THE ROLE OF BIGLEAF MAPLE IN SOIL CHEMISTRY AND NUTRIENT DYNAMICS IN COASTAL TEMPERATE FORESTS

by

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Abstract

The influence of bigleaf maple (*Acer macrophyllum* Pursh) in a forest dominated by Douglas-fir [*Pseudotsuga menziessi* (Mirb.) Franco] and western hemlock [*Tsuga heterophylla* (RAF.) Sarg.] was studied in a paired-plot design through an examination of the annual contribution of bigleaf maple litterfall to nutrient flux, its rate of decay, and its properties within the forest floor and mineral soil. Compared to conifer plots, bigleaf maple plots had litterfall significantly higher in all elements, and faster litter decomposition. Forest floor measurements revealed significantly higher pH and contents of N. Mineral soils beneath bigleaf maple had a lower bulk density, higher CEC, and total, mineralizeable and available N, compared to conifer plots. This suggests that bigleaf maple has the potential to increase nutrient cycling and availability in deciduous-conifer mixed stands, and may be a desirable species in temperate coastal forests.

Keywords: bigleaf maple; *Acer macrophyllum*; nutrient cycling; litterfall chemistry and decomposition; forest floor properties; mineral soil properties

Subject Terms: Forest Nutrient Cycling - British Columbia; Forest Ecology - British Columbia; Forest Soils - British Columbia; Maple - British Columbia; Litterfall Chemistry & Decomposition - British Columbia

Dedication

To my family, for their unconditional love and support. This would not have been possible without you.

And to Bill Bailey, who always urged me to learn to take risks in research and in life, and who constantly reminded me to Struggle Well.

Nature does nothing uselessly

Aristotle

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Chapter 1: Introduction

1.1 Research Rationale

Managing hardwoods together with conifers is gaining importance, with reliance on monocultures changing to management for mixed species forests (Rothe & Binkley, 2001). Research has indicated that the inclusion of a component of deciduous species in conifer stands may improve nutrient availability (Comeau, 1996). In contrast to conifers, broadleaves are generally higher in pH and have litter greater in element concentrations including nitrogen (N), potassium (K) and magnesium (Mg) (Fisher & Binkley, 1994; Augusto et al., 2002; Rothe & Binkley, 2001). Forest management has traditionally involved removing "invasive native" species (Washburn & Arthur, 2003) for the assumed integrity of commercially viable species (Simard et al., 2005). However, the presence of hardwoods in conifer forests may provide greater wood yield and better economic returns than pure stands, as demonstrated by the change in the Forest Practices Code of British Columbia (BC), which now requires a minimum number of broadleaved trees in their native habitat (Comeau, 1996). Beyond conifer integrity, several incentives exist to sustain naturally occurring hardwoods or "weed" species. In addition to aesthetic value, encouraging diversity in forest species subsequently encourages diversity of all other forest components, including wildlife (Carey & Harrington, 2001; Haeussler et al., 1990), understory species (Thomas, 1999), and soil flora and fauna, all of which encourage forest and ecosystem health.

Although research involving species influence on soils and forest health is not new, results are not consistent enough to state generalizations (Binkley & Giardina, 1998). Notions that nutrient cycling and availability are higher under broad-leaved than needle-leaved trees are no longer assumed, as experimental evidence does not consistently support this (Prescott, 2002). The influence of vegetation types on soil and forest productivity is an area that requires a number of studies encompassing a variety of species, further heightening the importance of studying 'native invasives' to determine their potential in forest ecosystems.

Vine maple (*Acer circinatum*) is an understory shrub or tree native to British Columbia, and like other hardwoods is managed to minimize its influence in conifer forests. Past research in mature coastal forests of BC suggest the presence of vine maple may improve site fertility (Ogden & Schmidt, 1997; Wardman & Schmidt, 1998; Tashe & Schmidt, 2001). Vine maple had nutrient-rich and faster-decomposing litter, a higher pH in the upper mineral soil, and greater concentrations of calcium (Ca), Mg and K in the forest floor relative to conifer-dominated plots (Ogden & Schmidt, 1997). Further research on vine maple in the same study area by Wardman & Schmidt (1998) revealed that the site index and tree heights of Douglas-fir (*Pseudotsuga menziesii*) were higher when adjacent to vine maple. Additional research indicated autumn litterfall (including needle litter) at vine maple plots was higher in N content compared to conifer plots (Tashe & Schmidt, 2001).

The largest maple in Canada, bigleaf maple (*Acer macrophyllum*) is also the only native tree-sized maple in British Columbia, and one of the major broadleaf species in the province (Thomas, 1999). Control, rather than culture of bigleaf maple guides forest

management in BC (Haeussler et al., 1990). The positive influence of vine maple on productivity in coastal forests suggests bigleaf maple may have an even greater impact on forest integrity due to its greater presence in the canopy. A study by Fried et al. (1990) revealed that when compared to Douglas-fir, bigleaf maple had greater litterfall weight and nutrient content, faster turnover rates for forest floor biomass, and mineral soils higher in N concentration. This implies that bigleaf maple may positively influence soil properties through accelerated nutrient cycling and improved site productivity (Thomas, 1999). These improvements may offset the influence of bigleaf maple as a competitor and justify its presence in commercial Douglas-fir stands.

1.2 Bigleaf Maple Research

1.2.1 Research Objectives

The goal of this research was to examine the influence of bigleaf maple on nutrient dynamics in a coastal Douglas-fir forest. The intention of this research was to expand and build upon the scope of the study conducted by Fried (1985). Despite the potential for improved nutrient availability due to the abundant nutrient-rich litter of bigleaf maple, Fried et al. (1990) found inconsistencies in forest floor and mineral soil nutrient contents when compared to Douglas-fir sites.

1.2.2 Research Hypotheses

The overall hypothesis of this research study was that the presence of bigleaf maple in a conifer forest will result in greater nutrient availability and enhanced soil fertility. Several sub-hypotheses follow.

The total weight of litterfall accumulated over one year is greater on sites with bigleaf maple as compared to sites with no bigleaf maple.

It was anticipated that bigleaf maple sites would contribute more total litterfall in the autumn season, as well as annually, compared to conifer sites. Fried et al. (1990) and Tarrant et al. (1951) found higher annual litterfall weights beneath bigleaf maple compared to Douglas-fir.

The nutrient concentrations of bigleaf maple litter is greater than Douglas-fir/hemlock litter.

Maple leaves were expected to input greater element concentrations compared to conifer needles, based on the notion that hardwoods have increased levels of nutrients compared to conifer foliage (Perry, 1994). Tashe and Schmidt (2001) measured significantly higher concentrations in vine maple foliage compared to Douglas-fir, in most nutrients analysed. In a comparison between bigleaf maple and Dougalas-fir litter, Fried et al. (1990) found greater concentrations of most macro and micronutrients in bigleaf maple.

Bigleaf maple litter has a faster decay rate and nutrient release compared to conifer needle litter. Litter decays faster at bigleaf maple plots.

Conifer needle litter is generally more acidic and has lower nutrient concentrations than deciduous litter, resulting in a slower rate of decomposition. Based on this assumption, it was hypothesized that bigleaf maple litter would decay faster than conifer litter. Harmon et al. (1990) found that bigleaf maple decayed faster than Douglas-fir at the end of 12

months. Fried et al. (1990) claimed faster decay in bigleaf maple compared to Douglas-fir when forest floor turnover times were calculated. A faster decay rate in bigleaf maple was expected to correspond with a faster rate of nutrient release compared to Douglas-fir and hemlock. In addition, it was expected that a faster decomposition of bigleaf maple litter at bigleaf maple plots would stimulate faster breakdown and decay of conifer litter.

Thinner LF horizons in the forest floor are present in bigleaf maple plots relative to conifer plots. A thicker Ah horizon is present beneath bigleaf maple relative to conifer plots.

Depths were expected to be thinner for the L and F horizons and thicker for the Ah horizon beneath bigleaf maple compared to conifer sites. Under the hypothesis that bigleaf maple would have hastened litter decay, the L and F horizons should be thinner, with a thicker Ah horizon representing the rapid breakdown of abundant litterfall. Total forest floor depths were thinner at vine maple sites compared to conifer sites in a study by Ogden and Schmidt (1997).

The majority of bigleaf maple plots have a mull humus form, while mor humus forms are found at conifer plots.

Mull forest floors are generally found where bases are well supplied, such as in hardwood forests (Fisher & Binkley, 2000). Hence, it was expected that the majority of forest floors beneath bigleaf maple would be classified as mull forest floors, as indicated by Krajina et al. (1982). Mor forest floors are mainly found in coniferous forests.

The nutrient content in the forest floor and mineral soil beneath bigleaf maple is higher relative to conifer plots. The pH of bigleaf maple plots is higher than conifer plots in both the forest floor and top 7 cm of mineral soil. Bigleaf maple plots have lower C/N ratio relative to conifer plots.

Litter from bigleaf maple plots was expected to have higher nutrient contents that would be reflected in the forest floor and incorporated into the mineral soil. It was expected that the input of Douglas-fir and hemlock litter would be demonstrated by a low pH in the forest floors and mineral soils at conifer plots. Higher total nitrogen concentrations in forest floors and mineral soils were expected to accompany hastened decomposition of nutrient-rich and basic litter, as well as a low C/N ratio. Ogden and Schmidt (1997) found lower C/N ratios, higher total N and higher pH in mineral soils beneath vine maple.

1.2.3 Thesis Overview

The purpose of my research is to examine the implications of bigleaf maple presence on forest soil chemistry and nutrient dynamics by examining several components of the forest nutrient cycle. This research will build a foundation for future studies examining the role of bigleaf maple in forest ecosystems, and will add to studies examining species influence on soils.

Chapter 1 is an introduction that presents the rationale for the research and reviews relevant literature. Chapter 2 presents the study location and methodology employed throughout the research for all measured components of the biogeochemical cycle. Results are presented in Chapter 3 and discussed in Chapter 4. The conclusion

chapter summarizes the study and its implications, and offers suggestions for further research.

1.3 Literature Review

1.3.1 Litterfall & Its Role in Nutrient Cycling

Nutrient cycling is crucial to soils in the Pacific Northwest, which are typically acidic and deficient in phosphorus (P) and N (Tarrant et al., 1951; Fisher & Binkley, 2000). Although mineral weathering and understory vegetation play an important role in nutrient flux, the forest canopy produces most of the litter reaching the forest floor and therefore has the largest influence on the development of the forest floor and its properties. Litterfall plays an important role in determining the properties of the forest floor and mineral soil, with aboveground species influencing the abundance and diversity of belowground organisms responsible for litter breakdown (Grayston & Prescott, 2005; Bjornlund & Christensen, 2005; Rothe & Binkley, 2001).

The effect a tree species has on nutrient availability is largely dependant on the chemistry of its litterfall (Thomas & Prescott, 2000; Prescott, 2002). In comparison to conifer litter, broadleaved litter is generally base-rich, contains higher concentrations of N, P, K, Ca and Mg (Fisher & Binkley, 2000), lower levels of lignin, and a larger surface area to mass component, all of which promote rapid decomposition (Perry et al., 1987; Prescott et al., 2000; Cornelissen, 1996). The greater abundance of soil macrofauna common in broadleaved forests (Killham, 1994) stimulates microbial activity and litter decomposition, suggesting an increase in the rate at which nutrients are released (Perry et al., 1987). Harmon et al. (1990) found vine maple, bigleaf maple and cottonwood

(*Populus trichocarpa* T&G) to decay faster than Douglas-fir during the initial stages of decay. In a study involving 14 litter types by Prescott et al. (2004a), broadleaved litter types decayed faster than conifer litter types during the first 2 years of decay, although differences were not statistically significant.

The nutrition of a forest stand may be improved in mixed-wood stands, especially if mixed foliage results in higher elemental inputs, faster decay, or if the species in question are limiting in different nutrients (Rothe & Binkley, 2001). Litterfall measurements comparing European beech (*Fagus sylvatica*) and Norway spruce *(Picea abies)* showed significantly higher contents of K, Ca and Mg between species, and little difference for N and P (Bucking, 1987; Rothe, 1997, as cited in Rothe & Binkley, 2001). Although seldom studied, preliminary research on black cottonwood (*Populus balsamifera* ssp. *trichocarpa*) suggests the species may enhance total nitrogen via nitrogen-fixing bacteria specific to its coarse woody debris (Haeussler et al., 1990).

1.3.2 The Role of the Forest Floor & Mineral Soil in Nutrient Cycling

The forest floor is made up of three organic horizons; litter (L), fragmented or partly decomposed litter (F) and humified or well decomposed organic matter (H) horizons. The humus form can be comprised of the organic horizons, or both the organic and mineral (Ah) horizons (Qian & Klinka, 1995; Green et al., 1993). In addition to providing insight to the rate of decomposition and productivity at a given site, horizon measurements can aid in humus form classification. The three orders of humus forms found in British Columbia, in order of increasing litter decomposition rate and biological activity, are Mor, Moder and Mull. Mors are typical under species with slow-decomposing litter (such as conifers), and are characterized by a large L and F horizon

due to the accumulation of litterfall over time. The most productive horizon, the H horizon, is typically thin in Mors due to the slow decay rate and consequently minimal incorporation of organic material into the mineral horizon. With rapid litter breakdown, one would expect a thin L and F horizons and a thicker H horizon, representing advanced stages of decomposition and high biological activity. In a study in the Malcolm Knapp Research Forest (MKRF) by Klinka et al. (1981, as cited in Green et al. 1993), Mors generally had lower pH, higher C:N, lower total N, and higher cation exchange capacity (CEC) than Moders and Mulls. The CEC is another parameter that provides insight into the potential of the forest floor or soil to supply nutrients; a higher CEC indicates that the soil is capable of holding a larger amount of cations compared to a soil with a low CEC (L. Lavkulich, UBC, 2006, *pers. comm.*). Lastly, Mulls are often seen beneath hardwoods with easily decomposed litter, and an abundance of bases (Fisher & Binkley, 2000). A high pH encourages the growth of bacteria (Grayston & Prescott, 2005) allowing chemical changes necessary for plant growth to occur.

1.4 The Ecology of Bigleaf Maple

1.4.1 Geographic Distribution

Bigleaf maple is abundant in western North America, with a native range starting in northern Vancouver Island (British Columbia Ministry of Forests, 1999), extending south to scattered areas in San Diego, California, and always within 300 km of the Pacific Ocean (Figure 1.1) (United States Department of Agriculture Forest Service [USDAFS], 2004; Peterson et al., 1999). Bigleaf maple often grows in conifer forests, and is a common component of Douglas-fir forests in the Coastal Western Hemlock (CWH) and Coastal Douglas-fir (CDF) biogeoclimatic zones, and with limited occurrence in the

Interior Douglas-fir (IDH) zone of BC (Thomas, 1999; Pojar & Meidinger, 1991; Krajina et al., 1982; Haeussler et al., 1990). Bigleaf maple is typically a low-elevation species, but can be seen at elevations of approximately 350 m on Burnaby Mountain in Burnaby, BC. Temperature and moisture conditions range from the coastal marine climate of British Columbia, to the warm and dry growing season of southern California (USDAFS, 2004). Although it is most often seen on moist soils with abundant seepage (Haeussler et al., 1990), bigleaf maple is not limited to moist sites and can be seen on dry hillsides in southwestern Oregon (USDAFS, 2004).

1.4.2 Morphology and Physiology

Bigleaf maple can reach heights of up to 30 m and can live up to 300 years of age (Haeussler et al., 1990; USDAFS, 2004). It has a narrow crown accompanied by a limb-free bole in low light, and a broad rounded crown with stout and opposite branching twigs in open conditions. Leaves are deep-lobed and can measure up to 30 cm (Figure 1.2). Flowers are yellowish-green, and the fruit is a winged samara with paired seeds (Haeussler et al.,1990).

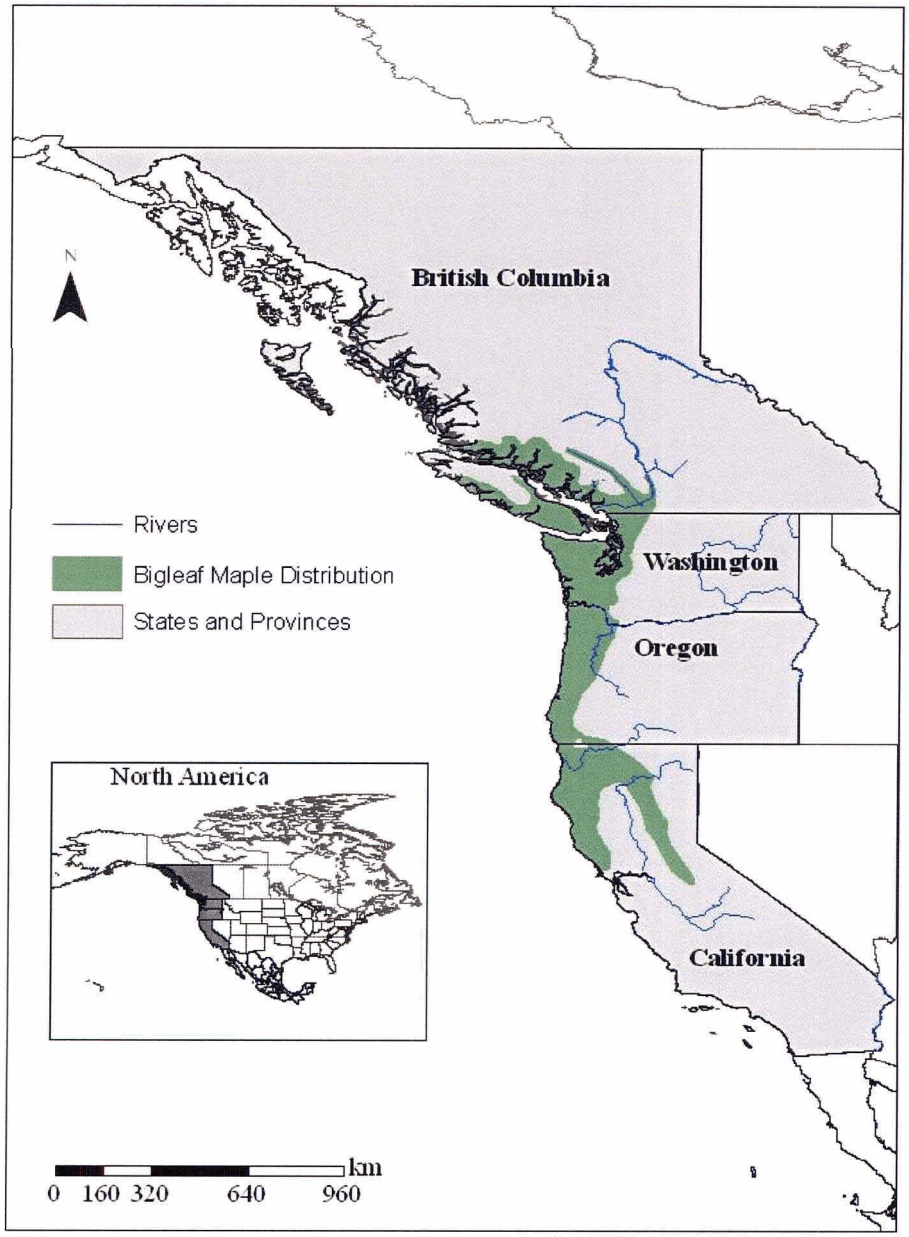

Figure 1.1. Geographic distribution of bigleaf maple in southwestern British Columbia (modified from Haeussler et al., 1990 & USDAFS, 2004).

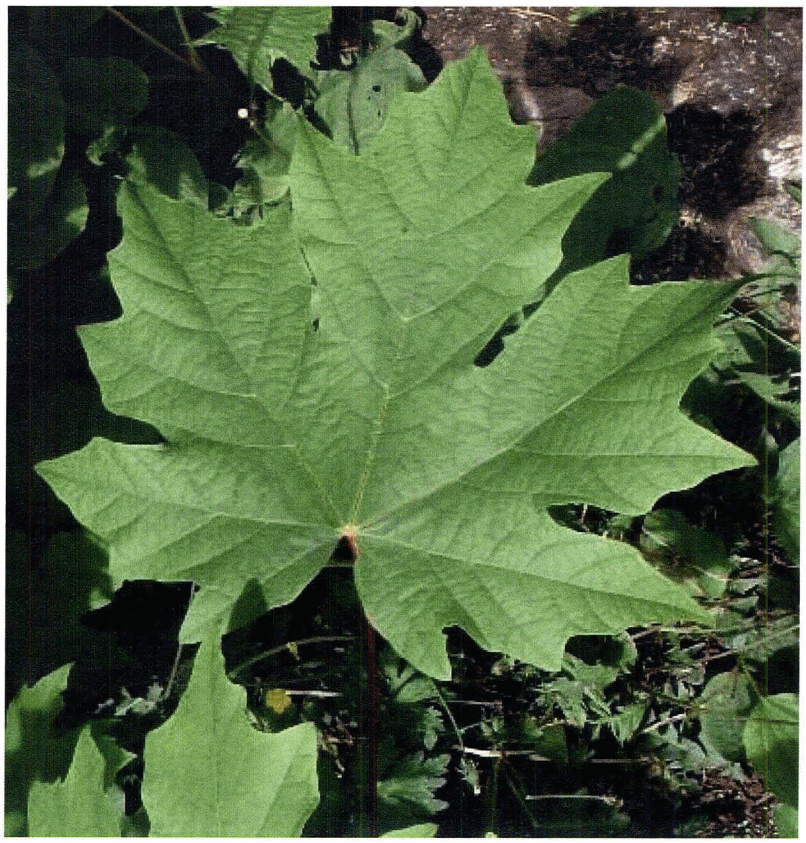

Figure 1.2. Bigleaf maple leaves are deep-lobed and can measure up to 30 cm.

In second-growth forests of southwestern BC, bigleaf maple is common but rarely dominates stands (Haeussler et al., 1990). It has a shallow and widespreading root system that likely has a competitive advantage over deeper rooted species in shallow soils (USDAFS, 2004). Bigleaf maple has a low to moderate shade tolerance (Krajina et al., 1982), and is not normally found as an understory tree (Haeussler et al., 1990). Due to its rapid initial growth, it often outgrows conifers to create a high overstory canopy component in the early stages of stand development (Comeau, 1996).

1.4.3 The Role of Bigleaf Maple in Nutrient Cycling

Because bigleaf maple competes for light in the forest canopy, it is considered a serious competitor to slower growing trees such as Douglas-fir, sitka spruce *(Picea sitchensis)*, western hemlock and grand fir (*Abies grandis)* (Thomas, 1999; Haeussler et al., 1990). The abundant litter during senescence in autumn can also smother small conifers. However, bigleaf maple litterfall is high in N, K and Ca compared to other northwestern tree species (Haeussler et al., 1990), and contains higher levels of most nutrients than conifer litter (Fried et al., 1990; Tarrant et al., 1951) supporting the notion that a small percentage of bigleaf maple trees can contribute a rich supply of nutrients to the forest nutrient cycle (Krajina et al., 1982). In old-growth forests along the west coast of the Olympic Peninsula, an area receiving up to 5000 mm of precipitation a year, large epiphyte populations on the bark of bigleaf maples contributed to nearly four times the foliar biomass of the host tree, demonstrating the crucial role it plays in nutrient cycling (Nadkarni, 1984).

