THE EFFECTS OF EXCESSIVE MOISTURE ON SOIL CARBON AND NITROGEN MINERALIZATION AND FOREST PRODUCTIVITY

by

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Abstract

Conifers of regenerating cedar-hemlock (CH) forests exhibit slow growth and nutrient deficiencies (N and P), which are not observed on adjacent cutovers of hemlock-amabilis fir (HA) forests. I test the theory that excessive moisture and resulting low oxygen availability in CH sites create the low N supply and poor growth in these ecosystems. A field experiment determined: 1) whether CH and HA forests differ in soil moisture and aeration, 2) whether decomposition rate and soil C stores differ in CH and HA forests, 3) whether composition of plant communities are related to soil moisture and aeration, and 4) the impact of harvesting CH and HA forests on moisture and aeration conditions. A laboratory experiment investigated the effects of moisture levels, from field capacity to saturation level, on C and N mineralization rates. Lastly, a field trial was carried out to assess drainage as a potential forest management solution in wetland forests by comparing C dynamics in drained and un-drained sites.

As hypothesized, CH forests were wetter, less aerated, had shallower aerated depth and higher frequency of anaerobic conditions compared with HA forests. Composition of plant species was related to soil moisture and aeration, however plant diversity was not. Soil aeration was the most important factor, explaining 25% of the variability of species within plant communities. Compared with HA forests with well-aerated soils, soils in HA clearcuts were anaerobic, had slower decomposition rate and shallower rooting depth. Microbial biomass, C mineralization and the soluble inorganic N: soluble organic N (SIN:SON) ratio all declined under water-saturated conditions. Concentrations of SIN increased with increasing moisture in HA soils; whereas in CH humus and soil, the SIN pool was small and decreased with increasing moisture. The results indicate that the low N availability on CH sites results from synergistic effects of litter quality and greater frequency of waterlogging. Drainage could be a useful silvicultural practice for improving the productivity of cedar-swamp ecosystems without stimulating loss of soil C, provided that redox levels are maintained at less than +300 mV, at which level oxygen is sufficient for plant growth but not for aerobic microbial decomposition.

Table of Contents

Abstract	ii
Table of Contents	iii
List of Tables	vi
List of Figures	viii
Acknowledgements	xi
Co-authorship Statement	xiii
Chapter 1 : Introduction	1
1.1 An ecological enigma	1
1.2 Relevance	6
1.3 Forest management effects on water-related soil processes	12
1.4 Objectives	13
1.5 Thesis structure	15
1.6 References	
Chapter 2 : The influence of soil moisture and aeration on organic matter of	dynamics, plant
communities and forest development	
2.1 Introduction	
2.2 Material and methods	32
2.2 Material and methods	32
2.2.2 Field measurements	
2.2.3 Laboratory measurements	
2.2.4 Data analysis	
2.2.5 Multivariate analysis	

2.3 Results	
2.3.1 Soil measurements	
2.3.2 Vegetation	41
2.3.3 Interactions between plant species and soil variables	
2.4 Discussion	
2.5 References	65
Chapter 3 : The effects of excessive moisture on soil C and N	mineralization in coastal
forests of British Columbia	73
3.1 Introduction	
3.2 Materials and methods	
3.2.1 Study area	
3.2.2 Field sampling	77
3.2.3 Laboratory protocols	77
3.2.4 Data analysis	
3.3 Results	
3.3.1 CH vs. HA	
3.3.2 Moisture effects	
3.3.3 Correlations among variables	
3.4 Discussion	
3.5 References	
Chapter 4 : Drainage effects on site productivity and soil car	bon stores in a cedar-swamp
ecosystem in coastal British Columbia	
4.1 Introduction	
4.1.1 Study site	
4.1.2 Soil sampling and vegetation analysis	
4.1.3 Soil biogeochemical analysis	
4.1.4 Incubation study	
4.1.5 Statistical analysis	

4.2 Results	
4.3 Discussion	
4.4 Management implications	
4.5 References	
Chapter 5 : Overall synthesis	
5.1 Clearcut effects on soil moisture and aeration (paludification)	
5.2 Drainage as a potential solution for forest management in wetland forests	
5.3 Strengths and limitations	
5.4 Recommendation for future studies	
5.5 References	
Appendix 1: Plant species coverage by classes in the four plots in each of five CH a	und HA
forest sites. Cover classes: $1 = \langle 1\%; 2 = 1-5\%; 3 = 5-25\%; 4 = 25-50\%; 5 = 50-75\%$; 6 = 75-
100%	

List of Tables

Table 2-1: Moisture content (%dry-weight basis) of soil horizons of CH and HA forests and clearcuts on the four sampling occasions. F=F-horizon, H_U = upper humus, H_L =lower humus, B= upper 20 cm of mineral soil
Table 2-2: Characteristics of the forest floors and mineral soils in CH and HA forests and clearcuts. F=F horizon; H= humus horizon; B= upper 20 cm of mineral soil
Table 2-3: Selected characteristics of forest floor and soil horizons CH and HA forests and clearcuts on the four sampling occasions. F=F horizon, H_U = upper humus, H_L =lower humus, B= upper 20 cm of mineral soil. (Numbers in paranthesis are standard errors. Different letters indicate significant difference between forest types. Capital letters indicate significant difference between clearcuts and forests of the same type. Numbers in brackets are standard errirs. * indicates difference at P<0.1 and ** indicates difference at P<0.05)
Table 2-4: The depth of the soil aerated zone in CH and HA forests and clearcuts on two occasions. 61
Table 2-5: Correlation coefficients between scores for plant species and the first three axes ofPCA. The first three axes explain 74% of the variation in the main matrix
Table 2-6: Multi-Response Permutation Procedures (MRPP) to test for overall differences in thestructures of the plant communities in CH and HA forests.62
Table 2-7: Correlation coefficient between scores for soil variables and the first three axes ofPCA. The first three axes explain 75% of the variation in the main matrix
Table 2-8: Characteristics of the three groups of CH sites identified by PCA analysis using the 10 soil variables that explained most of the variability in the dataset. Distinctive higher or lower values among the three groups are highlighted in bold
Table 2-9: Canonical correspondence analysis of soil variables in relation to plant species 64
Table 3-1: Concentrations of several N forms, mineralized C (measured as CO ₂ efflux), microbial biomass C and N and some other selected properties after 20-days of incubation in CH and HA forest floor at four different moisture levels
Table 3-2: Concentrations of several N forms, mineralized C (measured as CO2 efflux), microbial biomass C and N and some other selected properties after 20-days of incubation in CH and HA mineral soil at four different moisture levels

Table 4-1: Soil and stand properties in control (C) and drained (D) plots at the four (1-4) treatment areas.
Table 4-2: Selected properties of the forest floor in control (C) and drained (D) plots at the four (1-4) treatment areas.
Table 4-3: Variance explained by the first three axis of the PCA analysis
Table 4-4:Pearson and Kendall Correlations with Ordination Axes for 3-dimensional visualization. Variables with strongest r-values are indicated with bold font (n=12)

List of Figures

Figure 1-1: Some effects of excessive moisture on soil biogeochemical processes involved with N cycling
Figure 2-1: Average moisture content (% dry-wt) in soil horizons of CH and HA forests and clearcuts during two months of measurements. Different letters indicate significant difference between forest types; capital letters indicate significant difference between clearcuts and forests of the same forest type. F=F-horizon, H_U = upper humus, H_L =lower humus, B= upper 20 cm of mineral soil. 48
Figure 2-2: Average redox potential (mV) in soil horizons of CH and HA forests and clearcuts. Different letters indicate significant difference between forest types; capital letters indicate significant difference between clearcuts and forests of the same forest type. F=F-horizon, H_U = upper humus, B= upper 20 cm of mineral soil
Figure 2-3: Correlation between pH and redox potential in organic and mineral soil horizons 49
Figure 2-4: Correlation between average moisture content and redox potential in organic and mineral soil horizons in CH and HA forests. H_U = upper humus; B= upper 20 cm of mineral soil. 50
Figure 2-5: Relationship between clay concentration (%) and moisture content (% dry weight) in the upper 20 cm of mineral soil in CH and HA forests
Figure 2-6: Correlation between average redox potential and oxic depth in the upper humus (Hu) and upper 20 cm of mineral soil (B) horizons in CH and HA forests
Figure 2-7: Relationship between average moisture content and aerated depth in the (a) upper humus (H_U) and (b) upper mineral soil (B) soil horizons in CH and HA forests
Figure 2-8: Mass loss (% dry mass) of cellulose after a one-year incubation in the upper (H_U) and lower (H_L) humus layers in CH and HA clearcuts and forests
Figure 2-9: Soil carbon pool (kg m ⁻²) in the forest floor (FF) and the upper 20 cm of the mineral soil (B) in CH and HA forests and clearcuts
Figure 2-10: Ordination diagram of principal component analysis (PCA) of plant species in the two forest types (CH and HA). The 6 species explained 74% of the variation (Gas: <i>Gaultheria shallon</i> ; Bls: <i>Blechnum spicant</i> ; Kio: <i>Kindbergia oregana</i> ; Vac: <i>Vaccinium</i> spp.; Plu: <i>Plagiothecium undulatum</i> ; Hys: <i>Hylocomium splendens</i>)

Figure 2-11: Ordination diagram of principal component analysis (PCA) of soil characteristics in the two forest types (CH and HA). The 10 soil variables explained 75% of the variation (EhB: Eh of B horizon; EhHU: Eh of H_U horizon; MCHU: moisture content of H_U horizon; OMTH: organic matter thickness; OXD: oxic (aerated) depth; pHB: pH of B horizon; pHHU: pH of H_U horizon).

Figure 2-14: Correlation between % cover of deer fern (<i>Blechnum spicant</i>) and redox potential in the upper humus (H _U) horizon. % cover classes: $1 = <1\%$; $2 = 1-5\%$; $3 = 5-25\%$; $4 = 25-50\%$; $5 = 50-75\%$; $6 = 75-100\%$.	ו ; 7
Figure 3-1: Correlation between redox potential (mV) and moisture content (dry-weight basis) or humus from CH and HA forests	f 3
Figure 3-2: Mineralized carbon (mg C/ g soil C), measured as CO ₂ efflux, during a 20-day laboratory incubation of humus from HA and CH forest at four moisture levels	3
Figure 3-3: Mineralized carbon (mg C/ g soil C), measured as CO ₂ efflux, during a 20-day laboratory incubation of mineral soil from HA and CH forests at four moisture levels	9
Figure 3-4: Ammonium concentrations after a 20-day laboratory incubation of humus from HA and CH forests. Error bars are SEs (n=5)	9
Figure 3-5: Soluble organic nitrogen concentrations after a 20-day laboratory incubation of humus from HA and CH forests at four moisture levels	0
Figure 3-6: Soluble organic nitrogen concentrations after a 20-day laboratory incubation of mineral soil from HA and CH forests at four moisture levels	0

Figure 3-7: Amount of various N forms in the exchangeable labile N pool in humus from HA and CH forests after a 20-day laboratory incubation under field-moist (200%) and saturated (650%) conditions
Figure 3-8: Amount of various N forms in the exchangeable labile N pool in mineral soil from HA and CH forests after a 20-day laboratory incubation under field-moist (200%) and saturated (650%) conditions
Figure 3-9: Correlations between moisture content (% dry-weight based) and total C mineralized, measured as CO_2 efflux, from humus from HA and CH forests during a 20-day laboratory incubation (overall R^2 = 0.225 and overall p=0.0104)
Figure 3-10: Correlations between moisture content (% dry-weight based) and microbial biomass in a) humus, and b) mineral soil from CH and HA forests after 20-day laboratory incubation93
Figure 3-11: Correlations between soluble organic N (µg/g soil) and (a) moisture content (% dry- weight based), and (b) redox potental in humus from CH and HA forests after a 20-day laboratory incubation
Figure 3-12: Correlations between concentrations of total N (%) and (a)ammonium (μ g/g soil), and (b) soluble organic N (μ g/g soil) in humus from CH and HA forests after a 20-day laboratory incubation
Figure 3-13: Correlation between pH and total C mineralized (mg C/ g soil C) during a 20-day laboratory incubation of humus from CH and HA forests
Figure 4-1: Map of the Suquash drainage trial with four replicate drainage (treatment) areas and the control, drained, and semi-drained plots within each treatment area
Figure 4-2: Three-dimensional PCA biplot. Plant species: Sa (Salal, <i>Gaultheria shallon</i>); sB (salmonberry, <i>Rubus spectabilis</i>); hT (horsetail, <i>Equisetum arvense</i>); sC (skunk cabbage, <i>Lysichiton americanum</i>); Vac (<i>Vaccinium spp.</i>); Gr (Grasses); Ru (Rushes); Fer (Ferns); Mos (Mosses)
Figure 4-3: Daily mineralized carbon (mg C/ g soil C), measured as CO ₂ efflux, duringone month laboratory incubation of samples from drained and control sites
Figure 5-1: mechanism for how small variations in soil drainage could lead to the observed differences in nutrient supply and productivity of CH and HA ecosystems

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The three main chapters have been co-written with following co-authors: Cindy E. Prescott, Brad Seely, Annette Van Niejenhuis and Les Lavkulich. Toktam Sajedi, thesis author, designed individual experiments, selected the field sites, installed all experimental treatments and plots, collected and analyzed the data and in cooperation with the co-authors wrote the manuscripts. Cindy Prescott, research supervisor, identified the research program, assisted with study design, provided resources and guidance throughout the project, and commented on the three manuscripts. In addition to Toktam Sajedi and Cindy Prescott being co-authors of all the three main manuscripts, chapter 2 was co-authored by Brad Seely who assisted with study design and data analysis and provided feedback on the manuscript, and Les Lavkulich who helped with developing the methods for measuring redox in the field and the laboratory, provided the redox meter, and provided feedback on the manuscript. Chapter 3 did not have other co-authors. Chapter 4 was co-authored by Annette Van Niejenhuis who designed and installed the drainage experiment, provided the data for tree growth, assisted with logistics for the fieldwork and provided feedback on the manuscript.

Chapter 1: Introduction

1.1 An ecological enigma

The Wet Maritime Coastal Western Hemlock biogeoclimatic subzone (CWHvm1) on northern Vancouver Island contains two main ecosystems: upland forest and lowland swamps. Productive forests are a mixture of two major types: old-growth forests dominated by western red cedar (*Thuja plicata* Donn.) with a smaller component of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (CH type) and second-growth mature forests dominated by western hemlock and amabilis fir (*Abies amabilis* (Dougl.) Forbes) (HA type). Old-growth CH forests have no history of major disturbance for 8000 years (Kimmins 2004); whereas second-growth HA forests established after a major windstorm in 1906 and are even-aged. CH stands include very old and large cedars, up to 1000 years-old, and stands are relatively open (Keenan 1993). The understory is a dense cover of salal, an ericaceous shrub up to 2m tall. HA stands are more uniformly-sized and contain densely stocked trees ranging in age from 30 to 160 years. The understory consists of patches of salal and *Vaccinium* sp., and a ground cover of mosses and ferns.

Extensive parts of CH forests in the region exhibit slow growth and nutrient deficiencies that are not observed on adjacent HA forests. The symptoms appear before harvesting in old-growth forests and 5-8 years following clearcutting and slash burning. This phenomenon does not occur on adjacent HA cutovers (Weetman & Prescott 2000). Regenerating seedlings on CH sites almost cease growing and turn yellow, while those on HA sites grow rapidly and exhibit no signs of foliar chlorosis. Nitrogen and phosphorus deficiencies have been suggested as the main reasons for the chlorosis and associated growth stagnation of planted trees (hemlock, cedar and fir) on CH cutovers, with trees responding positively to nutrient (N+P) addition (Weetman et al. 1989b). A comprehensive research program called the Salal Cedar Hemlock Integrated Research

Project (SCHIRP) was established in 1986 to investigate the causes of, and solutions for, the nutrient deficiencies and regeneration problems occurring on CH sites. This understanding is fundamental to both short and long-term goals of improving forest productivity and sustainability.

Four hypotheses were initially proposed to explain low nutrient supply in CH cutovers:

a) Lack of disturbance

It has been argued that cyclic windstorms in HA forests have improved organic matter decomposition and nutrient cycling by disrupting hardpans in the mineral soil which improves drainage and soil aeration, accelerates decomposition, and increases rooting depth. These improved soil conditions resulted in growth increment of trees and created closed-canopy stands, which exclude salal and cedar by shading (Weetman & Prescott 2000). Keenen et al. (1994) examined short-term effects of mechanical mixing of forest floor and mineral soil after harvesting and found minimal soil and tree responses to the scarification. The small tree growth responses observed could easily have resulted from decreased competition with salal, which was disrupted through the mechanical mixing process.

b) Presence of salal

Expansion of the ericaceous shrub, salal (*Gaultheria shallon* Pursh) is coincident with nutrient deficiency symptoms in CH cutovers. Like other ericaceous sites, salal-dominated sites are frequently problematic for regeneration following forest harvesting. Salal is capable of gaining near complete occupancy of a site (Haeussler *et al.* 1990) and is considered to be a vigorous competitor with trees for water and nutrients (Fraser *et al.* 1993). There is evidence that salal competes strongly for nutrients on CH cutovers and that this contributes to poor hemlock growth (Fraser *et al.* 1999; Messier 1993, Weetman et al. 1989b). Messier and Kimmins (1990) showed that between 2 and 8 years after harvest, the biomass of ground vegetation (70% salal)

on CH cutovers increased from about 4 Mg/ha to 17 Mg/ha, of which over 10 Mg/ha was root biomass. With this large root biomass, salal would be a serious competitor for soil nutrients. Removal of vegetation (mostly salal) surrounding individual conifer seedlings through trenching and clipping led to a significant increase in growth of spruce, hemlock and cedar saplings and increased availability of N and P (Messier 1993, Chang *et al.* 1995). However, competition with salal does not account for the lower availability of nutrients in CH clearcuts, because N and P is also low in old-growth CH forest floors, which may contribute to the nutrient supply problems encountered by regenerating trees on cutovers of this forest type (Prescott et al. 1993). Also, manual removal of salal from field plots followed by herbicide (Garlon) applications did not improve conifer growth in the first three years following treatment (Weetman *et al.* 1990). Bennett et al. (2003) found that removal of salal by grubbing or herbicide did not have a large effect on tree growth rates, but nutrient addition had a large and long-lasting effect.

In addition to its competing role, salal has been proposed to decrease nutrient availability through its tannin-rich litter. Tannins have been shown to bind proteins, thus inhibiting the activity of extracellular enzymes and protecting nitrogenous compounds from enzymes. This would be beneficial for salal and disadvantageous for hemlock and cedar if the ericoid mycorrhizae associated with salal are better able to access organic nitrogen sources than the ecto- and arbuscular mycorrhizae associated with hemlock and cedar. This nitrogen "short-circuiting" hypothesis was described by Northup (1995) in pygmy forests of California. This hypothesis was tested by assessing the effect of salal leachates on cedar and hemlock seed germination and the use of organic and inorganic N sources by salal, cedar and hemlock. Mallik and Prescott (2001) found that leachates of salal leaf or litter did not significantly affect seed germination and primary growth of hemlock seedlings. Also, in a pot study, salal was not better able to use organic forms of nitrogen than cedar and hemlock (Bennett and Prescott, 2004).

Prescott and Sajedi (2008) reviewed the role of salal in forest regeneration problems and concluded that while short-term field experiments, laboratory and greenhouse studies provided some evidence of salal causing the low nutrient availability in CH sites, long-term results from silvicultural trials and associated ecological studies indicated that salal is not the fundamental problem for regenerating conifers on these sites. They concluded that salal should be viewed as a symptom of the underlying problem of poor nutrient availability on CH sites rather than a cause.

c) Tree species

The differences in tree species composition in both CH and HA forests has also been suggested as a reason for the lower nutrient supply on CH cutovers. Keenan (1993 & 1995) concluded that the quality and quantity of litter inputs to CH and HA forests are likely important controls of nutrient availability in these two forest types. Cedar litter had a lower nitrogen concentration, a higher nitrogen/lignin ratio, and more waxes and decomposed more slowly than hemlock litter. Cedar litter contains fungitoxic substances (thujaplicin and thujic acid) which make it highly resistant to decay (Swan et al. 1987). Cedar has also been reported to have slower rates of decomposition than the other species (Harmon et al. 1990), although Prescott and Preston (1994) found that cedar litter decomposed faster than Douglas-fir or hemlock litter in laboratory incubation.

Cedar also tends to produce litter and forest floors of relatively high pH and base cation concentrations (Turner and Franz 1985; Prescott et al. 1995) and a greater proportion of nitrate in soil (Turner and Franz 1985). High concentrations of nitrate have been interpreted as higher mineralization rate and available N; although it could also be the result of higher pH. There are inconsistencies in reports of decomposition and N mineralization rates of cedar relative to other tree species. Harmer and Alexander (1986) found higher rates of net N mineralization and nitrification in forest floors under cedar relative to 16 other species. However, Prescott and

4

Preston (1994) found lower N-mineralization rates in cedar forest floors than in hemlock and Douglas-fir. Similarly, Prescott et al. (1995) reported that cedar had lower N mineralization rates than 12 other species, including Sitka spruce, hemlock, and Douglas-fir, in single species plots in Ireland. Prescott et al. (2000) found redcedar to have a higher rate of nitrogen mineralization in forest floor than hemlock; however it had lower concentrations of nitrogen in litter than hemlock. Their results also revealed that the rates of N mineralization in the forest floors were not related to the rates of the decomposition in foliar litter. These findings suggest that the quality and quantity of litter inputs to CH and HA forests are not the cause of differing nutrient availability in these two forest types.

d) Anaerobic conditions in forest floor

Both CH and HA forests were initially classified as the same ecosystems with similar site characteristics (Lewis, 1982), with the same marco-morphological soil characteristics and topographic position; however, some differences between the sites have been documented. As cited by Keenan (1993), in classifying of this area, Lewis (1982) could not distinguish between the two types on the basis of topography or macromorphic mineral soil characteristics, and included them in the same ecosystem association. Germain (1985) found that forest floors of both types were deep mor humus, but generally deeper in the CH than the HA type, and mineral soils of both sites were duric or orthic Humo-Ferric Podzols. He reported that the CH type tended to occur on more poorly-drained situations, although he also observed gleying and evidence of periods of reducing conditions in mineral soils under the HA type.

Keenan (1993) did not find consistent differences in mineral soils among three sites of adjacent CH and HA forests; however deMontigny (1992) found a greater frequency of gleyed horizons in CH forests. The most common humus forms on CH sites were: humimors, lignomors, and hydromors, which develop under the influence of excessive moisture on poorlydrained soils and reflect fluctuating, stagnation or slowly moving water close to the ground surface (Green et al. 1993). Lignomors and hemimors were common on HA sites. Also, mineral soils in CH forests were compact with humus-enriched Bf layers over a continuous thin pan, while those in HA forests were well-aerated and well-drained with thin and discontinuous pans under humimors.

