THE DISTRIBUTION AND ROLE OF DOWNED WOODY DEBRIS IN NUTRIENT RETENTION AND CYCLING DURING EARLY STAND ESTABLISHMENT

by

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A Graduate Thesis Submitted in

Partial Fulfillment of the Requirements for the

Degree of Doctorate of Philosophy in Natural Resources Management

Faculty of Natural Resources Management

Lakehead University

September 14, 2012

ACKNOWLEDGEMENTS

This research would not have been possible without the support of many individuals and organizations. I would like to start by thanking the Natural Sciences and Engineering Research Council for the financial support that allowed me to work solely on my research. The program funding from the Ontario Ministry of Natural Resources not only supported the cost of field work, laboratory analyses, and staffing, but connected my work to the Province's continually evolving forest biofibre policy.

A special thank-you to the staff of the Centre for Northern Forest Ecosystem Research, specifically to Robert Whaley, Laura Edgington and Alissa Ramsay in the Stand Ecology branch. I borrowed enough equipment from the lab to warrant my own spot on the staff sign-out board, and without their helpfulness I would still be working on my research. The same can be said of the staff at the Forest Resources and Soils Testing Laboratory: Joel Symonds, Claire Riddell and Derek Lawrence, who were "instrumental" (pun intended) in helping me understand the ins and outs of my analyses. My summer staff, Neil Hillis and Christine Hague, was a joy to work with. Joan Lee, Greenhouse Manager, was patient and accommodating to the many, many reconfigurations of the greenhouse layout that I made to accomplish my *ex-situ* research trials. It was a pleasure to collaborate with Dr. Jay Malcolm, Jessica Iraci and the rest of the research team at the University of Toronto. I would be remiss if I did not also thank the entire faculty and staff in the Faculty of Natural Resources Management at Lakehead University for their willingness to assist in any way.

It is hardly fair that my name is the only one on the cover of this dissertation; my committee has provided support above and beyond what was expected. Dr. Leni Meyer provided excellent advice and helped me calibrate my soil measurement instruments. Dr. Douglas Reid was always active in my many committee meetings and his advice regarding experimental design and bigger picture thinking helped me form the pillars of my research. I don't think I can adequately thank Dr. Dave Morris enough for his role in shaping me as a researcher; the devout concern and attention that he has given my work has been exemplary from beginning to end. Lastly, it was Dr. Nancy Luckai who convinced me to pursue graduate studies, and I am indebted to her guidance and wisdom; her ability to see the best in everyone has inspired me to do likewise. Many thanks as well to the external examiner of this thesis, Cindy Prescott, who has provided a valuable comments and suggestions, particularly pertaining to the interpretation of the findings of the thesis.

I would like to end by thanking my friends and family, who have always been supportive of my goals. My two sons, Noah and Max, have kept me grounded in reality. My wife Angela has been my biggest support: she has truly shown her selfless and patient character through it all, and my gratitude for everything that she is cannot be expressed in words.

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EXECUTIVE SUMMARY

Coarse woody debris (CWD) in boreal ecosystems has been hypothesized to play an important nutritional role following stand-replacing disturbances such as fire or harvest. Sites with shallow soil over bedrock or those with coarse textured soils can be especially susceptible to overstory removal as low carbon and nutrient pools may limit stand productivity in subsequent rotations.

This dissertation includes results from a series of *in-situ* and *ex-situ* experiments examining the nutritional role of CWD. The *ex-situ* experiment was designed to evaluate whether species (aspen, spruce), origin (fire, harvest), and/or decay class (1-5) influence the timing, and rate of nutrient release from CWD. Source/sink relationships of CWD leachate were largely a function of CWD decay stage for C (source, peaking at decay class 4 and then a slight decline in decay class 5), N (initial sink to eventual source) and P (initially a large source followed by low rate of release). Leachate values from harvested logs were similar to those of fire origin, with the exception of N and Mn, suggesting considerable volatilization of these two nutrients during wildfire events.

The *in-situ* studies were conducted on sites that were experimental-harvested in 1994, with the regenerating stands now approaching crown closure. Two soil types (fresh, loamy : dry sandy), with stand replicates were chosen; the experimental harvest areas were designed to document carbon loss and nutrient fluxes after the application of four levels of biomass removal from mature black spruce stands in northwestern Ontario.

Nitrogen concentration in the CWD increased throughout the 14-year sampling period, but was largely a function of increasing carbon loss. When converted to N content in CWD (kg

ha^{-1}) however, nitrogen exhibited an initial upward trend (i.e., immobilization) through years 1-4 and a subsequent release in years 5-14. This trend was more apparent on the dry, sandy sites. Comparing the average loss of N from CWD in 4 to 14 years to the soil inorganic N pool revealed that the N loss from CWD represented a substantive portion of the available N pool, particularly on the dry, sandy sites. After an initial peak in year 4, black spruce foliar N decreased significantly ($p<.0001$) through to year 10, but began to rebound by year 14. This increase coincided with the documented release of N from CWD.

A 1-year, *in situ* study, using ion exchange resins, also found that nitrogen, in its available NH_4 form, was lower in the soil under CWD, indicating movement from the soil to the CWD.

These combined results suggest that CWD, although a small contributor to the total N pool, makes a significant contribution to the relatively small available N pool, especially on dry, sandy soils. The trend of initial N immobilization and subsequent release shows CWD may also serve to buffer the initial leaching of nutrients from the site following harvesting and provide an available source of N to the regenerating stand prior to crown closure.

The "zone of influence" of CWD on soil nutrient availability was found to not extend beyond the boundaries of the log. The abundance and distribution of CWD on the landscape is therefore important to quantify, especially post-harvest. In this study there was negligible difference of site nutrients between stem-only versus full-tree harvesting despite a near doubling of CWD in the stem-only treatment. This should not be surprising, however, as CWD is only one of a myriad of factors influencing site nutrient pools. It was rather unique to be able to isolate a nutrient signal from CWD in an *in-situ* experiment, as it has been difficult to accomplish in other studies.

To summarize, CWD does influence soil nutrient pool dynamics, notably at the scale of plant-available forms of nutrients (as opposed to total nutrient pool comparisons). This influence is normally small, but is greatly enhanced in dry, sandy soils. Current full-tree harvesting practices did reduce CWD retention levels when compared to stem-only harvesting, but still appear to retain adequate amounts of CWD; there was no evidence in this study to suggest there was a reduction in soil productivity in the full-tree harvesting treatments. Future forest policies regarding increased biomass removal should regard both i) the amount of CWD retained, and ii) the soil texture of the site. Research should be directed at creating a more detailed matrix of soil/CWD interactions to better inform policy directives.

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INTRODUCTION

Coarse woody debris (CWD), and its subsequent management, has been gaining momentum as a biological driver ever since it shifted in status from problem substrate (e.g. *how can we get rid of all this wood that's plugging up the stream?*), to a key ecological component. If publications can be used as a measure of scientific activity, this process began in the early 1980s, with works by Lambert, Lang, Harmon and others leading the way. Tracing this further back, part of the catalyst for this research can be traced to the energy crisis of the late 1970s, where governments, faced with intense public pressure to find alternative energy sources to fossil fuels, created publicly funded programs such as "Energy from the forest" (ENFOR). These programs were specifically designed to research the capacity of our forests for increased exploitation; that is, going beyond the traditional use of "logs" in forest manufacturing to considering the entire tree and even understory vegetation as fodder for biomass production.

Ecologists, of course, were eager to add their voice to this new direction, setting up research programs to explore issues of site productivity, sustainability and biodiversity. Very early on, coarse woody debris was singled out as an important component for two reasons; firstly, the "woody" component of CWD represents a significant portion of total woody biomass and is therefore easily converted to usable, economically viable energy. Secondly, the abundance and long residency of CWD on the natural forest landscape point toward CWD as a potentially important long-term ecological component that needs to be understood within the context of whole ecosystem function. Since Lambert et al. (1980) concluded their *Ecology* paper with the caution that "*… to neglect dead wood may be to miss a vital part of forest ecology",* the voices of ecologists have grown to a choir, and published articles relating to coarse wood have increased steadily, from a few articles in 1980 to over 150 by 2008.

Scandinavian forestry is famously “progressive” in management and utilization of forest resources, and it follows that many early research programs exploring the role of CWD on the landscape originate from that area. Canadian forests are not managed with the same intensity, but are unique, as they are managed primarily as a public resource rather than privately held land. As such, the mandate for most forested land in Canada is not necessarily optimal exploitation of resources but rather the maintenance or enhancement of existing ecosystems and management of all forest-based values (CFSA 1994). Subsequent management strategies primarily focus on emulating natural disturbances and are enforced through provincial policies and guidelines. Due to the ubiquity of CWD on the natural landscape, especially following disturbance, Canadian CWD research has been designed to inform public policy makers across the country of the implications of CWD removal to the natural ecosystem. The creation of the Canadian Intersite Decomposition Experiment (CIDET) in 1992 has developed a nation-wide linkage research on decomposition (Trofymow et al. 1998). Other related large-scale research projects that incorporate Canadian participation either in part or in whole include the North American Long Term Site Productivity (LTSP) network, Soils of the Ecosystem Management Emulating Natural Disturbance (EMEND), and BOReal Ecosystem-Atmosphere Study (BOREAS) (Powers 2006, Halliwell and Apps 1997, Kishchuk 2004).

Renewable energy is once again on the forefront of public interest, and it is interesting to see the parallels from a generation ago. While there have been many advances, especially in chemistry and microbiology, field-based research has remained relatively unchanged. Long term studies, many created from the last “energy crisis” have proved invaluable to present research.

This research project aims to build on work done through the LTSP network installation in northwestern Ontario by collating previous work, framing it within the context of contemporary issues, and performing the necessary tasks (additional experimentation, analysis) to successfully address Ontario's current forest management objectives.

Mounting interest in the use of biomass for fuel means that we need to understand more completely the impacts of intensive harvest on these sites. At the outset, we were prompted to more carefully consider the role of CWD in forest productivity by two hypotheses presented by Laiho and Prescott (2004). Specifically, that:

1. On sites where nutrients, especially N or P, limit plant growth, CWD accumulation may reduce primary productivity through immobilization of nutrients by decomposers, and
2. On dry sites, where lack of moisture limits plant and microbe growth, CWD may increase primary productivity and enhance element cycling by improving moisture retention.

On such sites, CWD may also be important for the retention and accumulation of soil organic matter. This dissertation will also attempt to more directly address the amount or form of nutrients sequestered within, and provided by, CWD. Using established experiments with a history of pertinent data supplemented by additional measurements, the goal of this dissertation is to clarify the role of CWD of these forest types and identify the potential effects of increased utilization for bio-fibre and bio-energy on these ecosystems.

1.0 LITERATURE REVIEW

The 1980 *Ecology* paper by Lambert *et al.* concludes with a caution: "*To neglect dead wood may be to miss a vital part of forest ecology*". Indeed, interest in coarse woody debris (CWD) has soared since 1980 (Figure 1.1), as the role of CWD has transformed from being viewed in the past as a problem substrate to its current status as key ecological component. A review by Jonsson and Kruys (2001) offers three main areas of current research: 1) understanding patterns of CWD following disturbance, including the effects of forestry, 2) the role of CWD in nutrient dynamics (especially carbon), and 3) the importance of CWD to biological diversity. This review will cover all three topics, although special emphasis will be given to nutrient dynamics of CWD as the research continuing from this paper will explore this theme.

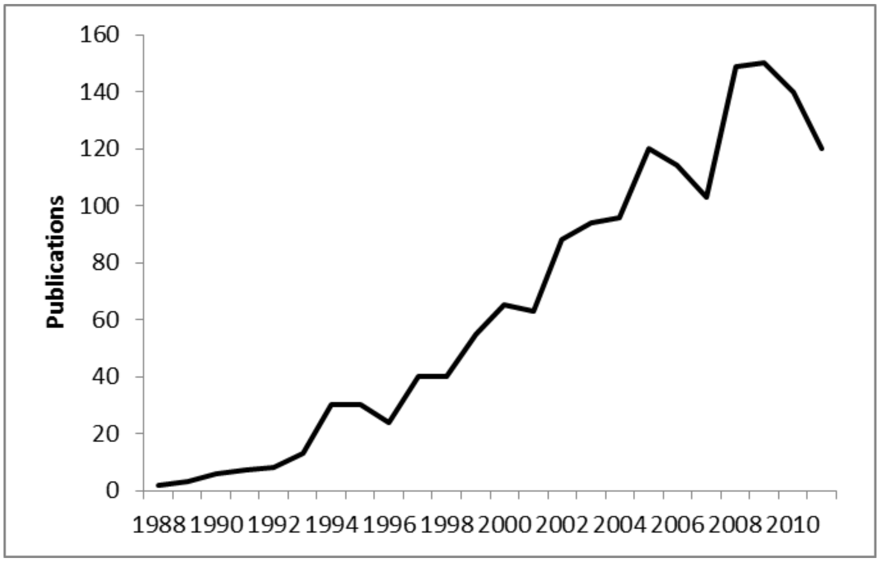

Figure 1.1. Items published per year since 1980 with key word "coarse woody debris". Source: Web of Science

1.1 Importance of dead wood

It is important to briefly review previous ecological research on CWD in general, as it will give greater insight on the importance of CWD in the broader forest ecosystem.

Coarse woody debris, or “deadwood” in the boreal forest generally refers to the bole of the tree, and, in the case of some hardwoods, large branches that enter the forest cycle through tree mortality. Stevens (1997) expands this definition to include *stumps and coarse wood in all stages of decay… material generally greater than 7.5 cm.* This coarse wood has long been hypothesized to play a role in the maintenance of forest productivity (Harmon *et al.* 1986) as well as many other ecological purposes. Stevens (1997) summarizes the role of coarse wood into four broad categories: 1] forest productivity, 2] habitat and structure to maintain biological diversity, 3] geomorphology of streams and slopes, and 4] long-term carbon storage (Table 1.1).

Table 1.1. Summary of the ecological role of coarse woody debris (*adapted from Stevens (1997)).*

Forest productivity	**Biological diversity**	**Streams & slopes**	**Carbon storage**
Adds organic matter to soil	Site for nests, dens and burrows	Large woody debris loads in streams	Important pool of carbon
Retain moisture in dry periods	Habitat for microbial decomposers	Slope stability	Storage capacity of large CWD
Represent a capital pool of nutrients for ecosystem	A primary energy source for complex food web	Soil surface stability, prevention of erosion	
Provide site for regeneration of conifers	Cover for both predators and prey	Control of storm surface runoff	
Contribute to soil acidification and podsolization	Moist microsite for amphibians, insects, worms, plants, etc.		
	Refugia during disturbance and stress		

1.2 Forest productivity

All forest litter (leaves, twigs etc.), including CWD, contains nutrients. Overall nutrient inputs from outside sources (e.g. atmospheric deposition) are low compared to the amount of cycling that occurs within the system (Harmon *et al.* 1986, Laiho and Prescott 2004, Ganjegunte *et al.* 2004). Decomposition of organic matter drives the recycling process, where the nutrients can be released from the various organic components (leaves, CWD, etc.) and returned to the system in available forms (Aber and Melillo 1991) (Figure 1.2). The “quality” of organic matter is dependent on both carbon and nutrient allocation strategies within the plant as well as the type of litter being decomposed. Coarse woody debris contains the largest pool of organic carbon in many forests (Zhou *et al.* 2007) and although nutrient concentrations may be lower than quickly decomposing fine litter, the actual amount (content) may be higher (Hafner *et al.* 2005), and so it is important to study the dynamics of decomposition to better understand how CWD is recycled into the ecosystem (Graham and Cromack 1982, Ganjegunte *et al.* 2004).

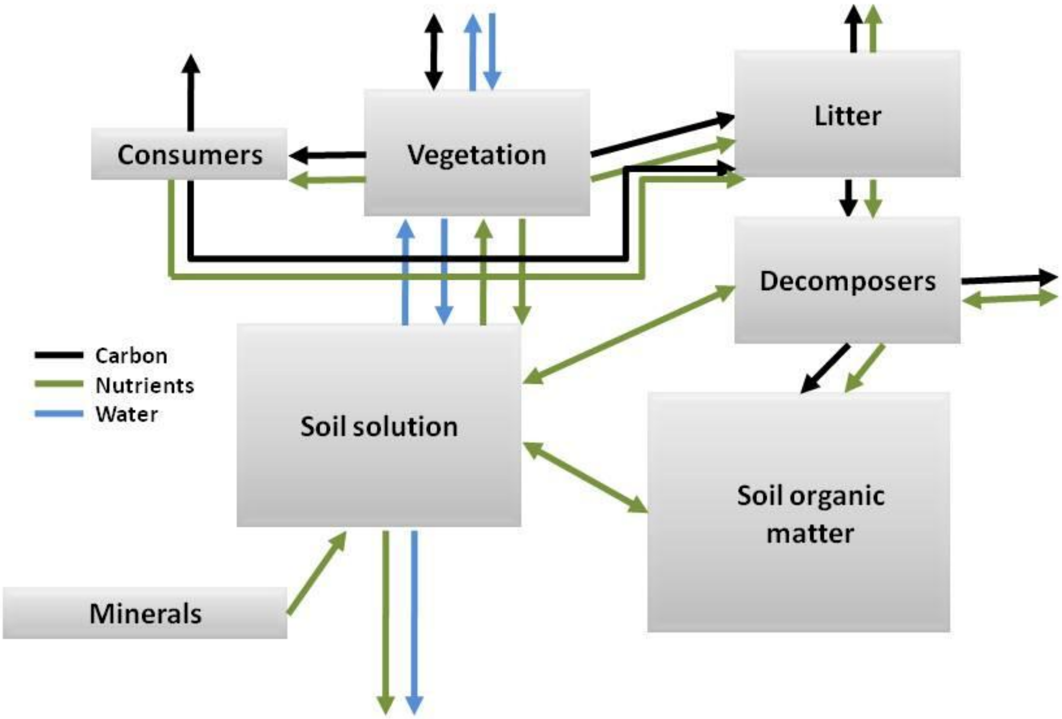

Figure 1.2 Nutrient dynamics in terrestrial ecosystems (*Adapted from Cole and Rapp 1981, Aber and Mellilo 1991*).

Wood is characteristically lower in sugars and starch than foliage or fine roots with the majority of carbon compounds in the form of cellulose (80%) or lignin (15%). Cellulose can be considered moderate in terms of quality as a decay substrate, as it requires external enzymes to break the large polymers into simple sugars. Lignin molecules, however, are very resistant to decay. Large amounts of energy are required for decomposition with almost no energy gain as a result (Aber and Melillo 1991). Current research on lignin may show a different picture, however, as Preston and Trofymow (2008) questions both the amount of true lignin in the wood and the amount of time it takes to decompose.

In many cases, the nutrient cycle in coarse wood starts with an initial immobilization of some essential nutrients (like nitrogen) as decomposer microbes consume available nutrients (Harmon *et al.* 1994, Moore *et al.* 2006, Herrmann and Prescott 2008). Moore *et al.* (2006), studying foliar litter, found that as litter decays (eventually leading to the formation of soil organic matter) it becomes a net source of nutrients, and it is this loss of nutrients from litter that contributes to overall productivity of the forest ecosystem. A sampling of the published nutrient values in CWD on a per-hectare basis is shown in Table 1.2. Tracking nutrient flux rates by decay class without accounting for mass loss can result in an overestimate of a given nutrient remaining or even accumulating in the log (Krankina *et al.* 1999). Holub *et al.* (2001) recently reanalysed many of the studies listed in Table 1.1 by applying a "volume-adjusted method". Using this method, Holub *et al.* (2001) found that i) Ca and K were lost from CWD over time, ii) N and P gained or and had no net change and iii) Mg results were mixed. Krankina *et al.* (1999) used a similar technique and found that nutrient stores generally remained stable or declined during decomposition with or without volume adjustment, but that the *magnitude* of change was affected between the two techniques.

Table 1.2. Total pool of nutrients in dead boles and in parentheses, the amount of nutrients stored in dead boles as a percentage of total above- and below-ground, living, forest floor, and dead wood detritus.

Study	Species	N (kg/ha)	P (kg/ha)	K (kg/ha)	Ca (kg/ha)	Mg (kg/ha)	Na (kg/ha)
Harmon *et al.* 1986	Doug. Fir – West. Heml.	100-244	5-13	-	-	-	-
Graham and Cromack 1982	Sitka spr. – west. Heml.	146-223	17-29	39-61	147-197	18-29	6-14
Arthur and Fahey 1989	Englemann Spr.-subalp. fir	92.2 (7%)	4.89 (5%)	67.9 (16%)	156.6 (12%)	28.9 (17%)	0.74 (9%)
Kim *et al.* 2006	Quercus spp.	15.2-16.8	1.0-1.9	3.9-7.7	30.8	1.5	0.1-0.6

1.2.1 ROLE OF NITROGEN

Available, biologically active nitrogen is relatively rare when compared to the large pool of inert N that exists in the atmosphere. Although the pool may be small, its importance is not, as it is the third most abundant element in plant dry matter (10-30 g kg^{-1}) after carbon (ca. 400 g kg^{-1}) and oxygen (ca. 450 g kg^{-1}) (McNeill and Unkovich 2007).

Plants cannot uptake organic N, but N can become available through mineralization (mineral N). An important term in the terrestrial N cycle is the mineralization-immobilization turnover (MIT), which is the continuous transfer of mineral N into organic materials through incorporation of N into soil microbial biomass and return of that immobilized N back into mineral N (McNeill and Unkovich 2007). CWD could alter N availability and transformations in the soil directly beneath the CWD, causing CWD to be an important controller of spatial heterogeneity in N dynamics (Hafner and Groffman 2005)

In the N cycle, decomposition is driven by microbial biomass, organisms that provide the necessary enzymes for decomposition; the dead biomass itself also provides a pool of available soil N. Harmon *et al.* (1986) found that CWD stored 100-244kg ha^{-1} of N, with more advanced decay classes accounting for the most N storage (see "Content vs. Concentration" section below).

Although CWD is itself low in nitrogen, it can become a significant contributor in some ecosystems by hosting free-living, nitrogen fixing bacteria. Boulanger and Sirois (2006) found that after fire, the fast decomposition of subcortical tissues (i.e phloem), leaching, and insect activity resulted in an initial pulse of N out of the CWD, but that N increased again in CWD at the oldest site, which could be the result of asymbiotic N-fixation. Microbial activity increases as logs decay, and determining the origin of the nutrient (in this case N) that is now residing in the CWD and the fate of the nutrients that originated in the CWD has not been explored. Holub *et al.* (2001) advocate that stable or radioactive isotope tracers might be able to solve this by tracing nutrients through CWD, although the high cost, uncertainty of technique and suitability of nutrient cations suggest that this procedure requires further development.

