QUANTITATIVE METRICS OF DEADWOOD DECAY CLASSES AS A FUNCTION OF MOISTURE REGIME AND TREE SPECIES

by

Emmarie Leeson

**FACULTY OF NATURAL RESOURCES MANAGEMENT
LAKEHEAD UNIVERSITY
THUNDER BAY, ONTARIO**

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Major Advisor   Second Reader

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ABSTRACT

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Keywords: biodiversity, black spruce, canonical discriminant analysis, coarse woody debris, decay class, jack pine, trembling aspen, wood density

The patterns and rates of decomposition of dead woody debris (DWD) in the boreal ecosystem throughout the wood decay process have been hypothesized to vary across moisture regimes and between species. A fundamental aspect of examining these patterns of temporal wood decay rates and patterns is distinguishing between deadwood decay classes. The study sites for this project were set up across northern Ontario, with 8 in the Northeast (Abitibi Lake Ecoregion) and 8 in the Northwest (Lake Nipigon Ecoregion) to allow for an examination of the impacts of ecoregion on temporal wood decay in future studies. Within each ecoregion, three study sites of Dry, Fresh, and Wet, moisture regimes were included to examine the impacts of moisture regime. Within each site species differences were examined by sampling of conifer and poplar (*Populus tremuloides* (Michx.)). A qualitative five decay class system was used to classify wood *in situ* via non-destructive methods, in order to examine how DWD would reclassify upon further quantitative analysis of physical and chemical properties. The patterns of decay observed in poplar DWD were significantly faster compared to conifer decay, as represented by shifts in density and the proportion of solid wood to decayed wood across the decay class continuum. DWD appeared to decay more quickly on fresh sites compared to dry and wet sites, which seemed to have an early delay in decomposition. C:N ratios decreased across the decay class continuum in our results, and appeared to reflect a three phase decay process, consisting of an initial slow phase, a second rapid stage of decay, and a third slow phase and coinciding release of N. Further reclassification of decay classes based on quantitative metrics was required and the middle decay classes were found to have significant amounts of overlap in quantitative patterns and classification. Despite this, some reclassification of the middle decay classes into decay classes 1 and 5 occurred indicating that a three decay class system may not be ideal. However, if all analysis was repeated using the quantitatively assigned decay classes, patterns across the decay class continuum may better reflect the three-phase decay process, and thus imply that DWD classification is well suited to a three decay class system.

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INTRODUCTION

Dead and decaying wood is a critical element of forest ecosystems that contributes to biodiversity and provides a variety of ecosystem services. It provides habitat for many species including saproxylic specialists that depend on deadwood at some point in their life cycle (Siitonen 2001). The presence of these organisms is critical in order for the ecosystems they inhabit to function. For example, it is through their interactions with each other and their environment that they provide various functions including the supply of soil organic matter, contributions to soil development and productivity, release of nutrients, microsite creation for plant establishment, nitrogen fixation, pest regulation, mulching, moisture retention, and erosion prevention (Berch *et al*. 2011). Deadwood also represents a significant component of carbon stocks in forest ecosystems, which is an important consideration in efforts to reduce greenhouse gas emissions (Ryan *et al*. 2010, Malmsheimer *et al*. 2011, McKinley *et al*. 2011). A more advanced understanding of deadwood decomposition and decay rates is necessary to better quantify changes in carbon stocks (Birdsey *et al*. 2006) and allow for the establishment of dynamic ecosystem models relating to deadwood (Russell *et al*. 2014).

The boreal forest region is driven by stand-replacing disturbances like fire, insect, wind, as well as other non-stand replacing disturbances (Bergeron *et al*. 2002). These common disturbances in many cases lead to significant dead wood inputs and a complex forest structure including large numbers of snags. Within the context of

"emulating natural disturbance", it has been recognized that standing and downed deadwood quantities observed in managed stands tend to be less than those found in comparably-aged natural stands (Franklin 1990, Kerr 1999, Omari and Maclean 2015). Intensive forest management and biomass harvesting in these historically dead wood-dependent ecosystems could significantly decrease the amount and quality of deadwood present, which could lead to losses in habitat, reduce carbon storage and impact a broad suite of ecosystem services (Venier *et al.* 2015). These effects have been observed in regions outside of North America (*e.g.*, Scandinavian countries) where intensive forestry has been practiced for centuries. As an example, reduction in deadwood has been identified as a major contributor to reductions in species diversity, such as in Sweden where it's loss represents the primary threat to more than 60% of 739 threatened invertebrate forest species (Berg *et al.* 1994).

Interest in forest biomass harvesting for woody biomass energy production is increasing globally. Informed policy that supports sustainable biomass harvesting will be necessary in order to maintain recruitment of deadwood to ecosystems in support of biodiversity conservation of deadwood-dependent species (Berch *et al.* 2011). Tree species, state of decay, and piece size appear to influence the use of deadwood among different groups of species. Recruitment (i.e., long-term supply of deadwood) of deadwood that includes the full suite of these factors may prove to be lacking after biomass harvesting (Bunnell and Houde 2010). Of particular importance is deadwood volumes in later stages of decay that provide more diverse habitat for many species (Berch *et al.* 2011).

Maintaining deadwood thresholds within the confines of forest management objectives will be essential to ensure sustainable deadwood recruitment. As part of this

assessment, quantifying the rate of change between deadwood decay classes, and how it differs between species, across soil moisture regimes (MR), and in various macroclimates will help in setting these thresholds and informing policy within an adaptive management framework (Titus *et al.* 2010). In order to obtain these data, a clearer understanding/definition of decay classes is needed beyond the currently used, field-based qualitative assessments.

OBJECTIVES AND HYPOTHESES

A fundamental issue in dead wood modelling is distinguishing between deadwood decay classes. Decay classification commonly occurs in the field through qualitative, non-destructive methods. This classification system is largely based on visual characteristics of the surface condition of the log (Bunnell and Houde 2010, Söderström 1988, Hofgaard 1993). Although decay classes may be classified by their qualitative characteristics, the quantitative metrics (*e.g.*, wood density, percent of bark remaining, ratios of sound versus rotted wood, cation exchange capacity, C:N ratios) obtained from further, more destructive measurements and analysis would supplement the field measurements that would provide for a more robust classification system. We predict that upon further assessment of their quantitative metrics, decay classes one and five will remain in their current classifications, while the middle classes, based only on the field-based, qualitative measurements, will often shift classes based on similarities in their physical and chemical properties. This analysis may suggest that decay classes two,

three and four may be reclassified into a single middle decay class if differences in their quantitative metrics are found to be insignificant. We also predict that the decayed hardwood samples will require more refined classification classes than the conifer samples largely due to the different internal structures of each and how white-rot (hardwood) versus brown-rot (conifer) fungi breakdown the internal wood structure. Since this thesis will only focus on the establishment (Time 0) data for a longer-term temporal wood decay study, we will be unable to assess differences in decay rates between sites of different moisture regimes as part of this thesis. It is anticipated that moisture regime will be a significant determinate factor controlling the time required for given log pieces to move into successive decay classes, but is beyond the scope of the current thesis. To quantify decay classes, this thesis will compare quantitative metrics of hardwood and conifer deadwood samples, representing the standard five decay classes collected from 18 study sites that cover a broad range of soil moisture regimes (dry, fresh, wet) located in two boreal ecoregions (Lake Nipigon and Lake Abitibi) within the Boreal Shield ecozone of northern Ontario.

LITERATURE REVIEW

THE CONTRIBUTION OF DOWNED WOODY DEBRIS TO FOREST CARBON

STORAGE

To manage and sustain carbon pools stored in forest ecosystems, there needs to

be a better understanding of the rates of deadwood decay across different forest types

and for a variety of different species (Herrmann *et al.* 2015). Distinctions between the

carbon stored in different tree species and how this varies as deadwood transitions

through decay classes is also critical to expand upon the current knowledge that is

largely based on expert opinion (Rock *et al.* 2008, Zell *et al.* 2009). Research has been

conducted to look at the importance of snags (standing dead volumes) in global carbon

pools (Hilger *et al.* 2012), yet similar research is currently lacking for downed woody

debris (DWD). A distinction between these two types of dead wood in terms of their

relative contributions to carbon stocks is of interest as downed woody debris tends to

decay at faster rates than standing snags (Harmon *et al.* 1986).

The development of a more robust wood decay classification system by

incorporating quantitative metrics in addition to the qualitative field measurements

should provide better ecosystem-level estimates of deadwood carbon pools. Field

classifications based only on visual and sensorial features do not take into account the

likely variability associated with internal conditions of the log that may not be visible on

the log surface (Herrmann *et al.* 2015). Commonly, decay classification in the field is used to determine DWD mass and C content based on average wood densities, measured volumes, and carbon concentrations in solid wood (Grove *et al.* 2009). This method of calculating ecosystem-level C pools can lead to significant errors without proper consideration of internal features that may alter the predicted density of the wood and C concentrations differences amongst different log components (*i.e.*, bark, solid wood, rotting wood of varying proportions) (Herrmann *et al.* 2015). This type of error can be greatly reduced by sampling for internal density through drill resistance methods (Kahl *et al.* 2009) or cookie sample collection and more detailed chemical analysis weighted by component.

ROLE OF DWD IN NUTRIENT CYCLING

Decomposition of organic forest matter, such as CWD, drives the nutrient recycling process, as nutrients are often released and returned to/ made available within the ecosystem (Aber and Melillo 1991). The relatively slow and steady decomposition of CWD provides essential nutrients to stands after disturbance until they are able to self sustain (Wiebe 2012). For CWD, this cycling of nutrients often begins with the immobilization of some essential nutrients such as nitrogen, through consumption by decomposer microbes (Harmon *et al.*1994, Moore *et al.* 2006, Herrmann and Prescott 2008). Concentrations of a variety of nutrients vary within CWD throughout the decay process as CWD acts as a sink or source for each within the ecosystem.

Although CWD can act as a relatively long-term sink for forest carbon (Guo *et al.* 2006), it can also be a source through release (Wang *et al.* 2002). Mass of CWD is primarily lost through carbon loss, as within-log carbon is released throughout the decay process. Carbon compounds in wood are mostly in the form of cellulose or lignin, allowing for carbon to be released through fragmentation of these compounds by basidiomycete fungi (Wiebe 2012). This release of carbon contributes to a carbon dioxide flux in forests (Wang *et al.* 2002). Carbon release varies throughout the decay process and is commonly slow in early stages of decay, more rapid in the middle stages often peaking in decay class 4 (Wiebe 2012), and finally slows down again in the later stages of decay (i.e. decay class 5) (Yatskov *et al.* 2003, Zell *et al.* 2009, Wiebe 2012).

Concentrations and content of nitrogen and phosphorous in decaying logs tend to increase initially with increasing mass loss, and as a result, CWD (particularly softwood CWD) may be a net sink for the two nutrients for as much as several decades (Means et al. 1992; Alban and Pastor 1993; Busse 1994). In later stages of decay, nitrogen content stops increasing as it begins to be released from the wood (Wiebe 2012). CWD can play a role in altering nitrogen availability in the soil directly beneath it, thus influencing nitrogen dynamics. The dead biomass of CWD also provides a pool of available soil nitrogen for plant uptake (Harmon *et al.* 1986). Since plants cannot uptake organic nitrogen, it must be made available through mineralization and converted to available forms such as ammonium (NH_4^+) and ammonia (NH_3). Nitrogen can be made available by soil microorganism activity in CWD. CWD can also host nitrogen-fixing bacteria that contribute to nitrogen availability in some ecosystems (Wiebe 2012).

Although the commonly accepted trend is that phosphorous concentration and content increases in decaying logs throughout the decay process, patterns of

phosphorous release are quite variable (Wiebe 2012). Phosphorous loss or increase may be associated with its initial concentrations within CWD. For example, Moore *et al.* (2006) suggest that CWD with high initial concentrations of phosphorous lost phosphorous during the decay process, while CWD with low initial concentrations retained it.

RELATIONSHIP BETWEEN SPECIES AND DECAY RATES

Decomposition may be influenced by the biological, physical, and chemical properties of the decaying wood. These properties change throughout the decomposition process and result in decreases in dimension and mass (Herrmann *et al.* 2015). Wood properties across tree species are known to vary and may lead to differences in rates and patterns in the decay process (Harmon *et al.* 2000, Mackensen and Bauhus 2003, Yatskov *et al.* 2003). Determining relationships between species and decay rates, therefore, is important for classifying decay characteristics, particularly when scaling up across large geographic areas. Provincial species-based forest inventories are collected across Canada making species a potentially useful parameter for classifying decay (Hilger *et al.* 2012).

Herrmann *et al.* (2015) found in a study of three common European species in Germany that the average decomposition rate of the hardwood species (*Fagus sylvatica* L.) was significantly faster when compared to that of the softwood species (*Picea* abies (L.) H. Karst. and *Pinus sylvestris* L.) when evaluated for all sites and diameter classes.

The study sites varied in altitude to represent a climatic gradient with sites varying in soil type, average annual temperature, and annual precipitation. In their study, *P. abies* and *P. sylvestris* took 21 and 22 years, respectively, to decay to 50% of their initial mass while *F. sylvatica* took only 13 years to reach this same level of decomposition. Although the initial rates of decay for softwood species were similar up until 18 years, the amount of decay in *P. abies* was significantly greater by year 36. Other studies have reported similar results for a variety of softwood and hardwood species measured in different locations (*e.g.*, Weedon *et al.* 2009, Russell *et al.* 2014).

Decay Rates Associated with Brown vs. White-Rot Fungi

Decomposition of DWD is driven mainly by microbial activity, although leaching, physical weathering and faunal activity are also responsible for some fragmentation of DWD (Harmon *et al.* 1986, Cornwell *et al.* 2009). The type of fungi present to decay the wood can alter decay rates in DWD (Harmon 2009). Most notably, whether wood-rotting basidiomycetes are present in the form of brown-rot versus white-rot fungi can determine the degree to which lignin is degraded. In this case, white-rot fungi have been shown to degrade lignin, whereas brown-rot fungi primarily breakdown cellulose (Gilbertson 1980). Lignin is resistant to biological, chemical, and mechanical decomposition. The concentration of lignin varies between species, and is generally higher in softwoods than hardwoods (Martínez *et al.* 2005). Furthermore, brown-rot fungi are most commonly responsible for the degradation of softwood species. It decays

wood with both non-enzymatic and enzymatic cellulose degrading systems but generally no lignin degrading enzymes are involved. Decay of hardwood species by white-rot fungi can result in a variety of wood decay patterns. Decay may occur in a uniform or pocket rot pattern when caused by white-rot fungi. Since white-rot fungi have lignin degrading enzymes in addition to the cellulolytic enzymes produced by brown-rot fungi, they have the ability to decay the entire wood structure when environmental conditions are right (Goodell *et al.* 2008). The presence and activity of this type of fungi may, therefore, influence both the decay rates of DWD and the endpoint of the decomposition process. Since hardwoods are most commonly affected by white-rot fungi, and have low lignin concentrations, it can be anticipated that they would decay more rapidly than their high lignin, brown-rot colonized softwood counterparts. Softwoods cannot be completely degraded if brown-rot fungi only decay them, meaning residues will be left behind and become an important constituent of stabilized Soil Organic Matter (SOM) (Harmon 2009). However, these generalizations may not always hold true under different conditions experienced across various forest ecosystems.

Structure and Composition of DWD Species

Spruce and pine logs often show low variation in their decomposition rates, which may be indicative of a higher resistance and more simplified decomposition process. For example, softwoods do not demonstrate the variable spatial pattern of solid and highly decomposed patches of wood adjacent to one another that are commonly

exhibited in hardwood logs (Herrmann and Bauhus 2012, Herrmann *et al.* 2015). Log respiration experiments conducted by Herrmann and Bauhus (2012), supported this statement as *F. sylvatica* had much higher variation in log respiration rates compared to those in either *P. abies* or *P. sylvestris*.

The initiation of decomposition in DWD is, however, dependent on microbial and invertebrate colonization (Harmon *et al.* 1986). Without facilitation through mechanical injury, colonization of the sapwood by these organisms may not occur until the bark has dried and cracked, or been penetrated by invertebrates digging galleries and/or microbes overcoming bark defenses (Käärik 1974, Ausmus 1977, Schowalter *et al.* 1992). Variable structure, composition, and dimensions of the bark could therefore further influence initial decay rates among tree species (Freschet *et al.* 2011). The bark of living trees functions to repel insects, pests, and pathogens, and this ability is likely maintained to some extent for a period of time after a tree dies. Both the thickness and resistance of a tree's bark, therefore, may limit microbial access to the wood substrate slowing the rate during the early stages of decay. However, the opposite may also occur where in some cases the bark moderates the internal microclimate of the DWD. In particular, intact bark may act as a biological sealant, thus causing high moisture retention within the DWD, which, in turn, could increase and create conditions that favour internal decomposition while the bark stays intact. This pattern of high internal moisture and decay is common in northern birch species (*Betula* spp.) (Cornwell *et al.* 2009).

The differences in structural composition between hardwoods and softwoods may also influence the way fungi colonize the wood. Specifically, the differences in xylem structures between hardwoods and softwoods could facilitate a more rapid spread

of fungi within hardwoods. The xylem structures in both hardwoods and softwoods are connected by pits, which act as barriers that restrict the spread of fungi between each individual element. In the case of hardwoods, the vessel elements can be much longer than the tracheids in softwoods (Cornwell *et al.* 2009). The short length and greater abundance of tracheids connected by pits in softwoods tends to result in the slower spread of fungal propagules compared to hardwoods (Boddy 2001). In addition, the high proportion of parenchyma in the sapwood of hardwoods, and the associated high nitrogen and starch contents in these cells, may also accelerate microbial decay processes (Evert and Esau 2007, Weedon *et al.* 2009). Deposits of extractives commonly found in the heartwood of trees, such as gums, tannins, and oils, can also play an important role in slowing the decay of the inner wood compared to the sapwood. If these extractives are active within the heartwood, a high heartwood to sapwood ratio may reduce decomposition rates (Cornwell *et al.* 2009). Tannins and lignin inhibit microbial decomposition, so species with high contents of these may be more resistant to decay (Day *et al.* 2007).

MOISTURE REGIME/ECOZONE AND DECAY RATES

Microclimate variables such as wood temperature and moisture have been found to influence the decomposition rate of DWD (Herrmann *et al.* 2015). The influence of wood moisture and temperature on deadwood decomposition has been studied via lab incubations by many, including Herrmann and Bauhus (2012). In these studies, it was

found that microclimate conditions like temperature and moisture contribute to short-term DWD mineralization in addition to substrate specific variables such as tree species, decay stage, and diameter. Of these two climatic variables, wood moisture tended to have a greater influence on mineralization than wood temperature, and these moisture effects were more pronounced in beech than in softwood species (Herrmann and Bauhus 2012). Hagemann *et al.* (2010) reported similar results from an *in situ* study in a black spruce forest in Labrador, Canada. In this study, they also found wood moisture content to be the dominant environmental control over DWD respiration, and that DWD respiration rates were lowest at wood moisture contents below a threshold level of 40%. Another field study by Herrmann *et al.* (2015) found that average annual temperature had significantly less impact than precipitation on the wood decay process. Herrmann *et al.* (2015) reported in their *in situ* deadwood study of *Fagus sylvatica* L., *Picea abies* (L.) Karst. and *Pinus sylvestris* L. in Germany that only 2% of the variation in mass remaining could be explained by average annual temperature. Certainly, interactions between climatic and substrate specific variables occur in forest ecosystems, and, therefore, should be considered together to improve our wood decay modelling efforts at the forest ecosystem level.

The response of decomposers to within-log moisture content is important to understand in order to more accurately model temporal patterns of DWD decay. When aerobic conditions dominate, deadwood decomposes through activity by brown-rot and white-rot basidiomycete fungi (Hicks and Harmon 2002, Schmidt 2006). Decomposition rates are altered as wood makes ground contact and increases in moisture content (Moroni *et al.* 2015). There is a threshold point at which moisture content increases so much that the pores of DWD fill with water, creating anaerobic conditions within the

wood. As oxygen becomes limiting, decomposition by brown and white-rot fungi decreases, which will slow the rate of decay (Harmon 2009). When this point is reached, decomposition becomes limited to activity by soft-rot ascomycetes fungi and bacteria, resulting in reduced rates of decay (Moroni *et al.* 2015).

Within-log moisture content is influenced by climatic and site conditions such as precipitation, temperature, and solar radiation. Certain climatic conditions can have a significant influence on decay rates. For example, warm and wet climatic conditions often create conditions optimal for decay compared to cold/wet or warm/dry conditions (Herrmann *et al.* 2015). Certain climatic extremes can also limit decomposition such as xeric sites where low moisture levels are limiting (Fasth *et al.* 2011). In contrast, deadwood can be preserved, or almost free of decay in very wet sites such as peat bogs where colonization by decaying agents is limited (Eckstein *et al.* 2009, Edvardsson *et al.* 2012).

RATE CHANGES THROUGH THE DECAY PROCESS

Herrmann *et al.* (2015) found that residence times per decay class increased from decay classes 1 to 4. The increase in residence time was greater in the softwood species compared to that of the hardwood species. Residence times in the hardwood species ranged from 6.7 years in decay class 1, to 21.6 years in decay class 4. The range in residence times per decay class for softwood species was even greater, ranging from 6 years in decay class 1 to 51.6 years in decay class 4. Herrmann *et al.* (2015) also found

the average dry density values to differ across species and decay classes. In decay class 3, dry densities of the hardwood species were significantly different from the softwoods, while no significant differences were found between species in decay class 4. Variation in wood density is commonly high in middle decay stages, as found by Herrmann *et al.* (2015) in the samples measured from decay class 3 for all species. Greater variation in density among this decay class was most pronounced in the hardwood species. These findings indicate that middle decay classes and hardwood species may require the most reclassification based on their quantitative variation. This could also indicate that merging middle decay classes into a single decay class may be unsuitable in some cases.