Battigelli (1994) found lower abundance and biomass of soil fauna and larger populations of copepods, which are aquatic animals, in CH forests. Finally, the tendency for CH sites to occupy slightly lower landscape positions than HA sites was documented by Albani and Lavery (2000), which could lead to excessive moisture and greater frequency of anaerobic conditions in CH forests.

1.2 Relevance

Soil moisture regime, reflective of climatic, topographic and edaphic factors, is a major determinant of the productivity of terrestrial ecosystems. Even in very humid ecosystems, variation in water supply plays an important role in determining ecosystem structure and function (Schuur & Matson, 2001). Distribution of plant species have been shown to be strongly connected with soil moisture, water-table depth and fluctuation. Soil physical or chemical characteristics such as organic matter thickness, soil porosity and redox potential are related to soil moisture regime and are important determinants of plant species distribution (Chambers *et al.* 1999; Castelli *et al.* 2000). In montane riparian meadows, Dwire *et al.* (2006) showed that species richness and total plant cover were negatively correlated with water-table depth and positively correlated with redox potential. Minkkinen *et al.* (1999) found that composition of plant communities of mires in central Finland changed drastically after the water level was drawn down by drainage. The growth rate, biomass production and root:shoot ratio of wetland

plant species are also strongly affected by low redox conditions (Pezeshki, 1994a; Kludze and DeLaune, 1994, 1995, Pezeshki 2001).

While the presence of soil moisture is typically beneficial for productivity in terrestrial ecosystems, the accumulation of soil moisture in excess of plant demand may suppress growth through a variety of mechanisms. For most upland plants, the supply of oxygen in the soil air must exceed 0.1 L/L (as compared to 0.2 in the atmosphere) (Brady and Weil 1999). Typically, poor soil aeration becomes a serious problem for plant growth when more than 80-90% of the soil pore space is filled with water. The effects of moisture on soil processes could be divided into direct and indirect effects (Fig 1.1). Direct effects do not involve major biological processes, whereas indirect effects are predominantly biologically-driven. With increasing moisture, anything in dissolved form becomes diluted. The dissociation of water produces H⁺ ions, which replace exchangeable cations. Thus, over time cations including NH4⁺ are leached out. On the other hand, organic material found in the soil (e.g. amino acids, amino sugars, simple proteins) may dissolve in water, causing dissolved organic nitrogen (DON) to increase. With the loss of cations through leaching, pH decreases; however, variation in pH depends on water movement in the soil and the amounts of alkalinity or acidity received as a result. In depressions where drainage is impeded by a restricting layer such as a pan layer, a small increase in the amounts of cations received from surrounding systems results in accumulation of cations in the soil solution, leading to increases in pH.

Extreme case of excess moisture occurs when all or nearly all of the soil pores are filled with water. The soil is then said to be *water-saturated* or *water-logged*. In these environments, organisms must survive with relatively low concentrations of oxygen and heterotrophic respiration may totally deplete oxygen. Under the conditions in which O_2 is limited, anaerobic microbial processes – denitrification, sulfate reduction, and methanogenesis – occur which

release N₂, H₂S, and CH₄ (Schlesinger, 1997). If a soil is well-aerated, oxidized states of Fe³⁺ in $Fe(OH)_3$ and N^{5+} in NO₃⁻ (nitrate) are dominant. In poorly aerated soils, the reduced forms of elements such as Fe^{2+} in FeO and N^{3+} in NH_4^+ (ammonium) will be present. The presence of these reduced forms is an indication of restricted drainage and poor aeration. As soon as soil O_2 becomes limited, anaerobic microorganisms begin borrowing oxygen from organic acids, metal oxides, and oxyanions in exchange for electrons (Sparks, 2000). One important chemical characteristic of soils that is related to soil aeration is the reduction-oxidation state of chemical elements, which expresses the tendency of an environment to receive or supply electrons. Redox potential (Eh) reflects the transfer of electrons from donors to acceptors; measured by means of a combined platinum electrode; expressed in millivolts (mV) (Gobbat et al. 2004). The reductionoxidation or redox potential (Eh) value varies with the specific chemical to be oxidized or reduced, so an Eh value explains the sequence of reactions that are known to occur when a wellaerated soil becomes saturated with water (Schlesinger 1997; Gobbat et al. 2004; Brady and Weil 1999). In general, well-aerated soils have an Eh range of +400 to +700 mV (adjusted for pH 7) while saturated soils generally have Eh values < +400 mV, reaching as low as -300 mV in extreme cases (Pezeshki 1991). Organic matter turnover, mineralization and nutrient release rates are strongly correlated with electron acceptor availability and redox condition in wetland soils and the rate of these processes slow as the soil becomes more reduced (McLatchey and Reddy 1998; Schuur et al. 2001).

Soil microorganisms are vital components of terrestrial ecosystems. They have fundamental roles in decomposition of organic matter and nutrient cycling as well as beneficial and antagonistic interactions with plants and animals. Microbial activities are affected by soil moisture directly and indirectly through the influence of moisture on soil aeration and temperature. With domination of facultative organisms under low-oxygen or anaerobic conditions, microbes seek alternate electron acceptors for their respiration or they undertake fermentative processes. Both processes are less efficient and result in less complete or slower decomposition in comparison with the aerobic form.

Heterotrophic respiration, measured as CO₂ efflux, has been commonly used to estimate the rate of C mineralization by microbial communities. CO_2 efflux has been shown to be strongly related to soil moisture directly or indirectly through the influence of soil moisture on temperature, which affects both degree of decomposition and production of CO_2 (Bouma and Bryla, 2000, Dilustro et al. 2004). Scanlon and Moore (2000) measured CO₂ production over twelve-day incubations under oxic and anoxic conditions in a cool-temperate peatland and found that production was lower under anaerobic conditions. Soil texture can also influence soil CO_2 efflux through its effects on soil moisture and temperature, both of which influence microbial and root activity. Enhanced populations of aerobic decomposers (Chmielewski 1991) and heterotrophic respiration (Minkkinen and Laine, 1998) due to increased oxidation status after draining soil have been suggested as the reason for higher CO₂ emissions in some cases (Glenn et al. 1993; Silvola et al. 1996; Byrne and Farrell 2005; Blodau et al. 2004). The effects of soil moisture on CO_2 efflux could be different in soils with different structures. Dilustro et al. (2004) found that soil CO₂ efflux was significantly related to soil moisture only in sandy sites when soil water content was above the wilting point threshold; no significant relationships were found between soil moisture and soil CO₂ efflux in clayey sites.

Microbial degradation of soil organic material is mediated by extracellular enzymes. Extracellular enzymes allow microbes to access energy and nutrients present in complex substrates, and catalyze the initial, rate-limiting step of decomposition and nutrient mineralization (Sinsabaugh 1994). Factors such as soil moisture, temperature and pH that influence soil microbial activity also exert control over soil enzyme production (Sinsabaugh et al., 1993). Activity of extracellular enzymes is lower under anaerobic conditions; Freeman et al. (2001) suggested that decomposition in peatlands is restricted by low phenoloxidase activity in the absence of oxygen. However, other studies suggest that phenoloxidase activity is influenced less by aeration than by the nature of the organic matter (Williams et al. 2000). Anaerobic conditions also change microbial populations, reduce microbial biomass, slow decomposition, and alter elements such as Fe, Zn and Cu (which are important cofactors for enzyme activities) in soil solution from oxidized to reduced forms, which can reduce extracellular enzyme activities essential for mineralization of nutrients such as nitrogen and phosphorus. The release of mineral nutrients has been shown to be strongly related to soil water across a broad geographic range (Silver et al. 1999; Chadwick et al. 2003; Holtgrieve et al. 2006; Sleutel et al 2008). At the ecosystem scale, nutrient mineralization increases with increasing moisture up to field capacity and then declines (Prescott 2005). Schuur (2001) showed that litter decomposition rates and nutrient release slowed with increased rainfall, as a result of both reduced soil oxygen availability, measured as redox potential, and the production of low-quality litter in wetter sites.

Nitrogen availability is thought to be highly sensitive to variations in soil moisture. However, the effects of soil moisture conditions on nitrogen mineralization and the potentiallymineralizable nitrogen content of the soil have not been well studied. The effect of soil moisture on N cycling is related to the moisture control over the redox potential. Pett-Ridge et al (2006) suggested that redox-control of soil microbial community structure was an important determinant of soil N-cycling rates. The N cycle is quite vulnerable to changes in soil redox, because redox acts as a master switch for microbe-catalyzed processes of nitrification (oxic), denitrification (hypoxic), and dissimilatory nitrate reduction to ammonium (anoxic) (Yu and Ehrenfeld 2009). Of all transformations and microorganisms involved in the N cycle, nitrification and nitrifying bacteria are thought to be the most sensitive to redox potential and their physio-chemical environment (NH₄ ⁺ and O₂ supply) (Bedard and Knowles 1989; Pett-Ridge et al 2006). Under anaerobic conditions, nitrification is reduced or eliminated (Pett-Ridge et al 2006); whereas processes that require anoxic conditions (notably denitrification) may increase (Pinay et al., 2002).

There is little information about constraining factors on N mineralization under anaerobic conditions and whether different forest types respond to excessive moisture in different ways. Holtgrieve et al. (2006) used a precipitation gradient in a tropical montane ecosystem of Hawaii to evaluate how changes in mean annual precipitation affect the processes resulting in the loss of N via trace gases. Volumetric soil moisture varied from 47% on the mesic sites to 82% in the wettest sites. They found that there was an increase in soil extractable NH₄⁺ and decline in NO₃⁻, while mean net mineralization and nitrification did not change from the mesic to intermediate sites, but decreased dramatically at the wettest site. Two other major N transformations-N immobilization and mineralization-generally do not involve either oxidation or reduction and therefore, may be expected to be unaffected by rapid fluctuations in soil moisture and consequently redox potential (Pett-Ridge et al 2006). Nitrogen mineralization, however, may be reduced under anaerobic conditions if organic N is associated with phenolic compounds which require oxidative decomposition (Schimidt-Rohr et al. 2004).

The significance of soluble organic N (SON) or the potentially dissolved organic N (DON) to plant nutrition relative to inorganic N pool ($NH_4^++NO_3^-$) seems to increase in less productive ecosystems with highly organic and acidic soils, such as peatlands and the Siberian Taiga (Jones and Kielland 2002; Jones et al. 2004). Kranabetter et al (2007) suggested that the assessment of DON, especially in relation to NH_4^+ and NO_3^- , provides more insights into N cycles and the nature of N uptake by plants than other indices such as soluble inorganic N (SIN). SON has been shown to be positively correlated with soil moisture (Hannam and Prescott, 2003); although the

11

mechanisms driving this process are not well understood. Larger microbial populations (Van Cleve and White 1980; Williams 1992) and higher SON uptake by microbial biomass coupled with high SON production (Hannam and Prescott, 2003) have been suggested as some of the mechanisms. Understanding the fate of SON and other forms of N under anaerobic conditions in upland forests will help us to better understand functional differences in N availability in these ecosystems.

1.3 Forest management effects on water-related soil processes

Compared to upland forests, wetland forests have generally poor tree growth due to inadequate oxygen in the rooting zone caused by persistently high water table levels (Dahl and Zoltai 1997; Westman and Laiho 2003). Forest management practices such as clearcut harvesting and drainage can have substantial effects on soil moisture and aeration dynamics in such ecosystems. The problem is intensified when wetland forests are harvested, which in turn raises the water table by reducing interception and evapotranspiration rates (Dube et al. 1995; Roy et al. 2000a). This generally results in peat accumulation or paludification, a process through which production of organic matter exceeds the decay rate (Paavilainen and Paivanen 1995; Charman 2002). The raising of the water-table level further limits tree growth (Paavilainen and Paivanen 1995; Paré and Bergeron 1995; Harper et al. 2002; 2003). Lavoie et al. (2005) concluded that waterlogged conditions (Joosten and Clarke 2002) cause colonization of mosses and Sphagnum on the forest floor, further reducing the soil aerated zone and nutrient turnover (Larson 1982; Taylor et al. 1987; Payette 2001). Increasing organic matter thickness through paludification is not itself the limiting factor for tree growth, but it does affect soil aeration and soil temperature, which in turn affects nutrient cycling and primary production (Lavoie et al. 2005).

12

Drainage has been used for decades to increase aeration in the surface organic layer in forest ecosystems. This improves timber growth by removing excess water from the rooting zone in paludified areas (Paavilainen and Paivanen 1995). Drainage improves oxygen availability in soils by lowering the water table level (Hillman 1992; Silins and Rothwell 1999) and increasing soil macro-porosity (Silins and Rothwell 1999; Roy et al. 2000*b*). Increased aeration of soil increases root metabolism and growth (Laiho and Finer 1996) and primary production and biomass (Dang and Leiffers 1989; Laiho and Finer 1996; Laiho and Laine 1997; Macdonald and Yin 1999; Minkkinen et al 1999; Roy et al. 1999, 2000a), and changes the vegetation composition and structure (Laine et al. 1995*a*, 1995*b*; Minkkinen et al. 1999; Laiho and Vasander 2003).

Drainage also increases populations of aerobic decomposers and microbial biomass (Jaatinen et al. 2007), which further increases mineralization of nutrients, organic matter decomposition and CO_2 efflux. Nevertheless, these losses of C may be offset by increased CO_2 sequestration in biomass (Byrne and Farrell 2005). It has been suggested that the increase in aboveground and belowground C stored in wetland forests compensates for the increase in peat mineralization after drainage (Martikainen et al. 1995; Hargreaves et al. 2003; Byrne and Farrell 2005). Therefore, whether drainage of wetland forests will result in greater or less sequesteration of atmospheric CO_2 remains uncertain.

1.4 Objectives

The aim of this study was to test the theory that the observed differences in nitrogen availability and regeneration growth between CH and HA sites arise from small, but ecologically significant, differences in soil moisture conditions at the two site types; specifically that excessive moisture in CH sites underlies the low N supply in these ecosystems. Specific objectives and hypothesis tested in this thesis are:

1) Determine whether CH and HA forests differ in soil moisture and aeration.

Hypothesis: CH sites have higher moisture content, lower redox potential (especially in lower soil horizons), shallower aerated zones, and greater frequency of anaerobic conditions in the forest floor and mineral soil than HA sites.

2) Determine whether decomposition rate and soil C storage differs between CH and HA forests.

Hypothesis: Mass loss rate is lower and soil C storage is higher in CH than HA forests.

3) Determine whether composition of plant communities is related to soil moisture and aeration.

Hypothesis: The composition of plant communities is related to the moisture and aeration in the forest floor and mineral soil.

4) Evaluate the impact of harvesting in CH and HA sites on moisture and aeration conditions.

Hypothesis: Clear-cut sites will be drier than old-growth sites in the surface horizons, but wetter and less aerated in the deeper soil horizons.

5) Test the effects of excessive moisture on mineralization of carbon and nitrogen.

Hypothesis1: Microbial biomass and CO_2 evolution will decrease under saturated conditions in humus and soil from both site types.

Hypothesis2: NO₃ concentrations and the proportion of N in the form of SIN (*i.e* SIN:SON) will decrease under saturated conditions in humus and soil from both site types.

6) Investigate the effects of drainage on tree growth, vegetation, and soil carbon storage and fluxes in a cedar-swamp forest.

Hypothesis: Drainage will alter the composition of plant species, and will increase tree growth, CO_2 flux, and microbial biomass, and decrease carbon storage in the soil.

1.5 Thesis structure

In Chapter 2, I investigate whether CH and HA forests differ in soil moisture and aeration, decomposition rates and soil C storage. I assess the degree to which the differences in the composition of plant communities are related to soil moisture and aeration. I also assess if harvesting intensifies the differences between the two forest types and results in wetter and less aerated condition in deeper horizons. Thus, I address objectives 1-4 in this chapter.

Chapter 3 deals with objective 5. In this chapter, I investigate how much control soil moisture has over C and N release in these soils and what mechanisms are involved by developing a gradient of moisture in the laboratory and monitoring mineralization of C and N during incubation.

In Chapter 4, I address objective 6 by assessing drainage as a potential solution for forest management in wetland forests. I investigate the effects of drainage on tree growth, vegetation, and soil carbon stores and fluxes in a cedar-swamp forest.

In chapter 5, I synthesize the results of the individual chapters, summarize my most important findings in the light of the current literature, identify weaknesses in the study and suggest directions for further research.



Figure 1-1: Some effects of excessive moisture on soil biogeochemical processes involved with N cycling

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Chapter 2: The influence of soil moisture and aeration on organic matter dynamics, plant communities and forest development ¹

2.1 Introduction

Soil moisture regime, reflective of climatic, topographic and edaphic factors, is a major determinant of the productivity of terrestrial ecosystems. Even in very humid ecosystems, variation in water supply plays an important role in determining ecosystem structure and function (Schuur & Matson, 2001). While the presence of soil moisture is typically beneficial for productivity in terrestrial ecosystems, the accumulation of soil moisture in excess of plant demand may suppress growth through a variety of mechanisms. Wetland forests commonly exhibit poor growth due to inadequate oxygen in the rooting zone caused by persistently high water-table levels associated with poor drainage (Westman and Laiho 2003, Dahl and Zoltai 1997). In such forests, seasonal fluctuations in water table depth often create alternating aerobic and anaerobic conditions, which significantly influence the dynamics of chemical and biological processes within the soil solution. Under water-saturated conditions where all or nearly all of the soil pores are filled with water, oxygen, the major oxidizing agent, becomes limiting. The degree to which oxygen availability limits oxidation reactions within the soil solution can be measured as the reduction-oxidation or redox potential (Eh) (Schlesinger 1997; Gobbat et al. 2004). In general, well-aerated soils have an Eh range of +400 to +700 mV with dominant oxidized states of Fe(III) in FeOOH and N(V) in NO₃⁻ while saturated soils generally have Eh values < +400 mV, reaching as low as -300 mV in extreme cases (Pezeshki 1991) and reduced forms of elements such as Fe(II) in FeO and N(III) in NH4⁺ are prevalent under saturation conditions.

¹ A version of this chapter will be submitted for publication.

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Organic matter turnover, mineralization rates, and enzyme activities appear to be strongly correlated with moisture and redox conditions in wetland soils. The rates of these processes generally slow as soil redox potential declines (McLatchey and Reddy 1998; Scanlon and Moore 2000, Schuur *et al.* 2001, Freeman *et al.* 2001). For example, in wet Hawaiian montane forests, litter decomposition rates and nutrient release slowed with increased rainfall, apparently as a result of both reduced soil oxygen availability and the production of low-quality litter in wetter sites (Schuur 2001). Under low-oxygen or anaerobic conditions, microorganisms require alternate electron acceptors for respiration. Anaerobic pathways are less efficient and result in less complete or slower decomposition of organic matter compared with the aerobic condition (Crumpton and Goldsborough, 1998). Over many years, anaerobic conditions can lead to an accumulation of dead organic matter.

Distribution of plant species have been shown to be strongly connected with soil moisture, water-table depth and fluctuation. Soil physical or chemical characteristics such as organic matter thickness, soil porosity and redox potential are related to soil moisture regime and are important determinants of plant species distribution (Chambers *et al.* 1999; Castelli *et al.* 2000). Most field investigations of interactions among hydrologic variables, redox potential, and plant species distribution have been carried out in salt marshes, riparian meadows or wetlands (Worner and Hackney 1997, Sanchez *et al.* 1998, Castelli *et al* 2000, Laiho *et al.* 2003). In riparian systems and wetland forests, the distribution of plant species has been correlated with water-table depth, frequency of flooding, duration of inundation (Stromberg *et al.* 1996, Yabe and Onimaru 1997, Castelli *et al.* 2000, Laiho *et al.* 2003) and slope position (Pojar and Meidinger 1987). In montane riparian meadows, Dwire *et al* (2006) showed that species richness and total plant cover were negatively correlated with water-table depth and positively correlated with redox potential. Minkkinen *et al* (1999) found that composition of plant communities of mires in central Finland

changed drastically after the water level was drawn down by drainage. The growth rate, biomass production and root: shoot ratio of wetland plant species are also strongly affected by low redox conditions (Pezeshki, 1994a; Kludze and DeLaune, 1994, 1995, Pezeshki 2001). Relationships among hydrology, soil redox potential and plant species distribution in other ecosystems such as temperate coniferous forests are less studied.

Forest management practices such as clearcut harvesting can substantially affect soil moisture and aeration. The presence of a forest canopy and associated root systems lowers the depth of the saturated zone in the soil through the processes of interception and transpiration. Accordingly, the removal of forest canopy through harvesting activities in wet forests can lead to reductions in total evapotranspiration (Dube *et al.* 1995; Roy *et al.* 2000; Grigal 2000) and temporary rises in the water table until vegetation recovers. Such elevations in the water table in wet forests over an extended period of time result in paludification, the processes whereby organic matter begins to accumulate to levels that can negatively impact tree growth (Paavilainen and Paivanen 1995, Paré and Bergeron 1995; Harper *et al.* 2002, 2003). In contrast, increased direct solar radiation following clearcut harvesting can result in drier conditions in the surface organic layer.

In this study we investigate whether low productivity and nutrient supply occurring in cutovers of cedar-hemlock (CH) sites on northern Vancouver Island, British Columbia, is attributable to conditions of excessive moisture. Regeneration of forests following clearcut harvesting of old-growth cedar-hemlock forests has been problematic with the frequent development of severe chlorosis and poor conifer growth associated with low availability of nutrients, particularly N and P. Symptoms of nutrient deficiency tend to appear 5-8 years following clear-cutting on CH sites, but curiously, do not appear on adjacent cutovers of second-growth hemlock-amabilis fir (HA) forests. Several mechanisms have been proposed and examined to explain the low nutrient supply in CH cutovers including competition from the ericaceous shrub,

30

salal (*Gaultheria shallon* Pursh) (Northrup 1995, Mallik and Prescott 2001, Prescott and Sajedi 2008), differences in tree species composition (Keenan 1993, Prescott *et al.* 2000), and lack of disturbance in CH sites (Keenen *et al.* 1994, Weetman & Prescott 2000). However, none of these studies has provided sufficient evidence that any of these suggested mechanisms account for the regeneration problems.

