics for the ILP.

Physiographic Region	Decomposition Rate Model		R^2	P-Value
			0.499	< 0.0001
ILP	$B_0 + B_1$ (decay)		**RMSE**	**Cp**
			0.033	3.41

Coefficient	Estimate	Standard Error	Partial R Square	P – Value
B_0	- 0.065	0.032		0.053
B_1	0.045	0.010	0.499	0.0001
Variable	**N**	**Mean (k)**	**Standard Error**	**Range**
Observed (k)	30	0.083	0.055	- 0.028 – 0.196
Predicted (k)	29	0.078	0.036	0.025 – 0.160

Note: The mean statistics are derived from the model validation data set.

CWD TSD Models

Models were developed to predict the time since death (TSD) for loblolly pine CWD in industrially managed cut-over plantations across all physiographic regions and for each physiographic region (Tables 47 – 52). An all regions model building data set was used to develop the model across physiographic region and an all regions validation data set was used to develop the correlations between the predicted variable and other stand level and tree level variables. Building data sets and validation data sets were also created for each physiographic region for model development (Tables 47 – 52).

To test for differences in estimated parameter coefficients for predicting TSD among physiographic regions a model was developed across all regions (Table 47). The model for all regions had six parameter estimates, which were all significant (Table 47). The model R^2 was 0.507 and model RMSE was 2.42 (Table 47). Three of the six variables in the model were interaction variables (Table 47). The interaction variables indicate the difference in the decay class parameter estimate for the ACP (z1decay), the importance of plot in O. Mt. (z4plot), and the importance of heating degree days (hdd) in the Piedmont (z3hdd) (Table 47).

Table **47:** Coarse woody debris time since death (TSD) model and parameter estimate statistics across all physiographic regions.

Physiographic Region	**Time Since Death Model**			**R^2**	**P – Value**
				0.507	< 0.0001
All Regions	$B_0 + B_1$ (decay) + B_2 (thin) + B_3 (len) + B_4 (z1decay) + B_5 (z4plot) + B_6 (z3hdd)			**RMSE**	**Cp**
				2.42	7.0
Coefficient	**Estimate**	**Standard Error**	**Partial R Square**	**P – Value**	
B_0	-0.314	0.600		0.600	
B_1	1.40	0.080	0.370	< 0.0001	
B_2	1.71	0.267	0.032	< 0.0001	
B_3	- 0.106	0.018	0.018	< 0.0001	
B_4	0.686	0.051	0.067	< 0.0001	
B_5	- 0.375	0.147	0.003	0.011	
B_6	0.0003	0.00005	0.017	< 0.0001	
Variable	**N**	**Mean (yrs)**	**Standard Error**	**Range**	
Observed	1045	7.96	3.72	2.00 – 22.0	
Predicted	1029	7.82	2.51	2.6 – 15.0	

Note: The mean statistics are derived from the model validation data set.

The predicted TSD and the observed TSD were significantly correlated (r = 0.679, p < 0.0001). The predicted TSD and observed decomposition rate were significantly correlated (r = 0.190, p < 0.0001). The predicted TSD and the observed specific gravity were significantly correlated (r = - 0.545, p < 0.0001).

The model developed for the ACP had one regressor variable: decay class (decay) (Table 48). The CWD TSD model for the ACP was significant (R^2 = 0.445, p < 0.0001) (Table 48). There was a significant correlation (r = 0.690, p < 0.0001) between predicted TSD and observed TSD. There was a significant correlation (r = - 0.652, p < 0.0001) between the predicted TSD and CWD observed specific gravity. Decomposition rate and predicted TSD were significantly correlated (r = 0.312, p < 0.0001).

Table 48: Coarse woody debris time since death (TSD) model and parameter estimate statistics for the ACP.

Physiographic Region	**Time Since Death Model**	**R^2**	**P – Value**
		0.445	< 0.0001
ACP	$B_0 + B_1$ (decay)	**RMSE**	**Cp**
		3.14	2.96

Coefficient	**Estimate**	**Standard Error**	**Partial R Square**	**P – Value**
B_0	0.666	0.646		0.3031
B_1	2.66	0.182	0.445	< 0.0001

Variable	**N**	**Mean (yrs)**	**Standard Error**	**Range**
Observed	345	8.83	4.14	3.0 – 21.0
Predicted	343	9.19	2.80	3.33 – 14.0

Note: The mean statistics are derived from the model validation data set.

The model developed for the GCP had two regressor variables (Table 49). The TSD model developed for the GCP was significant (R^2 = 0.313, p < 0.0001) (Table 49). There was a significant correlation (r = 0.569, p < 0.0001) between predicted CWD TSD and observed TSD. Predicted TSD and observed CWD specific gravity (SG_t) had a significant correlation ($r = -0.400$, $p < 0.0001$). There was not a significant correlation ($r = 0.096$, $p = 0.052$) between predicted TSD and observed CWD decomposition rate.