Nitrogen is most often made available in the form of NH^{+}_{4} (ammonium) or NH_3 (ammonia) by soil micro-organisms. Most of this mineralization takes place in the upper 5 cm of the soil surface, where biological activity is highest and the majority of the dead and decomposing plant and animal litter exists, including CWD. Immobilization occurs with the assimilation of NH_4 and NO_3 by soil microbes, which may also immobilize N through amino acids (McNeill and Unkovich 2007). Moore et. al (2006) point out that the accumulation of N in decomposing litter may be associated with chemical immobilization, where, for example, ammonia-N has an affinity for litter low in N concentration and the ammonia is then chemically fixed to the litter and humus. Brais *et al.* (2006) found that only white birch (*Betula papyrifera* Marsh.) acted as a net sink for N, while trembling aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* (Moench) Voss) and jack pine (*Pinus banksiana* Lamb.)were all net sources of N, although the latter two were of little magnitude. Similar increases of N (and P) content were found in logs of i) *Picea abies* between decay classes 3 and 5 (Butler *et al.* 2007) and ii) between 30 and 55 years following tree death in *Pinus contorta* (Fahey 1983). Garrett *et al.* (2008) found that nutrient contents of stumps and coarse roots of *Pinus radiata* (D. Don) also increased substantially during decay. In contrast, Krankina *et al.* (1999) reported N losses for three boreal tree species in Russia, and cite differences in methodology (e.g. accounting for bark loss), species, and environmental conditions as possible explanations. Krankina *et al.* (1999) hypothesized that abundant precipitation during frost-free days facilitates leaching while long winters, cool summers, and poor aeration may slow down nutrient immobilization from fungal and bacterial growth, root colonization, and atmospheric N fixation.

Postharvest retention of N may not actually be critical to long-term site productivity for several reasons, according to Laiho and Prescott (2004). First, nitrate is the nutrient most important in post-disturbance losses, as it increases following disturbance and is easily leached through the system. Nitrate is not readily immobilized by wood decay fungi (which do not use nitrate) and growth of these fungi is actually reduced in the presence of simple N forms, decreasing the likelihood of any immobilization of nitrate. Secondly, nitrate losses in the boreal forest region, which are often low in N, are small, and the utility of nitrate in cycling of nutrients for the future forest stand is subsequently low. Although Arthur and Fahey (1989) concluded that the role of CWD may not be as significant as expected, decaying CWD may be an important storage pool for base cations as well as stabilizing soil organic matter.

The type of soil that the CWD interacts with can also influence N availability, as soil structures such as clay lattices, or N adsorption to organic matter, can further immobilize ammonium through non-biological means (McNeill and Unkovich 2007).

1.2.2 PHOSPHORUS AND SULPHUR CYCLING

Phosphorus is used in nucleic acids (DNA and RNA), phospholipids, sugar phosphates and molecules with an energy rich pyrophosphate bond (e.g. ATP). Soil organic P dynamics are driven by microbial biomass (Bünemann and Condron 2007). Patterns of P release in CWD are quite variable, and Moore *et al.* (2006) hypothesize that there is a relationship between initial concentration of P in litter and the pattern of P loss. They found that litter with high initial P concentrations lost P, while those with low concentrations retained P. Initial loss of P in litter is reported by Monleon and Cromack (1996) and Titus and Malcolm (1999). According to Moore *et al.* (2006), initial retention of P in litter is reported by Staaf and Berg (1982), and Berg and Laskowski (1997). Harmon *et al.* (1986) found that older, more decayed logs accounted for the majority of P storage in *Pseudotsuga* dominated conifer stands. Smaller logs have a higher percentage of bark, which can also significantly alter P dynamics, as Krankina *et al.* (1999) reported initial P loss being driven by bark tissue loss.

Sulfur is contained in various coenzymes, vitamins and sulpholipids as well as two amino acids (cysteine and methionine). Microorganisms play an important role in S cycling, as they promote not only immobilization and mineralization, but also oxidation and reduction processes (Bünemann and Condron 2007).

1.2.3 MICRONUTRIENTS

Micronutrients are involved in structural and functional integrity of cell membranes as well as various enzymes and other active molecules in the plant. They are important for gene expression; biosynthesis of proteins, nucleic acids, growth substances, chlorophyll and secondary metabolites; metabolism of carbohydrates and lipids; stress tolerance, etc. (Rengel 2007). Micronutrients are therefore essential for plant growth, and there are eight that are generally accepted: Mn, Zn, B, Cu, Mo, Ni and Cl. The contribution of CWD in micronutrient cycling is not well-known (Krankina *et al.* 1999), as the majority of studies have focused on macronutrient dynamics.

1.2.4 CONTENT VERSUS CONCENTRATION

Changes in nutrient *concentrations* are more frequently reported than actual *content* changes, as most log surveys are done as a chronosequence (or a similar technique) and the initial mass of the log is not known. Laiho and Prescott (2004) investigated this, and discovered that nutrient content changes may be quite different than concentration changes. They report that studies by Lambert *et al.* (1980) and Alban and Pastor (1993) show net release of base cations and contrasting increases in contents of N and P as decay increases, although content changes are highly dependant on initial nutrient concentrations. For example, if the initial P concentration is low, the actual content of P within the log will also increase, although if P is initially high, P will increase very little, or even decrease – a phenomena reported by Alban and Pastor (1993), Arthur and Fahey (1990) and Prescott (1999). It is easy to understand how nutrient concentrations increase as mass decreases (most mass loss is carbon-based, so as C is lost, the nutrient proportion increases even if content stays the same, see Figure 1.3 and Figure 1.4). So why does content sometimes increase as well? Wood decaying fungi are the most likely source of nutrient accumulation in CWD, where they are eventually released from mycelia following grazing by invertebrates, interaction with other fungi or bacteria, or death (Boddy and Watkinson 1995). These fungal mycelia form long-lived networks that can relocate nutrients to areas many metres away from the source (Boddy and Watkinson 1995). Eventually, CWD does become a net source of nutrients, but this can take decades (Laiho and Prescott 2004). A conceptual model of basic CWD dynamics is shown in Figure 1.4, but clearly the role of CWD in nutrient dynamics is far more integrated into ecosystem function than simply determining the pattern of release of initial nutrient contents.

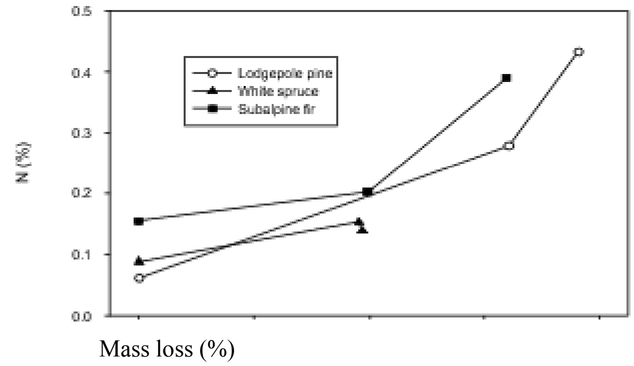

Figure 1.3 Concentrations of N and P in decaying log segments of three coniferous species. (Taken from Herrmann and Prescott 2008).

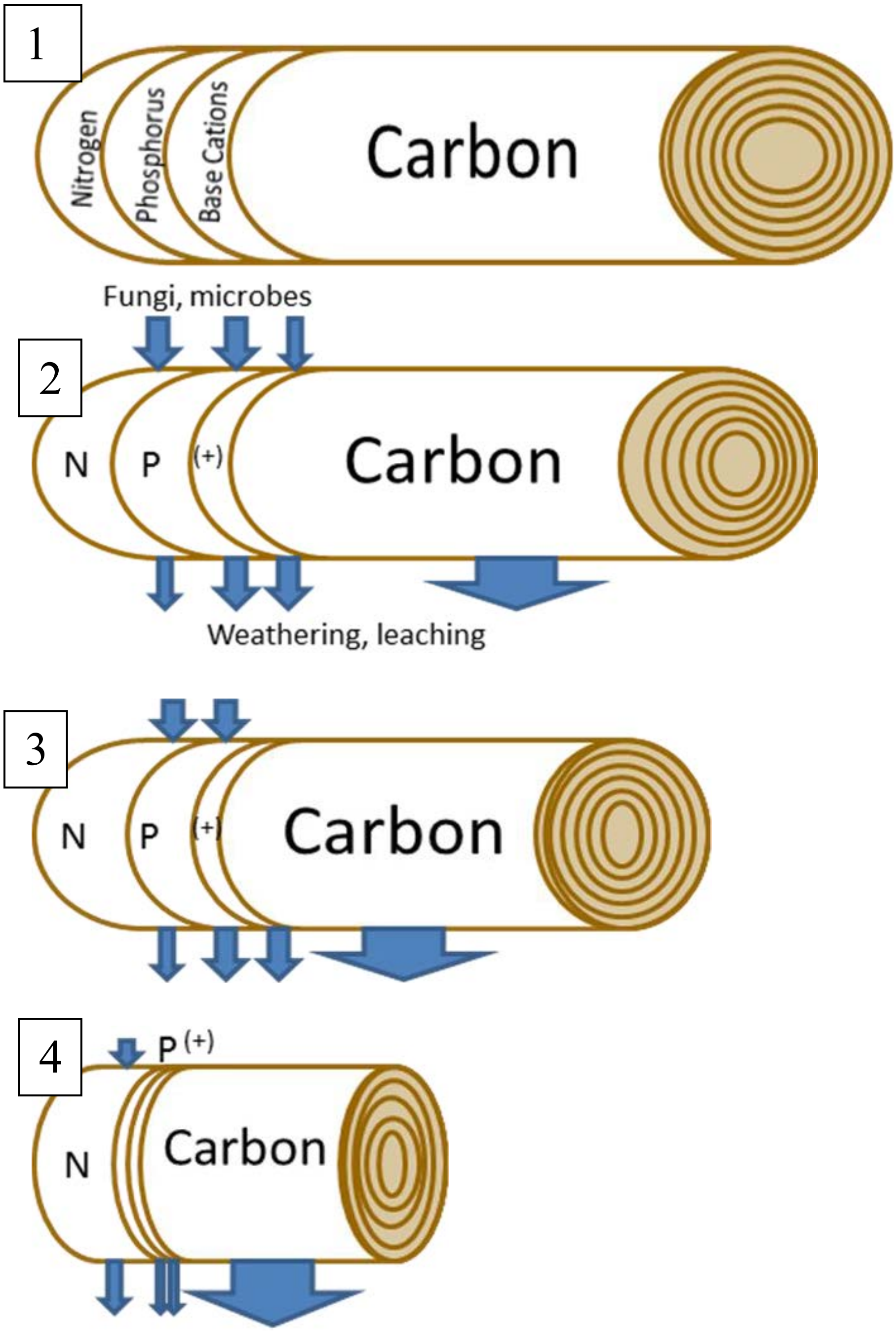

Figure 1.4 CWD dynamics during decomposition. Mass is lost primarily through carbon loss, nitrogen concentrations increase and N content also increases initially (up to stage 3) until being released. Phosphorus can be immobilized initially, but is often dependant on initial P concentration. Base cations are often variable, but often leach out of the system without immobilization.

1.2.5 SOIL ORGANIC MATTER

All CWD contributes to the soil organic matter of forest ecosystem. Stevens (1997) points out that in dry, inland forests, CWD is the most important organic material added to the forest soil in a rotation because it improves the moisture-carrying capacity and structure of the soil. Soil beneath CWD may be influenced by CWD leaching, affecting soil organic matter, microbial activity, and N availability (Hafner *et al.* 2005). As such, Stevens (1997) stresses the need for a continuous supply of organic materials to protect the productive potential of a forest soil. In fact, both Stevens (1997) and Harvey *et al.* (1987) point out that for forest managers, the manipulation of organic matter inputs is one of the most practical means of mitigating the effects of harvesting systems (such as clearcutting) that remove the standing crop from the forest site. The Long-Term Soil (or Site) Productivity (LTSP) research network is the most recognized program (several studies listed below are involved), and was developed to emphasize the impact of organic matter removal and compaction on forested sites (Powers 2006). Studies investigating the impact of harvest intensity on site productivity include: Phillips and van Lear 1984, Olsson *et al.* 1996, Morris 1997, Morris *et al.* 1997, Morris and Duckert 1999, Ballard 2000, Grigal 2000, Reich *et al.* 2001, Simard *et al.* 2001, Preston *et al.* 2002, Hannam *et al.* 2005, Kabzems and Haeussler 2005, Fleming *et al.* 2006, and Thiffault *et al.* 2007.

So far, results from studies on CWD removal through harvesting and soil organic matter effects have been mixed: Dai *et al.* (2001) found that clear-cutting resulted in the leaching of more highly decomposed organic matter, although the differences did not substantially alter the overall composition of SOM. Some studies (Bradley *et al.* 2001, Olsson *et al.* 1996) have found a net loss of nutrients in the soil after harvest regardless of harvest intensity, but in the case of Olsson *et al.* (1996) they do not factor in the role of CWD as an input to the soil nutrient pool. Pare *et al.* (1993) found that as time-since-(fire)-disturbance increased there was an accumulation of organic matter and total nutrients, although actual concentrations of available P and K decreased. Thiffault *et al.* (2006, 2007, 2008) found that harvesting treatments did not emulate wildfire biogeochemical conditions, which raises uncertainties about the long-term base nutrient availability (especially Ca and Mg) of harvested sites on Boreal Shield sites. Brais *et al.* (2000) investigated the impact of wildfire and subsequent salvage harvesting on the nutrient balance of boreal pine and spruce stands and found that salvage harvesting a severely burned site would result in depletions of Ca, Mg and K that would not recover in a 110-year rotation period.

1.2.6 SOIL TYPE

Highly productive soils can influence the nutrient content of the aboveground vegetation, which translates into CWD with higher nutrient contents. Vesterdal (1999) investigated the impact of soil type on decomposing foliage of beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst) and found that soil type may increase the decomposition of species that produce higher quality litter (i.e. deciduous trees). Research on soil type and decay of CWD is confounded with moisture availability, and needs further investigation.

1.3 Carbon storage

CWD is one of the largest pools of carbon in the forest ecosystem, accounting for 7-47% of all forest wood volume (Shorohova and Shorohov 2001). Krankina *et al.* (2001) also point out that many past assessments of carbon stores either ignore CWD completely or assume a relative proportion to live biomass. Carbon in the CWD pool is difficult to accurately assess, however, as CWD stores vary significantly over succession and do not necessarily parallel live biomass dynamics (Krankina *et al.* 2001). For example, Carmona *et al.* (2002) found that old-growth and primary forests had 10 times higher carbon storage in downed logs and snags than young-successional forests, creating a uneven CWD biomass distribution, which could also affect ecological functions and biodiversity. To alleviate some of the variation in C estimates, Sandstrom *et al.* (2007) developed biomass (density and carbon concentration) conversion factors based on decay class, based on visual characteristics that correlate to the degree of decay in the wood and are easily assessed in field surveys.

CWD reductions as a result of clearcutting can also change the chemical properties of the forest floor. For example, clearcuts were found to be higher in aromatic C and lower in phenolic C than uncut stands of boreal mixedwood aspen and spruce (Hannam *et al.* 2005). This change in C properties could result in C limitations and alter patterns of nutrient cycling as the forest floor has become more humified with reductions in C inputs following harvesting.

CWD not only plays a role in carbon storage, but also release. Wang *et al.* (2002) point out that carbon dioxide flux from CWD is an important source of CO_2 in forests with moderate to large amounts of CWD. In afforestation, woody debris can be a C sink that partly offsets the soil C loss after land use change (Guo *et al.* 2006).

1.4 Biological Diversity

Coarse woody debris provides habitat for many species of plants and animals (Samuelsson *et al.* 1994, Iraci *unpublished*) and many of the processes observed in CWD are foundational as a resource for living organisms. Siitonen (2001) conservatively estimates that 20-25% of all forest dwelling species in Finland are dependent on dead-wood habitats. Lonsdale *et al.* (2008) go so far as to label deadwood as an ecological “Noah’s ark”, storing and providing many of the elements needed for forest health and productivity.

1.4.1 AUTOTROPHS AND SAPROTROPHS

Many taxa of plants are associated with CWD, and as Harmon *et al.* (1986) specify, this includes not only saprotrophs (decomposer organisms) but also autotrophs that vary across the botanical spectrum, including green algae, diatoms, lichens, liverworts, mosses, horsetails, ferns, gymnosperms, and angiosperms. CWD is used in various ways by these autotrophs – some are only attached superficially to the surface of CWD (epiphytes)(Nascimbene *et al.* 2008), while some vascular plants may use CWD as a source of water and nutrients (Harmon *et al.* 1986, Lilja-Rothsten *et al.* 2008). CWD can act as an elevated microsite for ectomycorrhizal forest trees and fungi (Tedersoo *et al.* 2008). For example, commercial forest species such as Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Sitka spruce (*Picea sitchensis* (Bong.) Carriere) use CWD as a germinating substrate in their life cycle, and ericaceous species such as the gnome plant (*Hypopitis congestum*) and candystick (*Allotropa virgata*) are influenced by the availability of CWD substrate for growth (Lofoth 1998). Odor and Standovar (2001) found that bryophyte vegetation in beech stands was closely linked to CWD abundance and stressed the need for a strategy for retaining dead wood in managed forests, especially for habitat specialists with a limited dispersal capacity. Silviculture amendments using CWD retention (and creation) to generate mircosites for tree establishment and growth have shown initial success in Scandinavia (Vanha-Majamaa *et al.* 2007, Lilja-Rothsten *et al.* 2008).

One cannot mention the role of CWD for biological diversity of autotrophs without also including saprotrophic diversity (Stokland 2001). Lofroth (1998) identified 528 nonvascular plants, fungi and lichens closely associated with CWD in British Columbia. The abundance and distribution of CWD in the forest directly influence the species richness of these decomposer organisms (Lambert *et al.* 1980, Heilmann-Clausen and Christensen 2003, Lonsdale *et al.* 2008). Diversity of these species is also related to the diversity of the substrates, including variability in decay stages, log size etc. (Siitonen 2001). The association between producer organisms (such as those mentioned above) and decomposer organisms on CWD is generally mutually beneficial. Plant growth on CWD can influence substrate breakdown rates by entering the rotting wood with root systems and breaking up pieces of wood through expansive growth. Plants with root systems in CWD also influence decay by adding nutrients and labile carbon through root turnover or secretions for decomposer organisms to use (Harmon *et al.* 1986) and are fundamental in creating potential decay pathways (i.e. physical openings) and ecological succession. Fragmentation of forest areas, compounded by reductions in CWD have created concern for certain wood decay fungi that have short dispersal mechanisms and depend on contiguous areas of CWD (Stenlid and Gustafsson 2001).

1.4.2 ARTHROPODS

Arthropods constitute one of the most diverse (and least understood) groups of animals and their role in forests is equally varied. Arthropods (or terrestrial invertebrates in this review) use coarse woody debris for myriad purposes such as food, protection, nesting, and colonizing. (Harmon *et al.* 1986, Hanula *et al.* 2006). Invertebrates can actually create coarse wood by boring into and colonizing trees, effectively killing them (e.g. Mountain pine beetle), while others feed only on already decayed wood. Host specificity to the species of CWD evolves over time to that of habitat specificity (Harmon *et al.* 1986), changing from the importance of tree species contributing CWD (e.g. lodgepole pine and *Ips pini*) to the importance of the decay stage of the CWD (e.g. beetles able to enter only very decayed wood). The part of the tree that invertebrates use for food can be i) the nutrient-rich inner bark (e.g. bark beetles), ii) the actual wood (e.g. wood borers), or iii) the fungi that are growing on the decaying wood (Jonsell *et al.* 2001). Other invertebrates such as slugs, snails, earthworms and centipedes have been known to use CWD as protection from environmental extremes, while some (e.g. carabid beetle) use CWD as a hibernation site in the winter (Harmon *et al.* 1986). Many invertebrates, especially insects (bark beetles, wood boring beetles, etc.), spend much of their life cycle in CWD, as it is a safe site for breeding, nesting and reproduction. Although some organisms only utilize CWD for a short period of time in their life cycle, this need is no less critical for the need for CWD availability. In the boreal forest, colonizers such as termites (Order Isoptera) are not as prevalent as carpenter ants (*Camponotus spp.*), which chew snags, logs, and stumps to create galleries for nesting sites, although they do not ingest the wood (Harmon *et al.* 1986). This type of physical excavation is important, as it creates entryways for further CWD decomposition by other organisms. These arthropods also play a role in the release of nutrients in CWD by digesting the complex organic molecules in the wood and through their frass, returning the nutrients to the site (Stevens 1997). Also, species invading CWD (such as ants and bark beetles) are an important food source for prey species such as woodpeckers (Horn and Hanula 2008). Conservation of CWD for arthropods is important (Davies *et al.* 2008). For example, both Martikainen (2001) and Jacobs *et al.* (2007) studied threatened saproxylic beetle populations in clearcut areas and found that retention harvest systems can be valuable to maintain populations of threatened species. Interestingly, Gibb *et al.* (2008) released similar findings for parasitoids of saproxylic beetles in boreal Sweden, where forest operations have led to forest fragmentation and CWD loss.

For nutrient cycling in CWD, perhaps no other group of invertebrates are as important as the soil microarthropods, which have been shown to increase the availability and suitability of organic particles for other decomposer communities and contribute to nutrient cycling and soil formation (Stevens 1997).

Stevens (1997) sums up the overall influence of the arthropod community:

> *"Arthropod invaders inoculate their tunnels with fungi, bacteria, phoretic mites, nematodes and protozoans. Later, beetles that feed on sapwood and heartwood tunnel deeper into the log-opening access for other arthropods and micro-organisms. These processes involve hundreds or possibly thousands of species and are a critical link in the carbon and nutrient cycles in the forest"*

1.4.3 VERTEBRATES

Coarse woody debris provides an important structural component to the forest stand as standing and fallen dead trees are known to provide habitat for numerous organisms. This structural requirement is probably most noticeable for vertebrates such as amphibians, reptiles, birds and small mammals, which depend on CWD to maintain a continuity of habitat through natural disturbances (Harmon *et al.* 1986, Stevens 1997). In fact, coarse wood can be one of the most important habitat factors for small mammals (Carey and Johnson 1995, Samuelsson 1994), as it provides areas for nesting, cover, and safe travel corridors (Lofroth 1998, Ecke *et al.* 2001). Ecke *et al.* (2001) found that the positive relationship between structural factors such as CWD and species abundance and diversity was also closely linked to the amount of shelter and food available for small mammal habitat. Factors that affect the use of coarse woody debris for vertebrates include physical orientation of CWD, size (both diameter and length), decay state, species of CWD and overall abundance of CWD (Harmon *et al.* 1986). CWD can also alter the feeding habits of browsing mammals, as large aggregations of CWD can act as a barrier to palatable early-succesional tree species, allowing for their establishment despite heavy browsing elsewhere (de Chantal and Granstrom 2007).

Vertically oriented CWD (snags) functions in a critical role for cavity users, and Lofoth (1998) report that snag/cavity relationships may be one of the best documented wildlife/habitat relationships in North America. In British Columbia there are at least 26 endangered/threatened species that depend on CWD snags for all or part of their life history (Lofoth 1998).

Initial use of CWD by vertebrates is generally external (perches, cover), as the logs are hard, but becomes more internal as logs decay and soften enough for hiding, thermal cover, or excavating (Harmon *et al.* 1986). Also, CWD in mid-to-late stages of decay offer the best opportunities for food availability, as invertebrate populations are large and the logs are soft enough to access the prey species. Spatial patterns of CWD are also important, as clustered CWD is important as a nesting site, and continuous CWD may be important to connect populations of small mammals (Patrick *et al.* 2008) and enhance areas that would be otherwise inhospitable for prey species (e.g. clearcuts or burned areas) (Lee *et al.* 2008).