Although CH and HA forest types were initially classified as the same ecosystem association having similar topographic position and mineral soil characteristics (Lewis 1982, Germain 1985, Keenan 1993), several lines of evidence indicate that CH sites might be slightly wetter and less aerated than HA sites. Germain (1985) reported that CH sites tended to occur on more poorlydrained situations, and deMontigny (1992) found a greater frequency of gleved horizons in CH forests. Moreover, deMontigny (1992) observed that humus formations on CH sites were predominantly Humimors, which develop under the influence of excessive moisture on poorlydrained soils and reflect fluctuating, stagnation or slowly moving water close to the ground surface (Green et al. 1993). In contrast, Hemimors and Lignomors were common on HA sites. Battigelli (1994) found lower soil fauna abundance and biomass and larger populations of copepods, which are aquatic animals, in CH forests than HA forests. Furthermore, the tendency for CH sites to occupy slightly lower landscape positions than HA sites was documented through GIS analysis by Albani and Lavery (2000). Given the high precipitation levels in this coastal region (1900 mm/year), this small change in landscape position and / or drainage conditions might be sufficient to create waterlogged anoxic conditions that could lead to the low nutrient supply associated with CH sites.

In this study, we compared soil moisture, aeration, C storage, decomposition rate and plant species composition in CH and HA forests to test the hypothesis that the observed differences in nutrient supply and tree growth between CH and HA sites arise from small, but ecologically

31

significant, differences in moisture conditions among the site types. Specifically, we hypothesized that CH sites have a higher moisture content, lower redox potential (especially in lower soil horizons), shallower aerated zones, and greater frequency of anoxic conditions in the forest floor and mineral soil than HA sites. I hypothesize that soil aeration will be negatively correlated with soil moisture content in both forest floor and mineral soil and so will be lower in CH sites. I hypothesize that CH sites will have greater stores of C in soil and lower rates of decomposition than HA sites. I also hypothesized that the composition of plant communities will be related to the forest floor and mineral soil moisture and aeration. Finally, we evaluated the impact of harvesting in CH and HA sites on moisture and aeration conditions by comparing both recently harvested sites and unharvested sites. We hypothesized that clear-cut sites will be drier than old-growth sites in the surface horizons, but wetter and less aerated in deeper horizons.

2.2 Material and methods

2.2.1 Study area

The study sites are located on northern Vancouver Island, between Port Hardy and Port McNeill, British Columbia, in the very wet maritime Coastal Western Hemlock (CWHvm) biogeoclimatic zone (50° 60'N, 127° 35' W). The climate is characterized by cool, moist summers, and mild, wet winters. Mean annual precipitation is 1900 mm, 70% of which falls (mainly as rain) in the winter months (October to March). The summer months have less rainfall, but rainfall during the growing season prevents any soil moisture deficit in most years. Mean daily temperatures range from 3.3 °C in January to 14 °C in August. The area has gentle topography with an elevation no greater than 300 m a.s.l. Mineral soils are loamy Humo-Ferric Podzols that overlay unconsolidated morainal and fluvial outwash material (Prescott *et al.* 1993).

This study focused on two dominant forest types in the region, namely CH, or Cedar-

Hemlock, and HA, or Hemlock-Amabalis fir. The CH stands are old-growth, dominated by western redcedar with western hemlock as the co-dominant species. These forests are uneven-aged and have a relatively open canopy. Salal dominates the understory with smaller amounts of *Vaccinium spp.*, *Rubus spectabilis* (Pursh), *Blechnum spicant* (L.), *Cornus canadiaensis* (L.), and the mosses *Hylocomium splendens* (Hedw.) B.S.G., *Kindebergia oregana* (Sull.) *Ochyra*, and *Rhytidiadelphus loreus* (Hedw.)Warnst. (de Montigny, 1992). The HA stands are mature, predominantly second-growth, even-aged forests originating from a windstorm in 1906. Western hemlock and amabilis fir dominate the dense canopy. The sparse understory generally consists of *Blechnum spicant*, *Vaccinium spp.*, and the same mosses as at the CH sites (de Montigny, 1992).

2.2.2 Field measurements

Five replicate forest sites covered by mature CH and HA stand types and five replicate clearcut sites were randomly selected based on forest cover and ecosystem classification maps provided by Western Forest Products Inc. (Port McNeill, BC, Canada). The cutovers were mature CH and HA forests originally which were harvested 5-10 years prior to sampling and planted with the original species. These 10 sites, each of which had adjacent CH and HA stands, were distributed over an area of approximately 100 km². Clear-cut and old-growth sites were not always adjacent to each other. Clear-cut sites had been cut 7-10 years prior to sampling. At each site, a circular plot of 25-m diameter was established at least 50 m from the transition between forest types or the edge. Four 2m x 2m plots were randomly placed within each circle plot to study the response variables. A total number of 80 (4 plots x 20 stands) plots were studied. Composition of plant species and their coverage (%) were assessed within all 80 plots once in July 2006 over a two-week period. The coverage of plant species was determined in six classes: 0, 1-5, 6-25, 26-50, 51-75, 76-100 percent. A soil pit to a depth of 1 m, or to an impenetrable layer, was excavated beside each 2x2 plot and the principal horizons, their macro morphological characteristics and rooting depth were described. Samples were collected using a trowel from the F, upper H horizon (H_U), lower H horizon (H_L), and B horizons from each of the four replicate plots for field and laboratory measurements. Samples were collected from the lower H horizon (H_L) if the thickness of H horizon was >25 cm. Samples were kept in zip-lock bags at 4°C prior to analyses.

Relative rates of decomposition were determined using litterbags containing the standard substrate: cellulose filter papers. Litterbags with a 2-mm mesh size containing one piece of Whatman No. 42 filter paper were put into the upper H horizon in August 2005. A second litterbag was put in the lower H horizon if the thickness of the H horizon was >25 cm to compare decomposition rate of the upper and lower humus. Litterbags were collected in August 2006, the papers were removed, cleaned of roots and soil particles, dried and weighed. The weight lost in one year was used as a measure of mass loss rate.

Moisture content, pH and Eh of samples taken from different soil horizons of all 80 plots were measured four times bi-weekly. Each time, samples were collected from forest floor and mineral soil horizons as described above from a new soil pit on one side of the vegetation plot and one meter away from the plot. Sampling started in mid July and was completed in mid September. The composition of the plant community was studied during the first two weeks of sampling. pH and Eh were measured in the field and gravimetric moisture content was measured in a small laboratory in Port McNeill. Moisture content was measured as the actual amounts and not the potential. Approximately 50 gr of the collected samples was oven-dried at 70°C for 48 h to determine the moisture content of the samples taken from forest floor and at 105 °C for 24 h for samples taken from the mineral soil. To measure pH and Eh, a sample with a known volume was excavated from the same horizons as above with a small cylinder (5 cm in diameter and 7 cm long) and placed into a beaker in the field. Distilled water was added on a volume basis with the same cylinder to give a ratio of organic matter to water of 2:1 and mineral soil to water of 1:1. Samples were stirred and

34

allowed to equilibrate for 10 minutes with occasional swirling. After the last swirling, the electrode was inserted in the solution and allowed to stand for 5 min before reading. The readings were corrected for pH 7 by adding -59 mV per pH unit (Qualls et al. 2001; Bohn et al 1985). pH and Eh of the samples were measured using a digital pH meter and a digital waterproof redox tester (OAKTON ORPTestr BNC), respectively. Electrodes were calibrated with standard solutions on a daily basis before sampling. YSI 3682 Zobell solution was used for calibration of the redox meter.

Iron rods were used to assess maximum soil aerated depth over a one-year period (July 2005-July 2006. An iron rod (8 mm in diameter and 80 cm in length) was inserted into the soil at the centre of each vegetation plot, leaving at least 5 cm at the top exposed above the soil surface, to further explore the connection between aerated depth and plant community composition. Rust formation on the iron rods was examined one year later. The depth at which a rod remained unrusted represented the depth at which anaerobic conditions prevailed year-round. The depth from the soil surface to the unrusted zone was measured using a meter ruler. The aerated depth in the mineral soil was calculated by discounting organic matter thickness from the total aerated depth on the rod. An additional 16 iron rods were placed in randomly selected locations within each stand in July 2004 and collected in July 2005 to have a better understanding of the variation of the aerated depth at the stand level.

35

The soil C store (kg m⁻²) was then estimated as the product of C concentration (C%), bulk density (kg m⁻³) and organic layer thickness for forest floor and to a depth of 20 cm for mineral soil. Total carbon concentration was determined by the total combustion method (LECO, 1996). The average bulk density of F, upper H and lower H horizons was used to calculate the forest floor C store.

One out of the four plots within each of the 20 stands was chosen to fully describe soil morphological properties such as layer thickness, coarse fragment content, soil texture, structure, consistency, color, mottles, and rooting depth for each horizon according to the methods developed by the BC Ministry of Forests (Luttmerding *et al.* 1990). The thickness of the horizons and depth of mottling were recorded at all plots and on all four sampling occasions during the 2-month period of intense sampling.

2.2.3 Laboratory measurements

Soil samples taken from the last sampling occasion in September 2005 were transferred to the laboratory at the University of British Columbia for further analysis. A portion of the samples were air-dried prior to chemical characterization. Total nitrogen and carbon was determined by total combustion (LECO, 1996). Field capacity was measured in the laboratory using the pressure plate standard method (Klute, 1965). Soil particle-size distribution was determined using a combination of sieving and sedimentation steps for textural analysis as described by Kettler *et al.* (2001).

2.2.4 Data analysis

A split-split-plot experiment in a completely randomized design was used to analyze the data for variables measured at four time periods in the field (% moisture, pH, Eh, and organic matter thickness). Disturbance type (forest vs. clearcut) was the main treatment effect, and stand type (CH vs. HA) and time were the split plot factors (Kuehl, 1994). The stand and disturbance treatments (forest vs. clearcut and CH vs. HA) were fixed and the data were analyzed separately for each soil horizon. Site and observation (four sampling plots) were random effects and considered as the experimental error and sampling error, respectively. The GLM (General Linear Model) procedure in a SAS statistical package version 9.1 was used to test for differences in response variables between the two stand types within each disturbance type and also between the two stand types within each disturbance type and stand type, disturbance type and time, stand type and time and the three way interaction were also tested. To analyze the data for the variables measured only once, a split-plot experimental design was used and the rest of the analysis was similar.

2.2.5 Multivariate analysis

Several multivariate techniques were used to determine whether the structure of the plant communities was distinctively different between CH and HA stands and whether the variation in plant communities was associated with the variation in soil moisture and aeration. Principal components analysis (PCA), canonical correspondence analysis, multi-response permutation procedure (MRPP), and indicator species analysis were performed with the PC-ORD (ver. 5) program (McCune and Medford, 1997).

Principal component analysis (PCA) was used as an ordination method to explore the structure of the plant communities as well as the soil variables. PCA was also used to reduce the number of plant species from 18 to 6 of which representing the most information in the original data set. Canonical correspondence analysis (CCA) was then performed to determine whether variance in the plant community data (both the original and the reduced data set) could be explained by environmental variables. Stepwise selection in CCA provided an efficient way to eliminate environmental variables that did not explain significant variation in the plant community. Thus, 20 soil variables, including those measured separately at the three principal soil horizons, were reduced

to 10 variables (Fig 11) that explained 74% of the variation in the original data set (33% axes 1, 22% axes 2 and 19% axes 3). The null hypothesis (no structure in main matrix and therefore no relationship between matrices) was tested using MontCarlo simulation with 300 runs.

Multi-Response Permutation Procedure (MRPP) was used to test for the overall difference in the structure of the two groups (plant communities in CH vs. HA sites) and the homogeneity within each group. MRPP was performed using Sorensen distance. The Euclidian and ranked Sorensen values are also presented for comparison. Indicator Species Analysis (ISA) was used to find the possible indicator species associated with forest types, low redox potential (below 300 mV) and high moisture content (above 350% in the forest floor and 100% in the mineral soil). The data from forests and clearcuts were analyzed separately due to the significantly different plant communities between the two ecosystems. The analyses were performed first on all plots of each disturbance type (n=40) and then on all plots of each stand type (n=20).

2.3 Results

2.3.1 Soil measurements

2.3.1.1 CH vs. HA forests

All soil horizons were wetter in CH forests than HA forests, but only the differences in F and upper H horizons were significant (Table 2-1; Fig 2-1). Moisture content was highly variable, ranging from 100% to 780% in F horizons, 150% to 850% in H_U horizons, 260% to 800% in H_L horizons and 30% to 250% in the mineral soil of the forests. CH clearcuts were also on average wetter than HA clearcuts in all horizons, but the differences were smaller and not significant (Table 2-1). Soil moisture levels at both forest types were above field capacity even at the driest time of the year (Table 2-2).

CH forest soils were less aerated than HA forests as inferred from redox measurements. Average redox potentials in the H_U and B horizons were significantly lower in CH forests than in HA forests and the difference increased with depth (Table 2-3, Fig 2-2). There was no difference in the redox potential of the F horizon between the two forest types. Redox values were highly variable, ranging from +190 to +485 mV in forest floor and +50 to +470 mV in mineral soil. In clearcuts, redox potential was not significantly different between CH and HA stands in any of the horizons. Average redox values were lower in CH forests than HA forests on all four measurement occasions, but the difference decreased as the redox potential in HA forests declined in September when the rainy season started. In CH forests and in CH and HA clearcuts, redox potential did not change over the four measurement occasions (Table 2-3).

pH was significantly higher in F and H_U horizons of the CH forests than the HA forests but there was no difference between CH and HA clearcuts (p<0.05; Table 2-3). No difference was found in average pH values of B horizon between the two forest types in either forests or clearcuts. pH also did not change over the four measurement times (Table 2-3). Correlations between redox potential and pH were tested to check the credibility of the method used to measure redox. Redox potential was negatively correlated with pH at all horizons ($r^2=0.51$ in F horizon, $r^2=0.69$ in H_U and $r^2=0.58$ in B horizon; p<0.0001 at all horizons; Fig 2-3). Redox potential was moderately correlated with moisture content in H_U and weakly correlated in B horizons (Fig 2-4). Moisture content was positively correlated with clay concentration in the mineral soil; this correlation was stronger in the CH forests than HA forests (Fig 2-5).

Information collected from iron rods indicated that CH forests have a shallower aerated depth (p=0.016) in the soil profile and higher frequency of anoxic conditions in the soil than HA forests. 77% of the rods placed in 2005 indicated the presence of anoxic conditions in CH forests compared to 59% in HA forests (Table 2-4). The aerated depth in the soil profile was never less than 30 cm

from the soil surface in HA forests; whereas in CH forests it was as shallow as 6 cm at some plots. In clearcuts, CH stands also had a shallower aerated depth, but the difference between CH and HA stands was not statistally significant (p=0.69; Table 2-4). Similar to the total aerated depth, the thickness of the aerated zone in the mineral soil was similar in CH and HA clearcuts (Table 2-4). Aerated depth was positively correlated with redox potential both in the H_U (r^2 = 0.56; p<0.0001; Fig 2-6) and in the B horizons (r^2 = 0.60; p<0.0001; Fig 2-6) and negatively correlated with moisture content (r^2 = 0.27; p=0.002; Fig 2-7). Mottles, a sign of fluctuation of water and poor drainage, were observed at four out of five CH sites and at only one HA site. Out of a total of 80 soil pits at each unharvested forest type during the 2-months sampling period, 11 pits in CH sites exhibited mottling; whereas in HA forests, only 2 soil pits exhibited mottling.

Mass loss rates varied from 0 to 100 percent among all samples. There was no significant difference between CH and HA sites in either forests or clearcuts (Fig 2-8). Mass loss decreased with depth and was lower in the lower H than all other horizons; although the difference was not significant.

CH forests had significantly lower bulk density (p<0.1) and higher total carbon concentrations in the mineral soil than HA forests (Table 2-2). Total carbon concentration was similar in the forest floor in CH and HA forests. In clearcuts, HA stands had higher total carbon concentration in the mineral soil than HA stands (Table 2-2), but the difference was not significant. No difference was found in organic matter thickness between the two forest types in either forests or clearcuts (Table 2-3). Forest floor carbon pool was on average 16.4 kg m⁻² (2.7-55.1) in clearcuts and 12.2 kg m⁻² (1.4-34.1) in forests. The amount of C stored in the top 20 cm of the mineral soil was 11.2 kg m⁻² (2.2-34.0) and 9 kg m⁻² (1.7-30.4) in clearcuts and forests, respectively. There were no significant differences in total soil carbon pools between CH and HA sites in either forests or clearcuts (Fig 2-9).

2.3.1.2 Forests vs. clearcuts

Soil moisture was lower in upper soil horizons (F and H_U) horizons in CH clearcuts compared with CH forests ten years after clearcut; however differences decreased with depth and lower horizons (H_L and B) were similarly wet (Table 2-1). In the HA type, soil moisture content did not differ between forests and clearcuts in any horizon. Over the four sampling occasions, the differences in soil moisture content between forests and clearcuts increased and became most significant during month of August, the driest time of the sampling period, in all horizons.

Despite the similar average moisture content of the lower horizons in HA forests and clearcuts, redox values were significantly lower in the mineral soil in HA clearcuts (average of 288 mV) compared with HA forests (average of 324 mV; Table 2-3). Redox potential was similar in other soil horizons between HA forests and HA clearcuts and also between CH forests and CH clearcuts in all horizons (Table 2-3).

The iron rods indicated that harvesting improved soil drainage of CH sites but not HA sites. The thickness of the aerated zone in the mineral soil was significantly less in CH forests (average of 14 cm) than in CH clearcuts (average of 23 cm), but did not significantly differ between HA forests and clearcuts (average of 27 vs. 25 cm; Table 2-4). Average rooting depth was similar in CH forests and CH clearcuts, but was higher in HA forests (71 cm) than in HA clearcuts (56 cm; Table 2-2).

2.3.2 Vegetation

CH forests were dominated by *Gaultheria shallon, Blechnum spicant* and *Hylocomium splendens*. In HA forests, there were no dominant species, but compared with CH sites, Vaccinium *spp*. were more dominant (Table 2-5). Plant species diversity was significantly higher in CH forests with 15 species in total and 4.5 species per plot than in HA forests with10 species in total and 3.5 per plot (p=0.037). It was was similar in CH and HA clearcuts (p=0.428). Plant species diversity was significantly higher in clearcuts than in forests in both CH (p=0.023) and HA sites (p=0.002).

Sixty percent of species were identical between the two forest types. Six species present in CH forests did not occur in HA forests; however, these species were infrequent (less than 5% of the total coverage). Total plant coverage was higher in CH forests than HA forests. The percent cover of all species in CH and HA forest is presented in Appendix 1.

PCA results indicated that CH and HA forests had distinct plant communities (Fig 2-10). The reduced data matrix included 6 species with the first three axes explaining 74% of the variation in the plant communities (Table 2-5). The first axis explained most of the variability (35%) and was strongly negatively correlated with percent cover of *Gaultheria shallon* (salal) and *Blechnum spicant* (deer fern) and positively correlated with *Vaccinium* spp. Results from MRPP analysis also indicated a significant difference in plant community composition between CH and HA forests (Table 2-6). The two groups were well separated by a relatively high chance-corrected within-group agreement (A=0.22) and very low test statistics (T = -15.9). The average within-group distance was lower in CH forests than in HA forests indicating higher homogeneity of plant species within CH sites and greater dispersion within HA sites (Table 2-6).

PCA analysis was performed on all soil variables and the reduced soil matrix. The reduced soil matrix included 10 soil variables responsible for 75% of the variability in the original dataset (Table 2-7). HA forests had a relatively homogenous structure in soil characteristics represented by high oxic depth, redox potential and % sand in the mineral soil and forest floor (Fig 2-11). In contrast, CH plots separated into three distinct groups (Fig 2-11). Group 1 had saturated mineral soil underlying a very wet forest floor and was characterized by very low redox potential, low oxic depth and high pH (Table 2-8). In contrast, group 3 had characteristics similar to HA forests with moist soils, high redox, sandy soils, thick forest floor and high oxic depth. Group 2 was intermediate - like group1 it had saurated soils, but its redox potential was close to group 3. Soils in this group had very high silt and clay content and low sand.

2.3.3 Interactions between plant species and soil variables

Results from CCA analysis indicated that about 31% of the variation in plant communities (including all species) was explained by all the soil variables measured (Table 2-9). Moisture content alone explained 15% of the variability in plant communities (p=0.05 when all of species were used and p=0.01 when 6 species were used; Table 2-9). Interactions between soil aeration and plant community strucure were assessed using redox values of F, H_U and B horizons and the aerated depth data obtained from iron rods. Soil aeration explained about 25% of the variation in the structure of the plant communities (Table 2-9). Plant communities in CH and HA plots were well separated using the aeration matrix (Fig 2-12). Soil moisture and aeration together explained 30% of the variation in plant communities (Table 2-9; Fig 2-13).

I did not find any significant correlations between species diversity and redox potential $(r^2=0.013; p=0.93)$, or aerated depth $(r^2=0.19; p=0.006)$ in forests; however a weak correlation was apparent with moisture content $(r^2=0.22; p=0.002)$. Among the species present, the presence and coverage of *Blechnum spicant* (deer fern) was correlated with soil aeration of the humus layer (Fig 2-14). An Indicator Species Analysis (ISA) showed that deer fern was the only species associated with anaerobic conditions (Eh of <300 mV) in forests. Deer fern was covering more than 25% of the total understory cover under anaerobic conditions. In forests, the coverage of deer fern was moderately correlated with Eh (values were not adjusted for pH 7; r²=0.44; p=0.0001) and weakly correlated with aerated depth (r²=0.25; p=0.001).

2.4 Discussion

Measures of soil moisture and aeration were consistent with our first hypothesis that there are higher moisture content, more frequent anoxic conditions and lower aeration in CH forests than HA forests. The differences in moisture content between CH and HA forests were significant and large in upper horizons, but narrowed with depth. The smaller differences between the two forest types in moisture level of the lower soil horizons, which were higher than field capacity in both sites, indicate a high water table in both CH and HA forests. On the other hand, soils in CH forests were less oxidized than the adjacent HA forests in forest floor and in mineral horizons. This suggests that although HA stands might be as wet as CH stands, they have more dissolved oxygen in water, probably due to higher slope position or better drainage conditions in the mineral soil which maintains water flow. CH forests were more variable, ranging from moist soils that are well-aerated to poorly drained soils with high amounts of silt and clay. The moderate correlation between moisture and clay content in CH soils indicates that soil texture could be causing the higher soil moisture content in some CH forests. Also, higher frequency of mottles at CH forests, compared with HA forests, indicates that these sites are switching from oxidizing to reducing conditions throughout the growing season. The third group of CH forests is poorly drained, the water is almost stagnant with anaerobic conditions as redox potential is very low (average 245 mV) and the aerated depth is very shallow. Our field observations indicate that a pan layer close to the forest floor surface exists in almost all of those locations and some smell of sulphide was noted.