MATERIALS AND METHODS

Study Sites

A total of eighteen study sites were selected across northern Ontario to represent a broad range of environmental conditions that DWD decays in. *A priori* site selection criteria included: 1) 9 sites in each of two contrasting ecoregions (Lake Nipigon – northwestern Ontario; Abitbi Plains – northeastern Ontario), 2) within each ecoregion, 3 replicate sites for each of three soil moisture regimes (dry: MR 1-2; fresh: MR 3-5, wet: MR 7-8) were selected. The locations of these study sites are shown in Figure 1, and climatic norms for the two ecoregions are described in Table 2. Where possible, sites were selected and located around provincial growth and yield permanent growth plots to

capitalize on existing site and stand data (see Figure 1). On sites selected without existing stand/site data, the site/soil attributes were assessed to confirm the site was representative of the desired moisture regime. Dry sites were characterized by coarse-textured outwash sands, dominated by jack pine. Across fresh sites, the dominant soil texture was typically loams, and the species composition varied in mixtures of conifer and hardwood species. Wet sites were dominated by black spruce on organic soils. Detailed site/soil descriptions are provided in Table 1.

Table 1. DWD site/stand descriptions for the eighteen study sites.

Site Name/ Location	Ecoregion	Fresh/Wet/ Dry	Moisture Regime	Ecosite	Dominant Soil Texture	CF Content	Species Composition	Age (Years)
ERMTO	NW	Dry	0	NW20	Coarse Sandy	10	$Pj_{80}Sb_{10}Bw_{10}$	84
Sandbar	NW	Dry	0	NW14	Coarse Sandy	10	$Pj_{50}Sb_{20}Po_{10}Bw_{10}Bf_{10}$	119
Victoria	NW	Dry	1	NW14	Coarse Sandy	10	$Pj_{40}Sb_{30}Po_{20}Pr_{10}$	84
Shallownest	NW	Fresh	2	NW20	Fine Sandy	50	$Sb_{70}Pj_{30}$	109
Escape	NW	Fresh	4	NW21	Sandy Loam	30	$Sb_{50}Po_{20}Pj_{10}Bf_{10}Bw_{10}$	99
Escape 2	NW	Fresh	2	NW20	Sandy Loam	50	$Pj_{40}Po_{30}Bw_{20}Sb_{10}$	84
LTSP Area 6	NW	Wet	8	NW35	Organic	0	Sb_{100}	99
Keni Lake	NW	Wet	8	NW35	Organic	0	$Sb_{90}La_{10}$	89
LTSP Area 4	NE	Wet	6	NW31	Organic	40	Sb_{100}	146
Sultan	NE	Dry	1	NE2	Coarse Sandy	10	$Pj_{80}Sb_{20}$	56
Nimitz	NE	Dry	0	NE2	Loamy Medium Sand	20	$Pj_{90}Sb_{10}$	92
Island Lake	NE	Dry	0	NE2	Medium Sand	10	Pj_{100}	51
KM 38	NE	Fresh	3	NE3	Coarse Loamy	15	$Pj_{50}Po_{40}Bw_{10}$	53
Junction	NE	Fresh	1	NE4	Coarse Sandy	0	$Pj_{70}Po_{20}Sb_{10}$	61
Lower Fresh	NE	Fresh	2	NE2	Fine Loamy	0	Pj_{100}	66
KM 4	NE	Wet	8	NE11	Organic	0	$Sb_{90}Pj_{10}$	99
Shep Morse	NE	Wet	8	NE12	Organic	0	$Sb_{60}La_{20}Pj_{10}Po_{10}$	116
Highway	NE	Wet	8	NE8	Organic	0	$Sb_{90}La_{10}$	101

Table 2. Description of the climatic norms for the Lake Nipigon (NW Ontario) and Lake Abitibi (NE Ontario) ecoregions (Crins *et al.* 2009).

	Lake Nipigon ER (NW)	Lake Abitibi ER (NE)
Average Annual Precipitation Range	654-879 mm	652-1029 mm
Mean summer rainfall	231-298 mm	220-291 mm
Avgerage annual Temperature	-1.7°C to 2.1°C	-0.5°C to 2.5°C
Mean Growing Season Length	161 to 182 days	167 to 185 days

Short-term (1 month) results collected from the HOBO microclimate data loggers installed at each site highlight similarities and differences in soil microclimate conditions in the study sites. For example, average soil temperature revealed average soil temperature was slightly, albeit significantly ($p < .0001$), higher in northeast sites (11.3°C) compared to northwest sites (10.1°C) (Figure 1) (See Appendix II). As might be expected, average soil temperature was highest in the dry sites, and lowest in the wet sites across both regions.
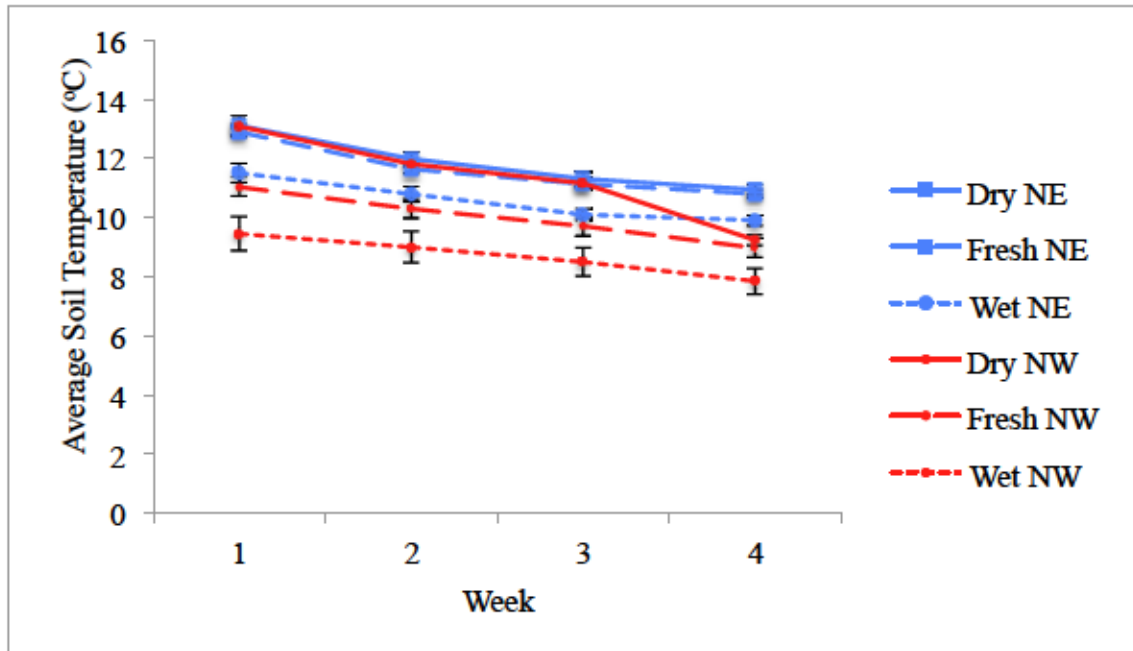
Figure 1. Average weekly soil temperature (°C) for dry, fresh, and wet sites in the northeast and northwest regions for the period of September 14th (week 1) to October 12th, 2016. Vertical bars represent standard error bars.

Average soil moisture did not vary significantly between regions (p=.2996). However, average soil moisture remained significantly higher (p<.0001) in wet sites, compared to dry and fresh sites. There was, however, a significant moisture regime*region interaction (p<.0001) suggesting the moisture regime differences in soil moisture did vary depending on region. The wet moisture regime sites had the highest in soil moisture content across both regions, during the 4-week sample period. However, in the northeast region, the "dry" sites had higher average soil moisture contents compared to fresh sites. The opposite was true in the northwest sites where the mean soil moisture content was greater in fresh versus dry sites (Figure 2).
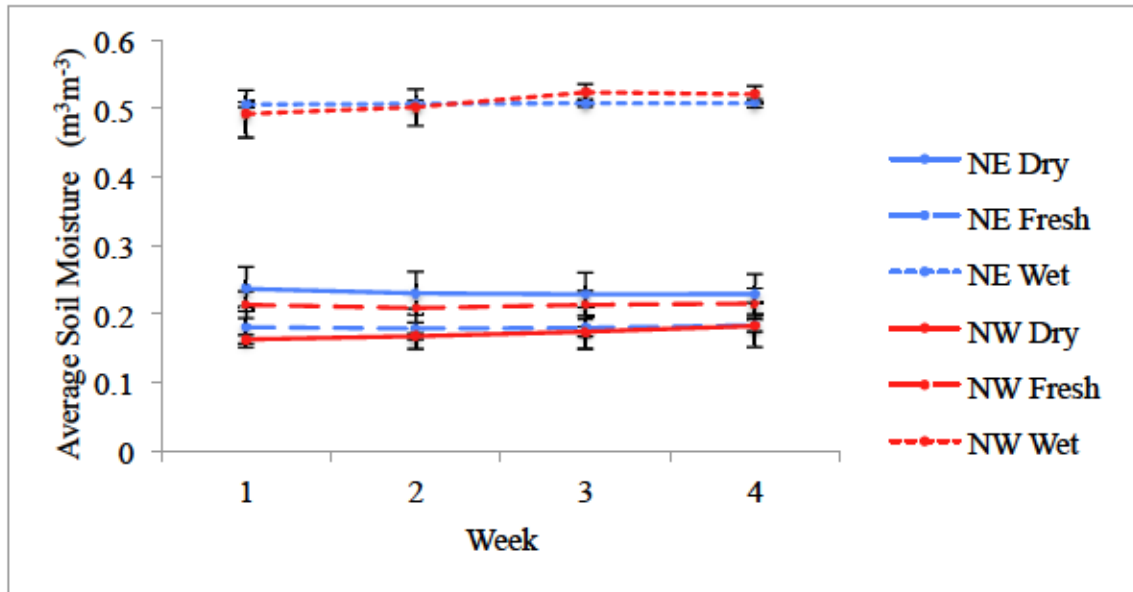
Figure 2. Average weekly soil moisture content (m^3m^{-3}) for dry, fresh, and wet sites in the northeast and northwest ecoregions for the period of September 14th (week 1) to October 12th, 2016. Vertical bars represent standard error bars.

DWD Selection/Measurement/Sampling

At each site, 30 individual DWD log bolts were selected and permanently marked for resampling. These log bolts represented 3 hardwood and 3 softwood replicate logs for each of the 5 decay classes, as described in Table 3. Trembling aspen (*Populus tremuloides* Michx.) logs were chosen for hardwood samples across all moisture regimes, while softwoods consisted mainly of black spruce on wet sites, and jack pine (*Pinus banksiana* Lamb.) on fresh and dry sites. In the case of the wet and dry sites, representative aspen logs across all decay classes were commonly not found *in situ*, so in these cases, logs were brought in from nearby sites and carefully placed on the forest floor in close proximity of the other selected logs. The logs chosen were to be a minimum of 7cm in diameter on at least one end, with an initial length of 1.50m. This

target was not always possible for the decay class 4 and 5 logs. In the end, only 6 log

bolts out of the 540 bolts selected/sampled were less than 1m in initial length. In some

cases, standing dead snags were felled and used for decay class 1 logs when 3 replicates

of DWD DC1 logs could not be found.

Table 3. Criteria used for classifying DWD by decay class in the field (Renvall 1995, Sollins 1981).

Decay class	Integrity of Wood	Bark	Other Characteristic
1	Solid wood	Intact	May have needles or leaves indicating recent mortality
2	Solid wood	Beginning to slough off	No indication of recent mortality
3	Outer layers of wood beginning to feel soft, core remains solid	May be present or absent	
4	Outer layers soft, can penetrate at least 1 cm into the wood surface but not all the way through	Variable (typically not present)	
5	Solid wood less than 25% of the sample	Variable (typically not present)	

Once located and permanently tagged, the decay class, lower and upper

diameters, initial length, species, percent moss cover, percent bark cover, presence of

fruiting bodies (yes/no), and length of the log elevated off of the ground were recorded

for each sample. In some cases, samples that had a large portion of their length elevated

off the ground were adjusted to ensure consistent ground contact across all samples.

After measurements were taken, a cookie was carefully removed from the end of each

sample The average diameter and width (based on 4 cardinal measurements) of the cookies were recorded (cookie volume calculated) and placed in paper bags for transport to the lab for further processing. Log bolt locations were mapped by recording the distance and bearing from a permanent centre stake to facilitate relocation over time for resampling.

Microclimate Monitoring

To monitor/contrast soil and near surface microclimate conditions at each of the study sites, HOBO H21-002 Micro Station Data Loggers (1 per site) were installed at a central location where the logs were identified/sampled (Figure 3). Each data logger had 2 soil temperature and 2 soil moisture probes inserted into the soil profiles at approximately 10cm in depth. In addition, an air temperature/relative humidity logger was installed at 1.5m off the ground attached to a nearby tree. All probes were programmed to take continuous readings 4 times per day (every 6 hours: midnight, 6am, noon, 6pm).

Figure 3. Hobo H21-002 Microclimate Data Logger site set up.

Laboratory Procedures

Once back in the lab, all samples were oven-dried at 50°C until constant weight was achieved, and total sample weight recorded. After total dry weight was determined, the samples were separated into their three main constituent components: bark, solid wood, rotted/decayed wood. Decayed wood was distinguished from solid wood based on the porosity, fragility, and in some cases, colour. Decayed wood was typically much softer and porous than solid wood, allowing it to easily crumble or break off of the solid wood portion. Decayed wood was also typically darker in colour than solid wood. Any unidentified fine particulate matter that did not clearly fall under one of these categories

was classified as chaff and weighed separately (Figure 4). Subsequently, subsamples were ground with a Whiley mill through a 20 mesh sieve to prepare them for carbon and nutrient analysis.
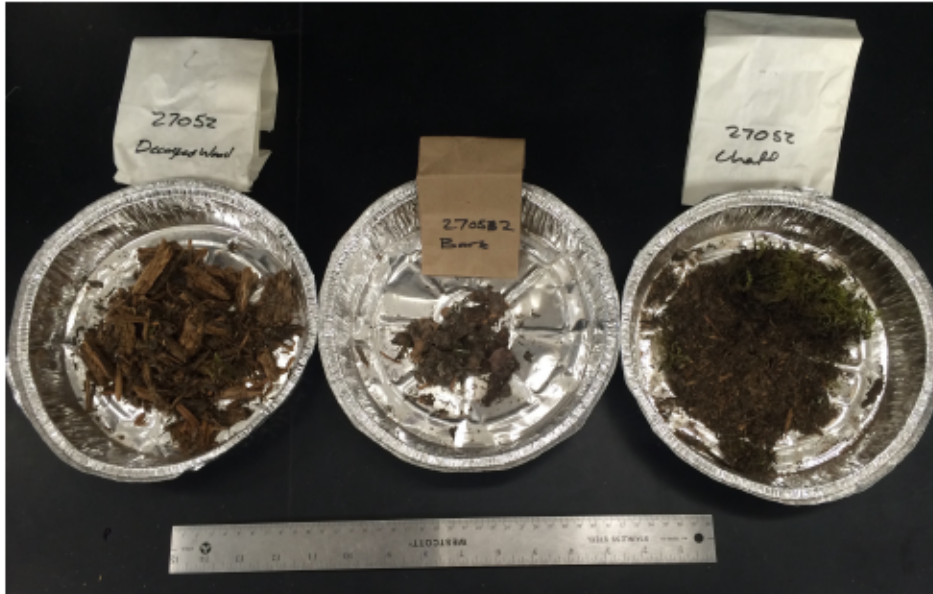
Figure 4. Deadwood sample separated into its three major components to allow for individual measurements.

For this thesis project, a subset of samples was analyzed to determine the carbon (C) and nitrogen (N) concentration, and C:N ratio by component. Overall mean weighted chemistry was calculated as well for C, N, and C:N. Concentrations of nutrients were quantified as a percent of the dry weight of each sample using a LECO CNS-2000 (LECO Corporation, St. Joseph MI). Three replicates of decay classes 1, 3 and 5 for softwoods and hardwoods were included from six of the eighteen sites. The subset samples came from one dry, one fresh, and one wet site from both the northwest and northeast regions. All three components of each sample (bark, solid wood, and decayed wood) were analyzed in this subset.

Physical Property Calculations and Statistical Approach

The quantitative values obtained in the lab for all samples were used in the primary linear model to quantify differences in decay classes across different moisture regimes, ecoregions, and species of DWD. The density data and percent composition by significant component (percent solid wood, percent decayed wood, percent bark, percent chaff) for all measured samples was analyzed as a 4-factor ANOVA using The GLM Procedure of SAS software using species, decay class, moisture regime, and block as factors. A series of ANOVAs were performed to evaluate the effect of species, decay class, and moisture regime on measures of density and the proportions of deadwood components. Student-Newman-Keuls (SNK) multiple range test (P=0.05) was used as the means separation test. Further analyses to investigate significant interactions were run through 1-way ANOVAs.

The data obtained from the analysis of the chemistry subset was analyzed in a separate linear model. A series of 2-way ANOVAs were performed using The GLM Procedure of SAS software for each deadwood component to evaluate the effects of species and decay class on the concentrations of carbon (C), nitrogen (N), and the carbon nitrogen (C:N) ratio. In order to examine the concentrations of nutrients in deadwood logs as a whole, total weighted averages for each of the chemical parameters were calculated. These weighted averages for C concentration, N concentration, and C:N ratio, were analyzed through a separate series of 2-way ANOVAs to examine the effects of species and decay class. Student-Newman-Keuls (SNK) multiple range test (P=0.05) was used as the means separation test.

The DISCRIM Procedure (SAS) was used to perform two canonical discriminant analyses. The first canonical discriminant analysis (CDA) was performed to determine the physical conditions of deadwood that provided the greatest degree of separation between the five qualitatively assigned decay classes. Reclassification of samples into five quantitatively derived decay classes provided an estimate of the accuracy of the derived discriminant analysis, and allowed for a comparison of how deadwood classifies based on qualitative and quantitative characteristics. The second CDA, included an additional three chemical variables to determine the physical and chemical conditions that provided the greatest degree of separation between decay classes. Because the subset of chemistry data only included DC 1, DC 3, and DC 5, reclassification of samples occurred only into these three decay classes rather than the full five as a result of the CDA. This quantitatively based reclassification provided an estimate of the accuracy of the derived discriminant function, based on both chemical and physical variables.

RESULTS

Based on preliminary analysis (*i.e.*, 4 factor general linear model with ecoregion, moisture regime, species, and decay class), ecoregion was found to be a non-significant factor (p>.30) for all ANOVAs run with the deadwood physical parameters, and as such, was removed from the model. All subsequent analysis were run as 3 factor models.

CHANGES IN PHYSICAL CHARACTERISTICS OF DEADWOOD

Density

The density (g cm^{-3}) of each deadwood cookie removed from the log bolts represents a combined contribution of existing wood components (*i.e.*, bark, solid wood, decayed wood) and would be expected to decline as deadwood decays. Based on the ANOVA results, significant differences in mean density occurred as a function of moisture regime (p<.0001), species (p<.0001), and decay class (p<.0001) (See Appendix I). In the case of moisture regime (MR), wood density remained significantly higher in logs sampled from the wet MR (0.2916 g cm^{-3}) compared to either dry (0.2683 g cm^{-3}) or fresh (0.2597 g cm^{-3}) MRs (Figure 5).
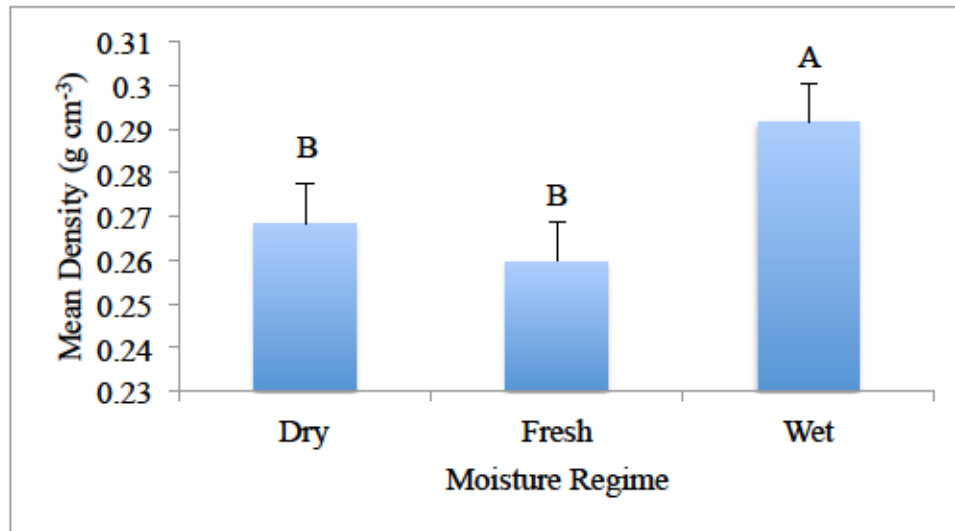
Figure 5. Differences in mean wood density values (g cm^{-3}) by moisture regime. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

Figure 4. Differences in mean wood density values (g cm^{-3}) by moisture regime. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

In terms of species differences, mean wood density for conifer logs (0.2884 g cm^{-3}) was significantly greater (p<.0001) than that of poplar logs (0.2581 g cm^{-3}) (Figure 6).
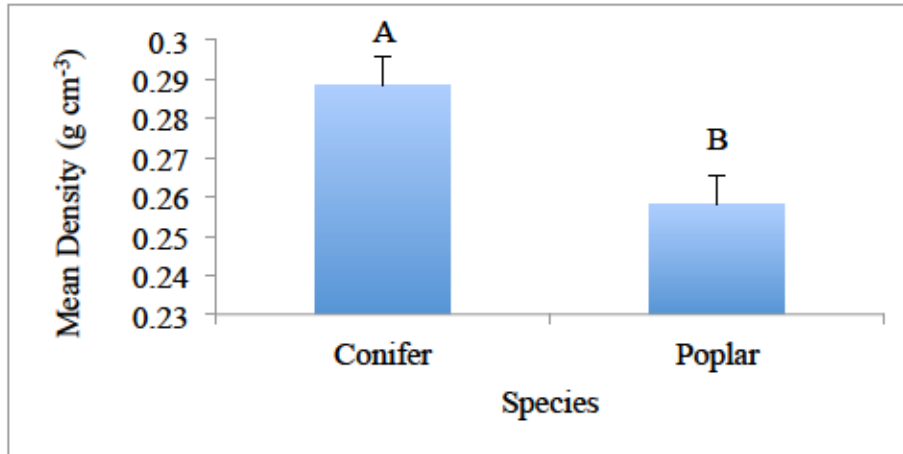
Figure 6. Comparison of mean wood density values (g cm^{-3}) as a function of species. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