Table 49: Coarse woody debris time since death (TSD) model and parameter statistics for the GCP.

Physiographic Region	**Time Since Death Model**	**R^2**	**P-Value**
		0.313	< 0.0001
GCP	$B_0 + B_1$ (decay) + B_2 (thin)	**RMSE**	**Cp**
		2.64	3.0

Coefficient	**Estimate**	**Standard Error**	**Partial R Square**	**P – Value**
B_0	- 6.38	1.21		< 0.0001
B_1	1.55	0.127	0.212	< 0.0001
B_2	4.04	0.521	0.101	< 0.0001

Variable	**N**	**Mean (yrs)**	**Standard Error**	**Range**
Observed TSD	415	7.15	3.22	2.0 – 21.0
Predicted TSD	408	7.14	1.92	3.25 – 13.5

Note: The mean statistics are derived from the model validation data set.

In the Piedmont physiographic region the full model for predicting CWD TSD reduced to a one parameter model: decay class (decay) (Table 50). The TSD model was significant ($R^2 = 0.604$, $p < 0.0001$) for the Piedmont physiographic region (Table 50). There was a significant correlation ($r = 0.730$, $p < 0.0001$) between observed TSD and predicted TSD. There was a significant correlation ($r = -0.725$, $p < 0.0001$) between observed CWD specific gravity and predicted TSD. Predicted TSD and CWD disk decomposition rate had a significant correlation ($r = 0.384$, $p < 0.0001$).

The model developed for the O. Mt. to predict TSD was significant (R^2 0.605, $p < 0.0001$) (Table 51). There was a significant correlation ($r = 0.412$, $p < 0.0001$) between

Table 50: Coarse woody debris time since death (TSD) model and parameter estimates for the Piedmont

Physiographic Region	**Time Since Death Model**	**R^2**	**P – Value**
		0.604	< 0.0001
Piedmont	$B_0 + B_1$ (decay)	**RMSE**	**Cp**
		1.78	2.0

Coefficient	**Estimate**	**Standard Error**	**Partial R Square**	**P – Value**
B_0	2.55	0.368		< 0.0001
B_1	1.87	0.110	0.604	< 0.0001
Variable	**N**	**Mean (yrs)**	**Standard Error**	**Range**
Observed TSD	167	8.57	2.89	2.0 – 16.0
Predicted TSD	167	8.61	2.26	4.42 – 11.9

Note: The mean statistics are derived from the model validation data set.

Table 51: Coarse woody debris time since death (TSD) model and parameter estimates for the O. Mt.

Physiographic Region	**Time Since Death Model**	**R^2**	**P – Value**
		0.605	< 0.0001
O. Mt.	$B_0 + B_1$ (decay)	**RMSE**	**Cp**
		1.55	2.0

Coefficient	**Estimate**	**Standard Error**	**Partial R Square**	**P – Value**
B_0	1.22	0.400		< 0.0001
B_1	1.59	0.140	0.605	< 0.0001
Variable	**N**	**Mean (yrs)**	**Standard Error**	**Range**
Observed TSD	94	5.78	2.86	3.0 – 14.0
Predicted TSD	92	5.45	1.9	2.8 – 9.16

Note: The mean statistics are derived from the model validation data set.

observed CWD TSD and predicted CWD TSD. Observed CWD specific gravity and predicted TSD were significantly correlated ($r = -0.235$, $p = 0.009$). Predicted TSD and observed decomposition rate were not significantly correlated ($r = 0.134$, $p = 0.656$).

The full model for predicting CWD TSD in the ILP reduced to a significant ($R^2 = 0.479$, $p < 0.0001$) one parameter model (Table 51). All the parameter estimates were significant (Table 51). There was a significant correlation ($r = 0.762$, $p < 0.0001$) between predicted CWD TSD and observed TSD. Predicted TSD and observed decomposition were significantly correlated ($r = 0.714$, $p < 0.0001$). Observed SG_t and predicted TSD were significantly correlated ($r = 0.801$, $p < 0.0001$).

Table 52: Coarse woody debris time since death (TSD) model and parameter estimate statistics for the ILP.

Physiographic Region	**Time Since Death Model**		**R^2**	**P – Value**
			0.479	0.0002
ILP	$B_0 + B_1$ (decay)		**RMSE**	**Cp**
			0.936	2.0
Coefficient	**Estimate**	**Standard Error**	**Partial R Square**	**P – Value**
B_0	3.39	0.889		0.001
B_1	1.22	0.271		0.0002

Variable	**N**	**Mean (yrs)**	**Standard Error**	**Range**
Observed TSD	30	7.2	1.69	5.0 – 12.0
Predicted TSD	29	7.25	0.979	5.82 – 9.47

Note: The mean statistics are derived from the model validation data set.