A study by Fried et al. (1990) in which the soil properties beneath Douglas-fir were examined with and without bigleaf maple found that the amount of bigleaf maple litter reaching the forest floor was enough to contribute a significant amount of nutrients to the forest floor and soil. Because bigleaf maple litter is rich in bases, the rate of decomposition was much faster than Douglas-fir needles (Fried et al., 1990). In addition, Fried et al. (1990) found that concentrations of K, Ca, Mg, Zn, and Mo in bigleaf maple litter were significantly greater beneath bigleaf maple than under Douglas-fir at all sites examined.

Chapter 2: Methods

2.1 Study Area

This study was conducted at the Malcolm Knapp Research Forest (MKRF), located in Haney, east of Vancouver, BC (49°16'40"N, 122°34'20"W) (Figure 2.1). The study area is located within the dry maritime subzone of the CWH (coastal western hemlock) biogeoclimatic zone. Mean annual precipitation is 2140 mm and mean monthly temperatures range from 1.4°C to 16.8°C (Pojar & Meidinger, 1991).

The MKRF was burned in the second half of the 1800s, extensively harvested between 1920-1931, and planted to Douglas-fir (*Pseudostsuga menziesii*) following slash-burning in 1957 (Klinka, 1976). Today, the forest consists primarily of mixed stands of Douglas-fir, western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*). Bigleaf maple, black cottonwood (*Populus balsamifera* L. ssp. *trichocarpa*), red alder (*Alnus rubra*) and vine maple (*Acer circinatum*) are also common.

Two 1 m-deep soil pits revealed that the soil in this area is a Gleyed Dystric Brunisol (Tashe, 1998) derived from parent material consisting of unconsolidated surficial deposits, including glaciomarine and glaciolacustrine materials (Klinka, 1976). Soil textures throughout the profile were identified as sandy loam and loamy sand (Tashe, 1998). Parent materials in the C horizon have been identified as colluvial and morainal deposits (Klinka, 1976).

2.2 Experimental Design

Soil properties and partial nutrient cycles were compared in plots with and without bigleaf maple. Four conifer-dominated stands with an admixture of bigleaf maple were located using forest cover maps (British Columbia Ministry of Forests, 1989) and local knowledge supplied by MKRF personnel (Figure 2.2). Of the four stands chosen, two were aged approximately 65 years, and two 125 years. The characteristics of these sites are listed in Table 2.1.

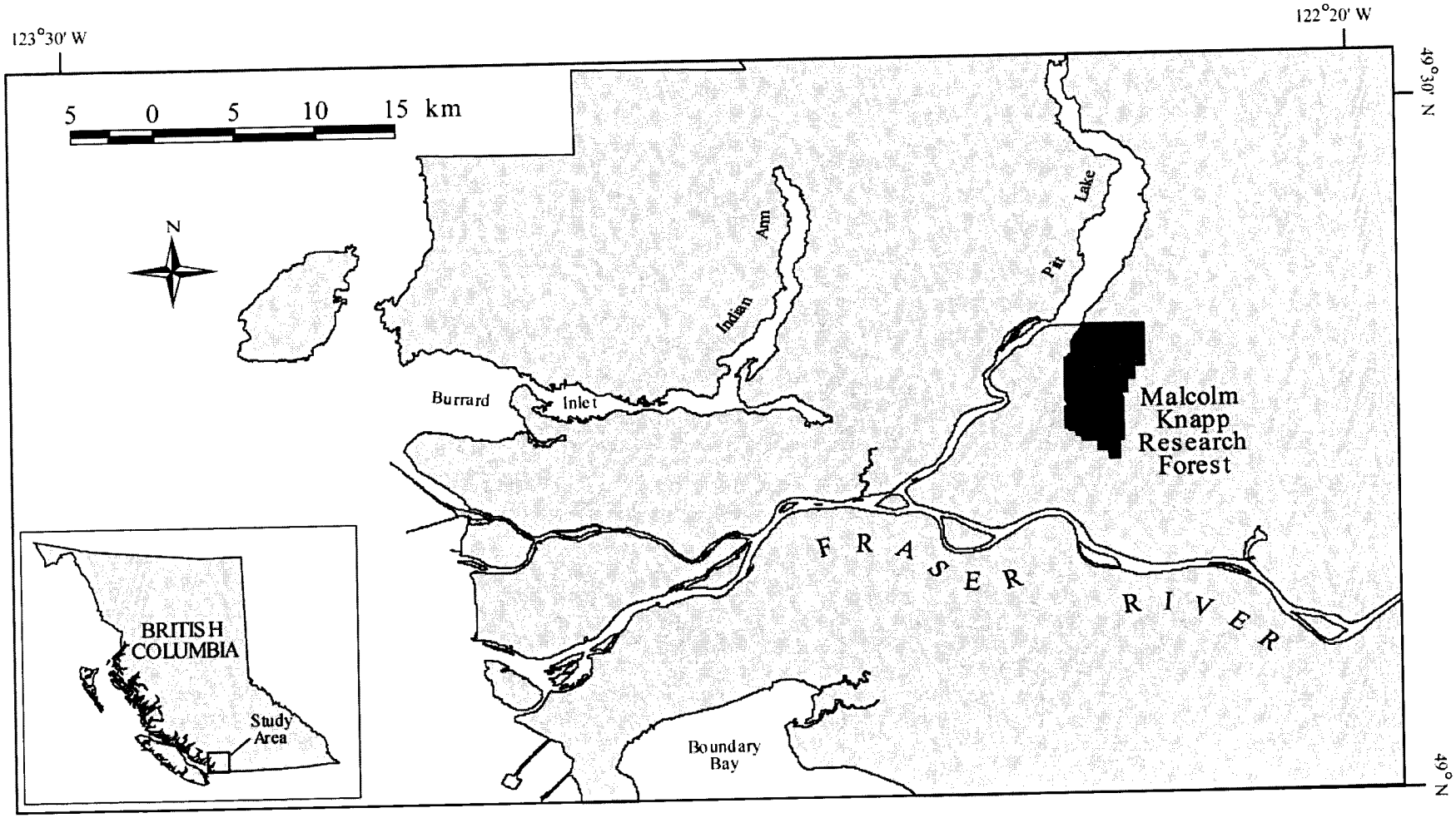

Figure 2.1. Location of Malcolm Knapp Research Forest in southwest British Columbia.

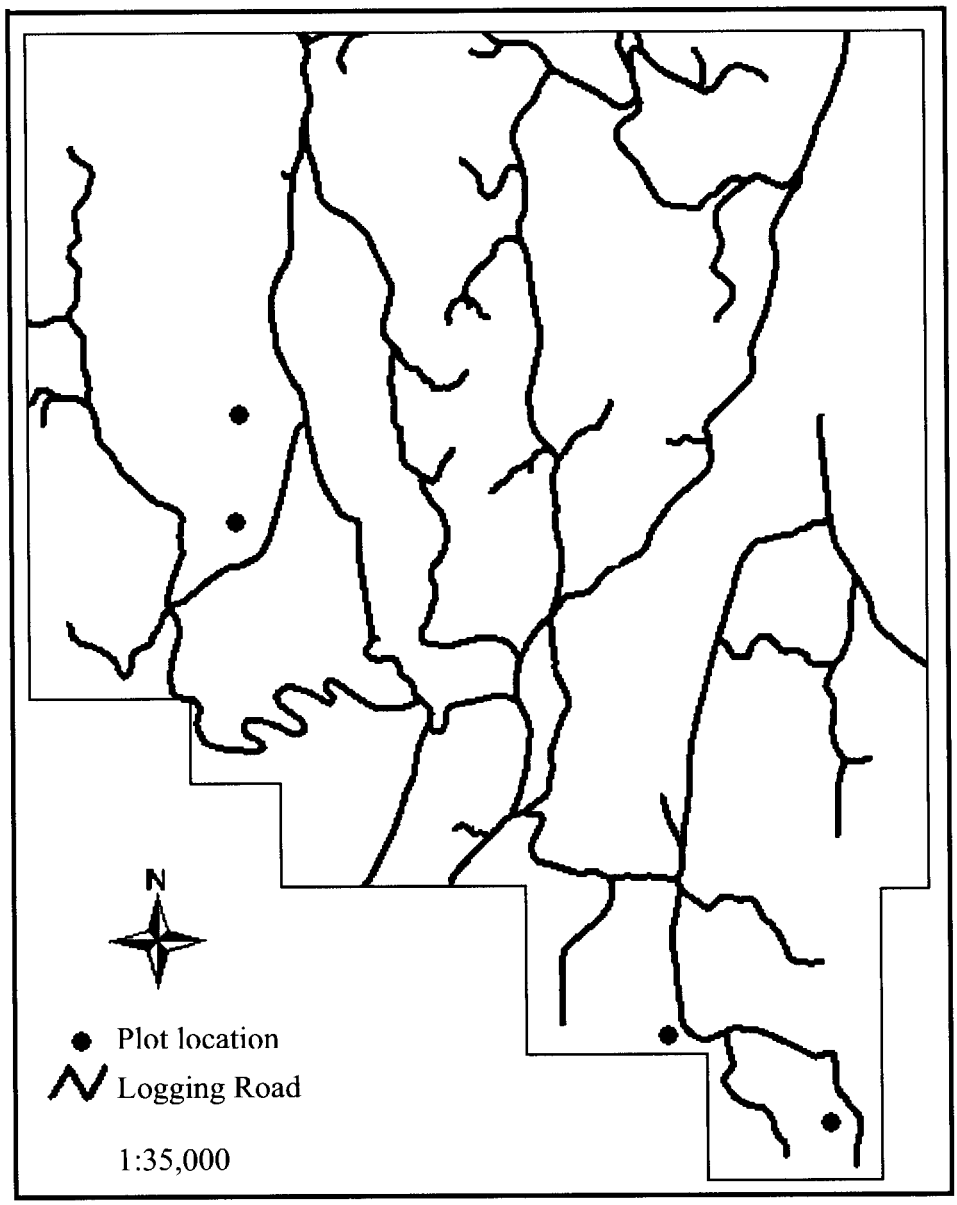

Figure 2.2. **Location of plots within the Malcolm Knapp Research Forest.**

Table 2.1. Characteristics of stands used at the Malcolm Knapp Research Forest

		Stand			
		A	B	C	D
Tree species composition (% canopy cover)	Douglas-fir	81	28	10	81
	western hemlock	9	40	60	9
	western redcedar	10	32	30	10
Height (m)		50	34	34	50
Age (y)		125	65	65	125
Site Class Code		Good	Good	Good	Good
Site Index		33.1	30.2	30.2	33.1
Crown Closure (%)		66-76	76-85	86-95	66-76

Source: Modified from UBC Malcolm Knapp Research Forest, 2006.

2.2.1 Plot Selection

Within each stand, three paired plots were selected, totalling 12 pairs, or 24 plots. Plots had a radius of 5 m, with the bole of a tree as plot center. Each bigleaf maple plot was paired with a conifer plot exhibiting similar site characteristics, such as slope, aspect and elevation. This allowed for comparison between sites with and without bigleaf maple.

Bigleaf maple plots were the first to be selected because this species is less frequent than conifers in these stands. Plots were centered on the bole of a dominant or co-dominant tree (Figure 2.3). All the plots met two further criteria: 1) they showed no signs of recent disturbance, and 2) they were at least 15 m distant from other deciduous trees.

Despite the latter precaution, one plot accumulated a considerable amount of black cottonwood litter during the observation period. Data from this plot were therefore

Figure 2.3. A bigleaf maple plot showing co-dominance in the canopy.

excluded from further analysis of litterfall (autumn and annual), forest floor and mineral soil. However, this plot was included in the litter decomposition portion of the study. Several studies show that at the local scale, site type does not significantly influence the rate of litter decay (DeCatanzaro & Kimmins, 1985; Xu & Hirata, 2005). Because differences in decay rates were minimal between plot types for this study, it was decided that the extra plot would be included in analysis.

Where possible, conifer plots were centred on the boles of dominant Douglas-fir trees. Western hemlock boles were used as the centre of plots only where no suitable Douglas-fir stems were present. Conifer plots were selected to match the slope, aspect, elevation and minor contributions from deciduous species of maple plots to which they

were paired. Conifer pairs selected were between 30 and 65 metres from established paired maple plots. Such placement should minimize the effects of bigleaf maple and of stand-scale variability.

2.2.2 Litterfall

2.2.2.1 Collection

Litterfall was collected beneath bigleaf maple and conifer plots using plastic greenhouse trays (0.125 m^2) equipped with drainage holes, and lined with fibreglass mesh. Five trays were randomly placed at each plot (120 trays total). Litterfall collection began in September 2004, and ended September 2005, with a total of four collection periods. Collection times were selected to represent each season; autumn (September 2004 – December 2004), winter (December 2004 – March 2005), spring (March 2005 – June 2005) and summer (June 2005 – September 2005). Litterfall from greenhouse trays was collected monthly, with the exception of the autumn collection. Collections throughout this period were made weekly to minimize the leaching of elements.

Litterfall collection followed the methods used by Tashe (1998) and Ogden (1993). Upon collection, the mesh lining was rolled up and placed into labelled plastic bags. Litter was spread out and left to air-dry overnight in the laboratory. The following day, litter was gently removed from the mesh, oven-dried at 70°C for 24 hours, and weighed. Samples from the autumn period were sorted into four categories; bigleaf maple leaves, Douglas-fir and hemlock needles, cedar, and 'other' debris (small twigs, cone scales, and any other litter). Branches larger than 2 mm in diameter, and bark greater than 2 cm in diameter were removed from the sample (Maguire, 1994). The oven-dry weight of each category for each plot was recorded. Litterfall weights were averaged per plot,

and an estimation of seasonal and annual litter input relative to each plot type was determined (Tashe, 1998). Grams of oven-dried litter in a 0.125 m^2 tray was converted to kg ha^{-1}.

2.2.2.2 Lab Analysis

Once oven-dried, sorted, and weighed, autumn litterfall samples were prepared for analysis. Each litterfall type was composited by species on a plot basis, and ground. After thorough mixing, a 10 g subsample was extracted and sent to the Ministry of Forests for cellulose, lignin and elemental analysis.

Litterfall samples were analysed for P, K, Ca, S, Mg, Mn, B, Zn, Fe, Cu and Al, following the closed vessel microwave digestion method, by Kalra and Maynard (1991), and modified by the Ministry of Forests laboratory. Each litterfall sample underwent digestion to break down the plant tissue and target the desired element. A standard control sample was digested with every 9 samples. Once removed from the microwave and cooled, samples were analysed by an inductively coupled plasma-atomic emission spectrometer (ICP). For analysis of total C and N, tissue samples were milled using a Wiley mill, and run through a Fisons NA-1500 Elemental Analyser.

Bigleaf maple and Douglas-fir/hemlock foliage from autumn litterfall was composited by stand, and analysed for cellulose and lignin (n = 4). Analysis followed the acid detergent method by Goering & Van Soest (1970) and Ryan et al. (1990).Using this method, a sample of leaf material was treated with a dilute acid detergent solution, made of sulphuric acid (0.5 M) and cetyltrimethylammonium bromide (CTAB) (20 g L^{-1}) solution (Fioretto et al., 2005). The treated sample was placed in a tube with Alundum

boiling stones, and kept at 100°C for one hour. After cooling, the stone and acid detergent-fibre (ADF) was rinsed well with hot distilled water. The remaining residue was then cooled in a dessicator for one hour and weighed (Eq 1). After weighing, sulphuric acid was added to the crucible and allowed to drain for one hour (repeated 2x) followed by thorough rinsing with hot water. The sample was then oven dried, cooled and weighed (Eq 2). Samples were then ashed at 500°C for 3 hours, cooled and weighed again (Eq 3). The remaining Acid Detergent Fibre contained lignin, cellulose and ash. The percentage of Acid Detergent Lignin (ADL) and Acid Detergent Cellulose were determined by the following equations;

Total Acid Detergent Cellulose (tADC) = (Eq 1) – (Eq 2)

ADC = tADC(100/tissue sample weight)*

Total Acid Detergent Lignin (tADL) = (Eq 2) – (Eq 3)

ADL = tADL(100/tissue sample weight)*

All values of elements, cellulose and lignin were expressed as concentrations ($\mu g\ g^{-1}$) and contents ($kg\ ha^{-1}$). Contents were calculated by multiplying concentrations by grams of oven dried litter in a 0.125 m^2 trap and converting to the appropriate SI units.

2.2.3 Litter Decomposition

2.2.3.1 Litter Bags

Litter decomposition was measured using methods similar to those of Prescott et al. (1993) and Taylor et al. (1991). Samples of litterfall were collected in September – October 2004 from greenhouse trays placed underneath various bigleaf maple and

Douglas-fir trees in the MKRF. Trays were lined with mesh, and had drainage holes in the bottom. Litter was collected frequently (once each week) from traps until the desired amount was obtained. Upon collection, litter was placed into plastic bags and brought back to the laboratory to air dry.

Decomposition bags were made of 2-ply fibreglass mesh that contained 1 mm square pores. After bags were filled with the equivalent of 2 g dry weight of litter, the open end was stapled across twice. Bigleaf maple litter was placed in 12 cm by 15 cm decomposition bags to account for the size of individual leaves, whereas Douglas-fir needles were placed in 6 cm by 12 cm bags. To find the equivalent of 2 g dry weight of bigleaf maple, five air-dried samples were weighed and recorded. Samples were then placed in an oven at 70°C for approximately 24 hours, and their dry weight recorded. Using the average of the oven-dried weights, as well as the average of the air-dried weights, the equivalent of 2 g of bigleaf maple dry weight was found. Two grams of Douglas-fir needles were placed in decomposition bags following oven drying. Litterbags were placed individually in labelled envelopes for transport to the field. Any spillage into envelopes was weighed and subtracted from the original weight (Prescott et al. 2004a, C. Staley, UBC, 2004, *pers. comm.*).

In December 2004, nine bags of each litter type (3 replicates x 3 collections) were randomly pinned to the forest floor at two paired plots per site, totalling 288 litterbags (16 plots x 9 bags x 2 litterbag types). Three bags of each litter type were collected from each site at 6, 12 and 18 months (Figure 2.4). Upon collection, litterbags were placed in labelled envelopes and brought back to the lab.

Figure 2.4. Litterbags at one plot at the MKRF. Larger bags contain bigleaf maple litter, and smaller bags contain conifer litter.

2.2.3.2 Lab Analysis

Litter was removed from individual mesh bags and rinsed under a gentle stream of water, above a sieve. This was done to remove any accumulated debris on the sample prior to weighing. After rinsing, samples were air-dried overnight. The following day, samples were oven dried at 70°C for 24 h. Each sample was weighed and the mass lost calculated. Samples were ground, composited on a plot basis, and sent to the Ministry of Forests for analysis of elements. Analysis of P, K, Ca, Mg, S, Mn, B, Zn, Fe, Cu and Al

followed the closed vessel microwave digestion method by Kalra & Maynard (1991), as described for litterfall samples. For analysis of total C and N, tissue samples were milled using a Wiley mill, and run through a Fisons NA-1500 Elemental Analyser.

2.2.3.3 Decay Rate Calculation

The annual litter decay constant *(k)* was determined using a single exponential decay equation, discussed in detail by Olson (1963), where the rate of decay is calculated as

$$-kt = \ln (X_t/X_o)$$

In this equation, X_t is the mass remaining at time t of year 1, and X_o is the original mass. This equation assumes that the decay rate of litter is the same throughout all stages of decay. However, the use of *k* as a decay constant can have limitations since litter decay generally goes through two different rates of decay over time. The use of a decay rate constant is often used to characterise the loss of mass, so that comparisons can easily be made with other data sets (Wieder and Lang 1982). Trofymow et al. (2002) found the single exponential decay model to be useful in comparing and analyzing 10 foliar litter types over 6 years at 18 sites across Canada, not including those sites that were especially cold.

2.2.4 Forest Floor

2.2.4.1 Humus Form Collection & Classification

Forest floor sampling occurred during November and December 2003, as well as January, March and November 2004. Due to the high variability of forest floors, a single sample is not sufficient to characterize the humus form of an entire plot (Green et al.,

1993). Three forest floor samples were extracted using randomly selected bearings and distances (between 1.5 and 4.0 metres) from the centre of each plot. The same sets of bearings and distances were used for all plots, however sampling at woody, rocky, or disturbed locations was avoided. If sampling at a randomly selected location was not suitable, sampling was conducted 0.5 metres in each of the cardinal directions (in the order north, south, east, west) until a suitable sampling location was encountered.

Because litter that has recently fallen on the forest floor is not a part of the humus form (Green et al., 1993), fresh leaves and needles were removed prior to extracting samples (Qian & Klinka, 1995). Samples extracted were approximately 20 x 20 centimetres, and extended to the depth of the organic-mineral soil interface. Humus form samples were removed with minimal disturbance to both the sample and the excavation sides and fitted into aluminium pans (Figure 2.5). Samples were sealed in plastic bags until described in the laboratory.

To reduce errors in depth estimation due to disturbance, depths of horizons affecting humus form classifications (e.g. L, F, H, Ah, and Ae) were recorded in the field. Mean depth of each horizon was determined by averaging mid-point depths from three undisturbed excavation sides (Carter & Lowe, 1986; Tashe, 1998). Where differentiation between organic and mineral material (typically H versus Ah material) was uncertain, sub-samples were removed from excavation sides for determination of organic matter content following the loss-on-ignition (LOI) method, described by Kalra & Maynard (1991).

Humus forms were classified to the group-level according to Green et al. (1993). Horizon designations for litter (L), fibric (F), humic (H), and organic-enriched mineral

(Ah) horizons were based on numerous properties including texture, fabric, composition, and organic matter content.

Figure 2.5. **A 20 X 20 cm extraction of the forest floor at one plot in the MKRF. Samples were fitted into aluminium pans, sealed in a plastic bag, and brought back to the laboratory.**

2.2.4.2 Forest Floor Sampling and Lab Analysis

Three additional forest floor samples were collected at each plot using random bearings, and followed the methods used for humus form sampling. Samples were approximately 20 cm X 20 cm. The total moist weight of the extracted forest floor was measured. Subsamples of the forest floor were weighed, oven-dried at 105°C for 48 h, and weighed again (Kalra & Maynard, 1991) to calculate the weight per unit area. An additional, equal-sized subsample was removed from each sample, oven-dried for 24 hours at 70°C, weighed, ground and composited per plot (Ogden, 1996; Tashe, 1998). After thorough mixing, composite samples from each plot were sent to the Ministry of

Forests and tested for pH, total N, C and S, mineralizable N, exchangeable cations, available P, ammonium and nitrates.