The ANOVA did however reveal a significant moisture regime*species interaction (p=.0015), suggesting the species differences in wood density did vary depending on moisture regime. Further analysis confirmed that conifer deadwood density was significantly higher than that found in poplar (p<.0001) when comparing samples taken from the moister sites (fresh or wet sites). However, samples taken from the dry sites did not vary significantly in density between poplar and conifer samples (p=.6527) (Figure 7).
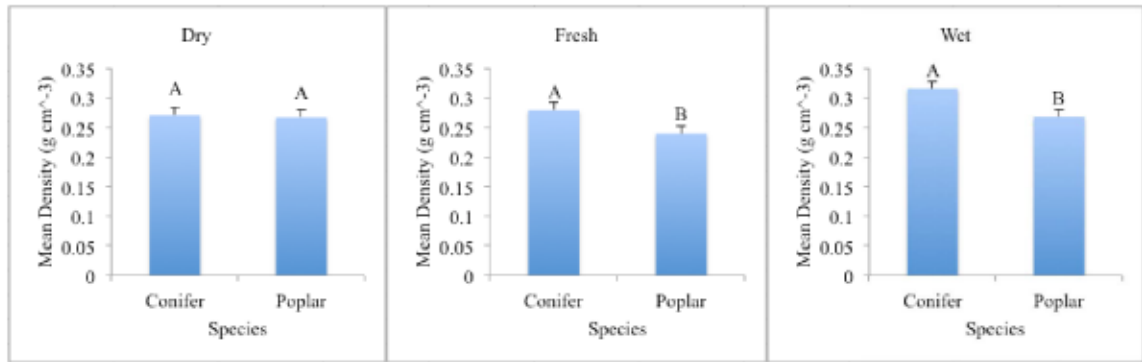
Figure 7. Species differences in mean wood density values (g cm^{-3}) as a function of moisture regime. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

Mean wood density declined significantly between each decay class (DC) along the DC continuum starting with DC 1 at 0.4147 g cm^{-3} and declining to nearly one-third the value in DC 5 logs at 0.1331 g cm^{-3} (Figure 8).
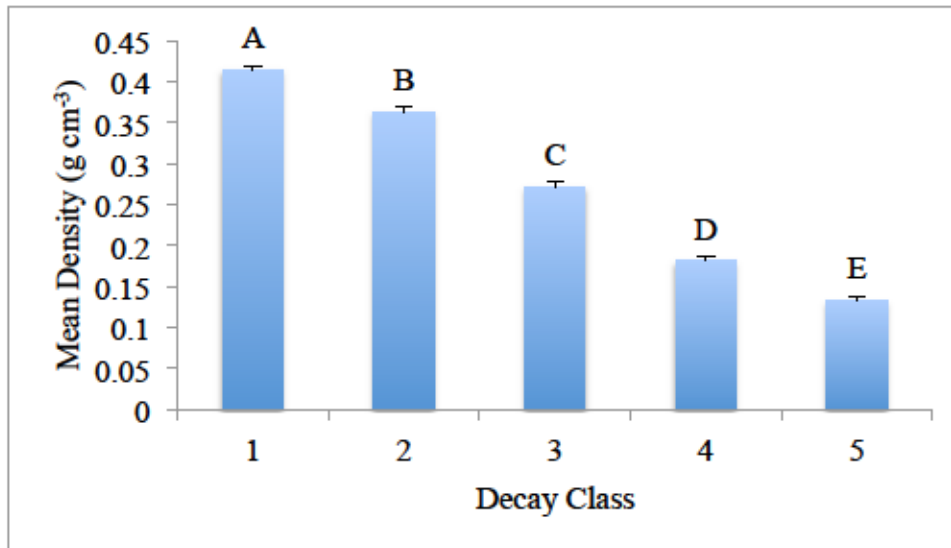
Figure 8. The gradient of mean wood density values (g cm^{-3}) along the decay class continuum. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

Proportions of Wood Components Along the Decay Class Continuum

The structural composition of each deadwood cookie removed from the log bolts was determined by measuring the proportion (%) that solid wood, decayed wood, and bark contributed to total log mass as modified by decomposition. Results from the ANOVAs (See Appendix I) conducted for each component revealed that there were significant shifts in component proportional contributions for all three components along the decay class continuum (p<.0001). Initially, solid wood represented nearly 85% of total log mass for DC 1 and DC 2, but then declined linearly through DC 3 (55%) to DC 5 (8%) as decomposition progressed (Figure 9). As would be expected, the opposite was true for decayed wood, with the percent contribution increasing from DC 1 to DC 5 (Figure 10). The loss of bark occurred quickly (*i.e.,* significant decline between DC 1 and DC 2), but then remained stable at 7-9% across the remaining decay classes (Figure 11).
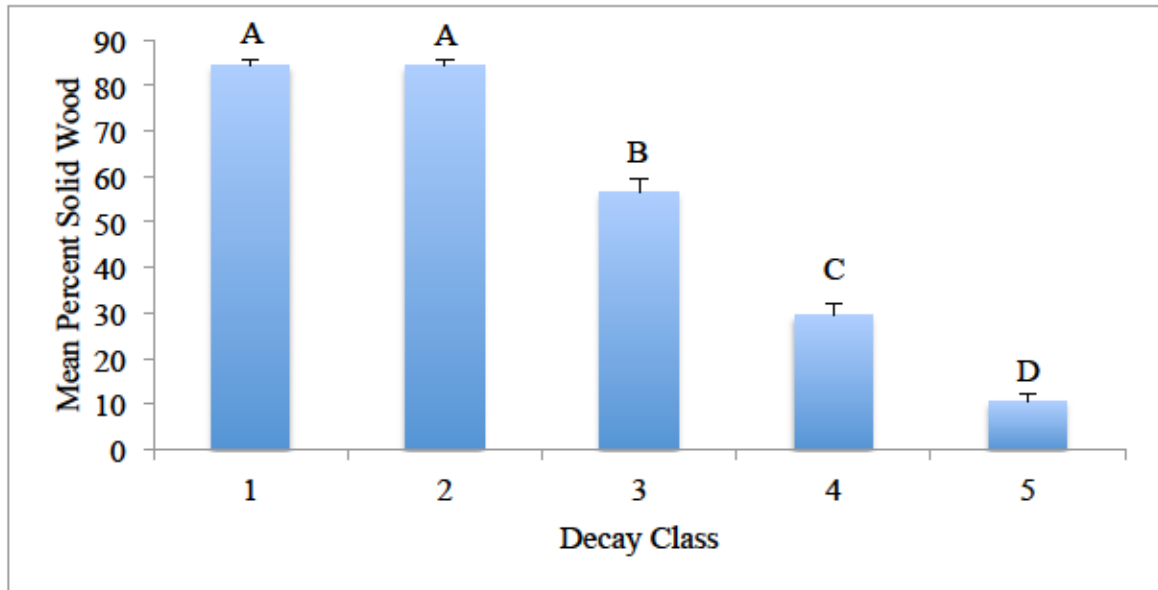
Figure 9. The gradient of mean proportion of solid wood (%) along the decay class continuum. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.
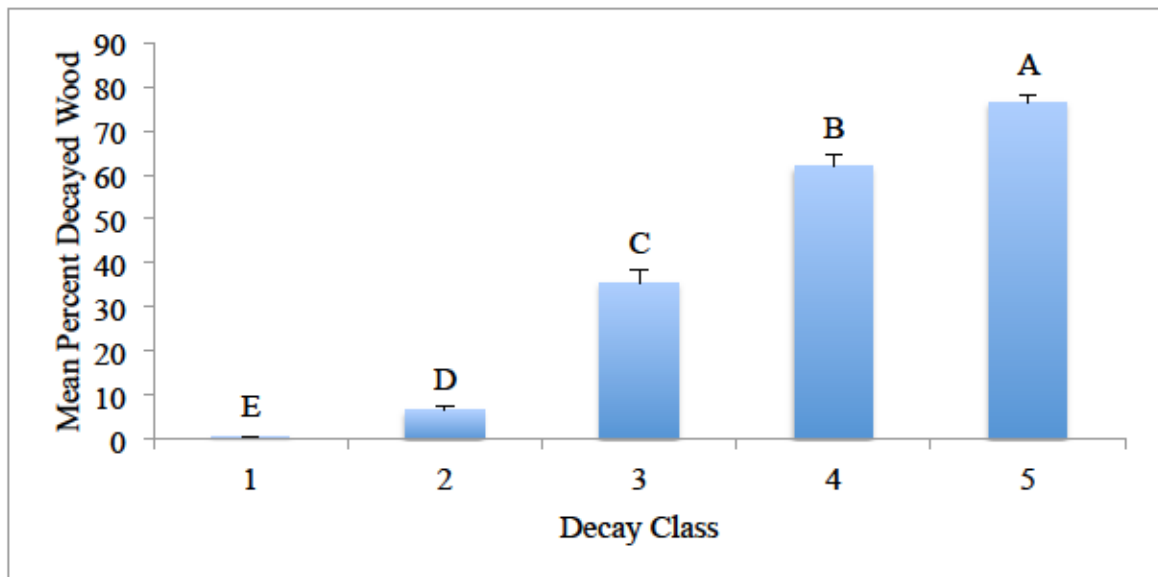
Figure 10. The gradient of mean proportion of decayed wood (%) along the decay class continuum. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.
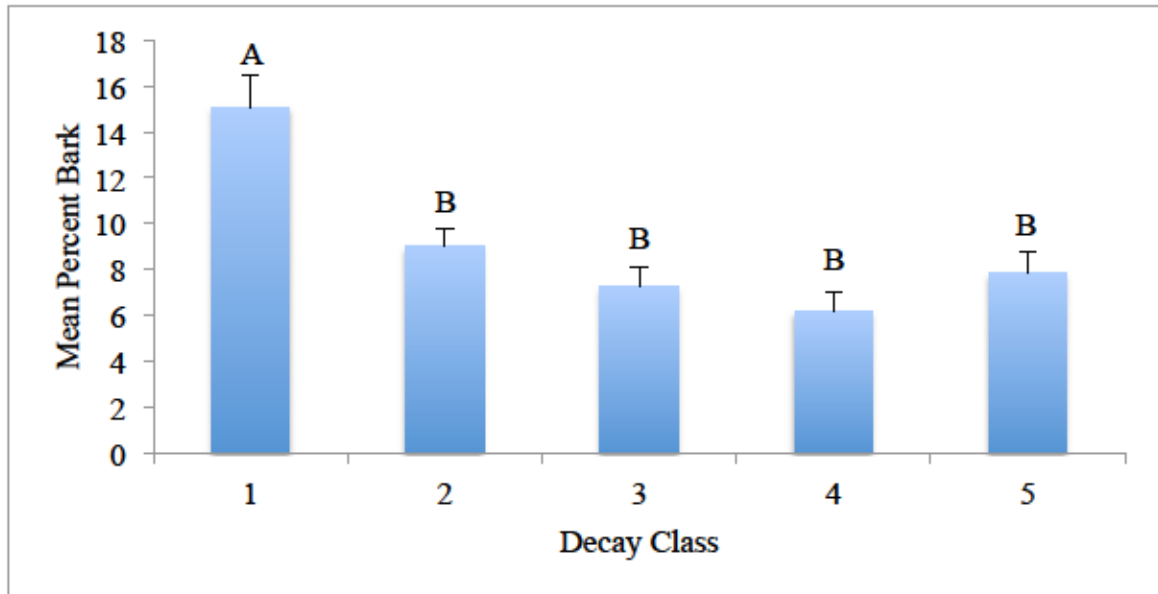
Figure 11. The gradient of mean proportion of bark (%) along the decay class continuum. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

The overall (species and DC combined) contribution to total log mass for both percent solid and decayed wood also differed significantly ($p=.01$ and $p=.005$, respectively) across moisture regimes. Results highlighted in Figure 12 (% solid wood) and Figure 13 (% decayed wood), suggest that decomposition (*i.e.,* as depicted by the shift of solid wood to decayed wood) is somewhat restricted (slowed) on both dry and wet sites. There was no significant difference ($p=.07$) in bark contributions across moisture regimes (data not shown), suggesting that bark loss maybe largely a mechanical process and unaffected by moisture conditions.
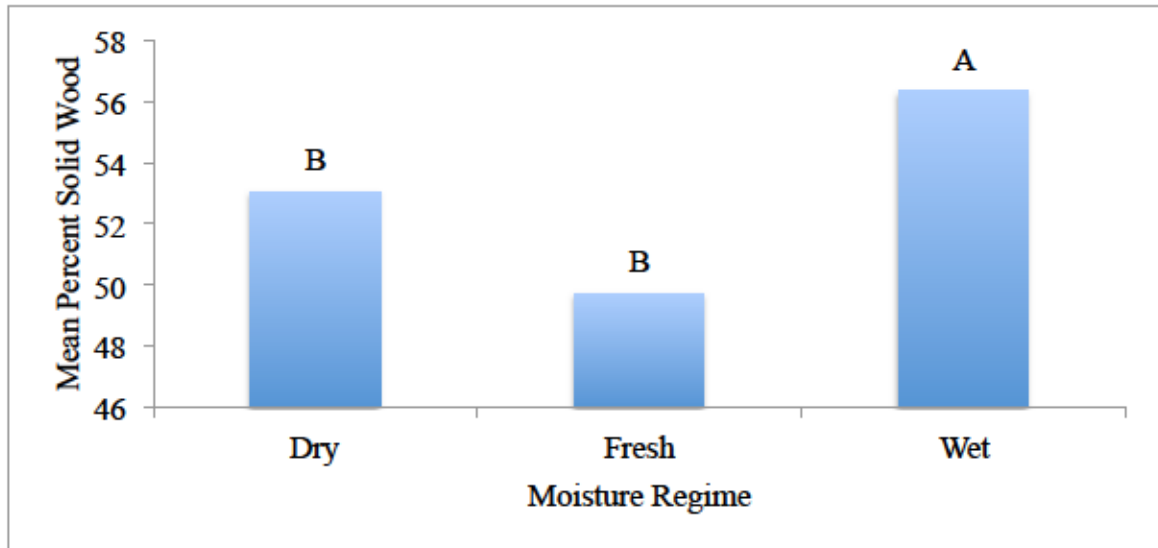
Figure 12. Differences in mean proportion of solid wood (%) by moisture regime. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.
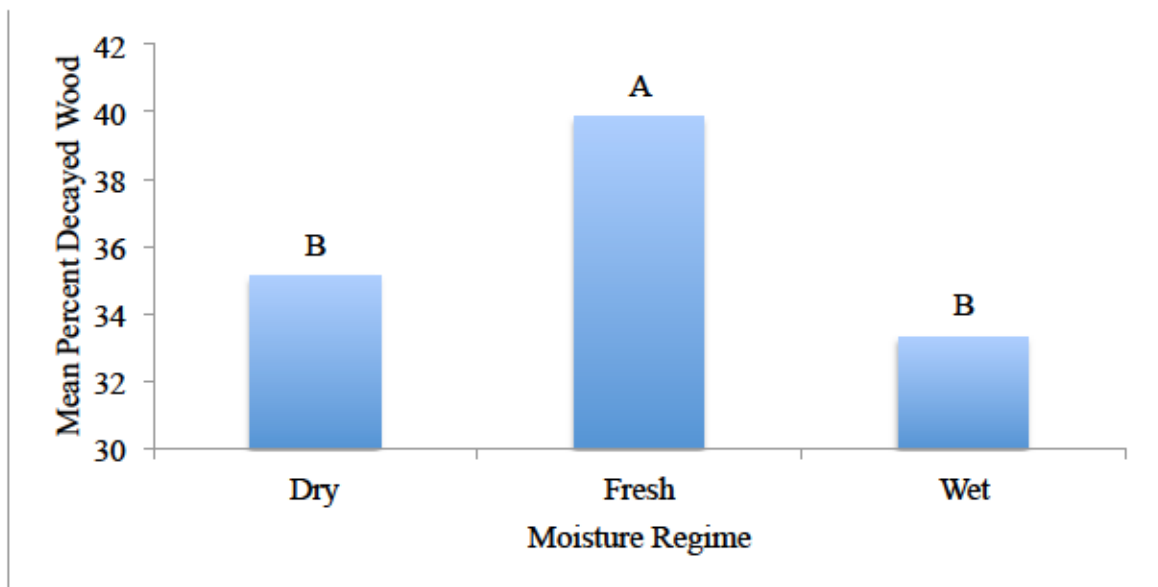
Figure 13. Differences in mean proportion of decayed wood (%) by moisture regime. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

In terms of species differences, the mean proportion of solid wood for conifer logs (55.45%) was significantly greater than that of poplar logs (50.66%). However, the opposite was true for the mean proportion of bark, for which poplar logs were significantly greater (12.33%) than conifers (5.79%).

The ANOVA did, however, identify a significant species*DC interaction for both the proportion of solid wood (p=.0093) and the proportion of bark (p < .0001), suggesting their proportions across decay classes differed depending on species. Further analysis revealed that the initial decline in solid wood (*i.e.,* DC 1 and DC 2) was slow between both species (Figure 14). For conifers, solid wood initially represented 90% of total log mass for DC 1 and DC 2, and then declined linearly from DC 3 (54.85%) to DC 5 (13.80%). Although solid wood represented less of the initial total log mass in poplar (DC 1 78.00%, and DC 2 79.43%) compared to conifers, poplar wood followed the same pattern of linear decline from DC 3 (57.94%) to DC 5 (7.08%).
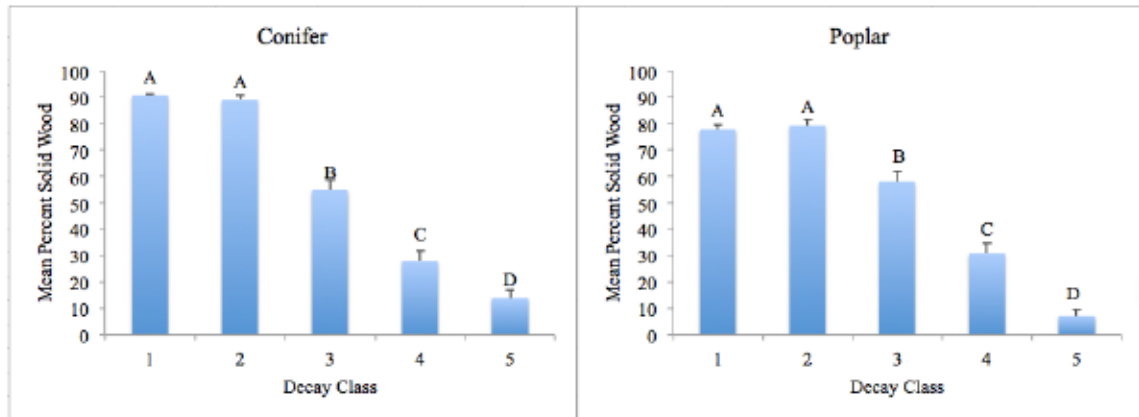
Figure 14. The gradient of mean proportion of solid wood (%) along the decay class continuum for conifer vs. poplar deadwood cookies removed from log bolts. Vertical bars represent standard error bars. Uppercase letters depict differences based on Student-Newman-Keuls (SNK) post-hoc means separation test.

Further analysis of the significant species*DC interaction for bark revealed that the loss of bark occurred quickly in conifer logs. The proportion of bark declined significantly between DC 1 (8.71%) and DC 2 (5.08%), but then remained stable across the remaining DCs (Figure 15). In poplar logs, no clear pattern was revealed across

decay classes apart from a rapid and significant loss of bark between DC 1 (21.43%) and DC 2 (12.90%). After this initial decline, the proportion of bark in poplar logs remained largely stable, apart from a minor, albeit significant, decline between DC 3 (10.22%) and DC 4 (10.04%).
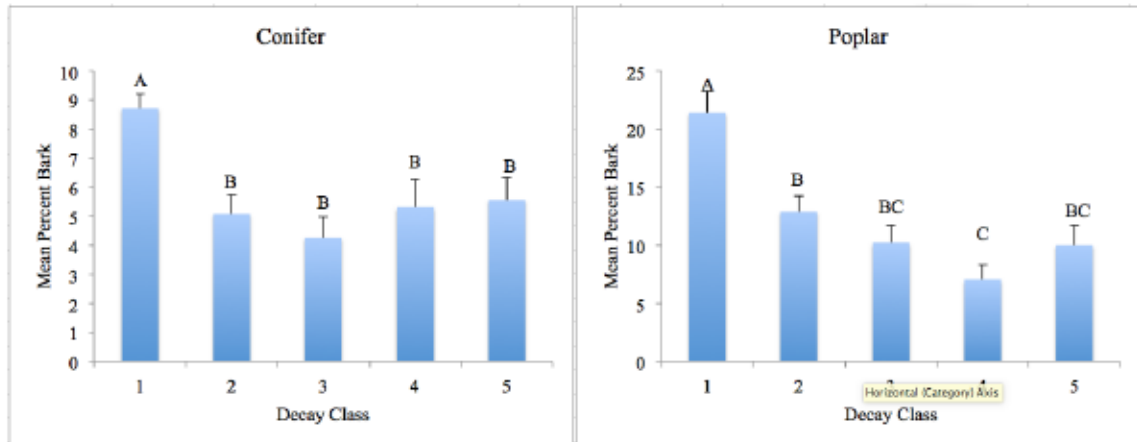
Figure 15. The gradient of mean proportion of bark (%) along the decay class continuum for conifer vs. poplar deadwood cookies removed from log bolts. Vertical bars represent standard error bars. Uppercase letters depict differences based on Student-Newman-Keuls (SNK) post-hoc means separation test.

