Canopy Gaps in The Bamfield Huu-ay-aht Community Forest: Baseline Information for Variable Retention Silviculture (Y073363)

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NUTRIENT AVAILABILITY IN NATURAL GAPS
IN OLD-GROWTH FORESTS
IN COASTAL BRITISH COLUMBIA

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By

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Abstract

In the last decade forest management shifted in the coastal forest region of British Columbia from clearcutting regardless of ecosystem type to harvest systems such as variable retention harvesting which imitate the natural disturbance regime. However, the selection of a silvicultural system that emulates natural disturbance requires an understanding of the influence of natural disturbance on post-disturbance nutrient supply rates. The effect of gap formation on the availability of 14 nutrients was investigated at two sites in coastal old-growth forests dominated by western redcedar (Thuja plicata Donn ex D. Don) and western hemlock (Tsuga heterophylla Raf.) in southern British Columbia. In summer and winter nutrient availability was measured using ion-exchange resins (Plant Root Simulator (PRS)™-probe) incubated in the forest floor for a burial period of 4 to 8 weeks in replicated plots in natural gaps and close-canopy forest. In addition, above-ground biotic and abiotic factors as vegetation coverage and light levels were examined for their influence on nutrient supply rates. Neither the canopy openness nor rooting substrate coverage was significantly different between forest and gaps. No significant changes in nutrient supply rates between gaps and forest were measured. Supply rates for all analysed nutrients had high microscale variability in each forest phase. Increased availabilities of inorganic NO$_3^-$, Mg$^{2+}$, and Al$^{3+}$ in gaps were inconsistently compared to the other evaluated nutrients within and between sites, and sample seasons. It is concluded that the general breakup of the canopy of the studied old-growth forests create pre-disturbance conditions of forest climate, understorey vegetation, and microbes which are similar to the post-disturbance conditions. On the basis of the high variability measured, it is recommends using several indices of nutrient availability simultaneously to assess differences between gaps and forest in nutrients supply rates.

Keywords: nutrient supply rates; ion-exchange resins; natural disturbance; temperate coastal old-growth forest
Zusammenfassung


_Schlüsselwörter:_ Nährstoffverfügbarkeit; Ionenaustauschmembran; natürliche Störung; gemäßigte Küstenurwälder
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1 Introduction

Forest soil as medium for forest growth and support of forest cover is the essential part of a forest ecosystem. Therefore any sustainable and reasonable forest management has to consider the implications of its management on the medium forest soil. Already in the early years of the eighteenth century the German forester H. Cotta pointed out the importance of soils for forest production. Since then a great amount of basic scientific research has been done, which shifted from the basic soil science research to the more applied research on issues like tree nutrition and response to fertilization; when the focus of forest management laid strongly on wood production in the twentieth century in Northern America (Fisher and Binkley 2000). One focus of the research was and still is the assessment of soil changes under intensive forest management. Changes in the availability of nutrients can be assessed as an indicator of the impact of disturbance on a forest ecosystem.

The change in the forest policy of British Columbia with the implementation of the *Forest Practices Code* in 1995 revealed the requirements of understanding the impacts of small scale disturbances because the forest management concept of the range of natural variability was introduced. It is defined as concept that maintains biodiversity and resilience in managed forests (Wong and Iverson 2004). Before 1994 clearcutting constituted 85 to 92 percent of the total area harvested in BC., which shifted to 43 percent in the coastal forest region after 2001 (Jull 2004). The remaining harvest area in coastal BC is managed under harvest systems which retain single trees or patches of trees. These figures indicate that forest management shifted from clearcutting regardless of ecosystem disturbance type to a more adapted natural disturbance type management. This new type of harvest systems is called variable retention harvesting. The level of retention left in the forest stand and therefore the severity of disturbance depends mainly on the professional forester who designs the timber harvest at the specific site. In contrast, the scales of natural disturbance depend on the nature of the disturbance regimes, their climatic and topographic drivers, and the lifespan of organisms (Wong and Iverson 2004). In general, disturbance of forest by nature or humans is often disliked by the general public as it is seen as “unnatural”. Nevertheless, using the concept of the range of natural variability means applying different scales and severities of disturbances in forest ecosystems.

This thesis focuses on the impacts of gap formation as natural process on nutrient supply rates, reviews the general processes of nutrient cycling and the impacts of human induced
disturbance on forest ecosystems, and discusses in light of the current knowledge the outcomes of this study. My investigation is part of a series of studies on gap formation with the long-term goal of developing ecologically-based spatial and temporal criteria to guide variable retention silviculture that emulates fine-scale canopy disturbances.
2 Literature Review

2.1 Nutrients cycling in Forest Soils

Soil development is influenced by many factors such as parent material, climate, topography, exposition, fauna and flora. In ecosystems, energy and material flows in cycles from ecosystem component to another; thus soil is part of an open ecosystem. Through the transport of water, energy, organic matter and mineral elements all ecosystems are more or less strongly linked with their neighbours. “One ecosystem’s output is its neighbour’s input”1.

Within the ecosystem nutrients occur in four basic compartments: the atmosphere, living and dead organic matter, in the soil as available nutrients, and in primary and secondary minerals (Likens and Bormann 1995). Nutrients in soils occur: as salts, absorbed and exchangeable at the surface of organic and inorganic soil particles, in less exchangeable forms in the internal adsorptive layer of clay minerals, in the organic matter and biomass, and immobile as a component of silicates (Schachtschabel et al. 1998). Nutrients are added to soils through weathering, atmospheric deposition, fertilization, fixation and mineralization. They can be lost or made unavailable through leaching, biological immobilization, and sorption and precipitation chemistry (van Bremen 1995; Cole 1995; Schachtschabel et al. 1998). The resulting nutrient cycles of these adding and removing processes of elements have a very complex relationship between air, water, soil, fauna and flora. Changes of the nutrient stocks of ecosystems, disruption of nutrient cycling and uptake affect the health and the succession status of forest ecosystems. Therefore, for a sustainable ecosystem management perspective it is important to understand nutrient cycling.

2.1.1 Nutrient Availability

Nutrient availability in soils is a function of the continuous addition and removal of nutrients of the soil solution depending on ecosystem conditions at a given site. In addition, soils differ widely in their ability to supply nutrients for plant growth due to their pedogenic history, 

1 quoted from Tokuchi et al. (1999), p. 361
specific site characteristics and local climate factors affecting the biogeochemical cycling of nutrients (Cole 1995; Knoepp and Swank 1997).

The accessibility of nutrients for plants depends on the following factors: (i) intensity or concentration (activity) of the dissolved nutrient element (species) with interactions between elements (ionic concurrence), (ii) total available amount (stock) of a nutrient in the rooting zone of a profile, (iii) rate of delivery between solid and dissolved solution phase which depends on soil moisture, temperature, microorganisms activity, and (iv) extracting potential of the plant which depends on root density, kind and amount of root excretions and the microorganisms activity in the surroundings of the root (Schachtschabel et al. 1998). Therefore the balance between addition and removal of nutrients is continually shifting, with rate and direction depending on the dominating ecosystem condition (Cole 1995). The resulting availability of the needed nutrients of plants is generally low, between 2 and 20%. In addition, the efficiency of root nutrient uptake depends on soil conditions as well as on the degree of suberization and mycorrhizal infection of the roots (Nilsson et al. 1995). The nutrients which can be taken up by plants occur in soils mostly as ions or in some cases as simple molecules, e.g. nitrogen as NO$_3^-$ and NH$_4^+$ ions, potassium as K$^+$ ion or phosphorus as H$_2$PO$_4^-$ and HPO$_4^{2-}$ ions (Cole 1995; Schachtschabel et al. 1998).

Weathering is the most important process that provides ecosystems (flora and fauna) with nutrients as the predominant part of the nutrients comes from parent material and bedrock. Acid hydrolysis (i.e. H$^+$ ions displace other ions from minerals) and organic complexation (i.e. organic acids comprise mineral ions) are the two primary processes which drive the weathering of soil minerals (Fisher and Binkley 2000). Although nutrients in soil minerals are made available for plants through weathering processes only a small portion of the total amount is available at any time (Schachtschabel et al. 1998). Mineral weathering supplies most nutrients for plant uptake at a rate normally faster than the rate of loss via leaching (Cole 1995). The rate of weathering differs widely between sites depending on the influencing site factors like the mineralogy, age of parent material and climate (Cole 1995). For instance April and Newton (1991)$^1$ found that glaciated sites had a significantly higher weathering potential than non-glaciated sites. Weathering of primary and secondary minerals represents a major process for the supply of cations (Ca$^{2+}$, Mg$^{2+}$, K$^+$) and anions (PO$_4^{2-}$, SO$_4^{2-}$) into the soil solution.

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$^1$ as cited by Cole (1995)
The exception is nitrogen (N), which occurs mainly in the atmospheric as N\(_2\). In the soil it is stored in organic forms and is not available until the organic matter has been broken down. Nitrogen may also enter ecosystems through fixation of atmospheric N by either free-living fixation or symbiotic organisms into soils. Fixation by symbiotic organisms (50 to 150 kg ha\(^{-1}\) yr\(^{-1}\)) is far more effective in adding N to the soil than the free-living organisms (1 to 2 kg ha\(^{-1}\) yr\(^{-1}\)) (Cole 1995). Nevertheless, N is the most growth limiting factor in many forest ecosystems (Mladenoff 1987; Nilsson et al. 1995; Briggs et al. 2000).

Another nutrient supply process is the decomposition of dead organic matter which is mostly independent of the nutrient stock in the soil. Whereas weathering of parent material and atmospheric deposition are important for the long-term supply of nutrients in forest ecosystems, the mineralization of organic matter provides the major source of the annual nutrient requirements (Prescott 2002). Through the process of mineralization, nutrients bound within the soil organic matter are released into the soil solution to become available for plant uptake (Cole 1995; Schachtschabel et al. 1998). Factors such as soil temperature, moisture, pH-value, chemical quality of the material, availability of energy sources (i.e. oxidized carbon compounds), and the activity of meso- and microfauna influence the rate of the mineralization process (Schachtschabel et al. 1998). The organic matter is broken down through an initial chopping process by primary decomposers followed by digestion into simple molecules or single ions through microbes such as bacteria and fungi (Cole 1995; Fisher and Binkley 2000). The major part of nutrient mineralization takes place in the humus layer and the adjacent soil layer. Consequently, the highest concentration of fine roots is found in these forest soil layers (Huang and Schoenau 1997; Prescott 2002; Nilson et al. 2005). The rate of N mineralization ranges from 1 to 2 % per year of the total soil organic matter N pool in temperate forest regions. In forest soils of the Pacific Northwest with approximately 2000 to 4000 kg ha\(^{-1}\) of total N, about 20 to 80 N kg ha\(^{-1}\) is available annually for uptake by plants (Cole 1995).

Atmospheric deposition of essential elements into soils historically has been very low depending on the proximity to sources; e.g. higher sulphur inputs (25 kg ha\(^{-1}\) yr\(^{-1}\)) in areas close to the oceans compared to less than 1 kg ha\(^{-1}\) yr\(^{-1}\) in areas away of the ocean. In the recent past, atmospheric depositions have increased through anthropological emissions in some forest regions. This is especially true for sulphur dioxides and for nitrogen compounds with deposition amounts up to 150 kg ha\(^{-1}\) yr\(^{-1}\). However, annual deposition is still very low in Pacific Northwest
with amounts of N less than 5 kg·ha\(^{-1}\) compared to 30 to 50 kg·ha\(^{-1}\)·yr\(^{-1}\) in Western Europe (Cole 1995; Schachtschabel et al. 1998).

The availability of nutrients is determined not only by supply rates of weathering, mineralization and atmospheric deposition but also by the soil characteristics. Especially, the pH of the soil influences the availability of nutrients. Soil nutrient elements may change chemical form in reaction to a change in pH. Nutrients are most available between pH 6 and 7 (Plaster 1996). With decreasing pH the solubility of Mn, Fe, Cu, Zn and especially of Mg and Ca increases. Therefore, soils with low pH experience greater leaching of Mg and Ca cations (Schachtschabel et al. 1998).

Nitrogen (N) occurs in both organic and inorganic forms in the soil. The most frequent inorganic forms are nitrate and (NO\(_3^\)) and ammonium (NH\(_4^+\)) ions which are taken up by plants. The major pathway for N availability is the decomposition and mineralization of dead organic matter, thus its dynamic is largely under the control of microorganisms. Phosphorus (P) is present in the soil in a number of ionic forms and can be strongly bound to mineral particles, thus only a very small fraction is soluble and available. The small mobile P pool is restocked by microbial processes and the weathering of minerals and consumed again by various competing sinks. Potassium (K), calcium (Ca) and magnesium (Mg) originate mainly from weathering of primary minerals in soils. Potassium is a very mobile nutrient that is present almost entirely as an unbound ion. It is easily released from living and decomposing plant tissues. Calcium is a relatively immobile nutrient if present in organic matter, and Ca dissolution is mainly determined by decomposition rates (Keenan and Kimmins 1993; Schachtschabel et al. 1998; Bradley et al. 2001).

### 2.1.2 Nutrient Losses

In general, the retention of nutrients within ecosystems is determined by the soil and vegetation at a given site (Pastor and Bockheim 1984). Nutrients becomes unavailable through biological immobilization by soil microorganisms and plant uptake, chemical and mineralogical reactions including precipitation and adsorption reactions, and ionic fixation within lattice structures of clay minerals (Cole 1995). Leaching and erosional events can cause losses of

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1 as cited by Tashe and Schmidt (2003)
nutrients from the soil polypedon depending mainly on precipitation surplus and ecosystem condition at a specified location (Nilsson 1995; Schachtschabel et al. 1998).

In soils nutrients are dissolved into the soil solution through acidification created by H\(^+\) ions. Under the influence of precipitation nutrients are transported from the top soil with the seepage water through the soil profile and may finally be leached. Soil texture and amount of seepage water determines the speed of leakage. The amount lost depends on the concentration of nutrients in the soil solution which is linked to the solubility and mobility of the specific chemical element. Any cation leached must be joined with an equivalent number of anions. The anions are bicarbonate, nitrate, organic acids, sulfates and chloride. The pH and the availability of these anions in the soils determine which specific anion is leached (Cole 1995, Schachtschabel et al. 1998). Due to the high solubility of bicarbonate it is often the cation with the highest rate of leaching (up to 45 to 85 kg Ca·ha\(^{-1}\)·yr\(^{-1}\)) in soils of the humid climate. In contrast, leaching of phosphorus with seepage water is very low (normally less than 1 kg P·ha\(^{-1}\)·yr\(^{-1}\)) due to strong sorption and fixing to the soil particles (Schachtschabel et al. 1998).