The pH of the forest floor was measured with a combination electrode and data acquisition system in a 1:1 forest floor to water solution (Kalra & Maynard, 1991; Atkinson et al., 1958; Peech, 1965). Total C, N, and S was measured on a Fisons NA-1500 Elemental Analyser. The calculated concentrations of C and N were used to calculate the C:N ratio of the forest floor. Exchangeable cations were determined using an ARL 3560 inductively coupled argon plasma (ICAP) spectrometer.

The sum of cations included in this method was used to measure effective CEC (Carter, 1993; Hendershot & Duquette, 1986). Available phosphate was extracted using the Bray P1 method. Afterwards, the phosphate in the extracting solution was complexed with ammonium molybdate and antimony potassium tartrate to form a stable antimony-phospho-molybdenum blue complex (Kalra & Maynard, 1991; John, 1970). Ammonium and nitrate were measured colorimetrically using an Alpkem Flow System IV analyzer (Carter, 1993; Bremmer, 1965). Mineralizable nitrogen was measured using an anaerobic incubation method, where a soil sample is incubated under anaearobic, water-logged conditions for 2 weeks at 30°C and measured colorimetrically by a Technicon Auto-analyzer II (Waring & Bremner, 1964a & 1964b; Bremner, 1996). Total concentration values were converted to kg ha^{-1} based on the oven-dry weight of the forest floor per unit of area.

2.2.5 Mineral Soil

2.2.5.1 Sampling

Three randomly selected mineral soil samples per plot were collected using a bulk density corer with a radius of 5.0 cm, height of 7.0 cm, and total volume of 549.8 cm^3. Bulk density cores were taken from areas directly beneath where forest floor samples were extracted. Mineral soil was recognised beneath the forest floor as having a lighter colour, and by the presence of gravel. Contamination of soil samples was avoided by thoroughly cleaning the bulk density core between plots (Tashe, 1998; Borchers & Perry, 1989).

2.2.5.2 Lab Analysis

The total moist weight of soil cores was measured. Subsamples from soil cores were weighed, oven dried at 105°C for 48 h, and weighed again (Kalra & Maynard, 1991) to calculate bulk density. To find the coarse fragment content, samples were passed through a 2 mm sieve, and the portion of soil material greater than 2 mm was weighed. The percentage of coarse fragments was then calculated by taking the mass of the coarse fragments, dividing by the mass of the sample, and multiplying the result by 100. Equal portions of the remaining soil subsamples were air-dried, composited, thoroughly mixed and sent to the Ministry of Forests for analysis of pH, total N and C, mineralizable N, exchangeable cations, available P, ammonium and nitrates (Tashe, 1998). Mineral soil samples were analysed using the same methods as described for forest floor samples.

2.2.6 Statistical Analysis

All quantitative data were statistically analyzed using S Plus 7.0 Software, with plots being considered individual sample units. Each sample unit represents the mean of sub-samples from each plot (Tashe, 1998). All data sets were plotted on a Quantile-Quantile (QQ) graph for visual inspection of normal to near-normal distribution. For all data analysis a significance level of 0.10 was used.

Data appearing normal were analysed using paired t-tests to test for statistically significant differences between bigleaf maple and conifer plots. Data not appearing to have a normal or near-normal distribution were log transformed prior to statistical analysis to achieve normality. Data that could not be corrected with log transformations were analysed using the nonparametric analogue to the t-test, the Wilcoxin signed rank (Zolman, 1993).

One-way analysis of variance (ANOVA) tests were performed on autumn litterfall data, to determine if statistical differences existed in the weight and nutrient content between bigleaf maple, Douglas-fir/hemlock, and cedar, within bigleaf maple plots. When analysis showed statistical significance between litterfall types, data sets were further analysed with the Tukey's multiple comparison test to determine which litter types were significantly different from each other (Tashe, 1998). In addition, at each plot type ANOVA tests were performed on each element analysed for litter decomposition, to determine significant differences between bigleaf maple and Douglas-fir/hemlock litter, at 0, 6, 12 and 18 months. Tukey's multiple comparison test followed, to determine where statistical differences existed. For clarity, only differences that existed between litter types at each sampling period were indicated in tables. In addition, underlying

assumptions were checked by inspecting the homogeneity of population variance through histograms and QQ graphs of the residuals.

The probability of committing a Type II (ß) error was calculated when paired t-tests yielded non-statistically significant results on normally distributed data. Power was determined by subtracting ß from 1, using a computer program created by Borenstein and Cohen (1988). A Type II error results in a failure to reject the null hypothesis when the alternative hypothesis is true (Kleinbaum et al., 1998). Hence, a small ß would increase the power and sensitivity of the test.

Chapter 3: Results

In the following chapter I describe the results of observations and experiments found in my study plots for each component of the forest nutrient cycle that was examined, in the following order: litterfall (seasonal and annual weights, followed by chemical composition), litter decomposition (percent mass loss, decay rate, and nutrient analysis), forest floor (humus form classification, forest floor properties and nutrient analysis), and mineral soil (properties and nutrient analysis).

3.1 Litterfall

3.1.1 Seasonal and Annual Litterfall Weights

When compared to conifer plots, bigleaf maple plots had significantly more litterfall in the autumn (Table 3.1, Figure 3.1, $P = 0.02$), and less in spring ($P = 0.06$). There was a weak trend for greater annual litterfall amounts in bigleaf maple plots as compared to conifer plots ($P = 0.20$). Summer litterfall amounts were higher in bigleaf maple plots and winter accumulations were higher at conifer plots, although these differences were not statistically significant.

Approximately half of the annual litter in bigleaf maple plots fell in autumn (Figure 3.2). Winter, spring and summer contributed equal portions of the remainder (17%). For conifer plots, autumn litterfall accounted for 35% of annual accumulations, with winter and spring both contributing approximately a quarter to the total. Summer contributions were approximately 18% of annual amounts.

Table 3.1. Seasonal litterfall (kg ha^{-1}) in bigleaf maple and conifer plots (mean ± 1 sigma; n = 11)

	Bigleaf maple plots		Conifer plots		P (t-test)	Power (1- ß)
Autumn	2272	(886)	1365	(654)	0.02*	
Winter	756	(298)	884	(291)	0.24	0.16
Spring	761	(204)	919	(236)	0.06*	
Summer	760	(370)	679	(324)	0.36*	0.08
Annual total	4549	(1229)	3847	(870)	0.20*	0.31

Single and double underlined values indicate significant differences at P < 0.1 and P < 0.05. *Data were log transformed to meet underlying statistical assumptions.

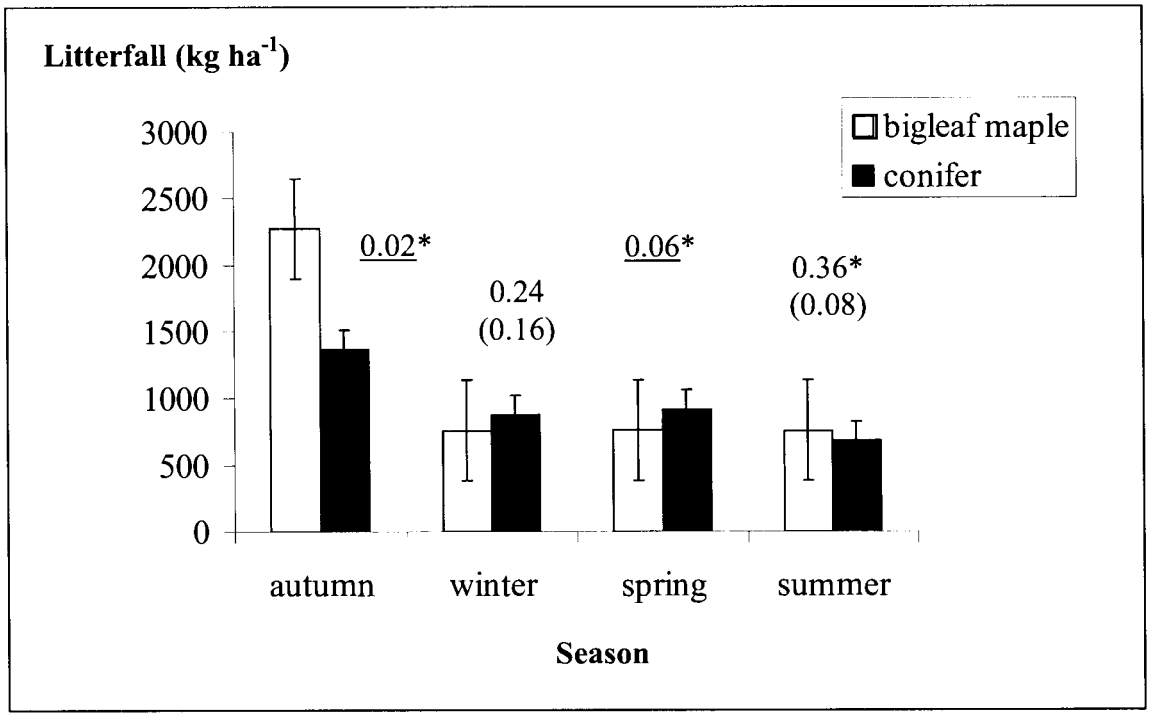

Figure 3.1. Mean seasonal litterfall amounts for bigleaf maple plots and conifer plots (mean of eleven replicates). Probability values (t-test) are shown on the graph. *Data were log transformed to meet underlying statistical assumptions. Single underlined values represent significant differences at P < 0.10. Values in parentheses represent Power (1- ß).

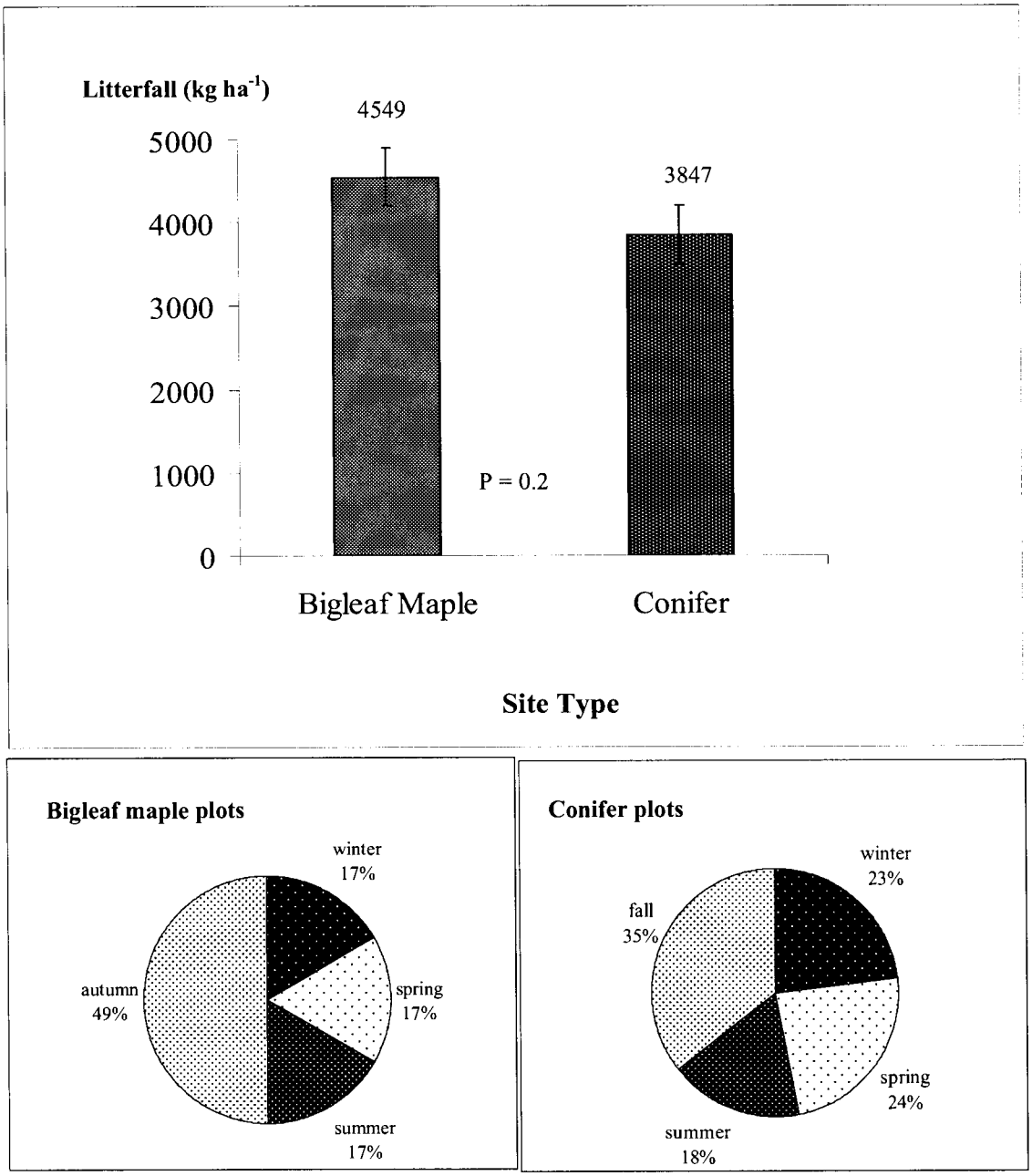

Figure 3.2. Total annual litterfall showing proportions of seasonal contributions by weight. Probability value (t-test) is shown on the graph. Power (1- ß) was 0.31.

There were no significant differences in the amount of conifer litter (fir/hemlock + cedar) that accumulated in autumn in the two site types (1015 and 1145 kg/ha for bigleaf maple and conifer plots respectively, Table 3.2). There was no bigleaf maple litterfall in the conifer plots. For bigleaf maple plots, the amount of bigleaf maple

litterfall (748 kg ha) was less than conifer (fir/hemlock + cedar, 1015 kg ha^{-1}, Table 3.2) but more than fir/hemlock litterfall (509 kg ha^{-1}). Fir/hemlock litterfall amounts were significantly greater at conifer plots than at bigleaf maple plots (P = 0.02). 'Other' litterfall (twigs, cones, black cottonwood leaves, seeds and moss) accounted for less than a quarter of autumn litterfall at bigleaf maple and conifer plots, however, differences between site types were not statistically significant (Figure 3.3). In bigleaf maple plots, maple contributed more litter than cedar (Table 3.2, P = 0.08).

Table 3.2. Autumn litterfall (kg ha^{-1}) in bigleaf maple and conifer plots (mean ± 1 sigma; n = 11)

	Bigleaf maple plots		Conifer plots		P (t-test)	Power (1-ß)
bigleaf maple	748	(377)				
conifer (fir/hemlock+cedar)	1015	(680)	1145	(589)	0.48*	0.07
fir/hemlock litterfall	509	(412)	819	(491)	0.02	
western red cedar	506	(753)	326	(304)	0.97*	0.10
'other'	509	(577)	220	(118)	0.15	0.34
total litterfall	2272	(886)	1365	(654)	0.02*	

Underlined values indicate significant differences at P < 0.05. *Data were log transformed to meet underlying statistical assumptions.

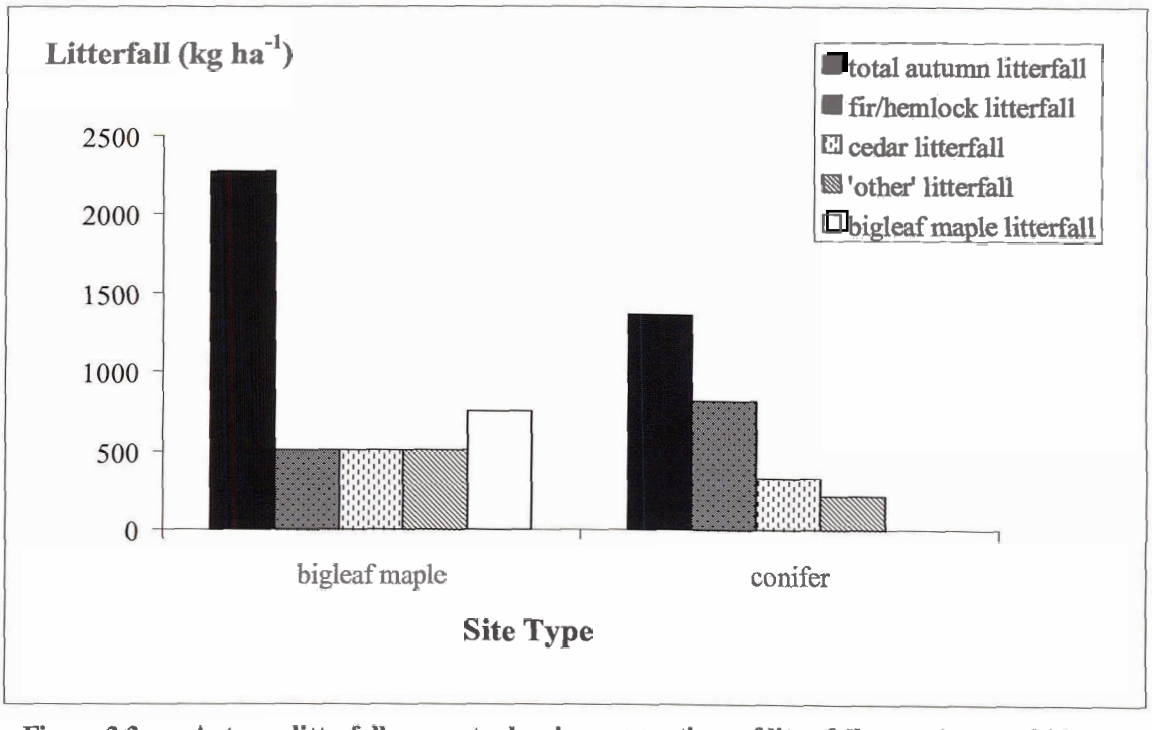

Figure 3.3. Autumn litterfall amounts showing proportions of litterfall types (mean of 11 replicates).

3.1.2 Litterfall Composition

Within bigleaf maple plots, all element concentrations showed statistically significant differences between litter types (bigleaf maple, Douglas-fir/hemlock, cedar), with the exception of Fe (Table 3.3). Bigleaf maple litter had higher concentrations and contents for all elements, except P, Mn and Fe than did Douglas-fir/hemlock litterfall, and higher concentrations and contents of all elements except Ca, Fe and Al than did cedar litterfall. Cedar had higher concentrations of Ca, and lower concentrations of K, S, and Mn than Douglas-fir/hemlock litterfall. Element contents of autumn litterfall (including all litter types at each site) were statistically different between site types (Table 3.4). Bigleaf maple plots had higher contents for all elements examined, relative to conifer plots.

Elemental concentrations for autumn Douglas-fir/hemlock litterfall were not significantly different between site types (Table 3.5) except for higher Zn concentrations at conifer plots, and higher Al concentrations at bigleaf maple plots. There were weak trends of higher K ($P = 0.11$) and lower Ca ($P = 0.14$) concentrations at bigleaf maple plots compared to conifer plots. Contents of all elements analyzed for Douglas-fir/hemlock litterfall were significantly lower at bigleaf maple plots compared to conifer plots. No significant differences in element concentrations or contents were observed in autumn cedar litterfall between bigleaf maple and conifer plots (Table 3.6). Significantly higher concentrations of N, K and Mn were found in 'other' litterfall at bigleaf maple plots compared to conifer plots (Table 3.7). No significant differences between site types were detected in element contents of 'other'.

An examination of the structural components between litter types at bigleaf maple plots revealed statistically significant differences in concentrations of total fibre, lignin and N (Table 3.8). Bigleaf maple litter was higher in concentrations of total fibre ($P = 0.003$), lignin ($P = 0.01$) and N ($P = 0.01$), respectively. There were weak trends for higher cellulose concentrations ($P = 0.13$) and lower lignin:N ratios ($P = 0.20$) for bigleaf maple litter compared to Douglas-fir/hemlock litter. Between plot types, there were no significant differences in fibre, cellulose, lignin or N for Douglas-fir/hemlock litter (Table 3.9).

Table 3.3. Element concentrations and contents of autumn litterfall from bigleaf maple plots (mean ± 1 sigma; n = 11)

	Bigleaf maple litter (blm)		Fir/hemlock litter (fir)		Red cedar litter (c)		Anova P (F stat.)	Tukey multiple comparison test		
								blm-fir	blm-c	c-fir
weight (kg ha^{-1})	748	(377)	509	(412)	506	(753)	0.079		+	
			Concentrations (μg g^{-1})							
C	497636	(10506)	536739	(7346)	536272	(11309)	0.000	++	++	
N	11017	(1395)	7070	(1084)	5902	(1812)	0.000	++	++	
P	636	(110)	548	(92)	431	(140)	0.001		++	
K	2817	(706)	1844	(827)	1059	(360)	0.000*	++	++	++
Ca	19719	(3835)	10211	(2857)	18622	(4191)	0.000	++		++
Mg	2018	(465)	895	(107)	772	(134)	0.000	++	++	
S	1238	(119)	743	(41)	617	(144)	0.000	++	++	++
Mn	253	(112)	217	(70)	131	(36)	0.000*		++	++
B	20	(6)	11	(2)	11	(3)	0.000	++	++	
Zn	49	(17)	28	(5)	19	(10)	0.000	++	++	
Fe	152	(45)	174	(91)	150	(54)	0.631*			
Cu	7	(1)	3	(0)	3	(1)	0.000	++	++	
Al	124	(27)	297	(112)	140	(50)	0.000*	++		++
			Contents (kg ha^{-1})							
C	373	(192)	275	(223)	275	(411)	0.114*			
N	8.30	(4.57)	3.55	(2.71)	2.54	(3.79)	0.002*	++	++	
P	0.48	(0.28)	0.27	(0.21)	0.19	(0.28)	0.006*		++	
K	2.26	(1.54)	0.79	(0.62)	0.44	(0.64)	0.001	++	++	
Ca	14.5	(7.25)	5.96	(5.52)	8.62	(12.21)	0.020*	++		
Mg	1.45	(0.72)	0.45	(0.37)	0.35	(0.49)	0.000*	++	++	
S	0.95	(0.53)	0.38	(0.31)	0.27	(0.39)	0.001	++	++	
Mn	0.18	(0.11)	0.11	(0.084)	0.080	(0.16)	0.007*		++	
B	0.015	(0.007)	0.006	(0.005)	0.005	(0.007)	0.002*	++	++	
Zn	0.038	(0.029)	0.015	(0.013)	0.008	(0.011)	0.000*	++	++	
Fe	0.11	(0.044)	0.082	(0.072)	0.054	(0.064)	0.032*		++	
Cu	0.005	(0.003)	0.001	(0.001)	0.001	(0.001)	0.000	++	++	
Al	0.092	(0.050)	0.13	(0.094)	0.054	(0.070)	0.017*		++	++

*Data were log transformed to meet underlying statistical assumptions. Single and double underlined values indicate significant differences at $P < 0.1$ and $P < 0.05$. ++ and + indicate significant differences at $P < 0.05$ and $P < 0.1$.