CWD Disk Specific Gravity Models

Models were developed to predict the CWD specific gravity at time of sampling (SG_t) across physiographic region and for each physiographic region (Tables 53 – 59). A model was developed across all physiographic regions using interaction variables to explore differences in estimated parameter coefficients among physiographic region. Models were also developed for each physiographic region. The models were created from building data sets for the all regions model and for each physiographic region. The correlations between observed stand level and tree level variables and the predicted SG_t were from the model validation data set across all regions or for each physiographic region.

The all regions model for prediction CWD disk SG_t reduced to four parameters, one of which was an interaction variable, indicating the importance of elevation in the O. Mt. (Table 53). The all physiographic regions model was significant (Table 49). Decay

Table 53: Coarse woody debris specific gravity (SG_t) model and parameter estimate statistics across all physiographic regions.

Physiographic Region	Specific Gravity Model	R^2	P – Value
		0.431	< 0.0001
All Regions	$B_0 + B_1$ (decay) + B_2 (pos) + B_3 (longdeg) + B_4 (z4eleve)	**RMSE**	**Cp**
		0.083	5.0

Coefficient	Estimate	Standard Error	Partial R Square	P – Value
B_0	0.236	0.043		< 0.0001
B_1	- 0.047	0.003	0.349	< 0.0001
B_2	- 0.029	0.004	0.049	< 0.0001
B_3	0.003	0.0005	0.009	< 0.0001
B_4	- 0.0001	0.00002	0.024	< 0.0001

Variable	N	Mean (sg_t)	Standard Error	Range
Observed SG_t	1045	0.267	0.120	0.030 – 1.47
Predicted SG_t	1029	0.267	0.074	0.124 – 0.456

Note: The mean statistics are derived from the model validation data set.

class comprised 0.349 of the total model R^2 (Table 53). Predicted CWD SG_t and observed SG t were significantly correlated ($r = 0.609$, $p < 0.0001$). Predicted SG_t and observed TSD were significantly correlated ($r = 0.592$, $p < 0.0001$). Predicted SG_t and observed decomposition rate (k) were significantly correlated ($r = 0.313$, $p < 0.0001$).

The CWD disk SG_t model developed for the ACP was significant ($R^2 = 0.453$, $p < 0.0001$) reducing to one parameter (Table 54). Observed disk SG_t and predicted disk SG_t were significantly correlated ($r = 0.652$, $p < 0.0001$). Observed disk decomposition rate and predicted disk SG_t were significantly correlated ($r = - 0.317$, $p < 0.0001$). Observed TSD and predicted SG_t were significantly correlated ($r = - 0.690$, $p < 0.0001$). The intercept for the linear fit between TSD and predicted SG_t was 0.369 for the ACP, which is an estimate of the average initial live specific gravity.

Table 54: Coarse woody debris specific gravity (SG_t) model and parameter estimate statistics for the ACP.

Physiographic Region	**Specific Gravity Model**	**R^2**	**P – Value**
		0.453	< 0.0001
ACP	$B_0 + B_1$ (decay)	**RMSE**	**Cp**
		0.083	2.0

Coefficient	**Estimate**	**Standard Error**	**Partial R Square**	**P – Value**
B_0	0.481	0.0166		< 0.0001
B_1	- 0.072	0.005	0.453	< 0.0001

Variable	**N**	**Mean (sg_t)**	**Standard Error**	**Range**
Observed SG_t	345	0.250	0.108	0.030 – 0.608
Predicted SG_t	343	0.257	0.076	0.127 – 0.415

Note: The mean statistics are derived from the model validation data set.

The CWD disk SG_t model developed for the GCP was significant ($R^2 = 0.227$, $p < 0.0001$) with two parameters (Table 55). Observed disk SG_t and predicted disk SG_t

were significantly correlated ($r = 0.535$, $p < 0.0001$). Observed disk decomposition rate and predicted SG_t were significantly correlated ($r = -0.275$, $p < 0.0001$). Observed TSD and predicted SG_t were significantly correlated ($r = -0.437$, $p < 0.0001$). The linear fit between observed TSD and predicted SG_t provided an intercept of 0.358, which is an estimate of the initial live disk specific gravity for the GCP.

Table 55: Coarse woody debris specific gravity (SG_t) model and parameter estimates for the GCP.