The ANOVAs identified a significant moisture regime*DC interaction for the proportion of solid wood (p<.0001), the proportion of decayed wood (p=.0022), and the proportion of bark (p = .0002). The mean proportion of solid wood was initially (*i.e.*, DC 1 and DC 2) high across all three moisture regimes (Figure 16). In samples from dry and wet sites, the proportion of solid wood declined significantly between DC 2 (dry: 79.5%, wet: 88.2%) and DC 3 (dry: 61.7%, wet: 62.8%), and then continued to decline significantly in the remaining decay classes to DC 5 (dry: 7.6%, wet: 9.3%). After an initial decline from DC 2 (85.2%) to DC 3 (44.7%) and DC 3 to DC 4 (16.4%) on fresh sites, the proportion of solid wood stabilized and was similar between DC 4 and DC 5 (Figure 16).
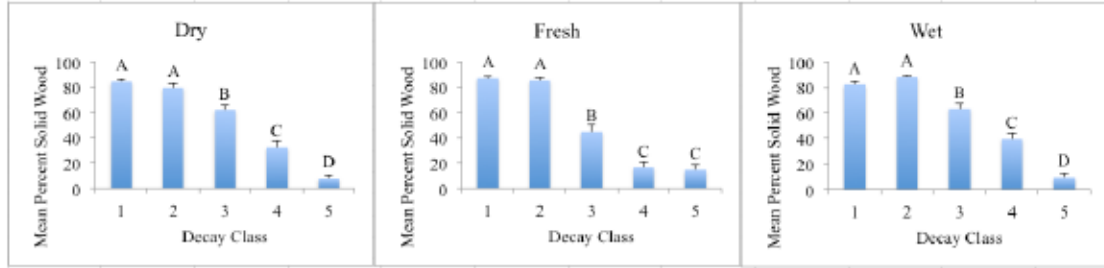
Figure 16. The mean proportion of solid wood (%) along the decay class continuum by moisture regime (Dry, Fresh, Wet) for deadwood cookies removed from log bolts. Vertical bars represent standard error bars. Uppercase letters depict differences based on Student-Newman-Keuls (SNK) post-hoc means separation test.

The mean proportion of decayed wood was initially (DC 1 and DC 2) very low across all moisture regimes (Figure 17). For dry and wet sites, there was a significant increase in the proportion of decayed wood in DC 3 (dry: 29.09%, wet: 29.51%), followed by consistently significant increase between DCs along the DC continuum to DC 5 (dry: 78.79%, wet: 78.00%). On fresh sites, decay occurred quickly between DC 2 and DC 3, as the proportion of decayed wood increased significantly from 8.24% to 48.02%. The proportion of decayed wood then increased significantly to 70.68% in DC 4, and remained stable in DC 5 (72.28%) (Figure 17).
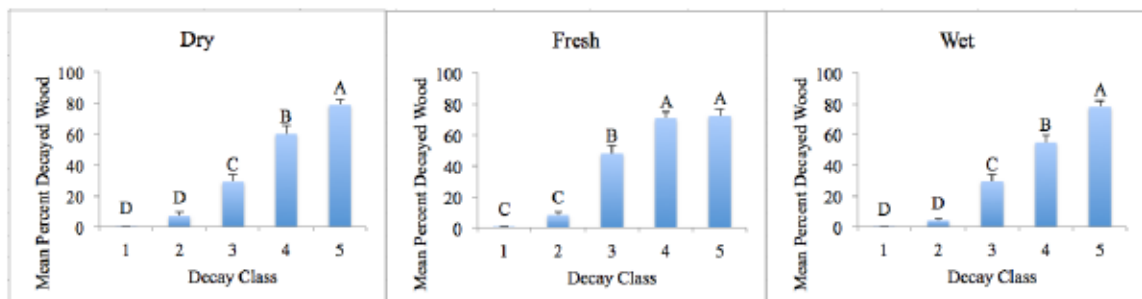
Figure 17. The mean proportion of decayed wood (%) along the decay class continuum by moisture regime (Dry, Fresh, Wet) for deadwood cookies removed from log bolts. Vertical bars represent standard error bars. Uppercase letters depict differences based on Student-Newman-Keuls (SNK) post-hoc means separation test.

The pattern of mean proportion of bark throughout the DC continuum also varied across moisture regimes. For dry sites, the proportion of bark was initially high, followed by a significant decrease between DC 2 (12.96%) and DC 3 (8.76%) (Figure 18). The proportion of bark then remained constant from DC 3 to DC 5.

For fresh sites, there was a rapid loss of bark between DC 1 (12.05%) and DC 2 (6.42%), after which the proportion of bark remained stable through to DC 3 (6.12%) (Figure 18). The proportion of bark then increased significantly in samples from DC 4 (9.60%) and DC 5 (8.50%), likely a function of high variability in the subsamples from the different logs.

For samples from wet sites, after an initial decrease in the proportion of bark from DC 1 (17.73%) to DC 2 (7.60%), the proportion of bark remained stable through to DC 5 (6.72%) (Figure 18).
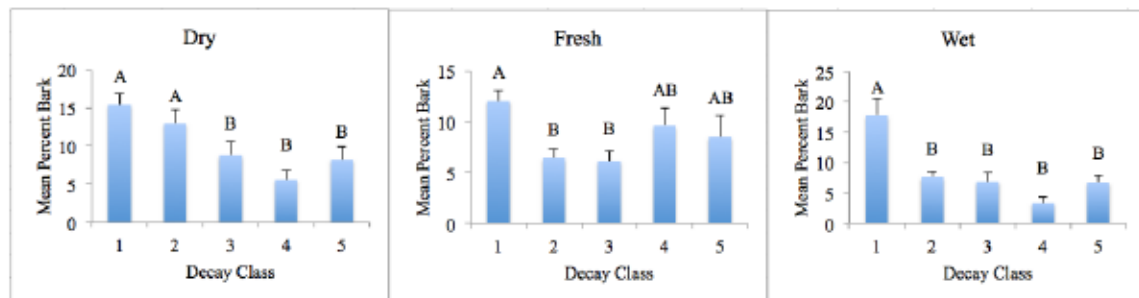
Figure 18. The mean proportion of bark (%) along the decay class continuum by moisture regime (Dry, Fresh, Wet) for deadwood cookies removed from log bolts. Vertical bars represent standard error bars. Uppercase letters depict differences based on Student-Newman-Keuls (SNK) post-hoc means separation test.

CHANGES IN CHEMICAL COMPOSITION OF DEADWOOD

Based on preliminary analysis (*i.e.*, 3 factor general linear model with moisture regime, species, and decay class), MR was found to be a non-significant factor (p>.40) for all ANOVAs run with weighted average chemical parameters, and as such, was removed from the model. All subsequent analysis for overall mean weighted chemistry was run as 2 factor models. However, all factors were found to be significant based on preliminary analysis for the chemistry by component, and therefore each was included in subsequent analysis.

Nitrogen

Based on the ANOVA results for overall weighted chemistry, significant differences in mean weighted nitrogen (N) concentration occurred as a function of DC (p<.0001). Nitrogen concentrations increased significantly between each DC along the DC continuum starting with DC 1 at 0.11%, and increasing nearly 3-fold by DC 5 at 0.30% (Figure 19).
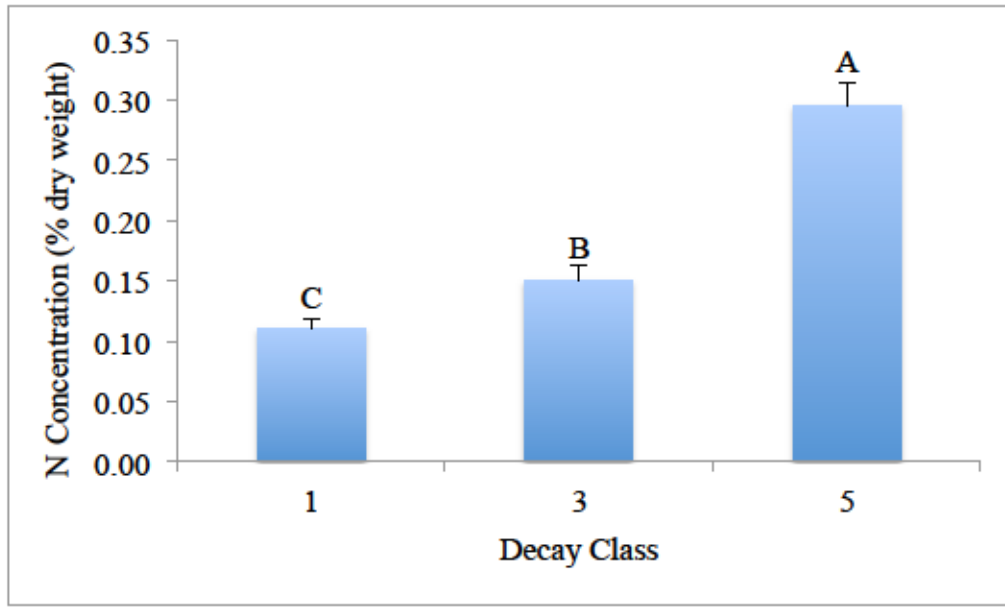
Figure 19. The gradient of mean weighted nitrogen values (%) along the decay class continuum. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

Results from two-way ANOVAs for each component (solid wood, decayed wood, and bark) also revealed significant differences ($p<.0001$) in N concentration for all components across decay classes. In solid wood, N was relatively low across all DCs sampled compared to bark or decayed wood, however, there was a slight, albeit significant, increase as decomposition proceeded (DC 1 ≠ DC 3 = DC 5) (Figure 20). Although N concentration increased across decay classes in decayed wood, there were insignificant changes in N during the early stages of wood decay (*i.e.,* DC 1 = DC 3) (Figure 21). In bark samples, N concentrations increased as decomposition proceeded from DC 1 (0.33%) to DC 5 (0.58%) (Figure 22).

Figure 20. Mean nitrogen concentration (percent dry weight) by decay class for solid wood component of samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.
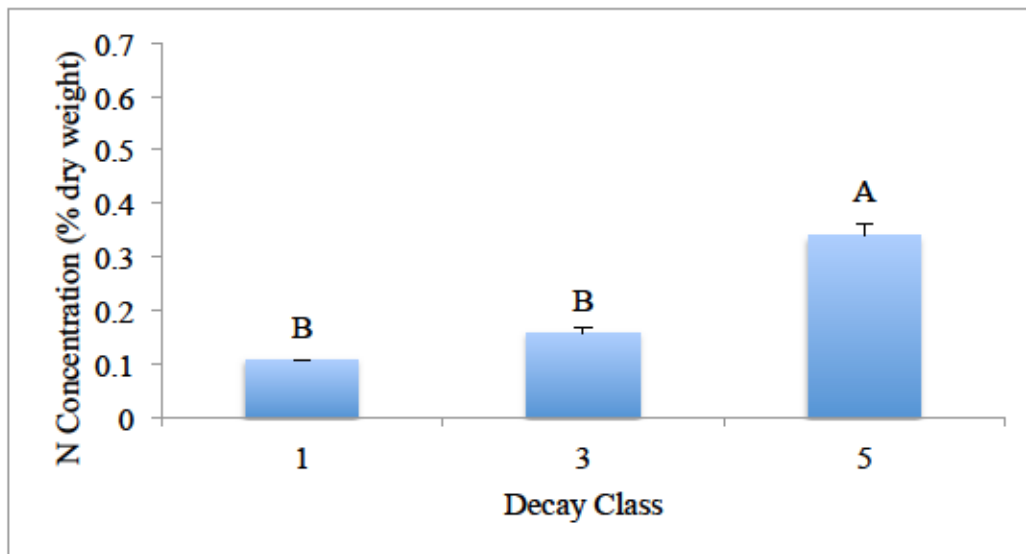
Figure 21. Mean nitrogen concentration (percent dry weight) by decay class for decayed wood component of samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

Figure 22. Mean nitrogen concentration (percent dry weight) by decay class for bark component of samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

Based on the ANOVA results for overall weighted chemistry, significant differences in mean weighted N concentration also occurred as a function of species ($p<.0001$) (See Appendix I). In this case, mean N concentration for poplar logs (0.24%) was significantly greater than that of conifer logs (0.13%) (Figure 23), and these lower values in the conifer samples occurred in all components (solid wood: $p<.0001$, decayed wood: $p<.0001$, bark: $p=.0015$) (Figures 24, 25, 26 respectively).
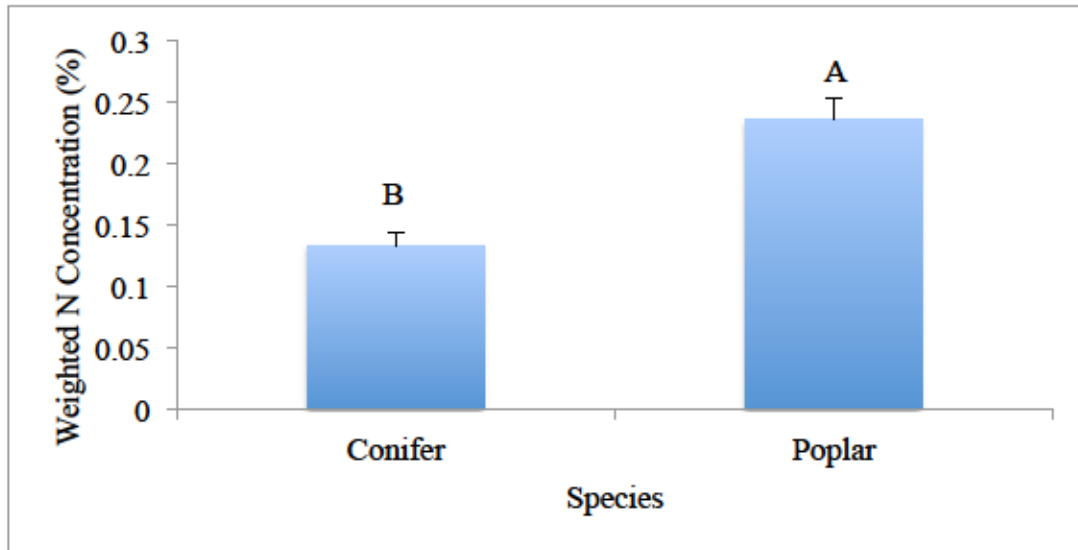
Figure 23. Comparison of mean weighted nitrogen values (%) as a function of species. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.
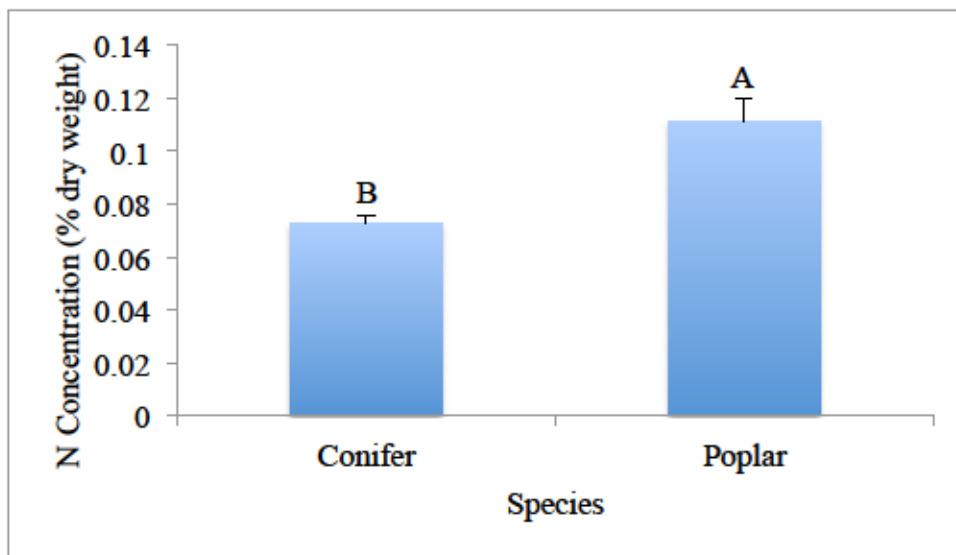
Figure 24. Mean nitrogen concentration (percent dry weight) by species for solid wood component of samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.
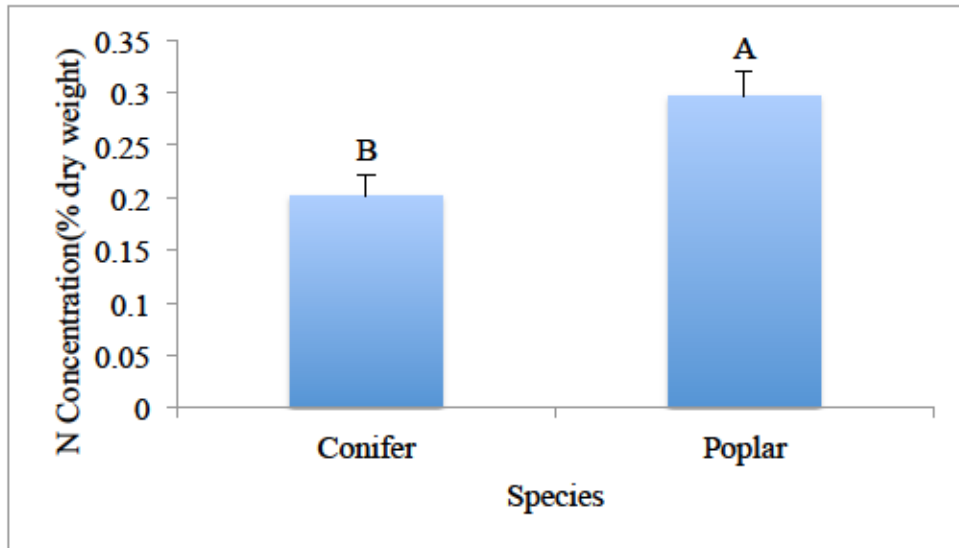
Figure 25. Mean nitrogen concentration (percent dry weight) by species for decayed wood component of samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

Figure 26. Mean nitrogen concentration (percent dry weight) by species for bark component of samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

In the case of bark and solid wood, there were significant species * decay class interactions (p=.0295 and p=.0064, respectively) for nitrogen, meaning that the decay

class pattern for N concentration differed between species. In conifer bark samples, N

concentrations increased significantly from DC 1 (0.23%) to DC 5 (0.60%) (Figure 27).

In contrast, the N concentration in poplar bark samples remained stable across all decay

classes sampled, with only a slight, non-significant increase in DC 5 samples (Figure

28).