Table 3.4. Element contents (kg ha^{-1}) of autumn litterfall in bigleaf maple and conifer plots in (mean ± 1 sigma; n = 11)

	Bigleaf maple		Conifer		P (t-test)
C	1179	(475)	730	(354)	0.026*
N	20.6	(7.77)	9.23	(3.67)	0.004
P	1.30	(0.49)	0.73	(0.36)	0.024
K	5.58	(2.97)	1.90	(0.94)	0.006
Ca	37.0	(13.7)	17.9	(9.32)	0.002*
Mg	3.13	(0.95)	1.18	(0.45)	0.000
S	2.23	(0.85)	1.02	(0.45)	0.004
Mn	0.51	(0.25)	0.29	(0.18)	0.083^{w}
B	0.034	(0.010)	0.015	(0.008)	0.001
Zn	0.12	(0.063)	0.050	(0.025)	0.005*
Fe	0.43	(0.12)	0.30	(0.13)	0.036
Cu	0.012	(0.004)	0.006	(0.003)	0.004*
Al	0.45	(0.11)	0.35	(0.16)	0.076

Single and double underlined values indicate significant differences at $P < 0.1$ and $P < 0.05$, respectively. *Data were log transformed to meet underlying statistical assumptions. ^{w}Wilcoxin Signed-Rank Test was used to determine probability value.

Table 3.5. Element concentrations and contents of autumn Douglas-fir and western hemlock needle litterfall in bigleaf maple and conifer plots (mean ± 1 sigma; n = 11)

	Bigleaf maple plots		Conifer plots		P (t-test)	Power (1-ß)
	Concentrations ($\mu g\ g^{-1}$)					
C	536739	(7346)	538048	(5794)	0.58	0.06
N	7070	(1083)	7047	(747)	0.95	
P	548	(92)	554	(126)	0.93[w]	
K	1844	(827)	1492	(554)	0.11	0.20
Ca	10211	(2857)	11483	(2383)	0.14	0.19
Mg	895	(107)	835	(135)	0.24	0.19
S	743	(41.5)	736	(52.8)	0.70	0.05
Mn	217	(70.2)	254	(121)	0.49*	0.13
B	11.0	(2.0)	10.3	(2.68)	0.36	0.10
Zn	27.9	(5.24)	35.1	(17.9)	0.054[w]	
Fe	174	(91.5)	143	(21.0)	0.77[w]	
Cu	3.0	(0.36)	2.93	(1.35)	0.70[w]	
Al	297	(112)	234	(34.3)	0.056	
	Contents ($kg\ ha^{-1}$)					
C	275	(223)	440	(265)	0.019	
N	3.55	(2.71)	5.68	(3.34)	0.021	
P	0.27	(0.21)	0.47	(0.34)	0.030	
K	0.79	(0.62)	1.22	(0.90)	0.057	
Ca	5.96	(5.52)	9.65	(5.98)	0.011	
Mg	0.45	(0.37)	0.67	(0.40)	0.044	
S	0.38	(0.31)	0.61	(0.37)	0.020	
Mn	0.11	(0.084)	0.21	(0.17)	0.050	
B	0.006	(0.005)	0.009	(0.007)	0.061	
Zn	0.015	(0.013)	0.03	(0.025)	0.006	
Fe	0.082	(0.072)	0.12	(0.076)	0.010	
Cu	0.001	(0.001)	0.003	(0.002)	0.065	
Al	0.13	(0.094)	0.18	(0.11)	0.031	

Single and double underlined values indicate significant differences at $P < 0.1$ and $P < 0.05$. *Data were log transformed to meet underlying statistical assumptions.
[w] Wilcoxin Signed-Rank Test was used to determine probability value.

Table 3.6. Element concentrations and contents of autumn cedar litterfall in bigleaf maple and conifer plots (mean ± 1 sigma; n = 11)

	Bigleaf maple plots		Conifer plots		P (t-test)	Power (1-ß)
			Concentrations ($\mu g\ g^{-1}$)			
C	536272	(11309)	538764	(9976)	0.55	0.10
N	5902	(1812)	6603	(2404)	0.21[w]	
P	431	(140)	500	(228)	0.45*	0.12
K	1059	(360)	1042	(527)	0.69*	0.03
Ca	18622	(4191)	19855	(4439)	0.20	0.09
Mg	772	(134)	749	(150)	0.71	0.05
S	617	(144)	645	(155)	0.62	0.06
Mn	131	(35.8)	166	(102)	0.26*	0.18
B	11.1	(2.72)	13	(4)	0.19	0.15
Zn	19.5	(9.60)	21	(9)	0.68	0.06
Fe	150	(54.4)	140	(38)	0.64	0.07
Cu	2.69	(0.92)	3	(1)	0.47	0.09
Al	140	(50.0)	138	(37)	0.82	0.03
			Contents ($kg\ ha^{-1}$)			
C	275	(411)	176	(166)	0.96*	0.10
N	2.54	(3.79)	1.77	(1.18)	0.77*	0.09
P	0.19	(0.28)	0.13	(0.083)	0.75*	0.09
K	0.44	(0.64)	0.28	(0.19)	0.92*	0.11
Ca	8.62	(12.21)	6.09	(5.42)	0.85*	0.09
Mg	0.35	(0.49)	0.23	(0.20)	0.96*	0.11
S	0.27	(0.39)	0.19	(0.16)	0.88*	0.09
Mn	0.080	(0.16)	0.044	(0.032)	0.72*	0.10
B	0.005	(0.007)	0.004	(0.003)	0.77*	0.06
Zn	0.008	(0.011)	0.005	(0.004)	0.71*	0.12
Fe	0.054	(0.064)	0.045	(0.047)	0.99*	0.05
Cu	0.001	(0.001)	0.001	(0.001)	0.75*	0.03
Al	0.054	(0.070)	0.046	(0.048)	0.96*	0.05

*Data were log transformed to meet underlying statistical assumptions. [w] Wilcoxin Signed-Rank Test was used to determine probability value.

Table 3.7. Element concentrations and contents of autumn 'other' litterfall in bigleaf maple and conifer plots (mean ± 1 sigma; n = 4)

	Bigleaf maple plots		Conifer plots		P (t-test)	Power (1-ß)
	Concentrations ($\mu g\ g^{-1}$)					
C	498800	(9003)	510118	(12007)	0.63[w]	
N	12010	(1068)	8543	(1969)	0.056	
P	777	(95)	675	(137)	0.32	0.18
K	3365	(1353)	1958	(663)	0.046	
Ca	14495	(2157)	10115	(5010)	0.25[w]	
Mg	1607	(243)	1355	(831)	0.29*	0.07
S	1222	(90)	1060	(236)	0.29*	0.19
Mn	278	(61)	196	(62)	0.025	
B	17	(4)	13	(5)	0.30*	0.19
Zn	121	(30)	76	(26)	0.14*	0.47
Fe	788	(1066)	746	(556)	0.99[w]	
Cu	10	(5)	10	(2)	0.81	0.03
Al	756	(996)	631	(442)	0.63[w]	
	Contents ($kg\ ha^{-1}$)					
C	277	(253)	192	(168)	0.39	0.07
N	6.71	(6.20)	3.67	(4.16)	0.27*	0.10
P	0.40	(0.35)	0.25	(0.25)	0.33	0.09
K	2.28	(2.35)	0.86	(1.03)	0.22	0.15
Ca	8.54	(8.01)	5.11	(6.79)	0.27	0.08
Mg	0.97	(0.95)	0.72	(1.02)	0.36	0.05
S	0.68	(0.61)	0.46	(0.52)	0.46	0.07
Mn	0.14	(0.12)	0.067	(0.059)	0.13[w]	
B	0.009	(0.008)	0.006	(0.008)	0.37	0.07
Zn	0.064	(0.054)	0.033	(0.040)	0.13[w]	
Fe	0.19	(0.097)	0.17	(0.048)	0.65	0.05
Cu	0.004	(0.003)	0.003	(0.002)	0.48	0.07
Al	0.18	(0.087)	0.14	(0.008)	0.41	0.12

Single and double underlined values indicate significant differences at $P < 0.1$ and $P < 0.05$. *Data were log transformed to meet underlying statistical assumptions.
.[w] Wilcoxin Signed-Rank Test was used to determine probability value.

Table 3.8. Characteristics of autumn litter composition in bigleaf maple and Douglas-fir/hemlock in bigleaf maple plots (mean ± 1 sigma; n = 4)

	Bigleaf maple		Douglas-fir/hemlock		P (t-test)	Power (1- ß)
	Concentrations (μg g^{-1})					
Fibre (total)	701852	(23391)	571977	(14893)	0.003	
Cellulose	355951	(12774)	317224	(17349)	0.13[w]	
Lignin	289871	(11790)	221282	(12709)	0.01	
N	11006	(939)	7167	(932)	0.01	
Lignin:N	26.5	(2.87)	31.2	(4.18)	0.20	0.35

Underlined values indicate significant differences at P < 0.1. [w] Wilcoxin Signed-Rank Test was used to determine probability value.

Table 3.9. Characteristics of autumn litter composition in Douglas-fir/hemlock from bigleaf maple and conifer plots (mean ± 1 sigma; n = 4)

	Bigleaf maple		Conifer		P (t-test)	Power (1- ß)
	Concentrations (μg g^{-1})					
Fibre (total)	571977	(14893)	583542	(38996)	0.60*	0.07
Cellulose	317224	(17349)	327513	(18877)	0.26	0.10
Lignin	221282	(12709)	226172	(35981)	0.77	0.04
N	7167	(932)	7043	(235)	0.79	0.04
Lignin:N	31.2	(4.18)	32.1	(5.0)	0.75	0.04

Underlined values indicate significant differences at P < 0.1.

3.2 Litter Decomposition

3.2.1 Percent Mass Loss

In bigleaf maple plots, percent mass loss was significantly greater for bigleaf maple litter than for Douglas-fir/hemlock litter (Table 3.10). Approximately 50% of the original mass of bigleaf maple litter remained after 6 months, compared to 70% in the conifer litter bags (Figure 3.4). At 18 months, only about 45% of the original bigleaf maple mass remained, whereas 60% of needle mass remained. Differences in mass loss of the same litter type between site types were minimal.

Table 3.10. Percentage of original litter remaining at bigleaf maple and Douglas-fir/hemlock sites (mean ● 1 sigma; n = 8)

	Bigleaf maple litter		Conifer needles		P (t-test)	P (Z stat.)
			bigleaf maple site			
6 months	50.1	(5.43)	70.0	(2.39)	0.000	
12 months	45.0	(3.89)	67.4	(3.10)	0.000	
18 months	42.1	(3.50)	58.1	(3.68)		0.008
			conifer site			
6 months	51.6	(8.39)	71.4	(2.50)		0.008
12 months	51.1	(3.96)	68.9	(2.15)	0.000	
18 months	47.1	(4.58)	59.4	(3.24)	0.000	

Underlined values indicate significance at $P < 0.05$

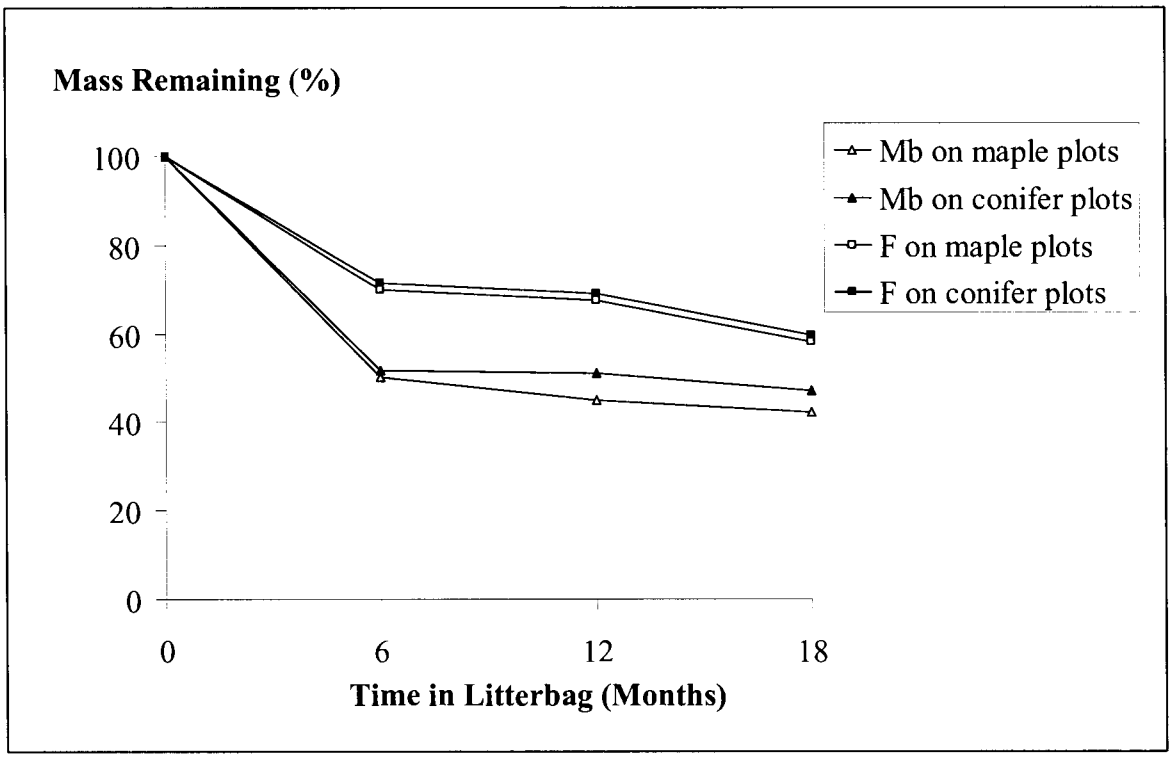

Figure 3.4. Percent of original litter mass remaining at 6, 12 and 18 months for bigleaf maple (Mb) and Douglas-fir/hemlock (F) litter, at bigleaf maple and conifer plots (mean of 8 replicates).

3.2.2 Annual Decay Rate

Bigleaf maple litter had a significantly higher annual decay rate (*k*) in bigleaf maple plots as compared to conifer plots (Table 3.10). The annual decay rate was significantly higher for bigleaf maple litter compared to conifer litter at both site types.

Table 3.11. Annual leaf litter decay (*k*) rates for bigleaf maple and conifer needles at bigleaf maple and conifer sites (mean ± 1 sigma; n = 8)

	Bigleaf maple		Conifer		P (t-test)	Power (1-ß)
		Site Type				
Bigleaf maple litter	0.83	(0.10)	0.69	(0.08)	0.007	
Conifer needles	0.40	(0.05)	0.37	(0.03)	0.22	0.27
		Litter Type				
Bigleaf maple site	0.83	(0.10)	0.40	(0.05)	0.000	
Conifer site	0.69	(0.08)	0.37	(0.03)	0.000	

Double underlined values indicate significance at $P < 0.05$

3.2.3 Element Analysis in Decaying Litter

Differences between bigleaf maple and Douglas-fir/hemlock litterfall were statistically significant for concentrations of N, Mg, S and B, in all measured stages of decomposition, with higher concentrations in bigleaf maple litter at bigleaf maple plots (Table 3.12), and bigleaf maple litter at conifer plots (Table 3.13). Differences in concentrations of Mn, Zn, and Cu were statistically significant at 6, 12 and 18 months for both plot types, with higher concentrations in bigleaf maple litter. In addition, concentrations of P were higher in bigleaf maple litter at 6, 12 and 18 months at conifer plots ($P = 0.00$). Ca concentrations were higher in bigleaf maple at both plot types, at 0 and 6 months ($P = 0.00$).

Bigleaf maple litter increased in N and P concentrations between 0 and 12 months, followed by a slight decrease at 18 months (Figure 3.5 and 3.6). Douglas-fir/hemlock litter increased steadily in N and P concentrations between 6 and 18 months,

with a slight decrease between 0 and 6 months. Overall differences between site types for N and P concentrations were minimal. Ca concentration decreased over time in bigleaf maple, and increased between 0 and 6 months in Douglas-fir/hemlock, followed by a steady decrease between 6 and 12 months (Figure 3.7). Differences between plot types in Douglas-fir/hemlock litter were minimal. For bigleaf maple, Ca concentration was lower at conifer plots, but decreased in a similar pattern as at maple plots.

Statistically significant differences were found at all measured stages for contents of N, S and Zn, with higher values in bigleaf maple litter at bigleaf maple plots (Table 3.14) and conifer plots (Table 3.15). At 0 months, contents of Ca, K and Mn were significantly higher in bigleaf maple litter at both plot types. In addition, C and B were higher in bigleaf maple at conifer plots for 0 months ($P = 0.00$). At 6 and 12 months, Cu was higher in bigleaf maple litter at both plot types ($P = 0.00$).

In bigleaf maple litter, N concentration steadily increased over time at both bigleaf maple and conifer plots (Figure 3.5). In Douglas-fir/hemlock litter, concentrations dropped slightly between 0 and 6 months, followed by a steady increase until 18 months. Differences between plot types were minimal. For bigleaf maple litter, P concentration steadily increased in bigleaf maple plots, but increases were not as rapid at conifer plots (Figure 3.6). For Douglas-fir/hemlock, initial concentrations of P dropped at 6 months, but increased thereafter. Ca concentrations steadily decreased in bigleaf maple over time at both site types (Figure 3.7). For Douglas-fir/hemlock, concentrations increased at 6 months, followed by a gradual decrease. Initial Mg concentrations decreased drastically in bigleaf maple litter at both plot types at 6 months, followed by a slight increase (Figure

3.8). Concentration of Mg in Douglas-fir/hemlock litter also decreased slightly, with a gradual increase up to 18 months.

For both litter types at both plots, N content decreased drastically between 0 and 6 months, followed by an increase at 12 months, and slight decrease at 18 months (Figure 3.9). P content drastically decreased between 0 and 6 months, with little change at 12 and 18 months (Figure 3.10). Initial Ca and Mg content in bigleaf maple decreased drastically at 6 months (Figure 3.11, Figure 3.12). Contents of Ca and Mg steadily decreased in at 6, 12 and 18 months.

Table 3.12. Element concentrations (µg g-1) of bigleaf maple (Mb) and Douglas-fir/hemlock (F) litter at bigleaf maple plots at 0, 6, 12 and 18 months (mean ± 1 sigma; n = 8)

	0 months†		6 months		12 months		18 months		Anova P
	Mb	F	Mb	F	Mb	F	Mb	F	(F stat)
C	496266[a]	535701[b]	503031[a]	536001[b]	502431	515957	509248	526784	0.000
	(9959)	(7777)	(15646)	(2922)	(14587)	(10148)	(14566)	(7544)	
N	11674[a]	7349[b]	13578[a]	7009[b]	16542[a]	10914[b]	16801[a]	11886[b]	0.000
	1972)	(1232)	(716)	(791)	(1131)	(993)	(1050)	(951)	
P	679	561	725[a]	498[b]	781	621	759	620	0.000
	(114)	(98.3)	(79.5)	(75.7)	(130)	(122)	(91.7)	(111)	
K	2553	2080	650	484	499	631	533	564	0.000
	(632)	(922)	(145)	(101)	(108)	(86.3)	(95.1)	(106)	
Ca	20208[a]	9566[b]	19366[a]	13268[b]	15476	12244	13420	11244	0.000
	(4129)	(3454)	(4923)	(648)	(1521)	(807)	(1385)	(679)	
Mg	2073[a]	885[b]	1013[a]	405[b]	1014[a]	554[b]	934[a]	554[b]	0.000
	(448)	(133)	(129)	(31.6)	(161)	(128)	(141)	(65.5)	
S	1245[a]	745[b]	1480[a]	741[b]	1625[a]	949[b]	1676[a]	1020[b]	0.000*
	(149)	(45.0)	(91.8)	(61.5)	(112)	(81.3)	(104)	(87.8)	
Mn	270	235	274[a]	146[b]	357[a]	185[b]	398[a]	219[b]	0.000
	(123)	(72.8)	(55.0)	(11.1)	(40.1)	(23.9)	(84.4)	(39.5)	
B	21.5[a]	10.8[b]	15.6[a]	8.70[b]	15.1[a]	9.43[b]	14.2[a]	9.78[b]	0.000
	(6.08)	(1.82)	(2.33)	(0.36)	(1.10)	(0.42)	(0.81)	1.18)	
Zn	50.2	28.5	122[a]	52.0[b]	151[a]	8.3[b]	143[a]	75.2[b]	0.000
	(18.8)	(5.85)	(40.1)	(9.65)	(34.6)	(12.4)	(21.3)	(13.5)	
Fe	169	172	305	237	1047[a]	479[b]	1184[a]	443[b]	0.000
	(44.2)	(97.7)	(77.7)	(87.2)	(507)	(170)	(634)	(193)	
Cu	7.36	2.62	98.0[a]	42.5[b]	90.6[a]	6.8[b]	97.8[a]	66.4[b]	0.000
	(1.20)	(0.31)	(28.9)	(11.3)	(34.3)	(15.4)	(16.1)	(12.5)	
Al	131	308	295	306	1038	550	1118[a]	509[b]	0.000
	(23.4)	(136)	(86.1)	(86.9)	(564)	(214)	(617)	(183)	

Underlined values indicate significant differences at $P < 0.05$. † Values obtained from autumn nutrient concentrations. [a,b] Different letters in same rows during one time period and between Mb and F are statistically different at $P < 0.05$. *Data were log transformed to meet underlying statistical assumptions.