Physiographic Region	Specific Gravity Model	R^2	P-Value
		0.227	< 0.0001
GCP	$B_0 + B_1$ (decay) + B_2 (pos)	**RMSE**	**Cp**
		0.112	3.0

Coefficient	Estimate	Standard Error	Partial R Square	P – Value
B_0	0.516	0.021		< 0.0001
B_1	- 0.038	0.007	0.189	< 0.0001
B_2	- 0.035	0.008	0.038	< 0.0001

Variable	N	Mean (sg_t)	Standard Error	Range
Observed SG_t	415	0.293	0.121	0.006 – 1.05
Predicted SG_t	407	0.296	0.064	0.187 – 0.443

Note: The mean statistics are derived from the model validation data set.

The CWD disk SG_t model developed for the Piedmont was significant ($R^2 = 0.571$, $p < 0.0001$) reducing to one parameter (Table 56). Observed CWD disk SG_t and predicted CWD disk SG_t were significantly correlated ($r = 0.725$, $p < 0.0001$). Observed disk decomposition rate and predicted SG_t were significantly correlated ($r = -0.384$, $p < 0.0001$). Observed TSD and predicted SG_t were significantly correlated ($r = -0.730$, $p < 0.0001$). The intercept for the linear fit between observed TSD and predicted SG_t was 0.401, which was an estimate of the loblolly pine initial live specific gravity.

Table 56: Coarse woody debris specific gravity (SG_t) model and parameter estimates for the Piedmont

Physiographic Region	Specific Gravity Model	R^2	P – Value
		0.571	< 0.0001
Piedmont	$B_0 + B_1$ (decay)	**RMSE**	**Cp**
		0.067	1.30

Coefficient	Estimate	Standard Error	Partial R Square	P – Value
B_0	0.441	0.015		< 0.0001
B_1	- 0.063	0.004	0.571	< 0.0001

Variable	N	Mean (sg_t)	Standard Error	Range
Observed SG_t	167	0.243	0.102	0.025 – 0.528
Predicted SG_t	167	0.236	0.076	0.124 – 0.377

Note: The mean statistics are derived from the model validation data set.

The CWD disk specific gravity model developed for the O. Mt. was significant ($R^2 = 0.482$, $p < 0.0001$) reducing to a one parameter model (Table 57). Observed disk SG_t and predicted disk SG_t were significantly correlated ($r = 0.235$, $p < 0.009$) for the O. Mt. Observed disk decomposition rate and predicted SG_t were not significantly correlated ($r = 0.042$, $p = 0646$). Observed TSD and predicted SG_t were significantly correlated ($r = -0.412$, $p < 0.0001$). The linear fit between TSD and predicted SG_t provide an intercept of 0.324, which was an estimate of the initial live specific gravity for the O. Mt.

The CWD disk specific gravity model developed for the ILP was significant ($R^2 = 0.621$, $p < 0.0001$) reducing to a one parameter model (Table 58). Observed disk SG_t and predicted disk SG_t were significantly correlated ($r = 0.801$, $p < 0.0001$). Observed disk decomposition rate and predicted SG_t were significantly correlated ($r = - 0.713$, $p < 0.0001$). Observed TSD and predicted SG_t were significantly correlated ($r = - 0.762$, $p <$

0.0001). The intercept for the linear fit between TSD and predicted SG_t was 0.574, which was an estimate of the initial specific gravity for the ILP.

Table 57: Coarse woody debris specific gravity (SG_t) model and parameter estimates for the O. Mt. physiographic region.

Physiographic Region	Specific Gravity Model	R^2	P – Value
		0.482	< 0.0001
O. Mt.	$B_0 + B_1$ (decay)	**RMSE**	**Cp**
		0.064	2.0

Coefficient	Estimate	Standard Error	Partial R Square	P – Value
B_0	0.386	0.017		< 0.0001
B_1	-0.051	0.006	0.482	< 0.0001

Variable	N	Mean (sg_t)	Standard Error	Range
Observed SG_t	93	0.264	0.096	0.070 – 0.043
Predicted SG_t	90	0.264	0.075	0.121– 0.363

Note: The mean statistics are derived from the model validation data set.

Table 58: Coarse woody debris specific gravity (SG_t) model and parameter estimates for the ILP.

Physiographic Region	Specific Gravity Model	R^2	P – Value
		0.621	< 0.0001
ILP	$B_0 + B_1$ (decay)	**RMSE**	**Cp**
		0.065	2.0

Coefficient	Estimate	Standard Error	Partial R Square	P – Value
B_0	0.631	0.062		< 0.0001
B_1	- 0.113	0.019	0.621	< 0.0001

Variable	N	Mean (sg_t)	Standard Error	Range
Observed Specific Gravity	30	0.261	0.106	0.049 – 0.523
Predicted Specific Gravity	29	0.271	0.091	0.065 – 0.404

Note: The mean statistics are derived from the model validation data set.