Average redox values were below +300 mV on all four measurement occasions during the driest time of the year in CH forest and clearcuts. This important redox threshold has been mentioned in the literature, below which oxygen does not exist and the soils become anaerobic (Dwire *et al.*, 2006; Faulkner and Patric 1992; Pezeshki 1991). It has been shown that redox values less than 300 mV result in complete or considerable cessation of root growth (Pezeshki 2001, Pezeshki 1991; Will *et al*, 1995). Implications of this threshold for microbiological processes need further research. Our results indicate that 40% of the samples taken from CH forests have an average redox value less than +300 mV during the summer when the soils are expected to be under the most oxidizing conditions.

Observations from rusting on iron rods also confirms that the aerated depth in CH forests is shallower and more variable than in HA forests. Strong correlations have been reported between steel-rod rusting depth and water-table depth (McKee 1978, Bridgham *et al* 1991), rooting depth (Carnell and Anderson, 1986) and soil oxygen concentration (Owens *et al.* 2008). My results indicte that aeration (both Eh and aerated depth) was only moderately correlated with moisture in the forest floor and weakly correlated in the mineral soil. In the mineral soil, stronger correlations were found between aerated depth and redox potential than between aerated depth and moisture content, suggesting that saturated conditions do not always result in developement of anaerobic conditions in the soil. Thus, dissolved oxygen could remain adequate despite the soils becoming saturated as long as the water does not stagnate. Direct measurements of dissolved oxygen therefore would be more preferable to moisture measurements for determining the ecological effects of water saturation of soils.

Analysis of the plant communities confirmed our second hypothesis that the composition of plant species would be related to soil moisture and aeration, but this was not true for plant diversity. Qian *et al.* (1997) showed that plant diversity increased with increasing soil moisture, from slightly dry to moist sites. In other studies, water-table depth, moisture and aeration in the soil have shown to be strongly to moderately correlated with the structure and composition of plant communities in floodplain and riparian meadows (Silvertown *et al.* 1999; Castelli *et al.* 2000; Dwire *et al.* 2006). In this study, composition of plant communities seems to be a more important metric in responding to the environmental variables than diversity. Wetter sites (CH forests) had higher plant diversity and abundance, but neither measures were directly correlated with moisture content, redox potential or aerated depth. Consequently, moisture or oxygen may not be the proximate factor in plant diversity.

Variation in plant community composition in the forests was not well explained by any of the measured soil variables. This was despite soil aeration being the most important factor driving

differences of plant species, explaining 25% of the variability within plant communities. Among all the species deer fern appeared to be an indicator of anaerobic conditions (Eh of <+300 mV) in CH and HA forests in that its presence and coverage was correlated with Eh and aerated depth. The results suggest that plant distribution could be affected by other factors such as light (Thomas *et al.* 1999, Hall and Harcombe 1998, Brinston 1990), nutrient availability (Wardle et al. 2004b), competition (Navas and violle 2009, Schenk 2006), and soil microbial communities (van der Heijden *et al.* 2006a, 2008) in these ecosystems.

The difference in moisture, aeration and composition of plant communities between CH and HA stands could cause significant differences in decomposition between the two forest types. Soil moisture has been shown to strongly affect heterotrophic respiration and decomposition (Bouma and Bryla, 2000, Dilustro *et al.*, 2004). Schuur (2001) showed that litter decomposition rates and nutrient release slowed with increased rainfall as a result of both reduced soil oxygen availability and the production of low-quality litter in wetter sites. Litter decay rates are similar in CH and HA sites, but not surprisingly since L and F horizons are well aerated but H horizon and mineral soil are not. This suggests that root decay may be impeded. The results also confirmed that rooting depth is deeper in HA sites than CH sites. More nutrients could be available for plant growth in HA sites because of greater rooting depth and better aeration.

The two forest types responded differently to clearcut harvesting. Moisture content was lower in all organic horizons in CH clearcuts than in CH forests; however the mineral soil was similarly wet in both CH forests and clearcuts. The drier soils in CH clearcuts did not result in better aeration, however, and the redox potential was similar to CH forests and still below the 300 mV threshold. Compared with forests however, in HA clearcuts the upper humus was drier, lower humus was wetter and mineral soil was similarly wet. Despite having similar moisture levels, mineral soil was anaerobic in HA clearcuts and not in HA forests. Redox potential in the mineral soil, which was always above +300 mV in HA forests, was lower in HA clearcuts; it was below this threshold and at similar levels as CH clearcuts. Likewise, the iron rods indicated that harvesting improved soil drainage in CH sites, but not in HA sites. The aerated depth of the mineral soil increased from 14 cm in CH forests to 23 cm in CH clearcuts, but remained similar (25 vs. 27 cm) in HA stands. The reduction of redox in HA cutovers suggests that clearcutting HA forests may cause this ecosystem to have poorly aerated soils like CH forests. Reductions in the soil aerated zone after harvesting have been noted elsewhere (Joosten and Clarke 2002; Lavoie *et al.* 2005) and are thought to reduce rates of decomposition and nutrient turnover (Payette 2001; Taylor *et al.* 1987) through the paludification process, which could negatively affect the productivity of HA sites. This theory needs to be tested.



Figure 2-1: Average moisture content (% dry-wt) in soil horizons of CH and HA forests and clearcuts during two months of measurements. Different letters indicate significant difference between forest types; capital letters indicate significant difference between clearcuts and forests of the same forest type. F=F-horizon, H_U = upper humus, H_L =lower humus, B= upper 20 cm of mineral soil.



Figure 2-2: Average redox potential (mV) in soil horizons of CH and HA forests and clearcuts. Different letters indicate significant difference between forest types; capital letters indicate significant difference between clearcuts and forests of the same forest type. F=F-horizon, H_U = upper humus, B= upper 20 cm of mineral soil



Figure 2-3: Correlation between pH and redox potential in organic and mineral soil horizons.



Figure 2-4: Correlation between average moisture content and redox potential in organic and mineral soil horizons in CH and HA forests. H_U = upper humus; B= upper 20 cm of mineral soil.



Figure 2-5: Relationship between clay concentration (%) and moisture content (% dry weight) in the upper 20 cm of mineral soil in CH and HA forests.



Figure 2-6: Correlation between average redox potential and oxic depth in the upper humus (Hu) and upper 20 cm of mineral soil (B) horizons in CH and HA forests.



Figure 2-7: Relationship between average moisture content and aerated depth in the (a) upper humus (H_U) and (b) upper mineral soil (B) soil horizons in CH and HA forests.



Figure 2-8: Mass loss (% dry mass) of cellulose after a one-year incubation in the upper (H_U) and lower (H_L) humus layers in CH and HA clearcuts and forests.



Figure 2-9: Soil carbon pool (kg m^{-2}) in the forest floor (FF) and the upper 20 cm of the mineral soil (B) in CH and HA forests and clearcuts.



Figure 2-10: Ordination diagram of principal component analysis (PCA) of plant species in the two forest types (CH and HA). The 6 species explained 74% of the variation (Gas: *Gaultheria shallon*; Bls: *Blechnum spicant*; Kio: *Kindbergia oregana*; Vac: *Vaccinium spp.*; Plu: *Plagiothecium undulatum*; Hys: *Hylocomium splendens*)



Figure 2-11: Ordination diagram of principal component analysis (PCA) of soil characteristics in the two forest types (CH and HA). The 10 soil variables explained 75% of the variation (EhB: Eh of B horizon; EhHU: Eh of H_U horizon; MCHU: moisture content of H_U horizon; OMTH: organic matter thickness; OXD: oxic (aerated) depth; pHB: pH of B horizon; pHHU: pH of H_U horizon).



Figure 2-12: Ordination diagram of canonical correspondence analysis (CCA) of plant species and soil variables related to soil aeration in the two forest types (CH and HA). The first three axes explained 25% of the variation (Gas: *Gaultheria shallon*; Bls: *Blechnum spicant*; Kio: *Kindbergia oreganum*; Vac: *Vaccinium* spp.; Plu: *Plagiothecium undulatum*; Hys: *Hylocomium splendens*; tSpe: total number of plant species; EhB: Eh of B horizon; EhF: Eh of F horizon EhHU: Eh of H_U horizon; OXD: oxic (aerated) depth).



Figure 2-13: Ordination diagram of canonical correspondence analysis (CCA) of plant species and soil variables related to soil moisture and aeration in the two forest types (CH and HA). The first three axes explained 30% of the variation (Gas: *Gaultheria shallon*; Bls: *Blechnum spicant*; Kio: *Kindbergia oregana*; Vac: *Vaccinium* spp.; Plu: *Plagiothecium undulatum*; Hys: *Hylocomium splendens*; tSpe: total number of species; EhB: Eh of B horizon; EhF: Eh of F horizon EhHU: Eh of H_U horizon; OXD: oxic (aerated) depth; MCF: Moisture content of F horizon; MCHU: Moisture content of H_U horizon; MCB: Moisture content of B horizon).



Figure 2-14: Correlation between % cover of deer fern (*Blechnum spicant*) and redox potential in the upper humus (H_U) horizon. % cover classes: 1 = <1%; 2 = 1-5%; 3 = 5-25%; 4 = 25-50%; 5 = 50-75%; 6 = 75-100%.

		Jul15-Jul 30		Aug 01-Aug 15		Aug 16-Aug 30		Sep 01-Sep 15		Average	
	Horizon	СН	HA	СН	HA	СН	HA	СН	HA	СН	HA
	Forests	333	305	385	347	448 ^a	347 ^{b*}	414	364	393 ^a	340 ^{b*}
F		(25.1)	(18.9)	(29.1)	(22.8)	(25.3)	(22.1)	(22.7)	(24.0)	(13.5)	(11.1)
	Clearcuts	297	318	280	273	274 ^{A**}	318 ^{Ab}	359	329	299 ^{A**}	308 ^{Ab}
		(30.6)	(18.3)	(34.4)	(21.1)	(21.1)	(18.3)	(21.4)	(20.4)	(14.9)	(10.1)
	Forests	447 ^a	349 ^{b*}	497 ^a	406 ^{b*}	496 ^a	396 ^{b**}	467	394	476 ^a	385 ^{b**}
${\rm H}_{\rm U}$		(33.6)	(16.8)	(33.3)	(36.0)	(22.9)	(23.2)	(25.3)	(20.2)	(14.6)	(12.3)
	Clearcuts	360	400	417 ^{A*}	364 ^{Ab}	362 ^{A**}	385 ^A	380	339	379 ^{A**}	372 ^{Ab}
		(23.3)	(20.9)	(20.1)	(35.2)	(13.9)	(32.8)	(33.1)	(22.3)	(11.7)	(13.8)
$H_{\rm L}$	Forests	424	336	560	416	540	365	534	371	495	372
		(24.6)	(19.8)	(67.9)	(39.7)	(48.2)	(27.1)	(8.5)	(11.5)	(24.3)	(12.1)
	Clearcuts	450	401.95	411	409	411	396	489	437	441	415
		(21.1)	(15.2)	(19.4)	(24.8)	(27.5)	(40.2)	(50.5)	(20.5)	(17.0)	(11.1)
	Forests	113	93	115	104	132 ^a	87 ^{b**}	94	84	114 ^a	92 ^a
В		(8.7)	(9.5)	(13.2)	(11.3)	(13.6)	(8.7)	(11.3)	(7.8)	(5.9)	(4.6)
	Clearcuts	113	99	108	83	88 ^{A**}	98^{Ab}	113	97	106 ^a	94 ^a
		(11.3)	(12.2)	(11.6)	(7.6)	(5.9)	(8.8)	(12.8)	(9.4)	(5.4)	(4.5)

Table 2-1: Moisture content (%dry-weight basis) of soil horizons of CH and HA forests and clearcuts on the four sampling occasions. F=F-horizon, H_U = upper humus, H_L =lower humus, B= upper 20 cm of mineral soil.

Numbers in parenthesis are standard errors. Different letters indicate significant difference between stand types (CH vs. HA). Capital letters indicate significant difference between clearcuts and forests of the same stand type. Numbers in brackets are standard errors. * indicates difference at P<0.1 and ** indicates difference at P<0.05.

		F		Н		В	
		СН	HA	CH	HA	СН	HA
Bulk density (g/cm3)	Forest	0.08 ^a	0.10 ^a	0.10	0.10	0.42 ^a	0.55^{b^*}
		(0.02)	(0.01)	(0.01)	(0.01)	(0.06)	(0.05)
	Clearcut	0.12 ^{A**}	0.10^{aA}	0.12	0.12	0.53	0.58
		(0.01)	(0.01)	(0.01)	(0.01)	(0.04)	(0.05)
Total carbon concentration %	Forest	-	-	48.1	47.4	10.7	8.4
				(0.4)	(0.3)	(1.5)	(0.5)
	Clearcut	-	-	-	-	11.0	10.9
						(1.3)	(0.9)
Rooting depth (cm)	Forest	-	-	-	-	50 (12.9)	67 (7.3)
	Clearcut	-	-	-	-	48 (3.8)	58 (6.6)
Field capacity (% dry weight)	Forest	-	-	248	261	65	64
				(38.7)	(10.3)	(9.2)	(7.3)
	Clearcut	-	-	259	288	82	85
				(17.2)	(44.4)	(4.2)	(3.4)
Clay%	Forest	-	-	-	-	11 (1.1)	10 (1.1)
	Clearcut	-	-	-	-	9 (1.1)	9 (1.8)
Silt%	Forest	-	-	-	-	24 (2.7)	24 (3.2)
	Clearcut	-	-	-	-	25 (3.5)	23 (3.9)
Sand%	Forest	-	-	-	-	65 (3.7)	66 (4.1)
	Clearcut	-	-	-	-	65 (4.0)	69 (5.0)

Table 2-2: Characteristics of the forest floors and mineral soils in CH and HA forests and clearcuts. F=F horizon; H= humus horizon; B= upper 20 cm of mineral soil.

Numbers in parenthesis are standard errors. Different letters indicate significant difference between the two stand types. Capital letters indicate significant difference between clearcuts and forests of the same stand type. * indicates difference at P<0.1 and ** indicates difference at P<0.05.
			Jul15	-Jul 30	Aug 01-Aug 15		Aug 16-Aug 30		Sep 01-Sep 15		Average	
			СН	HA	CH	HA	CH	HA	СН	HA	СН	HA
Eh (mV), adjusted												
for pH 7	F	Forest	303 (4.52)	315 (5.26)	297 (6.41)	301 (5.54)	303 (10.25)	334 (16.59)	294 (6.88)	290 (4.90)	299 (3.54)	309 (4.83)
		Clearcut	300 (5.02)	312 (5.56)	279 (4.21)	296 (3.68)	287 (8.76)	296 (7.67)	294 (6.53)	297 (4.49)	289 (3.25)	300 (2.92)
	Hu	Forest	303 (7.87)	330 (4.80)	292 (9.21)	304 (3.91)	309 (11.09)	336 (15.02)	298 (6.15)	297 (6.00)	300 (4.28) ^a	317(4.75) ^{b**}
		Clearcut	313 (5.11)	318 (6.12)	294 (4.11)	294 (4.37)	305 (8.69)	314 (6.42)	291 (3.72)	294 (4.01)	301 (3.06)	305 (2.94)
	H_{L}	Forest	312 (14.98)	314 (9.84)	271 (27.91)	303 (8.42)	291(20.17)	282 (46.63)	292 (11.94)	302 (6.02)	298 (10.17)	299 (12.42)
		Clearcut	306 (19.90)	324(8.89)	290 (6.40)	310 (10.09)	312 (11.69)	298 (21.37)	296 (4.08)	293 (5.15)	300 (4.78)	307 (5.66)
	в	Forest	294 (14.42)	336 (4.92)	281 (14.10)	303 (7.30)	298 (14.01)	350 (11.72)	281 (15.59)	307 (4.85)	288 (7.17) ^a	324 (4.40) ^{b**}
		Clearcut	274 (17.17)	293 (17.01)	267 (10.79)	297 (6.63)	288 (14.68)	282 (18.61)	280 (11.74)	279 (13.37)	277 (6.82) ^a	288 (7.21) ^{B**}
pH	F	Forest	4.58 (0.1)	4.14 (0.08)	4.66 (0.08)	4.18 (0.05)	4.52 (0.08)	4.10 (0.06)	4.59 (0.09)	4.16 (0.06)	4.59 ^a	4.14 ^{b**}
		Clearcut	4.58 (0.08)	4.29 (0.10)	4.43 (0.12)	4.39 (0.08)	4.20 (0.10)	4.16 (0.09)	4.43 (0.13)	4.42 (0.11)	4.43	4.31
	H_{u}	Forest	4.50 (0.15)	4.13 (0.09)	4.55 (0.14)	4.09 (0.09)	4.28 (0.14)	4.01 (0.12)	4.54 (0.13)	3.86 (0.04)	4.54 ^a	4.03 ^{b**}
		Clearcut	4.31(0.05)	4.14 (0.09)	4.04 (0.07)	4.09 (0.12)	4.06 (0.07)	4.02 (0.09)	4.16 (0.07)	3.99 (0.07)	4.16 ^{A*}	4.06
	H_{L}	Forest	4.48 (0.27)	4.00 (0.11)	4.13 (0.09)	4.10 (0.10)	4.32 (0.35)	4.15 (0.29)	4.65 (0.95)	3.82 (0.10)	4.65	4.00
		Clearcut	3.85 (0.17)	3.93 (0.10)	4.06 (0.06)	4.23 (0.32)	3.75 (0.11)	3.92 (0.17)	3.97 (0.06)	3.68 (0.10)	3.97	3.91
	В	Forest	4.93 (0.15)	5.00 (0.10)	4.97 (0.14)	4.90 (0.10)	4.94 (0.15)	4.98 (0.09)	5.20 (0.14)	5.03 (0.07)	5.01	4.97
		Clearcut	4.67 (0.1)	4.79 (0.11)	4.78 (0.11)	4.90 (0.08)	4.76 (0.10)	4.98 (0.09)	4.74 (0.11)	4.86 (0.11)	4.74	4.88
Organic matter thickness (cm)	LFH	Forest	31 (3.98)	24 (3.02)	18 (2.12)	31 (3.31)	25 (3.14)	24 (2.78)	21 (2.36)	29 (3.55)	24 (1.58)	27 (1.60)
		Clearcut	20 (3.77)	30 (3.38)	25 (3.41)	25 (3.03)	29 (4.31)	28 (3.76)	25 (4.36)	30 (5.01)	25 (1.96)	²⁸ (1.92) 60

Table 2-3: Selected characteristics of forest floor and soil horizons CH and HA forests and clearcuts on the four sampling occasions. F=F horizon, H_U = upper humus, H_L =lower humus, B= upper 20 cm of mineral soil. (Numbers in paranthesis are standard errors. Different letters indicate significant difference between forest types. Capital letters indicate significant difference between clearcuts and forests of the same type. Numbers in brackets are standard errirs. * indicates difference at P<0.1 and ** indicates difference at P<0.05).

	Forest 2005		Fores	Forest 2006		Clearcut 2006	
	СН	HA	CH	HA	CH	HA	
Average of aerated depth (cm)	42	56	37 ^a	56 ^{b**}	48	51	
from the forest floor surface	(2.62)	(2.17)	(4.75)	(3.58)	(3.66)	(3.47)	
Average of aerated depth (cm)			14 ^a	27 ^{b*}	23	25	
from the mineral soil surface			(2.8)	(3.1)	(3.7)	(2.8)	
Range of aerated depth (cm)			6 - 80	31 - 73	27 - 69	25 - 72	
Number of rods used	69	75	16	16	16	16	

Table 2-4: The depth of the soil aerated zone in CH and HA forests and clearcuts on two occasions.

Numbers in parenthesis are standard errors. Different letters indicate significant difference between forest types. Numbers in brackets are standard errors. * indicates difference at P<0.1 and ** indicates difference at P<0.05

Table 2-5: Correlation coefficients between scores for plant species and the first three axes of PCA. The first three axes explain 74% of the variation in the main matrix.

Variable	Axis 1	Axis 2	Axis 3	
Cumulative variance explained %	35.1	55.7	73.6	_
(Vaccinium spp.)	0.67	0.40	-0.30	_
(Gaultheria shallon)	-0.82	0.17	-0.16	
(Blechnum spicant)	-0.79	-0.18	-0.39	
(Hylocomium splendens)	0.03	-0.80	-0.30	
(Kindbergia oregana)	-0.35	-0.08	0.83	
(Plagiothecium undulatum)	0.45	-0.60	0.16	_

	Aver				
Group	SØresnsen	Ranked SØresnsen	Euclidean	A value*	Test statistics (T)
СН	0.25	0.26	3.96		
HA	0.41	0.44	4.42		
Average				0.22	-15.9

Table 2-6: Multi-Response Permutation Procedures (MRPP) to test for overall differences in the structures of the plant communities in CH and HA forests.

*Chance-corrected within-group agreement

Table 2-7: Correlation coefficient between scores for soil variables and the first three axes of PCA. The first three axes explain 75% of the variation in the main matrix.

variable	Axis1	Axis 2	Axis3	
pHHU	0.3085	-0.1471	-0.5050	
EhHU	-0.1206	0.0851	-0.6071	
MCHU	0.4111	-0.1775	0.0965	
pHB	0.4426	-0.0350	-0.2939	
EhB	-0.4355	0.1544	0.1762	
Sand	0.1098	0.5283	0.0477	
Silt	-0.2613	-0.5436	-0.0274	
Clay	-0.2186	-0.5342	-0.0576	
OXD	-0.3447	0.1946	-0.3677	
OMTH	-0.2979	0.1289	-0.3289	

	Group 1	Group 2	Group 3
	(n=6)	(n=8)	(n=6)
Mineral soil average moisture content (% dry wt)	122	119	87
Mineral soil average redox (mV)	245	304	312
Mineral soil average pH	5.5	4.8	4.7
Sand %	70	45	78
Silt %	21	40	15
Clay %	9	15	7
Mineral soil bulk density (g/cm ³)	0.69	0.30	0.45
Oxic depth (cm)	30	41	48
Organic matter thickness (cm)	19	23	33
Mineral soil organic matter concentration %	24	16	15

Table 2-8: Characteristics of the three groups of CH sites identified by PCA analysis using the 10 soil variables that explained most of the variability in the dataset. Distinctive higher or lower values among the three groups are highlighted in bold.

				canonical variance accounted			
				for by axes 1–3			
Species group	Environmental variables group	P value*	Sum of all canonical eigen values	Ι	II	III	
	Moisture	0.05	0.15	8.5	13.9	16.9	
All species	Aeration (Eh and oxic depth)	0.06	0.06	11.3	20.9	25.1	
	Moisture and Aeration	0.07	0.08	11.7	21.8	27.0	
	10 soil variables	0.14	0.14	12.2	22.6	31.2	
	Moisture	0.01	0.09	12.5	15.8	16.1	
Main 6	Aeration (Eh and OXD)	0.003	0.15	18.6	23.1	25.2	
species	Moisture and Aeration	0.016	0.17	18.7	24.9	29.5	
	10 soil variables	0.02	0.19	19.3	27.6	33.0	

Table 2-9: Canonical correspondence analysis of soil variables in relation to plant species.