Table 3.13. Element concentrations (μg g^{-1}) of bigleaf maple (Mb) and Douglas-fir/hemlock (F) litter at conifer plots at 0, 6, 12 and 18 months (mean ± 1 sigma; n = 8)

	0 months[†]		6 months		12 months		18 months		Anova P
	Mb[††]	F	Mb	F	Mb	F	Mb	F	(F stat)
C	496266[a]	536586[b]	497725[a]	541184[b]	506427	522933	515564	531520	0.000
	(9959)	(4544)	(9925)	(20292)	(17407)	(4955)	(11321)	(11952)	
N	11674[a]	7252[b]	13306[a]	6744[b]	16034[a]	9891[b]	17246[a]	11648[b]	0.000
	1972)	(605)	(2485)	(761)	(1277)	(1085)	(998)	(1306)	
P	679	584	689[a]	463[b]	688[a]	518[b]	759[a]	560[b]	0.000
	(114)	(133)	(122)	(46.8)	(80.5)	(64.5)	(86.9)	(89.8)	
K	2553[a]	1709[b]	658	426	501	580	545	498	0.000
	(632)	(642)	(136)	(64.6)	(113)	(86.0)	(112)	(72.5)	
Ca	20208[a]	10486[b]	17623[a]	13173[b]	13420	12361	11991	11320	0.000
	(4129)	(2662)	(1382)	(845)	(842)	(999)	(1727)	(1139)	
Mg	2073[a]	886[b]	969[a]	394[b]	823[a]	441[b]	811[a]	514[b]	0.000
	(448)	(129)	(98.9)	(32.9)	(131)	(73.8)	(110)	(106)	
S	1245[a]	749[b]	1515[a]	936[b]	1573[a]	900[b]	1685[a]	1010[b]	0.000
	(149)	(38.7)	(152)	(90.7)	(174)	(102)	(121)	(84.4)	
Mn	270	236	283[a]	155[b]	327[a]	188[b]	369[a]	240[b]	0.000
	(123)	(90.3)	(56.6)	(25.6)	(71.2)	(35.1)	(92)	(54.1)	
B	21.5[a]	11.2[b]	15.4[a]	8.80[b]	14.2[a]	9.31[b]	13.8[a]	9.54[b]	0.000
	(6.08)	(2.87)	(0.69)	(0.31)	(0.91)	(0.81)	(1.83)	(0.52)	
Zn	50.2	37.0	111[a]	47.8[b]	126[a]	61.5[b]	145[a]	75.3[b]	0.000
	(18.8)	(20.7)	(27.5)	(8.79)	(28.9)	(9.31)	(27.0)	(12.9)	
Fe	169	135	301	220	848[a]	440[b]	940[a]	414[b]	0.000
	(44.2)	(18.0)	(97.2)	(82.8)	(397)	(193)	(306)	(183)	
Cu	7.36	3.12	86.2[a]	44.2[b]	79.2[a]	39.2[b]	116[a]	65.2[b]	0.000
	(1.20)	(1.57)	(25.6)	(13.4)	(24.2)	(6.48)	(29.6)	(12.0)	
Al	131	242	320	289	870	509	918	483	0.000
	(23.4)	(43.6)	(158)	(117)	(662)	(239)	(381)	(225)	

Underlined values indicate significant differences at $P < 0.05$. [†] Values obtained from autumn nutrient concentrations. [††] Values obtained from autumn litterfall weights of bigleaf maple litter at bigleaf maple plots. [a,b] Different letters in same rows during one time period and between Mb and F are statistically different at $P < 0.05$.

Table 3.14. Element contents (mg) of bigleaf maple (Mb) and Douglas-fir/hemlock (F) litter at bigleaf maple plots at 0, 6, 12 and 18 months (mean ± 1 sigma; n = 8)

	0 months†		6 months		12 months		18 months		Anova P
	Mb	F	Mb	F	Mb	F	Mb	F	(F stat)
C	1320[a]	1057[b]	668[a]	748[b]	605	681	573	602	0.000
	(30.9)	(20.0)	(78.8)	(21.9)	(70.5)	(33.9)	(63.1)	(42.5)	
N	31.1[a]	14.5[b]	18.1[a]	9.76[b]	19.8[a]	14.4[b]	18.9[a]	13.6[b]	0.000
	(5.32)	(2.46)	(2.59)	(0.87)	(1.0)	(1.04)	(2.69)	(1.08)	
P	1.81[a]	1.11[b]	0.96[a]	0.69[b]	0.93	0.82	0.86	0.70	0.000
	(0.30)	(0.19)	(0.14)	(0.09)	(0.10)	(0.14)	(0.15)	(0.10)	
K	6.80[a]	4.10[b]	0.85	0.67	0.60	0.83	0.60	0.64	0.000
	(1.72)	(1.82)	(0.16)	(0.13)	(0.12)	(0.10)	(0.11)	(0.10)	
Ca	53.7[a]	18.9[b]	25.4	18.5	18.6	16.1	15.0	12.8	0.000
	(10.9)	(6.83)	(5.67)	(0.99)	(2.5)	(1.10)	(0.75)	(1.0)	
Mg	5.51[a]	1.75[b]	1.34[a]	0.57[b]	1.21	0.73	1.05	0.63	0.000
	(1.19)	(0.26)	(0.22)	(0.04)	(0.18)	(0.15)	(0.19)	(0.08)	
S	3.31[a]	1.47[b]	1.96[a]	1.03[b]	1.95[a]	1.25[b]	1.87[a]	1.16[b]	0.000
	(0.40)	(0.09)	(0.19)	(0.06)	(0.12)	(0.09)	(0.24)	(0.11)	
Mn	0.72[a]	0.46[b]	0.36	0.21	0.43	0.24	0.45	0.25	0.000
	(0.33)	(0.14)	(0.06)	(0.01)	(0.06)	(0.02)	(0.12)	(0.05)	
B	0.06[a]	0.02[b]	0.02[a]	0.01[b]	0.02	0.01	0.02	0.01	0.000
	(0.02)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.01)	(0.00)	
Zn	0.13[a]	0.06[b]	0.16[a]	0.07[b]	0.18[a]	0.09[b]	0.16[a]	0.09[b]	0.000
	(0.05)	(0.01)	(0.06)	(0.01)	(0.03)	(0.02)	(0.03)	(0.01)	
Fe	0.45	0.34	0.40	0.33	1.22[a]	0.63[b]	1.33[a]	0.51[b]	0.000
	(0.12)	(0.19)	(0.07)	(0.11)	(0.5)	(0.22)	(0.74)	(0.23)	
Cu	0.02	0.01	0.13[a]	0.06[b]	0.11[a]	0.06[b]	0.11	0.08	0.000
	(0.00)	(0.00)	(0.05)	(0.02)	(0.04)	(0.02)	(0.03)	(0.01)	
Al	0.35	0.61	0.38	0.43	1.22	0.74	1.25[a]	0.58[b]	0.000
	(0.06)	(0.26)	(0.08)	(0.11)	(0.57)	(0.28)	(0.71)	(0.20)	

Underlined values indicate significant differences at $P < 0.05$. † Values obtained from autumn nutrient concentrations. [a,b] Different letters in same rows during one time period and between Mb and F are statistically different at $P < 0.05$.

Table 3.15. Element contents (mg) of bigleaf maple (Mb) and Douglas-fir/hemlock (F) litter at conifer plots at 0, 6, 12 and 18 months (mean ± 1 sigma; n = 8)

	0 months[†]		6 months		12 months		18 months		Anova P
	Mb[††]	F	Mb	F	Mb	F	Mb	F	(F stat)
C	1320[a]	602[b]	685	771	699	710	651	623	0.000
	(30.9)	(42.5)	(116)	(48.7)	(55.9)	(22.63)	(57.6)	(42.4)	
N	31.1[a]	13.6[b]	17.9[a]	9.57[b]	22.1[a]	13.42[b]	21.7[a]	13.6[b]	0.000
	(5.32)	(1.08)	(2.39)	(0.84)	(2.16)	(1.54)	(2.11)	(1.21)	
P	1.81[a]	0.70[b]	0.93[a]	0.66[b]	0.95	0.70	0.95[a]	0.65[b]	0.000
	(0.30)	(0.10)	(0.13)	(0.05)	(0.09)	(0.09)	(0.10)	(0.08)	
K	6.80[a]	0.64[b]	0.89	0.61	0.69	0.79	0.69	0.58	0.000
	(1.72)	(0.10)	(0.13)	(0.08)	(0.16)	(0.13)	(0.17)	(0.07)	
Ca	53.7[a]	12.8[b]	24.3	18.8	18.6	16.8	15.2	13.3	0.000
	(10.9)	(1.0)	(4.53)	(1.39)	(2.35)	(1.35)	(2.55)	(1.82)	
Mg	5.51[a]	0.63[b]	1.35[a]	0.56[b]	1.14	0.60	1.03	0.60	0.000
	(1.19)	(0.08)	(0.34)	(0.05)	(0.25)	(0.12)	(0.19)	(0.13)	
S	3.31[a]	1.16[b]	2.06[a]	1.04[b]	2.17[a]	1.22[b]	2.12[a]	1.18[b]	0.000
	(0.40)	(0.11)	(0.20)	(0.04)	(0.24)	(0.15)	(0.20)	(0.08)	
Mn	0.72[a]	0.25[b]	0.38	0.22	0.45	0.26	0.46	0.39	0.000
	(0.33)	(0.05)	(0.04)	(0.03)	(0.07)	(0.04)	(0.10)	(0.07)	
B	0.06[a]	0.01[b]	0.02	0.01	0.02	0.01	0.02	0.01	0.000
	(0.02)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	
Zn	0.13[a]	0.09[b]	0.15[a]	0.07[b]	0.17[a]	0.08[b]	0.18[a]	0.09[b]	0.000
	(0.05)	(0.01)	(0.05)	(0.01)	(0.04)	(0.01)	(0.03)	(0.02)	
Fe	0.45	0.51	0.40	0.31	1.16[a]	0.60[b]	1.18[a]	0.49[b]	0.000
	(0.12)	(0.23)	(0.09)	(0.11)	(0.53)	(0.27)	(0.40)	(0.22)	
Cu	0.02	0.08	0.12[a]	0.06[b]	0.11[a]	0.05[b]	0.15[a]	0.08[b]	0.000
	(0.00)	(0.01)	(0.04)	(0.02)	(0.03)	(0.01)	(0.04)	(0.01)	
Al	0.35	0.58	0.42	0.41	1.19	0.69	1.16	0.57	0.000
	(0.06)	(0.20)	(0.16)	(0.16)	(0.90)	(0.33)	(0.53)	(0.26)	

Underlined values indicate significant differences at $P < 0.05$. [†] Values obtained from autumn nutrient concentrations. [††] Values obtained from autumn litterfall weights of bigleaf maple litter at bigleaf maple plots. [a,b] Different letters in same rows during one time period and between Mb and F are statistically different at $P < 0.05$.

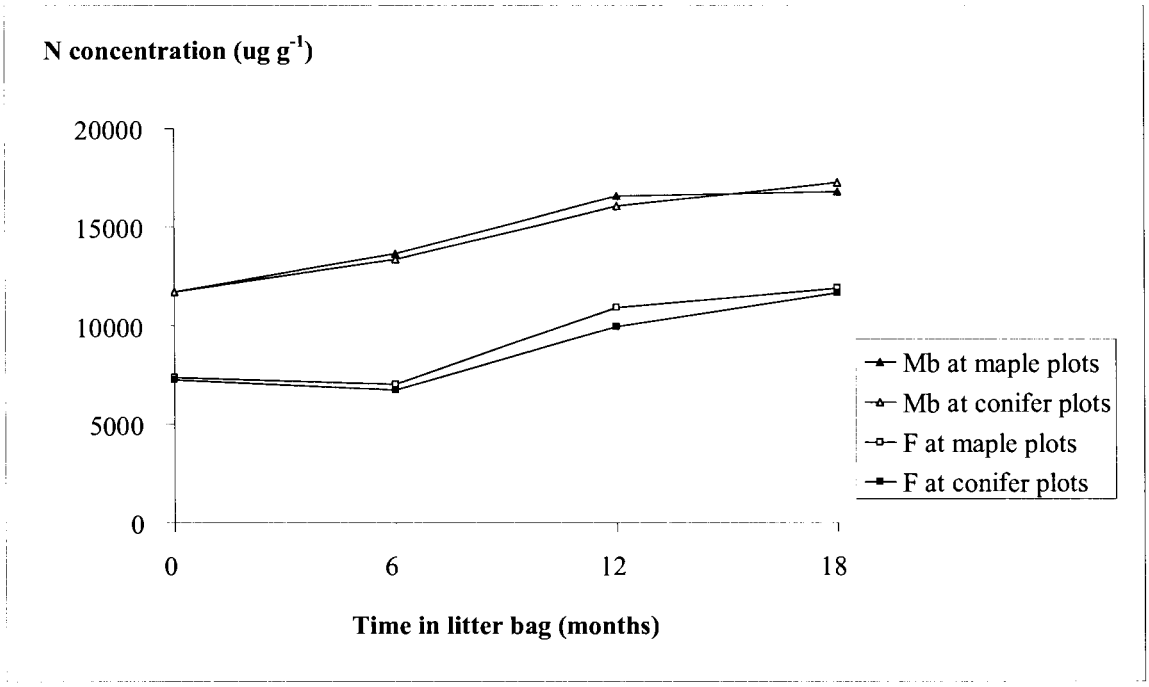

Figure 3.5. N concentration in bigleaf maple (Mb) and Douglas-fir/hemlock (F) litter at both plot types (mean of 8 replicates).

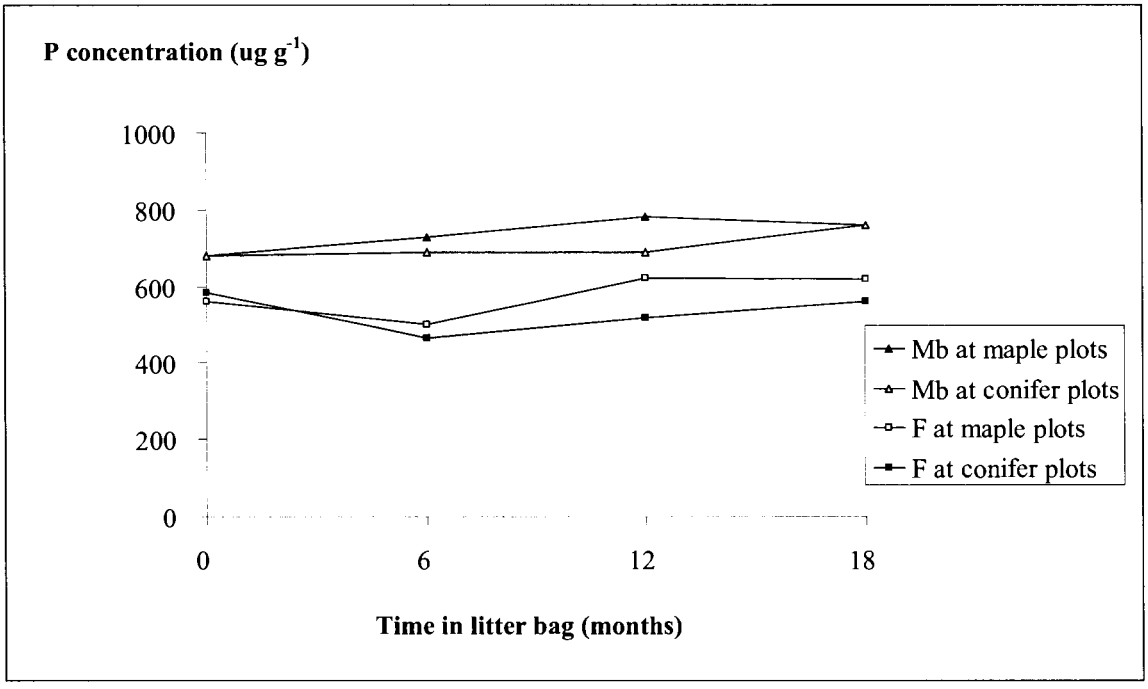

Figure 3.6. P concentration in bigleaf maple (Mb) and Douglas-fir/hemlock (F) litter at both plot types (mean of 8 replicates).

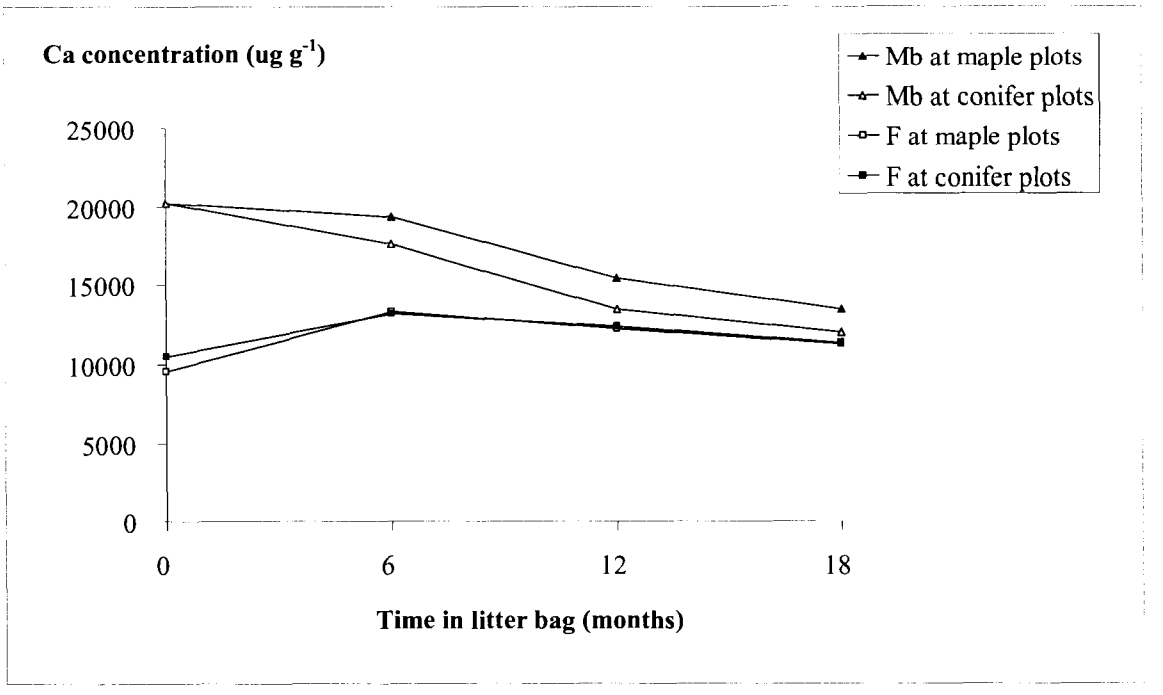

Figure 3.7. Ca concentration in bigleaf maple (Mb) and Douglas-fir/hemlock (F) litter at both plot types (mean of 8 replicates).

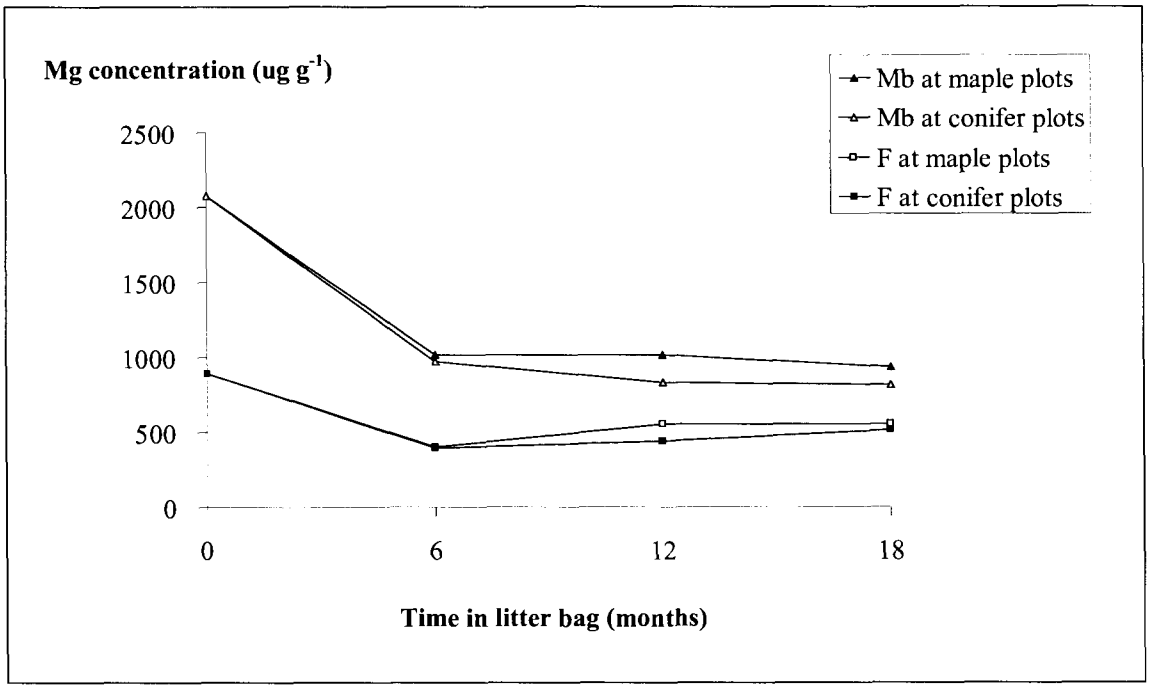

Figure 3.8. Mg concentration in bigleaf maple (Mb) and Douglas-fir/hemlock (F) litter at both plot types (mean of 8 replicates).

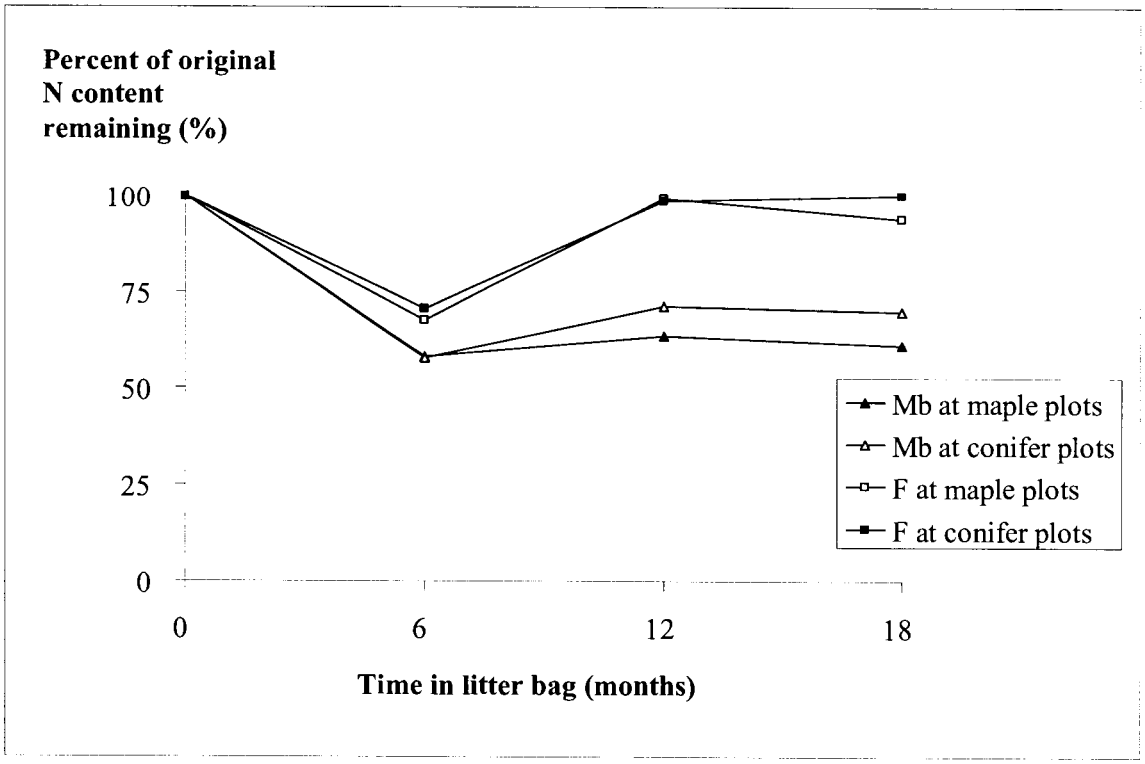

Figure 3.9. Percent of original N content remaining in bigleaf maple (Mb) and Douglas-fir/hemlock (F) litter at both plot types (mean of 8 replicates).