Losses via leaching are of particular concern because: i) important plant nutrients are lost; ii) NO\(_3\) ions and heavy metal ions losses to groundwater present a human health risk (Likens et al. 1970); iii) eutrophication of adjacent aquatic ecosystems might occur; iv) forest soils might experience a steady increase in acidification; and iii) alteration of the nutrient composition may alter the competitiveness of plant species (Lavoie et al. 1992).

### 2.2 Nutrients cycling affected by Harvesting

Long-term studies in undisturbed forests indicate that the nutrient status in soil changes during soil development over time. Several studies have shown that nutrient availability and pH often decrease over time (Troedsson and Nilsson 1984\(^2\), Binkley et al. 1989\(^3\); Billett et al. 1990\(^3\); Richter et al. 1994\(^3\), Brais et al. 1995). These changes result from modification of forest composition, sequestration of nutrients in aboveground biomass and/or leaching of nutrients (Knoepp and Swank 1994\(^3\); Brais et al. 1995).

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\(^1\) as cited in Grenon et al. (2004)
\(^2\) as cited in Nykvist and Rosén (1985)
\(^3\) as cited in Knoepp and Swank (1997)
Any silvicultural harvest technique affects soil nutrient cycling processes through changes in plant and canopy cover, reduction and redistribution of organic matter, soil compaction and modification of microclimate (Keenan and Kimmins 1993; Knoepp and Swank 1997; Barg and Edmonds 1999; Brigg et al. 2000; Marshall 2000; Bradley et al. 2001; Prescott 2002). The effects are complex and vary depending on the soil type, forest type and harvesting method (Knoepp and Swank 1997; Yanai 1998; Grenon et al. 2004). The mechanisms that lead to changes in nutrient cycling with any harvest system are still not completely understood due to the great variety of interacting factors involved in the biogeochemical cycling of nutrients in soils (Bradley et al. 2001; Hope et al. 2003). The most important factors causing these effects are thought to be the alteration of soil temperature and moisture conditions (Lübke 1992; Barg and Edmonds 1999; Marshall 2000; Bradley et al. 2001; Prescott 2002). Controversially, Prescott et al. (2002) observed that changes in the nature of forest soil following harvest had a greater influence on nitrate concentrations than the changes in environmental conditions.

Changes in abiotic conditions affect the soil biological communities that use the organic matter as energy substrate and nutrient sources (Barg and Edmonds 1999; Marshall 2000; Siira-Pietikäinen 2001). Soil organisms are influenced by all harvesting practices in the short-term whereas the long-term impacts are not well understood (Marshall 2000; Siira-Pietikäinen 2001). The alteration of the soil organisms may lead to a change of the decomposition rates in the forest floor but effects are inconsistent (Lübke 1992; Marshall 2000; Bradley et al. 2001). The reduction of organic matter in the forest floor and the reduction in the plant nutrient sink may lead to an increase in the nutrient concentration in the soil solution (Lübke 1992; Keenan and Kimmins 1993). Particularly, the availability of nitrogen and phosphorus is increased. This increase usually begins within 1 year of harvest and lasts 3-5 years (Prescott 2002). The growth of seedlings, ground vegetation and remaining trees may benefit from an increase in soil fertility known as the “assart effect” (Keenan and Kimmins 1993). On the other hand, greater nutrient availability could increase the movement of nutrients down the soil profile as the leaching of negative nitrate anions can cause concomitant movement of mobile cations through balancing of electrical charges in the soil solution (Cole 1995, Schachtschabel et al 1998).

Increased availability of ammonium and nitrate does not always happen after timber harvest. Barg and Edmonds (1999) observed no significant differences in net ammonification, nitrification, and total N mineralization rates and in soil microbial biomass among partial cutting and clearcutting. Grenon et al. (2004) found no effects of clearcutting on mineral N dynamics in
some coniferous ecosystems, and significant effects in others. These results question the assumption that a higher decomposition rate of organic matter after harvest causes higher nutrient availability due to higher moisture and temperature conditions. Prescott (2002) states that the assumption that faster decomposition is responsible for the flush of nitrate in clearcuts is not supported by experimental evidence. It is suggested that reduced input of fresh litter, reduced N uptake by plants and the resulting decline in carbon availability and immobilization of N into microbial biomass better explains the increase in N availability after clearcutting (Prescott 1997; Hope 2003; Bauhus et al. 2004).

The severity and duration of harvest-induced changes depend on the harvest system, and the soil and climate characteristics at the given site. Several studies of whole-tree harvesting have shown that nutrient losses increase through leaching after harvest (Knoepp and Swank 1997). Leaching decreased both total nitrogen and exchangeable base cations in the soil (Mroz et al. 1985\(^1\)) although amounts varied (Mann et al. 1988\(^1\); Tiedemann et al. 1988\(^1\); Swank 1988\(^1\)). Dahlgren and Driscoll (1994) found that whole-tree clear-cutting of a northern hardwood forest resulted in losses of nutrients from soil profile through leaching, increased acidification, and elevated concentrations of Al-ions in soil solution and stream water. The conclusion was that whole-tree harvest could lead to a severe ecosystem disturbance. In contrast, Briggs et al. (2000) found that net nutrient losses resulting from whole-tree harvest varied with the soil drainage class but did not exceed 5% of total capital for the nutrients studied. In a long-term study Knoepp and Swank (1997) found a significant increase in soil exchangeable cations (Ca, Mg, K) for the first 3 years after commercial sawlog harvest by clearcutting of a mixed hardwood forest. However, no adverse impacts on soil cation concentrations were observed in the long-term, as cation concentration was still above pre-treatment levels after 17-20 years.

Soil properties also change in other harvest systems that maintain more ecological functions of forests after the harvest than clearcuts. Bradley et al. (2001) compared soil properties among 4-year-old shelterwood treatment, 4-year-old clearcut, and adjacent old-growth plots in the montane coastal western hemlock biogeoclimatic zone. Forest floor pH, exchangeable Mg, total C and total N concentrations were similar in all treatments but there were differences among treatments in Bray-extractable P, exchangeable Ca, and exchangeable K. Both shelterwood and

\(^{1}\) as cited in Knoepp and Swank (1997)
clearcut harvesting significantly altered the availability of some nutrients, decreased available-C pools, and changed the functional diversity of microbial communities.

2.3 Nutrient cycling in gaps and smaller openings

Gap formation, a typical small scale disturbance created by forest management or ecosystem dynamics, is thought to have less severe effects on biogeochemistry stability of forest ecosystems than disturbance of bigger scales like clearcuts (Ritter 2004). Gaps from 0.002 ha to 0.25 ha have been examined (Mladenoff 1987; Parsons et al. 1994, Denslow et al. 1998; Luizao et al. 1998; Arunachalam and Arunachalam 2000; Ritter 2004). The largest gaps sizes studied have the same area of the minimum clearcut size definition found in the literature (Lüpke 1992, Keenan and Kimmins 1993). The ecological definition of clearcut is an area in which the majority of the opening is beyond the forest climate influence (Lüpke 1992, Keenan and Kimmins 1993). Therefore it is more ecologically rational to characterize gaps in forests as areas that are influenced by the forest climate. Ritter (2004) defines the term gap in forest ecology as “a canopy opening in a forest stand or a small area within a forest containing no trees or trees of a younger age class than the surrounding stand”\(^1\) (Fig. 2.1.).

Gap and opening conditions depend on diameter and tree height, on the shape and orientation of the gap, which influences the incoming light (Carlson and Groot 1997). The influence of a canopy gap extends into the forest (i.e. “extended gaps”) in which the forest conditions are influenced by adjacent gaps (Wong et al. 2004). The effect of the gap on nutrient cycling is modified by small-scale spatial variation in soil properties, topography, and the internal nutrient cycle of forests.

Canopy gaps generated by timber harvest or dying trees may change plant species composition, microclimate and soil nutrient availability (Mladenoff 1987; Bauhus and Bartsch 1995; Parsons et al. 1994; Gray et al. 2002; Ritter 2004). Conversely, changes in environmental factors such as temperature and moisture can be small, non-existent, or inconsistent (Bauhus and Bartsch 1995; Grey et al. 2002, Ritter 2004). Bauhus and Bartsch (1995) reported similar average daily temperatures in the gap centre and the forest, and Grey et al. (1995) found similar mean air

\(^1\) quoted from Ritter (2004), p. 4
temperatures between gaps of 40 to 2000 m$^2$ size. Soil temperature, moisture and solar radiation tend to increase from south to centre to north positions within a gap of the northern hemisphere. Soil temperatures at 5-cm soil depth increased up to 3°C above a gap size of 0.2 (tree height ratio) in the order south gap < centre < north gap (Grey et al. 2002). The most evident effect of a canopy gap is increased light levels with solar radiation levels twice and higher (2.5 to 20 mol-m$^{-2}$-day$^{-1}$) at the forest floor in gaps than in forest stands (Grey et al. 2002; Ritter 2004).

Effects of gap creation on nutrient cycling also include the creation of pit and mound topography created by root plates through windthrow, which can alter soil surface characteristics, decomposition and thus nutrient availability. In recent treefall micro-topographies ($\leq$ 30 years), mounds had significantly lower soil moisture, pH and Ca concentration than pits or undisturbed soils (Beatty and Stone 1986). However, in the long-term stand-level storage of carbon, nitrogen,

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1 quoted from Ritter (2004), p. 5
and organic matter in forest soils was not significantly altered by microtopography resulting from windthrow in old-growth forests (Liechty et al. 1997).

Predicting the effects of disturbance on nutrient cycling requires information on belowground response to gap formation. Parsons et al. (1994) suggested that a certain gap size exists, which represents a threshold above which significant losses of nutrients through leaching may occur. However, Denslow et al. (1998) found no evidence of a threshold gap size.

Denslow et al. (1998) suggest that nutrient availability in soils of treefall gaps may result from decomposition and mineralization of the large mass of fresh litter from the fallen tree. That holds only for the growing season and some studies have found no significant or inconsistent changes in decomposition, mineralization and nitrification between gaps and forest (Marrs et al. 1991; Luizao et al. 1998; Hope et al. 2003; Ritter 2004). On the other hand, several investigations have shown that N mineralization is increased in openings relative to uncut forest. Nitrogen mineralization rates increased within gaps of about 0.025 (Parsons et al. 1994) and 0.25 ha (Prescott et al. 1992) created in lodgepole pine forests, in a European beech forest in an opening of 30-m diameter (Bauhus 1996), and 65-611 m$^2$ gaps in a tropical wet forest (Denslow et al. 1998).

The effects of gap disturbance on net nitrification in the soil have been inconsistent. Mladenoff (1987) reported a large increase in soil nitrate concentrations in eastern hemlock (Tsuga canadensis) treefall gaps but little or no increase in a sugar maple (Acer saccharum) treefall gaps. Nitrate concentrations in soil also increased in small gaps in Costa Rica (Denslow et al. 1998), in the interior of British Columbia (Prescott et al. 2003), and in Denmark (Ritter 2004). However, Parker (1985)$^1$, Vitousek and Denslow (1986), and Marrs et al. (1991) found no significant increase in small gaps in tropical forests.

The effects of the specific timber harvest technique that is creating gaps are also not consistent. Removal of a 15-tree cluster (or larger) increased nitrate availability, but the removal of the same portion of trees by single-tree harvest did not have the same effect on nitrate availability (Parsons et al. 1994). On the contrary, Hope et al. (2003) found that single-tree selection harvesting increased the proportion of NO$_3^-$ in the forest floor compared to the uncut forest.

\[1\] as cited in Parsons et al. (2004)
It is commonly assumed that an “increased water availability concurrent with reduced nutrient uptake by roots in the gap can have an impact on drainage fluxes and thus export of nutrients in soil solution out of the ecosystem”\(^1\). Leaching losses of NO\(_3^-\) (64-126 kg N·ha\(^{-1}·yr\(^{-1}\)), Mg\(^{2+}\) (11 kg Mg·ha\(^{-1}·yr\(^{-1}\)), Ca\(^{2+}\) (21-24 kg Ca·ha\(^{-1}·yr\(^{-1}\)), Al\(^{3+}\) (35-69 kg Al·ha\(^{-1}·yr\(^{-1}\)), and nitrous oxide (3-11 kg N·ha\(^{-1}·yr\(^{-1}\)) were reported in gaps of 30 m diameter size in a German beech forest (Bauhus and Bartsch 1995; Bartsch 2000). They concluded that small scale disturbance can also cause large changes in element fluxes and pH with considerable element losses via leaching. In a later study of the same gaps they deduced that these losses were the result of reduced N uptake by plants, and were not caused by increased mineralization (Bauhus et al. 2004). The results were not significantly higher for Mg\(^+\) and Ca\(^{2+}\) compared to leaching losses under close-canopy forests. Mladenhoff (1987) reported that pH levels and phosphorus were significant greater in gaps and potassium and calcium levels were lower, consistent with ion mobility and greater leaching. In gaps of 65-611 m\(^2\), extractable PO\(_4^-\) was greater in gaps than in adjacent forest but did not vary as function of gap size (Denslow et al. 1998). Ritter (2004) found leaching losses of NO\(_3^-\) of about 2 kg·ha\(^{-1}\) in gaps relative to the closed forest but these losses were restricted to small areas within the whole stand.

Gap formation in forest ecosystems demonstrates only moderate changes in the nutrient cycle compared with disturbances of greater size like clearcuts. The initiated changes in nutrient availability seem to be only of short duration. In the study by Denslow et al. (1998) soil concentrations of NO\(_3^-\) and PO\(_4^-\) returned to pre-treatment levels within one year after disturbance. Furthermore, 21 months after gap formation no alteration between the gap and the beech stand was recorded in the forest floor mass, C and N content, and pH throughout the entire soil profile including the forest floor (Bauhus 1996). Bauhus et al. (2004) concluded that 8 years following silvicultural treatments gap-sized disturbance appeared to have minimal influence on soil C and N stocks.

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\(^1\) quoted from Ritter, 2004, p. 6
2.4 Gap disturbance of old-growth forests in coastal B.C.

Ecosystem

Old-growth forests have been defined by one, several, or all of the following criteria: the size of the trees, age of the trees, forest structure, species composition, and accumulation of dead organic matter (Kimmins 1992). Old-growth occurs as a part of a continuum of forest development and varies greatly over ecological gradients at several scales (Wells et al. 1998). Trees in old-growth forests have developed in the absence of allogenic processes (Oliver and Larson 1990); thus these ecosystems are the outcome of autogenic succession (Kimmins 2003).