1.4.4 AQUATIC LIFE

Coarse woody debris is often thought of a as parameter that exists only in terrestrial ecosystems. In fact, Harmon *et al.* (1986) point out that before the 1970's, wood was seen as a cause of oxygen depletion in streams and an interference to fish migration. Much of that paradigm has shifted to recognize the structural and formative role of CWD in fish habitat. Coarse wood in aquatic systems plays a very similar role to terrestrial CWD, e.g. provision of cover, reproductive sites, and food. In addition to this, CWD can create important hydrologic features like pools and backwaters which trap and store inorganic sediment and can be important rearing areas for juvenile fish as well as serve as refugia during high water periods (Harmon *et al.* 1986, Helmus and Sass 2008). Human activities such as CWD removal from the water and shoreline development have drastically reduced CWD loading in many aquatic systems, causing reductions in some fish populations and disrupting ecological communities (Helmus and Sass 2008).

The utility of CWD as a prerequisite for biological diversity in most forest systems is compelling, and recognizing the vast amount of research that occurred and is still ongoing helps to give credence to its role in terrestrial ecosystems. Coarse woody debris supports specific ecological niches that are not only species-rich within the niche, but are a microcosm of diversity to the entire forest stand or ecosystem. Studies on the effect of intensive forest management on CWD abundance and biodiversity in Fennoscandian boreal forests show that large-scale reductions of CWD appear to be the primary threat to both flora and fauna (Martikainen 2001, Siitonen 2001).

1.5 Wood decay process

It is important to survey the mechanics of decomposition; the process and rate, substrate quality and components and environmental influences to better understand and manage CWD on the landscape.

1.5.1 STARTING SMALL

Bacteria, fungi and other microbe populations invade deadwood, and are responsible for mass loss and breakdown of organic carbon and nutrients. Microbes produce enzymes capable of breaking chemical bonds in plant tissues. This production is limited by the quality of litter for microbial decay (Vesterdal 1999). Aber and Melillo (1991) outline three general characteristics that determine the quality of litter materials for microbial decay, 1] the types of chemical bonds and the amount of energy released by their decay, 2] the size and complexity of molecules, and 3] the nutrient content. To summarize, the production of enzymes require large amounts of carbon and nitrogen, and must be offset by gains associated in energy and nutrients. Glucose and other simple sugars offer the greatest return, as the carbon-carbon bonds are easily broken by the microbes and internally metabolized. This energy source is small, however, as most plant litter is in the form of large polymers and cannot be taken into microbial cells. Enzymes must instead be released into the environment where the decay process is far less efficient. The structure of enzymes must match the structure of large and complex molecules, which can also impede enzyme reactions and decrease decay rates. Lastly, microbial activity can be further inhibited if nutrient demands during decomposition are not met in low nutrient-to-energy ratio material.

Incomplete decomposition results in the formation of humus in forest ecosystems, and Prescott *et al.* (2000) list three major causes of humus formation: 1) climate, 2) chemical and physical characteristics (especially lignin and phenolics) and 3) abundance and composition of soil microbial and faunal communities. Of these three, Prescott *et al.* (2000) state that the chemical composition of the forest litter is perhaps the most significant factor, as the amount of structurally complex materials (acid insoluble materials such as cutin and lignin) inhibit decomposition and create humus. Extensive work by Caroline Preston (Preston and Trofymow 2000, Preston *et al.* 2002, Preston and Trofymow 2006) has led to advances in analyzing humus forms and the pros and cons of proximate analysis of lignin.

Boddy (2001) outlines the origins of decay from fungal communities. Most early decay originates from heartrot in the inner core of living trees, where there are few living cells and an extensive gaseous phase. This is much easier to colonize than sapwood, where defensive mechanisms prohibit intrusion, but are still made possible by “latent fungal propagules” (Boddy 2001).

Wood decomposing fungi are usually categorized as either brown or white rot species. Brown rot fungi feed on cellulose (component of the cell wall) and leave the lignin, which result in a brown colouration of the remaining wood. Because the cell walls are compromised, decay is evidenced by cracking along the grain and the wood turns to powder easily. White rot fungi, on the hand, break down both lignin and cellulose which causes the wood to appear whiter than normal. Affected wood generally shrinks and collapses when severely degraded and will lose strength and become spongy to the touch.

1.5.2 PHYSICAL FACTORS

There are two main physical forces that act on decomposition of CWD: leaching and fragmentation. Leaching is the process of water, temperature and gravity transporting nutrients and other soluble materials from CWD into the soil (Zhou *et al.* 2007). Of the two processes, leaching is perhaps the least studied, although its importance as a transport mechanism should not be ignored. For fresh CWD, there is little material to transport through leaching, but leaching becomes more important as material breaks down and carbon and nutrients are mobilized and available in older CWD.

Fragmentation is the breakdown of wood structure as a result of both physical and biological processes. Seasonal temperature and precipitation cycles fragment wood through expansion and contraction both by the freezing and thawing of water molecules as well as the swelling and shrinking of cells in the wood. The amount and timing of these climate variables determine how strongly physical fragmentation affects CWD. For example, Harmon *et al.* (1986) report that log moisture contents are lowest in summer and early fall and highest in winter and spring.

While climate conditions primarily affect the exposed surfaces of the bole, biotic factors are active in fragmenting its interior. Invertebrates, such as wood-boring beetles, tunnel extensively into the wood. This excavation not only compromises the structure of the wood, but the passageways act as conduits for water access and colonization of the interior with microbes. A secondary benefit to this biological activity is that the concentration of invertebrates attracts birds and other large mammals which further fragment the log to reach the source of food (Zhou *et al* 2007).

1.5.3 DECOMPOSITION RATE

Rates of decomposition are often reported as "*k*", the constant value used most frequently in exponential decay models. This can be confusing, as it is not the decay rate itself, but simply the constant used in the decay equation. A constant *k* value of "0.03" for instance, must be placed in context in order to understand what that number represents. The exponential decay model most frequently used (Harmon *et al.* 1986, Laiho and Prescott 2004, Tobin *et al.* 2007) is:

$$Y_t = Y_0\, e^{-kt}$$

Where Y_0 is the initial quantity of the material (mass or density), and Y_t is the quantity remaining at time t. Linear transformation of the equation to express k from the equation is as follows:

$$k = \frac{(lnY_0 - lnY_t)}{t}$$

The exponential decay rate is the most frequently reported; however, constants are highly variable for coniferous species, with mean and median around 0.02 year^{-1} reported by Laiho and Prescott (2004). For example, Harmon *et al.* (2000) report constants of 0.033 and 0.035 for spruce and pine, while Shorohova and Shorohov (2001) report a constant of 0.016 for spruce. Differences in methodologies are responsible for some of the discrepancy in constants, as there is no singular method that encapsulates all of the variability in dead wood, although a recent CWD global database of decomposition rates has been reported by Rock *et al.* (2008) as a collaborative effort. To further complicate matters, some decay rate estimates include standing dead wood, or "snags", that greatly lengthen the decay process due to log drying and reduced activity of decay organisms. In fact, Boulanger and Sirois (2006) reported a decomposition constant for postfire snags as *k*= 0.00! Wildfires may also create conditions where CWD becomes more recalcitrant to biochemical attack, further impeding decomposition rates (Gonzalez-Perez *et al.* 2004, Certini 2005). Other types of coarse wood, such as stumps and coarse roots have been found to have very similar decay rates to boles for *Pinus radiata* (Garrett *et al.* 2008).

Besides the variability from different studies, Herrman and Prescott (2008) found high decay rate variability within the same long-term study, cautioning the certainty of models that incorporate wood-decay estimates. Yatskov *et al.* (2003) reason that different stages of decomposition have different rates of decay and therefore different *k* values during decay – 1) an initial slow phase, 2) a rapid phase, and 3) a moderately slow phase (Figure 1.5). Different species also have unique curves. Yatskov *et al.* (2003) found that while some species follow the pattern in Figure 4 (*Betula costata, Picea* spp., *Pinus sylvestris*) there are at least three other possible decay patterns: 1) a gradual, almost linear decrease in density because of prolonged bark presence and absence of decay resistant substances in the heartwood, 2) species with decay-resistant heartwood, such as *Larix* spp., may not change in density until decay class 4 or later, and 3) species susceptible to heart rot (*Acer* spp., *Quercus* spp.) have complex decay patterns, as the heart wood may already be soft before the tree is dead thus rotting from both the outside and inside simultaneously.

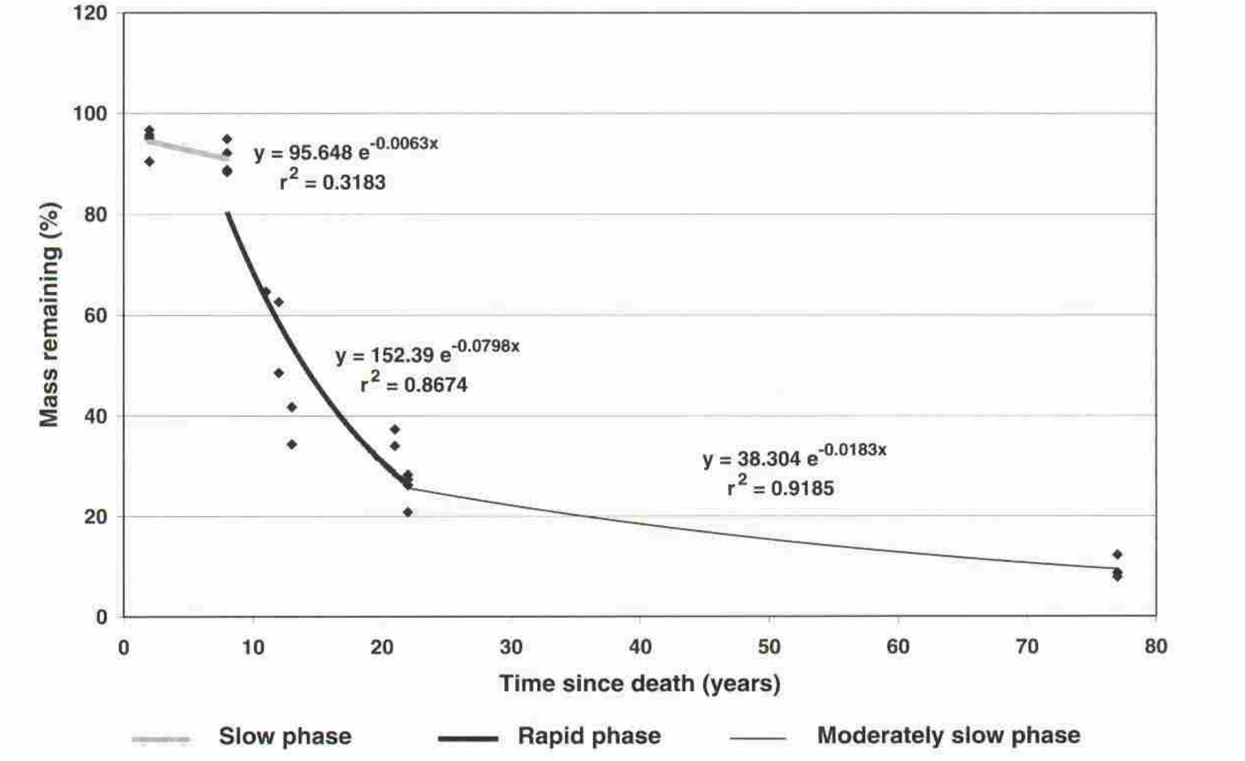

Figure 1.5 Mass loss by *Betula costata* logs, showing separate exponential curves for three phases of decomposition (slow, rapid, and moderately slow). (*Taken from Yatskov et al. 2003*)

Long term monitoring of CWD to assess mass, density, or volume changes over time is the most accurate and reliable method of calculating a constant value for decay (Tarasov and Birdsey 2001). Due to the long time period required and secured monetary investment, it is difficult to establish these types of research trials, and very few of these experiments exist or have been reported in the literature (Stone *et al.* 1998, Morris and Duckert 1999, Ganjegunte *et al.* 2003, Hafner *et al.* 2005, Herrman and Prescott 2008). Instead, chronosequence studies are more commonly employed, and the limitations of this type of study must briefly be mentioned. Chronosequencing can be used to select CWD across a spectrum of ages and its accuracy depends largely on the ability to correctly identify stands with similar site conditions and CWD type and amount. Dyck and Cole (1994) expand on these necessary assumptions and discuss benefits and alternative approaches. Despite these setbacks, numerous studies have successfully utilized chronosequence studies, such as Manies *et al.* (2005) and Metsaranta *et al.* (2008), the latter of which used dendrochronology and stand reconstruction techniques to obtain reliable data from up to 50 years in the past for boreal forest stands.

Another method often used in concert with chronosequence studies (as well as separately), is a decay classification system. There are no standardized classification protocols, although most studies separate decay into four or five basic categories: fresh, bark loose, bark not present, fragmentation occurring (often subdivided into exterior and interior fragmentation). Kuuluvainen *et al.* (2001) found that in a pristine *Picea abies* forest, distributions of four decay classes were as follows: Decay class 1 – 15%, 2 – 32%, 3 – 21%, 4 – 32%. Some studies are much more in-depth (Naesset 1999,Hafner *et al.* 2005, Butler *et al.* 2007), but the utility of any type of classification is questioned by Laiho and Prescott (2004). It is very difficult to match decay class to CWD age because of the many external factors (log position, climate, etc.) and large variation in decay time. Recent advancements using a repeated log survey method (Harmon *et al.* 2000) are attempting a hybrid approach, although Laiho and Prescott (2004) point out that this approach assumes a constant volume over time, which may not be the case. Kueppers *et al.* (2004) apply a unique approach that utilizes radiocarbon dating to overcome biases introduced with a chronosequence technique to obtain logs of similar age from fresh to advanced decay to more accurately determine decay rates. An overview of CWD assessment strategies has been published by Harmon and Sexton (1996) as well as Stahl *et al.* (2001). Maser *et al.* (1979) illustrate the 5 common decay classes and how standing dead trees can enter through time (Figure 1.6).

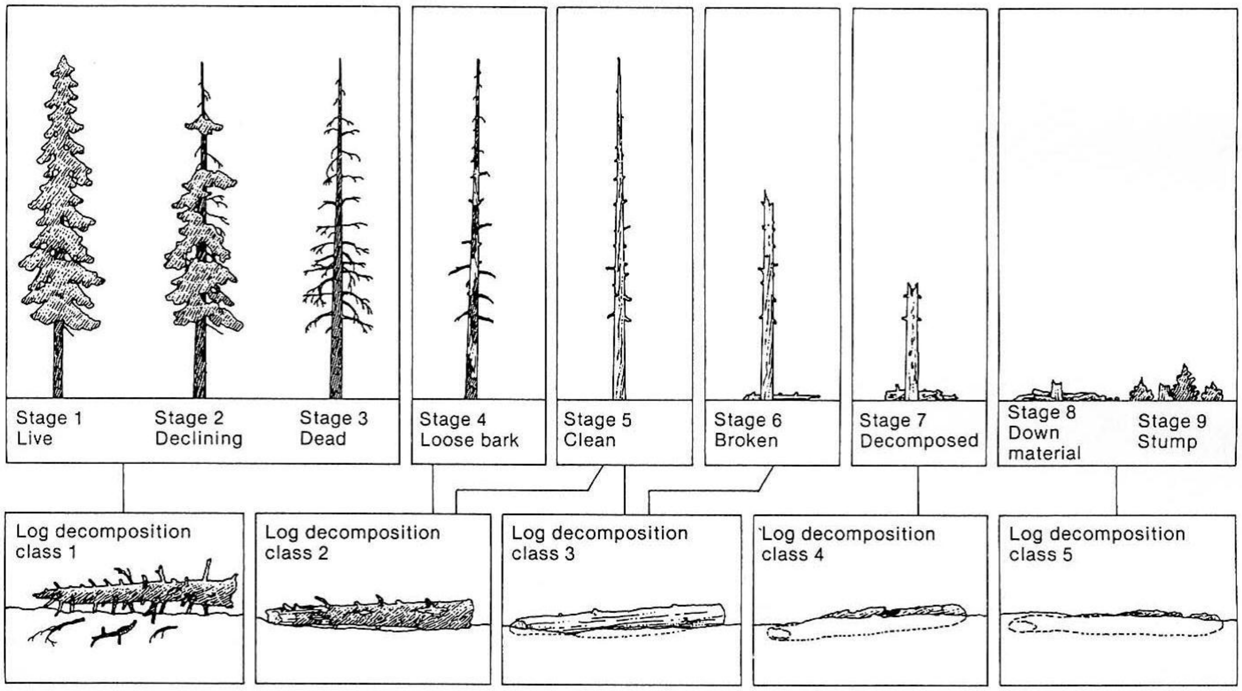

Figure 1.6 CWD decay classes showing inputs from standing dead trees (Taken from Maser *et al.* 1979).

1.5.3.1 Timeline

Fire or other event-driven phenomena (wind, insects) are the most common natural causes of mortality, with post-harvest wood residues accounting for the majority of CWD in forest stands after industrial activity. Forest ecosystems vary in mortality patterns, with some forest types (e.g. coastal rainforests) exhibiting an almost "steady-state" mortality pattern on the broader landscape scale and other forest types, such as *Abies balsamea* –dominated stands, demonstrating a "wave-mortality" effect where entire stands age and die at the same time, contributing to major "pulses" in CWD (Lambert *et al.* 1980, Lang 1984, Sprugel 1984). Broadly speaking, the pattern of disturbance in the boreal forest is driven by large-scale stand replacing events (such as fire or insect infestations), and large amounts of CWD deposition subsequently follow these disturbances. Increasing fire intensity has a positive correlation to

CWD amounts, with high intensity fires contributing the most CWD (Smirnova *et al.* 2008). Management directives aimed at emulating the amount and pattern of CWD deposition have been or are being developed for most forest areas (Jonsson *et al.* 2005). In Ontario, Natural Disturbance Emulation Guidelines (NDPEG), and more recently the Stand and Site Guide, are attempting this by promoting limited retention of some of the original forest stand following harvest.

If a tree dies without immediately falling over, it will remain standing for up to 35 years (Moroni 2006), depending on the species and age of the tree. Once on the ground, there are three general phases of decomposition. First, the log must become adequately saturated with moisture to allow for microbial habitation. Again, this process depends largely on climatic variables, general estimates (Fahey 1983, Laiho and Prescott 1999) show that this process takes about 5 years. The second stage is relatively fast, as simple carbon compounds and cellulose are decomposed through microbial activity. The last stage involves complex compounds (mostly lignin) that decompose very slowly (Laiho and Prescott 2004). Again broad variation is found among conifer species (mentioned in decay rate discussion previously).

1.6 Other influences

As mentioned earlier, decomposition of CWD relies largely on biotic activity. These organisms are influenced by many factors that control their activity, such as temperature, humidity and woody substrate (Harmon *et al.* 1986) as well as extractives and volatiles, pH, water availability and gaseous regime (Boddy 2001). It is therefore necessary to assess the organisms' requirement for each of the factors listed.

1.6.1 TEMPERATURE

The difference between a decomposer subsisting or thriving depends largely on the temperature of the surrounding substrate. Optimal temperatures for respiration by fungal species vary by region, but temperatures above 40^0 C are often lethal. Insects, however, have a larger optimum temperature spread as well as a higher temperature threshold (Harmon *et al.* 1986). One would expect that temperature differences would translate to differences in decomposition, where cold climates have slower decomposition than warmer ones, but Harmon *et al.* (2000) has found that it has not been the case. In fact, some studies in colder climates (Alban and Pastor 1993) showed faster decomposition rates than in warmer ones (Harmon 2000). Harmon (2000) attributes much of this to differences in methodology of the studies, including moisture, size, and species differences of the trees, indicating these factors may be more important than temperature in decomposition of CWD. Kueppers *et al.* (2004) and Pare *et al.* (2006) suggest that in the face of a changing climate, the C pool in forests could be reduced as increasing temperature causes increased respiration and a subsequent reduction in the turnover time of CWD .

1.6.2 WATER CAPACITY AND HUMIDITY

Moisture availability is a key factor for organisms inhabiting CWD. Low moisture contents are common in younger CWD, but as decomposition proceeds, increases in pore space also increase water holding capacity, creating a favourable habitat for larger more complex organisms (Samuelsson *et al.* 1994). CWD also affects the humidity in the microclimate surrounding the log and even small differences in log size, position and aspect can greatly vary humidity levels, which can help explain the broad variation in decomposition of CWD. CWD can also alter the microclimate surrounding the log, where logs on the ground have been found to increase soil moisture (Remsburg and Turner 2006). The boreal forest typically does not foster very high temperature or humidity levels (compared to other forest areas), which must be accounted for when comparing decomposition between regions.

1.6.3 **WOOD QUALITY**

CWD is not homogeneous (Boddy 2001), and can be separated into its various inventory characteristics: dimensions, components and species. Larger diameter logs have a much lower surface to volume ratio, resulting in lower rates of decomposition, although a few studies (e.g. Guo *et al.* 2006, Herrmann and Prescott 2008) have found diameter relationships in CWD decay rates inconclusive. An individual log also contains various components that decay at different rates. Outer bark, inner bark, sapwood and heartwood all have distinct physical characteristics and chemical compositions that influence the decay process. The transport system (phloem and xylem), situated in the inner bark, is the richest in energy (simple sugars etc.) and so is the first to be colonized and exploited by decay organisms. Outer bark is quite porous, and adequate moisture for microbial colonization is attained much faster than for the sapwood and heartwood. Krankina *et al.* (1999) found that smaller logs contain a greater percentage of bark, which also sloughs off and decomposes faster, and this loss of the nutrient-rich bark tissue determines the overall decrease in many nutrient stores in the CWD. When bark is sloughed off early, the sapwood can dry quickly, which hardens the wood and prolongs the decay process (Rock *et al.* 2008). Heartwood contains many decay-resistant, complex compounds which make extracting the little energy contained in the wood a laborious and difficult process. For this reason, the heartwood is usually the last to be recycled into the ecosystem.

Differences in decay between species largely rely on the combination of structural components associated with each species. Generally speaking, those species with higher proportions of high-energy simple sugars and proteins (e.g. many broadleaved spp.) will decay much faster than species with a high percentage of difficult to digest lignins (e.g. most conifers). Sapwood and heartwood proportions also vary widely among species and with age, which, as discussed above, influence the ability of organisms to easily break down the wood.

1.7 Leaching of coarse woody debris

Solutes leaching from CWD into the underlying soil may play a role in nutrient cycling, including dissolved organic carbon (DOC) and dissolved organic nitrogen (DON), but studies concentrating on leaching of CWD are rare (Hafner *et al.* 2005). Due to the dearth of leaching studies in the literature, the following section will concentrate on the work of Hafner *et al.* (2005). They collected throughfall, litter leachate, and CWD leachate *in situ* for one year at a mixedwood forest site in New York state, USA. Concentrations of DOC, DON, NH_4, NO_3, dissolved organic sulphur, SO_4, Cl, Al, Ca, K, Mg, Na, and P were measured to estimate flux from CWD. With the exception of inorganic nitrogen, all concentrations of nutrients were higher in CWD leachate than in throughfall or litter leachate (Figure 1.7). Although these results may suggest that CWD leachate may contribute significantly to nutrient fluxes (especially DON), the amount of CWD in the mixedwood forest was very low (2% of the total area), so overall contributions to nutrient cycling were negligible. It is certainly possible, however, that in forest ecosystems with greater CWD input (i.e. boreal forests following disturbance), CWD may play a greater role in nutrient cycling than previously thought.