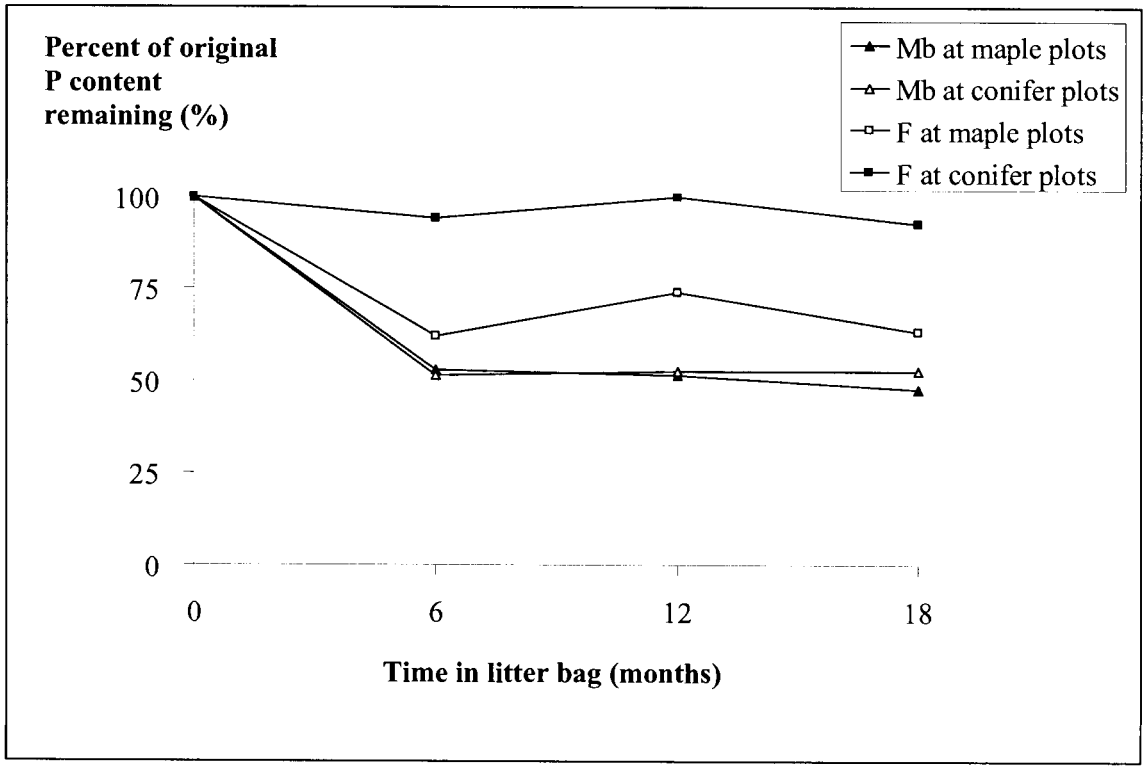

Figure 3.10. Percent of original P content remaining in bigleaf maple (Mb) and Douglas-fir/hemlock (F) litter at both plot types (mean of 8 replicates).

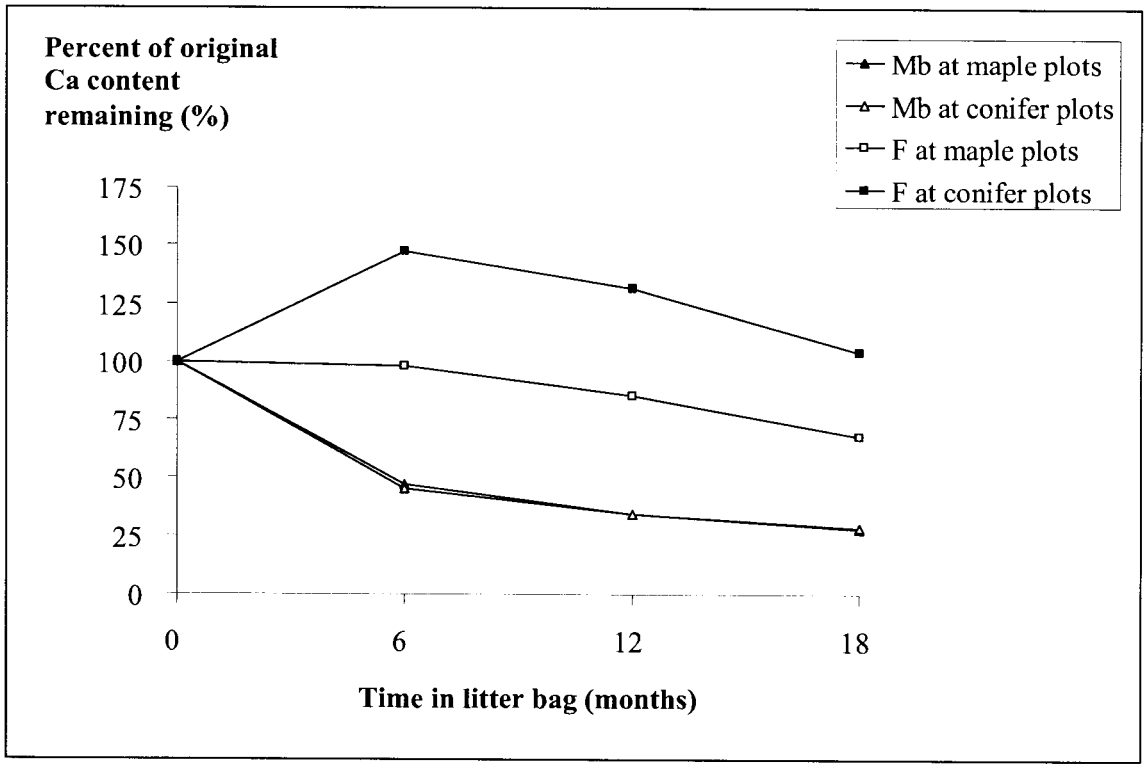

Figure 3.11. Percent of original Ca content remaining in bigleaf maple (Mb) and Douglas-fir/hemlock (F) litter at both plot types (mean of 8 replicates).

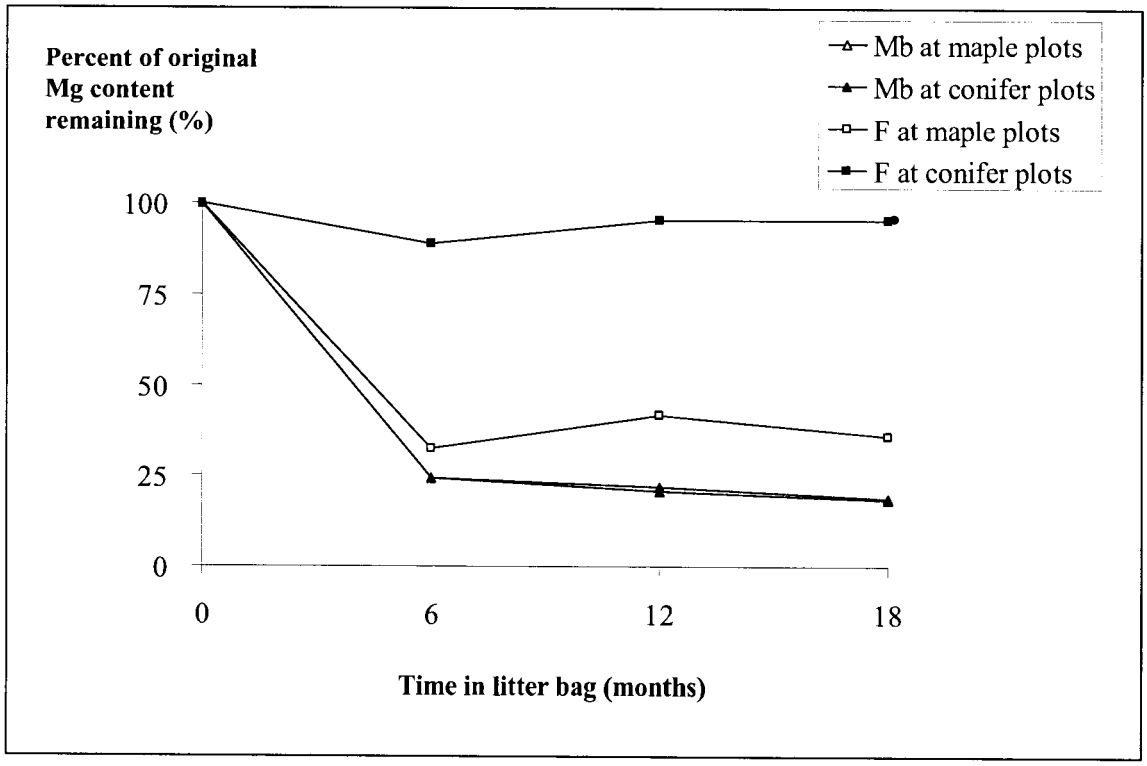

Figure 3.12. Percent of original Mg content remaining in bigleaf maple (Mb) and Douglas-fir/hemlock (F) litter at both plot types (mean of 8 replicates).

3.3 Forest Floor

3.3.1 Forest Floor and Ah Horizon Depths

All depths of the forest floor and upper mineral horizons, with the exception of the H horizon, showed statistical differences for bigleaf maple and conifer plots (Table 3.16). The Ah horizon was significantly thicker at bigleaf maple plots, when examined both alone (P = 0.01) and with the H horizon (P = 0.01). Total forest floor and Ah horizon were thicker at bigleaf maple plots (P = 0.06). Conifer plots had significantly thicker L, F, F+H, Ae, and total forest floor horizons (L+F+H) relative to bigleaf maple plots (Figure 3.13).

Table 3.16. Mean depths of the forest floor and upper mineral horizons for bigleaf maple and conifer plots (mean ± 1 sigma; n = 11)

	Bigleaf maple plots		Conifer plots		P (t-test)	P (Z stat.)
	Depth (cm)					
Litter horizon (L)	0.88	(0.60)	1.25	(1.00)	0.069	
Fibric horizon (F)	2.98	(2.18)	3.85	(1.84)	0.048*	
Humic horizon (H)	0.75	(1.00)	1.47	(1.11)		0.13
Ah	6.18	(2.68)	2.80	(1.59)	0.005	
Ae	0.19	(0.26)	0.54	(0.44)		0.05
Total Forest Floor	4.61	(2.07)	6.57	(2.40)	0.015*	
F plus H	3.73	(2.26)	5.32	(2.04)	0.024	
Ah plus H	6.93	(2.76)	4.27	(1.54)	0.005	
Forest Floor and Ah	10.79	(1.83)	9.37	(2.22)	0.055	

Single and double underlined values indicate significant differences at P < 0.1 and P < 0.05. *Data were log transformed to meet underlying statistical assumptions.

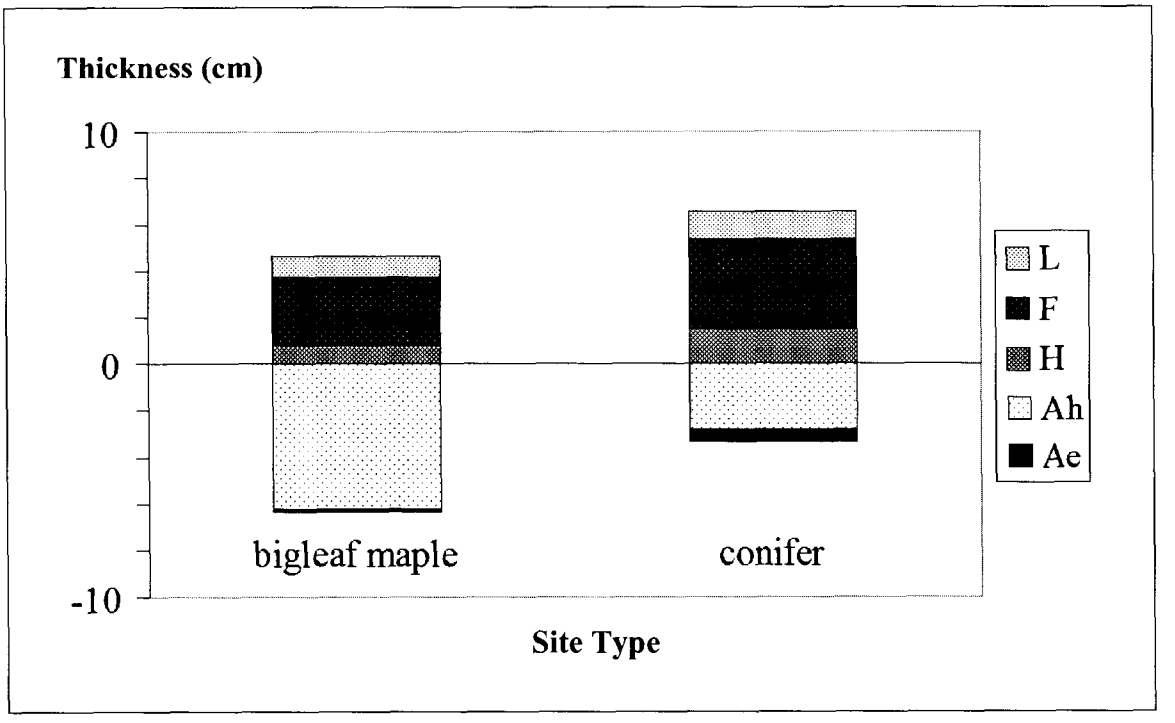

Figure 3.13. Mean thickness of forest floor and A horizons for bigleaf maple and conifer plots (mean of 11 replicates).

3.3.2 Humus Form Classification

Humus forms at bigleaf maple plots were not as variable as at conifer plots (Figure 3.14). Over 50% of humus forms at bigleaf maple plots were classified as vermimull; the remaining humus forms were mormoder (21%), mullmoder and leptomoder (12% each). Conifer plots were represented by 6 groups of humus forms, and were dominated by mormoder (42%) and hemimor (21%).

3.3.3 Forest Floor Chemical Properties

Forest floor weight per unit area, pH, mineralizable N contents, and NO_3-N concentrations and contents were significantly higher for bigleaf maple plots, when compared to conifer plots (Table 3.17). There was a weak trend for higher NH_4-N ($P = 0.12$) contents at bigleaf maple plots. Exchangeable Na, Fe and Al concentrations

were all significantly higher at conifer plots. There was a weak trend for higher (P = 0.15) exchangeable Ca in bigleaf maple plots compared to conifer plots.

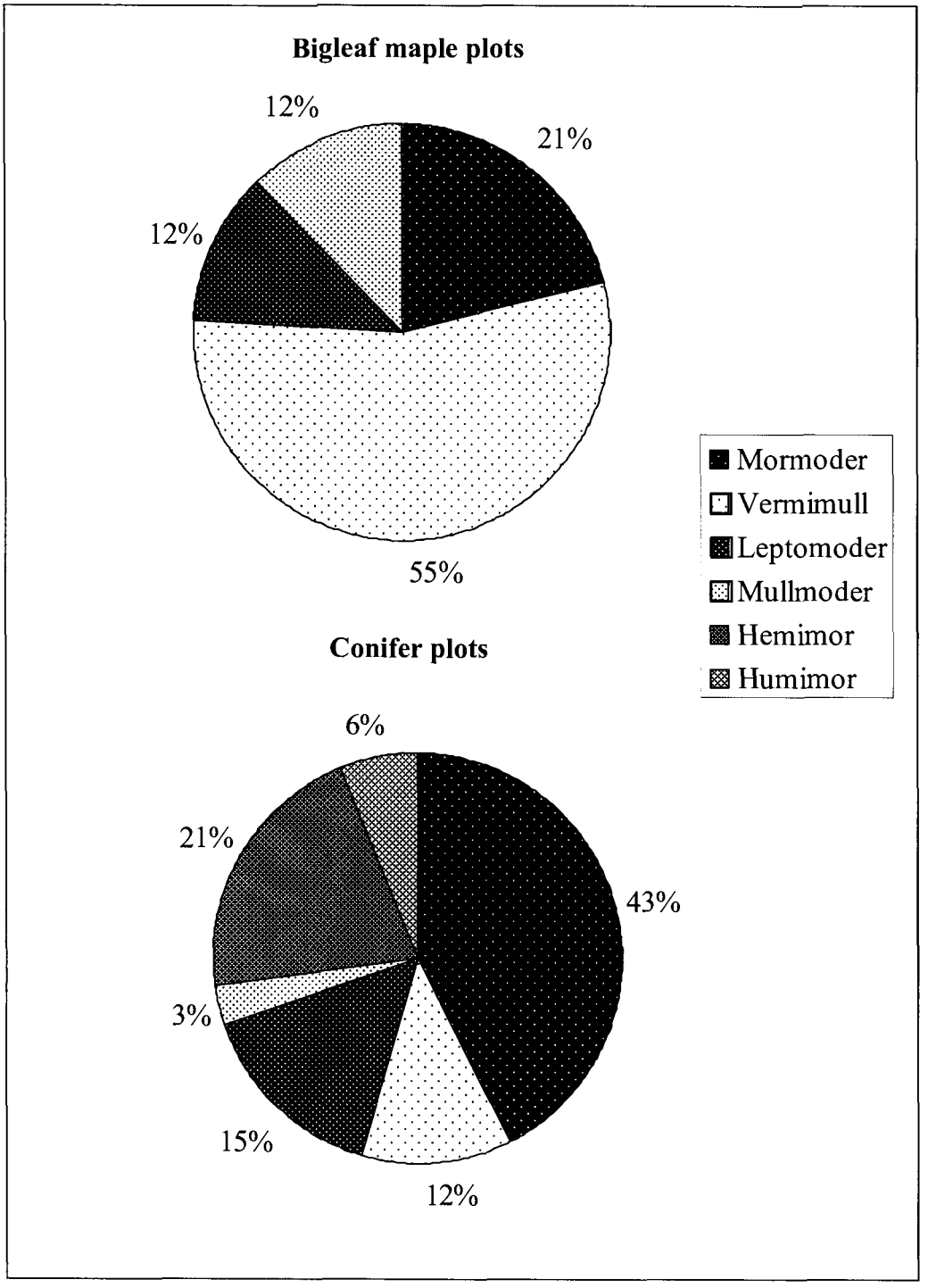

Figure 3.14. Frequency of humus forms at bigleaf maple and conifer plots (mean of 11 replicates).

Table 3.17. Forest floor chemical properties for bigleaf maple and conifer plots (mean ± 1 sigma; n = 11)

	Bigleaf maple plots		Conifer plots		P (t-test)	Power (1-ß)
Forest Floor (kg ha^{-1})	13602	(3672)	10027	(2562)	0.042	
pH (1:1 H_2O)	4.59	(0.50)	4.17	(0.33)	0.019	
Total C (g kg^{-1})	356	(83.4)	403	(71.0)	0.12	0.26
Total C (kg ha^{-1})	4931	(2123)	4032	(1265)	0.28	0.21
Total N (g kg^{-1})	12.9	(2.79)	14.1	(2.42)	0.25	0.19
Total N (kg ha^{-1})	178	(71.3)	142	(45.9)	0.21	0.27
C:N ratio	27.9	(4.40)	28.6	(2.35)	0.69	0.07
Mineral N (mg kg^{-1})	345	(77.7)	312	(77.3)	0.29	0.15
Mineral N (kg ha^{-1})	4.74	(1.79)	3.06	(0.81)	0.015	
NO_3-N (mg kg^{-1})	43.2	(39.1)	14.2	(17.4)	0.017*	
NO_3-N (kg ha^{-1})	0.59	(0.60)	0.15	(0.21)	0.005*	
NH_4-N (mg kg^{-1})	64.0	(24.5)	64.2	(29.4)	0.98	0.03
NH_4-N (kg ha^{-1})	0.87	(0.43)	0.63	(0.31)	0.12	0.30
Available P (mg kg^{-1})	54.5	(27.3)	50.5	(27.9)	0.75*	0.05
Available P (kg ha^{-1})	0.76	(0.52)	0.54	(0.41)	0.12*	0.18
Total S (g kg^{-1})	0.93	(0.44)	0.95	(0.57)	0.95	0.03
Total S (kg ha^{-1})	12.8	(7.63)	10.3	(7.76)	0.49	0.11
Exch K (cmol kg^{-1})	0.80	(0.27)	0.83	(0.29)	0.76	0.04
Exch Ca (cmol kg^{-1})	29.1	(7.77)	24.1	(7.51)	0.15[w]	
Exch Mg (cmol kg^{-1})	3.17	(0.79)	2.87	(1.27)	0.44	0.09
Exch Mn (cmol kg^{-1})	0.41	(0.16)	0.43	(0.17)	0.45	0.05
Exch Fe (cmol kg^{-1})	0.048	(0.066)	0.11	(0.68)	0.011*	
Exch Al (cmol kg^{-1})	1.22	(0.98)	2.79	(1.43)	0.021	
Exch Na (cmol kg^{-1})	0.082	(0.051)	0.12	(0.063)	0.075	
CEC (Ba) (cmol kg^{-1})	34.8	(9.01)	31.3	(8.70)	0.30	0.14

Single and double underlined values indicate significant differences at $P < 0.1$ and $P < 0.05$. *Data were log transformed to meet underlying statistical assumptions. [w] Wilcoxin Signed-Rank Test was used to determine probability value.

3.4 Mineral Soil

3.4.1 Mineral Soil Properties

Percent gravel content in the surface mineral soil was similar between site types (approximately 56%), and bulk density was significantly higher at conifer plots relative to bigleaf maple plots (Table 3.18). Total N concentration, mineralizable N concentration and content, NO_3-N concentration and content as well as exchangeable K, Ca, Mg and CEC were significantly higher at bigleaf maple plots. Exchangeable Fe was significantly higher at conifer plots. There was a weak trend for higher ($P = 0.20$) total C concentrations beneath bigleaf maple.