In general, old growth forests can be seen as “a phase of stand development in which the surviving individuals of the initial cohort are approaching maximum longevity, losing physiological vigour, and becoming increasingly susceptible to disease and damage.”¹ This development stage is characterized by an increase in large standing dead trees (snags) in various states of decay, with large amounts of coarse woody debris on the ground, breakup of the canopy by gaps with a decline in overstorey leaf area, and a productive understorey layer (Well et al. 1998; Kimmins 2003). As a result, most old-growth stands contain a structural mixture of young and old trees and diverse understorey vegetation.

Ecosystem dynamics

In the hypermaritime and maritime biogeoclimatic subzones of coastal BC; with its cool summers and mild winters (Kimmins 1997; Wong et al. 2004) the frequency of large-scale, stand-replacing disturbances is low relative to the longevity of the tree species. Fire is infrequent with mean return intervals that usually exceed 350 to 1000 years (Wong et al 2004). Wind in association with pathogens such as hemlock dwarf mistletoe is the major natural disturbance factor. Wind damage in these forests (windthrow, stem break, crown damage) creates small canopy gaps of ten trees or less, which does not push the ecosystem back to an earlier seral stage (Kimmins 2000; Wong et al. 2004). These gap processes allow tree establishment and recruitment to the upper canopy on a tree-by-tree basis (Kimmins 1997; Wells et al. 1998). In these unmanaged old-growth forests, gaps constitute about 16 to 39% of the forest area (Wong et

¹ quoted from Kimmins (2003), p.437
al. 2004) creating uneven-aged, structurally diverse forests with late-successional characteristics at both stand and landscape levels (Kimmins 2003).

Variable-Retention (VR) Harvesting

Forest management has become multipurpose and has not only to provide timber but also other values like ecosystem and landscape integrity, biodiversity, recreation, and drinking water. A variable-retention system is seen as a spatially variable strategy that accounts for different values, site types, economics of management, forest worker safety, in forest ecosystem management (Kimmins 2002). Retention means permanent, enduring conservation of various forest “structures” or habitat elements after harvest (Scientific Panel 1995). This silviculture system emerged in the late 1990s and focuses on the retention of biological values and aims to maintain structural and compositional attributes of old forests in coastal BC. Ecosystem structural elements that vary in their ecological rotations are sustained in the same area by creating gaps in a matrix of forest cover (Kimmins 2003). Therefore, it has been recommended as the sustainable approach for timber management of coastal old-growth forests (Scientific Panel 1995).

Because this silvicultural approach is new to B.C. and since gap studies in different forest ecosystems have shown diverse results, it is difficult to make assumptions about nutrient availability in variable-retention systems. VR is thought to be a more sustainable approach to forest management for nutrient cycling but it is yet to be determined if variable retention systems emulates short and long-term patterns of old-growth forests. A better understanding of gap dynamics regimes requires more research in old-growth forest ecosystems coastal B.C., especially if knowledge of gap dynamics is to be used in forest management.
3 **Objective and Hypothesis**

The objective of this Masterthesis is to investigate the effect of disturbance of the forest canopy on the availability of nutrients in temperate old-growth forests in coastal British Columbia. The survey evaluates natural gaps and close-canopy forest phases to determine if there is a consistent effect of gap formation on nutrient availability. It is also examined if above-ground biotic and abiotic factors like rooting substrate influence soil nutrient supply rates. Out of the investigated parameters this study will try to identify a key soil nutrient element or pattern of elements which indicate nutrient dynamics after gap creation. Implications of the results for variable retention silviculture and possible effects on gap regeneration will be discussed.

Based on the literature, it is hypothesised that the availability of nutrients will be higher in gaps, especially for inorganic NO\textsubscript{3}\textsuperscript{-} and Al\textsubscript{3+}. The availability of nutrients on plots of each treatment should decrease in the order Gap-North > Gap-South > Forest North > Forest South. It is expected that the difference between gap and closed-forest will be stronger than the spatial variation within each treatment. The expectations are based on the following arguments:

- Soil moisture, temperature and solar radiation tend to increase from south to centre to north positions within a gap and to decrease from forest north to forest south positions due to the increasing influence of the surrounding forest
- Increasing temperature and moisture in gaps causes higher microbial activity, greater ion movement and faster chemical reactions of ions in the soil
- Research has shown inconsistent effects of gap formation on decomposition and mineralization processes; therefore it is expected that higher N availability results from reduced uptake by trees
- Changes in the nature of forest soil following gap formation are minor

Thus, with respect to nutrient cycling, VR silviculture could be an appropriate management method to emulate fine-scale canopy disturbance.
4 Material and Methods

4.1 Study Site

This study was conducted in natural gap and closed-canopy forest plots situated in old-growth forests at two sites. One site was in the Capilano and Seymour Watersheds (GVRD) approximately 14 km north of North Vancouver; the other was in the Bamfield-Huu-ay-aht Community Forest approximately 1.5 km south of Bamfield on the south-west coast of Vancouver Island. At the Capilano watershed, plots were located in pairs of three within a west-east distance of approximately 3 km. In the Seymour Watershed two neighboring transects were established in west-east direction at a distance about 1.5 km to one single transect. A fourth transect was situated approximately 14 km north of the other plots. At the Bamfield site, 15 plots were located at two sites within approximately 2 km.

Bamfield

The plots were located at 10-30 m a.s.l. in two old-growth stands of the very wet hypermaritime Coastal Western Hemlock biogeoclimatic subzone\(^1\) with a Southern Variant (CWH vh1). The forest is dominated by western redcedar (*Thuja plicata* Donn ex D. Don) (68%; often spike-topped) followed by western hemlock (*Tsuga heterophylla* Raf.) (27%). Other tree species are in relatively equal proportions Sitka spruce (*Picea sitchensis* Bong.), western white pine (*Pinus monticola* Dougl.), lodgepole pine (*Pinus contorta var. Latifolia* Dougl.), Pacific silver fir (*Abies amabilis* Dougl. ex Loud.) and Pacific yew (*Taxus brevifolia* Nutt.). The average stand volume is 493 m\(^3\)·ha\(^{-1}\) with an average MAI of 2.78 m\(^3\)·ha\(^{-1}\)·yr\(^{-1}\) (Morgan 2002).

Average precipitation for the Bamfield area is approximately 2814 mm with 2801 mm as rain and 16 cm as snowfall. July and August are normally the driest months, 80-82% of the annual precipitation falls in the month October to March. The mean annual temperature is 9.8°C with mean monthly variations from 5.9°C in winter to 13.7°C in summer (Environment Canada 2002). The general topography is flat to rolling with occasional knobs and wet depressions with

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\(^1\) Ministry of Forestry of BC (n.d.)
many areas directly adjacent to salt water. Mineral soils within the Community Forest exhibit a
hummocky topography with some gentle inclines.

**Capilano and Seymour watershed (GVRD)**

The research plots are situated at 450-650 m a.s.l. in old-growth forest dominated by
western hemlock and Pacific silver fir with some western redcedar and Douglas-fir (*Pseudotsuga
menziesii* Mirb.). The investigated old-growth forest stands are approximately 850 years old
(Daniels et al. 1995). Common understorey species are deer fern (*Blechnum spicant* (L.) Roth),
bunchberry (*Cornus canadensis* L.), *Hylocomium splendens* (Hedw.) B.S.G., false azalea
(*Menzesia ferruginia* Sm.), *Rhytidiadelphus loreus* (Hedw.) Warnst., *Rhytidiopsis robusta*
(Hedw.) Broth., Alaskan blueberry (*Vaccinium alaskaense* Howell) and oval-leaved blueberry (*V.
* ovalifolium* Sm.) (Daniels 1994).

The site has a mean annual temperature of 6.9°C with a mean monthly variation from 3°C
in winter to 10.7°C in summer and is located in the Submontane Very Wet Maritime Coastal
Western Hemlock (CWHvm1) biogeoclimatic subzone¹. The mean annual precipitation is 3330
mm (75-78 % of the annual rainfall in the month October to March) with 2872 mm as rain and
465 cm as snowfall (Environment Canada 2002). The general topography is mountainous with
steep slopes which are moderately mounded.

**4.1.1 Soil description**

Soils at each site were classified as well to moderately well drained Ferro-Humic Podzols
(Centre for Land and Biological Resources Research Canada 1992, Capilano Watershed profiles
by Daniels 1993, Bamfield soil profile see Appendix pp. 63-65), derived from colluvial and
glacial till with gravelly loamy sand (GVRD) or gravelly sandy loam (Bamfield) surface textures
overlain by a forest floor of variable depth which contains a large component of decaying wood.
The thickness of the LFH layer was measured by taking forest floor cores at each of the Bamfield
plots. The average thickness of the forest floor was 10 cm with a range from 2 to 28 cm
(SD = 5.3 cm).

¹ Ministry of Forestry of BC (n.d.)
4.1.2 Natural Disturbance Type

According to the Forest Practices Code Biodiversity Guidebook 1 definitions, the natural disturbance type (NDT) of the Capilano and Bamfield plots are NDT1 (ecosystems with rare stand-initiating events\(^1\)). The major form of disturbance is windthrow of isolated individual trees and the forest replacement intervals by the created gaps range from 300 to 1000 years (CSSP 1995). Canopy trees grow to heights exceeding 60 m and diameters of up to 350 cm. The canopy of the forests at the examined plots in Bamfield and the GVRD is a multi-storied, with canopy gaps to snags and downed trees. The transition between forest canopy and canopy gap is often blurred (personal observation), which has led to a well-developed and diverse understorey vegetation layer. In unmanaged coastal old-growth forests, gaps constitute about 16% to 39% of the forest area (Wong et al. 2004).

4.2 Plot description

4.2.1 Gap assessment

Gaps were assessed and described in 2002 to 2004 Dr. Lori Daniels, Amanda Stan, Janneke Lade, Jennifer Passmore, and Dennis Morgan. At Bamfield, gap assessment started in 2004. The structure of the canopy of the forest was assessed by walking 100-m transects (Daniels et al. 2003). At each metre along the transect, the canopy was described as canopy gap, expanded gap, or closed-canopy (Lertzman et al. 1996) and the presence of subcanopy trees (“gap-fillers”) was noted.

At the GVRD site and the Bamfield site the size and shape of 10 gaps was assessed by measuring the azimuth and distance from the gap centre to the bole of each tree forming the boundary of the gap (Lertzman et al. 1996). The species, dbh, canopy position and location of gap-boundary trees and subcanopy gap-fillers were recorded. All gap-makers, boundary trees and gap-fillers were tagged for future reference. The species and decay stage was determined for each of the dead trees (gap-makers) that created the gaps. Logs and snags with a dbh > 20 cm occurring in the gap were identified as gap makers. The time of gap formation was determined by

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\(^1\) Ministry of Forestry (1995)
coring the gap makers and subsampling regeneration for age and growth rates using tree-ring analysis (Daniels et al. 1997; Pearson et al. 2003).

Canopy openness and understorey light environment were quantified in each plot using hemispheric canopy photographs (Frazer et al. 2000). Tree composition and density was assessed in each forest plot using the point-centre-quarter method (Cottam and Curtis 1956). For each plot, percent cover of substrate (mineral soil, wood, or organics), percent cover of bryophytes, herbs and shrubs by species, and density of seedlings and saplings stratified by species and substrate were measured (Pearson et al. 2003).

4.2.2 Gap description

Bamfield

A total of 94 gap makers (GM) were found. In every gap, snags and logs were thought to be the origin of gap formation. An average number of 9 gapmakers was found in gaps with range of 7 to 16 gapmakers. It was not possible to clearly identify if a snag or log actually formed the gap or just occurred where the canopy gap occurred. About 49 % of the total gap makers in the gaps were logs, 46 % were snags, 4 % were a combination of snags and logs, and one GM was a large fallen branch. Of the 94 GM, 32 were redcedars, 31 were hemlocks, 3 were fir, 1 was Pacific yew, and 27 could not be identified. The structure of the boundary trees was as follows: 29 % were emergent, 51 % were canopy trees, and 29 % were subcanopy and suppressed.

The forest had a moderate to patchy tree cover by western hemlock, western redcedar, and Pacific silver fir. Scattered very large trees (age > 250 years) rose above main canopy layer. The dense shrub layer in gaps was comprised of frequent and tall salal (Gaultheria shallon Pursh) with varying amounts of red huckleberry and evergreen huckleberry (Vaccinium ovatum Pursh). The herb layer was less dense but well-developed, consisting mainly of deer fern. Moss cover was variable and comprised of Oregon beaked moss (Kindbergia oregano (Sull.) Ochyra) and step moss (Hylocomium splendens (Hedw.) B.S.G) (Teversham 2003).

Of the total 800-m transect length the portion of closed-canopy was 62.4 % (SD = 20.5), canopy cap 10.0 % (SD = 10.7), and expanded gap 27.6 % (SD = 16.3). The mean gap size is 151.3 m² with a range of 28.8 to 274.9 m² (SD = 80.12 m²). The age of gaps are not known because assessment started only in 2004. The area of each gap was as follows: Gap 1 - 97.7 m²,
Gap 2 - 110.3 m², Gap 3 - 274.9 m², Gap 4 - 28.8 m², Gap 5 - 172.6 m², Gap 6 - 166.7 m², Gap 7 - 110.5 m², Gap 8 - 198.8 m², Gap 9 - 83.8 m², Gap 10 - 268.6 m². The gaps are not influenced by the aspect of their topographical position because the area is flat. The results of the determination of gap formation were not accomplished at the point of completion of this thesis.

**Capilano and Seymour watershed (GVRD)**

In gaps as well in forest common understorey species with ground coverage of 5 % and more were Alaskan blueberry (*Vaccinium alaskaense* Howell), deer fern (*Blechnum spicant* (L.) Roth), oval-leaved blueberry (*V. ovalifolium* Sm.), red huckleberry (*Vaccinium parvifolium* Sm.), false azalea (*Menzesia ferruginia* Sm.), False Lily of the Vally (*Maianthemum dilatatum* Wood). Occurring mosses were *Hylocomium splendens* (Hedw.) B.S.G., *Rhytidiadelphus loreus* (Hedw.) Warnst., *Rhytidiopsis robusta* (Hedw.) Broth., and regenerating tree species were Pacific Silver Fir, Western Hemlock, and western redcedar. In gaps additional ground vegetations consisted out of bunchberry (*Cornus canadensis* L.), devils Club (*Oplapanax horridus* (Sm.) Miquel), Lady Fern (*Athyrium filix-femina* (L.) Roth), fern goldenthread (*Pityrogramma triangularis*), salmonberry (*Rubus spectabilis* Pursh), spiny wood fern (*Dryopteris expansa* Presl), and thimbleberry (*Rubus parviflorus* Nutt.) (plot observations by Passmore 2004).