Cumulative percentage of

2.5 References

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Chapter 3: The effects of excessive moisture on soil C and N mineralization in coastal forests of British Columbia ¹

3.1 Introduction

Extensive parts of productive cedar-hemlock (CH) forests in northern Vancouver Island, Canada, exhibit slow growth and nutrient deficiencies (N and P) that are not observed on adjacent second-growth hemlock-amabilis fir (HA) forests. The symptoms appear 5-8 years following clearcutting on cutovers. Several potential causative factors have been investigated, including competition and alellopathic effects of the ericaceous shrub salal (Gaultheria shallon Pursh) and its associated ericoid mycorrhizae (Prescott and Sajedi 2008; Bennett et al 2003; Messier 1993; Weetman et al. 1989b), slow decay of cedar litter (Prescott et al. 2000; Weetman & Prescott 2000; Keenan et al. 1995), and lack of soil disturbance by windthrow in CH stands (Weetman & Prescott 2000; Keenan et al. 1994). However, none has provided sufficient evidence to explain the regeneration problems. Although CH and HA forest types were initially classified as the same ecosystem association having similar topography position and mineral soil characteristics (Lewis 1982, Germain 1985, Keenan 1993), several lines of evidence indicate that CH sites might be slightly wetter and less aerated than HA sites. Germain (1985) reported that CH sites tended to occur on more poorly-drained slope positions, and deMontigny (1992) found a greater frequency of gleyed horizons and hydromors, which develop under the influence of excessive moisture on poorly-drained soils in CH forests (Green et al. 1993). The tendency for CH sites to occupy slightly lower landscape positions than HA sites was documented through GIS analysis by Albani and Lavery (2000). Given the high precipitation levels in this coastal region (1900 mm/year), this small

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Title: The effects of excessive moisture on soil C and N mineralization in coastal forests of British Columbia

change in landscape position and poor drainage might be sufficient to create waterlogged anoxic conditions that could lead to the low nutrient supply associated with CH sites.

The primary mechanism through which excessive moisture affects nutrient cycling processes in the soil is the reduction in oxygen supply in soils in which nearly all of the soil pores are filled with water. In these environments, organisms must survive with low concentrations of oxygen and heterotrophic respiration may totally deplete oxygen. Under anaerobic conditions, aerobic microorganisms are replaced by facultative or obligate anaerobes, which seek alternate electron acceptors for their respiration or undertake fermentative processes. Lower rates of microbial respiration and lower microbial biomass are associated with waterlogged soils (Schimel et al 1999; Jaatinen et al. 2007, Chmielewski 1991). CO₂ production during twelve-day incubations of peat was lower under anoxic conditions than oxic conditions (Scanlon and Moore 2000), although CO₂ production rates were initially high. Changes in microbial populations and lower microbial biomass under low-oxygen or anaerobic conditions could result in slower decomposition of organic matter. For example, across a soil moisture gradient in Hawaii, litter decomposition rates and nutrient release slowed with increased rainfall as a result of both reduced soil oxygen availability and lower-quality litter in wet sites (Schuur 2001).

Nitrogen is thought to be highly sensitive to variations in soil moisture due to the influence of moisture on soil redox potential, a value that reflects the quantitative transfer of electrons from donors to acceptors and expresses the tendency of an environment to receive or supply electrons. Redox acts as a master switch for microbe-catalyzed processes of nitrification (oxic), denitrification (hypoxic), and dissimilatory nitrate reduction to ammonium (anoxic) (Yu and Ehrenfeld 2009). Nitrification and nitrifying bacteria are highly sensitive to redox potential (Bedard and Knowles 1989; Pett-Ridge et al 2006); under anoxic conditions, nitrification is reduced or eliminated (Pett-Ridge et al 2006). Devito et al (1999) measured large reductions in annual rates of net N mineralization and nitrification in forested peatlands compared to adjacent upland forests in

74

Ontario. Along a precipitation gradient from mesic to wet sites in Hawaiian forests, Holtgrieve et al. (2006) found the highest extractable NH_4 + but lowest NO_3 - and net N mineralization rates at the wettest site.

In many forest soils, soluble organic N (SON) or the potentially dissolved organic N (DON) constitutes the dominant form of N in the available N pool (Chang et al 1995; Devito et al. 1999; Hannam and Prescott 2003; Kranabetter et al. 2007). Kranabetter et al (2007) have suggested that the assessment of DON, especially in relation to NH_4^+ and NO_3^- , provides more insights into N cycles and the nature of N uptake by plants than other indices such as the inorganic N pool (SIN; NH_4 -N + NO_3 -N). The size of the SON pool and its significance to plant nutrition relative to the inorganic N pool (SIN) appears to be higher in less productive ecosystems with highly organic and acidic soils such as peatlands (Jones and Kielland 2002; Jones et al. 2005) where SIN is not abundant. SON abundance has been shown to be positively correlated with soil moisture (Hannam and Prescott, 2003), but little is known about the relative abundance and importance of SON in wet forest ecosystems.

In Chapter 2, I demonstrated that CH forest floors and soils were wetter and less aerated than those of HA sites. In this chapter I address the hypothesis that the low N supply on CH sites results from excessive moisture and associated anoxic conditions, by comparing rates of C and N mineralization between CH and HA humus and mineral soil along a realistic moisture gradient from field capacity to saturation. Rates were measured during a 20-day incubation in the laboratory under identical temperature conditions. The moisture gradient spanned the range of values measured in the field on CH and HA sites, with saturation being more prevalent on CH sites. I measured C mineralization (CO_2 evolution), microbial biomass C and N, soluble inorganic N (SIN) and soluble organic nitrogen (SON) at the end of the incubation. If excessive moisture at CH sites underlies the low N supply on these sites, I expected to observe the following:

- Microbial biomass and CO₂ evolution will decrease under saturated conditions in humus and soil from both site types.
- 2) NO₃ concentrations and the proportion of N in the form of SIN (*i.e.*, SIN:SON) will decrease under saturated conditions in humus and soil from both site types.

3.2 Materials and methods

3.2.1 Study area

The study sites are located on northern Vancouver Island, between Port Hardy and Port McNeill, British Columbia, in the very wet maritime Coastal Western Hemlock (CWHvm) biogeoclimatic zone (50° 60'N, 127° 35' W). The climate is characterized by cool, moist summers, and mild, wet winters. Mean annual precipitation is 1900 mm, 70% of which falls (mainly as rain) in the winter months (October to March). The summer months have less rainfall, but rainfall during the growing season prevents any soil moisture deficit in most years. Mean daily temperatures range from 3.3 °C in January to 14 °C in August. The area has gentle topography with an elevation no greater than 300 m a.s.l. Mineral soils are loamy Humo-Ferric Podzols that overlay unconsolidated morainal and fluvial outwash material (Prescott et al. 1993).

This study focused on two dominant forest types in the region, namely CH, or Cedar-Hemlock, and HA, or Hemlock-Amabalis fir. The CH stands are old-growth, dominated by western redcedar with western hemlock as the co-dominant species. These forests are uneven-aged and have a relatively open canopy. Salal dominates the understory with smaller amounts of *Vaccinium* spp., *Rubus spectabilis* Pursh, *Blechnum spicant* L., *Cornus canadiensis* L., and the mosses *Hylocomium splendens* (Hedw.) B.S.G., *Kindbergia oregano* (Sull.), and *Rhytidiadelphus loreus* (Hedw.)Warnst. (de Montigny, 1992). The HA stands are predominantly second-growth, even-aged forests originating from a windstorm in 1908. Western hemlock and amabilis fir dominate the dense canopy. The sparse understory generally consists of *Blechnum spicant*, *Vaccinium* spp., and the same mosses as at the CH sites (de Montigny, 1992).

3.2.2 Field sampling

Soil samples were collected in August 2006 from five replicate old-growth sites randomly selected based on forest cover and ecosystem classification maps provided by Western Forest Products Inc. (Port McNeill, BC, Canada). These five sites, each of which had adjacent CH and HA stands, were distributed over an area of approximately 100 km². At each stand (5 site x 2 stand type = 10), a circular plot of 25-m diameter was established at least 50 m from the transition between the two forest types or the edge.

A 500-g (wet weight) sample of each of two master horizons – the H horizon of the forest floor and the B horizon of the mineral soil – was collected from eight randomly selected points within each circular plot. Samples were collected from 10-20 cm from the top surface of each horizon. Samples were kept cool (approximately 4°C) during sampling and transported to the laboratory immediately after sampling for further analysis. All eight samples of a circular plot were then composited by site to reduce variability within sites and passed through a 5-mm sieve to remove all large pieces of wood and roots and coarse fragments. Moisture content of the sieved samples was determined by oven-drying 20 g of each sample at 70°C for 48 h.

3.2.3 Laboratory protocols

The moisture content of the H horizon samples were approximately at field capacity (as determined in Chapter 1) and slightly higher in CH samples than HA at the time of collection; whereas most of the mineral soil (B-horizon) samples were wetter than the field capacity in both forest types. Therefore, field capacity was used as the minimum moisture level that would occur in both forest types during the driest period of the years (summer). Field-capacity moisture contents (dry-weight basis) were on average 200% for H horizons and 60% for B horizons, respectively. To

remove water from mineral samples, 50 g of all mineral composited samples were saturated and held under 10 kPa pressure for one day to obtain field capacity (Klute, 1965).

Because these sites are known to be saturated for part of the year (Chapter 1), saturation was used as the maximum treatment in the simulated moisture gradient. To saturate the samples, a portion of each sample was put in plastic rings with Whatman No.42 filter paper on the bottom and put on porous plates covered with saturated sand. Plates were put in the refrigerator to impede evaporation from their surface. Capillary rise of water from the sand infiltrated the samples; saturation was considered to have occurred once the water was at the surface level of the sample. Saturation required between 2 and 7 days, depending on the carbon and clay content of the samples. Samples from the humus layer of the HA sites demonstrated water repellency and took longer to saturate than samples taken from CH sites. The moisture content of the saturated samples was then measured, and was on average 650% (dry-weight basis; Range: 506-713%) and 130% (dry-weight basis; Range: 107-172%) for H and B-horizon samples, respectively. To avoid the effects of the time required for samples to become saturated on microbial activity and C and N mineralization, a 100-g fresh portion of the sieved samples were taken to be used for the actual C and N mineralization studies and adjusted to its saturation moisture level by adding the previously determined quantity of water prior to the incubation.

Two additional moisture treatments between field capacity and saturation level were selected to form a moisture gradient: 350% and 500% for the H-horizon and 90% and 110% for the mineral soil (dry-weight basis). Two 100-g portions of each sieved sample were remoistened to these levels. Thus, the four treatments for humus were 200%, 350%, 500% and 650% and for mineral soil were 60%, 90%, 110% and 130%. Therefore, for each forest type-moisture treatment-soil horizon combination, there were five composited samples taken from site replicates for a total number of 80 samples (N=5).

An incubation system was developed to measure mineralization rate of C by estimating CO₂ efflux in incubated samples as well as relative rates of N mineralization (Prescott *et al.* 2000). After samples were adjusted for moisture treatments, 50 g of each sample was placed in glass canning jars (Kerr wide-mouth, 1 pint (0.6 L)). Jars were incubated in the dark at room temperature (about 20°C) for 20 days. To avoid side-effects of oxygen deficiency, the lids were removed twice a week for 20-30 min. Microbial biomass, concentrations of soluble organic N (SON), NO₃ and NH₄, pH and redox potential were measured after the incubation period.

Reduction-oxidation (redox, E_h) potential and pH were measured in 0.01 M CaCl₂ solutions (Sparks, 2000). The solutions were prepared in 1:1 (soil:solution) ratio and 1:3 (humus:solution) ratio. A digital waterproof oxidation-reduction potential tester (OAKTON ORPTestr BNC) was used to measure Eh values. The solution was stirred until the soil solution was well mixed and allowed to settle for 10 min with occasional swirling. After the last swirling, the electrode was inserted in the solution and allowed to stand for 5 min before reading. The readings were standardized relative to a hydrogen reference electrode at pH 7 (1244 mV at 17°C, -59 mV for each pH unit below pH 7) (Qualls et al. 2001; Bohn 1985). The pH was measured with a Pt electrode by a standard pH meter in the same solutions.

Total nitrogen and carbon concentrations were determined by total combustion using a LECO 1996 CNS analyzer (LECO Corp., Chicago, IL). Concentrations of extractable nitrate and ammonium were measured using colorimetric methods with K₂SO₄ extraction (Keeney & Nelson 1982). A 10-g subsample of each incubated sample was weighed and extracted in 100 ml of 0.5 mol/L K₂SO₄ and used to estimate concentrations of ammonium, nitrate and soluble organic N (SON) in each sample. The samples were then shaken for 1 h and gravity-filtered through Whatman No. 42 filter paper. Nitrate and ammonium concentrations were measured in a 10-mL aliquot of the filtrated solution with a Lachat QuickChem AE autoanalyser using the copperized cadmium reduction method. Soluble organic N (SON) concentrations were measured in the remaining

solution (Hannam and Prescott, 2003). Each extract was vacuum-filtered through a 0.45-µm Durapore PVDF membrane filter. Material passing through a filter of this pore size was considered dissolved (Hannam and Prescott, 2003). An adapted persulfate solution was used to convert dissolved N in the filtered extracts to nitrate (Cabrera and Beare 1993). Ten mL of the modified persulfate solution was added to 10 mL of each soil extract in 25 mL glass bottles. Equal volume of the persulfate solution to the soil solution has been shown to be sufficient for complete oxidation of dissolved N (Hannam and Prescott, 2003). After autoclaving at 121°C for 45 min, persulfate digests were analyzed for nitrate concentration using the same autoanalyser. SON was calculated by subtracting the SIN (sum of nitrate and ammonium) from total soluble N amounts in the extracts.

Microbial biomass N and C were measured using the chloroform fumigation-extraction technique (Parkinson & Paul, 1982, Voroney et al., 1993). A third 10-g subsample of each sieved incubated soil sample was fumigated under vacuum for 24 h. Fumigated samples were then extracted with 0.5 M K₂SO₄, gravity-filtered with Whatman No.42 filter paper, and then vacuumfiltered, oxidized and analyzed for nitrate as described above. Organic carbon was analyzed using the high-temperature combustion method, with the Shimadzu TOC-500 Carbon Analyzer. Microbial biomass C was estimated as the difference between fumigated and unfumigated samples and no correction factor was used. Microbial biomass N was calculated similarly.

Mineralization of carbon was measured by estimation of the total CO_2 evolved from incubated samples during 20 days (Prescott et al. 2000). A second incubation system under the same condition described above was developed to estimate rates of C mineralization. A 5-g and 10g dry weight subsample of each of the 80 organic and mineral soil samples that had been adjusted for moisture was transferred into canning jars (Kerr wide mouth, 1 pint (0.6 dm3)), with an air-tight septum on the lid, and incubated alongside the other 80 jars in the dark at room temperature (about 20°C). One mL of the headspace gas inside the jar was sampled with a syringe twice per week for a month. CO_2 concentration was measured with an infrared gas analyzer (Model LI-800, LI-COR

80

Inc., Lincoln, NE, USA) using nitrogen as a carrier gas. The jars were opened for 20 min immediately after each measurement. The concentrations of CO_2 were then converted to milligrams of CO_2 and C and summed for the six sampling occasions to estimate the total amount of C mineralized through microbial respiration during the incubation time.

3.2.4 Data analysis

The split-split-plot set of treatments replicated five times in a completely randomized design was analyzed with ANOVA (General Linear Model procedure) using SAS 9.1. Data from the organic and mineral horizons were analyzed separately. Forest type and laboratory-developed moisture levels were considered as the main and split-plot treatment effects, respectively. To compare mean values, α levels were adjusted for the number of comparisons using the Bonferroni test. Kolmogorov-Smirnov and Bartlett's Chi-square test were used to test whether the data were normally distributed and residuals were homogenous across treatment units, respectively. The values of C/N did not meet the normality assumption for ANOVA analysis, so they were transformed with log ⁻¹. The rest of the data met the normality assumptions.

3.3 Results

3.3.1 CH vs. HA

Inherent differences between CH and HA forest soils were evident in the field-moist samples. Relative to humus from HA forests, humus from CH forests had higher a pH, broader C:N ratio, lower concentrations of total N and NH₄-N and lower SIN:SON ratio (Table 3-1). Relative to mineral soil from HA forests, mineral soil from CH forests had higher concentrations of C and N (Table 3-2). Significant differences among the sites tended to be preserved in the moisture treatments.

3.3.2 Moisture effects

The expected decline in redox potential with saturation was apparent in the humus samples, but not in mineral soil. In humus, above 500% moisture content, Eh significantly decreased from average values of 196 and 197 mV in HA and CH humus, respectively, to 82 and 88 mV (Table 3-1). In mineral soil, Eh decreased above 90% soil moisture content, and then increased at saturation (Table 3-2). Eh was significantly negatively correlated with soil moisture content in humus (Fig 3-1), but not in mineral soil (R^2 =0.02; p=0.35). The correlation was curvilinear and a threshold of 500% was apparent, above which Eh declined sharply. pH was significantly higher under saturated conditions than at field condition in both CH and HA humus (Table 3-1), but pH of mineral soil did not change with increasing moisture (Table 3-2).

Microbial biomass C (MBC) declined with increasing moisture in humus and mineral soil (Table 3-1 and 3-2). The amount of carbon mineralized during the 20-day incubation, (measured as CO_2 efflux) increased with increasing moisture up to 500% and 110% levels in humus and mineral soil, respectively, but was lower at the highest moisture levels (Fig 3-2 and 3-3).

Almost all available inorganic N in the humus of both forest types was in the ammonium form (Table 3-1). Ammonium concentrations significantly increased with increasing moisture in HA humus; but did not change with increasing moisture in CH sites (Fig 3-4). As a result, the differences between the two sites increased with increasing moisture (Fig 3-4). In mineral soil, ammonium concentrations were low with the only significant difference being the decline above 350% in HA soil (p=0.005; Table 3-2).

In both CH and HA humus, nitrate concentrations declined with increasing moisture up to 500%, above which they increased. The increase in nitrate concentration between 500% and saturation (650%) was significant in CH humus (p=0.001), but not in HA humus (p=0.18; Table 3-1). Nitrate was more prevalent in the mineral soil but the apparent increase with increasing moisture was not significant (Table 3-2).

The amount of inorganic nitrogen mineralized after 20 days of incubation did not change with increasing moisture in HA humus and soil, from which substantial amounts of inorganic N $(NH_4^++NO_3^-)$ were produced (Table 3-1 and 3-2). The effect of increased moisture on N mineralization in CH humus and soil was highly variable, with both increases and decreases being evident.

Soluble organic N concentrations in humus from both forest types increased with increasing moisture, although the differences were significant only in HA humus (Table 3-1; Fig 3-5). In mineral soil, SON concentrations decreased with increasing moisture in both forest types but the differences were significant only in CH soil (Table 3-2, Fig 3-6). SON was generally lower in humus from CH sites than from HA sites; the difference between the two forest types was small at field moisture but increased with increasing moisture and became significant at 500% (p=0.0075) and saturation (p=0.0097). In mineral soil, there was no difference in SON concentrations between CH and HA forests at any moisture level.

Microbial biomass N (MBN) comprised 2.5% and 4.6% of the total N pool in humus from HA and CH sites, respectively. The response of MBN to increased moisture differed among the forest types. In CH humus, MBN declined with increasing moisture (Table 3-1 & 3-2) and was significantly lower MBN in the 500% (p=0.0078) and 650% (p=0.003) treatments compared with field-moisture. MBN did not change with increasing moisture in HA humus. In mineral soils, MBN declined with increasing moisture and was significantly lower under saturation condition than under field condition in CH soil (p=0.0004; Table 3-2), but not in HA soil.

The exchangeable N pool in humus was dominated by NH_4 in HA humus and by SON in CH humus (Fig. 3-7). Under saturated conditions the SON pool increased in proportion in both humus types. In mineral soil at field moisture, SON was the dominant N form in all forest types and moisture treatments (Fig 3-8) and most of the remainder was in the NH_4 form. Under saturated conditions the proportion in the inorganic N pool increased slightly and was mostly in the form of

 NO_3 . The SIN/SON ratio in HA humus decreased significantly with increasing moisture; a similar trend was apparent in CH humus, although the differences were not significant (Table 3-1). The SIN:SON in mineral soil was very small in all treatments (Table 3-2).

3.3.3 Correlations among variables

Carbon mineralization from humus was significantly correlated with soil moisture, increasing up to 350-500% moisture, above which rates declined (Fig 3-9). The correlation was strongest in HA humus. Microbial biomass C in both humus (Fig 3-10a) and mineral soil (Fig 3-10b) were weakly negatively correlated with moisture, declining with increasing moisture up to saturation. Concentrations of SON in humus were positively correlated with moisture (Fig 3-11a) and negatively correlated with Eh (Fig 3-11b) but no correlation was found between SIN and either moisture (R^2 =0.0002; p=0.93) or Eh (R^2 =0.0003; p=0.94). In the mineral soil, moisture was not correlated with any of the measured N forms.

Ammonium was strongly positively correlated with total N concentration in the humus (Fig 3-12a), but neither SON (Fig 3-12b) nor nitrate (R^2 =0.02; p=0.37) were significantly related to total N concentration. Nitrate was positively correlated with pH (R^2 =0.35; p=0.0001), as was C mineralization in humus (Fig 3-13).

3.4 Discussion

The saturation treatment was successful in creating anaerobic conditions in the laboratory study. Redox potential stayed relatively constant with increasing moisture up to 500% moisture in humus (and 90% in mineral soil), above which it decreased sharply. This suggests that anaerobic conditions, as measured by a decrease in Eh, and associated microbial processes occurred above this threshold. pH increased by about 0.5 unit under saturation conditions; changes of similar magnitude have been reported in field studies (Laiho and Laine 1990; Chapter 1).

Consistent with expectations, both CO_2 efflux and microbial biomass C declined under saturated conditions, after reaching maxima at intermediate moisture levels. This is consistent with other reports of lower microbial biomass and respiration under waterlogged conditions in soil and peat (Chmielewski 1991; Schimel et al 1999; Scanlon and Moore 2000; Jaatinen et al. 2007). Reductions in microbial biomass and respiration could be expected to lead to reductions in the rate or completeness of organic matter decomposition and thus accumulation of organic matter, as occurs on CH sites.