Table 3.18. Mineral soil properties at 0 to 7 cm depth (mean ± 1 sigma; n = 11)

	Bigleaf maple plots		Conifer plots		P (t-test)	Power (1-ß)
Bulk Density (g cm^{-3})	0.67	(0.15)	0.77	(0.09)	0.05	
Gravel Content (%)	55.9	(8.93)	56.1	(8.18)	0.94	
pH (1:1 H2O)	4.94	(0.41)	4.80	(0.21)	0.35	0.16
Total C (g kg^{-1})	81.8	(20.4)	68.1	(21.3)	0.20	0.31
Total C (kg ha^{-1})	39484	(8373)	38967	(13226)	0.70*	0.03
Total N (g kg^{-1})	3.60	(0.83)	2.88	(0.90)	0.09	
Total N (kg ha^{-1})	1734	(320)	1637	(519)	0.44	0.07
C:N ratio	22.7	(1.97)	23.8	(2.48)	0.30	0.18
Mineral N (mg kg^{-1})	78.4	(28.1)	53.4	(17.2)	0.04	
Mineral N (kg ha^{-1})	37.3	(10.0)	29.9	(8.10)	0.07	
NO_3-N (mg kg^{-1})	6.50	(3.75)	3.44	(4.14)	0.04[w]	
NO_3-N (kg ha^{-1})	3.05	(1.73)	1.92	(2.27)	0.07[w]	
NH_4-N (mg kg^{-1})	13.1	(5.12)	11.1	(3.04)	0.40	0.19
NH_4-N (kg ha^{-1})	6.22	(1.94)	6.23	(1.97)	0.99	0.03
Available P (mg kg^{-1})	14.1	(12.9)	25.5	(30.9)	0.43*	0.19
Available P (kg ha^{-1})	7.29	(7.88)	15.8	(20.1)	0.26*	0.23
Exch K (cmol kg^{-1})	0.095	(0.054)	0.060	(0.026)	0.04	
Exch Ca (cmol kg^{-1})	3.85	(2.54)	1.68	(1.01)	0.02	
Exch Mg (cmol kg^{-1})	0.36	(0.26)	0.19	(0.16)	0.09[w]	
Exch Mn (cmol kg^{-1})	0.073	(0.071)	0.036	(0.024)	0.19*	0.34
Exch Fe (cmol kg^{-1})	0.014	(0.012)	0.033	(0.032)	0.01*	
Exch Al (cmol kg^{-1})	1.79	(1.60)	2.00	(1.18)	0.34*	0.05
Exch Na (cmol kg^{-1})	0.027	(0.019)	0.027	(0.022)	0.99*	0.03
CEC (Ba) (cmol kg^{-1})	6.20	(3.03)	4.03	(2.06)	0.08	

Single underlined values indicate significant differences at $P < 0.1$. Double underlined values indicate significant differences at $P < 0.05$. *Data were log transformed to meet underlying statistical assumptions. [w] Wilcoxin Signed-Rank Test was used to determine probability value.

Chapter 4: Discussion

4.1 Litterfall

The amount of litterfall at bigleaf maple sites was compared to conifer sites to determine the degree of difference in litterfall biomass contribution. It was anticipated that bigleaf maple sites would contribute more total litterfall in the autumn season, as well as annually, compared to conifer sites. In addition, maple leaves were expected to input greater element concentrations compared to conifer needles. Measuring litterfall biomass between site types and analysing the concentration of nutrient elements within foliage can provide insight into the influence of bigleaf maple on nutrient cycling in conifer forests.

4.1.1 Seasonal and Annual Inputs

When compared to conifer sites, there was a weak trend ($P = 0.20$) for total annual litterfall weights to be higher (15%) at bigleaf maple sites. These findings are consistent with Fried et al. (1990) where annual litterfall was significantly greater in stands of bigleaf maple (33%), compared to Douglas-fir. Tashe and Schmidt (2001) found no significant differences ($P = 0.80$) in annual litterfall amounts between vine maple and conifer sites in a study carried out in the same general area as the present study. Since bigleaf maple occurs as a co-dominant or dominant tree in the canopy, whereas vine maple occurs as an understory tree, bigleaf maple contributes greater amounts of litter to conifer forests.

Fifty percent of annual litter fell in the autumn at bigleaf maple sites, compared to 35% at conifer sites. In the autumn, significantly more litter fell in bigleaf maple sites as compared to conifer sites (P = 0.02). These findings are consistent with those of Tarrant et al. (1951), where autumn litterfall weight was 38% larger beneath bigleaf maple canopies than Douglas-fir and of Tashe and Schmidt (2001) who found greater amounts of autumn litterfall for vine maple sites compared to conifer sites. Relatively equal portions of litter fell at bigleaf maple sites in winter, spring and summer, with winter and spring weights being larger at conifer sites (significant for spring, P = 0.06). In the autumn, there was no significant difference in conifer (fir/hemlock + cedar) litterfall weight between bigleaf maple and conifer sites (P = 0.48) indicating that the presence of bigleaf maple had not decreased the input of conifer litterfall. In conifer forests where bigleaf maple occurs, bigleaf maple appears to increase total litterfall inputs.

4.1.2 Chemical & Physical Composition of Litterfall

In the autumn, bigleaf maple litter had significantly greater concentrations and contents of N, K, Mg, S, B, Zn and Cu than did Douglas-fir/hemlock and cedar litter. Bigleaf maple litter was also significantly greater in concentrations and contents of Ca than Douglas-fir/hemlock, and significantly greater in P and Mn than cedar. These differences are in agreement with Valachovic et al. (2004) in which bigleaf maple had higher concentrations of N, P, K and Mg, than Douglas-fir and cedar and higher Ca concentrations than Douglas-fir. Fried et al. (1990) found greater concentrations of K, Ca, Mg, Zn, and Mo in bigleaf maple at all sites and concentrations of N and S greater at 4 out of 5 sites. In the same study, all element contents were higher at maple sites (Fried et al.,1990). Tarrant (1951) found contents of N, P, K and Ca higher in bigleaf maple, when

compared to Douglas-fir (100 year old stand), and contents of N, P, K and Ca higher in bigleaf maple compared to western hemlock. In agreement with the findings of Valachovic et al. (2004), Douglas-fir was significantly higher than both bigleaf maple and cedar in concentrations of C.

Higher concentrations and contents were expected for all nutrients in bigleaf maple as compared to Douglas-fir/hemlock. Vine maple litter has been shown to have higher concentrations of N, P, K and Mg (Ogden & Schmidt, 1997; Tashe & Schmidt, 2001; Valachovic et al., 2004) of Mn and B (Tashe & Schmidt, 2001), of Ca (Ogden & Schmidt, 1997; Valachovic et al., 2004) and of Zn (Ogden & Schmidt, 1997; Tashe & Schmidt, 2001). In a comparison of nutrient concentrations between 14 litter types, N, K and Mg were higher in red alder, black cottonwood and vine maple than Douglas-fir and hemlock (Prescott et al., 2004b). In the same study, vine maple was higher in P concentration, and black cotton wood was higher in Ca concentration, than both Douglas-fir and hemlock.

The element contents in total autumn litterfall between bigleaf maple and conifer sites were compared. For total autumn litterfall between sites, all measured element contents were significantly greater at bigleaf maple sites, compared to conifer sites. This is in agreement with Fried et al. (1990), in which total mass for each element was significantly greater under maple. As expected, bigleaf maple foliage contributed a greater percentage to total element input in this study. Between 32-46% of all elements measured at bigleaf maple sites came from bigleaf maple foliage, with the exception of Fe and Al (for these elements, bigleaf maple contributed 26% and 20%, respectively). These findings are in agreement with Tashe and Schmidt (2001), where vine maple

contributed more than 25% of inputs from each measured nutrient in the autumn (Tashe & Schmidt, 2001).

In a comparison of element concentrations in Douglas-fir/hemlock litter between sites, higher Zn concentration existed at conifer sites, and higher Al concentrations at bigleaf maple sites. There were no differences in the concentrations for all other elements tested in Douglas-fir and hemlock between site types. It was expected that the presence of bigleaf maple would enhance nutrient availability in the forest floor and mineral soil due to a greater input of element-rich biomass, resulting in a greater uptake of nutrients by Douglas-fir and hemlock at bigleaf maple sites, compared to conifer sites. This would suggest a higher concentration of nutrients would be found in needles at maple sites. In another study, Tashe and Schmidt (2001) found Douglas-fir and hemlock needles to be significantly higher in N concentration at vine maple sites compared to conifer sites, at both stands that were studied. In addition, one study site showed vine maple sites to have Douglas-fir and hemlock needles significantly greater in concentrations of Mn, and another study site exhibited needles with significantly higher concentrations of P.

Douglas-fir/hemlock litter was higher in all element contents measured at conifer plots, compared to bigleaf maple plots. This is likely due to the greater amount of Douglas-fir and hemlock litterfall at conifer sites, compared to bigleaf maple sites, where Douglas-fir and hemlock were not dominant in the canopy.

Element concentrations in 'other' litterfall between sites were significantly higher at bigleaf maple sites for N, K and Mn. This is likely due to the difference in composition of 'other' litterfall between site types. The 'other' litter type at both sites consisted of small portions of black cottonwood, vine maple, coarse woody debris, small twigs and

moss. Due to the phenology of the species; the samara or "fruit" of bigleaf maple ripen in early autumn, and dispersal begins mid-season (Haeussler et al., 1990). The 'other' litter type at maple sites included portions of samara, and likely influenced nutrient concentrations.

At bigleaf maple sites, concentrations of total fibre, lignin and N were significantly higher in bigleaf maple compared to Douglas-fir/hemlock litter. The higher concentrations of total fibre and lignin in bigleaf maple were not expected, as several studies suggest decomposition is slower in litter high in lignin (Girisha et al., 2003; Prescott et al., 2000; Taylor et al., 1991; Xu & Hirata, 2005; Fisher & Binkley, 2000). However, studies by Berg and Staaf (1980), Berg (1984, as cited in Taylor et al., 1991) and Fioretto et al. (2005) suggest nutrients control litter decay rates until 20-25% of the mass is lost, after which point rates are determined by cell wall components such as lignin. In a study by Prescott et al. (2004a), broadleaf litters decayed faster than conifer needles only during the initial stages of decay, after which point rates were slower. Several studies suggest the lignin:N ratio is inversely related to decay rates (Taylor et al., 1991; Melillo et al., 1982; Xu & Hirata, 2005). This may explain why bigleaf maple would still have a faster initial decay rate despite higher lignin levels, compared to Douglas-fir and hemlock. There was a weak trend ($P = 0.20$) for Douglas-fir and hemlock litter to have higher lignin:N concentrations compared to bigleaf maple, at maple sites. There were no significant differences in concentrations of fibre, cellulose, lignin and N, or in lignin:N ratio for Douglas-fir/hemlock litter from bigleaf maple sites compared to conifer sites. This suggests that the presence of bigleaf maple had no significant effect on the measured parameters of Douglas-fir/hemlock litter.

4.2 Litter Decomposition

The mass loss of bigleaf maple and Douglas-fir/hemlock litter was examined at both bigleaf maple and conifer sites, over 18 months. For the initial stages of decay, it was hypothesized that bigleaf maple litter would decay faster than conifer litter, and conifer litter would decay faster at bigleaf maple sites compared to conifer sites. A faster decay rate was expected to correspond with a faster rate of nutrient release with bigleaf maple litter compared to Douglas-fir and hemlock. These trends were expected as rapidly-decaying litter speeds up the nutrient cycle and creates nutrient-rich tissues that will eventually become palatable for microbes and should be easily decomposed (Perry, 1994).

4.2.1 Percent Mass Loss

Differences in percent mass loss in litter were statistically significant for all months measured, with faster decay in bigleaf maple compared to Douglas-fir/hemlock litter at 6, 12 and 18 months. This pattern was seen at both bigleaf maple and conifer sites. These results are in agreement with Harmon et al. (1990), in which bigleaf maple had 57% and 50% of its initial litter weight remaining at 6 and 12 months, respectively, and Douglas-fir had 77% and 73% remaining at 6 and 12 months, respectively. A study by Prescott et al. (2005) in which decay rates were compared between combinations of spruce/aspen, Douglas-fir/alder, and Douglas-fir/paper birch/lodgepole pine revealed that broadleaf species decay faster than conifer in the initial stages of decay, but over time differences were not statistically significant. In the same experiment, vine maple decomposed faster than all litters examined (14 total), losing 75% of its original mass after the first year (Prescott, 2005). Ogden (1996) reported a 37-68% mass loss for vine

maple litter and a 32-42% mass loss for conifer litter after 1 year. Turnover times for forest floor litter were calculated by Fried et al. (1990), and also revealed bigleaf maple litter to decay faster than Douglas-fir litter. An opposite pattern was revealed by DeCatanzaro and Kimmins (1985), in which bigleaf maple lost 24% and 57% of its initial weight after 12 and 18 months, respectively, and conifer needles lost an average of 35% and 75% of their weight after 12 and 18 months, respectively. Different results may be due to differences in sampling methodology. In addition to using litter bags with a mesh size of 1 mm for bigleaf maple, litter bags made of nylon material with a mesh size of 4 mm were used (DeCatanzaro & Kimmins, 1985). Other differences in methodology include size of litter bags (20 X 20 cm), number of replicates (2), and litterbag mixtures for conifer litter (cedar, Douglas-fir and hemlock). In our study, all litter was placed in 1 mm litter bags made of fibreglass material, and replicated 3 times within each site, with a total sample size of 8.

4.2.2 Decay Rate Constant

Bigleaf maple litter had a significantly higher annual decay rate at bigleaf maple sites compared to conifer sites. In a review of several papers, studies suggest litter often decays faster beneath the canopy in which it is found due to the presence of specific soil fauna and microflora, a concept otherwise known as "home advantage" (Augusto et al., 2002; Valachovic et al., 2004). In our study, bigleaf maple only occurred at the bigleaf maple sites and thus it had a 'home advantage' at these sites. For conifer needles, there was no significant difference in annual decay rate between bigleaf maple and conifer sites. Since Douglas-fir/hemlock was present at both bigleaf maple and conifer sites, both sites provided a 'home advantage'.

The annual decay rate was significantly higher for bigleaf maple litter than for Douglas-fir/hemlock litter at both bigleaf maple and conifer sites. In addition to its high nutrient concentrations, bigleaf maple litter has a larger surface area to mass ratio, resulting in a litter more accessible and palatable to microbes for rapid breakdown. The decay rate calculated for bigleaf maple and Douglas-fir/hemlock are in agreement with other studies in which *k* was calculated. In a study comparing the decay rate constant between eleven species of leaf litter, Harmon et al. (1990), as cited in Valachovic et al. (2004), obtained a *k* value of 0.67-0.69 for bigleaf maple, 0.87 for vine maple, and 0.29-0.39 for Douglas-fir. Valachovic et al. (2004) calculated a decay constant of 0.34 for bigleaf maple, 0.82 for vine maple and 0.27 for Douglas-fir. DeCatanzaro and Kimmins (1985) also used a single exponential decay constant, and calculated *k* values of 0.33 for bigleaf maple and 0.43 for conifer (Douglas-fir/cedar/hemlock). In addition, Lee and Weber (1983) obtained a *k* value of 1.5 for bigleaf maple, the highest out of a total 10 species calculated. The difference in values for conifer litter may be a result of litterbag mixtures. In the present study, litterbags contained Douglas-fir and hemlock, whereas the litterbags used by Valachovic et al. (2004) and Harmon et al. (1990) contained pure Douglas-fir needles. In addition, DeCatanzaro and Kimmins (1985) used litterbags containing Douglas-fir, hemlock and cedar. The variations used in the litterbags likely has an impact on the decay rate constant calculated, because cedar decays the slowest, followed by Douglas-fir and hemlock (Prescott, 2005; Prescott et al., 2000).

4.2.3 Nutrient Analysis

Nutrients in litter have different patterns of decomposition and release over time, with some nutrients being held in the litter structure more strongly than others (Girisha et

al., 2003). Between litter types, bigleaf maple was generally higher in most nutrient concentrations and contents at all stages of decay. Bigleaf maple litter had an overall increase in N and P concentrations, and an overall decrease in N and P contents at both site types; a pattern not seen in Douglas-fir and hemlock litter. Differences in N concentration between litter types were significantly higher for bigleaf maple at both sites. Concentrations of N and P were expected to be higher in bigleaf maple litter due to the higher nutrient quality observed in maple leaves in the present study. During the initial stages of decay, mass loss is dominated by easily-decomposed carbohydrates, followed by the slower decay of more recalcitrant compounds, such as lignin (Perry, 1994; Corbeels, 2001). Because N and P are limiting nutrients, over time concentrations likely increased because they were immobilized in the structural components of the litter by microbes during C respiration (DeCatanzaro & Kimmins, 1985; Girisha et al., 2003). N contents may have increased by inputs through N in precipitation, insect frass, or leaching from new litter (DeCatanzaro & Kimmins, 1985; Bocock, 1964). These results are similar to DeCatanzaro and Kimmins (1985) in which N and P concentrations of bigleaf maple litter generally increased over 18 months.

Between litter types, concentrations of Ca were significantly higher in bigleaf maple at both site types, at 0 and 6 months. Concentrations of Mg were also significantly higher in bigleaf maple litter at both site types, at all months measured. Over months measured, concentrations of both Mg and Ca decreased in bigleaf maple litter at both site types; a pattern not seen in the decay of Douglas-fir and hemlock litter. A decrease in Ca and Mg concentrations were expected because these elements are soluble cations, enhancing their susceptibility to leaching. DeCatanzaro and Kimmins (1985) suggest the

loss of Ca in decomposing litter is largely a result of leaching in coastal Douglas-fir/western hemlock forests. In addition, bigleaf maple's nutritional requirement for Ca and Mg are quite high (Thomas, 1999; Krajina et al., 1982). DeCatanzaro and Kimmins (1985) found Ca and Mg concentrations to generally decrease up to 12 months in bigleaf maple. In the present study, concentrations of Mg and Ca in Douglas-fir and hemlock litter were expected to show trends similar to bigleaf maple, but at a smaller scale due to the difference in initial nutrient concentrations. However, in Douglas-fir and hemlock, overall concentrations of Ca increased and Mg decreased. In a litter decay study on a variety of eucalyptus species, Attiwill (1968) suggests Ca is immobilized until just prior to litterfall, resulting in an increase of mobile Ca soon after litterfall in some litter types. This may have been the case of Ca concentration in Douglas-fir and hemlock litter – although not seen in bigleaf maple litter, Ca might have been a limiting element and thus immobile until 6 months, at which time it became available to microbes, decreasing its concentration. In addition, external inputs of Ca may have increased contents of Ca in Douglas-fir and hemlock, through leaching of Ca in bigleaf maple litter (Bocock, 1964).

4.3 Forest Floor

Humus forms (L, F, H and Ah) from both bigleaf maple and conifer sites were classified and measured, and the organic horizons were analysed for chemical properties to provide insight to the productivity of the site (Green et al., 1993).

4.3.1 Forest Floor and Ah Horizon Depths

Statistically significant differences were found in the forest floor depths between maple and conifer sites for all parameters measured, with the exception of the H horizon.

As expected, the L and F horizons were thinner at bigleaf maple sites, and when combined, the H and Ah horizons were thinner at conifer sites. The Ae horizon was also thicker at conifer sites. Due to its rapidly decomposing litter, it was expected that bigleaf maple sites would have thinner L and F horizons, and thicker H and Ah horizons compared to conifer sites.

These results are in agreement with Ogden and Schmidt (1997) in which total forest floor depth (L, F, H) was thinner at vine maple sites compared to conifer sites. Although Tashe and Schmidt (2003) found no statistical differences between vine maple and conifer sites for the L, F or H horizons, vine maple did have significantly thicker Ah horizons.

Results from the present study reveal that bigleaf maple is responsible for a large input of litterfall over a short period of time (i.e. autumn), compared to conifer sites. In addition, results suggest a rapid rate of bigleaf maple litter decay compared to Douglas-fir and hemlock, supporting the notion that thin L and F horizons beneath bigleaf maple are due to hastened decay. The greater thickness in the combined H and Ah horizons beneath bigleaf maple suggest rapid cycling and incorporation of nutrients from the organic horizon into the mineral horizon. The depth of the H horizon may not have been significant between site types when analyzed alone, due to errors in sampling. The H and Ah horizons are often difficult to differentiate due to the presence of organic matter in the A horizon.

4.3.2 Humus Form Classification

It was expected that bigleaf maple sites would be dominated by Mulls, because Mulls are most common beneath species with rapidly decomposing litter (Green et al., 1993). More than half of humus forms examined at bigleaf maple sites were classified as belonging to the Mull order (vermimull). The remaining humus forms were different groups of the Moder order. At conifer sites, the dominant humus form orders were Moder and Mor, with a larger variation in groups, compared to maple sites. Moder humus forms often have an accumulation of the F horizon similar to Mors, but they are also biologically active and have an abundance of faunal droppings, similar to Mulls (Green et al., 1993). The findings in the present study are in agreement with Tashe and Schmidt (2003), in which Mulls were identified beneath vine maple and Mor and Moder humus forms were abundant beneath conifer sites. Krajina et al. (1982) also suggest Mulls are typical of bigleaf maple litter.

Results in this present study suggest bigleaf maple can influence humus forms within mixedwood stands. Bigleaf maple is likely influencing the formation of humus form types wherever it is abundant and its rapidly decomposing, nutrient-rich litter is falling, consequently affecting the abundance and diversity of microbes in the organic horizons and the rate at which nutrients are made available for plant uptake. If the type of humus form in the forest floor is an indicator of site productivity (Green et al., 1993), then bigleaf maple can benefit the integrity and growth of the surrounding forest.

4.3.3 Forest Floor Properties

Forest floors beneath bigleaf maple had a larger weight per unit area, compared to conifer sites. Fried et al. (1990) found inconsistent differences in forest floor weights

between Douglas-fir and bigleaf maple sites. It is interesting to note that the forest floor weight per unit area is larger at maple sites, but the depth of the L, F and H horizons is significantly thinner than conifer sites. This may be a result of the forest floor samples being extracted in the summer; a time when most litterfall beneath bigleaf maple has had nearly a year to flatten and decompose. Litter at conifer sites falls throughout the year, so much of the L and F horizon may not have been as mature and decomposed, compared to those at maple sites.

Mineralizable N contents, as well as nitrate concentration and contents were also higher at bigleaf maple sites. These results are in agreement with those found within Mull humus forms, which typically have low pH and higher available N (Green et al., 1993). Tashe and Schmidt (2003) also found forest floors beneath vine maple to have higher mineralizable N concentrations.

Although all element concentrations in total litterfall were greater at maple compared to conifer sites, these results were not evident in the forest floor chemical properties. I expected to find greater concentrations of exchangeable Ca, Mg and K beneath bigleaf maple, due to its inputs of base-rich litter, but I did not find this. However, I did find a weak trend of significantly higher concentrations of exchangeable Ca for bigleaf maple plots as compared to conifer plots. The high concentration of nutrients in bigleaf maple litter, coupled with the rapid rate of decomposition in forest floors beneath bigleaf maple may indicate that these nutrients are being taken up by surrounding vegetation as soon as they become available. Fried et al. (1990) also experienced high variability in forest floor nutrient elements beneath bigleaf maple,

despite high nutrient elements found in litterfall. However, Ogden and Schmidt (1997) found higher concentrations of Al, Ca, Mg and K in forest floors beneath vine maple.

4.4 Mineral Soil

Mineral soil samples were extracted from sites to determine the difference in bulk density and chemical properties between sites. Samples were taken from the top of the mineral horizon, where species effects on soils are most obvious (Binkley & Valentine, 1991).

4.4.1 Mineral Soil Properties

Bulk density of the surface mineral soil was lower at bigleaf maple sites compared to conifer sites. It was expected that bigleaf maple sites would have lower mineral soil bulk densities because of the greater amount of organic matter being added to these sites in litterfall and the faster decay rates, compared to conifer sites. This is in agreement with Fried et al. (1990) in which bigleaf maple stands had lower bulk densities in the top 10 cm of mineral soil. This suggests that soils surrounding bigleaf maple are higher in organic matter and better aerated, encouraging microbial survival and water infiltration.