All gap makers in the GVRD are exclusively uprooted trees. The mean gap size is 297.5 m² with a range of 139.9 to 558.7 m² (SD = 131.1 m²). Area of each gap was as follows: Gap 1 – 216.4 m², Gap 2 – 558.7 m², Gap 3 – 139.9 m², Gap 4 – 224.7 m², Gap 5 – 384 m², Gap 6 – 241.1 m², Gap 7 – 151.5 m², Gap 8 – 429.1 m², Gap 9 – 309.3 m², Gap 10 – 317 m². The slopes of gaps were not measure in the gap assessment. The topographical aspect of six gaps is to the South to Southeast, whereas the other four gaps are faced to the Northwest. The age of gap formation at the GVRD site could not be included in this study due to the fact that these data is used by other researchers for their own surveys.
4.3 Nutrient availability

4.3.1 Plant Root Simulator (PRS)™-Probes

Nutrient availability was measured using ion-exchange resins (Plant Root Simulator (PRS)™-probes; Western Ag Innovations Inc., Saskatoon, Saskatchewan) incubated in the forest floor for a burial period of 4 to 8 weeks. The ion-exchange membrane (IEM) method is an in situ soil testing tool which promotes a measure of dynamic ion fluxes in soils according to actual field conditions (i.e. soil type, moisture, temperature, microbial activity) (Qian and Schoenau 2002; Hangs et al. 2004; Western Ag Innovations Inc. 2004). Long-term burial of ion-exchange resins provides information of nutrients supply rates from ions diffusion from greater distance, cation exchange and slow release of nutrients from decomposition and mineralization (Qian and Schoenau 2002). When chemically pre-treated with 0.5N HCL and 0.5N sodium bicarbonate (NaHCO₃), the anion and cation exchange resin membranes exhibit surface characteristics and nutrient sorption phenomena that closely resemble a plant root surface. The anion (PRS)™-probes (orange) adsorbs all nutrients anions and through a chelating pre-treatment also micronutrients metals. The cation exchange probes (purple) adsorb nutrients cations (Western Ag Innovations Inc. 2005). (PRS)™-probes (15 cm x 3 cm x 0.3 cm) consist of either cation- or anion-exchange resin membrane (approximately 17.5 cm² including both sides of the membrane) encased in a plastic holding device.

4.3.2 Sampling of Probes

Four permanent plots (2 m x 2 m) were installed in each identified gap on a north to south axis in order to sample four different environmental conditions (Gap-North (GN), Gap-South (GS) representing gap conditions, and Forest-North (FN), Forest-South (FS) representing close-canopy conditions). The geographically centre of gaps was located and Gap-North and Gap-South plots were then installed half way to the gap boundaries. The Forest-North and Forest-South plots were set up inside the forest 10 m from the respective gap boundary. In some case forest plots would be in another opening in the forest. The procedure was then to go across the
gap and install the plot 10 m in the forest from this gap boundary. This sample design created 40 observations for the Bamfield site and 40 observations for the GVRD watershed sites.

In Bamfield additionally 5 axes were installed in closed-canopy forest (20 observations) as pre-treatment measurement plots for three variable retention treatments. These plots also were sampled for four different locations on the axis Forest-South-VR (FS-VR), Gap-South-VR (GS-VR), Gap-North-VR (GN-VR), and Forest-North-VR (FN-VR).

At each plot, four (PRS)™-probes for each cation and anion exchange capacity were inserted vertically into the FH layer using a soil knife (a long, tapered blade with the diameter size of the soil probes) causing minimal soil disturbance. Complete contact between the soil and the resin membrane was ensured. The (PRS)™-probes were randomly distributed over the 2 x 2 plots but at every spot one probe of each exchange capacity was put in the soil only 2 to 5 cm apart. Before installation, during transport to sites and after collecting the (PRS)™-probes were stored in plastic bags in a cool box to ensure that they stayed wet and cool. At the end of the burial period, the probes were removed from soil and residual soil was cleaned of the membrane surface using a coarse brush. In the lab they were thoroughly washed with deionised water ensuring the complete removal of any residual soil in cracks or plastic casting. The cleaned (PRS)™-probes were transferred to Ziploc® bags and shipped to the Western Ag Innovations Inc. laboratory in Saskatoon, Saskatchewan for chemical analysis (Hangs et al. 2004; Western Ag Innovations Inc. 2004). The (PRS)™-probes were analysed for the following cations and ions: NO$_3^-$, NH$_4^+$, Ca$^{2+}$, Mg$^{2+}$, K$^+$, H$_2$PO$_4^-$, Fe$^{2+}$, Mn$^{2+}$, Cu$^{2+}$, Zn$^{2+}$, B(OH)$_3$, SO$_4^{2-}$, Pb$^{2+}$, Al$^{3+}$. The four (PRS)™-probes of each exchange capacity of each plot were analysed together making up one composite sample, for a total of 160 samples (two sites + one replication at the Bamfield site).

At the GVRD watersheds (PRS)™-probes were installed on July 23$^{rd}$ 2004 and collected on September 20/21 2004 (burial time = 59 days). The July and the period until the 21$^{st}$ of August 2004 were very dry with only 20 mm of precipitation falling over this time$^1$. Therefore it was decided to leave the (PRS)™-probes for another month in the forest floor. At Bamfield site the first set of (PRS)™-probes were inserted on August 7/8 2004 and collected on September 11/12 2004 (burial period = 35 days), and the 2nd set of (PRS)™-probes were installed on December 15/16 2004 and collected on January 27/28 2005 (burial period = 43 days).

$^1$ Environment Canada (n.d) Weather data, [On-line]
In situ burial of ion-exchange resins membrane express the nutrient supply rate into a ion
sink as the amount of nutrient absorbed per surface area of IEM during the duration of burial
(Qian and Schoenau 2002; Hangs et al. 2004). The nutrient availability in the soil thus was
expressed as μg Ion·10 cm⁻² burial period⁻¹.

Fig. 4.1. (PRS)™-probes were inserted vertically in the FH layer of the forest floor.

4.4 Statistical Analysis

Objective: Test for differences in availability of nutrients between natural gaps and forest using
a controlled, replicated experiment.

All analyses were conducted using SAS for Windows software (version 8.02, SAS
Institute Inc., Cary, N.C.). Before each analysis, data outliers appropriate to the design of the
analysis were removed that were greater than 3 standard deviations from the mean prior the test
for differences in availability of nutrients. The accepted level of significance was P < 0.05, unless
stated otherwise.
The GLM procedure as a split-plot design was used to analyse for difference in availability of nutrients between replication (summer/winter) and environmental condition (n = 2 x 10 plots) in Bamfield.

Also in SAS the GLM procedure as a replicated randomized complete block design was used to analyse for difference in availability of nutrients between environmental conditions and bioclimatic zone for the summer burial period. Nutrient supply rates for each environmental condition of 10 plots are used of the summer sampling at the GVRD site and in Bamfield.

To compare the closed-canopy plots of the natural gap assessment and the pre-treatment plots of the variable retention treatments only Forest-North and Forest-South plots are analysed in SAS as a split-plot design. Due to the fact that for the VR plots only five replication were sampled five replication of the data set for FN and FS were randomly removed for the test for differences.

For all analyses mean comparison were performed with use of the least significant difference (LSD) at a significant level of 0.05. The LSD option was used to carry out pairwise t tests of the different means between treatments. All data were tested for homogeneity of variance and normality. For data which had an insufficient homogeneity (ChSq < 0.05) the data were standardized using a power transformation (Kuehl 1999). In some case transformation could not be performed because no regression could be found between the standard deviation of the residuals and the mean.

One plot was lost due the construction of a new logging road at the Bamfield site. Five additional plots were not replicated because they where not revisited at the second installation of (PRS)™-probes at Bamfield.
5 Results

5.1 Environmental conditions

5.1.1 Bamfield

Light levels measured as canopy openness were on average 3.6 % higher in gaps than in forest plots. However, this was only statistical significant if just gap and forest plots were evaluated. If forest-VR plots were included in the analysis the difference diminished and a significantly greater canopy openness was evaluated between forest and forest-VR plots. Forest-VR plots had the highest light levels of the subcanopy light environment with average 14.8 % open canopy, followed by gap plots with 12.4 %, and forest plots with 8.8% (Fig. 5.1 and Table 5.2).

The vegetation cover of the understorey including mosses in the 2 x 2 m plots did not differ between gap or forest canopy. Only cumulative vegetation cover of shrubs in gaps (average cover 55 %) was significantly greater compared to forest plots (average cover 32%) if forest-VR plots were excluded in the statistical analyses (Fig 5.1 and Table 5.1). Also for the rooting substrate significant difference occurred only if forest-VR plots were excluded from the analysis. Then the percentage cover of forest floor was consistently greater in open canopy plots with average cover of 57.5 % than in forest plots with 45.6 % (Fig 5.2 and Table 5.2). The difference in decaying wood as rooting substrate is the opposite of the forest floor because the rooting substrate forest floor and decaying wood are summed up to a total coverage of 100 percent. Regeneration of trees evaluated as numbers of seedlings and sapling in the 2 x 2 m plots is rare with a total numbers of 11 seedlings and 1 sapling in forest plots, 15 seedlings and 3 saplings in gaps, and one of each in forest-VR plots.
**Table 5.1. Percentage of vegetation cover in the 2 x 2 m plots of gaps, forest, and forest-VR**

<table>
<thead>
<tr>
<th>Plot</th>
<th>Trees</th>
<th>Shrubs</th>
<th>Ferns</th>
<th>Herbs</th>
<th>Mosses</th>
</tr>
</thead>
<tbody>
<tr>
<td>GN</td>
<td>3.8 ± 8.1</td>
<td>45.4 ± 24.1</td>
<td>1.9 ± 2.1</td>
<td>37.8 ± 17.4</td>
<td>70.9 ± 21.5</td>
</tr>
<tr>
<td>GS</td>
<td>1.8 ± 2.5</td>
<td>57.6 ± 21.4</td>
<td>2.1 ± 2.7</td>
<td>38.1 ± 12.3</td>
<td>66.3 ± 16.6</td>
</tr>
<tr>
<td>FN</td>
<td>2.7 ± 6.5</td>
<td>29.8 ± 8.8</td>
<td>2.1 ± 1.7</td>
<td>38.1 ± 16.8</td>
<td>63.1 ± 12.5</td>
</tr>
<tr>
<td>FS</td>
<td>0.7 ± 1.5</td>
<td>33.7 ± 13.2</td>
<td>1.9 ± 2.3</td>
<td>34.0 ± 21.2</td>
<td>60.4 ± 15.7</td>
</tr>
<tr>
<td>FN-VR</td>
<td>0.6 ± 1.3</td>
<td>52.5 ± 20.2</td>
<td>0.1 ± 0.2</td>
<td>26.0 ± 15.6</td>
<td>79.9 ± 17.6</td>
</tr>
<tr>
<td>FS-VR</td>
<td>0.1 ± 0.1</td>
<td>47.0 ± 29.8</td>
<td>0.4 ± 0.9</td>
<td>32.1 ± 17.5</td>
<td>58.2 ± 25.1</td>
</tr>
</tbody>
</table>

Note: "Mean ± standard deviation (n = 10 for GN, GS, FN and FS; n = 5 for FN-VR and FS-VR); No significant difference was observed between plots of pre-treatment Forest North-VR (FN-VR), control Forest North (FN), Gap North (GN), pretreatment Forest South-VR (FS), control Forest South (FS), and Gap South with the LSD option; vegetation cover for trees with a diameter less than 10 cm"
Table 5.2. Percentage of canopy openness relative to visible sky beneath forest canopy and percentage coverage of rooting substrate in gap, forest and forest-VR plots

<table>
<thead>
<tr>
<th>Plot</th>
<th>% Canopy Openness</th>
<th>Light Source</th>
<th>Rooting Substrate%</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Decaying Wood</td>
<td>Forest Floor</td>
</tr>
<tr>
<td>GN</td>
<td>12.01 ± 2.66</td>
<td>41.1 ± 19.6</td>
<td>58.9 ± 19.6</td>
</tr>
<tr>
<td>GS</td>
<td>11.96 ± 3.71</td>
<td>44.2 ± 24.6</td>
<td>55.8 ± 24.6</td>
</tr>
<tr>
<td>FN</td>
<td>9.26 ± 2.91</td>
<td>63.0 ± 15.2</td>
<td>37.0 ± 15.2</td>
</tr>
<tr>
<td>FS</td>
<td>8.30 ± 4.02</td>
<td>45.2 ± 24.2</td>
<td>54.2 ± 24.2</td>
</tr>
<tr>
<td>FN-VR</td>
<td>12.84 ± 6.04</td>
<td>55.1 ± 14.0</td>
<td>44.9 ± 14.0</td>
</tr>
<tr>
<td>FS-VR</td>
<td>16.72 ± 4.15</td>
<td>27.0 ± 18.2</td>
<td>73.0 ± 18.2</td>
</tr>
</tbody>
</table>

Note: Mean ± standard deviation (n = 10 for GN, GS, FN and FS; n = 5 for FN-VR and FS-VR); no significant difference was observed between plots of pre-treatment Forest North-VR (FN-VR), control Forest North (FN), Gap North (GN), pre-treatment Forest South-VR (FS), control Forest South (FS), and Gap South with the LSD option.

Fig. 5.2. Mean percentage coverage of surface rooting substrate (i.e. forest floor or decaying wood) in gap, forest and forest-VR in the 2 x 2 m plots; error bars refer to one standard deviation.

Note: No significant difference was observed between plots of pre-treatment Forest North-VR, control Forest North, Gap North, pre-treatment Forest South-VR, control Forest South, and Gap South with the LSD option.
5.1.2 GVRD

Environmental information of understorey light environment and the time of gap formation could not be included in this thesis because these data are being used by other researchers for their own surveys.