My findings with respect to N pools do not support my hypothesis that saturated conditions lead to reductions in supply of available N. Total pools of exchangeable N (SIN+SON) were larger in saturated than in field-moist humus and soil. Concentrations of SIN were not related to moisture content; ammonium concentrations were most closely related to total N concentration, and nitrate concentrations were correlated with pH. This indicates that N mineralization is more closely related to the C:N ratio of the material than the rate of C mineralization. Bridgham et al. (1998) also found that C mineralization rates were more affected by anaerobic conditions than were N mineralization rates in soils from cedar-swamp sites incubated under both aerobic and anaerobic conditions.

SON was the most responsive N form to the changes in moisture and redox - SON concentrations increased with increasing moisture and decreasing redox potential. The accumulation of SON under saturated conditions could be the result of a reduction in mineralization rate under high levels of moisture. However, concentrations of SIN (especially ammonium) also increased with increasing moisture in HA soils, suggesting that excessive moisture did not inhibit N mineralization in HA forests. Nitrogen mineralization is generally not affected by low oxygen availability, because it does not involve either oxidation or reduction processes (Pett-Ridge et al. 2006). The accumulation of ammonium in HA soils at high moisture could also result from reduced microbial assimilation of ammonium in the saturated soils, in which microbial biomass and

85

respiration were reduced. Reduced microbial growth efficiency has been reported under anaerobic conditions (Chappin et al, 2002, Silivia et al 2005), which would result in microbes incorporating less C and N into their biomass.

In contrast, in CH humus and soil, the SIN pool was small and decreased with increasing moisture. This may indicate that equilibrium is already established between N mineralization and assimilation under saturated conditions in CH sites. The reduction in SIN above 350% moisture (compared with field moisture) in CH humus could not have been caused by immobilization of N into microbial biomass, as microbial biomass N significantly declined with increasing moisture in both humus and mineral soil from CH sites. The reduction in SIN in CH humus and soil at high moisture levels may have resulted from immobilization of ammonium N as a consequence of the nature of the organic matter on CH sites. Schimidt-Rohr et al. (2004) showed that N mineralization can be reduced under anaerobic conditions if organic N is associated with phenolic compounds which require oxidative decomposition. Cedar litter has higher levels of phenolic compounds such as lignin than most tree species in this region (Prescott et al. 2004), and the dense understory of salal in CH forests has been shown to have high concentrations of phenolic compounds such as tannins (Preston 1999). Excessive moisture and resulting low oxygen conditions would further constrain decomposition and N release from this organic matter, leading to the very low rates of N mineralization from CH humus and soil at the highest moisture level. Interestingly, Bridgham et al (1998) found the lowest rates of N mineralization in cedar-swamp ecosystems, compared with bog, fen and meadow ecosystems.

The decrease in nitrate concentrations with increasing moisture (up to 500%) is consistent with findings of decreased nitrate with increasing precipitation in montane Hawaiian forests (Holtgrieve et al. 2006). The increase in nitrate concentrations at the highest moisture level (650%) was not expected, and may be related to the 0.5-unit increase in pH of these samples.

86

The results of the laboratory incubation were largely consistent with my hypotheses that microbial biomass, C mineralization and the SIN:SON ratio would all decline under water-saturated conditions. The concentration and proportion of SON increased at the highest moisture levels, but concentrations of SIN were not related to moisture content. Ammonium concentrations were most closely related to total N concentration, and nitrate concentrations were correlated with pH. The expected decline in SIN at saturation occurred in CH samples but not in the HA samples, indicating that the low N availability on CH sites results from synergistic effects of higher phenolic contents of the organic matter and greater frequency of waterlogging of soils on CH sites.



Figure 3-1: Correlation between redox potential (mV) and moisture content (dry-weight basis) of humus from CH and HA forests.



Figure 3-2: Mineralized carbon (mg C/ g soil C), measured as CO_2 efflux, during a 20-day laboratory incubation of humus from HA and CH forest at four moisture levels.



Figure 3-3: Mineralized carbon (mg C/ g soil C), measured as CO_2 efflux, during a 20-day laboratory incubation of mineral soil from HA and CH forests at four moisture levels.



Figure 3-4: Ammonium concentrations after a 20-day laboratory incubation of humus from HA and CH forests. Error bars are SEs (n=5).



Figure 3-5: Soluble organic nitrogen concentrations after a 20-day laboratory incubation of humus from HA and CH forests at four moisture levels.



Figure 3-6: Soluble organic nitrogen concentrations after a 20-day laboratory incubation of mineral soil from HA and CH forests at four moisture levels.



Figure 3-7: Amount of various N forms in the exchangeable labile N pool in humus from HA and CH forests after a 20-day laboratory incubation under field-moist (200%) and saturated (650%) conditions.

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Figure 3-8: Amount of various N forms in the exchangeable labile N pool in mineral soil from HA and CH forests after a 20-day laboratory incubation under field-moist (200%) and saturated (650%) conditions.



Figure 3-9: Correlations between moisture content (% dry-weight based) and total C mineralized, measured as CO_2 efflux, from humus from HA and CH forests during a 20-day laboratory incubation (overall R^2 = 0.225 and overall p=0.0104).



Figure 3-10: Correlations between moisture content (% dry-weight based) and microbial biomass in a) humus, and b) mineral soil from CH and HA forests after 20-day laboratory incubation.



Figure 3-11: Correlations between soluble organic N (μ g/g soil) and (a) moisture content (% dry-weight based), and (b) redox potential in humus from CH and HA forests after a 20-day laboratory incubation.



Figure 3-12: Correlations between concentrations of total N (%) and (a)ammonium (μ g/g soil), and (b) soluble organic N (μ g/g soil) in humus from CH and HA forests after a 20-day laboratory incubation.



Figure 3-13: Correlation between pH and total C mineralized (mg C/ g soil C) during a 20-day laboratory incubation of humus from CH and HA forests.
	200%		350%		500%		650%	
	HA	СН	HA	CH	HA	СН	НА	СН
Eh (mv)	196(8) ^a	197(4) ^a	195(8) ^a	184(13) ^a	180(8) ^a	$178(11)^{a}$	82(23) ^{b**}	88(9) ^{b**}
pН	3.46(0.14) ^{a**}	3.65 (0.17) ^{a**}	3.17(0.15) ^b	3.40 (0.17) ^b	3.45(0.21) ^a	3.35(0.17) ^b	3.85(0.15) ^{c**}	4.07 (0.21) ^{c**}
Total N (%)	1.18 (0.06) ^{**}	1.08(0.03)	1.25 (0.05) ^{**}	1.06(0.03)	1.25 (0.04) ^{**}	1.06(0.03)	1.23 (0.05) ^{**}	1.04(0.03)
Total C (%)	46.9(0.6)	47.3(0.9)	47.6(0.7)	47.4(1.0)	47.2(0.7)	48.4(0.9)	47.9(0.7)	48.1(0.8)
C/N	40(1.9)	44(1.6)	38(1.6)	45(1.4)	38(1.6)	45(1.2)	39(1.8)	46(1.2)
C mineralization	$0.64(0.07)^{a^{**}}$	0.65(0.15)	1 11(0 08) ^{b**}	0.01(0.26)	$1.23(0.21)^{b}$	0.04(0.16)	$1.13(0.12)^{b}$	0.79(0.10)
(mg C/g C)	0.04(0.07)	0.03(0.13)	1.11(0.08)	0.91(0.20)	1.23(0.21)	0.94(0.10)	1.15(0.12)	0.79(0.19)
Microbial biomass C	$1.65(0.2)^{ab}$	1.86(0.2)	2.02(0.3) ^{a**}	1.59(0.3)	0.66(0.3) ^b	1.11(0.4)	1.78(0.3) ^{ab}	1.20(0.4)
(mg C/g soil)	1.05(0.2)	1.80(0.2)						
NO_3^+ -N (µg /g soil)	1.37(0.8)	$1.64(0.4)^{abc}$	0.45(0.1)	$0.17(0.1)^{ab}$	0.19(0.1)	$0.43(0.1)^{b}$	0.96(0.2)	2.40(0.6) ^{c**}
NH4 ⁻ -N (µg /g soil)	153.1 (33) ^{**}	46.1(20)	241.7 (49) ^{**}	52.1(8)	204.0 (38) ^{**}	9.6(5)	256.8 (44) ^{**}	39.5(20)
SON ($\mu g / g$ soil)	52.7(5.5) ^{a**}	70.2(4.1)	94.6(7.8) ^b	72.7(6.9)	95.2 (12.6) ^{bc}	65.2(4.7)*	$122.4(6.5)^{abc}$	93.6(7.2)*
SIN/SON	3.00 (0.62) ^{**}	0.84(0.37)	2.47 (0.45) ^{**}	0.77(0.17)	2.39 (0.59) ^{**}	0.14 (0.06)	2.06 (0.23) ^{**}	0.40(0.18)
Microbial biomass N	0.20(0.07)	$0.46(0.04)^{a}$	0.15(0.00)	0.27(0.06)	0.15(0.05)	$0.22(0.02)^{b*}$	0.25(0.06)	0.10(0.06) ^{c**}
(mg N/g soil)	0.29(0.07)	0.40(0.04)	0.13(0.09)	0.27(0.00)	0.13(0.03)	0.23(0.02)	0.23(0.00)	0.19(0.00)

Table 3-1: Concentrations of several N forms, mineralized C (measured as CO₂ efflux), microbial biomass C and N and some other selected properties after 20-days of incubation in CH and HA forest floor at four different moisture levels.

Note: Each value is the least squares mean of five replicates with standard errors in brackets. Different letters indicate significant differences within one forest type among moisture treatments. Numbers in bold indicate significantly higher values in comparison between CH and HA forest types within each moisture treatment. ** indicates significant differences at p<0.05 level, * indicates significant differences at p<0.1 level.

	60%		90)%	110%		130%	
	HA	СН	HA	СН	HA	СН	HA	СН
Eh (mv)	223(9) ^a	233(2) ^a	244(4) ^{ac}	255(6) ^a	186(17) ^{b**}	195(7) ^{b**}	257(6) ^{c**}	256(9) ^a
рН	4.5(0.07)	$4.4(0.12)^{ab}$	4.5(0.04)	$4.3(0.09)^{ab}$	4.6(0.03)	4.5(0.13) ^a	4.5(0.05)	$4.3(0.09)^{b^*}$
Total N (%)	0.21(0.02)	0.25 (0.02) ^{**}	0.21(0.02)	0.25 (0.01) ^{**}	0.23(0.03)	0.23(0.02)	0.21(0.02)	0.23(0.01)
Total C (%)	6.6(0.8)	7.4 (0.6) [*]	6.7(0.8)	7.4 (0.6) [*]	6.9(1.0)	7.2(0.7)	6.7(0.9)	7.2(0.6)
C/N	31((0.9)	$30(2.1)^{a}$	31(1.1)	$30(2.0)^{a}$	29(1.6)	31(2.1) ^{ab}	31(0.6)	32(2.2) ^{b**}
C mineralization	$0.27(0.04)^{ab}$	$0.27(0.06)^{a^{**}}$	0.22(0.05)a**	0.34(0.05) ^{ab}	0.43(0.08) ^b	0.40(0.00) ^b	0.38(0.00) ^{ab}	0 40(0 08) ^{ab}
(mg C/g C)	0.27(0.04)	0.27(0.00)	0.22(0.03)	0.34(0.03)	0.43(0.08)	0.49(0.09)	0.38(0.09)	0.40(0.00)
Microbial biomass C	0.4(0.1)	0.5(0.2)	0.3(0.1)	0.2(0.1)	0.3(0.1)	0.1(0.1)	0.2(0.1)	0.1(0.03)
(mg C/g soil)	0.4(0.1)	0.5(0.2)						
NO_3^+ -N (µg /g soil)	1.61(0.72)	0.06(0.02)	0.35(0.27)	0.09(0.03)	1.60(0.66)	3.09(1.46)	2.91(1.36)	2.60(0.89)
NH_4^N (µg /g soil)	$0.72(0.6)^{ab}$	0.00(0.0)	$2.69(1.2)^{a^*}$	1.69(0.8)	$0.00(0.0)^{b}$	0.43(0.4)	$0.00(0.0)^{b}$	0.55(0.5)
SON (µg /g soil)	38(4.7)	28(3.7) ^{ab}	39(4.6)	36(4.1) ^{a**}	32(6.1)	$18(1.9)^{b}$	34(3.4)	25(2.0) ^{ab}
SIN/SON	0.15(0.62)	0.00(0.37)	0.08(0.45)	0.05(0.17)	0.06(0.59)	0.21(0.06)	0.07(0.23)	0.13(0.18)
Microbial biomass N	46 3(11 0)	52 4(11 1) ^{a**}	14 1(6 0)	22 2(5 c) ^{ab}	21.2(10.7)	26 8(5 2) ^{ab}	10.1(7.6)	$155(53)^{b}$
(µg C/g soil)	40.3(11.0)	55.4(11.1)	14.1(0.9)	22.2(3.0)	21.2(10.7)	20.0(3.3)	17.1(7.0)	15.5(5.5)

Table 3-2: Concentrations of several N forms, mineralized C (measured as CO2 efflux), microbial biomass C and N and some other selected properties after 20-days of incubation in CH and HA mineral soil at four different moisture levels.

Note: Each value is the least squares mean of five replicates with standard errors in brackets. Different letters indicate significant differences within one forest type among moisture treatments. Numbers in bold indicate significantly higher values in comparison between CH and HA forest types within each moisture treatment. ** Indicates significant differences at p<0.05 level, * indicates significant differences at p<0.1 level.

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Chapter 4: Drainage effects on site productivity and soil carbon stores in a cedar-swamp ecosystem in coastal British Columbia ¹

4.1 Introduction

Globally, about 14 million hectares of wetlands have been drained for forest establishment, mainly in Nordic countries and Russia (Paivanen and Paavilainen 1995; Paivanen 1997). Drainage as a forest management tool is very recent in Canada, where the drainage-related studies have focused on the hydrological aspects of drainage in forested peatlands and the impacts on regeneration and stand growth in the black spruce forests of eastern Canada (e.g. Lieffers and MacDonald 1990; Sundstrom and Jeglum 1992; Hillman 1992; Rothwell et al. 1996; Prevost et al. 1997, Roy et al. 1999).

Compared to upland forests, wetland forests and swamps² generally have poor tree growth due to inadequate oxygen in the rooting zone caused by persistently high water table levels (Dahl and Zoltai 1997; Westman and Laiho 2003). The problem is intensified when wetland forests are harvested, which may lead to a rise in water table due to reductions in canopy interception and transpiration (Dube et al. 1995; Roy et al. 2000a). The raising of the water-table level further negatively affects tree growth (Paavilainen and Paivanen 1995; Paré and Bergeron 1995; Harper et al. 2002; 2003). This commonly results in peat accumulation or paludification, a process by which the production of organic matter exceeds the decay rate (Paavilainen and Paivanen 1995; Charman 2002). In a review of paludification and management of forested peatlands in Canada, Lavoie et al.

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 $^{^{2}}$ A swamp, by the North American definition, is a wetland dominated by trees or tall shrubs, on either mineral or organic soils, which is influenced by minerotrophic groundwater.

(2005) concluded that waterlogged conditions (Joosten and Clarke 2002) favour colonization of the forest floor by mosses and Sphagnum, which further reduces soil aeration and nutrient turnover (Taylor et al. 1987; Payette 2001). The reduction in mineralization rate of soil organic matter under waterlogged conditions is suggested to be a result of the chemical composition of Sphagnum litter, which contains secondary polyphenolic metabolites such as sphagnol (Verhoeven et al. 1990; Johnson and Damman 1991) that are known to restrict organic matter decomposition. Increased organic matter thickness through paludification is not itself the causal factor of limited tree growth under waterlogged conditions; but a thicker organic layer can affect soil aeration, which in turn affects nutrient cycling and primary production (Lavoie et al. 2005).

Improving drainage through the use of trenches can be an effective method to enhance timber growth by removing excess water from the rooting zone in paludified areas and poorly drained sites (Paavilainen and Paivanen 1995). Drainage can be used to increase oxygen availability in soils by lowering the water table (Hillman 1992; Silins and Rothwell 1999) and increasing soil macroporosity (Silins and Rothwell 1999; Roy et al. 2000*b*). Increased aeration of soil has been shown to increase root metabolism and growth (Laiho and Finer 1996), increase forest production and biomass accumulation (Dang and Leiffers 1989; Laiho and Laine 1997; Macdonald and Yin 1999; Roy et al. 2000a), and may lead to changes in vegetation composition and structure. Water-table draw-down has been shown to initiate forest succession, from an original sphagnum and graminoid-dominated site, towards an arboreal vegetation type within two decades (Laine et al. 1995*a*, 1995*b*; Minkkinen et al. 1999; Laiho and Vasander 2003). The magnitude of the drainage effects on composition of plant species has been related to the nutrient status of the site with more impact on minerotrophic sites compared with ombrotrophic ones (Laine et al. 1995*b*; Korpela 1999; Minkkinen et al. 1999).

Drainage in wetland forests also has implications for the sequestration and long-term storage of organic carbon, but the net effect of drainage on total ecosystem carbon balance remains uncertain. Higher CO₂ emissions have been measured following drainage (Glenn et al. 1993; Silvola et al. 1996; Byrne and Farrell 2005; Blodau et al. 2004) and attributed to enhanced populations of aerobic decomposers (Chmielewski 1991, Jaatinen et al. 2007) and increased soil heterotrophic respiration (Minkkinen and Laine, 1998) due to increased oxidation after draining. Drainage may also lead to increases in productivity and thus enhanced C sequestration in vegetation, root and microbial biomass (Byrne and Farrell 2005); it has been suggested that the increases in aboveground and belowground C production in wetland forests may offset and even surpass C losses associated with increases in peat decomposition following drainage (Martikainen et al. 1995; Hargreaves et al. 2003; Byrne and Farrell 2005). Therefore, C fluxes to the atmosphere due to drainage could be substantially different in ecosystems such as fens and wetlands (where trees are growing) than in peatlands and bogs. Laiho (2006) showed that a peatland site could become a C source for the atmosphere, remain a C sink or become a stronger C sink after drainage, depending on the nutrient level, vegetation type and climatic conditions (Martikainen et al. 1995; Laiho 2006).

Extensive portions of the productive forest land-base in coastal British Columbia exhibit below-average timber productivity, which is believed to result from excess soil water as a consequence of poor drainage, coupled with high levels of precipitation or overland flow (van Niejenhuis and Barker 2002). There have been no long-term studies to evaluate the use of drainage as a potential treatment to enhance forest productivity in such sites. In this study, we investigated tree growth, understory vegetation, and soil C stores and C mineralization in drained and undrained areas in a cedar-swamp forest that had been operationally drained 10 years earlier. Rates of soil CO₂ efflux were measured during laboratory incubation. Based on conclusions from other drainage

trials, we hypothesize that drainage will alter the composition of understory plant species from communities dominated by mosses and ferns to those dominated by vascular plants, and will increase tree growth, CO_2 flux, microbial biomass and carbon stores in the soil.

4.1.1 Study site

The study site was located on the Suquash flats on northern Vancouver Island, Canada (50° 38'N, 127° 15'E). The Suquash is a coal-bearing sub-basin within the Georgia basin with Sediments of sandstone, some shale, and minor amounts of conglomerate and coal (Kenyon 1991). Erosion of the soft Cretaceous sedimentary beds has produced the low-lying topography within the Suquash Basin. Ponded water in depressions covers more than 30 percent of the area throughout much of the year (van Niejenhuis et al. 2002). The site is classified as a CWHvm1, the Submontane Very Wet Maritime Coastal Western Hemlock Zone (Green and Klinka 1994) with a mean annual precipitation of 1870 mm and mean annual temperature of 8.1°C. The original vegetation before harvesting was dominated by shore pine (*Pinus contorta* Dougl. ex Loud. var. *contorta*) and western redcedar (*Thuja plicata* Donn.) with sphagnum (*Sphagnum* spp) and skunk cabbage (*Lysichiton americanum* Hultén & H. St. John) in the understory. The soils in the Suquash Basin included depressions of poorly-drained mucky organics over marine silty clays, combined with raised hummocks of freely drained organic matter with significant portions of rotting wood (Lewis 1982). An undulating hardpan restricts the drainage of this site (van Niejenhuis et al. 2002).

A 22-ha cutover that had characteristics of productive forests, but was influenced by excess soil moisture throughout much of the year, was chosen as the study site. Following harvesting and slash burning in 1993-1994, the cutover was planted in 1995 to western redcedar. The entire cutover was operationally fertilized in 2006 with nitrogen and phosphorus (225N, 75P Kg/ha) for timber growth improvements.

In 1997, four replicate drainage areas (Fig. 4-1) with a total area of approximately 9.8 ha were established within the cutover by digging open channels (ditches) 150 m in length and at 30-m intervals using a V-notch bucket. To minimize erosion, ditch lines were mapped perpendicular to the topographical slight slope to maximize interception of seepage and minimize the ditch bottom slope. Five parallel ditches comprised a drainage area. Three treatments were compared in a randomized block design as follows. Three 0.09-ha plots representing three drainage treatment levels were randomly established at each replicate drainage area: an undrained control plot, a partly drained plot placed along a border ditch, and a highly drained plot placed between two central drainage ditches. The centre of any control plot was at least 45 m from any existing ditch line. The partly-drained plots were established 20 m away from control and highly drained plots, a distance well beyond the extent of the root growth of the seedlings. An initial hydrology study (van Niejenhuis et al. 2002) showed that the effects of ditching on subsurface drainage did not extend beyond15 m.

4.1.2 Soil sampling and vegetation analysis

In August 2007, height and diameter (dbh) of the 20 largest trees were measured within each 0.09-ha treatment plots as an indicator of site productivity. At the centre of each tree plot, understory vegetation was recorded in one 2 x 2 m subplot. The percent cover of each species, including mosses, ferns, and vascular was recorded for each of the 12 treatment plots. Seedling measurements and vegetation surveys were made before trenching and 2, 4 and 10 years afterward (van Niejenhuis et al. 2002).

In August 2007, at four randomly selected locations within each treatment plot, soil samples (approx. 500 g) were collected using a trowel from the top 20 cm of the humus layer (H horizon). A second sample was collected from the 30-50 cm depth if the H horizon was more than 30 cm thick.

Soil samples were placed in plastic bags, kept cool at 4 °C in a chilly bin during field work, and then transported to the laboratory and stored at 4 °C until analysis. The four samples collected in each plot were composited and passed through a 5-mm sieve to remove all large pieces of wood and roots before incubation. Moisture content was determined by oven-drying at 70°C for 48 h. Total C and N were measured by combustion (LECO 2000).