Figure 27. Mean nitrogen concentration (percent dry weight) by decay class for conifer bark samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.
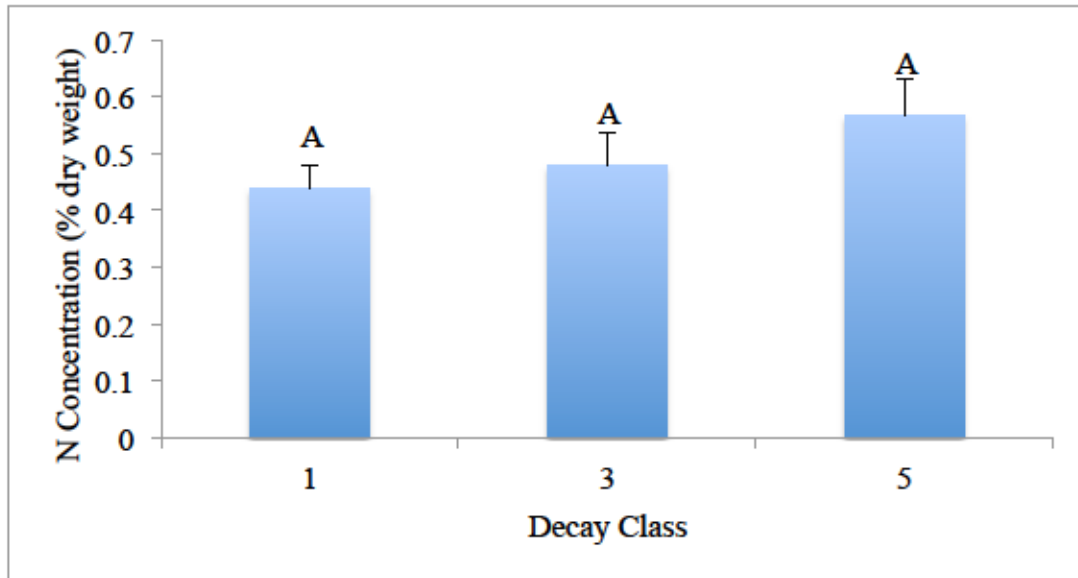
Figure 28. Mean nitrogen concentration (percent dry weight) by decay class for poplar bark samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

For conifer solid wood samples, N concentration increased significantly between all decay classes measured from DC 1 (0.05%) to DC 5 (0.09%) (Figure 29). Poplar solid wood samples followed the same pattern shown for conifers (Figure 30), however, N concentrations in poplar solid wood were consistently higher ranging from 0.08% in DC 1 to 0.17% in DC 5.
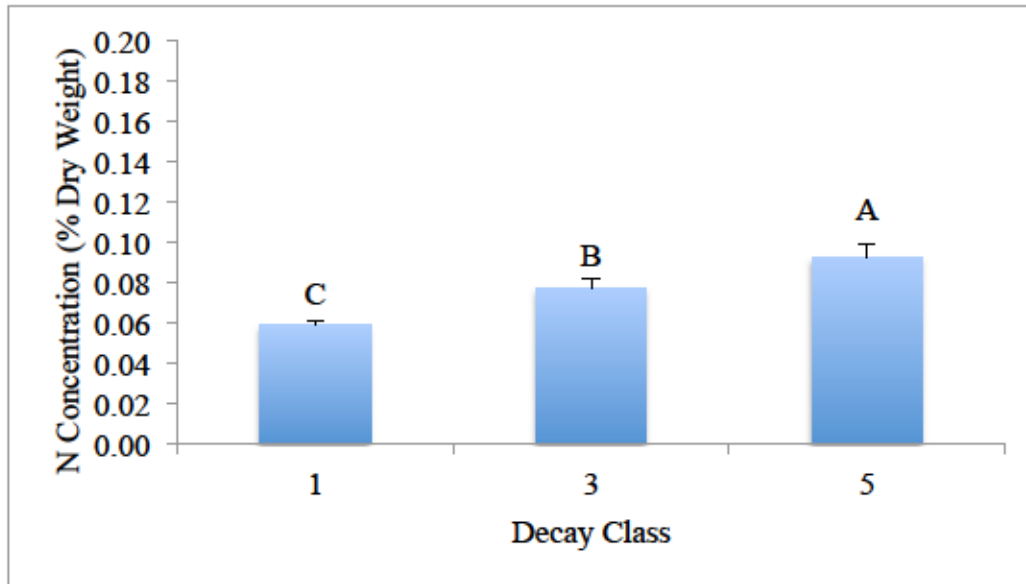
Figure 29. Mean nitrogen concentration (percent dry weight) by decay class for conifer solid wood samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.
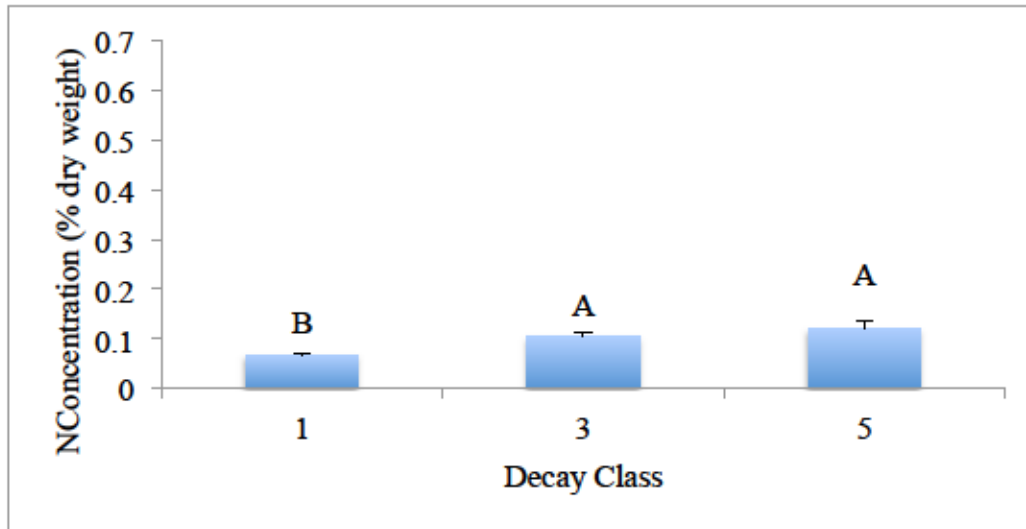

Figure 30. Mean nitrogen concentration (percent dry weight) by decay class for poplar solid wood samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

Carbon

Based on the ANOVA results (See Appendix I), there were no significant differences in weighted C concentrations between species (p=0.3852). However, significant differences in mean weighted C concentration did occur as a function of DC (p=.0001). Mean weighted C concentration remained significantly higher in logs sampled from DC 1 (48.47%) and DC 3 (48.13%) compared to DC 5 (45.25%) (Figure 31).
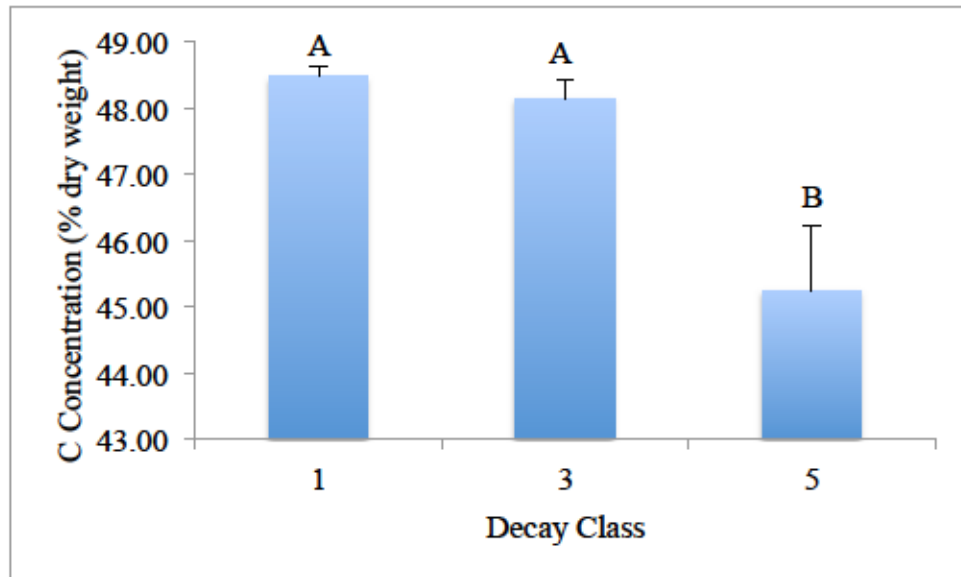
Figure 31. The gradient of mean weighted carbon values (%) along the decay class continuum. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

Results from the two-way ANOVAs for each component (solid wood, decayed wood, and bark) revealed significant differences in carbon concentration for solid wood and decayed wood (p=.0006 and p=.0241, respectively) across decay classes. Although carbon concentrations increased across decay classes in decayed wood, these increases

were not significant (Figure 32). Carbon concentrations increased across decay classes

in solid wood, however, there were insignificant changes in C concentrations until later

stages of decay (*i.e.*, DC 1 = DC 3 ≠ DC 5) (Figure 33).
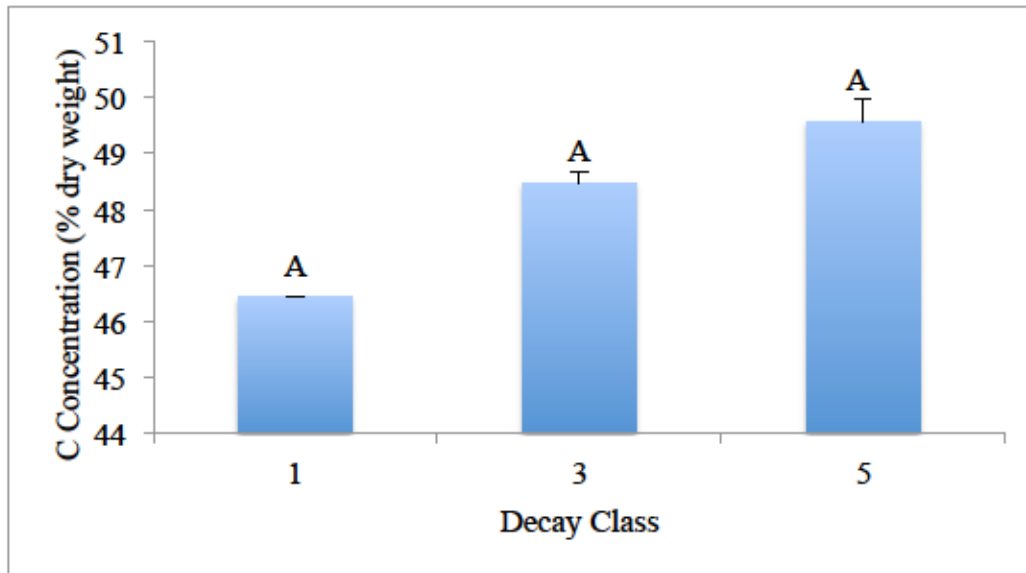
Figure 32. Mean carbon concentration (percent dry weight) by decay class for decayed wood component of samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.
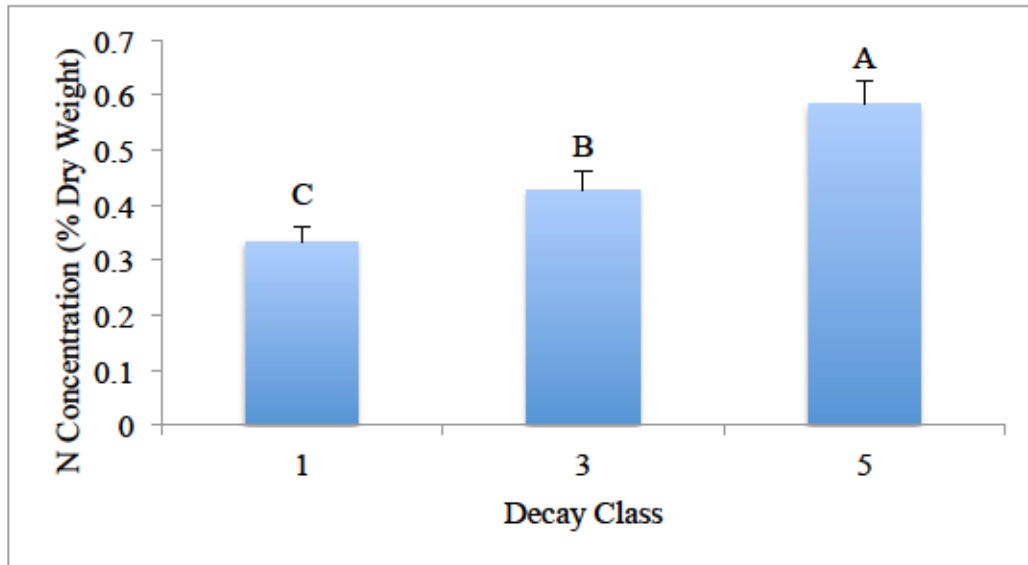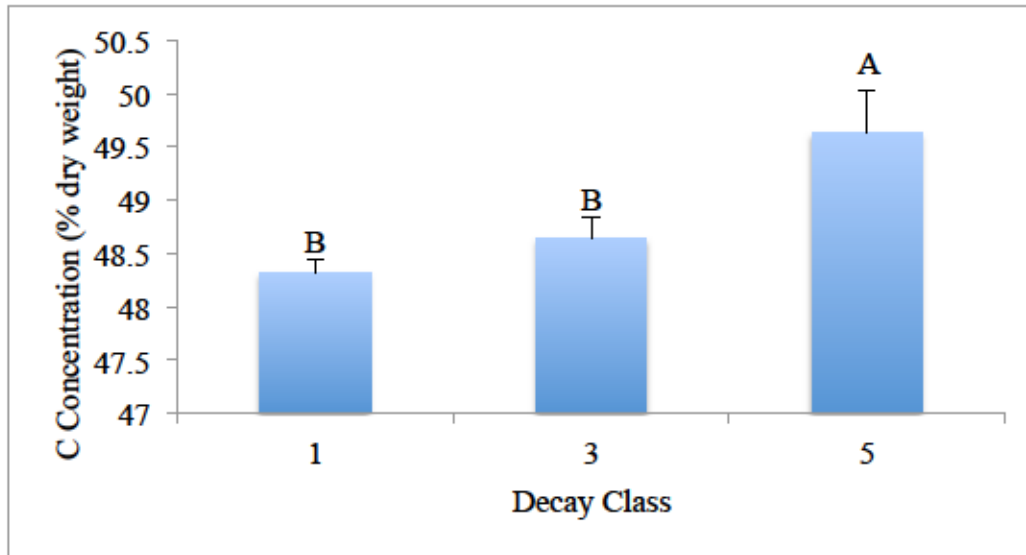
Figure 33. Mean carbon concentration (percent dry weight) by decay class for solid wood component of samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

Significant differences were found in C concentration between species for bark and solid wood (p=.0105 and p<.0001, respectively). In the case of bark, carbon concentrations were lower in conifer samples compared to poplar samples (Figure 34). The opposite was true for solid wood components, with C concentrations being higher in conifer samples compared to poplar (Figure 35).
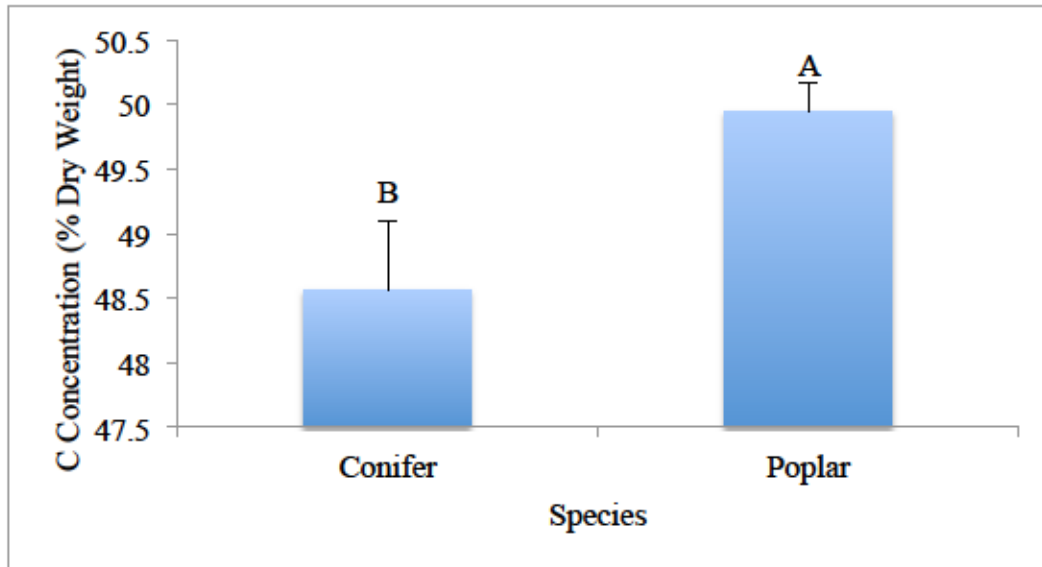
Figure 34. Mean carbon concentration (percent dry weight) by species for bark component of samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

Figure 35. Mean carbon concentration (percent dry weight) by species for solid wood component of samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

The ANOVA for bark did also reveal a significant species * decay class

interaction (p=.0022), meaning that the DC pattern for C concentration differed between

species. In conifers, the bark C concentrations decreased significantly across the DC
continuum from DC 1 (49.63%) to DC 5 (46.41%) (Figure 36). On the other hand, bark
from poplar samples did not differ between DC 1 (49.83%) and DC 3 (49.23%), but
increased significantly in DC 5 (51.04%) (Figure 37).
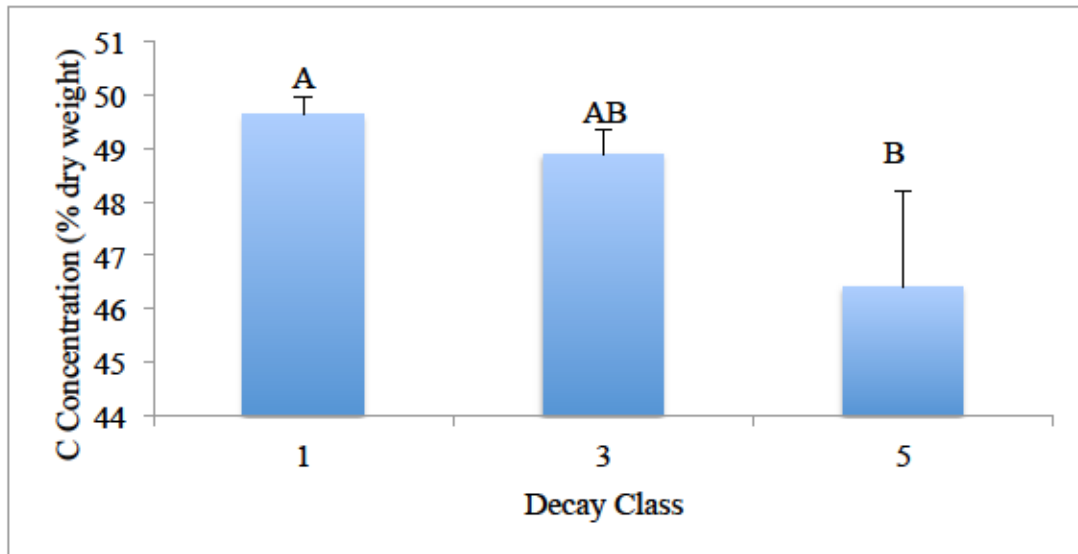
Figure 36. Mean carbon concentration (percent dry weight) by decay class for conifer
bark. Vertical bars represent standard error bars. Uppercase letters depict significant
differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.
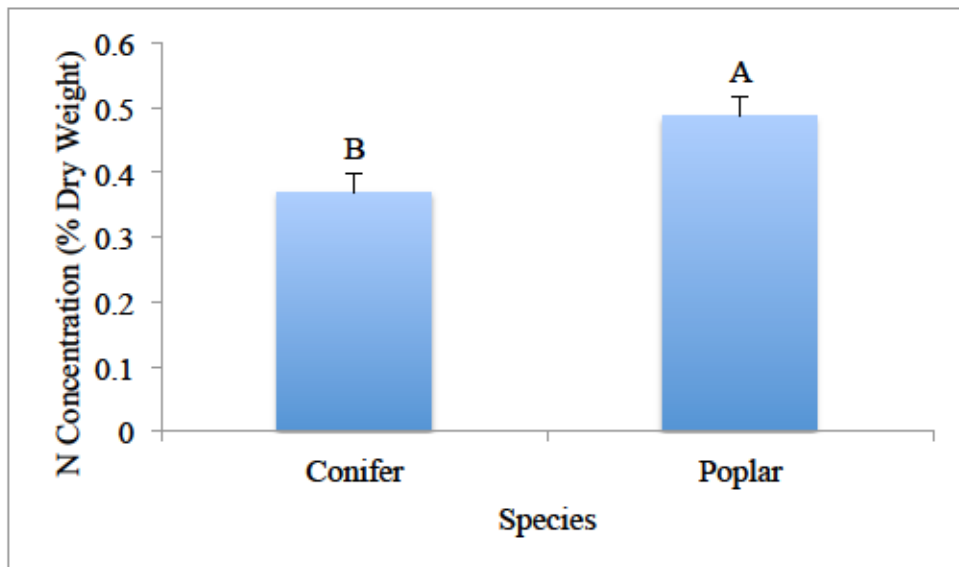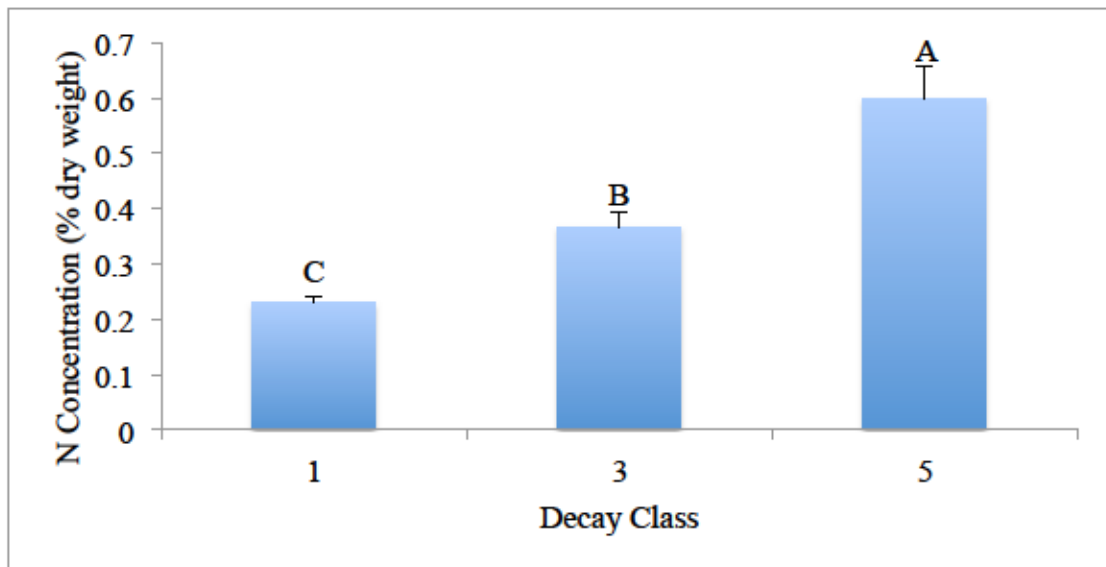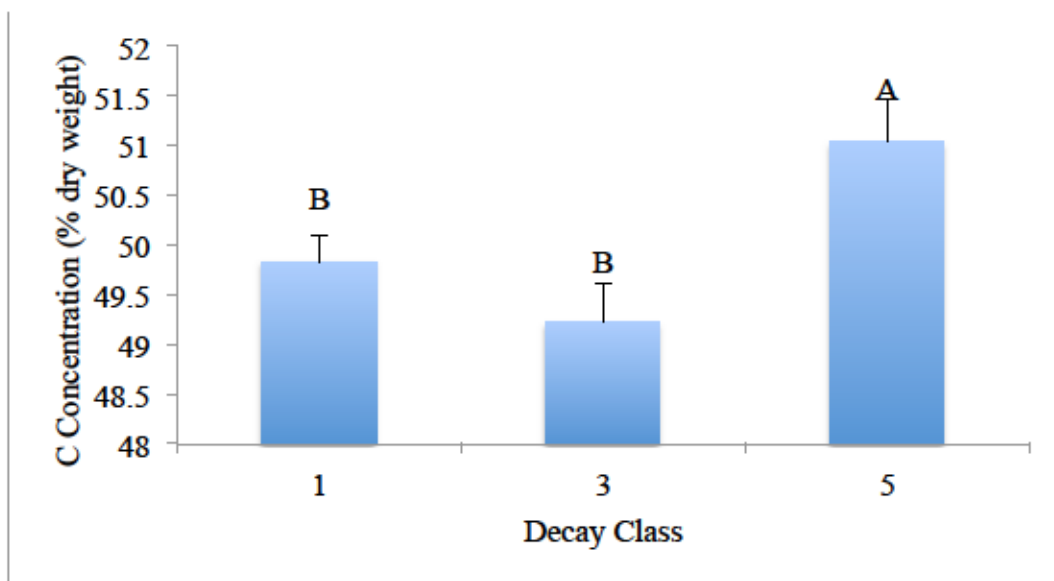

Figure 37. Mean carbon concentration (percent dry weight) by decay class for poplar
bark. Vertical bars represent standard error bars. Uppercase letters depict significant
differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

C:N Ratio

The ANOVA results highlighted significant differences in mean weighted C:N ratios between species and decay classes (p<.0001) (See Appendix I). In terms of species differences, mean weighted C:N ratio for conifer logs (452.46) was significantly greater than that of poplar logs (269.12). Across the DC continuum, C:N ratio decreased starting at 503.83 for DC 1, and declined by nearly 3-fold by DC 5 (179.67).