Percentage of coverage of rooting substrate in the 2 x 2 m plots of gaps and forest plots was homogenous with large variability within plots (Table 5.3 and Fig. 5.3). The vegetation coverage was more heterogeneous between plots but only cumulative average coverage of shrubs (P < 0.1) and ferns in gaps was higher than in forest plots (Table 5.3 and Fig. 5.4.). In contrast to the Bamfield site, mosses were non-existent in most plots (data not shown). As with the Bamfield site, for all other coverage observations no significant differences were observed between gaps and forest at the GVRD site.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Rooting substrate%</th>
<th>Vegetation cover %</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Decaying Wood</td>
<td>Forest Floor</td>
</tr>
<tr>
<td>GN</td>
<td>17.2 ± 18.9</td>
<td>82.5 ± 18.8</td>
</tr>
<tr>
<td>GS</td>
<td>17.8 ± 14.9</td>
<td>74.9 ± 26.7</td>
</tr>
<tr>
<td>FN</td>
<td>14.9 ± 15.4</td>
<td>79.0 ± 18.6</td>
</tr>
<tr>
<td>FS</td>
<td>16.5 ± 16.0</td>
<td>80.6 ± 14.9</td>
</tr>
</tbody>
</table>

Note: *Mean ± standard deviation (n = 10 for GN, GS, FN and FS), no significant difference was observed between plots of control Forest North (FN), Gap North (GN), control Forest South (FS), and Gap South with the LSD option.*
Fig. 5.3. Mean percentage coverage of surface rooting substrate (i.e. forest floor or decaying wood) in gap, and forest plots; error bars refer to one standard deviation

Note: No significant difference was observed between control Forest North, Gap North, control Forest South, and Gap South plots with the LSD option

Fig. 5.4. Mean percentage of coverage of trees (diameter < 10 cm), shrubs and ferns in gap and forest plots, error bars refer to one standard deviation

Note: No significant difference was observed between control Forest North, Gap North, control Forest South, and Gap South plots with the LSD option
5.2 Nutrient supply rates

5.2.1 Bamfield

Gap plots versus forest plots

Supply rates of nitrogen tended to be higher in north position with no clear tendency of a gap effect for the summer burial period. In contrast, availability of \( \text{NO}_3^- \) and \( \text{NH}_4^+ \) and thus Total-N was noticeable greater in both gap plots for the winter burial time (Fig. 5.5, Fig 5.6 and Table 5.4, 5.5). However, a significant increase of supply rates could not be determined from Forest South to Gap North plots. Only cumulative nutrient supply rates of \( \text{NO}_3^- \) were found to be slightly higher in gaps in the winter burial period (P < 0.1).

The nutrient supply rates of the cations were inconsistent with changeable availabilities between positions for both sample seasons; all means were not significantly different. The observed order of the availability changed between the summer and the winter sampling. For calcium the nutrient supply rates decreased in the order GS > FN > GN > FS in summer, which changed in the winter to GS > FS > GN > FN (Fig. 5.7.). Availability of magnesium was in the order GS > FN > FS > GN in summer and in winter FS > GS > FN > GN; potassium showed following availability FN > GN > GS > FS in summer and in winter GN > FN > FS > GS (Fig. 5.7 and 5.8).

Availability of \( \text{Al}^{3+} \) in winter and of \( \text{Fe}^{2+} \) in summer showed an increasing order from Forest South to Gap North but it was nevertheless not statistically significant and also the order of availability changed between seasons (Fig 5.10. and Table 5.4.). In contrast, nutrient supply rates of sulphur for the summer burial time showed the opposite availability of \( \text{SO}_4^{2-} \) than expected (FS > FN > GS > GN), which could be an indication of higher aerosol deposition caused by the higher interception of trees in forest plots. Nevertheless, this change as well was not significant and in the winter burial period supply rates increased in a different order (FS < GN < FN < GS). For the other analysed micronutrients no difference between gaps and forest plots could be found. Supply rates of \( \text{Pb}^{2+} \) were not compared because most observations were beneath the detection limit of the method.
5 Results

Forest plots versus forest VR plots

As expected, no differences in nutrient supply rates were found between forest plots and forest-VR plots for all nutrients except Ca\(^{2+}\). Supply rates of calcium were significantly greater in Forest North-VR plots than in Forest North plots in the summer burial period.

Comparison of nutrient supply rates was not sensible for NO\(_3^+\) for both burial periods and for Cu\(^{2+}\) and Pb\(^{2+}\) for the winter measurement because too many values were below the analytic method detection limit. Nutrient supply rates were found to be considerable greater for Ca\(^{2+}\), Zn\(^{2+}\), B(OH)\(_3^0\), and a slightly greater for H\(_2\)PO\(_4^-\) (P < 0.1), Mn\(^{2+}\) (P < 0.1), and SO\(_4^{2-}\) (P < 0.1) for the burial period August/September. Sampling seasons had no effect on the availability of Total-N, NH\(_4^+\), Mg\(^{2+}\), K\(^+\), Fe\(^{2+}\) and Al\(^{3+}\).

Including the Forest-VR plots in the comparison of nutrient supply rates diversified even more the picture of availability of nutrients observed in Bamfield because all nutrient ions were inconsistent in their availability among positions. The availability of NO\(_3^+\) and Total-N in Forest South-VR plots was almost as high as in Gap North plots in winter. The nutrient supply rates of Ca\(^{2+}\) were the highest in pre-treatment Forest North-VR plots for both sampling seasons but almost as low in pre-treatment Forest South as in Forest South plots in summer. The highest availability of Al\(^{3+}\) and SO\(_4^{2-}\) was in pre-treatment Forest South-VR and control Forest South plots.

Summer versus winter

Significant higher nutrient supply rates were found for Total-N, NO\(_3^+\), Fe\(^{2+}\), and a slightly greater availability for Al\(^{3+}\) (P < 0.1) for the burial period December/January. In contrast, availability of Ca\(^{2+}\), Mg\(^{2+}\) (P < 0.1), K\(^+\), H\(_2\)PO\(_4^-\), Zn\(^{2+}\), and B(OH)\(_3^0\) was considerably greater for the burial period August/September. No difference in availability of nutrients between seasons was recognized for NH\(_4^+\), Mn\(^{2+}\), SO\(_4^{2-}\), and Cu\(^{2+}\).
Fig. 5.5. Mean nutrient supply rates of NO$_3^-$ and NH$_4^+$ in summer (burial period = 35 days) and winter (burial period = 43 days) at the Bamfield site; error bars refer to one standard deviation.

Note: No significant difference was observed between plots of pre-treatment Forest North-VR (FN-VR), control Forest North (FN), Gap North (GN), pre-treatment Forest South-VR (FS-VR), control Forest South (FS), and Gap South with the LSD option; a only one observation was made; b no observations, nutrient supply rates were below method detection limits.

Fig. 5.6. Mean nutrient supply rate of Total-N in summer (burial period = 35 days) and winter (burial period = 43 days) at the Bamfield site; error bars refer to one standard deviation.

Note: No significant difference was observed between plots of pre-treatment Forest North-VR, control Forest North, Gap North, pre-treatment Forest South-VR, control Forest South, and Gap South with the LSD option; Total N is based on addition of NO$_3^-$ and NH$_4^+$ prior to adjustment for method detection limits.
Fig. 5.7. Mean nutrient supply rates of Ca\(^{2+}\) and Mg\(^{2+}\) in summer (burial period = 35 days) and winter (burial period = 43 days) at the Bamfield site; error bars refer to one standard deviation; values with different letters are significant different among treatments (p < 0.05)

Note: No significant difference was observed for Mg between plots of pre-treatment Forest North-VR, control Forest North, Gap North, pre-treatment Forest South-VR, control Forest South, and Gap South; and for Ca between plots of Gap North, pre-treatment Forest South-VR, control Forest South, and Gap South with the LSD option.

Fig. 5.8. Mean nutrient supply rates of K\(^{+}\) and SO\(_4\)\(^{2-}\) and in summer (burial period = 35 days) and winter (burial period = 43 days) at the Bamfield site; error bars refer to one standard deviation.

Note: No significant difference was observed between plots of pre-treatment Forest North-VR, control Forest North, Gap North, pre-treatment Forest South-VR, control Forest South, and Gap South with the LSD option.
Fig. 5.9. Mean nutrient supply rates of $H_2PO_4^-$ in summer (burial period = 35 days) and winter (burial period = 43 days) at the Bamfield site; error bars refer to one standard deviation.

Note: No significant difference was observed between plots of pre-treatment Forest North-VR, control Forest North, Gap North, pre-treatment Forest South-VR, control Forest South, and Gap South with the LSD option.

Fig. 5.10. Mean nutrient supply rates of $Al^{3+}$ in summer (burial period = 35 days) and winter (burial period = 43 days) at the Bamfield site; error bars refer to one standard deviation.

Note: No significant difference was observed between plots of pre-treatment Forest North-VR, control Forest North, Gap North, pre-treatment Forest South-VR, control Forest South, and Gap South with the LSD option.
Table 5.4. Nutrient supply rates in gap, forest, and forest-VR plots for the summer sampling at the Bamfield site*

<table>
<thead>
<tr>
<th>Plot</th>
<th>Total-N</th>
<th>NO$_3^-$</th>
<th>NH$_4^+$</th>
<th>Ca$^{2+}$</th>
<th>Mg$^{2+}$</th>
<th>K$^+$</th>
<th>H$_2$PO$_4^-$</th>
</tr>
</thead>
<tbody>
<tr>
<td>GN</td>
<td>8.24 ± 4.58</td>
<td>5.90 ± 3.85</td>
<td>3.69 ± 1.03</td>
<td>772.2 ± 236.0</td>
<td>462.1 ± 158.5</td>
<td>173.6 ± 73.5</td>
<td>2.67 ± 2.42</td>
</tr>
<tr>
<td>GS</td>
<td>6.71 ± 3.15</td>
<td>3.76 ± 0.20</td>
<td>2.80 ± 0.91</td>
<td>833.5 ± 375.5</td>
<td>532.2 ± 158.9</td>
<td>167.9 ± 89.9</td>
<td>1.01 ± 0.66</td>
</tr>
<tr>
<td>FN</td>
<td>8.68 ± 6.30</td>
<td>5.05 ± 3.62</td>
<td>3.33 ± 1.42</td>
<td>799.5 ± 305.6</td>
<td>498.1 ± 163.0</td>
<td>185.1 ± 117.5</td>
<td>0.96 ± 0.35</td>
</tr>
<tr>
<td>FS</td>
<td>6.40 ± 1.93</td>
<td>3.80 ± 0.28</td>
<td>3.28 ± 1.55</td>
<td>710.3 ± 298.6</td>
<td>491.8 ± 205.9</td>
<td>165.1 ± 81.9</td>
<td>2.02 ± 1.93</td>
</tr>
<tr>
<td>FN-VR</td>
<td>2.80 ± 0.47</td>
<td>.</td>
<td>2.48 ± 0.61</td>
<td>1029.5 ± 460.1</td>
<td>476.9 ± 133.8</td>
<td>157.3 ± 95.7</td>
<td>2.37 ± 3.19</td>
</tr>
<tr>
<td>FS-VR</td>
<td>6.12 ± 5.91</td>
<td>14.40 ± .</td>
<td>2.96 ± 0.89</td>
<td>714.0 ± 289.9</td>
<td>548.2 ± 204.4</td>
<td>130.6 ± 135.6</td>
<td>0.45 ± 0.17</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Fe$^{2+}$</th>
<th>Mn$^{2+}$</th>
<th>Zn$^{2+}$</th>
<th>Cu$^{2+}$</th>
<th>B(OH)$_3$</th>
<th>SO$_4^{2-}$</th>
<th>Pb$^{2+}$</th>
<th>Al$^{3+}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>GN</td>
<td>17.06 ± 39.36</td>
<td>13.48 ± 6.99</td>
<td>4.77 ± 1.17</td>
<td>0.70 ± 0.33</td>
<td>0.62 ± 0.20</td>
<td>52.32 ± 28.88</td>
<td>0.26 ± 0.04</td>
</tr>
<tr>
<td>GS</td>
<td>24.28 ± 51.90</td>
<td>15.33 ± 7.54</td>
<td>4.50 ± 0.67</td>
<td>0.65 ± 0.39</td>
<td>0.61 ± 0.15</td>
<td>59.99 ± 56.12</td>
<td>.</td>
</tr>
<tr>
<td>FN</td>
<td>7.10 ± 8.05</td>
<td>15.52 ± 9.45</td>
<td>4.78 ± 0.94</td>
<td>0.71 ± 0.37</td>
<td>0.69 ± 0.19</td>
<td>60.74 ± 41.02</td>
<td>0.32 ± .</td>
</tr>
<tr>
<td>FS</td>
<td>6.09 ± 5.28</td>
<td>15.38 ± 8.69</td>
<td>4.97 ± 0.97</td>
<td>0.65 ± 0.21</td>
<td>0.63 ± 0.15</td>
<td>72.88 ± 52.28</td>
<td>0.21 ± 0.01</td>
</tr>
<tr>
<td>FN-VR</td>
<td>3.72 ± 2.81</td>
<td>17.64 ± 9.97</td>
<td>4.43 ± 1.10</td>
<td>0.66 ± 0.27</td>
<td>0.56 ± 0.12</td>
<td>58.23 ± 29.49</td>
<td>0.15 ± .</td>
</tr>
<tr>
<td>FS-VR</td>
<td>7.99 ± 7.01</td>
<td>8.57 ± 4.14</td>
<td>5.35 ± 1.53</td>
<td>0.67 ± 0.30</td>
<td>0.71 ± 0.07</td>
<td>84.07 ± 28.54</td>
<td>53.64 ± 39.81</td>
</tr>
</tbody>
</table>

Note: No significant difference was observed for all investigated nutrient ions between pre-treatment Forest North-VR (FN-VR), control Forest North (FN), Gap North (GN), pre-treatment Forest South-VR (FS-VR), control Forest South (FS), and Gap South with the LSD option.