Five additional soil samples were collected in the field from the top 20 cm of the humus layer at each sampling location to determine bulk density. A wooden frame was used to excavate a 0.10 x 0.10-m square sample. The exact dimensions and depth of each sample was re-measured and each sample was placed in a separate plastic bag, transported to the laboratory and weighed after removing large woody debris. A subsample was used to measure moisture content, and bulk density was calculated by dividing the equal dry mass of the sample by its volume.

4.1.3 Soil biogeochemical analysis

4.1.3.1 Redox and pH

Reduction-oxidation (redox, Eh) potential and pH were measured both in the laboratory and in the field. In the laboratory, redox potential and pH of the sieved fresh samples were measured in 1:3 (soil:0.01 M CaCl₂) solution (Sparks, 2000). A digital waterproof oxidation-reduction potential tester (OAKTON ORPTestr BNC) was used to measure Eh values. The soil solution was stirred until it was well mixed and then it was allowed to settle for 10 min with occasional swirling. After the last swirling, the electrode was inserted in the solution and allowed to stand for 5 min before reading. The readings were corrected for pH 7 by adding -59 mV per pH unit (Qualls et al. 2001; Bohn et al 1985).

Additionally, in October 2007, the Eh and pH of soil samples were measured in the field. The soil samples were taken from the same depth as previously, at three randomly selected points in the

drainage treatment plots. Large particles were removed from the collected samples and solutions were prepared with distilled water, using the ratios, equipment and procedure described above.

4.1.3.2 Soil carbon storage

Carbon density was calculated as the product of C concentration (%C) and bulk density. Soil C storage was then estimated as the product of C density and organic layer thickness, assuming that C density did not vary with depth.

4.1.3.3 Microbial biomass and soluble organic carbon (SOC)

Microbial biomass was measured using the chloroform fumigation-extraction technique (Parkinson and Paul, 1982, Voroney et al., 1993) on fresh soil samples from the field. Samples (10 g) were fumigated under vacuum for 24 h, extracted with 0.5 M K₂SO₄, gravity-filtered through Whatman No.42 filter paper, and then vacuum-filtered through a 0.45-µm Durapore PVDF membrane filter. Material that passed through a filter was considered to be dissolved (Hannam and Prescott, 2003). The filtrate was analyzed for organic carbon using the high-temperature combustion method, with a Shimadzu TOC-500 Carbon Analyzer. Microbial biomass C was estimated as the difference between fumigated and unfumigated samples, and no correction factor was used. Measurements from unfumigated samples are reported as SOC.

4.1.4 Incubation study

An incubation system was developed to measure mineralization rate of C by estimation of CO_2 efflux in incubated samples (Prescott *et al.* 2000). Sub-samples (50g) of the sieved composited soil samples from each treatment plot were aerobically incubated in glass canning jars (Kerr wide mouth, 1 pint (0.6 L)) in the dark at room temperature (about 20°C) for a month.

4.1.4.1 Carbon mineralization

A 5-g and 10-g dry weight equivalent portion of the organic soil samples, respectively, were transferred into glass jars (0.6 dm³), with an air-tight septum on the lid. Samples were incubated in the dark at room temperature (about 20°C) for 27 days. One mL of the headspace gas inside the jar was sampled with a syringe twice per week for four weeks. CO_2 concentration of each sample was measured with an infrared gas analyzer (Model LI-800, LI-COR Inc., Lincoln, NE, USA) using nitrogen as a reference gas. The jars were opened for 20-30 min immediately after each measurement. The concentrations of CO_2 were then converted to mg of CO_2 and C and summed for the eight sampling occasions to estimate the total amount of C mineralized through microbial respiration during the incubation period.

4.1.5 Statistical analysis

One-way ANOVA was used to test for treatment effects on the response variables, where site and drainage were the block and main treatment factors, respectively, in the randomized block design (n=4). To compare mean values, α levels were adjusted for the number of the comparisons using the Bonferroni test. Kolmogorov-Smirnov and Bartlett's Chi-square test were used to examine the normality of the distribution of the data and the homogeneity of the residuals, respectively. The preliminary results showed that the partly-drained treatment was not significantly different with either control or highly-drained treatments. Thus, mean values of the measured variables are given only for control (C) and highly-drained (D) treatments; although all the three treatments were used in the ANOVA as well as correlation analysis.

Principal component analysis (PCA) was used as an ordination method to examine the variation of the ground vegetation species in response to drainage. The use of the technique and its qualifications are explained in detail by McCune and Grace (2002) and Manly (2000). To reduce

the variation in the analysis, which would be caused if all plant species recorded were included, only the sum of the fern, moss, grass, rush, and *Vaccinium* species were used.

4.2 Results

Drainage decreased the moisture content of the forest floor by 100% overall (p = 0.04, adjusted $\alpha = 0.033$; Table 4-1). Redox potential (Eh-CaCl₂) was 64 mV higher in the top humus layer of the drained plots than the control plots (p=0.04; Table 4-1). pH (H₂O) was significantly lower in drained sites (P = 0.03; Table 4-1).

Drainage significantly improved growth of regenerating trees. Average tree height and diameter were 22% (p = 0.003) and 29% (p = 0.02) higher in drained sites, respectively (Table 4-1). The average height of the 20 dominant trees varied from 4.1-5.9 m (Table 4-1). Results from PCA analysis indicated that ground vegetation composition differed between the drained treatments and the control (Fig. 4-2). The first three axes explained 72% of the variation (Table 4-3). The majority of the variance accounted for was in the first axis, which indicates the high heterogeneity among control plots. The species correlated to the first axis were more abundant in control plots (skunk cabbage (*Lysichiton americanum*) and sum of grass, rushes and moss species) and those species correlated to the second axis were more abundant in drained plots (Salal (*Gaultheria shallon*), salmonberry (*Rubus spectabilis*) and ferns (Table 4-4).

Drained plots had a slightly higher carbon concentration than undrained, control plots, but the differences were not significant (p = 0.90; Table 4-1). Bulk density of the top humus layer did not differ between the control and drained plots overall (P = 0.86). There was a tendency for drained plots to have greater C density than in the control (mean of 59 kg/m3 vs 53 in control plots), but the difference was not significant (p = 0.36). The variation among sites was high. In site 1 and 2, C density was 15 and 19 kg/m³ higher in drained plots than control plots. At site 3 and 4 this amount

was 2 and 9 kg/m³, respectively. Total organic layer thickness was on average 19 ± 19 cm (mean \pm SD; range from 4-45 cm; p = 0.19) higher in drained sites than the control and this was consistent across all replicates (Table 4-1). The total C storage in the humus layer was 131 t/ha higher in drained than the control treatment. Drained plots had higher average C:N ratio than the control (Table 4-1) plots, but the differences were not significant at the treatment level (p = 0.15).

Rate of C mineralization in forest floors over the one-month incubation varied from 0.02 to $0.20 \text{ mg g}^{-1} \text{ d}^{-1}$ among all plots. CO₂ flux was on average 47% higher in the control than in the drained plots (p=0.07, Table 4-2). Average daily CO₂ flux over the incubation time was significantly higher in control than drained plots in each site. At site 2, the control plot had unusually high CO₂ fluxes through the entire incubation period than all other plots. Daily CO₂ emission differed significantly between control and drained plots during the first two weeks of incubation but converged during the last two weeks (Fig. 4-3).

Microbial biomass values varied between 2.7-9.4 mg g⁻¹ dry organic matter across all plots (Table 4-2). Drained plots had significantly lower microbial biomass values than the control plots (p = 0.023). Soluble organic C was slightly higher in drained than control areas in each site. Again the difference was not significant (p = 0.23).

4.3 Discussion

Drainage clearly improved productivity of the site measured as height and diameter of regeneration. There was also a shift in the composition of plant communities after drainage. Species that are indicators of very wet and nutrient-poor sites, such as mosses, skunk cabbage and rushes, which were present in the original swamps, have been replaced by species such as salal, salmonberry and ferns. Changes in composition of plant communities and increases in tree growth have been reported in several other drainage studies (Martikainen et al. 1995; Laiho and Laine

1997; Roy et al. 1999 & 2000c). Although we did not measure understory biomass in this study, field observations suggested a substantive increase in the biomass of understory vegetation in drained areas.

More surprising was our finding that soil C stores were greater in drained sites than control sites. This finding contrasts with other drainage studies, which have shown that oxic conditions created by water level drawdown (Silins and Rothwell 1999; Roy et al. 2000b) favor microbial activity and accelerate decomposition rate and carbon loss (Martikainen et al 1995, Silvola et al. 1996, Ueda et al. 2000, Blodau et al. 2004). Our laboratory incubation also indicated that decomposition rates were not enhanced in drained areas; in fact, CO₂ efflux and microbial biomass were lower in incubated soils taken from the drained plots compared to soil taken from the control plots. The lack of increase in CO₂ release in our drained sites may indicate that the oxygen limitation was not entirely overcome through drainage. Although drainage improved soil aeration, the difference in Eh values between drained and control plots was not significant, and all Eh values in both drained and control sites were still much lower than 300 mV, the critical threshold below which anaerobic conditions develop (Dwire et al., 2006; Faulkner and Patrick 1992; Pezeshki 1991). Under such low redox conditions, facultative anaerobes and less efficient microbial communities become more prevalent in the soil, and nutrients such as Fe, Mn, and Zn, which are important cofactors in enzyme activities, are reduced and unavailable (Gobat et al. 2004). This results in the reduction of key soil enzyme activities that catalyze the mineralization of organic matter. The maintenance of low redox conditions in drained plots would explain the lack of stimulation of decomposition and CO₂ efflux.

The lower emission of CO_2 and microbial biomass in soil from drained sites compared with control sites may, in turn, have resulted from the significant reduction in pH in drained areas (average of 3.10 compared to 3.76 in control plots). Reductions in pH after drainage have been

reported in other studies (De Vries and Breeuwsma 1987, Laiho and Laine 1990, Laine et al. 1995b). Laiho and Laine (1990) found an average decrease of 0.5 units (from 3.5 to 3.0) in pH (CaCl₂, suspension) for mesotrophic sites after drainage. Several mechanisms have been proposed to explain the reduction of the pH in drained areas, including greater uptake of base cations by trees and longer nutrient retention in the biomass, leaching of nutrients as the result of water fluctuation, and increased SOC in drained areas (Laine et al. 1995a). We also found that SOC concentrations were 20% higher in drained than in undrained plots.

It may be that under drained, but still low-redox and low-pH conditions, plants are better able to survive and grow but soil microbial communities remain inhibited. Root oxygenation and elongation are common mechanisms used by many plants growing in wetlands and flooded soils to overcome low redox conditions and maintain aerobic respiration (Pezeshki, 1991). Kludze et al. (1994) found three-fold higher oxygen loss through roots of *Taxodium distichum* seedlings growing in flooded soils than those growing in drained soils. In contrast, the biomass and activities of microbial communities remain negatively affected by low oxygen and pH under such circumstances. Thus, drainage of this cedar-swamp ecosystem appears to have had the serendipitous effect of improving vegetation growth without stimulating losses of soil C.

Increases in soil C stores in the drained sites could arise through increases in litter and root production associated with the observed stimulation of aboveground vegetation growth. However, the magnitude of the increase in soil C stores, especially in areas 2 and 3, is surprising. The difference in soil C storage between drained and control areas declines from 131 to 70 Mg/ha once plot 2 removed from the data set. It is possible that the differences in soil C stores in these areas existed prior to drainage, as there were no pre-treatment soil measurements. It is unlikely that all four control areas had larger C stores prior to drainage; on balance our findings suggest that there was not a net loss of C from the soils at any of the four treatment areas following drainage. Thus,we

suggest that higher soil C store in drained siteswas related to the soil redox conditions remaining under 300mV despite drainage.

4.4 Management implications

Our results indicate that drainage could be a useful silvicultural practice for improving the productivity of cedar-swamp ecosystems in coastal B.C. Fertilization is commonly used to increase nutrient supply after harvesting in the area (Bradley et al. 2000; Bennett et al. 2003); field experiments comparing the relative and additive effects of drainage and fertilization would be beneficial in establishing the optimal silvicultural practices for these sites.. The study also indicated that it may be possible to improve tree growth without stimulating loss of soil C; we hypothesize that this may occur if drainage is sufficient to improve aeration in the rooting zone while maintaining redox levels of less than 300 mV in the bulk soil. This hypothesis needs to be tested in replicated experiments testing a range of drainage intensities under a variety of site conditions to determine its generality.



Figure 4-1: Map of the Suquash drainage trial with four replicate drainage (treatment) areas and the control, drained, and semi-drained plots within each treatment area.



Figure 4-2: Three-dimensional PCA biplot. Plant species: Sa (Salal, *Gaultheria shallon*); sB (salmonberry, *Rubus spectabilis*); hT (horsetail, *Equisetum arvense*); sC (skunk cabbage, *Lysichiton americanum*); Vac (*Vaccinium spp.*); Gr (Grasses); Ru (Rushes); Fer (Ferns); Mos (Mosses)



Figure 4-3: Daily mineralized carbon (mg C/ g soil C), measured as CO_2 efflux, duringone month laboratory incubation of samples from drained and control sites.

	C1	D1	C2	D2	C3	D3	C4	D4	Average C	Average D
Moisture (% dry mass)	468	385	635	536	446	308	459	372	502 (28) ^{a*}	400 (28) ^b
Eh (mv) - $CaCl_2$	118	208	60	194	176	193	183	198	134 (17.4)	198 (17.4)
Eh (mv) - dH ₂ O	110	111	70	119	96	116	-	-	92 (9.7)	115 (9.7)
pH - CaCl ₂	2.74	2.62	2.67	2.45	2.58	2.32	2.44	2.67	2.61	2.52
pH - dH ₂ O	3.74	3.18	3.49	2.99	4.04	3.12	-	-	3.76 (0.10) ^{a*}	3.10 (0.10) ^b
Total N (%)	1.13	0.90	1.43	1.28	1.28	1.11	1.03	1.12	1.22 (0.05)	1.10 (0.05)
Carbon (%)	49	48	41	49	36	41	47	48	43 (1.42)	46 (1.42)
C/N	44	53	29	38	28	37	45	43	36 (2.17)	43 (2.17)
OM thickness (cm)	33 ± 30^{1}	37 ± 19	12 ± 5	57 ± 19	7 ± 2	30 ± 20	11 ± 7	15 ± 5	16 (6.07)	35 (6.07)
bulk density (kg/m3)	88 ± 17	131 ± 18	125 ± 29	135 ± 24	144 ± 51	120 ± 37	141 ± 38	121 ± 17	125 (8.21)	127 (8.21)
C density(kg/m ³)	44	62	51	66	52	50	66	57	53 (4.05)	59 (4.05)
C store (t/ ha)	143	231	62	376	37	147	74	86	79 (4.57)	210 (4.57)
N density(kg/m ³)	1.00	1.18	1.79	1.72	1.84	1.33	1.45	1.35	1.52 (0.10)	1.40 (0.10)
N store (t/ ha)	3.28	4.38	2.15	9.78	1.29	3.93	1.64	2.02	2.09 (1.20)	5.03 (1.20)
Tree height (m)	4.66 ± 1.29	5.91 ± 0.67	4.4 ± 0.75	5.35 ± 0.85	4.64 ± 0.68	5.41 ± 0.69	4.14 ± 0.79	5.16 ± 1.02	4.37 (0.14) ^{a**}	5.38 (0.14) ^b
Tree diameter (m)	0.07 ± 0.02	0.10 ± 0.02	0.06 ± 0.01	0.09 ± 0.02	0.07 ± 0.02	0.08 ± 0.02	0.07 ± 0.02	0.08 ± 0.02	0.07 (0.005) ^{a*}	$0.09 \pm (0.005)^{b}$

Table 4-1: Soil and stand properties in control (C) and drained (D) plots at the four (1-4) treatment areas.

Different letters indicate significant difference between the averages of the two treatments; ^{**} level of significance with p< 0.05; ^{*} level of significance with p< 0.10; The numbers in parenthesis are standard errors; ¹ standard deviation

	C1	D1	C2	D2	C3	D3	C4	D4	Average C	Average D
total CO ₂ emission (mg/g C)	4.27	2.76	10.41	2.79	5.30	2.58	3.71	3.69	5.92 (0.95)	2.95 (0.95)
Daily emission ¹ (mg C-CO ₂ /g soil)	0.086 (0.006) ^{a**}	0.051 (0.006) ^b	0.153 (0.006) ^{a**}	0.047 (0.006) ^b	0.078 (0.006)	0.038 (0.006)	0.066 (0.006) ^{a**}	0.069 (0.006) ^b	0.096 (0.006) ^{a**}	0.051 (0.006) ^b
Daily emission (mg C-CO ₂ /ha)	2.37	2.44	2.33	3.79	0.74	1.37	1.01	1.20	1.61 (0.46)	2.20 (0.46)
MBC mg/g	3.93	2.74	9.40	3.67	7.11	4.31	7.02	5.81	6.86 (1.12) ^{a*}	4.13 (0.65) ^b
SOC (mg/g soil)	1.66	2.17	2.51	3.59	1.80	1.50	1.97	2.24	1.99 (0.20)	2.37 (0.20)

Table 4-2: Selected properties of the forest floor in control (C) and drained (D) plots at the four (1-4) treatment areas.

¹ These values are the average of 8 times of measurement over a month of incubation; Different letters indicate significant difference between the averages of the two treatments; ^{**} level of significance with p < 0.05; ^{*} level of significance with p < 0.10; Numbers in parenthesis are standard errors.

	% of Variance	Cum.% of Var
Axis1	33.85	33.85
Axis2	23.28	57.13
Axis3	15.67	72.81

Table 4-3: Variance explained by the first three axis of the PCA analysis

Table 4-4:Pearson and Kendall Correlations with Ordination Axes for 3-dimensional visualization. Variables with strongest r-values are indicated with bold font (n=12).

	Axis1	Axis2	Axis3
Sa (salal)	0.130	0.294	0.175
sB (salmonberry)	0.000	0.538	0.212
hT (horsetail)	0.007	0.574	0.091
sC (skunk cabbage)	0.792	0.001	0.075
Vac (Vaccinium spp.)	0.373	0.84	0.344
Gr (grasses)	0.800	0.004	0.004
Ru (rushes)	0.511	0.008	0.002
Fer (ferns)	0.075	0.375	0.451
Mos (mosses)	0.357	0.217	0.056

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Chapter 5: Overall synthesis

Extensive parts of coastal western redcedar-western hemlock (CH) forests exhibit slow growth and nutrient deficiencies (N and P), which are not observed on adjacent mature secondgrowth hemlock-amabilis fir (HA) forests. The symptoms appear 5-8 years following clearcutting. Several potential causative factors have been investigated but none has provided sufficient evidence for the theories proposed to explain the cause of low N supply in CH sites.Emerging evidence from earlier studies indicated that CH sites might be wetter than HA sites and may be waterlogged for most of the year. Waterlogged conditions could lead to development of anaerobic conditions and low nutrient supply in CH soils. CH forests have some characteristics of wetland forests (ecosystems with similarities to both swamps and upland forests). Soil water could play a pivotal role in the function and productivity of wet ecosystems because of its impact on the decomposition process, nutrient mineralization and distribution of plant species. Soil moisture dynamics and the consequent impacts on soil processes differ among forest types. Forest management practices such as harvesting and site preparation can also significantly impact hydrological and related biogeochemical processes in the soil. Research in northern B.C., eastern Canada and southern Alaska suggests that productive forests can develop into bogs through paludification, the processes whereby organic matter accumulates to levels that can negatively impact tree growth (Paavilainen and Paivanen 1995, Paré and Bergeron 1995; Harper et al. 2002, 2003). After harvesting in wet forests, the decrease in canopy interception increases the amount of soil moisture and the frequency and duration of waterlogged conditions. It is therefore possible that clearcut harvesting on CH sites will raise the water table level and intensify the low nutrient supply in CH cutovers.

The objectives of this study were to develop an understanding of how one ecosystem component - soil moisture - relates to other components like nutrient cycling, plant species

distribution and site productivity, and how these relationships differ in two adjacent forest ecosystems with similar soil macromorphological characteristics (Lewis (1982; Germain 1985; Keenan 1993). I also examined the effects of clearcutting on soil moisture and aeration.

Three approaches were used to examine the effects of excessive soil moisture on site productivity:

1) Field research: a field experiment was carried out to:

- Determine whether CH and HA forests differ in soil moisture and aeration.
- Determine whether decomposition rate and soil C storage differs between CH and HA forests.
- Determine whether composition of plant communities was related to soil moisture and aeration.
- Evaluate the impact of harvesting CH and HA forests on moisture and aeration conditions.
- Laboratory research: an incubation study was conducted to investigate the effects of moisture levels, from field capacity to saturation level, on C and N mineralization rates.
- *3) Management implications for the research*: A field study was carried out to assess drainage as a potential solution for forest management in cedar-swamp forests by comparing C dynamics and soil C storage in drained and un-drained sites.

Following are some of my most important findings with regards to the objectives of this study:

CH forests were wetter and less aerated, had shallower aerated depth, and had higher frequency of anaerobic conditions compared with HA forests (objective 1). Soil moisture was high and above field capacity in forest floor and mineral soil of both forest types even at the driest time of the year. As infered from redox measurements, more than 40% of the sampling plots in CH forests had an average redox value less than +300 mV, a threshold below which anaerobic conditions exist (Dwire et al., 2006; Faulkner and Patrick 1992; Pezeshki 1991) during the summer when the soils are expected to be under the most oxidizing conditions. The differences in moisture content between the two forest types were large in the upper horizons, but narrowed with depth. Soils were semi-saturated in lower horizons, indicating a high water table in both forest types. On the contrary, the differences in redox potential between CH and HA forests increased with depth. This suggests that although HA stands might be as wet as CH stands, they have more dissolved oxygen in water, probably due to their higher slope position or better drainage conditions in the mineral soil, which maintains a better water flow. Thus, the line of difference between the two ecosystems is very narrow. My findings suggest that the slightly lower landscape position of CH forests (Albani and Lavery, 2000) and consequently the greater amount of water received increases the moisture content of these soils to maximum waterholding capacity, which results in the development of anaerobic conditions. However, the physiographic position does not seem to be the only reason for the wetter and less-aerated conditions in CH forests, as CH forests are widely distributed over a range of topographic positions. I found CH sites to be highly variable, ranging from moist soils that are well-aerated(mainly in the surface), to poorly drained soils with high amounts of silt and clay. This variability may explain why no consistent differences among CH and HA sites were found in soil characteristics in previous studies (Lewis (1982; Germain 1985; Keenan 1993); although deMontigny (1992) reported a greater frequency of gleyed horizons in CH forests. Several factors could cause wetter and less aerated conditions in CH soils. A pan layer was observed in

several plots, which would impede drainage. High levels of silt and clay content were found in some sampling locations, which could significantly increase water retention and reduce redox potential. In other CH sites, soils were not saturated but mottling was observed, indicating a tendency for the soils to become saturated after rain events and switch between aerobic and anaerobic conditions. These findings suggest that micro-site conditions play an important role in ecosystem structure and function in CH forests.