There was, however, a significant species*DC interaction for mean weighted C:N ratio (p=.0002), suggesting different patterns in C:N ratios occurred across decay classes depending on the species. The ANOVA confirmed that conifer logs declined in mean weighted C:N ratio across the DC continuum starting at 650.64 for DC 1, and decreasing to 217.20 for DC 5 (Figure 38). In the case of poplar logs, mean weighted CN ratio remained significantly higher in DC 1 (357.01) and DC 3 (306.11) before declining to 144.23 in the DC 5 samples (Figure 39).
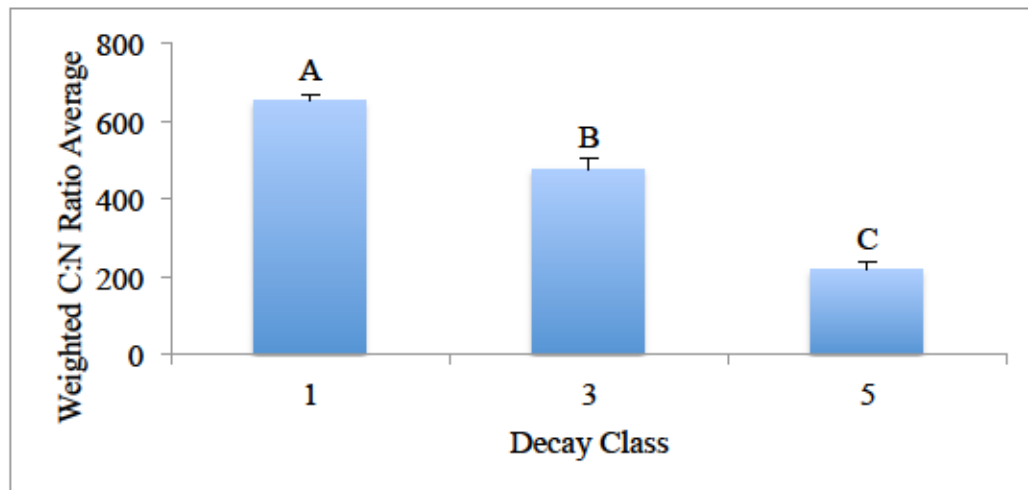
Figure 38. Differences in mean weighted carbon nitrogen ratios along the decay class continuum for conifer logs. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.
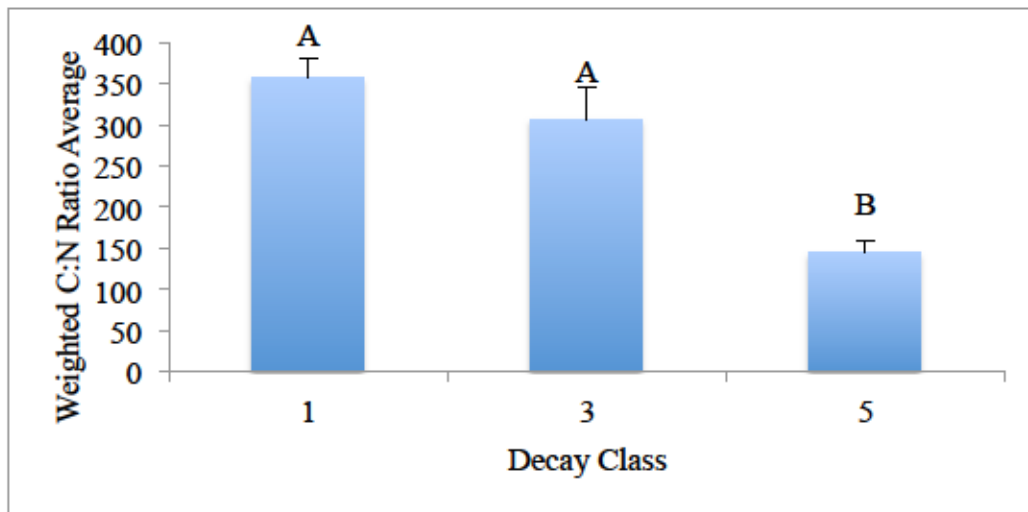
Figure 39. Differences in mean weighted carbon nitrogen ratios along the decay class continuum for the poplar logs. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

Results from the two-way ANOVAs for each component (solid wood, decayed wood, and bark) revealed significant differences ($p<.0001$) in the C:N ratio for all components across decay classes. In bark, C:N ratio decreased as decomposition proceeded from DC 1 (177.80) to DC 5 (96.05) (Figure 40). In contrast, significant declines in C:N ratio for decayed wood samples did not occur until DC 5 (170.39), which was significantly lower compared to DC 1 (433.55) and DC 3 (354.41) (Figure 41). Although C:N ratios decreased across decay classes for solid wood, there were insignificant differences in C:N ratio during the later stages of wood decay (*i.e.,* DC 3 = DC 5) (Figure 42).
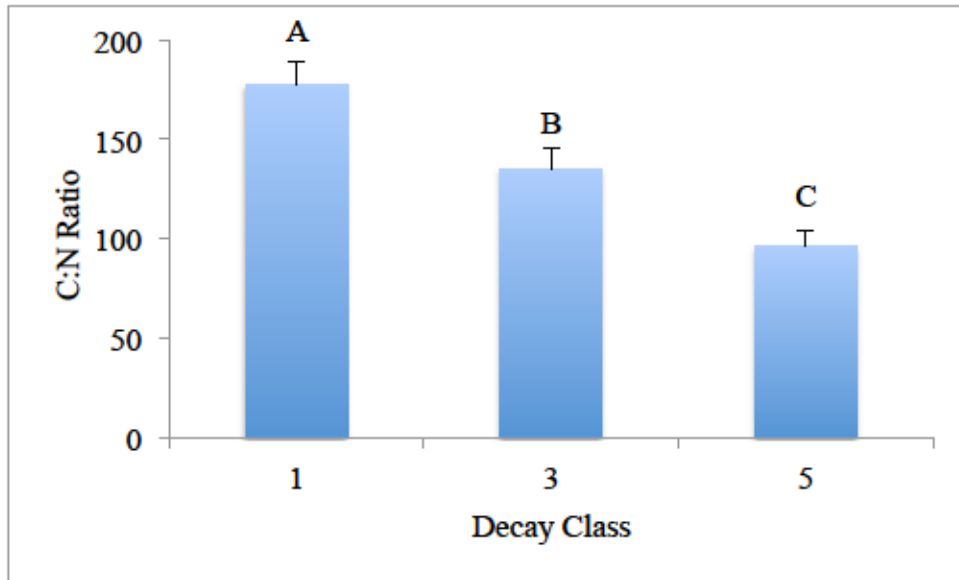
Figure 40. Mean carbon nitrogen ratio by decay class for bark component of samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.
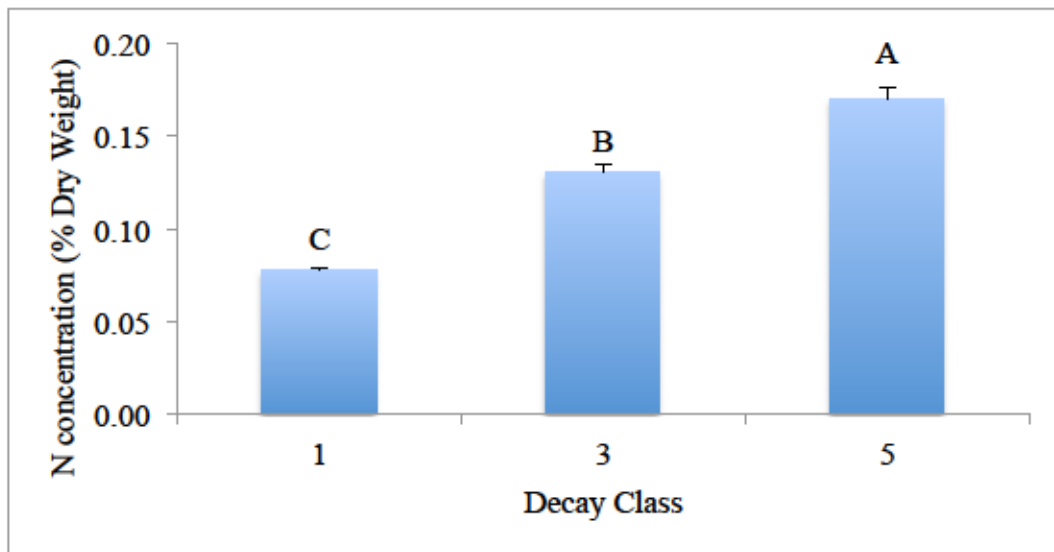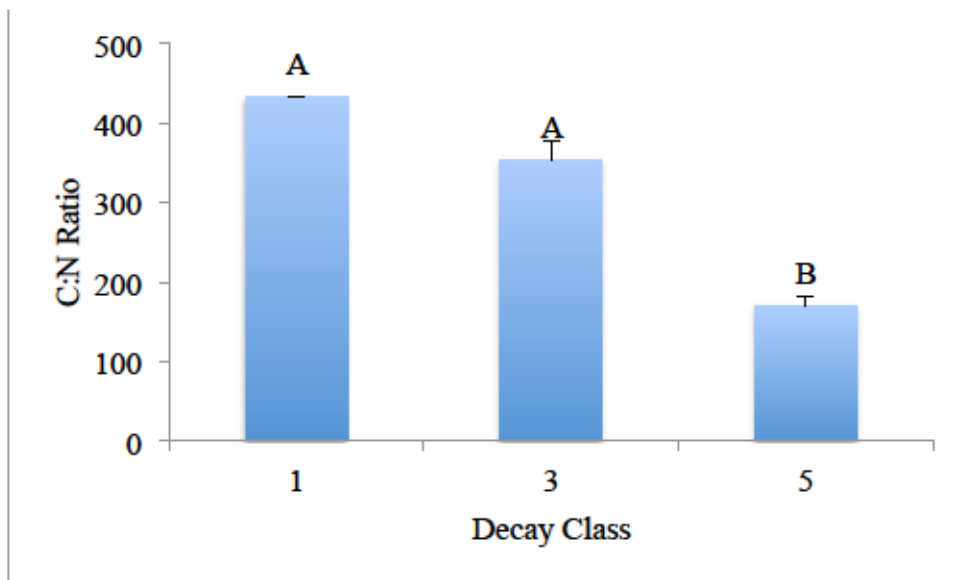

Figure 41. Mean carbon nitrogen ratio by decay class for decayed wood component of samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.
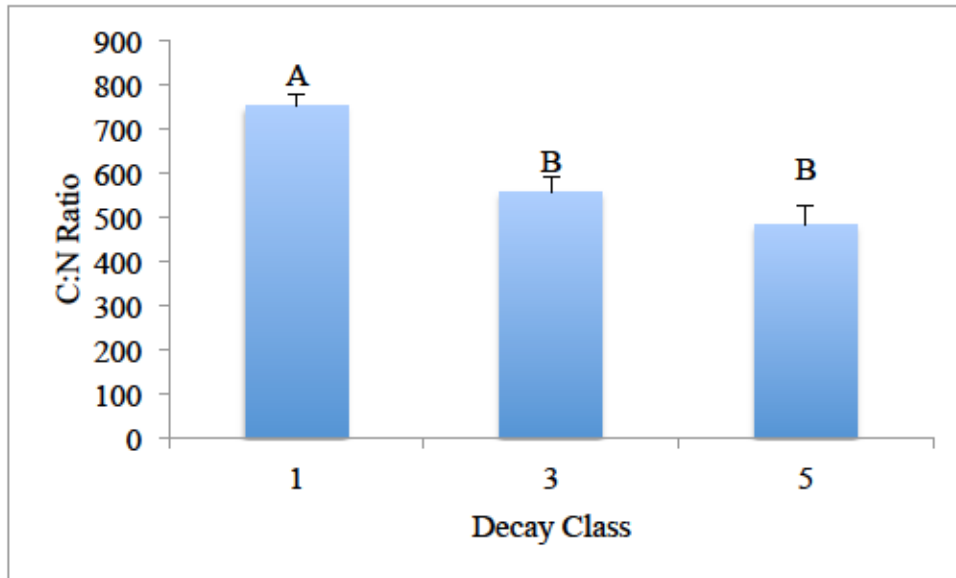
Figure 42. Mean carbon nitrogen ratio by decay class for solid wood component of samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

In terms of species differences, the mean C:N ratio was consistently greater in conifer samples compared to poplar across all components (bark: p=.0002, decayed wood: p<.0001, solid wood: p<.0001) (Figure 43, 44, 45 respectively).
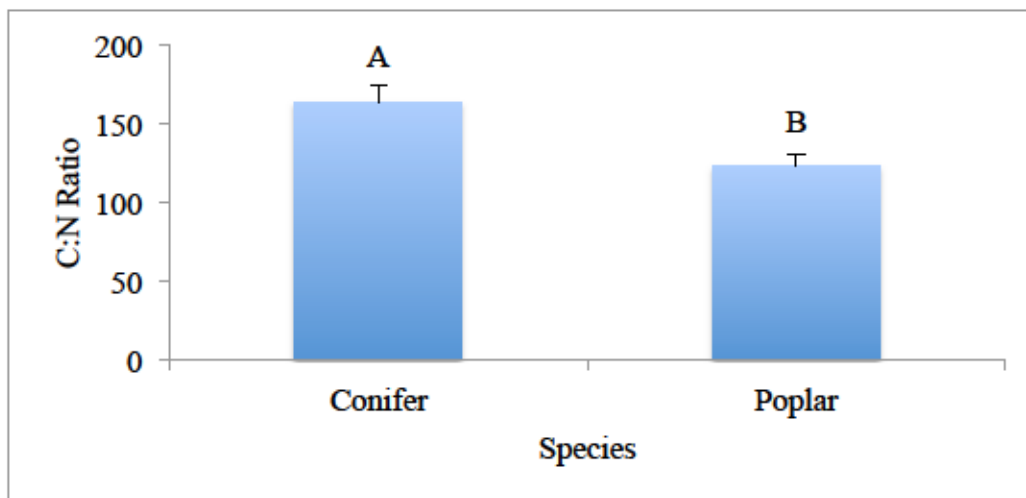
Figure 43. Mean carbon nitrogen ratio by species for bark component of samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.
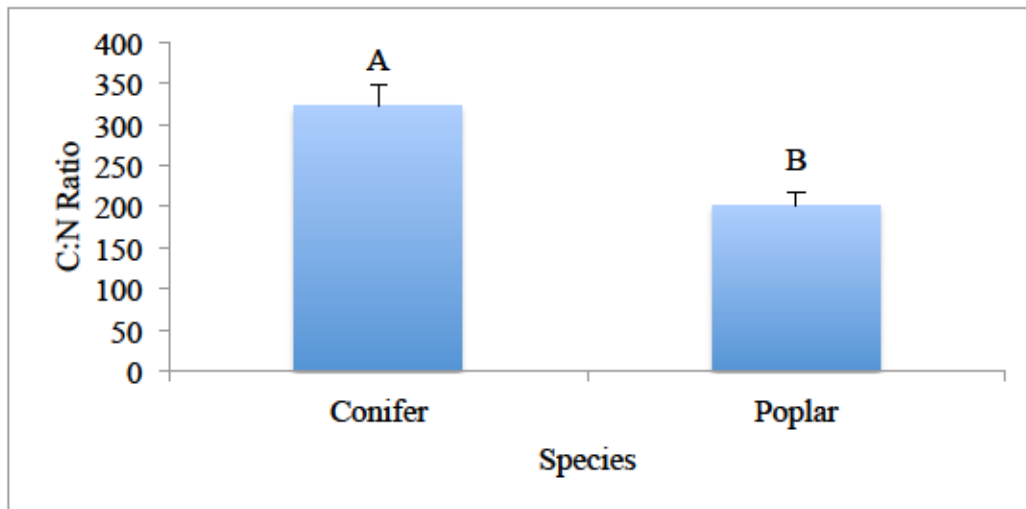
Figure 44. Mean carbon nitrogen ratio by species for decayed wood component of samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.
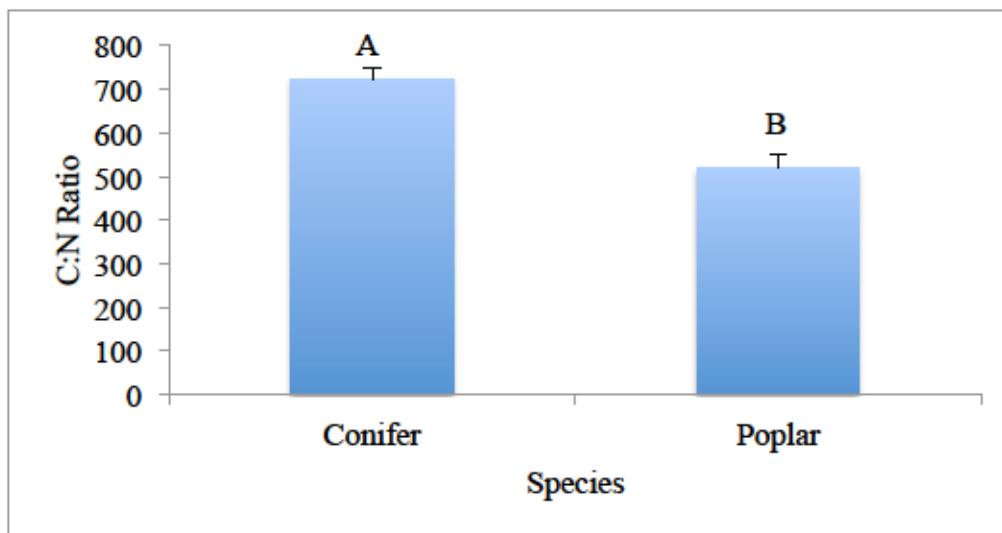
Figure 45. Mean carbon nitrogen ratio by species for solid wood component of samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

In the case of bark and decayed wood, the ANOVAs revealed significant species*DC interactions (p<.0001 and p=.0033, respectively), meaning that the decay class pattern for C:N ratio differed between species (Figure 46 and Figure 47). The mean C:N ratio for conifer bark declined significantly between DCs along the DC continuum

from 226.75 in DC 1 to 88.53 in DC 5 (Figure 46). In contrast, there was no significant

change in C:N ratio of bark (ranging between 128.9 and 102.9) for poplar logs (Figure

47).
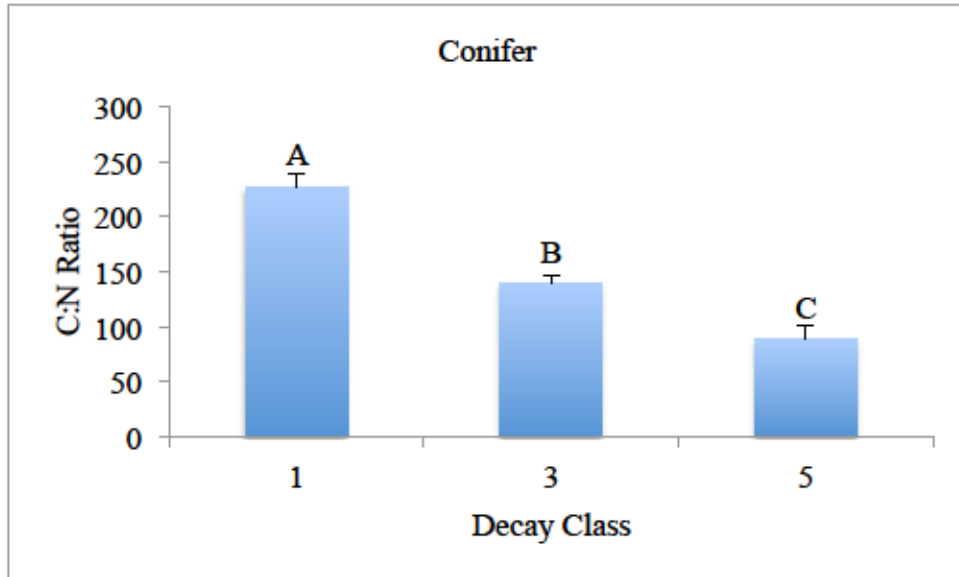
Figure 46. Mean carbon nitrogen ratio by decay class for conifer bark samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.
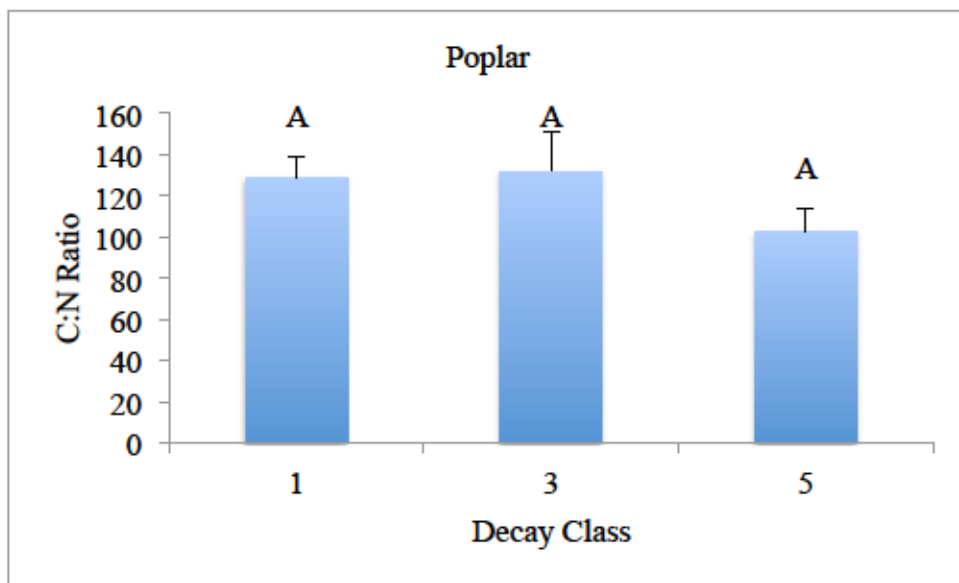
Figure 47. Mean carbon nitrogen ratio by decay class for poplar bark samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