* Mean ± standard deviation (n = 10 for GN, GS, FN and FS; n = 5 for FN-VR and FS-VR); nutrient supply rates as μg Ion ⋅ 10 cm$^{-2}$ burial period$^{-1}$; supply rates are rounded off to the last digit; burial time 35 days

* Total N is based on addition of NO$_3^-$ and NH$_4^+$ prior to adjustment for method detection limits

* Indicates that supply rates were below method detection limits

* ± Indicates that only one observation was made, the other supply rates were below method detection limits
Table 5.5. Nutrient supply rates in gap, forest, and forest-VR plots for the winter sampling at the Bamfield site

<table>
<thead>
<tr>
<th>Plot</th>
<th>Total-N ( \text{g Ion} \cdot 10 \text{ cm}^{-2} \text{ burial period} )</th>
<th>( \text{NO}_3^- )</th>
<th>( \text{NH}_4^+ )</th>
<th>( \text{Ca}^{2+} )</th>
<th>( \text{Mg}^{2+} )</th>
<th>( \text{K}^+ )</th>
<th>( \text{H}_2\text{PO}_4^- )</th>
</tr>
</thead>
<tbody>
<tr>
<td>GN</td>
<td>13.62 ± 7.98</td>
<td>10.62 ± 6.87</td>
<td>3.00 ± 1.33</td>
<td>560.6 ± 215.5</td>
<td>440.1 ± 176.9</td>
<td>152.4 ± 84.2</td>
<td>0.75 ± 0.53</td>
</tr>
<tr>
<td>GS</td>
<td>11.45 ± 6.06</td>
<td>8.23 ± 4.96</td>
<td>3.36 ± 1.76</td>
<td>662.8 ± 288.1</td>
<td>463.8 ± 149.1</td>
<td>101.3 ± 72.7</td>
<td>0.57 ± 0.36</td>
</tr>
<tr>
<td>FN</td>
<td>10.29 ± 6.20</td>
<td>5.93 ± 3.69</td>
<td>2.33 ± 0.61</td>
<td>553.8 ± 150.7</td>
<td>449.0 ± 192.8</td>
<td>144.0 ± 65.5</td>
<td>0.54 ± 0.34</td>
</tr>
<tr>
<td>FS</td>
<td>9.02 ± 3.47</td>
<td>6.56 ± 3.85</td>
<td>2.47 ± 0.94</td>
<td>643.4 ± 386.1</td>
<td>479.1 ± 270.2</td>
<td>107.9 ± 61.4</td>
<td>0.67 ± 0.45</td>
</tr>
<tr>
<td>FN-VR</td>
<td>5.67 ± 3.07</td>
<td>4.40 ± 2.96</td>
<td>2.40 ± .( ^c )</td>
<td>903.3 ± 458.3</td>
<td>577.1 ± 170.0</td>
<td>126.7 ± 141.7</td>
<td>0.96 ± 0.99</td>
</tr>
<tr>
<td>FS-VR</td>
<td>12.90 ± 7.36</td>
<td>10.40 ± 7.78</td>
<td>2.50 ± 1.01</td>
<td>809.2 ± 271.3</td>
<td>470.4 ± 165.6</td>
<td>117.4 ± 34.4</td>
<td>0.26 ± 0.05</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>( \text{Fe}^{2+} )</th>
<th>( \text{Mn}^{2+} )</th>
<th>( \text{Zn}^{2+} )</th>
<th>( \text{Cu}^{2+} )</th>
<th>( \text{B(OH)}_3^- )</th>
<th>( \text{SO}_4^{2-} )</th>
<th>( \text{Pb}^{2+} )</th>
<th>( \text{Al}^{3+} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>GN</td>
<td>96.24 ± 104.99</td>
<td>10.79 ± 6.42</td>
<td>2.78 ± 1.18</td>
<td>0.16 ± .( ^c )</td>
<td>0.21 ± 0.04</td>
<td>55.44 ± 32.91</td>
<td>0.18 ± 0.03</td>
</tr>
<tr>
<td>GS</td>
<td>31.62 ± 60.54</td>
<td>12.17 ± 14.48</td>
<td>2.08 ± 0.72</td>
<td>0.18 ± .( ^c )</td>
<td>0.25 ± 0.11</td>
<td>65.51 ± 52.08</td>
<td>0.28 ± 0.01</td>
</tr>
<tr>
<td>FN</td>
<td>60.86 ± 96.29</td>
<td>7.97 ± 3.92</td>
<td>2.21 ± 1.05</td>
<td>0.20 ± .( ^c )</td>
<td>0.22 ± 0.02</td>
<td>60.50 ± 39.03</td>
<td>.</td>
</tr>
<tr>
<td>FS</td>
<td>19.08 ± 39.82</td>
<td>18.99 ± 16.86</td>
<td>2.24 ± 0.67</td>
<td>0.16 ± 0.01</td>
<td>0.23 ± 0.08</td>
<td>42.84 ± 41.31</td>
<td>.</td>
</tr>
<tr>
<td>FN-VR</td>
<td>6.86 ± 4.97</td>
<td>7.65 ± 5.99</td>
<td>2.22 ± 1.66</td>
<td>0.17 ± .( ^c )</td>
<td>0.20 ± 0.02</td>
<td>70.47 ± 62.56</td>
<td>.</td>
</tr>
<tr>
<td>FS-VR</td>
<td>3.48 ± 3.04</td>
<td>6.27 ± 3.72</td>
<td>1.79 ± 0.22</td>
<td>.( ^d )</td>
<td>0.32 ± 0.14</td>
<td>49.71 ± 39.01</td>
<td>0.22 ± .( ^d )</td>
</tr>
</tbody>
</table>

Note: No significant difference was observed for all investigated nutrients ions between pre-treatment Forest North-VR (FN-VR), control Forest North (FN), Gap North (GN), pre-treatment Forest South-VR (FS-VR), control Forest South (FS), and Gap South with the LSD option.

\( ^a \) Mean ± standard deviation (n = 10 for GN, GS, FN and FS; n = 5 for FN-VR and FS-VR); nutrient supply rates as \( \mu \text{g Ion} \cdot 10 \text{ cm}^{-2} \text{ burial period} \); supply rates are rounded off to the last digit; burial time 43 days

\( ^b \) Total N is based on addition of \( \text{NO}_3^- \) and \( \text{NH}_4^+ \) prior to adjustment for method detection limits

\( ^c \) Indicates that supply rates were below method detection limits

\( ^d \) Indicates that only one observation was made, the other supply rates were below method detection limits
5.2.2 GVRD

A significant effect of gap formation on availability of nutrients could not be determined comparing even the most contrasting environmental conditions (i.e. Gap North – Forest South). Availability of nitrogen tended to be higher in north position (Fig. 5.11 and 5.12). Average nutrient supply rates of NO$_3^-$ were less in Gap North than in Forest North plots and higher in Gap South than in Forest South plots. Nutrient supply rates of NH$_4^+$ were similar in Gap North and Forest North plots. In Gap South plots availability of ammonium was reduced compared to Forest South locations. Total-N (which combines the different nutrient supply rates of nitrate and ammonium) had increased availability in Gap North and Gap South locations compared to corresponding forest plots (Table 5.5).

In contrast to the stated hypothesis nutrient, supply rates of Mn$^{2+}$ were significantly higher in Forest South compared to Gap South plots but no difference was observed between the other treatments (Fig. 5.14). If nutrient supply rates within gaps and forests were summed up then only supply rates of Mg$^{2+}$ ($P < 0.5$) and Al$^{3+}$ ($P < 0.1$) were significantly higher in gaps. Supply rates of Al$^{3+}$ followed the expected decreasing order of availability (i.e. Gap North to Forest South) however the effect was not significant.

Supply rates of nutrients are conspicuously larger for K$^+$ in Gap South plots, increased by almost half for SO$_4^{2-}$ in Gap North plots, by a quarter for Gap South plots, and almost doubled for Fe$^{2+}$ in Gap South compared to the respective forest plots. However, no gap effect is noticeable for SO$_4^{2-}$ due to the large variability within replicates. Although the nutrient supply rates for Fe$^{2+}$ in Gap North and Gap South were twice as high as the Forest South location, the Forest North plots had the highest availability of Fe$^{2+}$. Comparing Forest North and Gap North plots, soluble iron decreased by approximately a quarter in Gap North plots.

Availability of nutrients was noticeably less in Gap North and Gap South for Ca$^{2+}$ and H$_2$PO$_4^-$, therefore adsorption rates of these nutrients were greater in forest plots. Nutrient supply rates were also less for K$^+$ in Gap South (-18.9%) and for Cu$^{2+}$ in Gap North plots (-16%). For these nutrients and for Zn$^{2+}$, and B(OH)$_3$ no trend in availability of nutrients between forest and gaps plots was observed. Nutrient supply rates of Pb$^{2+}$ tended to be higher in south plots.
Fig. 5.11. Mean nutrient supply rates of Total-N, NO$_3^-$, and NH$_4^+$ in summer at the GVRD site (burial period = 59 days); error bars refer to one standard deviation

Note: No significant difference was observed between control Forest North, Gap North, control Forest South, and Gap South plots with the LSD option; Total N is based on addition of NO$_3^-$ and NH$_4^+$ prior to adjustment for method detection limits

Fig. 5.12. Mean nutrient supply rates of Ca$^{2+}$, Mg$^{2+}$, and K$^+$ in summer at the GVRD site (burial period = 59 days); error bars refer to one standard deviation

Note: No significant difference was observed between control Forest North, Gap North, control Forest South, and Gap South plots with the LSD option
Fig. 5.13. Mean nutrient supply rates of $H_2PO_4^-$ in summer at the GVRD site (burial period = 59 days); error bars refer to one standard deviation

Note: No significant difference was observed between control Forest North, Gap North, control Forest South, and Gap South plots with the LSD option.

Fig. 5.14. Mean nutrient supply rates of $Al^{3+}$, $SO_4^{2-}$ and $Mn^{2+}$ in summer at the GVRD site (burial period = 59 days); error bars refer to one standard deviation, values with different letters are significant different among treatments ($p < 0.05$)

Note: No significant difference for $Al$ and $S$ was observed between control Forest North, Gap North, control Forest South, and Gap South plots with the LSD option.
Table 5.6. Nutrient supply rates in gap and forest plots in summer at the GVRD site

<table>
<thead>
<tr>
<th>Plot</th>
<th>Total-N $b$</th>
<th>NO$_3$</th>
<th>NH$_4^+$</th>
<th>Ca$^{2+}$</th>
<th>Mg$^{2+}$</th>
<th>K$^+$</th>
<th>H$_2$PO$_4^-$</th>
</tr>
</thead>
<tbody>
<tr>
<td>GN</td>
<td>34.33 ± 19.29</td>
<td>14.90 ± 11.31</td>
<td>15.06 ± 6.85</td>
<td>1080.0 ± 341.9</td>
<td>183.0 ± 61.2</td>
<td>225.8 ± 101.6</td>
<td>0.66 ± 0.53</td>
</tr>
<tr>
<td>GS</td>
<td>29.90 ± 14.27</td>
<td>12.47 ± 7.00</td>
<td>12.96 ± 5.19</td>
<td>1010.4 ± 428.1</td>
<td>197.2 ± 59.9</td>
<td>166.0 ± 111.4</td>
<td>0.68 ± 0.54</td>
</tr>
<tr>
<td>FN</td>
<td>32.08 ± 14.20</td>
<td>17.06 ± 13.67</td>
<td>15.02 ± 4.57</td>
<td>1289.8 ± 374.0</td>
<td>139.4 ± 47.1</td>
<td>175.8 ± 70.8</td>
<td>1.16 ± 1.73</td>
</tr>
<tr>
<td>FS</td>
<td>27.43 ± 10.42</td>
<td>9.68 ± 5.95</td>
<td>14.51 ± 4.49</td>
<td>1112.4 ± 428.3</td>
<td>152.2 ± 36.2</td>
<td>204.7 ± 129.4</td>
<td>0.92 ± 0.78</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Fe$^{2+}$</th>
<th>Mn$^{2+}$</th>
<th>Zn$^{2+}$</th>
<th>Cu$^{2+}$</th>
<th>B(OH)$_3$</th>
<th>SO$_4^{2-}$</th>
<th>Pb$^{2+}$</th>
<th>Al$^{3+}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>GN</td>
<td>4.12 ± 3.87</td>
<td>25.60 ± 17.13</td>
<td>8.71 ± 2.09</td>
<td>0.42 ± 0.24</td>
<td>0.78 ± 0.15</td>
<td>50.80 ± 28.74</td>
<td>1.92 ± 0.70</td>
</tr>
<tr>
<td>GS</td>
<td>3.92 ± 4.89</td>
<td>16.40 ± 8.69 a</td>
<td>9.58 ± 2.32</td>
<td>0.48 ± 0.19</td>
<td>0.80 ± 0.13</td>
<td>45.60 ± 31.90</td>
<td>2.32 ± 0.60</td>
</tr>
<tr>
<td>FN</td>
<td>5.62 ± 8.23</td>
<td>23.06 ± 13.19</td>
<td>7.52 ± 1.68</td>
<td>0.50 ± 0.17</td>
<td>0.78 ± 0.15</td>
<td>34.80 ± 15.30</td>
<td>1.68 ± 0.46</td>
</tr>
<tr>
<td>FS</td>
<td>1.99 ± 1.23</td>
<td>28.40 ± 11.48 b</td>
<td>8.54 ± 1.93</td>
<td>0.48 ± 0.26</td>
<td>0.81 ± 0.15</td>
<td>36.70 ± 25.97</td>
<td>2.44 ± 0.74</td>
</tr>
</tbody>
</table>

Note: Mean values for Mn with different letters are significant different among treatments (p < 0.05), for all other investigated nutrient ions no significant difference was observed between control Forest North (FN), Gap North (GN), control Forest South (FS), and Gap South with the LSD option.

$^a$ Mean ± standard deviation (n = 10); nutrient supply rates as μg Ion·10 cm$^{-2}$·burial period$^{-1}$; supply rates are rounded off to the last digit; burial time 59 days

$^b$ Total N is based on addition of NO$_3^-$ and NH$_4^+$ prior to adjustment for method detection limits
6 Discussion

The results of this investigation are consistent with other studies reporting no significant changes in decomposition, mineralization and nitrification between gaps and forest (Marrs et al. 1991; Luizao et al. 1998; Bauhus et al. 2004; Ritter 2004). In addition, rates of net mineralization of nitrogen in partial cuts of 1.5 ha have been similar to those in the uncut old-growth forests at the MASS installation near the Campbell River on Vancouver Island (Prescott 1997). Also Barg and Edmonds (1999) reported no change in net mineralization in green tree retention plots (20-30 trees/ha) in coastal Washington.

The observations made are in contrast to the produced evidence of many studies that supply rates of nitrogen are increased in gaps relative to undisturbed forest (Mladenhoff 1987; Parsons et al. 1994; Prescott et al. 1992; Bauhus 1996; Denslow et al. 1998; Prescott et al. 2003). Furthermore, at the Opax Mountain experiment in the dry southern interior of BC, increased nitrate concentrations occurred in partially harvested areas (50% canopy removal in a 20 ha block), between 2 and 11 meters from the forest edge on a north-to-south transect but without any effect of aspect or direction of the edge (Hope et al. 2003). However, ammonium concentrations were not affected. These data indicated that the influence of forest edge disappeared within 16 m of the edge.