Negative Decomposition Rates

There were a total of 178 samples with negative decomposition rates (k). A cause of death was recorded for 168 of the 178 total negative decomposition rates (Table 59). Ten out of 178 samples with a cause of death and a decomposition rate were thinned. Seventy – five percent of the samples with negative decomposition rates were classified as dying to suppression, and 24% were classified as dying from insect attack or disease.

Table 59: Summary of negative decomposition rates, specific gravity at time of sampling (SG_t) and estimated initial specific gravity (isg) by cause of death (cause). (k) is the decomposition rate, (SG_t) is the specific gravity at time of sampling, and (isg) is the estimated initial specific gravity.

Cause	N	(k)	Standard Error	Range
1 – lightning	2	- 0.098 [a]	0.114	- 0.178 – (- 0.173)
2 – insect or disease	40	- 0.060 [a]	0.100	- 0.178 – (-0.007)
3 – suppression	126	- 0.037 [a]	0.043	- 0.270 – (- 0.00005)
	N	**SG_t**	**Standard Error**	**Range**
1 – lightning	2	0.892 [b]	0.816	0.315 – 1.47
2 – insect or disease	90	0.366 [a]	0.152	0.091 – 0.852
3 - suppression	166	0.401 [a]	0.134	0.062 – 1.05
	N	**(isg)**	**Standard Error**	**Range**
1 – lightning	2	0.394 [a]	0.156	0.284 – 0.505
2 – insect or disease	40	0.373 [a]	0.089	0.150 – 0.523
3 - suppression	126	0.379 [a]	0.890	0.053 – 0.521

Note: Different letters above each mean specific gravity value represent significantly different values according to the Tukey's W Test at alpha = 0.05. The letters indicating significant differences apply to each column separately.

Coarse woody debris resulting from insect or disease mortality had a higher mean decomposition rate than CWD resulting from suppression, however the difference was not significant (Table 59). The mean SG_t was higher for CWD than the mean estimated initial specific gravity of CWD for the trees dying as a result of lightning and suppression (Table 59). The control treatment had 46% of the samples with negative decomposition rates (Table 60). The lightly thinned plot had the highest mean negative decomposition rate, but it was not significantly different from the other treatment mean decomposition rates (Table 60).

Table 60: Summary of negative CWD disk decomposition rates by treatment: control, lightly thinned, and heavily thinned

Treatment	N	(k)	Standard Error	Range
Control	81	- 0.033 [a]	0.0324	- 0.167 – (- 0.0005)
Lightly Thinned	53	- 0.058 [a]	0.096	- 0.629 – (- 0.0007)
Heavily Thinned	44	- 0.040 [a]	0.043	- 0.197 – (- 0.0008)

Note: Different letters above each mean specific gravity value represent significantly different values according to the Tukey's W Test at alpha = 0.05. The letters indicating significant differences apply to each column separately.

Discussion

I chose the single exponential model for determining CWD decomposition rate (Olson 1963; Grier 1978; Barber and van Lear 1984; Mattson et al. 1987; Edmonds and Eglitis 1989; Stone et al. 1998; Mackensen and Bauhus 2003). The overall mean loblolly pine CWD disk decomposition rate (k) according to the single exponential model across all physiographic regions and treatments was 0.07, which was within the range determined by Barber and van Lear (1984).

The mean decomposition rate (k) of loblolly pine CWD according to physiographic region ranged from 0.068 in the Piedmont to 0.088 in the O. Mt. (Table 19). These rates are similar to those observed for loblolly pine (0.072) by Barber and van Lear (1984), who also used the single exponential model. Loblolly pine decomposed faster than either Douglas fir or western hemlock (Table 2). The differences in loblolly pine CWD decomposition rates among physiographic regions indicate the variability of decomposition rate across a climatic gradient and provide an example of the spatial heterogeneity of decomposition rates across a landscape.

Stand-Level Interactions

The influence of climate on CWD decomposition was assessed using surrogates such as: air temperature, precipitation, latitude, longitude, and heating degree days. Fluctuations in the air temperature and precipitation change the moisture content and temperature of CWD and the surrounding soil influenceing the habitat quality for decomposers (Mackensen et al. 2003). The quality of the habitat provided by CWD for fungi, bacteria, and macroinvertebrates subsequently affects the decomposition rate of CWD. Several studies have monitored fluctations in air temperature and determined that increases were followed by enhanced decomposition rates (Edmonds 1987; Marra and Edmonds 1996; Mackensen et al. 2003). Mean annual temperature showed a stonger relationship to CWD decomposition rate than precipitation, diameter, or elevation (Mackensen et al. 2003). Coarse woody debris disk decomposition rate was significantly correlated with latitude, longitude, maximum temperature, minimum temperature, average annual temperature, and heating degree days (Table 25), indicating an influence of climatic variables on the decomposition process.