Analysis of the plant communities revealed that the composition of the plant community was related to soil moisture and aeration, however plant diversity was not. Soil aeration was the most important factor driving differences in plant species I measured, explaining 25% of the variability within plant communities (Objective 3). Soil moisture explained only 16% of the variation, indicating that plant communities are more sensitive to changes in soil aeration than moisture. The stronger correlations I found between aerated depth and redox potential than between aerated depth and moisture content in the mineral soil, suggest that saturated conditions do not always result in development of anaerobic conditions in the soil. Redox potential is driven by factors other than moisture, such as soil texture, soil organic matter and oxygen. Redox and aerated depth both can exert control over rooting depth, root structure and biomass. It has been shown that redox values less than +300 mV result in complete or considerable cessation of root growth (Pezeshki 2001, Pezeshki 1991; Will et al, 1995) and changes in cellular structure in the cortex (Pezeshki 1991). The results also confirmed that rooting depth is shallower in CH than HA sites. Fewer nutrients could be available for plant growth in CH sites because of shallower rooting depth and less aeration. Thus, species that can grow under water fluctuation would be expected to dominate CH forests. This explains the distinct plant communities in CH and HA forests despite the generally similar soil characteristics.

CH sites are dominated by salal and deer fern (*Blechnum spicant*). Salal tolerates a wide range of moisture and nutrient conditions, but is most abundant on nutrient-poor, slightly dry to moist sites, and on some very wet sites (Prescott and Sajedi 2008). One of the most effective mechanisms for salal to grow under anaerobic conditions and shallow mineral soil is related to its ability to spread vegetatively through layering, sprouting and suckering (Haeussler *et al.* 1990; Huffman *et al.* 1994;Tappeiner *et al.* 2001). Deer fern appeared to be an indicator of anaerobic conditions (Eh of <+300 mV) in CH and HA forests in that its presence and coverage was correlated with Eh and aerated depth. Deer fern covered more than 25% of the total understory cover under anaerobic conditions.

The difference in moisture, aeration and composition of plant communities between CH and HA stands could cause significant differences in decomposition and nutrient availability between the two forest types. Soil moisture has been shown to strongly affect heterotrophic respiration and decomposition (Bouma and Bryla, 2000, Dilustro et al., 2004). In my field study, cellulose decay rate was similar between CH and HA forests and declined with depth (Objective 2). This was probably because L and F horizons are well aerated but H horizons and mineral soil are not. The reduction in decomposition rate in lower humus suggests that root decay is partially impeded on CH sites. The results also confirmed that plant rooting depth is greater in HA sites than CH sites. More nutrients could be available for plant growth in HA sites because of deeper rooting depth and better aeration. Schuur (2001) found contradicting results compared with the similar decay rates I found between wet (CH) and moist (HA) sites. He showed that litter decomposition rates and nutrient release slowed with increased rainfall as a result of both reduced soil oxygen availability and the production of low-quality litter in wetter sites. The differences in these findings could be explained by the method we applied to measure decay rates. Cellulose is an easily decomposable food source for microbes, and so may
decompose faster in CH sites than in HA sites due to the lack of labile carbon in CH sites; this could be misinterpreted as fast decomposition.

The findings that **microbial biomass and C mineralization declined under watersaturated conditions (objective 5)** in the laboratory incubation were largely consistent with my hypotheses regarding C mineralization. This is consistent with the lower rates of microbial respiration and lower microbial biomass associated with waterlogged soils reported in other studies (Schimel et al 1999; Jaatinen et al. 2007, Chmielewski 1991). Scanlon and Moore (2000) also found lower CO₂ production under anoxic conditions than oxic conditions during twelveday incubations of peat. Lower microbial biomass and activity under low-oxygen or anaerobic condition would result in slower decomposition of organic matter.

As hypothesized, SIN:SON ratio declined under water-saturated conditions, but my findings with respect to N pools do not support my hypothesis that saturated conditions lead to reductions in supply of available N (Objective 5). Total pools of exchangeable N (SIN+SON) were larger in saturated than in field-moist humus and soil. The concentration and proportion of SON increased at the highest moisture levels and was correlated with moisture. Consistent with my finding, Hannam and Prescott (2003) found SON abundance to be positively correlated with soil moisture. Concentrations of SIN on the other hand was more closely related to the C:N ratio of the material than to moisture content or the rate of C mineralization. Ammonium concentrations were most closely related to total N concentration and were much lower in CH than HA forests. Nitrate concentrations were very low in both forest types and were correlated with pH.

Contrary to my expectations, the two sites responded differently to excessive moisture with regards to N mineralization. SIN declined at saturation moisture level in CH samples but not in the HA samples. Like HA forests, Holtgrieve et al. (2006) found the highest extractable NH_4 ⁺ at the wettest site along a precipitation gradient from mesic to wet sites in Hawaiian forests.

However, N mineralization is generally thought not to be affected by low oxygen availability, because it does not involve either oxidation or reduction processes (Pett-Ridge et al. 2006). Like CH forests, Schimidt-Rohr et al. (2004) showed that N mineralization can be reduced under anaerobic conditions if organic N is associated with phenolic compounds which require oxidative decomposition. Cedar litter has higher levels of phenolic compounds such as lignin than most tree species in this region (Prescott et al. 2004), and the dense understory of salal in CH forests has been shown to have high concentrations of phenolic compounds such as tannins (Preston 1999).

These findings indicate that excessive moisture and resulting anaerobic conditions in soil play a fundamental causal role in the low nutrient supply in cedar-hemlock forests in coastal BC. The effects of moisture on low N availability in CH sites appear to be indirect and arise through interactions with vegetation and litter quality (Fig 5-1). The high precipitation regime in the region, coupled with the slightly lower slope positions and/or poor drainage caused by the presence of a pan layer or fine soil texture on CH sitescause the moisture content of these soils to be at or above maximum water-holding capacity. The resulting conditions of excessive moisture and low oxygen have probably been the major factors leading to domination of cedar and salal on CH sites. These species produce litter with high levels of phenolic compounds. Nitrogen mineralization can be reduced under anaerobic conditions if organic N is associated with phenolic compounds (Schimidt-Rohr et al. 2004) which require oxidative decomposition. This combination of low-oxygen conditions and association of organic N with phenolic compounds would constrain decomposition and increase humification and the binding of N into complex humic materials, leading to very low rates of N mineralization from CH humus and soil. Such conditions could create a positive feedback for growth of species like cedar and salal which compete well with other species under very wet and low nutrient conditions, thereby exacerbating the differences between CH and HA sites.

Thus, I suggest that low N availability on CH sites results from synergistic effects of the greater frequency of water-logging of soils and the resulting dominance of plant species with high phenolic contents, which promote humification and binding of N in humus, rather than mineralization into plant-available N forms. Implication for forest management

5.1 Clearcut effects on soil moisture and aeration (paludification)

The hypothesis that clear-cut harvesting results in wetter and less aerated conditions in the deeper soil horizons was partially supported (Objective 4). The two forest types responded differently to clearcut harvesting. CH clearcuts were drier than CH forests in all organic horizons. The drier condition in the forest floor in CH clearcuts did not result in better aeration, however, and the redox potential was similar to CH forests and still below +300 mV threshold. As expected the upper humus was drier and mineral soil was similarly wet in HA clearcuts compared with HA forests, but lower humus was wetter. Higher moisture content and lower redox potential in the lower humus layer in HA forests could indicate that slight increase in water table might have resulted in development of anaerobic condition and paludification. Clearcut harvesting can raise the water table by reducing interception and evapotranspiration rates (Dube et al. 1995; Roy et al. 2000a). Despite having similar moisture levels, mineral soil was anaerobic in HA clearcuts and not in HA forests. Redox potential in the mineral soil, which was always above +300 mV in HA forests, was lower in HA clearcuts, and below this threshold and at similar levels as CH clearcuts. Likewise, the iron rods indicated that harvesting improved soil drainage in CH sites, but not in HA sites. The reduction of redox in HA cutovers despite similar moisture levels suggests that clearcutting HA forests may (at least temporarily) shift these ecosystems towards more anaerobic conditions similar to CH sites. Reductions in the soil aerated zone after harvesting have been noted by others (Joosten and Clarke 2002; Lavoie et al. 2005) and are thought to reduce rates of decomposition and nutrient turnover (Payette 2001;

Taylor *et al.* 198) through the paludification processes, which could negatively affect productivity. My cellulose mass loss data confirm slower decomposition rates in HA cutovers than HA forests. The higher mass loss rates in both upper and lower humus layer in CH cutovers compared with CH forests is consistent with improved aeration in CH cutovers. In HA clearcuts, cellulose mass loss was higher in the upper humus layer, as was aeration, but lower in the lower humus layer than HA forests, consistent with reduced aeration in HA clearcuts. Also, rooting depth was not different between CH clearcuts and forests, but it was shallower in HA clearcuts than HA forests. These findings suggest that clearcutting reduced aeration in HA forest soils, The potential for clearcut-harvesting to promote paludification of productive HA sites warrants further examination.

5.2 Drainage as a potential solution for forest management in wetland forests

The hypothesis that drainage would alter the composition of plant species, and will increase tree growth, CO₂ flux, microbial biomass, and carbon store in the soil was partially supported (Objective 6). Drainage improved soil aeration, measured as redox potential, and tree growth, measured as height and diameter. Although drainage improved soil aeration, the difference in Eh values between drained and control plots was not significant, and all Eh values in both drained and control sites were still much lower than +300 mV. The composition of plant communities on swamp sites shifted from domination of species that indicate very wet and nutrient-poor sites, such as mosses, skunk cabbage and rushes, to communities dominated by forest-understory species such as salal, salmonberry and ferns on drained sites. Changes in composition of plant communities and increases in tree growth have been reported in several other drainage studies (Martikainen et al. 1995; Laiho and Laine 1997;

Roy et al. 1999 & 2000c). As expected, soil carbon store increased after drainage, but CO₂ efflux and microbial biomass were surprisingly lower in drained plots compared to control plots. This finding contrasts with other drainage studies that have shown that oxic conditions created by water-level drawdown (Silins and Rothwell 1999; Roy et al. 2000*b*) favor microbial activity and accelerate decomposition rate and carbon loss (Martikainen et al. 1995, Silvola et al. 1996, Ueda et al. 2000, Blodau et al. 2004). Our results indicate that drainage could be a useful silvicultural practice for improving the productivity of cedar-swamp ecosystems in coastal B.C. The study also suggests that it may be possible to improve tree growth without stimulating loss of soil C if drainage is sufficient to improve aeration in the rooting zone while maintaining redox levels of less than 300 mV in the bulk soil.

5.3 Strengths and limitations

The major strength of my thesis research was examining the nutrient deficit issue in CH sites from a more integrated and ecosystem-function perspective. Integration of field and laboratory studies helped to overcome some of the inherent limitations of independent studies. Comparing CH with adjacent HA sites, where the symptoms of low nutrient supply does not occur, helped to distinguish the effects of moisture from other influencing factors, such as litter quality, while testing my hypotheses. The study was carried out in both forest floor and in mineral soil layers, while in many other studies only one or the other layer is examined. Comparing forest floor and mineral soil provided useful information about dynamics of soil moisture and aeration through the soil profile and the relationships between the organic layer and the underlying mineral soil, and how upper versus lower horizons play different roles in decomposition and nutrient mineralization.

Through a detailed determination of the variability and characteristics of CH and HA sites in the field I was able to explain some of the complexities in these ecosystems and identify the potential cause of the low nutrient supply in CH forests. Repeated measures of soil moisture, redox (Eh) and pH provided a better understanding of the relationship between soil moisture and aeration dynamics and the differences among sites. Also, rusting depth from iron rods provided very useful information about water table fluctuations and the maximum aerated depth over a one-year time period. However, I did not capture seasonal trends and fluctuations in soil moisture and aeration, which may be different in CH and HA ecosystems.

Redox potential is a very useful indicator of the overall oxidation-reduction status in the soils. Under very wet condition and when oxygen becomes limiting, methods used in welldrained soils to quantify oxygen content cannot be employed efficiently (Pezeshki 2001). On the contrary, Eh is a very useful measurement in wet soils by providing an excellent estimation of soil chemical status both in the field and under laboratory condition. My study is among the very few studies in Canada to address redox measurements and dynamics in forest ecosystems and to explore relationship between Eh and other ecosystem components. Redox measurements were well correlated with other soil measurements such as pH, moisture, rusting depth from iron rods, as well as regeneration growth and plant species distribution. My findings also showed that redox potential and the important +300 mV redox threshold is a valuable ecological indicator in wet forest ecosystems that could be used to address forest management practices and, for example, reduce the potential for paludification. Similar to moisture I did not capture seasonal changes in redox potential. Also, I did not test for the number of observations necessary to determine the natural variation in soil redox potential. Based on my field observations, variability in redox potential increased with increasing soil moisture. More observations in each site would have resulted in less variability and better estimations of differences in Eh among sites and treatments. Another weakness in field study was using cellulose papers to measure

decomposition rates. I chose a standard substrate because I thought it would better distinguish the differences in the rates of decomposition between CH and HA sites. However, results indicate that cellulose papers decomposed faster in CH sites than in HA sites due to lower litter quality and lack of fresh carbon which could be misinterpreted as faster decomposition rate in CH sites.

The laboratory incubation study was useful to test for the effects of excessive moisture on C and N mineralization by eliminating other influential variables such as temperature. Most studies carried out to investigate the effects of moisture on nutrient mineralization are restricted to precipitation (or physiographical) gradients or drainage trials. The moisture gradient I developed in the laboratory was based on realistic moisture levels adapted from the field study. One of the most important outcomes of the incubation study was to reach a threshold in moisture content (350-500% in forest floor and 90% in mineral soil) above which C mineralization and microbial biomass declined in both CH and HA sites along with a sharp reduction in redox potential. Nitrogen mineralization also declined above this threshold in CH sites but not in HA sites. However, I did not test for this threshold in the field.

The size of the soluble N pool after the incubation period does not reflect the actual available pools in the field and gives limited information about how much N may become available for plant uptake in the field. Nitrogen production in the absence of roots is expected to be lower than in their presence as labile C and N sources from root exudation are excluded (Burger and Jackson 2004). However, it gives the potential of exchangeable labile pool and in this particular study it shows how moisture can affect this potential pool, thus shedding light on the mechanisms and processes involved in N mineralization with regards to moisture. A weakness in my incubation study was that I did not partition SON into the simple low-weight molecules (such as amino acids) and high-weight molecules. I found SON to be the dominant form of nitrogen in N-poor CH sites and in the mineral soil and it increased with increasing

moisture. It has been shown that SON could be a potential source for N uptake by plants in simple forms such as amino acids (Chang et al 1995; Devito et al. 1999; Hannam and Prescott 2003; Kranabetter et al. 2007). Thus, partitioning SON could have provided useful information regarding the exchangeable pool.

In addition to the field and laboratory study to investigate the effects of excessive moisture on C and N mineralization, my findings have direct implications for two of the most important management practices for these sites. Finding a drainage trial developed 10 years prior to this study gave me an opportunity to test some of my hypotheses. Thr major weakness in the drainage trial was the lack of site replication. The lack of pre-treatment soil measurements also made for uncertainties regarding some of the surprising results, such as distinctively higher soil C store and relatively lower CO_2 efflux on drained sites compared with control undrained sites.

5.4 Recommendation for future studies

My findings revealed that soil moisture and aeration play an fundamental role in the function and structure of these wet ecosystems. A hydrological study that measures long-term water fluctuations along with long-term redox measurements would bring a better understanding of soil biogeochemical processes and site productivity. Direct measurements of dissolved oxygen would be preferable to single moisture measurements for determining the ecological effects of water saturation in soils.

There are controversies in the literature regarding N mineralization under anaerobic conditions. Findings from my incubation study along with other studies (Schimidt-Rohr et al. 2004) suggest that nitrogen mineralization declines under anaerobic conditions if organic N is associated with phenolic compounds, which require oxidative decomposition. This hypothesis needs to be tested. Also, I found SON to be the dominant form of nitrogen in N-poor CH forest

floors and mineral soil. Considering the very low levels of SIN in the forest floor in CH sites, the potential for cedar and other species to take up SON should be examined.

The microbial degradation of organic matter and nutrient release is mediated by extracellular enzymes. Activity of extracellular enzymes (e.g. phenoloxidase) could be inhibited or reduced under anoxic conditions, which could slow the decay of organic matter and mineralization of nutrients. The study of enzyme activity in relation to redox potential and concentrations of coenzymes such as Fe, Mo or Zn, which could be in reduced forms and unavailable for enzymatic activities under anaerobic conditions, could provide useful information for better understanding of the mechanisms involved in N mineralization under anaerobic conditions. I found that under anaerobic conditions, microbial biomass N decreased despite an increase in concentrations of ammonium. This suggested that microbial assimilation of N is prohibited under anaerobic conditions. It is likely that reduction in some other nutrients such as C, P or Fe associated with the anaerobic condition indirectly inhibits N assimilation. This needs further research. Also, a direct measure of nutrients and particularly N forms along with moisture and Eh in the field would compliment this research. Results from my study indicate that lower soil horizons and thus root decay are more affected by excessive moisture and related anaerobic conditions than upper soil horizons and litter decay. Thus, a detailed assessment of nitrogen availability and mineralization in upper and lower soil layers separately would be advantageous.

Pezeshki (1991) has shown that under anaerobic conditions and below a critical redox threshold, root growth could be inhibited or reduced and the cellular structure of the roots changes. He suggested that this redox threshold is species-specific and varies from +350 to +200 mV. Cedar is one of the tree species that grows under a wide range of moisture and can grow better than many other species in wet soil. In one of the control plots in cedar-swamp sites (Chapter 4), I found seedlings of cedar growing in soils with redox values as low as -75 mV,

suggesting that cedar might have a special physiological structure in its roots that enables this species to survive under both oxic and anoxic conditions. This hypothesis needs further research.

Our results indicate that drainage could be a useful silvicultural practice for improving the productivity of cedar-swamp ecosystems in coastal B.C. Fertilization is commonly used to increase nutrient supply after harvesting (Bradley et al. 2000; Bennett et al. 2003); field experiments comparing the relative and additive effects of drainage and fertilization would be beneficial in establishing the optimal silvicultural practices for these sites.. My study also indicated that it may be possible to improve tree growth without stimulating loss of soil C; I hypothesize that this may occur if drainage is sufficient to improve aeration in the rooting zone while maintaining redox levels of less than 300 mV in the bulk soil. This hypothesis needs to be tested in replicated experiments under a variety of site conditions to determine its generality. I recommend field measurements of CO_2 and NH_4 efflux before and after drainage to better assess drainage as a potential solution for forest management and its impacts on C dynamics.

Expansion of forest disturbance and global climate change has increased the need for ecosystem models that can cope with the changes in ecosystem dynamics produced by recent forest management, natural disturbance and climatic conditions. One aspect of forest ecosystems, particularly sensitive to these types of changes, is the effect of soil moisture conditions on tree growth and other ecosystem processes. Several models have included soil moisture as a parameter in the calculation of forest production, but few consider the effects of stand management on the dynamics of forest hydrology. ForWaDy is a stand-level hydrology model developed to simulate the effects of vegetation removal on stand-level water dynamics (Seely et al 1997). Hydrologic dynamics in the forest floor and rooting zone are simulated in the model using a multi-layered approach in which inflows and outflows are estimated sequentially for each soil layer. My results indicate that upper and lower horizons play different but equally

important role in moisture dynamics, decomposition and nutrient mineralization. Thus, this approach makes ForWaDy a suitable model to apply in CH and HA ecosystems. This model could be further integrated with the forest ecosystem models such as FORCEE and FORECAST (Kimmins 1999) to simulate the effects of forest water dynamics on stand growth and development. FORECAST could simulate and explore the effects of excessive moisture on stand development through time. Another pathway for integrating the two models is through the use of simulated water content in the forest floor layers for the calculation of litter decomposition rates in the ecosystem model. When combined with litter quality parameters, such a relationship will allow the integrated model to have more flexibility in predicting the effects of various silviculture systems on forest floor moisture contents and thus, litter decomposition rates.



Figure 5-1: mechanism for how small variations in soil drainage could lead to the observed differences in nutrient supply and productivity of CH and HA ecosystems

5.5 References

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Appendix 1: Plant species coverage by classes in the four plots in each of five CH and HA forest sites. Cover classes: 1 = <1%; 2 = 1-5%; 3 = 5-25%; 4 = 25-50%; 5 = 50-75%; 6 = 75-100%.

Forest type	СН													HA																										
Site	1				2				3				4				5			1				2				3				4				5				
Plot#	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Number of species	5	4	5	3	5	3	4	4	3	5	4	4	3	5	6	3	7	4	4	8	4	4	4	2	3	3	4	5	3	4	2	4	3	3	3	3	4	6	5	3
Total plant coverage	6	6	6	5	6	6	6	5	3	6	6	6	6	5	6	6	6	5	5	6	5	3	4	2	3	3	5	3	4	6	4	5	6	5	4	3	5	5	5	6
Total moss coverage	3	3	3	3	3	4	3	4	2	3	3	3	3	4	3	3	5	5	4	5	3	3	3	2	3	3	3	3	2	3		2	6	5	3	3	2	3		4
Vaccinium spp.	3				3			3						3						3	4	2	2	2		2	3	2	2	3	3	3	3		3	2	3			4
Gaultheria shallon	6	6	5	6	6	6	5	5	3	3	5	6	6	5	4	6	4	4		3	4	2	3			3	5	3	4	4	3	4			2		2		5	
Rubus spectabilis												3			2					4																				
Lysichiton																																								
americanum										3																														
Streptopus roseus										2																														
Fragaria chiloensis																	2																							
Cornus canadiansis											3								2																					
Menziensia ferruginea															3																									
Polystichum munitum																																						2	2	
Athyrium felix-feminia																				2																		4	2	
Blechnum spicant	4	3	6			4	4	2		6	3	3		3	4		4		2	5							2	3				2						3	2	
Sphagnum spp.	2		3																	3																	5		3	5
Hylocomium																																								
splendens	3	2	3	3	3	4	3	4	2	3	3	3	3	4	3	3	5	4	3	5	3	3	3	2	3	3	3	3				2	6	5	3	3		3		
Kindbergia oreganum		3	2		2		2		2				2	3		3	4	3	3	4					2				2	3				3		3		2		4
Plagiothecium																																								
undulatum				3											3		2	2	2		3	3	3		2			3		2			3	4			2			
Rhizomnium																																								
glabrescens																	3																							