All these studies (except Denslow et al. 1998) measured net mineralization of NO$_3^-$ and NH$_4^+$ through the incubation of soil probes in plastic bags of forest floor and mineral soil either in the lab or in the field for 30 to 174 days. Denslow et al. (1998) extracted chemically NO$_3^-$ and NH$_4^+$ after collecting soil probes periodically until 319 days after gap creation. The incubation method measures the potential net supply rate of nutrients in soils, but does not take into account the entire dynamic of nutrient cycling in the soil, especially in the forest floor. Ion diffusion, moisture and carbon fluxes into, and out of the neighbouring soil are excluded through inclusion, when soil is isolated in plastic bags. The only factor unmodified from the surrounding soil is the temperature. Net mineralization rates estimated by the incubation method do not take into account uptake by plants roots or microbes. Stark and Hart (1997) reported that microbial assimilation of nitrate constitutes an important mechanism for nitrogen retention in mature forest ecosystems. As the highest density of fine roots is in the H and F horizon, the highest demand for nutrients is in the forest floor (Huang and Schoenau 1997). The efficiency of nutrient removal from the soil solution by plant roots depends then on soil conditions (i.e. moisture, temperature
and texture), fine root density as well as on the degree of suberization and mycorrhizal infection (Nilsson et al. 1995).

In my study availability of nutrients was monitored only in the forest floor as net nutrient supply rates, so it is not examined if gap formation increased leaching of nutrients. Nutrients such as calcium, magnesium and potassium may have lower availability in gaps because of their higher ion mobility and greater leaching (Mladenhoff 1987). Nitrate concentration was significantly increased in the soil solution below 90 cm after gap formation in two beech forests in Denmark (Ritter 2004). Bauhus and Bartsch (1995), and Bartsch (2000), also reported considerable leaching losses of nutrients due to gap formation in German beech forests.

On the other hand, nitrogen is thought to be tightly cycled in coastal temperate forest ecosystems of British Columbia because they have had much less nitrogen depositions in the past than forest ecosystems in Denmark or Germany (cp. chapter 2.1.1 pp. 5-6). Additionally, most of the nutrients are adhered in the organic matter of Podzols due to its high water absorption and retaining capacity (CSSP 1995; Schachtschabel 1998). Vital nutrients for plants and microbes growth are adsorbed from the soil solution before they can be leached (Fisher and Binkley 2000). Furthermore, disturbance of an ecosystem does not automatically lead to intensification of leaching. On the contrary, nitrate leaching of soil of a high natural N status in New Zealand decreased sharply after clearcutting because vegetation and microbial biomass removed N from the soil solution (Parfitt et al. 2002). Commonly, Al$^{3+}$, SO$_4^{2-}$, and organic anions have the highest share of nutrients which are leached in podzols because these soils have already been strongly weathered in the past (Schachtschabel 1998). Furthermore, nutrient supply rates between gaps and forest were similar; therefore the amount of leached nutrients should be the same in gaps and forests.

It was expected that the difference between gap and closed-forest canopy would be stronger than the spatial variation within each forest phase. That was found to a limited extent for NO$_3^-$ (P < 0.1) in winter in Bamfield, and for Al$^{3+}$ (P < 0.1) at the GVRD site, and significantly for supply rates of Mg$^{2+}$ at the GVRD site. Therefore the hypothesis of an effect of gap formation on nutrient supply rates with a decreasing order Gap-North > Gap-South > Forest North > Forest South in coastal temperate old-growth rainforest is rejected. The increased availability of Mg$^{2+}$, inorganic NO$_3^-$ and Al$^{3+}$ in gaps is not consistent compared to the other evaluated nutrients within and between ecosystems, and sample seasons. Thus these increased nutrient fluxes cannot be used as verification for higher microbial activity (i.e. biologically-based nutrient cycles), greater
ion movement and faster chemical reactions of ions in canopy gaps. The slightly higher availability of inorganic nitrate may be caused by reduced uptake by herbs and shrubs in gaps in the winter time at the Bamfield site. The size of gaps at the GVRD site was significantly greater than those at the Bamfield site, which may explain the higher adsorption of magnesium and aluminium by ion-exchange resins at GVRD. However, other nutrients should have been similarly influenced by the greater gap size at the GVRD site but were not.

The lack of difference in nutrient supply rates to resins in forest and gaps may indicate that either nutrients are not mineralized faster in gaps, or are taken up immediately by corresponding plants and microbes (if any increased availability of nutrients exists through gap formation), or the naturally variability of nutrients supply rates is too high within each forest phase, or the formation of gaps was so long ago that vegetation and microbes have adapted to the created conditions. The heterogeneous canopy structure of studied rainforests may be the main reason why no differences in nutrient fluxes in forest and gaps were detected. Neither the canopy openness (i.e. light conditions in Bamfield) nor rooting substrate coverage was significantly different between forest and gaps for both ecosystems, which indicates that the diverse canopy leads to homogeneous understorey conditions in old-growth forests. Through the general breakup of the canopy by gaps or standing, dying trees the overstorey leaf area had declined and an abundant, multiple strata understorey layer had formed, fuzzying the distinctions between gaps and closed-canopy forest (cp. Fig. 6.1 to 6.4). Frazer et al. (1999) reported that old-growth canopy was heterogeneously open and maintained a low effective leaf area on southern Vancouver Island. Canopy openness at the Bamfield site was 8.30 to 16.72 % similar to the observations by Frazer et al. (1999). Unexpectedly, the forest plots had the highest (i.e. forest-VR plots) and the lowest (i.e. forest plots) canopy openness, while taking gaps were intermediate. The observed difference in canopy openness between forest and forest-VR plots shows the strong diversity of the canopy structure in these old-growth forests, which is a major source of variation in the character of understorey light environments (Frazer et al. 1999). Bauhus and Bartsch (1995), Grey et al. (2002), and Ritter (2004) reported that changes in temperature and moisture in gaps is very small. Thus, the heterogeneous canopy and additionally the already existing lush understorey at Bamfield (cp. Fig. 4) has probably created uniform moisture, temperature and light levels at the forest floor, which prevent changes in nutrient fluxes between forest and gaps.
Fig. 6.1. Closed canopy old-growth forest with lush understorey vegetation through the low leaf area of the old-growth forest at the Bamfield site (December 2004)

These ecosystems have in general a tight nutrient cycle due to a low availability of nutrients. Especially parent material and high annual precipitation has lead to the development of Ferro-Humic Podzols. Also the understorey vegetation of the investigated sites indicates that the soil is poor in nutrients through the presence of Alaskan blueberry, deer fern, *Rhytidiadelphus loreus*, and salal (Klinka et al. 1989). Nutrients additionally made available in these ecosystems by the means of increased moisture and temperature levels are taken up by the competing plants and microbes. Ritter (2004) reported that the effect of canopy gap on biogeochemical processes was modified by the growth response of vegetation in and around the gap. Roots of gap-bordering trees extend into the canopy gap which makes the below-ground gap smaller than the above-ground gap (Parsons 1994; Ritter 2004). Therefore, roots of bordering trees continue to supply carbon and remove nutrients from the area of the canopy gap (Ritter 2004). Mycorrhizal networks may extend into the gap and act as sink for nutrients and transfer nutrients to gap-bordering trees (Simard and Durall 2004). Siira-Pietkäinen et al. (2001) reported that selective felling and gap felling did not alter the community structure or the microbial biomass in a period
of 2 years after harvest. On the other hand, soil microbial biomass decreased in gaps in the second year after tree felling due to the removed carbon supply from tree roots (Bauhus and Barthel 1995). Thus, the microbial biomass in gaps would not act as a nutrient sink after disturbance. However, it is likely that the existing lush understorey vegetation could have taken over the carbon supply for microbes due to higher assimilation rates by increased light conditions. Therefore, the carbon supply was not disrupted hence no increased microbial assimilation of nutrients took place. In addition, Schilling et al. (1999) reported that fine roots of herbaceous and woody understorey vegetation play are large role in carbon and nutrient storage after disturbance.

It has been reported that ion-exchange resins in strong nitrogen-poor environments are poor competitors with microbes and plant roots especially for nitrogen because ions are bounded to resins by relatively weak ionic bonds, and are freely exchangeable with other ions in the soil solution (Subler et al. 1995; Fisher and Binkley 2000). Nevertheless, under normal field conditions which existed at the research sites the only nutrient sink whose adsorption strength is
Fig. 6.3. Predominated tall salal coverage in a natural gap at Bamfield (December 2005)

superior to PRSTM-probes are plant roots (Hangs 2005, personal communication). Therefore it is unlikely that nutrient ions were removed from the probes by microbes like mycorrhiza or bacteria during the burial period. Natural death or harvest of trees normally lead to an increase in the availability of nutrients because nutrient uptake by tree roots has declined, thus the competition for nutrients should be reduced in gaps (Prescott 2002; Bauhus et al. 2004). However, microorganisms and plant roots still remove ions from the available soil nutrient pool resulting in reduced nutrient adsorption by resins. In conclusion, it is assumed that any additional nutrient flux through gap formation may be counter balanced by the nutrient uptake of the lush understorey vegetation, bordering tree roots, and microbes in gaps.

Supply rates for all analysed nutrients had high microscale variability in each forest phases, which diminished any difference in nutrient fluxes. This variability may be exacerbated by using the ion-exchange probe technique. Resins take into account all factors influencing nutrient fluxes (i.e. soil moisture and temperature, mineralization and immobilization, ion activity, cation exchange buffer, and ion diffusion). Soil moisture and temperature affected into a great extent the other factors (Turrion et al. 1997; Western Ag Innovations Inc. 2005 [On-line]1).
Also other studies have reported high spatial variability and temporal fluctuations in nutrient concentrations when accessing nutrient supply rates in forest soils (Qusnel and Lavkulich 1981\(^1\); Arp and Krause 1984\(^1\); Johnson and Todd 1987\(^1\); Cole 1995). Especially nitrogen availability may fluctuate widely over short periods of time and short distances in responses to minor changes in the external environment (Huang and Schoenau 1996). Prescott (2002) stated that increasing canopy complexity will increase the spatial variability in nutrient cycling within forest. This is supported through the nutrient supply rates found in this study.

The last essential consideration is whether or not any difference was found in nutrient supply rates were related to the time of gap formation. In Bamfield gaps have seemed to be created and maintained over a longer time period because some of the gapmakers were very decayed (Lade 2004, personal communication). However, the assessment of time of gap creation was not finished for both sites at the point of completion of this thesis. Most investigations have reported that increased availability of nitrogen takes places in the subsequent year (Denslow

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\(^1\) as cited in Huang and Schoenau (1997)
1998, gap size 65-611 m²; Bauhus 1996, 30 m diameter), and after 0 to 3 years after gap creation (Mladenhoff 1987, 90-250 m²). Furthermore, Denslow (1998) and Bauhus (1996) found that the initiated effect on the availability of nutrients was only of short duration and diminished within the second year after disturbance (cp. chapter 2.3 p. 13). Therefore, the effect of gap formation was maybe not observed due to the fact that natural creation of gaps occurred approximately 3 and more years ago.

The size of the gaps investigated is not considered as a reason why no difference in nutrient fluxes between gaps and forest was measured. Many studies have observed higher availability of nutrients in gaps which had similar or smaller gap sizes (Mladenhoff 1987; Parsons et al. 1994; Prescott et al. 1992; Bauhus 1996; Denslow et al. 1998).

Calcium had the highest availability among the evaluated nutrients, which is common for forest ecosystem of the Pacific Northwest (Cole 1995). Cumulative nutrient supply rates were in the order $Ca^{2+} > Mg^{2+} > K^+ > SO_4^{2-} > Fe^{2+} > Al^{3+} > Mn^{2+} > NO_3^- > NH_4^+ > Zn^{2+} > H_2PO_4^- \geq Cu^{2+} \geq B(OH)_3^0 \geq Pb^{2+}$ for Bamfield; and for the GVRD site $Ca^{2+} > K^+ > Mg^{2+} > SO_4^{2-} > Al^{3+} > Mn^{2+} > NH_4^+ > NO_3^- > Zn^{2+} > Fe^{2+} > Pb^{2+} > H_2PO_4^- \geq Cu^{2+} \geq B(OH)_3^0$.

At the GVRD site nutrient supply rates of Total-N, $NO_3^-$, and $NH_4^+$ were significantly higher. This is consistent with the presence of understorey vegetation like False Lily of the Vally, devils Club, Lady Fern, salmonberry, and thimbleberry as indicators of a richer nitrogen status. Shrub and fern coverage in gaps was higher than in forest plots; however the overall vegetation coverage was less than in Bamfield. Nevertheless, understorey coverage was of almost 50 % beneath the forest canopy, which may have prevented significant increase in nutrient fluxes after the canopy is opened up through gap disturbance at the GVRD site.

The close proximity of the Bamfield site to the Pacific Ocean resulted in higher nutrient supply rates of $SO_4^{2-}$ at the Bamfield site (Cole 1995; Schachtschabel et al. 1998). However, a more comprehensive evaluation of the nutrient supply rates between both sites is not reasonable because moisture levels and burial periods have been utterly different (i.e. 84 mm rainfall and 24 days incubation difference).

Nutrient supply rates of base cations, phosphorus, zinc, and boron were all higher in summer than in winter. Ion sorption sometimes diminishes in summer because it is strongly affected by soil water regime (Turrion et al. 1997). This was not the case in Bamfield, probably because forest floor moisture levels were still high enough to allow ion diffusion. Approximately 99 mm precipitation fell during the summer burial period compared to 215 mm during the winter.
burial period (Environment Canada n.d.)\(^1\). Average temperatures were 16°C during the summer incubation and 4.9°C during the winter incubation. Thus nutrient supply rates were rather driven by the temperature than by moisture levels. The higher rates for nitrate in the winter time could relate to initial NH\(_4^+\) availability and organic matter addition through the litterfall of shrubs and herbs in the autumn (Huang and Schoenau 1997). At Bamfield, winter mean temperatures remain above zero (Environment Canada n.d.)\(^1\), which allows continuous decomposition of organic matter. Increased dissolution of Al hydroxides caused by the lower pH and the reduction of Fe\(^{3+}\)-oxides to Fe\(^{2+}\) due to high moisture levels may be the main reason for increased supply rates of Al\(^{3+}\) and Fe\(^{2+}\) in the winter (Bauhus and Bartsch 1995; Schachtschabel 1998).

These comparisons of nutrient supply rates must be made with caution because of differences in burial times. The burial time in winter was 43 days compared to 35 days in summer. Adsorption of nutrients on the resins is not linear over time depending on initial labile nutrient pool (Western Ag Innovations Inc. 2004); thus values for the 2 incubation periods cannot be directly compared. Some repeated samples were 2 times higher or lower than the first sampling, which is most reasonably attributed to moisture differences (Hangs 2005, personal communication).

Ion-exchange resins continually remove nutrient ions that come into solution through chemical-biological processes, thus preventing equilibrium between the ions on the solid phase and in the soil solution. The observed soil nutrient supply rates of the forest floor showed the availability of nutrients in the soil solution as a net nutrient supply rate (i.e., soil supply - plant uptake) over time.