In the case of decayed wood, there was a significant decrease in C:N ratio between DC 3 (436.51) and DC 5 (200.03) for conifer samples, however, there were no results for DC 1 to compare to the other classes (Figure 48). Poplar decayed wood decreased significantly in C:N ratio along the DC continuum from DC 1 (433.55) to DC 5 (142.39) (Figure 49).
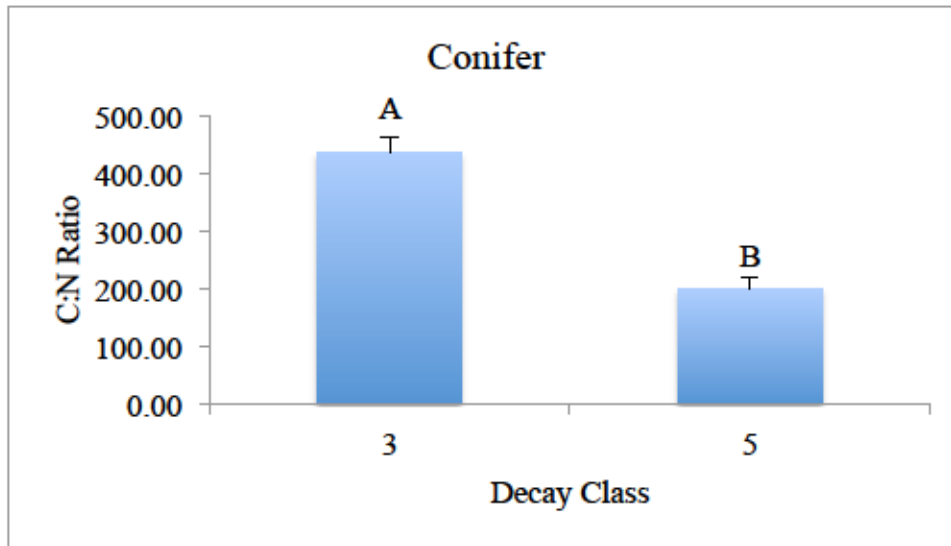
Figure 48. Mean carbon nitrogen ratio by decay class for conifer decayed wood samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.
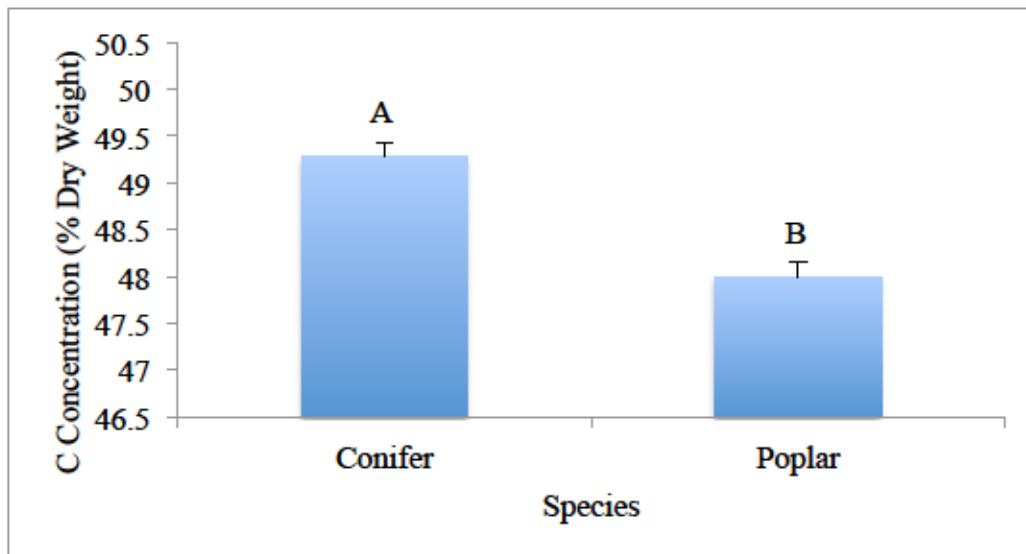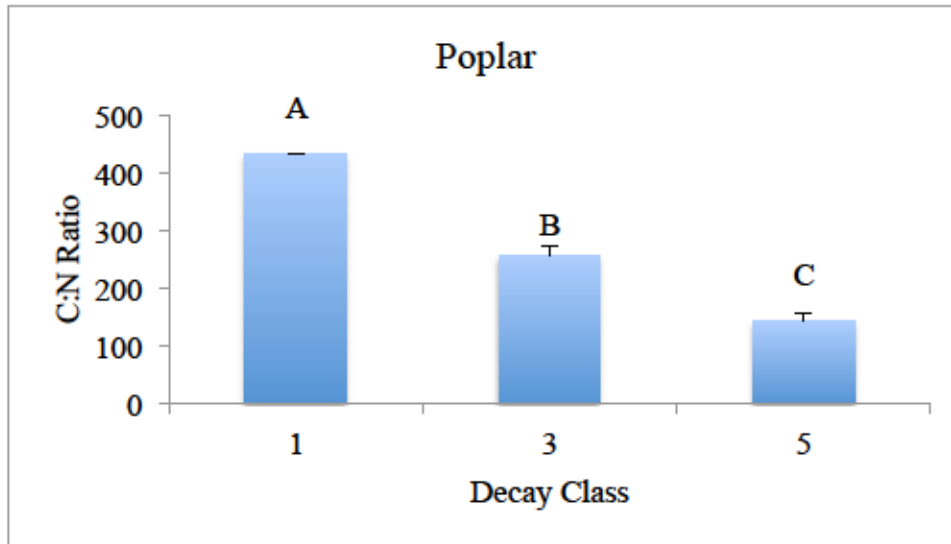
Figure 49. Mean carbon nitrogen ratio by decay class for poplar decayed wood samples. Vertical bars represent standard error bars. Uppercase letters depict significant differences based on the Student-Newman-Keuls (SNK) post-hoc means separation test.

RECLASSIFYING DECAY CLASSES BASED ON QUANTITATIVE VARIABLES

To determine the collective conditions that influence the classification of deadwood into decay classes, a series of variables were included in two separate Canonical Discriminant Analyses (CDAs). The first, included eight physical variables, and allowed for reclassification of individual samples from their originally assigned qualitative decay classes, into five new quantitatively-derived decay classes. The second CDA included the eight physical variables with the addition of three chemical variables. This CDA allowed for a reclassification of samples into quantitatively driven decay classes based on both physical and chemical characteristics.

Analysis with Physical Variables

Eight measured physical variables were included in the CDA (Table 4). This analysis combined all the variables to produce two uncorrelated discriminant functions that provided the maximum separation possible between the five, qualitatively-driven decay classes (See Table 3 for descriptions of classes). Separation between all decay classes occurred primarily on the first canonical axis (Figure 50). Some additional separation occurred along the second canonical axis, particularly between DC 1 and DC2, as well as between DC 4 and DC 5. A summary of the standardized canonical function coefficients for the two canonical functions, the cumulative variance explained by the two axes, and the reclassification success rate is provided in Table 4. The standardized canonical functions can be viewed as weighting factors and generally indicate the relative importance of each variable in the derived functions.

Of the eight physical variables included in the analysis, seven were highly significant ($p<.0001$) in the univariate ANOVA, while the eighth (elevation) was only marginally significant ($p=.0460$) (Table 4). Of the highly significant variables from the univariate ANOVA, density and percent solid wood were the dominant positive factors in the first canonical function (1.2437 and 1.1812, respectively). In the second canonical function, percent solid wood increases in magnitude in its coefficient (3.1200), while density decreases and reverses in sign (-1.0479). Of the characteristics observed at the original site of the log, bark cover was the dominant positive factor in the first canonical axis (0.4026), while moss cover and elevation were less important (-0.2749 and 0.0419, respectively).

Table 4. Results of canonical discriminant analysis of physical variables for decay classes one to five for both species of deadwood samples.

	Univariate test statistics		Standardized canonical function coefficient	
Variable	F value	Pr>F	Canonical function 1	Canonical function 2
Bcover	66.19	<.0001	0.4026	-0.3219
Mcover	54.21	<.0001	-0.2749	-0.5741
Elevation	2.44	0.046	0.0419	0.3266
Density	367.05	<.0001	1.2437	-1.0479
Percsolid	233.61	<.0001	1.1812	3.1200
Perdecay	269.49	<.0001	0.5270	2.1371
Perbark	14.44	<.0001	0.3520	0.2601
perchaff	29.76	<.0001	0.0000	0.0000
Cumulative variance (%)			95.4	99.0
Samples correctly reclassified (%)			57.5460	
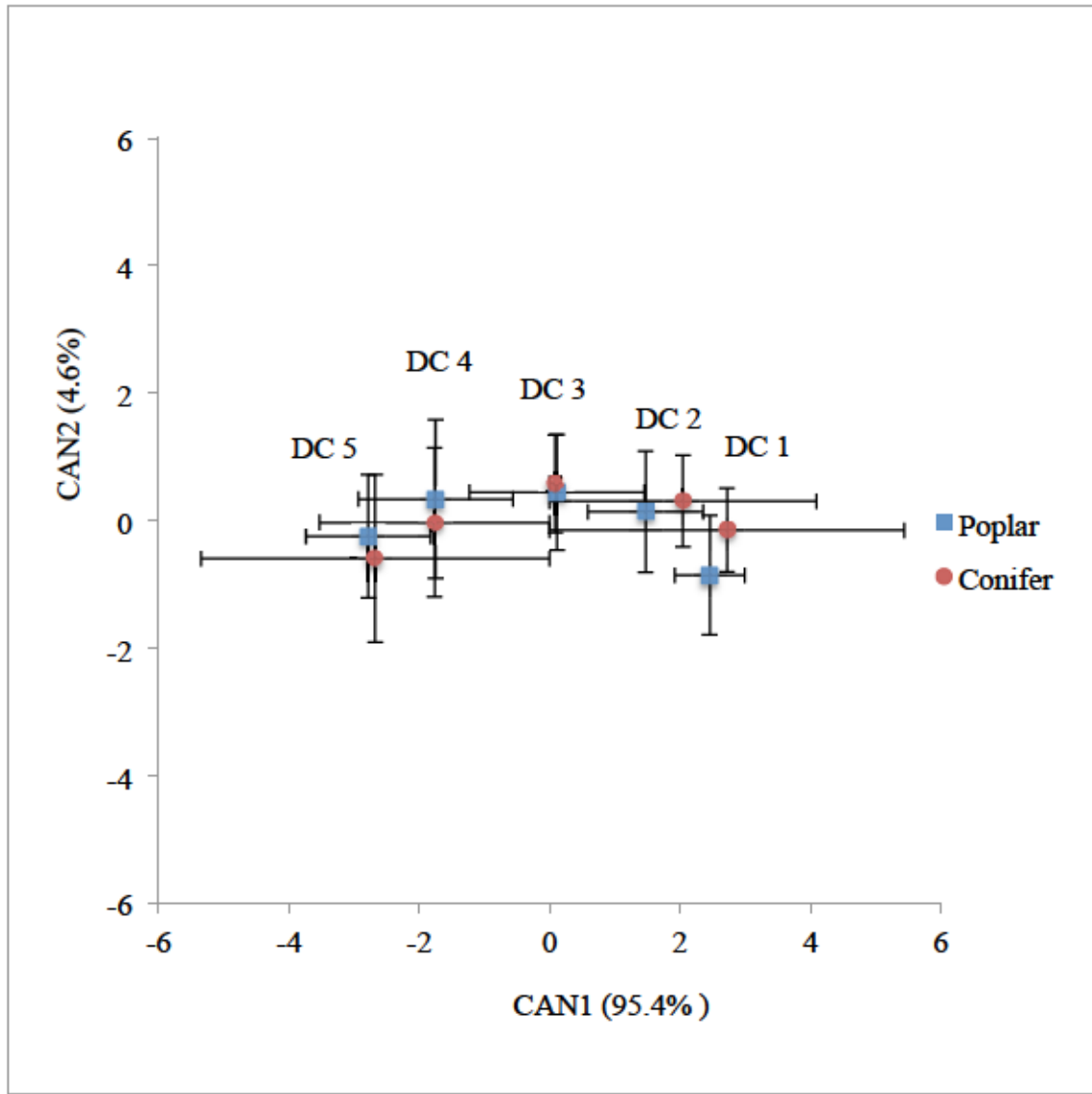
Figure 50. Two-dimensional ordination between decay classes 1 to 5 for both poplar and conifer logs using canonical discriminant analysis. Horizontal and vertical lines represent 1 standard deviation to each side of decay class means.

In terms of model performance, 57.5% of individual samples were correctly reclassified into their decay classes (Table 4) using the derived discriminant function. Reclassification success was greatest for decay classes 1 (71.30%) and 5 (73.83%), while reclassification rate for the middle classes, particularly DC 3 (46.30%) and DC 4 (37.04%), was considerably lower.

Analysis with Chemical and Physical Variables

A second canonical discriminant analysis was carried out with three chemical variables in addition to the eight physical variables (Table 5). This analysis combined all eleven variables to produce two uncorrelated discriminant functions that provided the maximum separation possible between decay classes. Because a subset (only DC 1, DC 3, and DC 5) of deadwood cookie samples was used in the chemical analysis, the CDA provided maximum separation between these three decay classes. With the addition of these chemical variables, separation between the three decay classes occurred primarily on the first canonical axis (Figure 51). Some additional separation of DC 3 occurred on the second canonical axis. Table 5 summarizes the standardized canonical function coefficients for the two canonical functions, the cumulative variance explained by the two axes, and the reclassification success rate.

Of the physical variables that were highly significant in the univariate ANOVA (P<.0001), density, percent solid wood, and percent decayed wood were the dominant positive factors in the first canonical function (1.8769, 1.1130, and 0.8988, respectively) (Table 5). Although the signs are reversed, only percent solid wood and percent decayed wood increase in magnitude in their coefficients (-6.7058 and -6.1961, respectively) in the second canonical function. All of the chemical variables were highly significant in the univariate ANOVA. Of these chemical variables, N concentration was the dominant factor in both canonical functions (-0.2829 and 1.3353). Carbon concentration also had a relatively large coefficient in both canonical functions (-0.2141 and 1.0607), while C:N ratio remained lowest in both (0.0325 and 0.6120).

Table 5. Results of canonical discriminant analysis of physical and chemical variables for decay classes 1, 3, and 5, for both species of deadwood.

Variable	Univariate test statistics		Standardized canonical function coefficient	
	F value	Pr>F	Canonical function 1	Canonical function 2
Bcover	30.99	<.0001	0.3933	0.7818
Mcover	43.11	<.0001	-0.6724	0.6533
Elevation	2.23	0.1129	0.1006	-0.2459
Density	227.24	<.0001	1.8769	1.1826
Percsolid	112.37	<.0001	1.1130	-6.7058
Perdecay	106.07	<.0001	0.8988	-6.1961
Perbark	2.84	0.0629	0.3728	-2.1911
perchaff	21.68	<.0001	0.0000	0.0000
weightN	48.60	<.0001	-0.2829	1.3353
weightC	9.31	0.0002	-0.2141	1.0607
Cnratio	43.83	<.0001	0.0325	0.6120
Cumulative variance (%)			95.63	100
Samples correctly reclassified (%)			89.7067	
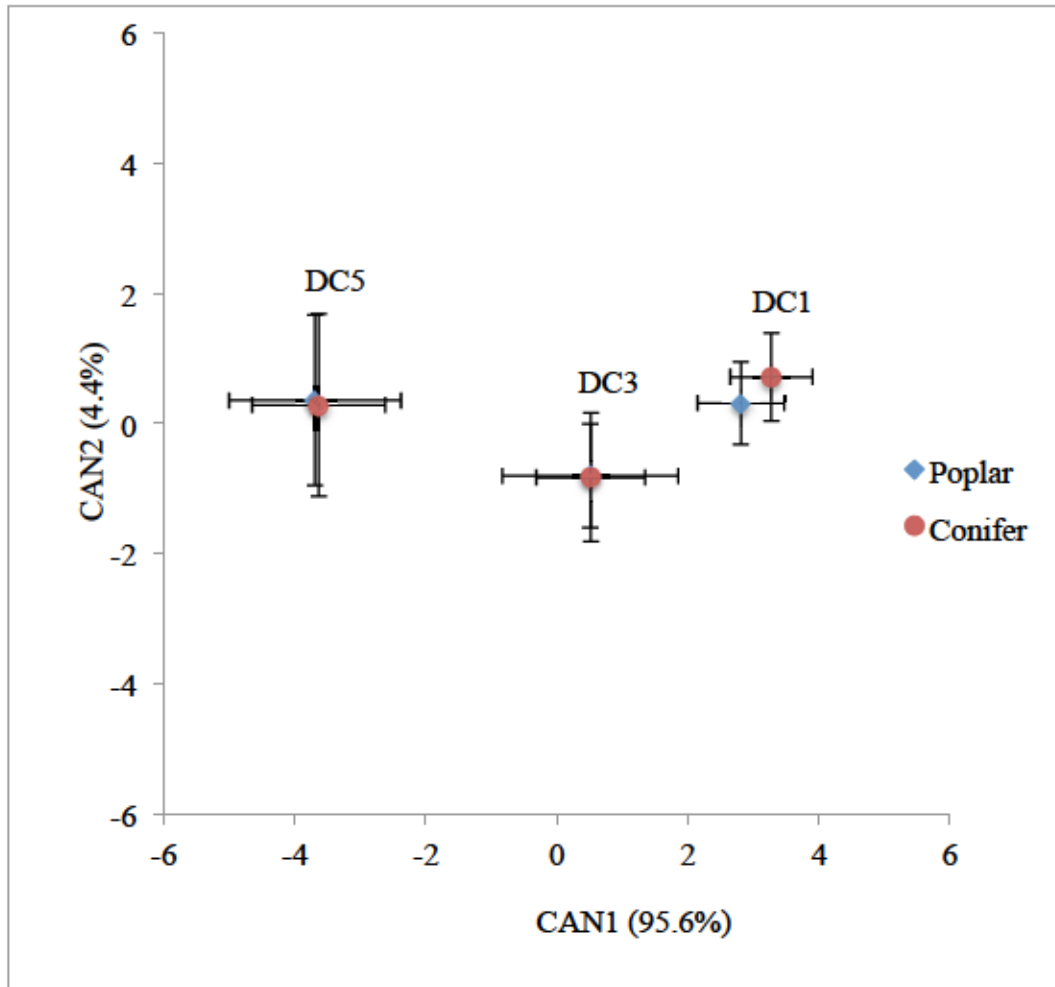
Figure 51. Two-dimensional ordination between decay classes 1, 3, and 5 for both poplar and conifer logs using canonical discriminant analysis. Horizontal and vertical lines represent 1 standard deviation to each side of decay class means.

Compared to the results of the CDA using only physical variables, this analysis resulted in much higher reclassification success. A large percent of individual samples (89.71%) were correctly reclassified into their decay classes (Table 5) using the derived discriminant function. Reclassification success was greatest for DC 1 (94.44%), followed by DC 5 (88.57%), but also remained high for the middle class, DC 3 (86.11%). Based on the results of this analysis, it may be implied that the predictive strength of the model improved with the addition of chemical variables. However, it must be recognized that this analysis only compares three decay classes rather than all

five classes used in the CDA for only physical variables. By their nature, these three classes are more distinct from each other than say DC 1 compared to DC 2, so a complete set of chemical analysis and a CDA with all five decay classes would be needed to truly confirm that the chemical properties improve the quantitative classification.

DISCUSSION

CHANGES IN DENSITY AND THE PROPORTION OF WOOD COMPONENTS

Moisture Regime

While discussing the differential patterns in deadwood decay as a function of moisture regime in this study, it must be recognized that in the case of wet and dry sites, some aspen log replicates in various DCs were brought in from nearby sites when they could not be found *in situ*. Although all logs brought into the study sites were from sites of similar site and stand conditions located in close proximity to study sites, minor differences in site conditions may have contributed to a differential effect in the logs decay process prior to movement.

The effect of moisture regime on the decay process is depicted in the results by the difference in overall (species and decay classes combined) density of samples across

moisture regimes, as well as by differences in the proportion of solid versus decayed wood across decay classes in each moisture regime. The greater amounts of decayed wood, indicative of faster rates of decay, in samples from fresh compared to dry and wet sites, reflects a well-documented relationship between moisture regime and wood decay. For example, Herrmann *et al.* (2015), found no differences in the decomposition constants of the DWD they studied between 'cold and wet' and 'warm and dry' sites, which they assumed reflected different types of climatic limitations for wood decaying fungi, that may not be present on the 'warm and wet' sites more optimal for decay. These observations reflect similarities in the pattern and rate of decay between wet and dry sites from our studied, compared to fresh sites, which appeared to host more favourable conditions for decay.