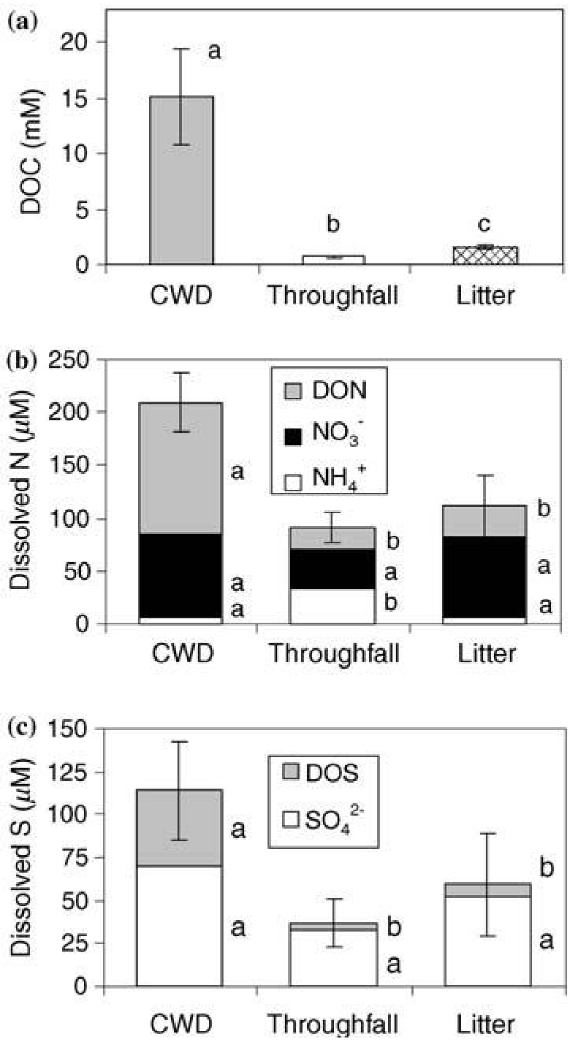

Figure 1.7 Mean concentrations in throughfall and CWD and litter leachate of DOC (a), dissolved N (b), and dissolved S (c). (Source: Hafner *et al.* 2005)

1.8 Importance of CWD to the broader ecosystem

Coarse woody debris has been shown to be a very important component of the forest ecosystem, especially for biological diversity of many types of flora and fauna. From a nutrient standpoint, however, there is conflicting evidence about the role that CWD plays in nutrient release in the overall ecosystem. It has been proposed numerous times (Graham and Cromack 1982, Lang 1984, Tenhagen *et al.* 1996, Krankina *et al.* 1999), that CWD acts as a buffer against nutrient losses that occur during site disturbances. The theory is that the nutrient-rich leaves, small branches and roots are quickly decomposed and that CWD, with its slow and steady decomposition, provides essential nutrition to the emerging stand until crown closure once again enables that stand to be self-sufficient. Laiho and Prescott (2004) critically examine this hypothesis, pointing out that it is based on C/nutrient ratios and observed increases in nutrient content of wood during decay.

If CWD does contribute to nutrient cycling, it appears to be small. Hart (1999) found that CWD in old growth forests (*Pseudotsuga menziesii*) contributed between 4-6% of plant N uptake. Laiho and Prescott (1999) simulated N and P release in *Pinus contorta, Picea glauca,* and *Abies lasiocarpa – Picea engelmannii* forests and found that CWD contributed less than 5% of total N and P released from aboveground litter, similar to the estimates of Arthur and Fahey (1989). Laiho and Prescott (2004) point out that although the data are scarce, it does not appear that CWD makes a significant contribution to N and P cycling. This subject is still open to great debate, as Krankina *et al.* (1999) and others (Hafner *et al.* 2005, Butler *et al.* 2007) point to the broad range of nutrient and carbon pool estimates in the literature as evidence that further research is required to fully understand nutrient dynamics.

Laiho and Prescott agree with further research needs, and offer three hypotheses that need to be tested regarding the role of CWD in soil fertility. Specifically, that 1) on sites where nutrients, especially N or P, limit plant growth, CWD accumulation may reduce primary productivity through immobilization of nutrients by decomposers, 2) on dry sites, where lack of moisture limits plant and microbe growth, CWD may increase primary productivity, enhance element cycling by improving moisture retention as well as be important for soil organic matter buildup, and 3) CWD may not be a constraining factor in elemental cycles in nutrient-rich sites.

CWD may also influence nutrient cycling in different ways than has been traditionally researched. For example, Arthur and Fahey (1990) concluded that although CWD may not significantly contribute directly to nutrient pools, CWD may indirectly play an important role as a storage pool for base cations as well as stabilize soil organic matter.

1.8.1 MANAGEMENT OF CWD FOR NUTRIENT RETENTION

Management of CWD is a major research interest in Scandanavia (Siitonen 2001, Lilja-Rothsten *et al.* 2008), and Canadian researchers have been following suit (i.e. LTSP collaborators, etc.). There are two factors driving this charge: Firstly, although research on CWD is abundant, from a nutrient/site productivity standpoint, relatively little research has been done (in comparison to biodiversity, decay rates, abundance, etc. studies), and so it can be considered one of the "final frontiers" of forest stand dynamics. Secondly, interest in "unutilized" forest biomass left after harvesting is growing as Canada searches for renewable and sustainable energy alternatives to traditional fossil fuel consumption. Existing forest management does not account for CWD adequately, and Kabzems and Haeussler (2005) caution that "current operational guidelines and regeneration monitoring techniques lack sufficient resolution to identify the extent and severity of site compaction"; a caution that could also be echoed for any number of site disturbance issues including organic matter (especially CWD) removal from forested sites. Policy makers in Canada are looking to scientists for advice on future government action in forest management guidelines. To properly answer this, well-designed, long-term experiments are required to see differences in forest productivity. Existing long-term experiments in Canada are maturing and it may be that many "insignificant" nutrient values of CWD have simply not been explored long enough or that scientists have not been asking the right questions. CWD is listed in Ontario's Criteria and Indicators under element 2.3

in “maintaining and conserving forest ecosystem resilience”, and new research to investigate new questions regarding the role of CWD in forest ecosystems will continue to evolve and subsequently influence forest management in Canada.

2.0 NUTRIENT RETENTION AND LEACHING POTENTIAL OF COARSE WOOD BOLTS COLLECTED FROM LOGGED AND BURNED UPLAND BOREAL SITES: A GREENHOUSE MISTING EXPERIMENT

2.1 Introduction

Renewable energy is once again on the forefront of public interest, and jurisdictions are increasing renewable fuel standards (EIA. 2007) to offset fossil fuel consumption. Older programs, such as “Energy from the forest” (ENFOR) are being re-examined (Lambert *et al.* 2005, Hall and Richardson 2001), and new projects (Morris and Duckert 1999, Gan and Smith 2007) are being specifically designed to investigate the capacity of our forests for increased utilization beyond traditional forest products. In part, utilization of unmerchantable or low value coarse wood, commonly by-passed during normal forest operations, is likely to be a targeted fibre source as this new bio-economy matures (Perez-Verdin *et al.* 2009, Nechodom *et al.* 2008, Borjesson 2000, Rudolphi and Gustafsson 2005, Gan and Smith 2006).

It has been acknowledged (Graham and Cromack 1982, Lang 1985, Tenhagen *et al.* 1996, Krankina *et al.* 1999) that CWD acts as a buffer against nutrient losses that occur during site disturbances. Compared to nutrient-rich leaves, small branches and roots that decompose quickly, CWD is thought to provide essential nutrition to the developing stand through slow and steady decomposition. This contribution is important through to crown closure where stands become self-sufficient in terms of cycling nutrients. This impact has been hypothesized to be large (Krankina *et al.* 1999) and species-dependent (Brais 2006). Laiho and Prescott (2004) point out that although there are limited studies in this area, it does not appear that CWD makes a large contribution to N and P cycling.

Solutes leaching from CWD into the underlying soil may play a role in nutrient cycling in forest ecosystems, especially in plant-available forms of N and P. Leaching is an important mechanism of CWD nutrient release, and, as Kuehne *et al.* (2008) point out, leaching delivers nutrients directly to the soil in soluble form, not bound to woody debris (via fragmentation) or fungi (mycelia), which require additional steps to become available to plants. While there is evidence that plants may directly remove nutrients from CWD (Arthur *et al.* 1993, Marx and Walters 2006) or use CWD as a seedbed (Harmon *et al.* 1986), the soluble nutrients in the soil remain an important nutrient source for plant uptake. Spears *et al.* (2003) found the largest differences in solutions and soils between CWD and controls were in the middle decay classes, but that overall there were no differences in N, P, microbial biomass, Biolog plate assays, or enzyme activity in soils. Microclimatic conditions and varied underlying soil characteristics of individual CWD locations has been shown to vary significantly (Spears *et al.* 2003, Metzger *et al.* 2008).

This study was designed to simplify the decomposition process to understand the dynamic nature of nutrient flux directly from CWD. Moisture content in CWD can have a large impact on the nutrient dynamics (Boddy 1983). High moisture content and associated restriction of aeration are factors limiting activity of mycelia fungi (Boddy and Rayner 1983, Progar *et al.* 2000, Barker 2008). High moisture content may also lead to anaerobic activity, which limits nitrogen fixation and may lead to denitrification (Brunner and Kimmins 2003). Low moisture content can also limit respiration, and Jomura *et al.*, (2008) found that maximum respiration occurred at an intermediate water content. Isolating the log in a warmer, more humid, soil-less *ex-situ* environment does not directly mimic field conditions, as soil interface relationships are removed, but trends found will be used to develop testable hypotheses for longer-term *in situ* investigations. This short, carefully controlled experiment explored the following questions:

1. What nutrients are most susceptible to leaching, and what is the general trend over time?
2. Is immobilization of nutrients a result of soil/log interactions, microbial/fungal activity or both?
3. How do a common and widespread boreal softwood (*Picea mariana* L.) and hardwood (*Populus tremuloides* Michx.) differ in nutrient retention/leaching?
4. Does harvest debris CW have a similar pattern of nutrient leaching compared with CWD originating from wildfire disturbances (i.e., charred wood)?

2.2 Materials and Methods

Stem (bole) samples of CWD were collected from 2 wildfire-origin (recent, 15-year-old) and 2 harvested (recent, 15-year-old) sites. The recent wildfire site/stand burned in the spring of 2007 and was approximately 50 years of age (previously harvested in the late 1950's) comprised of a mixture of trembling aspen and black spruce (At_7Sb_3) growing on shallow, morainal till. The 15-year-old wildfire site/stand was a mature (80-year-old) stand of jack pine and black spruce (Pj_6Sb_4), with scattered clumps of trembling aspen at the time of the fire (1992). The soil was also a shallow, morainal till. The recent harvest site was part of a commercial thinning trial established during late winter of 2007 in a mid-rotation (40-year-old) black spruce plantation (Sb_8At_2) growing on a deep, fine-medium sandy outwash plain. The final site, the 15-year-old harvest, was a mature (100-year-old) mixed conifer stand (Sb_8Pj_2) with scattered trembling aspen growing on a very shallow (<20 cm) morainal till. The greenhouse experiment examined three fixed factors: 1) two origins –fire and harvest, and 2) two species – black spruce (Sb) and trembling aspen (At), and 3) five decay classes. The collections from the recent fire and harvested sites, combined with the collections from the 15 year old stands provided replicates along the decay class continuum from 1 to 5, similar to Maser *et al.* (1979), Sollins (1982) and Naesset (1999): 1] Recently dead tree, bark intact 2] bark mostly intact, wood of outer layers (sapwood) of the log has started to soften due to rot, 3] bark sloughing or absent, soft outer layers of log and are easily removed with a knife, heartwood mostly sound, 4] bark detached, wood soft, no solid core, 5] Fragmented, no structural integrity. The recent “fire” and “harvest” samples were taken from sites where the disturbance occurred less than one year previously, and had Sb and At as constituents of the pre-disturbance stand. The older CWD were collected from boles with known disturbance type (wildfire and clearcut harvest) and age; care was taken to select harvest debris wood (evidence of cut) or tipped up charred stems (roots intact), thereby assuming these samples were sourced from the disturbance event.

After collection, physical properties of each log bolt were documented, including percentages of bark, cracks, ash, frass, moss and knots. The remaining sections were suspended above separate containers and placed in the greenhouse in a completely randomized design (Figure 2.1). In addition, eight (8) blank containers were randomly placed in the design to account for any particulates from the water source, tubing, etc. Each bole was suspended with nylon line above separate containers to ensure that the bole had no contact with any surface and was sufficiently aerated. A water-misting apparatus with flat-nozzle spray tips (TeeJet TP800067) was placed 20 cm above the logs. The spray coverage was contained to the length of each log, collecting water from the top, sides and bottom of the log. A zero-tension lysimeter was connected to each container to drain log leachate into 20 litre collection containers. The containers were emptied once per week, the volume recorded to ensure equal distribution, and a

200 ml sample taken for chemical analysis. Containers were not treated with anti-bacterial/fungal chemicals, but were rinsed out weekly. Each log was immersed in water for 48 hours prior to start-up, after which a misting schedule of four minutes every 12 hours (500 ml per cycle) was set to keep logs moist but not saturated. We compared the water inputs and collected leachate to the control (no log) amounts to ensure that logs were not absorbing excess water, as Sexton and Harmon (2009) found actual absorption of CWD accounted for only 3-11% of throughfall inputs. In addition, a clear plastic covering was put over the entire set-up and two temperature/relative humidity probes were placed at opposite ends to monitor heat/moisture distribution. Temperature was regulated and averaged 23.3^0C (std. dev. $\pm 4.0^0$C), but some large temperature fluctuations from 15 – 35^0C were recorded due to the placement in the greenhouse, sunlight intensity, and daily cycle of heating. The 16 week experiment of 2016 growing degree days, compared to about 1200 per year in actual *in-situ* conditions. The total length of time for the experiment was 16 weeks, after which the logs were dried out and samples were taken again to determine changes in volume and nutrient content.

Leachate samples were immediately filtered (P5 filter paper, pore size:.05 mm), decanted into 15 ml centrifuge tubes and frozen until analysis. Dissolved organic carbon (DOC) and total soluble nitrogen (TSN) were measured with the Technicon Instruments AutoAnalyzer II (Pulse Instrumentation Ltd., Saskatoon, SK) using Industrial Method Nos. 455-76W/A and G-086-93 A, respectively (N detection limit = 0.009 mg).

Figure 2.1 Photograph of greenhouse experiment showing log suspension, overhead misting and collection containers.

Quality control samples were included every 10 samples to ensure accuracy. Aluminum, B, Ca, K, Mg, Mn, Na, P, S and Zn were analyzed with a Varian Vista Pro inductively coupled argon plasma spectrometer (ICAP/ICP) AES (Varian Inc.) for trace elements in water (> 5ppm). The mean weekly blank water values were subtracted from the solute concentration.

Solid wood samples taken both pre- and post-experiment were dried at 50^0C until they reached a stabilized dry weight. Each wood cookie was separated into bark, sound, and unsound components. To determine the ratio of the three components within each log, and to account for airspaces, the end of each log was scanned and the average area of each component was delineated using SigmaScan Pro 5 (Systat SSI Products, USA). Samples were then ground into 2g portions using a Thomas Scientific Wiley Mini-Mill (Model 3383-L10), with a 0.85mm sieve (20 mesh). Total carbon, nitrogen and sulfur were analyzed using a combustion technique with a LECO CNS-2000 (LECO Corporation, St. Joseph MI). Al, B, Ca, K, Mg, Mn, Na, P, S and Zn analysis was completed with the same ICP instrument as the leachate, following a 10% HNO3 acid digestion (adapted from Miller 1998).

Concentrations of carbon and nutrients leached from the CWD were analyzed as a repeated measures ANOVA to isolate changes in solute concentration over the 16 week period. The collection and analysis of leachate occurred weekly, and so there were 16 repeated, weekly measurements**.** The amount (flux) of carbon and nutrients leached was calculated, as the weekly collected volume of water was tracked and the original mass of CWD (at the start of the experiment) was known. Flux values were reported as mg of solute leached from CWD. Carbon and nutrient contents were then summed for a “cumulative flux”. Descriptive statistics (e.g., skewness, kurtosis, boxplot etc.) revealed one outlier log, which was removed from the analysis. The design was then analyzed as an unbalanced, 3-factor Completely Randomized Design

(CRD) ANOVA using SPSS 16.0 (SPSS Chicago) using age, species and "Decay Groups" as factors. The decay groups of "freshly cut" and "original to the disturbance" were used to ensure the preliminary ANOVA model retained all factor combinations. Carbon, nitrogen and phosphorus were found to be only significantly different ($p<=0.05$) among decay groups, and so a separate unbalanced CRD ANOVA was run with the five decay classes as the only factor to improve the replication across the decay classes. Decay class frequency was: 18, 3, 5, 6, and 7 for classes 1 through 5, respectively. This was done as some classes were not represented for some of the species x origin combinations in the full model.

2.3 Results and Discussion

2.3.1 CARBON

Cumulative solute contents were measured as mg of solute leached over the length of the experiment, and were largely driven by decay class for C ($p<0.001$) (**Table 2.1**, Table 2.2). C leaching was a source in all stages of decay (

Table 2.1), which was small for the first three decay classes (437.6, 536.5, 1019.7 mg, respectively), peaked as a strong source in the fourth (3228.5 mg), and was reduced in the fifth and most advanced decay class (1805.9 mg) (Figure 2.2). SNK post-hoc test revealed only decay class 4 was significantly different in C release from the other classes.

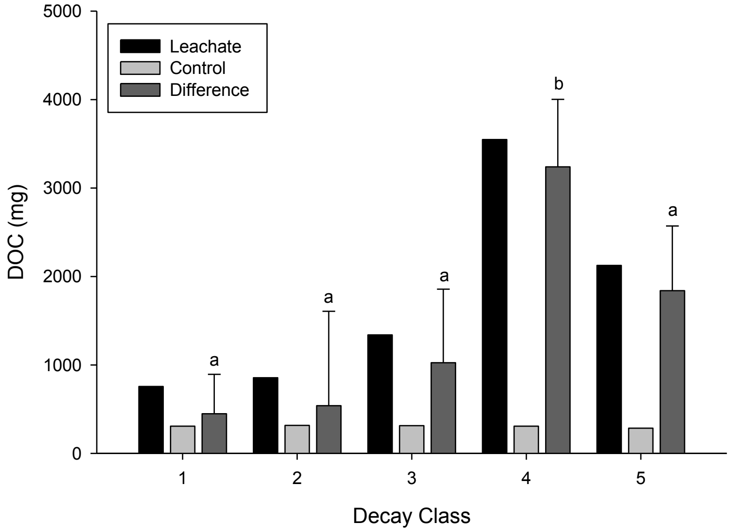

Figure 2.2. Cumulative dissolved organic carbon (DOC) collected over 16 weeks, by log decay class.

Decay rates (C remaining) are most frequently reported as a negative exponential curve (Harmon *et al.* 2000, Rock *et al.* 2008). Carbon leachate trends in this experiment were not consistent with this process, but were similar to polynomial carbon/mass loss curves reported in other CWD decay studies for certain species (Harmon *et al.* 2000, Shorohova and Shorohov 2001, Yatskov *et al.* 2003). In our case, low C leachate corresponded with early decay and high C release was indicative of the later stages of decay. The carbon leachate pattern through the five decay classes mirror the three phase decay model (Yatskov *et al.* 2003, Zell *et al.* 2009) showing 1) an initial slow phase, 2) a rapid phase, followed by 3) a moderately slow phase. Our data suggest that C loss peaks in decay class 4 and starts to slow down in decay class 5.

Table 2.1. Average leachate concentration, cumulative leachate content and wood element concentrations of CWD treatments.

		Nutrients												
Source	**Decay Class**	**C**	**N**	**Al**	**Ca**	**Cu**	**Fe**	**K**	**Mg**	**Mn**	**Na**	**P**	**S**	**Zn**
Average concentration for 16 week period (ppm)														
Leachate														
	1	5.51	0.45	0.03	13.56	0.02	0.02	2.07	2.92	0.04	3.69	0.05	1.21	0.02
	2	6.10	0.49	0.03	13.00	0.01	0.03	1.45	2.86	0.03	3.68	0.02	1.22	0.02
	3	9.24	0.59	0.03	13.16	0.02	0.03	1.36	2.87	0.03	3.77	0.01	1.25	0.03
	4	25.00	0.61	0.04	12.77	0.03	0.06	1.42	2.79	0.06	3.67	0.01	1.22	0.03
	5	16.97	0.73	0.04	13.17	0.02	0.03	2.09	2.94	0.01	3.73	0.02	1.23	0.03
Control (Blank)		2.30	0.56	0.03	13.76	0.02	0.02	0.91	2.81	0.00	3.64	0.01	1.16	0.03
Difference														
	1	3.21	-0.12	0.00	-0.20	-0.01	0.00	1.16	0.11	0.04	0.05	0.05	0.05	-0.01
	2	3.80	-0.07	0.00	-0.76	-0.01	0.01	0.54	0.05	0.03	0.04	0.01	0.05	-0.01
	3	6.93	0.02	0.00	-0.60	0.00	0.01	0.45	0.06	0.03	0.13	0.00	0.08	-0.01
	4	22.69	0.04	0.01	-0.99	0.00	0.04	0.51	-0.01	0.06	0.03	0.01	0.06	0.00
	5	14.66	0.17	0.00	-0.59	-0.01	0.01	1.18	0.13	0.00	0.09	0.01	0.06	-0.01
Cumulative content for 16 week period (mg/kg)														
Leachate														
	1	756.9	62.27	4.14	1945.72	2.43	3.03	302.39	417.21	6.21	516.05	6.55	167.04	3.02
	2	855.5	71.52	3.92	1912.82	1.93	4.26	210.22	419.08	4.62	518.61	2.32	168.61	3.31
	3	1338.8	84.26	3.99	1901.91	2.83	3.48	201.00	415.48	5.00	526.71	1.53	172.09	3.99
	4	3547.5	85.59	5.40	1815.79	3.69	8.37	206.11	397.10	8.60	512.06	1.65	168.28	4.66
	5	2124.9	95.12	4.84	1729.30	2.31	3.52	297.93	386.47	0.80	499.96	2.40	160.55	3.49
Control (Blank)		319.0	78.27	3.93	1913.05	3.47	2.65	127.08	388.78	0.21	508.18	0.89	162.07	4.79
Difference														
	1	437.9	-16.00	0.21	32.67	-1.05	0.38	175.32	28.44	6.00	7.87	5.66	4.97	-1.77
	2	536.5	-6.75	-0.01	-0.22	-1.55	1.61	83.15	30.30	4.40	10.43	1.44	6.54	-1.48
	3	1019.7	5.98	0.06	-11.13	-0.64	0.83	73.92	26.70	4.79	18.53	0.65	10.02	-0.81
	4	3228.5	7.32	1.48	-97.25	0.21	5.72	79.03	8.32	8.39	3.88	0.77	6.21	-0.13
	5	1805.9	16.85	0.91	-183.75	-1.16	0.87	170.85	-2.31	0.59	-8.22	1.51	-1.52	-1.31
Wood element concentrations														
	Type	%		mg/kg										
		C	N	Al	Ca	Cu	Fe	K	Mg	Mn	Na	P	S	Zn
	Sound	51.1	0.06	32.7	1217.7	0.8	43.0	459.4	180.3	60.9	-18.9	31.9	92.1	13.4
	Unsound	52.7	0.33	43.0	11984.2	10.6	39.3	1181.2	595.1	317.8	4.8	338.0	500.8	128.7
	Bark	53.6	0.40	303.8	5433.6	10.0	409.9	901.9	641.4	70.1	15.6	214.3	429.6	49.5

Table 2.2. Carbon and nutrients' significance tests of CWD leachate by univariate and repeated measures ANOVA for phosphorus.