Precipitation alone and in combination with temperature, influences the decomposition rate of CWD (Mattson et al. 1987; Chambers et al. 2000; Mackensen and Bauhus 2003; Mackensen et al. 2003). Excess or limited precipitation influences the soil and log moisture content, subsequently affecting the habitat for fungi, bacteria, and macroinvertebrates (Boddy 1983). In the wet forests of the Pacific Northwest changes in decomposition rate of western hemlock CWD followed seasonal precipitation patterns with increased precipitation followed by increased decomposition rates (Carpenter et al. 1988; Progar et al. 2000). Sitka spruce and Douglas fir decomposition rate were positively correlated with moisture content but pine CWD was not correlated (Laiho and Prescott 1999). The decomposition of loblolly pine CWD was not significantly correlated ($p = 0.302$) with average annual precipitation. There was no pattern between loblolly pine disk decomposition rate and average annual precipitation. For example, there were ten states visited during the study, Maryland had the highest average decomposition rate but the fourth lowest average annual precipitation.

Incorporating temperature, precipitation, latitude, and longitude into the decomposition rate model development was another tool for examining the importance of climatic variables on the decomposition process. Longitude was the only climatic variable to enter into any of the regression models for predicating decomposition rate (Table 41 and 43). The absence of the climate variables from the all regions model indicated that the tree level variables possibly had more influence on predicting the decomposition rate than the climatic variables. The absence of climate variables in the region specific regression models may have resulted from a small range in values of the regressor variables.

Disk specific gravity at time of sampling (SG_t) was significantly correlated with all stand level variables except average annual precipitation and elevation (Table 25). Studies have reported for loblolly pine an inverse relationship between live disk specific gravity and latitude (Talbert and Jett 1981; Megraw 1985). The CWD disk specific gravity at time of sampling (SG_t) displayed a direct relationship with latitude (Table 25). Within physiographic region the pattern observed for CWD disk SG_t compared to the pattern observed by Tasissa and Burkhart (1998) for live disk specific gravity was similar for the coastal plains regions with the GCP having a higher SG_t than the ACP (Table 23). The estimated initial specific gravity using the model developed by Amateis (personal communication) followed the pattern of initial specific gravity found by Tasissa and Burkhart (1998) (Table 12). However, when comparing mean estimated initial specific gravity (isg) of the Piedmont, O. Mt., and ILP from this study to the live specific gravities of loblolly pine from other studies the values were low (Table 12 and 13) (Talbert and Jett 1981; Byrum and Lowe 1988; Tauer and Loo-Dinkins 1990; Tasissa and Burkhart 1998; Jokela et al. 2004).

Another stand level variable examined was thinning. There were no significant affects of thinning on the mean decomposition rate of loblolly pine CWD (Table 30), which is contrary to the hypothesis considering the change in light dynamics that would occur on the forest floor due to canopy removal and subsequent patch development. The change in forest floor light interception hypothetically could influence soil and CWD temperature and moisture content changing the microhabitat for the fungi, macroinvertebrates, and bacteria. However, thinning did affect the average CWD disk SG_t at the time of sampling. The control treatment and heavily thinned treatment were statistically the same according to Tukey test (Table 30). However, the lightly thinned treatment had significantly different average CWD disk SG_t from both the control and the heavily thinned treatments. The difference in SG_t was because the lightly thinned CWD samples were on average dead 8.2 years while the control and heavily thinned plot CWD samples were on average dead 7.7 years. The difference in mean time of death (TSD) between control and heavily thinned treatments compared to the lightly thinned treatment was significant according to the Tukey's test. The increased TSD allowed time for further colonization by insects, bacteria, and fungi causing more fragmentation

Tree-Level Interactions

A variety of tree level variables were measured during the CWD study (Table 11). The distribution of CWD according to decay class peaked in decay class III (707) and was low in decay classes I (82) and V (318) (Table 14). A similar distribution was observed by Graham and Cromack (1982). A study of CWD in the Harvard forest found an even distribution of CWD according to decay class in pine forests (Currie and Nadelhoffer 2002). Coarse woody debris disk decomposition rate had a significant positive correlation ($p < 0.0001$) with decay class (Table 22). The decomposition rate of loblolly pine CWD according to decay class was significantly different between decay class I – II, III – IV, while decay classes II – III and IV – V were statistically similar according to a Tukey test (Table 21). The rates for decay class ranged from 0.023 to 0.098 for decay class I – V respectively (Table 21). A similar relationship between decomposition activity and decay class was observed in forests of western Montana (Larsen et al. 1978). In old–growth coniferous forests of Washington decomposition was most active in decay class I and V and least active in decay class III (Marra and Edmonds 1994). Still another pattern was observed by Hicks et al. (2003) where decomposition was enhanced in the middle stages of decay. Decay class entered into the final all regions decomposition rate model explaining 1% of the variation in the total R^2 (Tables 41) and into the models for the Piedmont and the ILP tables (44) and (46).