Wood moisture content has been well documented as a dominant environmental control over DWD respiration (Hagemann *et al.* 2010). The slower decreases in solid wood observed in samples from wet sites are likely in response to anaerobic conditions within the wood as a result of DWD pores filling with water. Decomposition by organisms such as brown and white-rot fungi becomes limited under these wet conditions, and the rate of decay may ultimately be slowed as it occurs only as a function of bacteria and soft-rot ascomycetes fungi (Moroni *et al.* 2015). The more rapid shift from solid wood to decayed wood and greater declines in density in samples from fresh sites may be a result of DWD achieving adequate/optimal moisture content required to promote microbial colonization without reaching anaerobic conditions (Harmon *et al.* 2000).

The pattern of slow initial decay followed by consistent decay after DC 3 in deadwood samples from dry sites is likely the result of moisture limiting conditions,

that, in turn, influence microbial colonization and activity (respiration). As these moisture-limited pieces of DWD become buried by forest litter, their moisture levels may increase. This increase in moisture content may allow decomposing agents to invade the DWD and increase the rate of decomposition (Fasth *et al.* 2011, Moroni *et al.* 2015).

The lack of significant differences in bark contributions across moisture regimes suggests bark loss is largely a mechanical process unaffected by moisture conditions. Since bark is the component of DWD most directly exposed to its outer environment, it is most vulnerable to physical factors that contribute to decomposition such as fragmentation. Fragmentation can occur by biological and physical processes such as precipitation cycles that fragment wood directly, and also result in internal freezing and thawing of water molecules, which causes swelling and shrinking of cells within the wood (Wiebe 2012). Other mechanisms of fragmentation unaffected by moisture regime include invertebrates that tunnel into wood and beneath the bark of deadwood, thus compromising its structure. As a result, fragmentation of bark by birds and large mammals may increase as they use the wood to reach their food source (Zhou *et al.* 2007). These forms of fragmentation that are largely unaffected by MR, are reflected in the quick initial loss of bark (*i.e.*, DC 1 and DC 2) observed across all moisture regimes.

Species

Species differences in density and the proportion of solid and decayed wood across the decay class continuum, follow a commonly reported pattern of significantly faster decomposition rates in hardwood compared to conifer logs (*i.e.* Wiebe 2012, Herrmann *et al.* 2015, Weedon *et al.* 2009, Russell *et al.* 2014). The differences in the composition of the wood, as well as the agents responsible for decay between the two, are likely responsible for the different decomposition rates observed. Brown rot fungi, which are most commonly responsible for the decay of conifer deadwood, feed on cellulose, but do not contribute to the degradation of lignin. White rot fungi that degrade both cellulose and lignin largely decompose hardwood species, many of which have higher proportions of high-energy simple sugars and proteins compared to conifer DWD (Wiebe 2012, Goodell *et al.* 2008). As a result, many hardwood species decay much faster and more completely than conifer species with high percentages of difficult to digest lignin (Wiebe 2012). This pattern was observed in the results, as density was, on average, significantly greater in conifer logs than poplar logs across all samples. This pattern was also reflected by a more rapid and complete loss of solid wood in poplar compared to conifer logs.

CHANGES IN THE CHEMICAL COMPOSITION OF DEADWOOD

Nitrogen

Increases in N concentrations throughout the decay process are reflected in the results by a consistent increase in the weighted average and component concentrations of N across the DC continuum. This increase demonstrates a pattern of N concentrations throughout the decay process observed by many (*e.g.* Wiebe 2012, Butler *et al.* 2007, Fahey 1983, Garrett *et al.* 2008). The increase of N concentrations in DWD as decomposition progresses is largely a result of translocation and retention (immobilization) by fungi (Lambert *et al.* 1980, Schimel and Hättenschwiler 2007), and fixation by bacteria (Brunner and Kimmins 2003).

Jack pine, the species most commonly representing conifers in this study, is characterized by low N content (Strukelj *et al.* 2013), as was demonstrated in our results by the significantly higher concentrations of N in poplar compared to conifer logs.

Although DWD N pools are small compared to underlying soils (Kuehne *et al.* 2008, Wiebe 2012), DWD should not be dismissed as an important contributor to N cycling and plant nutrition. Initial increases in N concentrations in DWD with increasing mass loss, as reflected in our results, mean that DWD can be a net sink for N for as much as several decades (Means et al. 1992, Alban and Pastor 1993, Busse 1994). This period of retention of N in DWD may be important as it occurs during the same time as

a stage of nutrient excess in the soil. In later stages of decay when N concentrations stop increasing and N is released from DWD, it can contribute to N availability in the soil, particularly for uptake by plants in the form of ammonium and ammonia (Harmon *et al*. 1986, Wiebe 2012). This period of release commonly coincides with a stage of nutrient deficit within the soil, which further supports the argument that the small amounts of N in DWD may play a significant role in plant nutrition (Kuehne *et al*. 2008).

Carbon

From the results for mean weighted C concentration, as well as concentrations by significant component, it would appear that a rapid stage of decomposition and resulting loss of C does not occur until after DC 3, at which point significant changes begin. In this rapid middle phase of decomposition, simple carbon compounds and cellulose are decomposed through microbial activity (Wiebe 2012) resulting in significantly lower C concentrations by DC 5.

Greater carbon concentrations in the solid wood component of conifer compared to poplar samples may be explained in part by the greater proportions of lignin in conifer DWD, as well as the different basidiomycete fungi acting in the decay process. These species differ in the chemistry of their lignins, quality of their hemicelluloses, and quantity and quality of their resins, all of which may play a role in species differences in nutrient cycling. Conifer wood contains almost exclusively guaiacyl lignin, which is typically more resistant to microbial decomposition than the syringyl lignins contained

in the wood of hardwoods. Secondary compounds like resins deposited in the heartwood can inhibit microbial decomposition through direct toxicity as observed in many conifer species (Cornwell *et al.* 2009, Hennon *et al.* 2007).

Carbon compounds in wood are mostly in the form of cellulose or lignin, so carbon is released by action of these fungi throughout decay (Wiebe 2012). Since conifer wood is typically more abundant in lignin, and is decomposed mostly by brown-rot fungi that do not break down lignin, carbon release in conifer wood may be less rapid than in hardwoods. The overall concentration of C may remain at higher level or appear to increase, as complex C rich compounds like lignin within the wood progress very slowly through decomposition. As this is occurring, the rest of the wood has been significantly degraded and a significant amount of mass loss will have occurred.

C:N Ratio

The combination of increasing N concentrations as decomposition progressed, along with C concentration declines in the later stages of decay, resulted in a continuous decrease in C:N ratio for both weighted average and component based analysis. Decreases observed in C:N ratio may be a result of mycelial N translocation by wood dependent fungi (Schimel and Hättenschwiler 2007) and by asymbiotic N fixation (Brunner and Kimmins 2003). The stability of the C:N ratio observed in early stages (DC 1 to DC 3) of decay reflects a well-recognized first phase of decomposition (*e.g.* Strukelj *et al.* 2013, Wiebe 2012, Yatskov *et al.* 2003) in which all concentrations of

organic fractions remain mostly stable. This stability occurs as organic compounds are degraded simultaneously (Strukelj *et al*. 2013). Wiebe *et al*. (2012) found that this initial phase of slow decay and N immobilization is followed by a subsequent release during a phase of rapid decay that may serve to provide an available source of N to regenerating plants prior to crown closure. Our results did not provide any indication of reaching the final stage of extended, moderately slow decomposition in which few changes in chemical composition occur (Wiebe *et al*. 2012). A long term temporal wood decay study examining chemical composition in DWD over time, or a similar analysis with a full scope of all five decay classes may be useful in reaching a better understanding of the three stages of decay highlighted above.

RECLASSIFYING DECAY CLASSES BASED ON QUANTITATIVE VARIABLES

The qualitative variables initially used to classify log bolts were largely based on log surface characteristics such as the integrity of the wood, and bark cover. Classification of deadwood using these qualitative variables lacked consideration of the complete internal structural components of deadwood bolts that are considered in the quantitative analysis. Our results from the discriminant analysis for physical variables only, showed that density, the proportion of solid wood, and the proportion of decayed wood are the physical factors that contribute most to quantitative classification of DWD into decay classes. However, the physical variables that were less important in showing the greatest differences between decay classes are also valuable in contributing to a more

robust decay classification system for DWD as all showed significant differences. Variables such as the proportion of log elevated that held little importance in distinguishing between decay classes may prove to be of greater significance with longer-term sampling.

The results of this discriminant analysis strictly based on physical variables demonstrated that as hypothesized, DC 1 and DC 5 were considerably more distinct than the middle decay classes based on their qualitative characteristics, with 71.3% of DC 1 and 73.8% of DC 5 reclassifying successfully into their respective qualitative decay classes. However, a considerable amount of reclassification of DC 1 and DC 5 into other quantitatively derived decay classes still occurred. The qualitative middle decay classes (DC 2, DC 3, and DC 4) had substantial overlap when reclassified based on their quantitative characteristics, as hypothesized. However, further overlap of some of these middle decay classes occurred into DC 1 and DC 5. For example, a portion of the logs qualitatively classified as DC 3, reclassified into quantitative DC 1 (2.8%) and DC 5 (4.63%) as a result of the discriminant analysis. Because of the lack of consistently clear distinction between DC 2, DC 3, and DC 4 from DC 1 and DC 5, grouping these middle classes into one middle decay class is not an obvious choice based on this quantitative model. However, it could be investigated whether the patterns and processes within our results linked to the three-phase decomposition process, might correspond more closely to the reassigned DCs, compared to the original qualitative assignments. If this was found to be true, and the statistical analyses (i.e. ANOVAs) were rerun using the quantitatively assigned DCs, the patterns in density and the proportion of components throughout the decay process may more closely resemble the three-phase decomposition

process, and as a result be deemed well suited to a 3 DC deadwood classification system that corresponds with the three phases.

In order to directly compare the results of the CDA with physical variables only and the CDA with physical and chemical variables included, a full scope of samples from all five decay classes in both is necessary. This was not feasible in the scope of this thesis, but would be useful in future studies. Some comparison can, however, be made between the results from the two CDAs performed in this thesis. For example, in the physical only CDA, 4.6% of samples qualitatively classified as DC 3 were reclassified into DC 5, whereas in the second CDA, only 2.8% reclassified this way. This may imply an improved predictive strength of the model with the addition of chemical variables, although, if DC 2 and DC 3 were included in the second CDA, further reclassification may have still occurred. Because of this, making conclusions regarding the differences in predictive strength of decay classification models that include just physical compared to physical and chemical variables remains difficult at this time. However, because of the importance of DWD in nutrient cycling as discussed in previous sections, and the significant patterns of nutrient concentrations and ratios observed in the results, the inclusion of these chemical variables likely contributes to a more robust classification system. In addition, re-running the statistical analysis (*i.e.* ANOVAs) for chemical variables using the quantitatively derived decay classes rather than the original qualitative assignments, could reveal a closer resemblance to the three-phase decomposition process as it relates to nutrient patterns in DWD.

CONCLUSION

MANAGEMENT CONSIDERATIONS

This study has shown that the physical and chemical properties of DWD vary between species, and throughout the decay process. With the anticipated increase in utilization of forest biofibre previously considered unmerchantable (i.e., other uses beyond traditional wood products) continues to rise, maintaining DWD within the thresholds defined in forest management and/or biomass harvesting guidlines will become even more critical to ensure adequate deadwood recruitment that reflects levels observed in natural stands. Management requirements for DWD recruitment should ensure deadwood retention that includes a variety of hardwood and conifer species, and at various stages of decomposition. Maintaining this variety of DWD in managed forests will ensure long-term availability of deadwood habitat for saproxylic species and contribute to a variety of ecosystem functions and services.

CLASSIFICATION SYSTEM

As this thesis examines the establishment data for a longer-term temporal wood decay study, the quantitative classification system can be applied to the logs that will be

observed over time. Using the results of this thesis to reclassify logs at the study sites into quantitatively-based decay classes may provide a better basis for long term examination of changes in DWD throughout the decay process. The quantitative classification system provides a more robust set of baseline data for the log bolts at each site compared to the qualitative decay classes originally assigned.

Using a 3-class DC system may be a possibility as middle three decay classes largely reclassified into each other upon quantitative analysis. However, further investigation of this possibility through a study involving a CDA including physical and chemical parameters for all five decay classes may clarify how model performance and distinction between decay classes improves with the inclusion of chemical variables. Until this type of study is possible, a 5 decay class system will ensure that DWD log bolts significantly different in their quantitative characteristics are properly classified.

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APPENDICES

APPENDIX I

ANALYSES OF VARIANCE FOR PHYSICAL AND CHEMICAL VARIABLES

This section presents the outputs from a series of ANOVAs performed using the PROC GLM procedure of SAS software to evaluate the effect of moisture regime, species, and decay class, on various quantitative physical and chemical variables.

ANOVA results for density as the dependent variable.

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
MR	2	0.09770669	0.04885335	13.66	<.0001
Block2 (MR)	15	0.09587853	0.0063919	1.79	0.0335
Spp	1	0.12130239	0.12130239	33.93	<.0001
Dclass	4	6.04277407	1.51069352	422.55	<.0001
MR*Spp	2	0.04719131	0.02359565	6.6	0.0015
MR*Dclass	8	0.02999074	0.00374884	1.05	0.3983
Spp*Dclass	4	0.02674098	0.00668525	1.87	0.1145
MR*Spp*Dclass	8	0.01692047	0.00211506	0.59	0.7851
Error	494	1.76614356	0.00357519		
Total	538	8.24464874			

ANOVA results for PercSolid (percent solid wood) as the dependent variable.

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
MR	2	3899.6136	1949.8068	4.59	0.0106
Block2 (MR)	15	16616.5013	1107.7668	2.61	0.0009
Spp	1	3008.6973	3008.6973	7.08	0.008
Dclass	4	468363.5176	117090.8794	275.58	<.0001
MR*Spp	2	1219.2380	609.6190	1.43	0.2392
MR*Dclass	8	15886.1569	1985.7696	4.67	<.0001
Spp*Dclass	4	5777.5854	1444.3963	3.40	0.0093
MR*Spp*Dclass	8	10520.4115	1315.0514	3.10	0.0020
Error	494	209891.5113	424.8816		
Total	538	735183.2329			

ANOVA results for PerDecay (percent decayed wood) as the dependent variable.

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
MR	2	4095.8963	2047.9482	5.19	0.0059
Block2 (MR)	15	14859.4382	990.6292	2.51	0.0014
Spp	1	253.2979	253.2979	0.64	0.4235
Dclass	4	478815.0603	119703.7651	303.17	<0.0001
MR*Spp	2	1124.8808	562.4404	1.42	0.2416
MR*Dclass	8	9701.8388	1212.7298	3.07	0.0022
Spp*Dclass	4	3772.119	943.0298	2.39	0.0501
MR*Spp*Dclass	8	6209.2424	776.1553	1.97	0.0489
Error	494	195048.5679	394.8352		
Total	538	713880.3416			

ANOVA results for PerBark (percent bark) as the dependent variable.

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
MR	2	351.939121	175.96956	2.66	0.0707
Block2 (MR)	15	3567.826619	237.855108	3.6	<.0001
Spp	1	5699.389036	5699.389036	86.25	<.0001
Dclass	4	5340.237873	1335.059468	20.2	<.0001
MR*Spp	2	1052.134387	526.067194	7.96	0.0004
MR*Dclass	8	2020.570454	252.571307	3.82	0.0002
Spp*Dclass	4	1844.756255	461.189064	6.98	<.0001
MR*Spp*Dclass	8	1970.395409	246.299426	3.73	0.0003
Error	494	32643.57919	66.08012		
Total	538	54490.82834			

ANOVA results for PerChaff (percent chaff) as the dependent variable.

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
MR	2	8.427025	4.213512	2.66	0.0707
Block2 (MR)	15	555.064313	37.004288	3.6	<.0001
Spp	1	22.348009	22.348009	86.25	<.0001
Dclass	4	2103.727203	525.931801	20.2	<.0001
MR*Spp	2	140.983518	70.491759	7.96	0.0004
MR*Dclass	8	68.520580	8.565072	3.82	0.0002
Spp*Dclass	4	265.992220	66.498055	6.98	<.0001
MR*Spp*Dclass	8	263.570904	32.946363	3.73	0.0003
Error	494	8237.299420	16.6747		
Total	538	11665.933192			

ANOVA results for C:N ratio as the dependent variable for the solid wood component.

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
Species	1	884896.633	884896.633	39.49	<0.0001
DC	2	1150701.761	575350.881	25.68	<0.0001
Species*DC	2	4512.919	2256.459	0.1	0.9043
Error	78	1747731.902	22406.819		
Total	83	3787843.215			

ANOVA results for C:N ratio as the dependent variable for the decayed wood component.

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
Species	1	250923.3584	250923.3584	36.62	<0.0001
DC	2	586100.0054	293050.0027	42.77	<0.0001
Species*DC	1	63914.114	63914.114	9.33	0.0033
Error	64	438524.994	6851.953		
Total	68	1339462.472			

ANOVA results for C:N ratio as the dependent variable for bark component.

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
Species	1	35455.53	35455.53	15.14	0.0002
DC	2	93556.05	46778.02	19.97	<0.0001
Species*DC	2	54702.67	27351.33	11.68	<0.0001
Error	81	189721.11	2342.24		
Total	86	373435.36			

ANOVA results for N as the dependent variable for the solid wood component.

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
Species	1	0.0317	0.0317	34.13	<.0001
DC	2	0.0413	0.0207	22.27	<.0001
Species*DC	2	0.0100	0.0050	5.4	0.0064
Error	78	0.0723	0.0009		
Total	83	0.1553			

ANOVA results for N as the dependent variable for the decayed wood component.

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
Species	1	0.1558744	0.1558744	19.18	<.0001
DC	2	0.56282126	0.28141063	34.63	<.0001
Species*DC	1	0.00096968	0.00096968	0.12	0.7309
Error	64	0.52000434	0.00812507		
Total	68	1.23966968			

ANOVA results for N as the dependent variable for the bark component.

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
Species	1	0.29678074	0.29678074	10.74	0.0015
DC	2	0.85049333	0.42524666	15.38	<.0001
Species*DC	2	0.20344981	0.1017249	3.68	0.0295
Error	78	2.23890909	0.02764085		
Total	83	3.58963297			

ANOVA results for C as the dependent variable for the solid wood component.

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
Species	1	34.35154813	34.35154813	43.7	<.0001
DC	2	12.97268334	6.48634167	8.25	0.0006
Species*DC	2	3.40230387	1.701151935	2.16	0.1217
Error	78	61.3182115	0.786130917		
Total	83	112.0447468			

ANOVA results for C as the dependent variable for the decayed wood component.

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
Species	1	5.92100859	5.92100859	1.73	0.1928
DC	2	27.019751	13.5098755	0.0241	0.0241
Species*DC	1	0.76937876	0.76937876	0.6368	0.6368
Error	64	218.7685787	3.418259		
Total	68	252.4787171			

ANOVA results for C as the dependent variable for the bark component.

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
Species	1	41.99020682	41.99020682	6.87	0.0105
DC	2	14.52381237	7.26190619	1.19	0.3099
Species*DC	2	80.62809055	40.31404527	6.6	0.0022

Error	81	494.9217289	6.1101448	
Total	86	632.0638386		

2-way ANOVA results for weighted nitrogen averages by species and decay class. MR and Block were dropped from the model as they were insignificant

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
Species	1	0.27882012	0.27882012	66.99	<.0001
Dclass	2	0.65933216	0.32966608	79.21	<.0001
Species*DC	2	0.02934632	0.01467316	3.53	0.0331
Error	101	0.42038051	0.004162183		
Total	106	1.38787911			

2-way ANOVA results for weighted carbon averages by species and decay class. MR and Block were dropped from the model as they were insignificant

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
Species	1	8.6933658	8.6933658	0.76	0.3852
Dclass	2	223.0237566	111.5118783	9.76	0.0001
Species*DC	2	74.8188661	37.40943305	3.27	0.0419
Error	101	1154.164013	11.42736647		
Total	106	1460.700002			

2-way ANOVA results for weighted C:N ratio averages by species and decay class. MR and Block were dropped from the model as they were insignificant

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
Species	1	899098.441	899098.441	76.18	<.0001
Dclass	2	1885473.035	942736.5175	79.88	<.0001
Species*DC	2	217205.727	108602.8635	9.2	0.0002
Error	101	1191961.142	11801.59547		
Total	106	4193738.35			

APPENDIX II

ANALYSES OF VARIANCE FOR MICROCLIMATE MONITORING RESULTS

This section presents the outputs from a series of ANOVAs performed using the PROC GLM procedure of SAS software to evaluate the effect of Ecoregion and Moisture Regime on soil moisture and soil temperature.

2-way ANOVA to investigate the effect of ecoregion and moisture regime on average soil temperature (°C).

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
Region	1	32.11420907	32.11420907	31.46	<.0001
MR	2	45.99751587	22.99875794	22.52	<.0001
Region*MR	2	6.27462547	3.137312735	3.07	0.0529
Error	66	67.3631235	1.020653386		
Total	71	151.7494739			

2-way ANOVA to investigate the effect of ecoregion and moisture regime on average soil moisture (m^3m^{-3}).

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
Region	1	0.00122534	0.00122534	1.09	0.2996
MR	2	1.53092635	0.765463175	682.88	<.0001
Region*MR	2	0.02612029	0.013060145	11.65	<.0001
Error	66	0.07398189	0.001120938		
Total	71	1.63225387			

1-way ANOVA to investigate the effect of MR on average soil moisture (m^3m^{-3}) in the NE region as indicated by the significant MR*Ecoregion interaction.

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
MR	2	0.74044765	0.370223825	265.66	<.0001
Error	33	0.04598812	0.001393579		
Total	35	0.78643577			

1-way ANOVA to investigate the effect of MR on average soil moisture ($m^3 m^{-3}$) in the NW region as indicated by the significant MR*Ecoregion interaction.

Source	DF	Type I Sum of Squares	Mean Square	F Ratio	Pr > F Ratio
MR	2	0.81659898	0.40829949	481.32	<.0001
Error	33	0.02799377	0.000848296		
Total	35	0.84459275			