Cumulative		Nutrients															
		C		N		P		K		Ca		Mg		S		Mn	
Source	df	F	Prob.	F	Prob.	F	Prob.	F	Prob.	F	Prob.	F	Prob.	F	Prob.	F	Prob.
Decay Group (D)	1	20.61	0.000	20.25	0.000	63.24	0.000	4.97	0.033	1.74	0.197	0.70	0.408	0.04	0.846	1.36	0.253
Origin (O)	1	0.59	0.450	3.90	0.057	0.42	0.522	2.26	0.143	0.08	0.786	0.14	0.710	0.13	0.719	26.77	0.000
Species (S)	1	1.42	0.243	1.19	0.284	3.25	0.081	12.55	0.001	0.03	0.871	0.00	0.978	1.48	0.232	65.91	0.000
D*O	1	0.09	0.763	0.82	0.374	1.10	0.301	4.46	0.043	0.27	0.606	0.67	0.419	1.06	0.311	1.53	0.226
D*S	1	1.76	0.194	0.01	0.932	0.64	0.564	0.65	0.426	0.02	0.884	0.05	0.827	0.31	0.582	1.52	0.227
O*S	1	1.67	0.206	1.65	0.209	0.42	0.520	3.04	0.091	0.21	0.649	0.47	0.500	0.50	0.486	27.44	0.000
D*O*S	1	1.00	0.325	1.87	0.181	1.32	0.259	0.16	0.695	0.50	0.485	0.94	0.341	0.72	0.404	1.27	0.268
Error	31																

Decay Class																	
		DOC		N		P		K		Ca		Mg		S		Mn	
Source	df	F	Prob.	F	Prob.	F	Prob.	F	Prob.	F	Prob.	F	Prob.	F	Prob.	F	Prob.
Decay class	4	11.90	0.000	4.92	0.003	21.567	0.000	2.12	0.099	0.75	0.566	0.38	0.821	0.55	0.704	2.08	0.105
Error	34																

Repeated Measures (Phosphorus)							
		Content			Concentration		
Source	df	MS	F	Prob.	MS	F	Prob.
Week (W)	15	0.38	52.377	0.000	0.019	58.158	0.000
W*D	15	0.222	30.387	0.000	0.013	41.455	0.000
W*O	15	0.006	0.786	0.684	0.000	0.993	0.459
W*S	15	0.013	1.618	0.071	0.001	1.622	0.070
W*D*O	15	0.003	0.345	0.988	0.000	0.351	0.986
W*D*S	15	0.003	0.252	0.998	0.001	0.631	0.840
W*O*S	15	0.004	0.468	0.949	0.001	0.817	0.651
W*D*O*S	15	0.002	0.065	1.000	0.001	0.35	0.987
Error	465	0.008			0.000		

As outlined by Laiho and Prescott (2004) the log must first become adequately saturated with moisture to allow for microbial habitation and decay is very slow. The second stage is relatively short lived, as simple carbon compounds and cellulose are rapidly decomposed through microbial activity. The last stage involves complex compounds (mostly lignin) that decompose very slowly. Our oldest, most highly decomposed logs were 15 years old, so it stands to reason that some were approaching the final, moderately slow stage of decomposition.

2.3.2 NITROGEN

We found that N in CWD leachate from decay class 1 and 2 was below the control N levels (-16.0, -6.8 mg, respectively, $p \leq 0.003$), indicating immobilization of N (Figure 2.3). In decay classes 3 through 5, however, CWD leachate was an increasing source of N (5.98, 7.32, 16.85 mg, respectively) (

Table **2.1**).

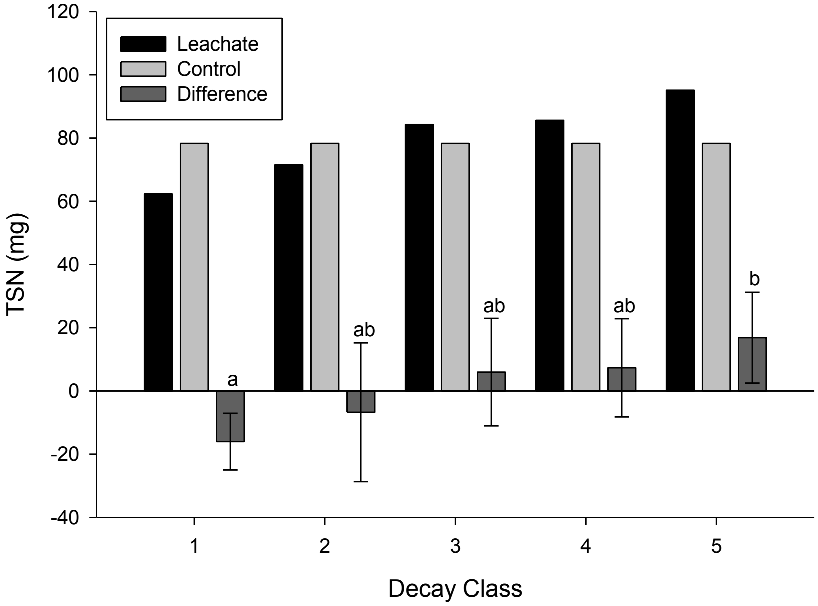

Figure 2.3 Cumulative total soluble nitrogen (TSN) collected over 16 weeks, by log decay class.

Initial immobilization of N in early decay classes has been well documented (Yavitt and Fahey 1985, Herrmann and Prescott 2008, Harmon *et al.* 1994, Moore *et al.* 2006) where C:N ratios are high, requiring decomposer microbes to access nutrients (such as N) from the CWD to begin decomposition of cellular structures in the wood. This trend from sink to source is still debated, as Brais *et al.* (2006) found only white birch (*Betula papyrifera* Marsh.) acted as a net sink for N, while trembling aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* (Moench) Voss) and jack pine (*Pinus banksiana* Lamb.) were all net sources of N, although the latter two were of little magnitude. Similar increases of N (and P) content in leachate were found in *Picea abies* between decay classes 3 and 5 (Butler *et al.* 2007) and between 30 and 55 years following tree death in *Pinus contorta* (Fahey 1983). Garrett *et al.* (2008) found that nitrogen content of stumps and coarse roots of *Pinus radiata* (D. Don) also increased substantially during decay. In contrast, Krankina *et al.* (1999) reported N losses from CWD of three boreal tree species in Russia, and cite differences in methodology (e.g., accounting for bark loss), species, and environmental conditions as possible explanations.

Log origin was not a significant factor for N (p=0.057), but the fire-origin logs leached more N than harvest logs. Higher N leaching from fire-origin logs could be due to decomposition of subcortical tissues (i.e. phloem), leaching, and insect activity, as was suggested by Boulanger and Sirois (2006) to explain their similar observation of an initial pulse of N following fire.

2.3.3 PHOSPHORUS

The phosphorus pattern differed from that of C and N, in that the first decay class was the largest source of P (5.6 mg, p<0.001), with a decline to the third decay class (0.65 mg) and a small (non-significant) rebound in decay classes four (0.77 mg) and five (1.51 mg) (Figure 2.4).

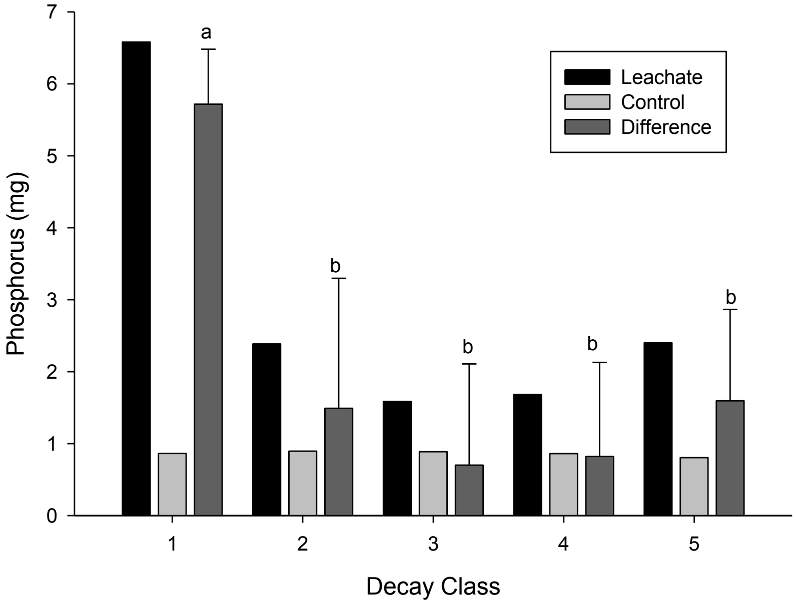

Figure 2.4 Cumulative phosphorus collected over 16 weeks, by log decay class.

When P leachate concentrations were tracked over the 16-week time period, there was a clear pattern of rapid release of P in the fresh logs ($p<0.001$). Initially high levels of P in leachate from fresh CWD dropped rapidly to a level similar to the older logs and very close to the detection limits of the instruments (Figure 2.5). This rapid loss of P following tree mortality may help explain the variability in patterns of P in the literature, which report CWD as both a P sink and source (Moore *et al.* 2006). As most of the P in fresh logs was accounted for in the bark (ten times higher in bark than sound wood, Table 2.1), this "pulse" loss of P in fresh logs is largely driven by bark tissue decomposition (Krankina *et al.* 1999) and can be easily missed if bark is not included or if there is a delay in CWD nutrient assessments following tree mortality.

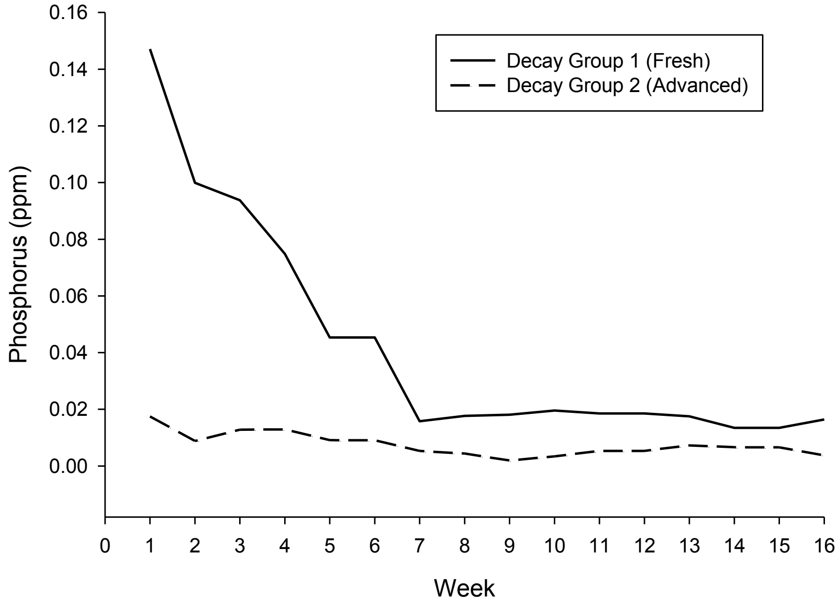

Figure 2.5 Phosphorus leachate trends by log age (fresh and old) over the 16 week experiment.

A small "rebound" of P solute was observed in the latter stages of decay, mostly originating from unsound wood in the log (Fig. 4). Harmon *et al.* (1986) found that older, more decayed logs accounted for the majority of P storage in *Pseudotsuga* dominated conifer stands, and this increase of P in the wood could be from microbial activity or previous activity of the soil interface with the log prior to the experiment. Similar to DOC, origin and species did not significantly differ ($p>0.05$) in P leaching output.

2.3.4 OTHER NUTRIENTS

Log origin was a significant ($p<0.001$) factor for Mn, with harvest-origin logs leaching more Mn (8.06 mg kg^{-1}) than fire logs (2.02 mg kg^{-1}). Mn also had a species ×

origin interaction ($p<0.001$) as Mn content and leachate was almost exclusively linked to spruce and was also strongly associated with harvest-origin logs. Almost no Mn leachate was detected in aspen logs (< 0.2 mg kg^{-1}), and spruce Mn leachate was five times higher in harvested logs (15.9 mg) than fire-origin logs (3.6 mg), possibly as a result of quick volatilization of Mn in fire situations.

Species differences were also detected for K (Table 2.2: $p=0.007$). Higher initial contents of K in aspen log samples translated directly to higher leachate concentrations of these cations than from the spruce logs (Table 2.1).

2.3.5 OTHER OBSERVATIONS

A singular older log was observed to leach over 95 mg kg^{-1} of N and 32 mg kg^{-1} of P, 10 and 15 times, respectively, more than all other older logs combined. While this log was considered an outlier, the advanced decay and biological activity (e.g. germination of seeds within the log, visible mesofauna on leachate filter paper) suggest that this exceptional log may have been simply farther along the decay spectrum than the rest of the sample logs collected and likely an older log that did not originate from the disturbance event. This also highlights the variability of logs, especially as decay progresses, and the limitations of using a decay classification system (Laiho and Prescott 2004).

2.4 Conclusions

Misting CWD in the absence of soil media exhibited similar source/sink trends from *in-situ* studies, indicating that 1] microbial and fungal processes occur on CWD without soil, and 2] that these processes act quickly after felling. The *ex-situ*, soil-less environment of this study made it possible to identify clear source/sink dynamics of carbon and nutrients of two commonly occurring boreal species as decay progressed.

Source/sink relationships of CWD leachate were largely dependent on the stage of decay of the log for C (source, peaking at decay class four and slowly decreasing), N (initial sink to eventual source) and P (initial pulse, subsequent low source). Leachate differences between aspen and spruce (higher K, Ca, Mg output in aspen; higher S and Mn output in spruce CWD) were largely a function of the relative difference in the content of these nutrients in the bark and wood prior to the experiment. Harvested log leachate values were similar to those of fire origin, with the exception of N and Mn, suggesting considerable volatilization of these two nutrients during wildfire events.

As this study has shown, CWD is quite dynamic, even in the absence of interaction with the forest floor. In light of initiatives calling for increased utilization of unmerchantable or low value wood within typical boreal harvesting systems, careful consideration of the type and amount of CWD (species, decay class) should be left, as well as consideration for CWD “recruitment” (i.e., standing trees) should be regarded. Testable hypotheses regarding the assessment of site nutrient pools and associated metrics (e.g. soil type, structure, depth; site quality) should be studied to determine if removal of CWD will significantly affect these pools over the longer term.

3.0 COARSE WOODY DEBRIS DYNAMICS FOLLOWING BIOMASS HARVESTING: TRACKING THE CARBON AND NITROGEN PATTERNS FROM HARVEST TO CROWN CLOSURE IN UPLAND BLACK SPRUCE ECOSYSTEMS.

3.1 INTRODUCTION

The use of forest biomass for energy/fuel may result in increased utilization, requiring a better understanding of the potential impacts of intensive harvest on forested sites. Coarse woody debris (CWD) has been shown to be a very important component of the forest ecosystem, especially for biological diversity of many types of flora and fauna (Samuelsson *et al.* 1994, Siitonen 2001, Lonsdale *et al.* 2008). There is less clarity in the role CWD plays as a significant contributor to site nutrient pools, the temporal pattern of nutrient release, and the timing of this release compared to plant uptake demand. CWD has often been described as a "buffer" against nutrient losses following site disturbance (Graham and Cromack 1982, Lang 1984, Tenhagen *et al.* 1996, Krankina *et al.* 1999). Laiho and Prescott (2004) reported declining C /nutrient ratios and increased nutrient content of wood during early phases of decay suggesting that CWD plays an active role in maintaining site quality. Following the flush of more rapidly decomposing components (i.e. leaves, small branches, roots), commonly referred to as the assart effect (Romell 1957, Titus *et al.* 2006), CWD could provide essential nutrition to the emerging stand until crown closure when other cycling processes (e.g. litterfall, throughfall, stemflow) once again enable self-sufficiency.

Observed contributions of CWD are roughly 4-6% of plant uptake (Hart 1999) and less than 5% of total N released from aboveground litter (Arthur and Fahey 1989, Laiho and Prescott 1999). While CWD has been dismissed as a non-significant contributor to total N cycling (Laiho and Prescott 2004), the timing of N immobilization and subsequent release by CWD has not been related to forest stand requirements following stand disturbance and initiation. Krankina *et al.* (1999) and others (Hafner *et al.* 2005, Butler *et al.* 2007) point to the broad range of nutrient and carbon pool estimates in the literature as evidence that further research is required to fully understand nutrient dynamics. This will be particularly critical should forest biomass be increasingly utilized as a renewable energy source in the coming decades

In a recent review, Laiho and Prescott (2004) pose two hypotheses with respect to the role of CWD in forest productivity. Specifically, that 1) on sites where nutrients, especially N or P, limit plant growth, CWD accumulation may reduce primary productivity through immobilization of those nutrients by decomposers, and 2) on dry sites, where lack of moisture limits plant and microbe growth, CWD may increase primary productivity and enhance element cycling by improving moisture retention. On such sites, CWD may also be important for the retention and accumulation of soil organic matter. The current study was designed to address the amount or form of nutrients sequestered within and provided by the CWD. Using established experiments with a history of pertinent data supplemented by additional measurements, our goal is to clarify the role of CWD in these forest types and identify the potential effects of increased utilization for bio-fibre and bio-energy on these ecosystems. Another important aspect to consider is the timeframe when CWD might contribute to site nutrition in terms of the ecological rotation of forested stands. The stands examined in this project have been tracked for 14 years post-harvest and are now approaching the critical period of time between stand establishment and canopy closure. As this monitoring effort includes repeated measures of CWD nutrient levels, it is possible to quantify the change in both biomass and nutrient retention throughout this timeframe.

Our specific research questions related to Laiho and Prescott's (2004) over-arching hypotheses were:

1. Is soil type a significant factor in determining the role of CWD (i.e. source or sink for nutrients)?
2. How do CWD-C pools compare to total soil C reserves, and does this vary depending on soil type and level of biomass removal?
3. How do mass and nitrogen content change in CWD over time since disturbance, and does this pattern differ depending on soil type?
4. Does the pattern of CWD nitrogen retention/release correspond to the temporal patterns in planted black spruce foliar nutrition?

3.2 MATERIALS AND METHODS

3.2.1 SITE LOCATION

For this study, four sites were selected that represented two soil types and site quality classes (good – fresh, coarse loamy tills; poor - dry, sandy outwashes). The fresh, coarse loamy sites are situated approximately 60 km north of Thunder Bay, ON, CAN (latitude: $49^{o}07^{'}$N, longitude: $89^{o}41^{'}$W), and represent well drained, fresh (moisture regime 2) sites dominated by black spruce (*Picea mariana* L.) and jack pine (*Pinus banksiana* Lamb.) with a scattered occurrence of trembling aspen (*Populus tremuloides* Michx.). These sites are shallow (<20 cm) morainal tills overtopping granitic bedrock (Dystric Brunisols – Can. Soil Classification Working Group 2006).

The two dry, sandy sites are located north of Geraldton, ON, CAN (latitude: $50^{o}42^{'}$N, longitude: $86^{o}24^{'}$W). Both sites are representative of sandy outwash soils dominated by black spruce and jack pine, and have well-developed Humo-ferric podzolic profiles (Can. Soil Classification Working Group 2006).One site is a deep, fine to medium sand that is rapidly drained, and has a moderately dry moisture regime (MR: 1), while the second site is very rapidly drained, and represents a slightly drier (MR: 0), medium-coarse sandy site.

3.2.2 EXPERIMENTAL DESIGN

The study was designed as a 2 x 4 Completely Randomized Design (CRD), with two soil types, as described above, and 4 levels of biomass removals. These removal treatments during the winter of 1994/5, and included: Stem only [SO]– delimbed at the stump, Full-tree chipping [CH] – chipped debris returned to the harvest plot, Full-tree [FT] – delimbed at the roadside, and Full-tree + Blading [FT + B]– complete removal of vegetation and forest floor. Each site included three replicated treatment plots (30 x 30 m), separated by 20 m buffers. On each treatment plot, two 4 m^2 slash plots were established immediately after harvest in the centre of two randomly-selected plot quadrats. The slash on each sub-plot was sorted by component (bole, branches, bark, cones, twigs, needles), weighed and sub-samples collected for dry weight and nutrient analysis. Slash was then returned to the plot according to the original distribution. Slash loadings and their associated nutrient pools were calculated for each biomass removal level x site combination for the period immediately following harvest ($Time_0$), 4 and 14 years after harvest (summer 2008). At each sampling period, sub-samples of CWD (i.e., branches and stems > 7 cm in diameter) remaining from slash plots was removed and analyzed for total carbon and nitrogen. In total, 96 slash plots were tracked through the 14 year period.

To determine if the original 4 m^2 slash plots were representative of the overall slash loadings for each biomass removal treatment x site combination, additional transects were measured in 2008 (48 in total). Transects were 10 m in length and 2 m wide and were situated diagonally within one quadrant that had an existing slash plot. Log diameters and lengths were recorded and converted to mass using density. Density was determined by classifying each log into decay classes similar to Maser *et al.* (1979), Sollins (1982) and Naesset (1999): 1] Recently dead tree, bark intact 2] bark mostly intact, wood of outer layers (sapwood) of the log has started to soften due to rot, 3] bark sloughing or absent, soft outer layers of log and are easily removed with a knife, heartwood mostly sound, 4] bark detached, wood soft, no solid core, 5] Fragmented, no structural integrity. Average densities for each decay class were determined through volume displacement of subsampled logs. Overall, the plots did appear to be representative when compared to the transects, with a percent difference of 2.6%. There was a tendency, however, for underestimates in the SO treatments due to the clumpy nature of the slash distribution.

Field sampling of soil for the determination of mineralizable N (anaerobic incubation) and inorganic N (fresh extraction) occurred in the summer of 2008 ($Time_{14}$). One forest humus (O horizon) and one upper mineral soil sample (0 to 20cm) were randomly taken from each treatment plot. Samples were air dried, organic samples were hand ground, removing cones and branch fragments > 2 cm in diameter; mineral samples were sieved (2 mm) to remove coarse fragments. Soil carbon and nitrogen pools, by horizon, were calculated as horizon depth (cm) x elemental concentrations ($mg \cdot kg^{-1}$) x fine fraction bulk density ($g \cdot cm^{-3}$), then converted to a per hectare basis. Bulk density measurements were done as part of the ongoing monitoring of these Long-term Soil Productivity (LTSP) trials.

Foliar sampling was conducted repeatedly (Year 4, 8, 10, 15) on 9 randomly selected planted black spruce seedlings on each of the 4 study sites and 12 treatment plots per site (432 seedlings x 4 sampling periods). Current foliage was clipped from 10 branches (bulked into 1 sample per tree) located in the upper one-third of the crown at the end of August in each of the sampling years. Samples were processed/analyzed in the lab following the procedures described below for the CWD samples. Time 0 samples were obtained from 9 trees at the time of felling.