The average loblolly pine disk SG_t for each decay class was significantly different ranging from 0.393 to 0.171 for decay classes I through V (Table 21). Consistently, a significant inverse relationship between CWD SG_t and decay class has been demonstrated in different forested ecosystems (Sollins 1982; Sollins et al. 1987; Carmona et al. 2002). For example, lodgepole pine SG_t had a negative linear relationship with decay class ranging from approximately 0.370 to 0.130 (Holub et al. 2001) and for Douglas fir CWD SG_t ranged from 0.416 to 0.080 for decay classes I through V respectively (Means et al. 1985). During specific gravity model development, decay class was the first variable to enter using the stepwise selection technique for all models. Decay class explained between 62% and 18% of the variability in predicting specific gravity (Tables 53 – 58).

Coarse woody debris position was another important factor influencing decomposition rate, with 56% of the samples found in position class III (Table 14). Position class and decomposition rate displayed a significant positive linear relationship ($p < 0.0001$) (Table 22). There was a significant increase in the decomposition rate with ground contact (Table 24), similar to the pattern of CWD decomposition determined in other studies (Mattson et al. 1987; McMinn and Crossley 1993; Laiho and Prescott 1999). The ground decomposition rate (0.081) and aerial decomposition rate (0.051) of loblolly pine CWD determined by Barber and van Lear (1984) were similar to the rates observed in this study (Table 24). In coniferous stands of western Oregon snags were determined to decompose quicker than ground contact CWD contrary to our findings, possibly because the forested ecosystems of the Pacific Northwest are wet and the drier conditions of aerial CWD could enhance the decomposing environment for fungi, bacteria, and macroinvertebrates (Sollins 1982). Ground contact enhances the opportunity for macroinvertebrates, fungi, and bacteria to colonize decomposing CWD. The moisture content and temperature of CWD are often stabilized as a result of ground contact establishing a more habitable environment for decomposing organisms. Water and nutrient availability in ground contact CWD is enhanced for decomposing organisms (Mackensen et al. 2003). Position class entered into the final decomposition rate models for three out of the six models (Tables 41 – 46).

Aerial loblolly pine CWD had an average disk SG_t of 0.370 and ground contact CWD had a significantly different average SG_t of 0.275 (Table 24). The relationship between loblolly pine CWD SG_t and position were similar to the results of Barber and van Lear (1984) where ground contact CWD had an average specific gravity of 0.316 and aerial CWD was 0.343. Position entered into the final specific gravity models for all regions, and the GCP (Tables 53 and 58). The decreased SG_t with position class could be from the increased colonization by macroinvertebrates, bacteria, and fungi causing fragmentation and biological breakdown of the CWD resulting in a decreased wood specific gravity.

Thinned loblolly pine in the lightly and heavily thinned treatments provided a unique opportunity to compare decomposition rates of CWD that had immediate ground contact at the time of mortality versus CWD that had natural death and the potential to progress through different position stages before obtaining ground contract. There were no significant differences in the mean decomposition rates of CWD that were thinned versus CWD that had natural mortality (Table 28). The importance of mortality (thin) entered into the model for the GCP explaining about 2% of the variation (Table 43). The entrance of the mortality variable was not a sampling artifact because the largest number of trees sampled with anthropogenic mortality was in the Piedmont (124), GCP (61), ACP (24), and O. Mt. (17). However the entrance of the (thin) variable into the model could be because position explained the most variation in the GCP decomposition rate model mortality (thin) is connected to position class (Table 43).

Several different diameter (cm) measurements were collected, all having significant correlations with CWD decomposition rate (Table 22). In the western forests of the United States and Canada small diameter CWD was determined to decay faster than larger diameter pieces of CWD (Graham and Cromack 1982, Stone et al. 1998). Another study in the western USA found small diameter logs decayed slower than larger diameter logs attributing the difference in decay rates to the increased stability of temperature and moisture in the larger CWD (Edmonds and Eglitis 1989). Small loblolly pine CWD in South Carolina decomposed slower than large and medium CWD, the difference in rates attributed to case-hardening (Barber and van Lear 1984). Still other researcher's have found no affects of diameter on decomposition rate (Mattson et al. 1987; Marra and Edmonds 1996). In this study loblolly pine CWD had significant negative correlations with all diameter measurements recorded ($p < 0.0001$) (Table 22). The smaller CWD logs had a greater surface area to volume ratio increasing the decomposable surface for colonizing bacteria, macroinvertebrates, and fungi subsequently increasing the decomposition rate. The difference in results between my study and the Barber and van Lear (1984) study could be attributed to the difference in study site environment. The Barber and van Lear (1984) study was conducted on CWD from old clear-cuts, where the light interception by the CWD and bare soil would increase the temperature and decrease CWD moisture content making case-hardening a phenomenon that could affect decay rates. However, my study was conducting in forested ecosystems having canopy cover. The forest canopy intercepts incoming solar radiation decreasing the extreme temperatures at the forest floor and CWD interface and allowing for moisture content stabilization, which makes is less likely that small CWD will develop case-hardening.