Although nearly 400 journal articles have been published related to use of ion-exchange resins (Qian and Schoenau 2002), only a few studies have evaluated nutrient supply rates in forest soils. It is difficult to compare nutrient supply rates measured in this study with those from other forests. These are constraints in comparing nutrient supply data from different studies because the methodologies differ (i.e. resin type, burial time, seasons, ions, soils, etc.). Furthermore, PRSTM™-probe nutrient supply rate data cannot be compared to conventional nutrient extraction methods and data (for instance mg/ha) because PRSTM™-probes measure ion flux over time to a sink with a fixed surface area whereas chemical extractions evaluate a static or indices

\(^1\) Weather station VICTORIA INT'L A, [On-line]
of nutrient pools in the soil (i.e., total, extractable in soil solution, and organic) at one point in time (Western Ag Innovations Inc. 2005).

Ion-exchange resin technique has other issues which have been discussed in the literature (Turrion et al. 1997; Qian and Schoenau 2002; Western Ag Innovations Inc. 2005 [On-line]). In this study and also in others it has been observed that during the burial times membranes become darker as organic matter (such as fulvic acids) accumulates on the membranes. Low-molecular-weight humic substances or organometal complexes are common in acid forest solutions (Schachtschabel 1998). Resins may lose their exchange efficiency by reacting with substances or organic complexes (Turrion et al. 1997). However, it has been argued that most organic matter is trapped in the resin lattice, so the exchange capacity is largely unaffected (Qian and Schoenau 2002). The degree to which organic substances restrict the exchange capacity of the ion-exchange resins needs to be thoroughly evaluated.

It has to be pointed out that the observed nutrient supply rates could be also limited because of the maximum ion capacity of the PRSTM-probes. So far the maximum ion adsorption capacities of PRSTM-probes for single ions have been examined, for instance for Ca\(^{2+}\) (3920 ions \(\mu g \cdot 10 \ cm^{-2}\)) and for K\(^{+}\) (7650 ions \(\mu g \cdot 10 \ cm^{-2}\)) (Western Ag Innovations Inc. 2004). In this study maximum loads of added up ions were found between 2300 to 2600 ions \(\mu g \cdot 10 \ cm^{-2} \cdot \text{burial period}\) for both sites and sample periods; most of the maximum loads were in the forest plots.

As ion-exchange resins resemble plant roots, ions may interact and compete for exchange bounds at the membrane lattice of the probes. Thus binding of some ions may be hindered. The maximum ion capacity of the resins membrane will decrease depending on the specific ion activity in soil solution relative to the other nutrient ions (Hangs 2005, personal communication). This is especially true for Ca\(^{2+}\) and K\(^{+}\) due to the higher ionic valence of Ca\(^{2+}\) (Schachtschabel 1998; Western Ag Innovations Inc. 2005 [On-line]). Thus nutrient supply rates of some ions could theoretically be higher than indicated by the ion-exchange resins. On the other hand, plant roots would not take up the free cations either. In addition, it is already known that ion-exchange resins do not take up all free Mg\(^{2+}\) and K\(^{+}\) ions in the soil solution, which a traditional chemical extraction would detect (Hangs 2005, personal communication).

These issues lead to the following question: what measure of nutrient status is most appropriate for evaluating the effect of gap formation or timber harvest on nutrient availability? Is it the total nutrient pools (i.e. pressure disintegration with HNO\(_3\)), available of nutrients measured with a traditional method (i.e. chemical extraction of nutrients; collecting of soil
solution by lysimeters, centrifugation, or leaching by gravity; soil probe incubation in the lab or under field conditions), or supplies of nutrients as encountered by the plant roots (i.e. ion-exchange resins)? As Fisher and Binkley (2000) point out, all methods have advantages and disadvantages. Measures of nutrient pools quantify the site potential but not the rate at which nutrients become available. The traditional collection of soil solution and the incubation has the issue of quantifying temporal fluctuations of nutrient fluxes during the year (Fisher and Binkley 2000; Grenon et al. 2004). The incubation method encounters the issue that the normal labile carbon input (i.e. carbohydrates) by plant roots is removed during the incubation time (Fisher and Binkley 2000). The release of carbon is important for the soil microbial activity which determines the rate at which nutrients are mineralized from organic matter (Grayston et al. 1996). Nutrient supply rates measured with ion-exchange resins are meaningful because they provide an estimate of nutrient supply rate to a sink (such as plant roots) under actual field conditions (Qian and Schoenau 2002; Hangs 2005, personal communication). Nevertheless, ion-exchange resins may not measure the total amount of nutrients adsorbed by plant roots as mycorrhizal fungi play an important role transporting nutrients to plant roots (Simard and Durall 2004).

The most appropriate technique depends on the objectives of the study. Considering the implications of disturbances on forest ecosystem functions from short- and long-term perspectives, it is crucial to measure changes in nutrient supply rates and total nutrient pools. Nutrient cycling is an important feature of forest management practices for long-term sustainability of forest ecosystems. However, in the long-term it can be assumed that temperate ecosystems are resilient against changes in the total nutrient pool through continued mineral weathering and nutrient deposition. It has been shown that clearcutting had no negative impacts on the total nutrient pool of forest ecosystems (Knoepp and Swank 1997, Briggs et al. 2000; Kranabetter and Coates 2004, cp. chapter 2.2 p. 9). Measurements of nutrient supply rates on a year-to-year basis are more likely to detect impacts of changes in the canopy structure of forests. Most studies have focused on net nutrient supply rates (i.e. mineralization and decomposition) during the first 1 to 5 years after disturbance. Most of the research has been on supply rates of nutrients which either limit the productivity of forest ecosystems (such as nitrogen and phosphorus), or might negatively affect the health of the ecosystem and humans (like Al$^{3+}$ and nitrite). Furthermore, if one wishes to fully understand the effect of harvesting one should consider gross production of nutrients separate from their immobilization by microbes,
understorey vegetation and regenerating trees. Additionally, changes in the rate of nutrient leakages indicate if harvest systems have negative impacts on nutrient pools.

How much change in nutrient cycling is acceptable in general from a perspective of sustainable forest management which emulates natural disturbance in variable retention or shelterwood harvest systems? Kimmins (2002) points out that sustainability is a non-declining pattern of change at a forest stand level of 1-100 ha. Losses of nutrients also occur in undisturbed forest ecosystems as natural process (Schachtschabel 1998; Fisher and Binkley 2000). Therefore, disturbance of an ecosystem is a prerequisite to either implement changes or maintain ecosystem form and function; otherwise a productive forest ecosystem may change slowly to unproductive ecosystem conditions (Kimmins 2000). In the absence of large-scale disturbances, succession turnover rates of gaps in coastal western hemlock forests range from approximately 300 to 1400 years, depending on growth rates of trees in gaps (Wong et al 2004).

“It depends” on the ecosystem is probably as so often the right answer. Forest management should respect the ecological role of natural disturbance and therefore balance the frequency and severity of disturbance so that the ecological and biological diversity of the forest ecosystem is maintained.
7 Conclusions and Recommendations

Natural formation of gaps in coastal temperate old-growth forest did not change the biogeochemical nutrient cycles of 14 investigated nutrient ions. The already existing heterogeneity of the forest canopy buffered the effect of gap disturbances on the understorey ecosystem, which is consistent with the findings by Ritter (2004). The index of canopy closure is apparently not a good measure to indicate environmental conditions and thus nutrient availability at the ground in these old-growth forests. The made observations are attributed to consistency of the nature of the forest soil, understorey vegetation and the biomass of the microbial community after gap formation. Moreover it is assumed that understorey vegetation and bordering trees replaced the carbon and litter supply of the gapmakers on and into forest floor and forest soil.

The high microscale variability of nutrient supply rates measured by the PRSTM-probes shows that nutrient fluxes are the result of different, partly antagonistic factors (i.e. soil moisture and temperature, mineralization and immobilization, ion activity, cation exchange buffer, and ion diffusion) and players (i.e. fungi, bacteria, and plant species) in the soil. The distribution of these parameters is not homogenous which resulted in the high variability. Of the 14 analysed nutrients no real key nutrient or pattern of nutrient was indicated as a predictor of a gap effect. For further investigations it is recommended to examine nutrients which could explain most the effect of disturbance on forest ecosystems. Because no conclusion can be drawn from this investigation, it is reported that these nutrients are NO\textsubscript{3}\textsuperscript{−}, NH\textsubscript{4}\textsuperscript{+}, Ca\textsuperscript{2+}, Mg\textsuperscript{2+}, H\textsubscript{2}PO\textsubscript{4}\textsuperscript{−}, and Al\textsuperscript{3+}.

The results also indicates that canopy gaps larger than those studied here are needed to induce changes in nutrient cycling in these old-growth forests. Therefore, with respect to nutrients supply, variable retention systems are an appropriate harvest system to manage coastal temperate rainforests. However, it is concluded qualified by the limitations of this study that the used retention level has to maintain the integrity of the understorey and forest floor conditions to maintain biogeochemical processes. In contrast that may hinder the successful establishment of regeneration after harvest because no additional flush of nutrients and a higher competition by the understorey flora would not support the next generation of trees.

Many questions need to be addressed before it can be concluded that variable retention harvesting will maintain the integrity of forest ecosystems with respect to biogeochemical cycles. These include the role of microbial biomass and understorey vegetation in retention and uptake of nutrients after gap disturbance and their function of providing resilience against disturbances-
induced changes. In addition, the assessment if gap disturbance in coastal temperate rainforests lead to changes in nutrient losses with the seepage water.

As ion diffusion is strongly affected by the temperature and moisture of the soil, it is very sensible to measure these factors if nutrient fluxes are assessed by ion-exchange resins for a more comprehensive understanding of the effect of gap formation. Furthermore, the interaction of roots as source of carbon and the microbial community in below-ground gaps has to be evaluated. The high microscale variability measured in this study recommends using several indices of nutrients availability simultaneously to assess if difference between gaps and forest existed.

"Conservation is paved with good intentions which prove to be futile, or even dangerous because they are devoid of critical understanding either of the land, or of economic land-use”

Leopold 1989
8 References


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9 Appendix

Soil profile description

Date of Examination: 28.01.2004

Location: Bamfield east side, 2 km south east from Bamfield, road incision @ 25 m after start of new logging road

Elevation: 30 m a.s.l.

Surrounding landform: undulating, moderately mounded

Slope on which profile is sited: very gentle slope with a southwest aspect

Land-use / Vegetation: productive woodland, western redcedar dominated old-growth forests, age approximately 800 to 1000 years

Climate: very wet hypermaritime, average precipitation approximately 2814 mm with 2801 mm as rain and 16 cm as snowfall. The mean annual temperature is 9.8°C with mean monthly variations from 5.9°C in winter to 13.7°C in summer.

Parent Material: sedimentary sand, colluvial, fragmental,

Drainage: well drained to moderately drained, slow surface runoff

Moisture Conditions in the profile: moist throughout

Depth of Ground Water Table: moderate water table (100-200 cm)

Presence of surface stones: non stony

Stoniness Class: none rocky, moderately deep to bedrock (100-200 cm)

Evidence of Erosion: none
## Soil type: Humo-Ferric Podzol

<table>
<thead>
<tr>
<th>Horizon</th>
<th>Depth (cm)</th>
<th>Colour &amp; Mottling</th>
<th>Texture</th>
<th>Structure</th>
<th>Stoniness</th>
<th>Consistence</th>
<th>Other Features</th>
</tr>
</thead>
<tbody>
<tr>
<td>L</td>
<td>+12 - +11</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Humus layer not closer examined due to the disturbance by the road construction</td>
</tr>
<tr>
<td>F</td>
<td>+11 - +4</td>
<td></td>
<td>Moder Humus</td>
<td>weak, loose - friable</td>
<td>granular to subangular</td>
<td>fine to very coarse</td>
<td>friable, slightly sticky</td>
</tr>
<tr>
<td>H</td>
<td>+4 - 0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>very frequent fine to very coarse roots, horizon discontinuous</td>
</tr>
<tr>
<td>E</td>
<td>0 - 6</td>
<td>10YR 5/2 grayish brown</td>
<td>loamy Sand</td>
<td>weak, loose - friable</td>
<td>granular to subangular</td>
<td>fine to very coarse</td>
<td>none</td>
</tr>
<tr>
<td>Bfh</td>
<td>6 - 14</td>
<td>5YR 3/3 dark reddish brown</td>
<td>Silt</td>
<td>weak</td>
<td>subangular</td>
<td>fine to very coarse</td>
<td>greasy, slightly sticky and slightly plastic</td>
</tr>
<tr>
<td>Bfg</td>
<td>14 - 62</td>
<td>10YR 4/4 dark yellowish brown, 2% very few mottles 5YR 2.5/2 dark reddish brown, many coarse prominent mottles 10YR 5/6 yellowish brown, also patches with a more greyish colour</td>
<td>loamy Sand, slightly gravelly</td>
<td>weak, loose - friable</td>
<td>subangular</td>
<td>fine to very coarse</td>
<td>very few stones, gravel, weathered</td>
</tr>
<tr>
<td>Bg</td>
<td>62+</td>
<td>2.5Y 5/4 Reddish Brown, @ upper boundary and in patches 10YR 4/2 dark grayish brown</td>
<td>Sand, slightly gravelly</td>
<td>weak</td>
<td>subangular</td>
<td>fine to very coarse</td>
<td>very few stones, gravel, weathered, angular</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>massive in pedon but friable</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>no roots</td>
</tr>
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</table>
10 Acknowledgement

This thesis would not have been possible without the help, supervision and support of a number of people. I would like to thank my supervisor Prof. Cindy Prescott and Dr. Heiner Flessa for their support and help with this work. Especial thanks to Cindy Prescott for her constructive criticism and professional scientific phraseology. Further thanks to Dr. Lori Daniels, and her research group (Amanda Stan, Janneke Lade, Jennifer Passmore), which contributed a great amount of the prerequisite data for my investigation. Without this data the completion of this research would not have been possible. I acknowledge the assistance in the field by Candi Staley and Dennis Morgan; we had good times in Bamfield. Lucie Jerabkova and Dr. Antal Kozak I have to thank for their assistances with statistical issues regarding this investigation.

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Declaration of Honour

I hereby declare in accordance with § 26 para. 6 of the Bachelor and Master examination regulation from March 24\textsuperscript{th} 2000, that I conducted the submitted thesis on my own and did not use any other references and resources than cited.

Ehrenwörtliche Erklärung

Hiermit versichere ich gemäß § 26 Abs. 6 der Bachelor- und Master-Prüfungsordnung vom 24.03.2000, daß ich die vorliegende Arbeit selbstständig verfaßt und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Vancouver, June 2nd 2005 __________________________________________________

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