3.2.3 ANALYSIS

Solid wood samples were dried at 50^0C until they reached a stabilized dry weight. Each wood cookie was separated into bark, sound, and unsound components. Samples were then ground into 2g portions using a Thomas Scientific Wiley Mini-Mill (Model 3383-L10), with a 0.85mm sieve (20 mesh). Total carbon, nitrogen and sulfur were analyzed using a combustion technique with a LECO CNS-2000 (LECO Corporation, St. Joseph MI). Al, B, Ca, K, Mg, Mn, Na, P, S and Zn analysis was completed with a Varian Vista Pro inductively coupled argon plasma spectrometer (ICAP/ICP) AES (Varian Inc.) following a 10% HNO_3 acid digestion (adapted from Miller 1998).

Mineralizable nitrogen was determined using an anaerobic incubation procedure to measure the potential of the soil, collected in 2008, to provide available nitrogen. Ten grams of the air-dried mineral sample or five grams of the organic sample were added to 50 mL of deionized water and placed in an incubator for 14 days at 30^0C [following the procedures outlined by Powers (1980)]. Following incubation, 4 M KCl solution was added to the samples, which, when combined with the deionized water yielded a 2 M extraction solution (Binkley *et al.* 1990). Samples were then agitated for one hour at 180 rpm, filtered, and analyzed for ammonium using a Technicon Instruments AutoAnalyzer II (Pulse Instrumentation (1992) Ltd., Saskatoon, SK)(Kalra and Maynard 1991). In addition, inorganic nitrogen (NH_4 + NO_3) was measured to obtain a point-in-time ($Time_{14}$) reading of available N, and was similarly obtained using 2 M KCl extraction on fresh soil, following Kalra and Maynard (1991).

Data were analyzed as a 2 x 4 CRD ANOVA with site and biomass removal treatment as factors using SPSS (ver. 17). To examine changes in nutrient concentrations and content through time a repeated measures approach was employed. Post hoc analysis was performed using Student Neuman Kuels (SNK) means separation test.

Decay rate was calculated using a standard CWD exponential decay model (Harmon *et al.* 1986, Laiho and Prescott 2004, Tobin *et al.* 2007) and is expressed as:

$$Y_t = Y_0 e^{-kt} \quad ,$$

[1]

Where Y_0 is the initial quantity of the material (mass or density), Y_t is the quantity remaining at time t, and k is the decay constant. Linear transformation of the equation to express k from the equation is as follows:

$$k = \frac{(\ln Y_0 - \ln Y_t)}{t}$$

[2]

Decay constants were then computed for the different sampling periods (years 0,4, and 14, as well as an average constant).

3.3 Results

3.3.1 CWD MASS AND CARBON LOSS

Initial CWD slash loadings for the SO, CH, and FT treatments were in the range of 13-23 Mg ha^{-1}, with significantly higher values on the loam sites for the FT and FT+B treatments (Figure 3.1). After 14 years, the CW remaining was less than 4 Mg ha $^{-1}$, dropping on average nearly 10 Mg ha^{-1} across the treatments. There was no significant difference in the amount of material lost between the SO, CH and FT treatments at time 0 (p=0.952), year 4 (p=0.323) or year 14 (p=0.193). The FT + B treatment, as expected, had little to no CWD after the treatment was applied.

Average CWD mass decreased on both soil types over the 14 year time period, with loam decreasing from 15.0 to 4.7 Mg ha^{-1} and sand decreasing from 13.1 to 3.0 Mg ha^{-1}, with the rate of decrease similar across treatments (Figure 3.1). We did not detect any difference in average CWD mass loss between soil types at year 0 (p=0.363) year 4 (p=0.950) or year 14 (p=0.258).

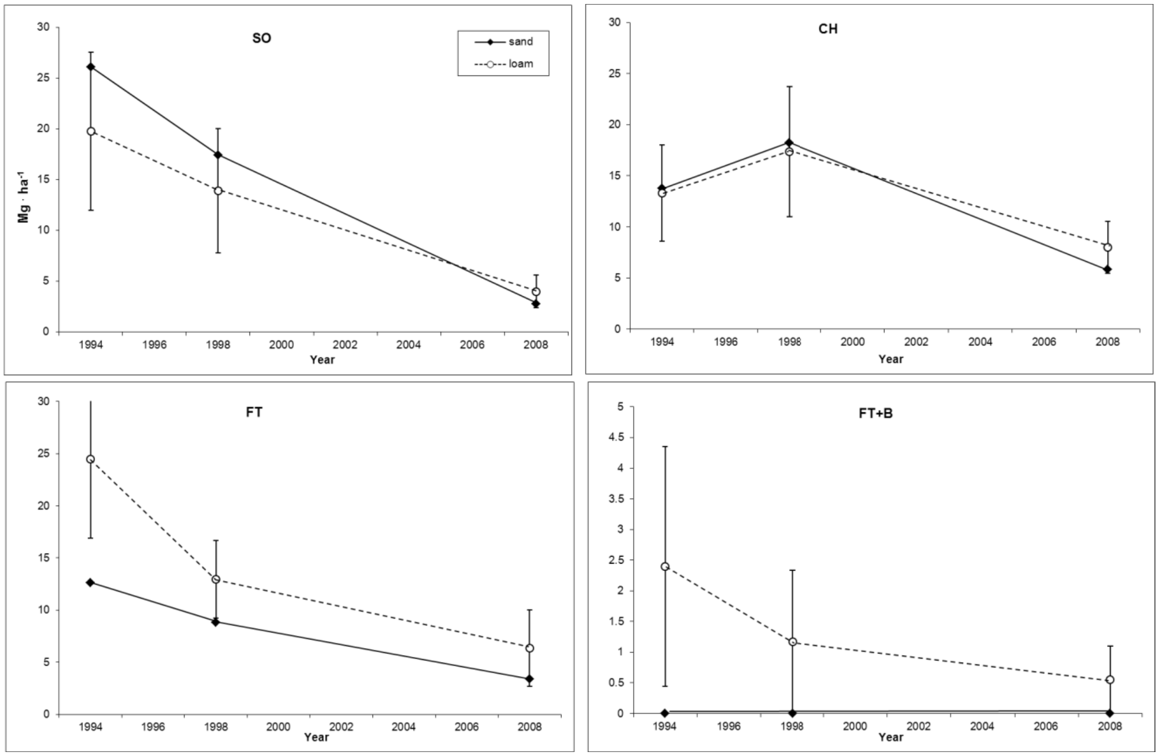

Figure 3.1 Average CWD mass loss, by harvest treatment and soil type, tracked over a 14 year sampling period. SE bars have been included for the loamy sites to provide an example of the within-treatment variability for each of the sampling years.

It is worth noting, however, that the CWD decay constants from year 0 to 4 were lower on sandy soils (k=0.05) than on the loamy sites (k=0.12) (Table 3.1). From years 4 to 14, the decay rate for CWD on loamy sites remained relatively constant (k=0.10), while CWD on sandy sites decayed at a much faster rate (k=0.13) during this phase of decomposition compared to the first four years, suggesting a “decompositional delay” on the dry, sandy sites.

Table 3.1 Decay constants (k) by soil type for the various sampling periods.

Decay period (Year)	Sand (decay *k*)	Loam (*k*)
0 to 4	0.05	0.12
4 to 14	0.13	0.10
0 to 14	0.10	0.11

In both soil types and all harvest treatments, there was greater carbon content in the soil (mineral and organic) compared to CWD in Year 14 (Figure 3.2). Total C reserves (CWD-C + soil C) averaged 56.8 (sand) and 83.6 Mg ha^{-1} (loam) 14 years after treatments were imposed. The high within-site variability is largely a function of the difference between treatments (mainly the low C pool in the FT + B treatment). Total C in CWD at 14 years after harvest was <8% of total C reserves for both soil types, with the majority of C contained in the O horizon (nearly 70%), with the exception of the severe FT+B treatment.

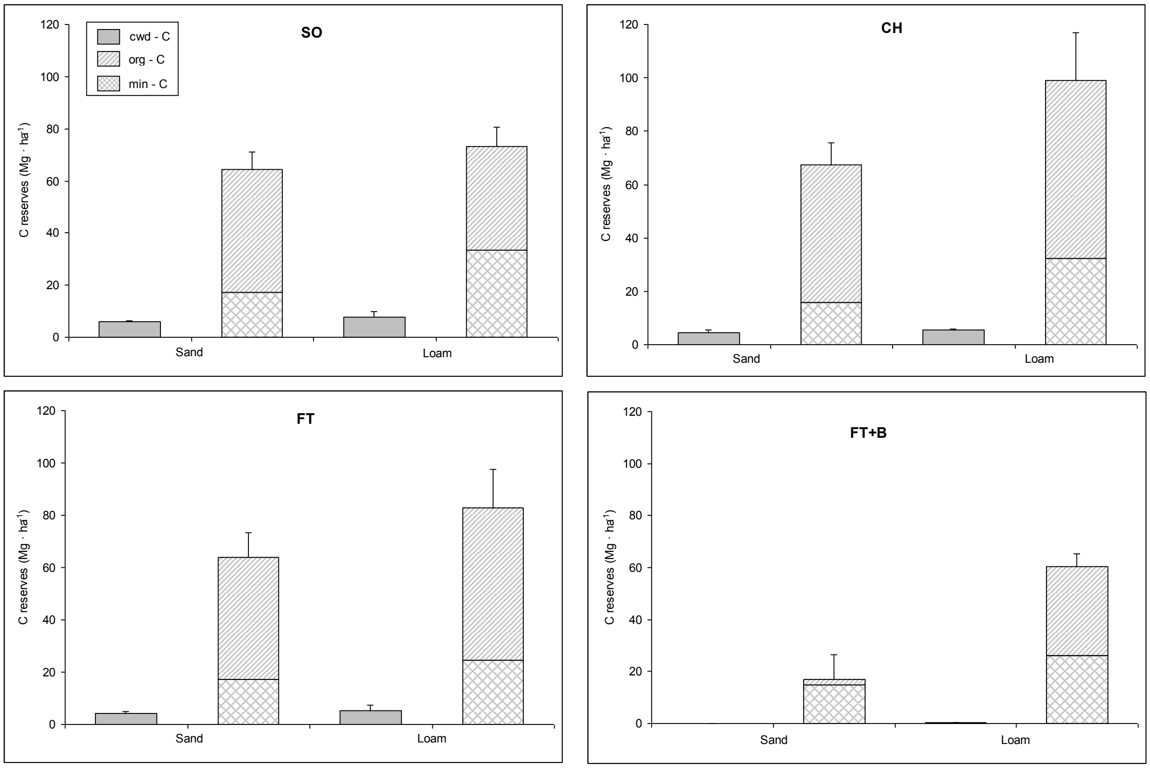

Figure 3.2 Carbon content in CWD (CWD-C) and organic (ORG-C) and mineral (MIN-C) soil pools , by harvest treatment and soil type, 14 years after harvest; values. SE bars for CWD-C and the total soil carbon pool have been included.

3.3.2 NITROGEN CONCENTRATION, CONTENT AND POOLS

Overall, nitrogen concentration in CWD increased through time from 900 ppm to over 2400 ppm (nearly a threefold increase) regardless of removal treatment or soil type (Figure 3.3). Initial N concentrations in CWD were similar at year 0 for all treatments, with the exception of the FT+B, but were significantly higher ($p<0.001$) on the sandy sites (2091 ppm, ranging from 1814 (SO) to 2593 ppm (CH)) compared to CWD on the loam sites (850 ppm, ranging from 743 (FT+B) to 933 ppm (SO)) at year 4. Although concentration remained higher in year 14 on the sandy sites, (2728 *vs.* 2163 ppm) they were not significantly different for any of the treatments due to the high variability associated with the highly decomposed CWD (majority (65%) of CWD was at least decay class 4).

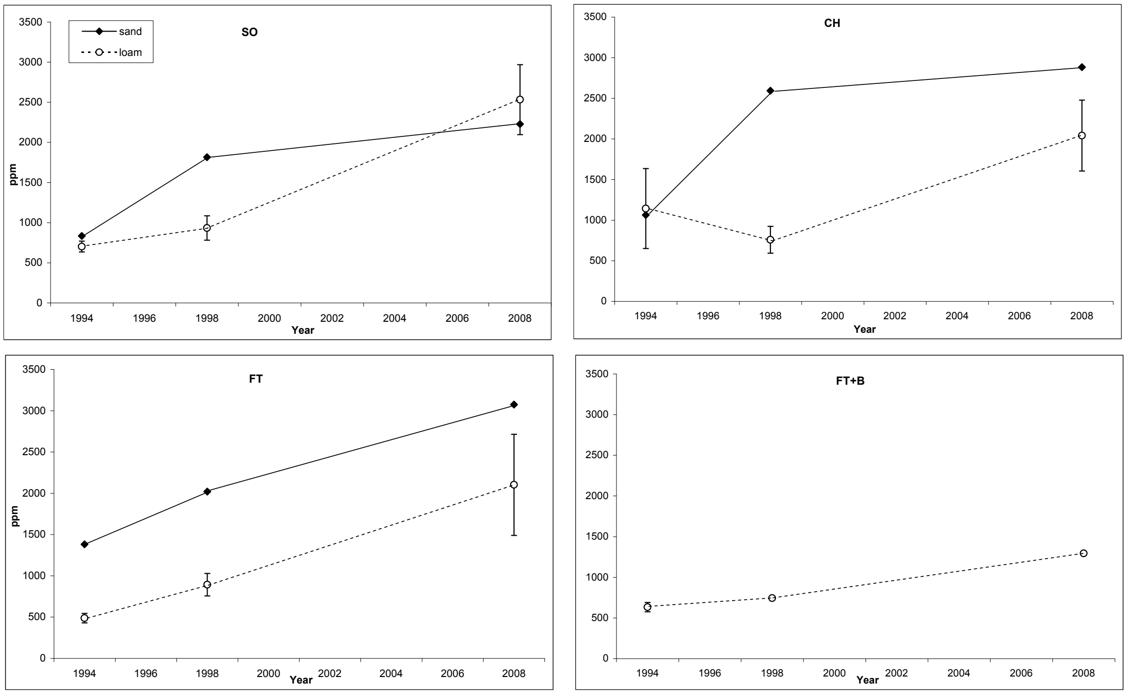

Figure 3.3 Changes in nitrogen concentration in CWD by harvest treatment and soil type, over a 14 year sampling period. SE bars have been included for each sampling year. Note: no samples were available for chemical analysis for the FT+B treatment on the sandy sites.

In terms of nitrogen content, the CWD on both soil types displayed immobilization for the first four years (sand: -12.7 kg ha^{-1} yr^{-1} ; loam: -2.4 kg ha^{-1} yr^{-1}) , with subsequent release from years 4 to 14 (sand: 7.1 kg ha^{-1} yr^{-1} ; loam: 3.4 kg ha^{-1} yr^{-1}) (Figure 3.4).

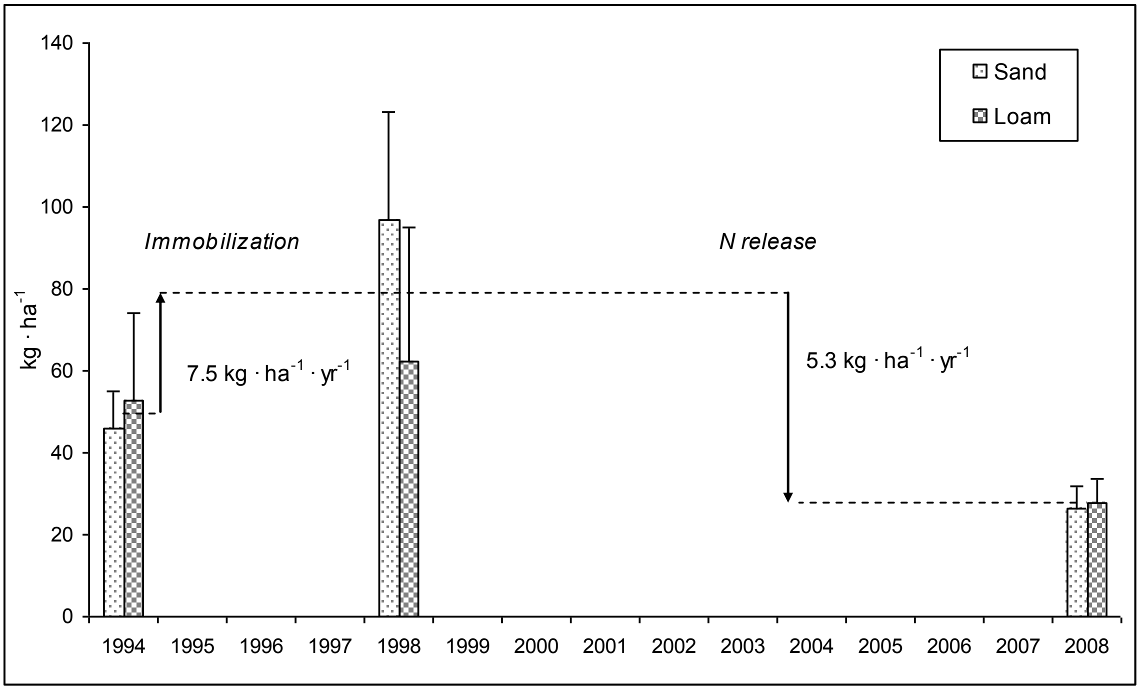

Figure 3.4 Changes in N content in CWD, by soil type, over a 14 year period following harvest. SE bars have been included for each sampling year.

This N release average of 5.3 kg ha^{-1} from years 4 to 14 can be compared to the inorganic and mineralizable N pools measured in studies with comparable soil and climate conditions. Some studies (Pare and Van Cleve 1993, Brais et al. 1995, and Huang and Schoenau 1997) indicate that this input of available N would constitute a much larger proportion of the available N pool than the 2-5% contribution that CWD makes to the total N pool. A specific study of jack pine-dominated outwash sands (post wildfire chronosequence) found N mineralization rates to average 25 kg ha^{-1}, dominated by NH_4^+ (>90%). [1]

3.3.3 TEMPORAL PATTERNS IN FOLIAR N

In terms of planted tree (*Picea mariana* – black spruce) response, Figure 3.5 illustrates the temporal pattern in foliar N concentration during the first 15 years following harvest. For both soil types, a significant peak in foliar N occurred at Year 4, presumably resulting from a soil assart flush (*i.e.*, increased soil mineralization following harvesting and rapid decompositiion of fine logging residues – foliage and twigs). At this point in time, the seedlings established on the FT + B treatments had significantly lower ($p<.0001$) foliar N concentration than the other 3 treatments on both soil types.

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[1] Morris, D.M., Edgington, L.E., and Duckert, D.R. 2006. Carbon and nitrogen dynamics associated with post-wildfire stand development for jack pine-dominated sites in northwestern Ontario. *In* The Soil Science Society of America annual meeting, Nov. 12-16, 2006, Indianapolis, Indiana.

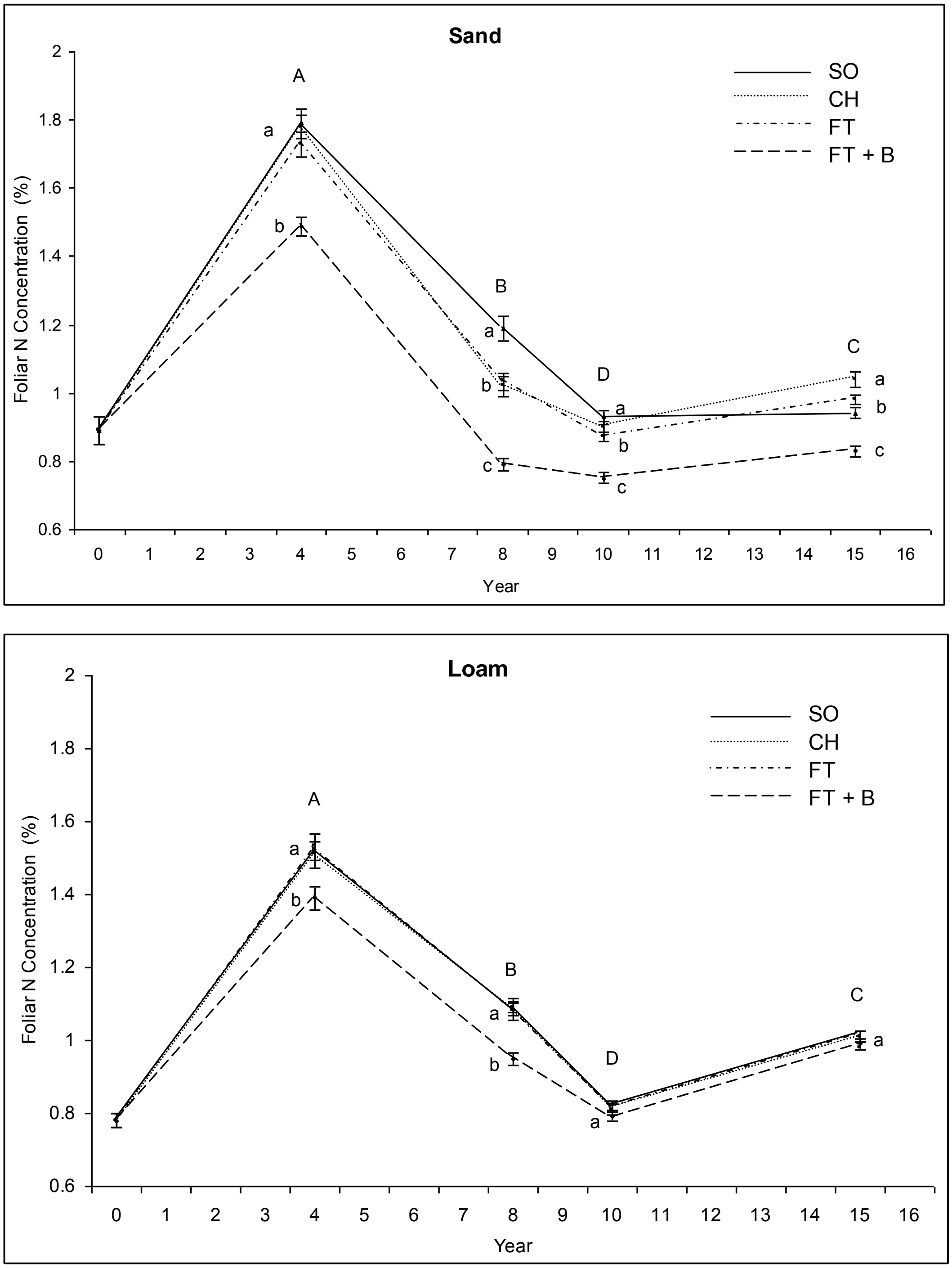

Figure 3.5 Temporal patterns in planted black spruce foliar N (current foliage only) for the various harvest treatment x soil type combinations. Lower case letters denote significant ($p<.05$) differences between treatments. Capital letters denote significant differences between sampling times.

After this peak, foliar N decreased significantly (p<.0001) through to year 10, but began to rebound by year 15 particularly on the loam sites. This increase, presumably was, in part, the result of the documented release of N from CWD from Year 8 to 14 (Figure 3.4). On the sandy sites, foliar N on the FT + B treatment remained significantly lower (p<.0001) where little to no CWD had been retained.

3.4 Discussion

The exponential decay pattern of CWD among biomass removal treatments was similar to natural patterns of CWD decay (Harmon *et al.* 1986, Tobin *et al.* 2007). When separated by soil type, however, the CWD on the sandy sites exhibited a distinct increase in decay rate after year four, which more closely follows a three stage decay function, described by Yatskov *et al.* (2003): 1) an initial slow phase, 2) a rapid phase, and 3) an extended period of moderately slow decay. This difference in decay rate pattern across soil types could be a reflection of moisture retention differences between the dry, freely draining sand *vs.* the fresh loam soil types. CWD must achieve an adequate moisture content to promote microbial colonization (Harmon *et al.* 2000), and this may be delayed on the rapidly drained sandy soils compared to the moderately drained loamy soils.