Length (len) of the entire CWD piece, unlike in the study by Mattson et al. (1987), was significantly correlated ($p < 0.0001$) with decomposition rate (Table 22). Coarse woody debris microhabitat is heterogeneous along the length of the bole (Harmon and Sexton 1986). This microhabitat heterogeneity influences colonization of organisms that decompose CWD. For example, Graham and Cromack (1982) found within a 10 cm section of a bole there was sound wood, brown rot fungi which mainly decompose cellulose (Allen et al. 2000), and slimy white rot fungi, which decompose cellulose and lignin (Allen et al. 2000). Indicating, depending where along the bole's length the disk is sampled could affect the decomposition rate. Another variable correlated with decomposition rate and related to length was disk height (m). The estimated height along the bole a disk was sampled (hdisk) was significantly correlated with CWD disk decomposition rate (Table 22).

There was one negative mean decomposition rate, which occurred for decay class I CWD sampled from the heavily thinned treatment (Table 34). There were a total of 178 samples with negative decomposition rates (Table 59). The control treatment had 48% of the samples with negative decomposition rates (Table 60). The heavily thinned plot had the least number of CWD samples with a negative decomposition rate (Table 60). The increased distribution of negative decomposition rate samples coming in the control was hypothesized. The control treatment had greater competition due to increased stem density. The increased stem density can perpetuate disease, insect colonization, or suppression due to high levels of competition.

The CWD samples with negative decomposition rates had higher SG_t values than estimated initial specific gravity, causing a negative decomposition rate. The cause of death of these samples, as recorded by the remeasurement team, was insect infestation, disease, or suppression (Table 59). All three causes of mortality could result in elevated live wood specific gravities. Insects can transport dirt and other materials into the sample increasing the density, disease such as fusiform rust causes a resin build up in the wood increasing the live wood specific gravity, and suppression which increase the proportion of latewood to earlywood and therefore increases the initial live specific gravity of the CWD sample. The model for estimating specific gravity was not sensitive to these issues and therefore underestimated the initial specific gravity of these samples (Table 59).

The dynamics of loblolly pine CWD decomposition in industrially managed plantation ecosystems was spatially heterogeneous at the resolution of the stand and tree. For example, CWD dynamics varied at the stand level, with significant differences in decomposition rate (k) and specific gravity at time of sampling (SG_t) across physiographic region. Coarse woody debris dynamics also varied at the tree level. Coarse woody debris decomposition was significantly related to length, diameter, position, or decay class (Table 22). Changes in these variables can be indicators of fluctuations in CWD microhabitat. Length, position, decay, and diameter differences create fluctuations in CWD moisture content and temperature leading to microhabtatiat variability. These variable interactions influence the colonization of bacteria, fungi, and macroinvertebrates, and it is these organisms that dominate the breakdown and release of carbon, nitrogen, phosphorus, and calcium from CWD.

The interrelation between stand and tree level factors make it difficult to determine which variables are essential in the decomposition process of CWD. For example, there has been an inconsistent relationship found by researchers between decomposition rate and diameter (Abbott and Crossley 1982; Graham and Cromack 1982; Mattson et al. 1987; Edmonds and Eglitis 1989; McMinn and Crossley 1993; Marra and Edmonds 1994; Stone et al. 1998; Mackensen et al. 2003). It has been determined that ground contact enhances decomposition (Barber and van Lear 1984; Edmonds 1987; Mattson et al. 1987; Marra and Edmonds 1994; Wei et al. 1997;

Mackensen et al. 2003), because of increased colonization by decaying organisms, elevated CWD moisture content and stabilized temperature. However, if the CWD having ground contact was located in a moist environment, the increased moisture content of the log could retard decomposition by creating an anaerobic environment (Laiho and Prescott 1999) or if the grounded CWD was in a clear – cut case hardening could result from hot temperatures and low moisture content retarding decomposition of CWD (Barber and van Lear 1984).

In the decomposition rate models the variable that explained the greatest amount of variation was consistently different (Tables 41 – 46). The variability in findings could be due to true interactions between these different stand and tree level variables or could be a result of a sampling problem, or a data structure problem. Decomposition is a complicated process that is often generalized on a large spatial scale such as physiographic region, but for a greater understanding of what drives the decomposition of CWD it needs to be better understood at the tree level.

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