Carbon pools in CWD have often been oversimplified in past assessments of carbon stores (Krankina *et al.* 2001), largely in part to the significant variation of CWD inputs over forest succession. Many models simply apply a relative proportion to live biomass, but CWD does not parallel live biomass carbon storage patterns. The contribution of CWD in our study to total carbon reserves after 14 years (<8%) was comparable to other coniferous systems (Harmon *et al.* 1986), but relatively low compared to many other forest types (Shorohova and Shorohov 2001). Complete removal of all CWD, as in the FT + B treatment, may create a carbon deficit that could have a detrimental effect on long term soil carbon stores and ecosystem energetics and therefore should be monitored over the longer term.

While patterns of CWD N retention, release, or a combination of the two over time have been observed previously (Fahey 1983, Boulanger and Sirois 2006, Brais *et al.* 2006), studies showing these N patterns as related to substrate (i.e. soil type) are not available. We found N retention to be large on the nutrient limited sandy site, consistent with Laiho and Prescott's (2004) hypothesis. However after year 4, we found net N release from CWD at just slightly lower annual rates, meaning that the initial N immobilization is countered by subsequent N release. Comparing the timing of this immobilization and release to the stages of stand development (Figure 3.6), the timing of N immobilization occurs at a period of low demand, while its release occurs during peak demand, as the stand nears crown closure. This pattern coincided with a rebound in planted black spruce foliar N concentrations between Year 10 and 15.

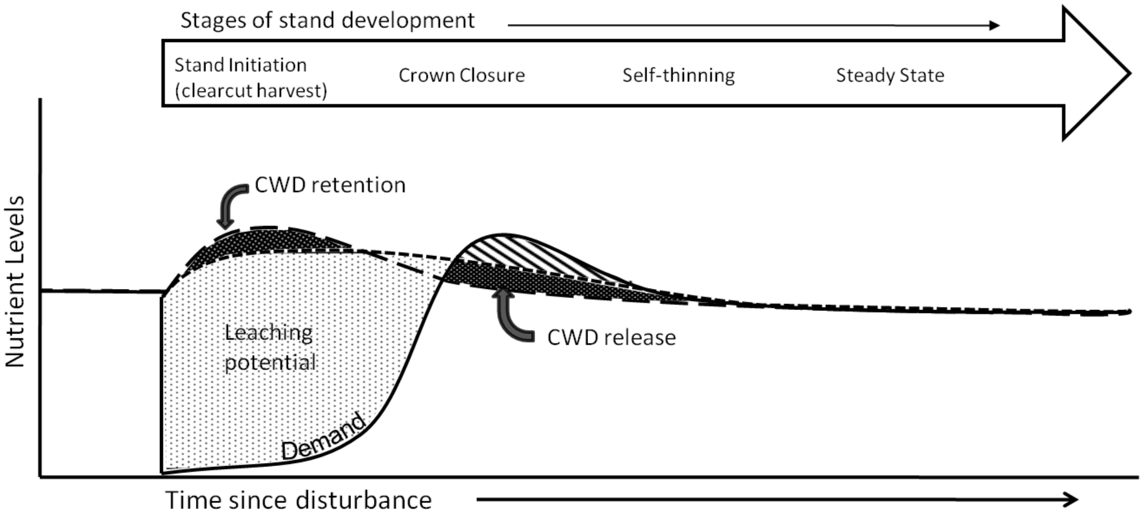

Figure 3.6 Conceptual diagram of the role of CWD in N retention and subsequent release during the stages of stand development.

Most studies, when comparing CWD to soil/aboveground N pools use total N, and CWD contributions are 2-5% of this total (Sollins *et al.* 1980, Means *et al.* 1992, Laiho and Prescott 2004). Our study found similar percentages when compared to total N pools. However, when we compared available N pools, the N release from CWD on the nutrient poor, sandy sites was equivalent to the estimates of inorganic N pools (Figure 3.6). In contrast, the CWD contribution to the available N pool was negligible compared to the large inorganic N or mineralizable N soil pool on the loamy sites.

Management of CWD is becoming increasingly integral to biomass harvesting operations, especially in Scandanavia (Siitonen 2001, Lilja-Rothsten *et al.* 2008). North American researchers have been following suit with long term research projects (i.e. LTSP collaborators, etc.) as interest in “unutilized” forest biomass left after harvesting grows in the search for renewable and sustainable energy alternatives to traditional fossil fuel consumption. CWD has already been recognized as an important component of site structure for biodiversity of flora and fauna (Lonsdale *et al.* 2008), but comparisons of biomass harvesting intensity and CWD nutrient/site productivity impacts are few. Many of these long term studies are now approaching or are past the crown closure stage of stand development, and it is imperative that impacts to long term site productivity are thoroughly examined. While CWD nitrogen pools are small compared to underlying soils, there are two reasons why these small amounts may be important to plant nutrition: 1] The timing of retention and release of N in CWD coincides with stages of nutrient excess and deficit (respectively) and 2] N released from CWD is in plant-available form (Kuehne *et al.* 2008) which should have a positive impact on growth in N limited boreal ecosystems. CWD may also indirectly play an important role as a storage pool for base cations as well as stabilized soil organic matter (Arthur and Fahey 1990).

The limited scope of this study in terms of study sites (*i.e.,* 2 site replicates for each of the soil types) and CWD subplots (2) per replicated (3) treatment plot does need to be recognized, and is reflected in the large standard errors across treatments and sampling periods. These results, however, do suggest that on nutrient and/or moisture-limiting sites, the importance of CWD may be magnified and become a critical factor to maintaining long term productivity. Research focusing on these less-productive sites may show more conclusively the unique role of CWD and better inform policy directives for biomass harvesting operations to ensure continued sustainability.

3.5 Conclusions

1. Soil type is a significant factor in determining the role of CWD. Sandy sites, which are poorer quality than loamy sites, show greater response (sensitivity) to CWD decay rates and N dynamics. Forest management should include monitoring of CWD abundance based on soil type. Biomass removals beyond that of harvests for traditional wood products could have detrimental effects on soil C and N pools, particularly on nutrient poor, sandy sites.
2. Studying active (available) pools of nutrients may provide a more accurate assessment of the role of CWD in nutrient retention and cycling. In this study, N release from CWD was only 5% of total N stores, but can constitute a greater percentage of *available N* during the critical growth phase prior to crown closure.
3. The contribution of CWD to site N reserves changes over time, particularly evident on sandy sites, with an initial immobilization of N followed by a period of release during phase 3 (extended period of moderately slow decay). This release coincides with an increase in tree foliar N concentrations by Year 15.
4. In a managed forest scenario, nutrient retention by CWD occurs during a period of minimal demand and may serve to minimize leaching potential from the site. Conversely, nutrient release by CWD release occurs as the stand approaches crown closure, which is a critical period of maximal demand.

4.0 CWD AS A MICROCOSM: ITS INFLUENCE ON SOIL QUALITY AT THE LOG-SCALE

4.1 Introduction

Government policies are being developed to address increased utilization during forest harvesting, specifically the use of previously unmerchantable timber typically left on site. In the past, this unutilized timber remains in the forest ecosystem as coarse woody debris (CWD), which has been hypothesized to play an important role (habitat, C retention, etc.) following stand-replacing disturbances such as fire or harvest. Sites with shallow soil over bedrock or those with coarse-textured soils can be especially susceptible to overstory removal as inherently low carbon and nutrient pools may be further reduced to levels that limit stand productivity in subsequent rotations. On these kinds of sites CWD, with its slow and steady decomposition, can provide essential nutrition to the developing 2nd growth stand prior to the reestablishment of internal cycling processes stabilizing at crown closure (15-20 years after stand initiation). The current study sites were established in 1994, and are now approaching crown closure. The experiment was designed to document carbon loss and nutrient fluxes associated with residual CWD remaining after the application of four levels of biomass removal from mature black spruce forested stands in northwestern Ontario. Two soil types (fresh, loamy : dry, sandy) with stand replicates were selected to test if CWD represents a source or sink for nutrients(especially N and P), and if the decay pattern varied depending on soil type.

This chapter continues the investigation of the two questions posed by Laiho and Prescott (2004) with respect to the role of CWD in forest productivity. Specifically, that 1) on sites where nutrients, especially N or P, limit plant growth, CWD accumulation may reduce primary productivity through immobilization of those nutrients by decomposers, and 2) on dry sites, where lack of moisture limits plant and microbe growth, CWD may increase primary productivity and enhance element cycling by improving moisture retention. On such sites, CWD may also be important for the retention and accumulation of soil organic matter.

One key finding that carries through to this chapter is that while total nutrients may be abundant within a forest ecosystem, they need to be in ionic form to be available for plant uptake and use.

This chapter describes an *in* situ study that examined the influence of CWD on its substrate (soil) following disturbance in the FTH experimental plots. This experiment adds to examination of the research questions presented in Chapter 3, but is designed to focus in and isolate the individual log, namely:

1. What effect does CWD have on soil quality?
2. What is the spatial extent of the influence of CWD?

4.2 Methods

This study utilizes the four sites that were selected for study in chapter two (See full description, page 59). Again, sites were selected that represented two soil types and site quality classes (good – fresh, coarse loamy tills; poor - dry, sandy outwashes).

Each site included replicated (three plots per treatment) experimental harvest treatments with four levels of biomass removal (Stem only [SO]– delimbed at the stump, Full-tree chipping [CH] – chipped debris returned to the harvest plot, Full-tree [FT] – delimbed at the roadside, and Full-tree + Blading [FT + B]– complete removal of vegetation and forest floor). This study focused exclusively on the FT and SO treatments.

4.2.1 ION EXCHANGE RESINS – ESTIMATING AVAILABLE NUTRIENT POOL

Exchange resins (designed to capture cations and anions in soil water) were placed at the organic/mineral interface directly under the log as well as three locations every 30 cm away from CWD (30, 60 and 90 cm, Figure 4.1). CWD selected for this study averaged 11cm in diameter (min 9, max 14cm), were at least 2m in length with the entire CWD being no closer than 2m from the edge of the treatment plot boundary. A total of 192 resins were placed in the field on June 1, 2009 for one year in the following design: 2 sites x 2 harvest treatments x 6 replicates x 2 resins (cation and anion) x 4 distances (under and 30, 60 and 90 cm away from log). After one year, the resin bags were removed from the site, cleaned with deionized water and stored at 4^0C (Beyer 1998).

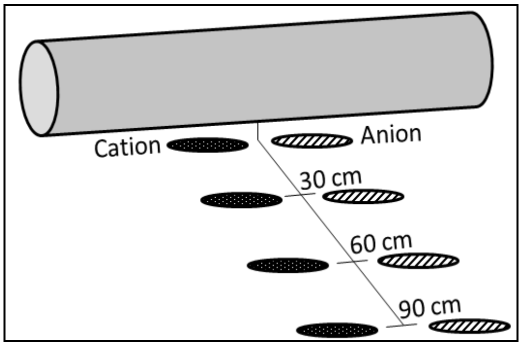

Figure 4.1 Locations of ion exchange resin bags relative to individual logs. All were placed at the depth of the organic/mineral interface.

Resin bags were constructed out of a fine mesh material and measured 6 cm by 6 cm. The mesh was sufficiently fine to restrict the resin beads from falling out without impeding aeration or water flow. Each mesh bag was filled with three grams of resin. Both anion and cation resins were made by Sigma-Aldrich; the anion resin, a strong base (IRA 400, Cl^-, 3.8 $meq \cdot g^{-1}$ exchange capacity) and the cation resin, a strong acid (IR 120 Plus, H^+ 4.4 $meq \cdot g^{-1}$ exchange capacity). Anion exchange sites were saturated with counter ions using 0.5 M $NaHCO_3$ solution at a volume of 300 ml per resin bag with two saturation periods of one hour each (Sibbesen 1978). Similarly, cation resins were saturated using 1 M NaCl solution at a volume of 150 ml per resin bag with three saturation periods of one hour (Krause and Ramlal 1987, Beyer 1998).

After retrieval, the resin bags were cleaned thoroughly in de-ionized water, and were extracted using 150 ml of 0.05 M HCl (Anion, as per Sibbesen 1978, Lajtha 1988, Qian and Schoenau 1997) or 0.1 M HCl (Cation, as per Krause and Ramlal 1987). After the resin bag and chemicals had been added to a sealed bottle, it was shaken for one hour at 180 rpm and then filtered using Fisherbrand Q2 filters and placed in 15ml centrifuge tubes and stored at frozen at -10^{0}C.

4.2.2 SOIL SAMPLING

At the time of resin bag retrevial, soil samples representing these same locations were collected and used for laboratory analyses and incubations. Soil samples were taken directly under the logs ("under" samples) used for resin analysis as well as 1m away ("away" samples); soil samples were taken a sufficient distance from the area the resin bags were placed. Each soil sample was 10cm in depth, and the ratio of organic and mineral soil in each sample was recorded. Organic and mineral components were separated before analysis if possible; bulk density, coarse fragments, and other site characteristics were taken from 10yr measurements from a previous study. Total carbon, nitrogen and sulfur were analyzed using dry combustion with a LECO CNS-2000 (LECO Corporation, St. Joseph MI). Al, B, Ca, K, Mg, Mn, Na, P, S and Zn cations and anions were analyzed with a Varian Vista Pro inductively coupled argon plasma spectrometer (ICAP/ICP) AES (Varian Inc.), following a 10% HNO3 acid digestion (adapted from Miller 1998).

Mineralizable N was estimated through a 14-day anaerobic incubation at 30°C, where air-dried and sieved soil samples (10 g) were placed in sealed containers with 50 ml of deionized water, incubated, extracted with a 2M KCl solution (Powers 1980). Analysis for net NH_4 was measured with the Technicon Instruments AutoAnalyzer II (Pulse Instrumentation Ltd., Saskatoon, SK) using Industrial Method Nos. 455-76W/A.

4.2.3 STATISTICAL ANALYSIS

Resin data were analyzed as a 2 x 4 CRD ANOVA with site (sand, loamy) and distance (under, 30, 60 and 90cm away) as factors using SPSS (ver. 17). Harvest treatment (FT and SO) was not included in the analysis; these data were pooled into similar soil sites. Soil samples were analyzed using a 2 x 2 CRD ANOVA with site and distance (under and away) as factors. Post hoc analysis was performed using Student Neuman Kuels (SNK) means separation test.

4.3 Results and Discussion

4.3.1 SOIL

There were clearly significant differences in soil nutrient pools between the two soil types (loam vs. sand). Carbon and nutrient pools on the loamy sites were significantly greater for Carbon ($p = 0.009$), N ($p = 0.001$), P ($p < 0.001$), K ($p < 0.001$), Ca ($p < 0.001$), Mg ($p < 0.001$), and Al ($p < 0.001$),), N ($p = 0.001$) and). In addition, the mineralizable N estimates also reflected these differences ($p < 0.001$). (Table 4.1). This coincides with previously published work for this test site (Morris and Duckert 1999), as the soil at dry, sandy sites was generally more nutrient poor, with much lower cation exchange capacity than the fresh, coarse loamy soil.

The resins, however, did not pick up as clear of a signal of these site differences, as only Al ($p < 0.000$) was significantly higher on the loamy sites (Table 4.1). The lack of differences, despite the large disparity in soil nutrient pools between the soil types, could indicate either that the cation exchange sites on the resins were limiting the amount of nutrients that could be absorbed, or alternatively that the actual exchange of available nutrients for each site was relatively equal. In this instance, the latter is most likely true, considering similar resin experiments have been carried out on these sites (Wrigley 2007), the amount of resins used in this study (3g per bag). The exchange capacity associated with the resin bags used is roughly triple the value needed for these soils for the one year placement period.

4.3.2 POSITION AND DISTANCE

Determining the effect of Position, the "under" and "away" treatment, was far more complex. Most of the total nutrients (Al, Ca, K Mg, Mn, P) and the NH_4 incubation (Mineralizable N) in the soil did not differ significantly ($p < 0.05$) between locations (under the log vs. 1m away (Table 4.1). Total carbon, however, was much higher under the logs, but only significantly ($p = 0.009$) on the loamy sites (104.4 Mg ha^{-1} under vs. 36.0 Mg/ha away, Figure 4.2, Table 4.2).

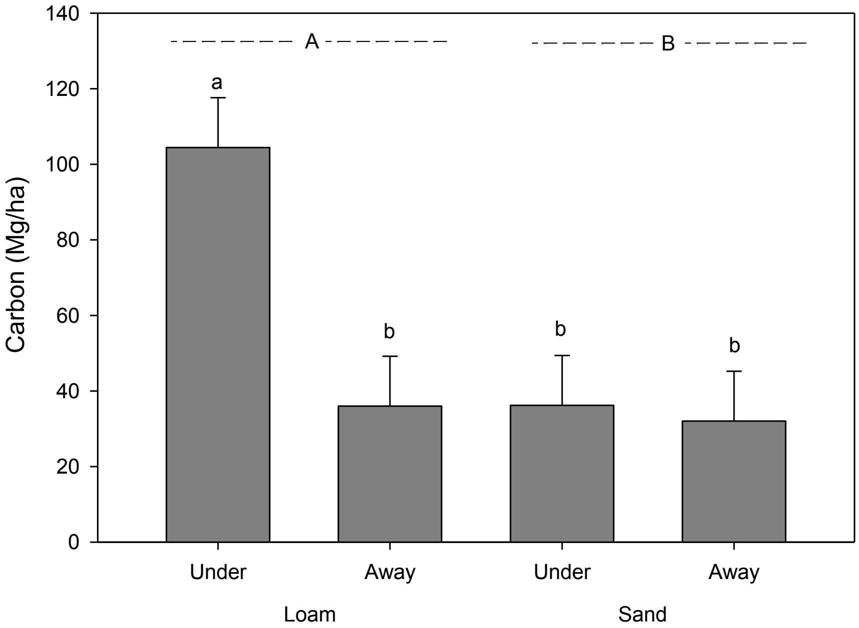

Figure 4.2 Soil carbon nutrient contents at 0-10cm under and away (1m) from the log on two soil types. Capital letters denote differences between soil types, lower case letters denote differences between "under" and "away" treatments using SNK post hoc tests.

One possible explanation for the large differences occurring under logs on the loamy sites is that the sampling was taken for the 0-10cm layer, and immediately under the log contained greater organic material (possibly a legacy from the pre-disturbance conditions) than away from the log. Aside from this, the higher carbon levels under the log are not surprising as it is well-documented that carbon is released from CWD both as pieces of fragmented recalcitrant C and as dissolved organic carbon (Yavitt and Fahey 1986, Solinger *et al.* 1991, Fitzhugh *et al.* 2001, Zhou *et al.* 2007). Another explanation could be that of reduced decay of organic matter once a log falls on top of it, which could result from poorer aeration or interrupted flushing of the soil beneath the log with throughfall which would replenish it with 02 and many elements as well as flush out all the microbial decay products. The mobility of carbon in sandy soils vs loamy soils may also provide some explanation for this variance.

Total N was also significantly higher ($p=0.02$, Table 4.1) under the logs, but only on the loamy sites (1082.8 kg ha^{-1} away vs. 2030.2 kg ha^{-1} under, Table 4.2, Figure 4.3).

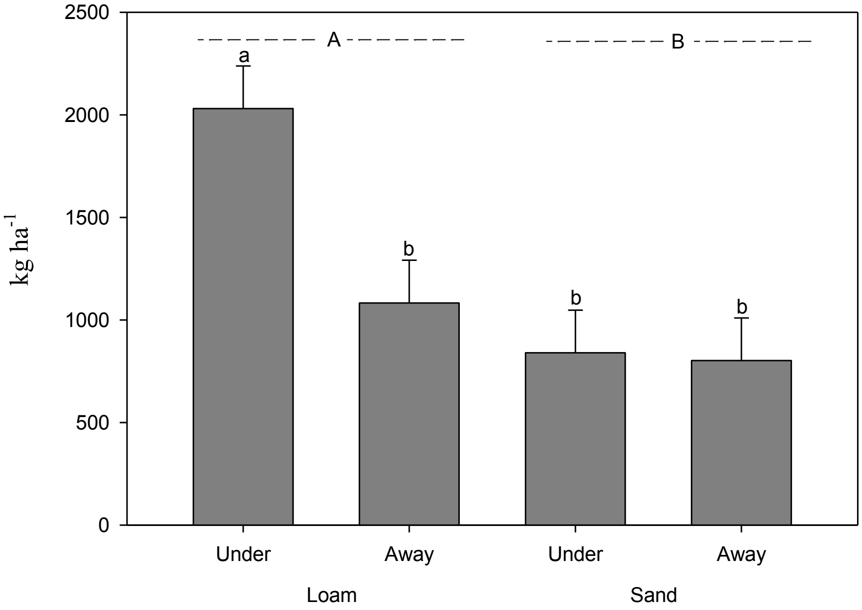

Figure 4.3 Soil nitrogen nutrient contents at 0-10cm under and away (1m) from the log on two soil types. Capital letters denote differences between soil types, lower case letters denote differences between “under” and “away” treatments using SNK post hoc tests.

Table 4.1 Nutrient analysis at 0-10cm using soil (under and away - 1m from log) and resins (0, 30, 60 and 90 cm away from log) on two soil types.

Soil																					
		Carbon		TN		NH4 Inc.		NH4		Al		Ca		K		Mg		Mn		P	
Source	df	F	Prob.	F	Prob.	F	Prob.	F	Prob.	F	Prob.	F	Prob.	F	Prob.	F	Prob.	F	Prob.	F	Prob.
Soil (S)	1	7.4	0	12	0	1.21	0.3	6	0	263	0	25	0	26	0	80	0	2	0.16	31	0
Position (P)	1	7.5	0	5.6	0	0.22	0.6	12	0	0.9	0.4	0.5	0.5	1.3	0.3	0	0.9	0.1	0.79	0	0.9
S*P	1	5.9	0	4.8	0	2.93	0.1	0	0.8	0	1	3.2	0.1	2.1	0.2	0.3	0.6	0.6	0.44	4.9	0
Error	44																				
Resins																					
	df																				
Soil (S)	1							0.1	0.8	12	0	0.5	0.5	3.3	0.1	0.6	0.4	3.2	0.08	1.5	0.2
Distance (D)	3							2.8	0.1	0.1	1	1.8	0.2	0.1	0.9	1.3	0.3	2.7	0.05	0.5	0.7
S*D	3							0.1	1	0.9	0.4	0.3	0.8	0.4	0.8	0.1	1	1.2	0.33	0.7	0.5
Error	61																				

Table 4.2 Soil nutrient contents at 0-10cm under and away (1m) from the log on two soil types.

		Al	Ca	K	Mg	Mn	P	NH4[a]	Min. N	TN	Carbon
Soil	Position					Kg ha^{-1}					
Loam											
	away	10958.0[+]	1201.3[+]	234.0[+]	3457.6[+]	73.0	124.8[+]	10.7[+*]	21.1	1082.8[+*]	36.0[+*]
	under	10228.5[+]	1603.9[+]	309.0[+]	3604.7[+]	90.7	152.2[+]	5.8[+*]	22.6	2030.2[+*]	104.4[+*]
Sand											
	away	2765.7[+]	695.1[+]	128.0[+]	820.4[+]	62.0	86.1[+]	12.7[+*]	18.1	801.7[+*]	32.0[+*]
	under	1983.7[+]	526.6[+]	118.7[+]	631.9[+]	53.3	62.4[+]	9.3[+*]	19.3	839.5[+*]	36.2[+*]

[a] NH_4 denotes a fresh extraction, while "Min. N" denotes an NH_4 incubation

[+] denotes significant ($p<0.05$) differences between "loam" and "sand" treatments

[*] denotes significant ($p<0.05$) differences between "away" and "under" treatments

Soil incubation (Figure 4.4) results showed no differences between soil or position. However, the fresh extraction showed marked differences within the treatment on both sites, as under the log (sand = 9.3 kg/ha, loam = 5.3 kg ha^{-1}) was significantly smaller ($p<0.001$) than away from the log (sand = 12.7, loam = 10.7 kg/ha, Figure 4.5).

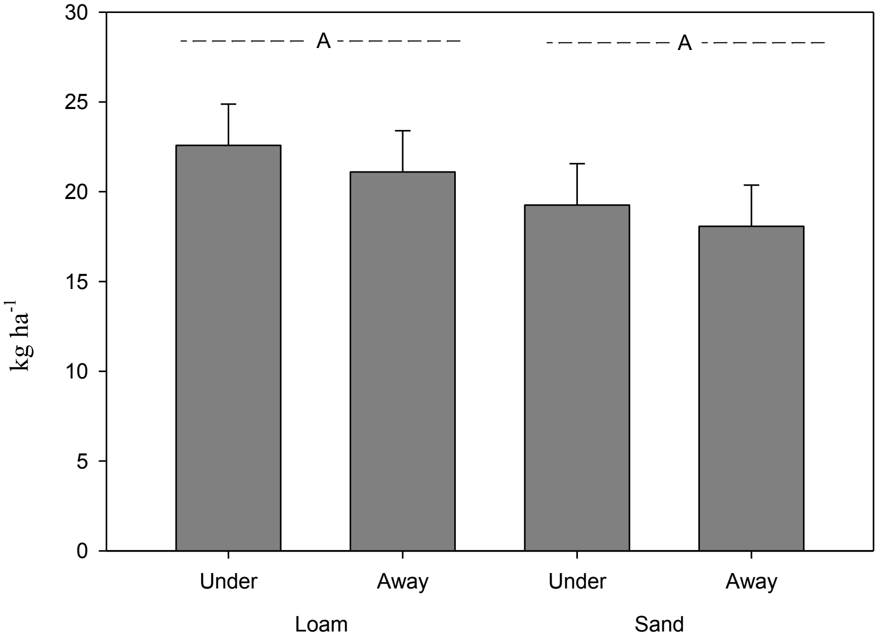

Figure 4.4 Soil incubation (Mineralizable NH_4) nutrient contents at 0-10cm under and away (1m) from the log on two soil types. Capital letters denote differences between soil types, lower case letters denote differences between "under" and "away" treatments using SNK post hoc tests.

Although a fresh extraction is a simple "point in time" reference of soil nutrients, it is interesting to compare the lower NH_4 under the logs to the nutrient dynamics occurring in the CWD (Figure 4.5). As CWD decomposes, the activity of microbes, fungi and other organisms require nitrogen in the biological processes of breaking down carbon to release energy.

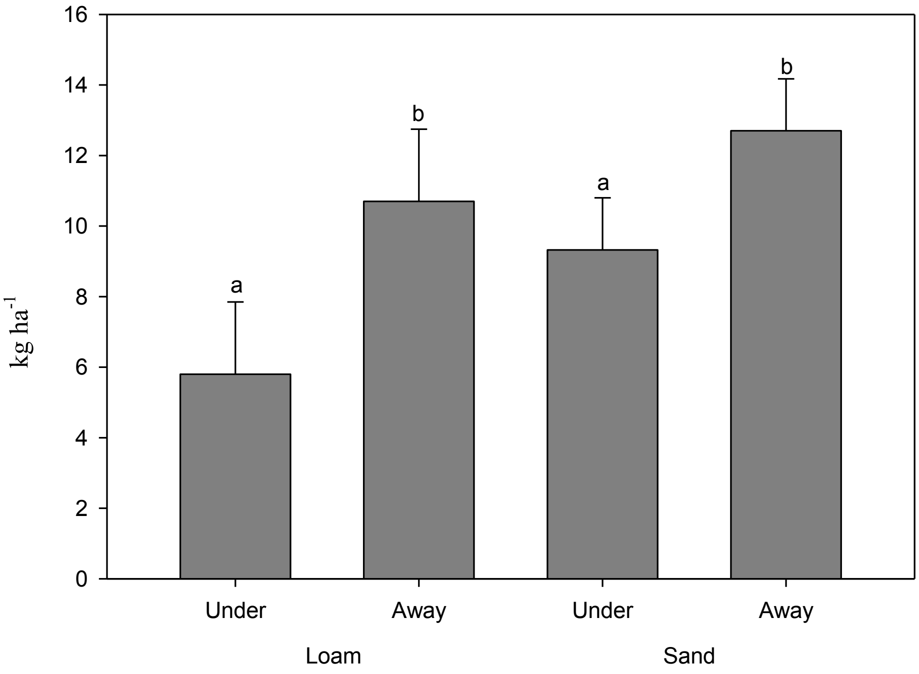

Figure 4.5 Soil NH_4 nutrient contents (fresh extraction) at 0-10cm under and away (1m) from the log on two soil types. Capital letters denote differences between soil types, lower case letters denote differences between "under" and "away" treatments using SNK post hoc tests.

The greenhouse experiment in Chapter 1 has also shown an import of soluble nitrogen into the log as CWD decay progresses. It seems logical that the N in the soil is providing at least some of the required N needed to offset the N deficit in the CWD. N^{15} isotope analysis, or a similar test, would be required to test this hypothesis. This N is also at some point released (beyond the 'critical C:N ratio', the point of maximum N accumulation), and has been documented by others (McClaugherty *et al.* 1985, Palviainen *et al.* 2010).

The distance treatment results for the ion exchange resins were more detailed than the total soil nutrients, as bags were placed every 30 cm to a distance of 90 cm from the log. Results were similar to the total soil nutrients, as Al, Ca, K, Mg, Mn and P were not significantly different under the log or at any distance away from the log (Table 4.1 and Table 4.3). The calcium results, however, showed a potential (although weak) trend. Under the log and 30cm away from the log had higher amounts of Ca, especially on the sandy sites (Figure 4.6), but were not strong enough to be statistically significant (p=0.153,Table 4.1). Calcium can be relatively high on tree-length sites (Hendrickson *et al.* 1989), which corresponds to elevated levels of calcium in CWD, especially in the bark (Harmon *et al.* 1986). Harvest treatment was not considered in this analysis; a calcium difference may have been shown for harvest treatment with greater replication, and warrants further study.

Table 4.3 Resin nutrient contents at 0-10cm at 0, 30, 60 and 90cm away from the log on two soil types.

		Al	Ca	K	Mg	Mn	P	NH4
Soil	Distance (cm)	Kg ha^{-1}						
Loam	0	1.6	12.5	76.3	7.2	0.4	1.9	3.0
	30	2.2	13.4	95.7	7.7	0.7	0.8	1.7
	60	2.0	10.6	93.0	5.9	0.3	1.2	1.8
	90	2.2	9.3	83.6	5.5	0.3	1.1	1.7
Sand	0	1.4	14.7	78.5	7.1	0.7	1.3	2.9
	30	0.9	17.3	58.4	8.3	1.4	1.8	1.8
	60	0.9	9.4	52.4	3.9	0.4	2.1	2.0
	90	0.8	10.2	59.9	4.4	0.3	1.4	1.8

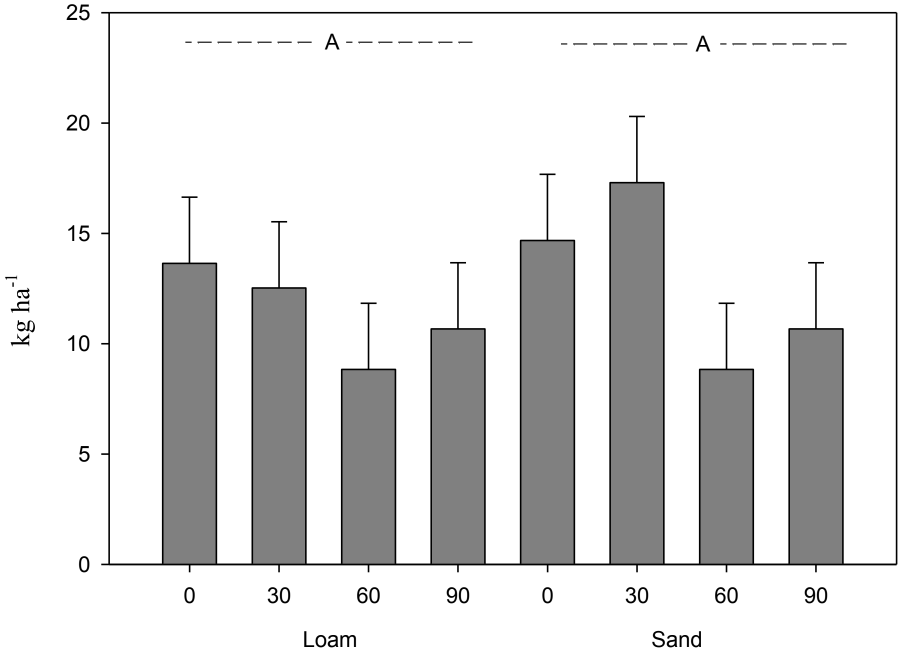

Figure 4.6 Calcium resin nutrient contents at 0-10cm at 0, 30, 60 and 90cm away from the log on two soil types. Capital letters denote differences between soil types, lower case letters denote differences between "under" and "away" treatments using SNK post hoc tests.

Available N (NH_4), from the fresh extraction, was signifcantly ($p<0.05$) higher under the logs, almost doubling (~40%) the amount away from the logs, which were roughly equal at every distance beyond the log (Figure 4.7). This relationship seen with NH_4 is contrary to the NH_4 trend in the incubation, where there was *less* N under the log than away. The resin bags simply measure nutrient movement, not absolute amounts, and so it is reasonable, and strengthens the argument, to suggest that the N that is labile is moving from the soil to the CWD. Ammonium is weakly held on cation exchange sites, and other studies suggest that ion exchange resins do not reflect actual soil nitrogen pools (Stark and Hart 1997, Driscoll *et al.* 1999) but are more accurately a static measure of available soil nitrogen during the ion exchange period (Hangs *et al.* 2004).

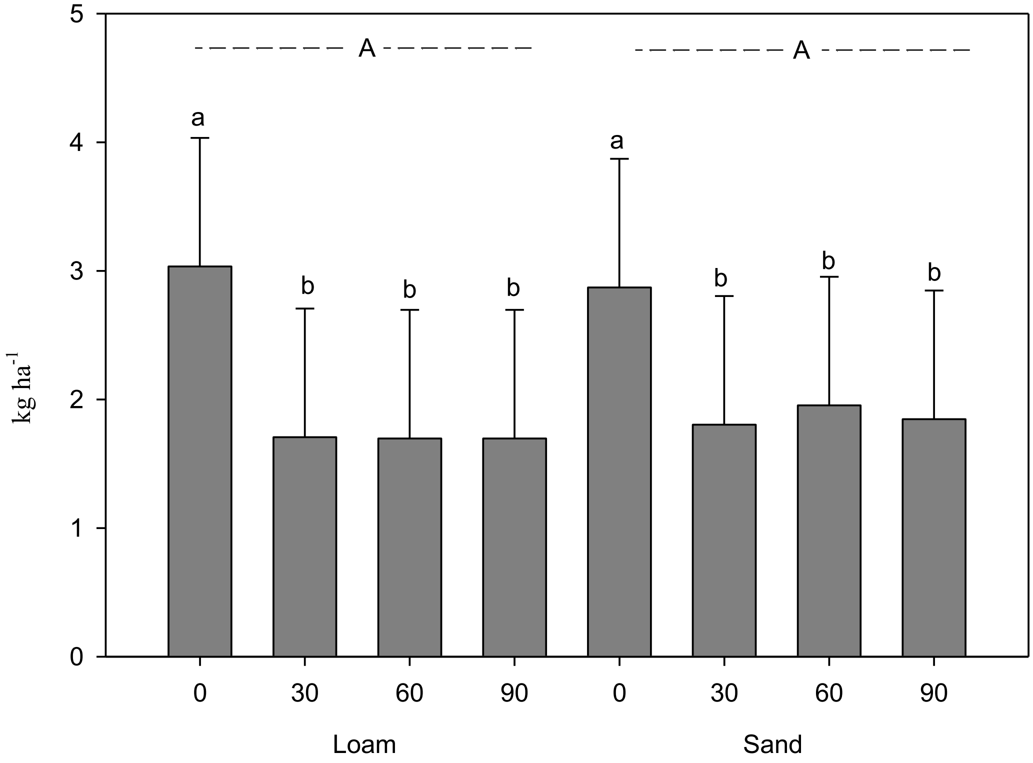

Figure 4.7 NH_4 resin nutrient contents at 0-10cm at 0, 30, 60 and 90cm away from the log on two soil types. Capital letters denote differences between soil types, lower case letters denote differences between "under" and "away" treatments using SNK post hoc tests.

4.3.3 ZONE OF INFLUENCE

The results from the exchange resins failed to show any clear pattern of nutrient dynamics between the three distances beyond the CWD. An exception could be made for Ca, which seemed to be higher nearest the CWD and extending to the 30cm range, but the high variability exhibited in the data failed to show any statistical significance. This lack of any "zone" beyond the bounds of the CWD confirms that the nutrients moving in or out of the log interacts directly with the soil beneath; the excess or deficit seen in the soil remains isolated to the area covered by the CWD.

4.3.4 RELATING CWD NUTRIENT DYNAMICS TO HARVEST INTENSITY: SCALING UP

CWD, as seen above, does influence the soil nutrient pool directly beneath the log, with little to no extension beyond the outer portion of the log. Relating this influence on a broader, landscape-scale is not as clear. It is important to quantify the overall effect of CWD on the landscape, especially as harvest intensity increases and CWD, as a percentage of ground coverage, decreases. CWD, or "slash" loadings, from the experimental harvest sites were tracked and recorded (Chapter 2.0) and were typically 4-7% of the total area. Despite the nearly doubling of CWD in the stem-only treatment vs. full-tree, when viewed on a per hectare basis, the role of CWD remained negligible (Figure 4.8). Although CWD can be shown to impact the immediate soil pool, the overall effect of CWD on the landscape remains only a small piece of the total picture of maintaining soil health, and current harvest practices (i.e. whole trees) do not appear to impact the contribution of CWD.

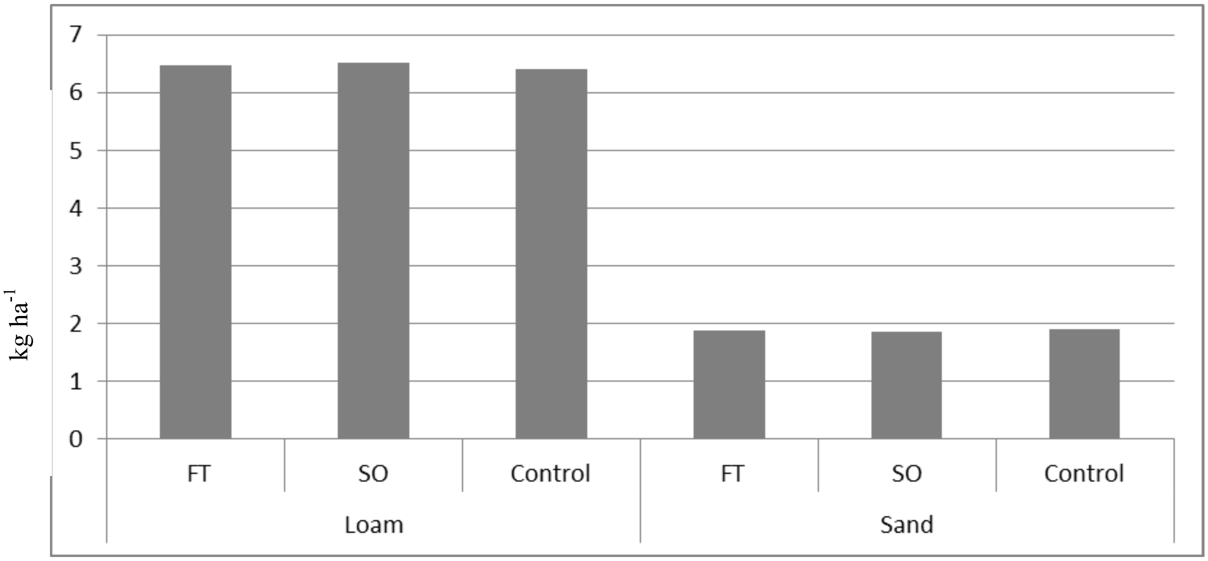

Figure 4.8 Soil incubation (Mineralizable NH_4) nutrient contents at 0-10cm under the log on two soil types, two harvest types, and a control. The "control" treatment was created by scaling up only the "away" results to a per ha scale.

4.4 Summary and conclusions

The impact of CWD on soil was measurable, as adequate signal responses from some nutrients, especially carbon and available N show CWD interacting with and impacting the soil nutrient pool. As expected, total carbon was higher under the log, which corroborates previous chapters' work with dissolved organic carbon leaching from the CWD into the soil. Physical breakdown and remnants of recalcitrant CWD contribute to soil organic matter (SOM) and soil structure, which are well-documented (Harmon *et al.* 1986).

Nitrogen, in its available NH_4 form, was lower in the soil under CWD, but had much higher activity, as seen in the exchange resin results. As discussed earlier, this N movement can be hypothesized to move from the soil and into the log. Although CWD is generally low in N as compared to the total soil N pool (2-5% of total, Laiho and Prescott 2004), it is the active, plant-available N pool that is important. The traceable, dynamic movement of labile N from the soil to the log is more aptly compared to the available soil pool, which has been discussed in earlier chapters. Focusing on CWD in comparison to this smaller, more relevant soil pool suggests a greater impact of CWD and its influence on nutrient availability for plant uptake.

The soil quality differences between the nutrient-rich loamy vs. the poor sandy sites did not dramatically alter the CWD-soil nutrient dynamics. This can be explained by reiterating that the active soil nutrient (especially N) pool is actually quite similar between the soils and the CWD-soil interaction reflected this relationship.

The "zone of influence" of CWD on soil nutrient availability does not extend beyond the boundaries of the log. The abundance and distribution of CWD on the landscape is therefore important to quantify, especially post-harvest. In this study there were negligible differences in site nutrients between the two harvesting systems (FT vs. SO) despite a nearly doubling of CWD in the stem-only treatment. This should not be surprising, however, as CWD is only one of myriad factors influencing site nutrient pools. In fact, other studies have had difficulty isolating a nutrient signal from CWD in *in-situ* experiments, so the signal I observed is quite unique.

The following conclusions can be derived from this study:

- Soil carbon is higher under CWD
- Total N is not noticeably affected by CWD, but labile NH_4 was shown to be especially dynamic under CWD
- CWD does not affect soil nutrient levels beyond the area directly beneath the log.
- On a landscape level, CWD plays a minor role, as total CWD coverage is not sufficient to significantly alter total soil pool dynamics.

5.0 SUMMARY

This dissertation has focused on isolating the particular role of CWD in boreal ecosystems, specifically on sites with shallow soil over bedrock or those with coarse textured soils. Although CWD has been hypothesized to play an important nutritional role following stand-replacing disturbances such as fire or harvest, it is only on these identified sites that CWD removal would be especially susceptible; low carbon and nutrient pools may limit stand productivity in subsequent rotations.

Beginning with the *ex-situ* experiment, it was evident very early on that CWD leachate varied tremendously by the stage of decay. This should not be surprising, considering the work of Mark Harmon and many others who have chronicled the breakdown of CWD through time. This study supported the proposed three-stage decay model of i) slow initial decay, ii) rapid decay, and iii) gradual final release of recalcitrant material. Nitrogen, on the other hand, has been much more difficult to ascertain, and my experiment was able to demonstrate N changing from an initial sink to an eventual source, becoming stronger as decay progressed. Phosphorus was quickly leached from the system; considering that most of the initial pulse of P was leached in less than 4 weeks, it is reasonable to assume that many studies may have missed this initial input to the ecosystem.

To give context to the dynamics documented in the *ex-situ* experiment, it was necessary to conduct *in-situ* studies and attempt to assess the signal strength associated with CWD regarding soil nutrients where all the ecological noise associated with field trials. I was fortunate enough to study four established (1994) biomass removal experimental sites, part of the North American network of Long Term Site Productivity (LTSP). These sites have had excellent pedigree, recording data essential to answering questions related to the ecological effect of biomass removal at various times throughout its 14 year (and counting) history.

I focused on the two soil types (shallow, fresh loamy : dry sandy), identified as susceptible to CWD removal. Through the series of experiments outlined in Chapters 3 and 4, I was able to ascertain the following broad trends of CWD dynamics:

> **Soil type must be considered when determining the role of CWD**. As Laiho and Prescott (2004) rightly hypothesized, nutrient poor sandy sites show greater response to CWD decay rates and N dynamics than nutrient rich loamy sites. This difference in soil type was more pronounced in the N dynamics measured in the CWD itself than in the underlying soil.

> **Active, available pools of nutrients are a critical aspect of plant growth, and may provide a more accurate assessment of the role of CWD in nutrient retention and cycling.** Using N content in CWD measurements taken over the length of the 14 year study, I found that N release from CWD was only 5% of total N stores, but contribute a greater percentage of available N during the critical growth phase prior to crown closure. Labile NH_4 was especially dynamic in the soil under CWD, and corroborated with the initial *ex-situ* results. Further studies

focusing on the plant-available pool of nutrients would better understand the significance of CWD.

The timing of CWD nutrient retention and release, especially nitrogen, appears to complement the changes occurring in the regenerating stand. When nutrient demand is low, N is retained in the CWD, and the subsequent release of N from CWD coincides with maximal demand prior to crown closure of the regenerating stand; N release from CWD was found to correspond to a rebound in tree foliar N concentrations by year 15.

Coarse woody debris does not appear to affect the soil beyond the boundaries of the log. There was a clear delineation past the log's edge where nutrient dynamics seen in the soil under the CWD suddenly dropped off to a consistent level, up to 1m away from the CWD.

The underlying concern of the investigations in this dissertation was to determine how these nutrient dynamics seen in CWD translate to the stand level, and if current harvesting practices limit the productivity of future generations of forest stands. It is important to quantify the abundance and distribution of CWD, especially post-harvest. Current full-tree harvesting practices did reduce CWD retention levels when compared to stem-only harvesting, but still appear to retain adequate amounts of CWD; there was no evidence in this study to suggest there was a reduction in soil productivity in the full-tree harvesting treatments.

At a stand scale, the influence of CWD remains small, but in dry, sandy soils, this effect is enhanced and appears to result in an increase in foliar N concentrations during maximal demand. It is imperative that future biomass harvesting guidelines controlling CWD removal consider soil type of the stand as a critical factor to determine threshold levels of removal.

This dissertation was able to accomplish unique and insightful observations and results. Concentrating on the most susceptible soils for study was a valid and useful strategy, a benchmark for establishing more comprehensive studies to better understand the complex ecosystem dynamics in the boreal forest.

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