The mineral soil at bigleaf maple sites were characterized by significantly higher total N concentrations, compared to conifer sites. The greater amount of nitrogen made available to plants beneath bigleaf maple may explain why differences in mineralizable N and NO_3-N concentrations and contents were significantly higher beneath maple. These trends were expected since bigleaf maple litter was significantly higher in N concentration compared to Douglas-fir/hemlock litter, in addition to several other

nutrients. Tarrant et al. (1951) and Fried et al. (1990) also found bigleaf maple litter higher in N, P, K, Ca and Mg compared to Douglas-fir and hemlock.

The significant differences in the quality of litterfall between sites suggested similar patterns might be evident in the mineral soil. In a review of several papers, Augusto et al. (2002) proposes that differences in soils beneath various tree species are partially due to differences in litter characteristics. Fried et al. (1990) also found higher means of total N and mineralizable N concentrations and contents at bigleaf maple sites (although only statistically significant for total N concentration).

It was expected that the addition of base-rich litter would be reflected in a higher organic matter concentration in the mineral soil, compared to conifers and I did find a weak trend ($P = 0.20$) for higher total C beneath bigleaf maple. This is likely why the cation exchange capacity (CEC) at maple sites was significantly higher relative to conifers (Brady & Weil, 1999). Exchangeable K, Ca and Mg were significantly higher at bigleaf maple sites. This is consistent with total litterfall results in the present study, where differences between litterfall types were highest in favour of maple for K, Ca and Mg (as well as B). These findings are in agreement with Tashe and Schmidt (2003), in which vine maple sites had significantly higher total exchangeable bases at maple sites, compared to conifer sites. Fried et al. (1990) found bigleaf maple sites to have higher K concentration, with results statistically significant at 2 out of 5 sites.

Chapter 5: Conclusion

5.1 Summary of Findings

Because the structure and function of coniferous and deciduous species differ from each other, their influence on forest ecosystems also differ. This study set out to determine the influence of bigleaf maple in a coastal temperate forest dominated by Douglas-fir and western hemlock on nutrient cycling, through an examination of its litterfall, rate of decay, and chemical properties within the forest floor and mineral soil (Figure 5.1).

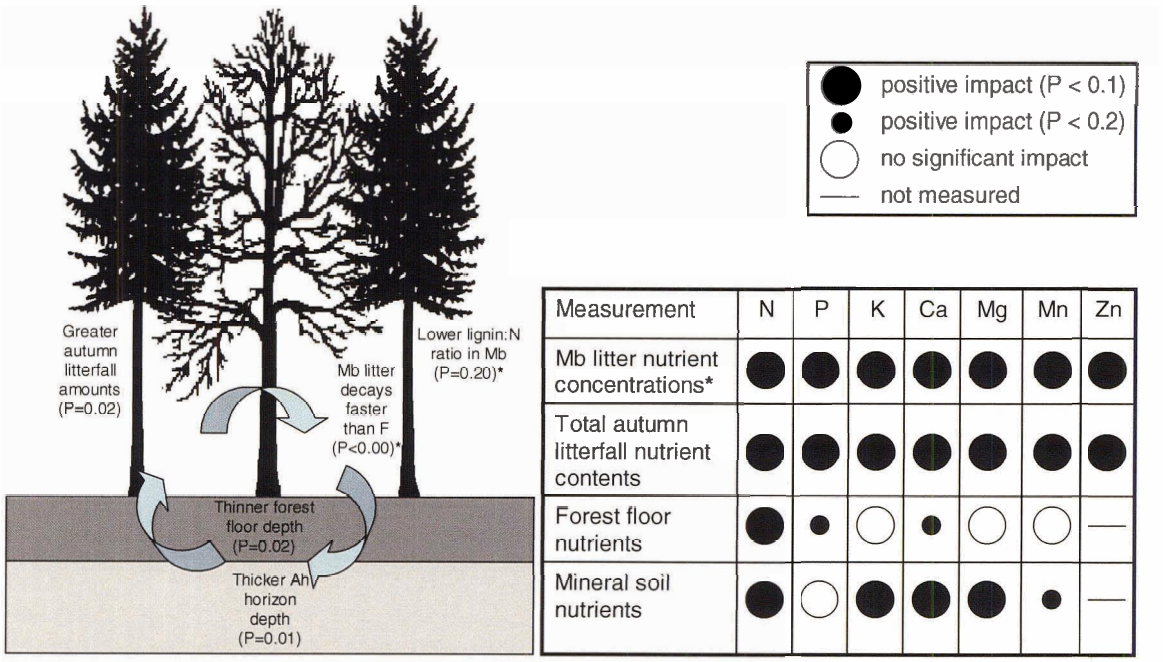

Figure 5.1 Summary diagram illustrating the influence of bigleaf maple (Mb) on forest floor and mineral soil chemical properties in a conifer forest through an examination of forest floor nutrient concentrations (Exchangeable K, Ca, Mg & Mn) and contents (P & N), and mineral soil nutrient concentrations (N, P and Exchangeable K, Ca, Mg and Mn). Forest floor N represents mineralizable N & NO_3 contents. Mineral soil N represents total N concentrations, and mineralizable N & NO_3 concentrations and contents. Parameters displayed represent differences in sites with and without Mb. *Represents differences in Mb and Douglas-fir/hemlock (F) litter types.

An examination of seasonal and annual litterfall weights and nutrient concentrations at two site types (bigleaf maple and conifer sites) provided insight to the differences each species contributes to nutrient flux. Compared to conifer canopies, bigleaf maple canopies have greater litterfall containing higher elemental concentrations, and with senescence will eventually be incorporated into the forest floor. With bigleaf maple litter contributing a third of the total elements measured, areas without its litter are receiving less nutrient inputs. Compared to Douglas-fir/hemlock and cedar, bigleaf maple litter is higher in concentrations of all macronutrients (except for C) as well as the micronutrients Mn, B, Zn and Cu. In the same context, when weight contribution is taken into consideration, bigleaf maple sites are higher in contents of all macronutrients (except C) and micronutrients (except Al).

The difference in litter quality and quantity between species suggests there may be differences in microbiological activity in the presence of bigleaf maple, which in turn has an effect on litter decay rates and nutrient release. Because of higher nutrient concentrations and lower recalcitrant fractions such as lignin, broadleaved litter has a faster rate of decay compared to conifer litter (Berg & McClaugherty, 2003). Compared to bigleaf maple, Douglas-fir/hemlock litter is lower in N concentration, adding to the stress on microbial populations that require a sufficient amount of N to thrive. This research confirmed these assumptions by measuring the rate of decomposition between species over the 18 month study period. Although litter decay was faster in bigleaf maple litter compared to Douglas-fir/hemlock litter, macronutrient concentrations in bigleaf maple remained greater than in conifer litter at all months measured. Not only is bigleaf maple litter higher in initial element concentrations, but its rapid decay suggests

significantly larger quantities of nutrients are continuously being incorporated into the forest floor and mineral soil, at least during initial stages of decay.

A measurement of the forest floor revealed significantly thicker L and F horizons at conifer sites, and significantly thicker H and Ah horizons at bigleaf maple sites. These results correspond well with the hastened litter decomposition measured in bigleaf maple. Beneath maple canopy, nutrients are not held as tightly in the forest floor as is the case beneath the conifer canopy. Rather, nutrients from foliage are broken down for a quicker return to an organic-enriched mineral soil for eventual plant root uptake. In the case of slower decomposing conifer foliage, litter accumulates over time resulting in thick L and F horizons with nutrients unavailable for efficient uptake by the surrounding tree species. These postulations are supported with an examination of humus form types found between species. The majority of humus forms beneath bigleaf maple were identified as Mull – the most biologically active, base-rich and productive humus form group supporting nitrification (Fisher & Binkley, 2000). An examination of the mineral soil revealed lower NO_3-N concentration in areas where bigleaf maple is absent, likely due to microbial immobilization. Mineral soils beneath bigleaf maple were lower in bulk density supporting the notion of higher organic matter content in the upper 7 cm of the soil horizon, which should result in better aeration, water infiltration, and an overall better environment for microbial functioning. Bigleaf maple may also contribute to higher CEC, exchangeable bases and N in the mineral soil.

The lack of differences in nutrient concentrations in Douglas-fir/hemlock litterfall between site types was not expected. Higher litterfall nutrient concentrations at bigleaf maple plots were expected to be evident in the forest floor and mineral soil, resulting in

greater nutrient uptake by surrounding conifers, and higher nutrient concentrations in needle litter. Nutrient concentrations, especially Ca and Mg, usually increase in litter as their availability in soil increases (Berg & McClaugherty, 2003). This suggests that although bigleaf maple is contributing significant nutrients to the forest floor and mineral soil, it may be taking up those nutrients for its own benefit, with little left over for surrounding conifers.

5.2 Significance of Research

The incorporation of deciduous species into conifer monocultures is receiving more attention in silviculture. If the goal of forest management is conifer integrity, then why are nutrient-rich and soil building broadleaved species being removed from monocultures? In the case of bigleaf maple, its presence has been deemed competitive and even detrimental to conifer survival. Following removal, bigleaf maple can proliferate from stumps or seedlings, its rapid growth often out-competing Douglas-fir for light and dimming shade-intolerant species. However, these reasons are not sufficient to warrant the removal of the species from conifer forests. Rather, it stresses the need to further examine how management needs to be reinvented to reap the benefits of a soil building species proven to enhance nutrient cycling.

Through its abundant, base-rich and quickly decomposing litterfall, bigleaf maple influences soils wherever it is present. However, results obtained in this research were not all expected, and raise several questions on the role of bigleaf maple in conifer forests. Studies on this species are not as abundant as on other deciduous species such as alder and birch. Considering the complexity of forest ecosystems, an incentive to conserve bigleaf maple in coniferous forests is to research further on the species and its

influence in various forest types. Beyond nutrient cycling, the presence of bigleaf maple encourages biodiversity. Carey and Harrington (2001) claim bigleaf maple presence increases forest complexity, and can benefit coniferous populations through its influence on mammals. The nutritional seeds produced by bigleaf maple may reduce interaction and mammal predation on cone populations. A recent discovery of a new fungal species associated with bigleaf maple, *Fibulobasidium*, stresses that we still do not fully understand its potential in ecosystems (Bandoni, 1998). Additionally, it would be beneficial to encourage native species such as bigleaf maple so that future generations will be able to enjoy the species our generation was able to experience.

5.3 Future Research

As a master's project, this research had limitations on the scope and length of the study to ensure it remained within financial constraints and within a realistic timeline. For future research designs, it may be useful to consider the suggestions that follow.

Some statistical analyses conducted during paired t-tests encountered low power. Oftentimes, low power is encountered if the sample size chosen for a given experiment is small (Zolman, 1993). To determine the appropriate number of samples required to gain significance, sample sizes can be calculated on a number of computer programs, including Statistical Power by Borenstein and Cohen (1988). However, low power is sometimes unavoidable because a sufficiently large sample size can be time consuming and costly, and beyond the limits of research (Hurlbert, 1984).

Results obtained for lignin concentration in bigleaf maple were unexpected, as deciduous species are typically low in lignin compared to conifers. Despite high

concentrations, bigleaf maple litter had a faster rate of decomposition. Future research might include an examination of lignin at several stages of decay to determine the rate of lignin breakdown, and how it differs from concentrations in other species. In addition, it would be interesting to study the decay rate of both litterfall types over a longer period of time to determine how nutrient breakdown changes over time.

There was no difference in nutrient concentrations of Douglas-fir/hemlock litter between site types. However, a low power was encountered. Future research might examine this parameter more closely by calculating the appropriate sample size prior to experimentation. In addition, the nutrient concentration of foliage prior to senescence could be examined to determine if differences exist before nutrients are translocated to other parts of the tree. It would also be interesting to determine the effect bigleaf maple has on the growth of surrounding species by measuring the diameter of growth of nearby conifers.

This research found a greater number of Mull humus forms at maple sites, but the extent of bigleaf maple is still unclear. It would be interesting to examine the extent of influence of bigleaf maple in a conifer forest, and to also examine the extent of influence in a more controlled research site. Ideally, a fully grown and isolated bigleaf maple tree would be studied to minimize influence of other vegetation types. This would allow for segregation of parameters measured in this research. Research for this project also stressed the importance of microbial populations in belowground ecosystems. It would be useful for further research to examine the abundance and diversity of such populations beneath bigleaf maple, compared to areas in which the species is absent.

The forest canopy has the largest influence on the development of the forest floor and its properties. In addition to contributing to litterfall, the canopy modifies the composition of precipitation reaching the forest floor either by reducing snow accumulation, removing soil water through transpiration or washing off dry deposited solutes (Prescott, 2002; Tobon et al., 2004). Accountable for 70-90% of gross precipitation, stemflow and throughfall are the main hydrological processes responsible for spatial distribution of moisture and solutes from the canopy to soil, and have been documented to significantly impact forest biogeochemical cycles (Parker, 1983; Escudero et al., 1991; Stockli, 1991 and Soulsby, 1997, as cited in Levia and Frost, 2003). In south central Ontario, throughfall and stemflow beneath coniferous and deciduous canopy cover demonstrated enrichment of all ions sampled except for H^+, NH_4^+, and Na^+ (Neary & Gizyn, 1994). It would be useful for further research to include an examination of the composition of throughfall and stemflow beneath bigleaf maple canopies, compared to Douglas-fir. Results may aid in explaining the spatial variation of forest floor properties and patterns of apparent nutrient decay in litterbag studies.

The role of bigleaf maple in conifer forests is still not fully understood. Bigleaf maple contributes a large quantity of nutrients to the forest floor and mineral soil, but how this affects surrounding conifers is still unclear. As such, it would be beneficial to examine additional parameters to measure bigleaf maple influence in conifer forests. In addition, research involving optimal management strategies that include balancing a deciduous component in coniferous forests are necessary to maintain the survival of the species.

Literature Cited

Atkinson, H.J., Giles, G.R., MacLean, A.J. and Wright, J.R. 1958. Chemical methods of soil analysis. Contr. 169. Chem. Div. Sci. Serv. Canada Department of Agriculture, Ottawa, ON.

Attiwill, P.M. 1968. The loss of elements from decomposing litter. Ecology 49(1):142-145.

Augusto, L., Ranger, J., Binkley, D. and Rothe, A. 2002. Impact of several common tree species of European temperate forests on soil fertility. Ann. For. Sci. 59:233-253.

Bandoni, R.J. 1998. On an undescribed species of *Fibulobasidium*. Can. J. Bot. 76:1540-1543.

Berg, B. 1984. Decomposition of root litter and some factors regulating the process: long-term root litter decomposition in a Scots pine forest. Soil Biology and Biochemistry 16: 609-618.

Berg, B. and McClaugherty, C. 2003. Plant Litter: Decomposition, Humus Formation, Carbon Sequestration. Springer, New York. 286 pp.

Berg, B. and Staaf, H. 1980. Decomposition rate and chemical changes of Scots pine needle litter. II. Influence of chemical composition. In: Persson, T. (Ed.), Structure & Function of Northern Coniferous Forests – An Ecosystem Study. Ecol. Bull. (Stockholm) Vol. 32, pp. 373-390.

Binkley, D. and Giardina, C. 1998. Why do species affect soils? The warp and woof of tree-soil interactions. Biogeochemistry 42:89-106.

Binkley, D. and Valentine, D. 1991. Fifty-year biogeochemical effects on green ash, white pine and Norway sprice in a replicated experiment. For. Ecol. Manage. 40: 13-25.

Bjornlund, L. and Christensen, S. 2005. How does litter quality and site heterogeneity interact on decomposer food webs of a semi-natural forest? Soil Biology & Biochemistry 37: 203-213.

Bocock, K.L. 1964. Changes in the amounts of dry matter, nitrogen, carbon and energy in decomposing woodland leaf litter in relation to the activities of the soil fauna. Journal of Ecology 52(2): 273-284.

Borchers, S.L. and Perry, D.A. 1989. Growth and ectomycorrhiza formation of Douglas-fir seedlings grown in soils collected at different distances from pioneering hardwoods in southwest Oregon clear-cuts. Can. J. For. Res. 20:712-721.

Borenstein, M. and Cohen, J. 1988. Statistical Power Analysis: A Computer Program.

Brady, R.H. and Weil, R.R. 1990. The Nature and Properties of Soils. Twelfth Edition, Prentice Hall, Upper Saddles River, New Jersey. 881 pp.

Bremner, J.M. 1965. Inorganic forms of nitrogen In Methods of Soil Analysis, Part 2. Edited By C.A. Black et al. Agronomy 9:1179-1237. Am. Soc. Of Agron., Inc. Madison, Wisconsin.

Bremner, J.M. 1996. Nitrogen Availability Indexes In Methods of Soil Analysis, Part 2. Edited By C.A. Black et al. Agronomy 9:1324-1345. Am. Soc. Of Agron., Inc. Madison, Wisconsin.

British Columbia Ministry of Forests. 1989. Forest Cover Mapsheets 1: 10 000 UTM Zone 10, NAD 83. Timberline Forest Inventory Consultants.

Carey, A.B. and Harrington, C.A. 2001. Small mammals in young forests: implications for management for sustainability. Forest Ecology and Management 154:289-309.

Carter, M.R. 1993. Soil Sampling and Methods of Analysis. Canadian Society of Soil Science, 1993. pp. 25-37.

Carter, R.E. and Lowe, L.E. 1986. Lateral variability of forest floor properties under second-growth Douglas-fir stands and the usefulness of composite sampling techniques. Can. J. For. Res. 16:1128-1132.

Comeau, P.G. 1996. Why mixedwoods? *In* Silviculture of temperate and boreal broadleaf-conifer mixtures. *Edited by* P.G. Comeau and K.D. Thomas. BC Min. For. Res. Branch, Victoria, British Columbia. Land Manage. Handbook No.36. pp. 1-7.

Corbeels, M. Plant litter decomposition: general concepts and model approaches. NEE Workshop proceedings: 18-20 April 2001.

Cornelissen, J.H.C. 1996. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. J. Ecol. 84: 573-582.

DeCatanzaro, J.B. & Kimmins, J.P. 1985. Changes in the weight and nutrient composition of litterfall in three forest ecosystem types on coastal British Columbia. Can. J. Bot. 63:1046-1056.

Escudero, A., Hernandez, M.M., and Del Arco, J.M. 1991. Spatial patterns of soil composition around isolated trees. *In* Diversity of environmental biogeochemistry. *Edited by J. Berthelin.* Elsevier, Amsterdam. pp. 507-517.

Fioretto, A., Di Nardo, C., Papa, S. and Fuggi, A. 2005. Lignin and cellulose degradation and nitrogen dynamics during decomposition of three leaf litter species in a Mediterranean ecosystem. Soil Biology & Biochemistry 37:1083-1091.

Fisher, R.F. and Binkley, D. 2000. Ecology and Management of Forest Soils. 3rd edition. John Wiley & and Sons, New York (Chapter 11).

Fried, J.S. 1985. Two studies of *Acer macrophyllum*: I. The effects of bigleaf maple on soils in Douglas-fir forests. II. The ecology of bigleaf maple seedling establishment and early growth in Douglas-fir forests. M.Sc. thesis, College of Forestry, Oregon State University. Corvallis, Oregon.

Fried, J.S., Boyle, J. R., Tappeiner II, J. C. and Cromack, K. Jr. 1990. Effects of bigleaf maple on soils in Douglas-fir forests. Can. J. For. Res. 20:259-266.

Girisha, G.K., Condron, L.M., Clinton, P.W. and Davis, M.R. 2003. Decomposition and nutrient dynamics of green and freshly fallen radiate pine (*Pinus radiata*) needles. Forest Ecology and Management 179:169-181.

Goering, H.K., and Van Soest, P.J. 1970. Forage Fiber Analyses (Apparatus, Reagents, Procedures and Some Applications). U.S. Dep. Agric. Handbook No. 379. Washington, DC.20pp.

Grayston, S.J. and Prescott, C.E. 2005. Microbial communities in forest floors under four tree species in coastal British Columbia. Soil Biology and Biogeochemistry 37:1157-1167.

Green, R.N., Trowbridge, R.L. and Klinka, K. 1993. Towards a taxonomic classification of humus forms. Forest Science Monograph 29. Society of American Foresters. Bethesda, MD. 49 pp.

Harmon, M.E., Baker, G.A., Spycher, G., and Greene, S.E. 1990. Leaf-litter decomposition in the *Picea/Tsuga* forests of Olympic National Park, Washington, U.S.A. For. Ecol. Manage. 31:55-66.

Haeussler, S., Coates, D., and Mather, J. 1990. Autecology of common plants in British Columbia: A literature review. BC Min. For. and Can. For. Serv. FRDA Rep. No. 158. Victoria, British Columbia.

Hendershot, W.H., Duquette, M. 1986. A simple Barium chloride method for determining cation exchange capacity and exchangeable cations. Soil Science Society of America Journal 50:605–608.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field studies. Ecological Monographs. 54:187-211.

Insightful Corporation. 2005. S Plus® Version 7.0 copyright 1988, 2005. Insightful corp.

John, M.K. 1970. Colorimetric determination of phosphorus in soil and plant materials with ascorbic acid. Soil Sciences 109:214-220.

Kalra, Y.P. and Maynard, D.G. 1991. Methods manual for forest soil and plant analysis. For. Can., Northwest Reg,. North. For. Cent., Edmonton, Alberta. Inf. Rep. NOR-X-319.

Killham, K. 1994. Soil ecology. Cambridfe University Press. New York. 242 pp.

Kleinbaum, D.G., Kupper, L.L., Muller, K.E. and Nizam, A. 1998. Applied Regression Analysis and Other Multivariable Methods (3rd Ed.). Duxbury Press, Toronto. 798 pp.

Klinka, K. 1976. Ecosystem Units: Univeristy of British Columbia Research Forest, Maple Ridge, BC 1: 10000. Sheet 3 within NTS sheets 92G/7, 92G/2. Faculty of Forestry, University of British Columbia. Vancouver, British Columbia.

Krajina, V.J., Klinka, K., and Worrall, J. 1982. Distribution and ecological characteristics of trees and shrubs of British Columbia. Faculty of Forestry, University of British Columbia. Vancouver, British Columbia.

Lavkulich, L. 2006. Personal communication. UBC.

Lee, J.J. and Weber, D.E. 1983. Effects of sulfuric acid rain on decomposition rate and chemical element content of hardwood leaf litter. Can. J. Bot. 61:872-879.

Levia, D.F., and Frost, E.E. 2003. A review and evaluation of stemflow literature in the hydrologic and biogeochemical cycles of forested and agricultural ecosystems. J. of Hydrol. 274: 1-29.

Maguire, D.A. 1994. Branch mortality and potential litterfall from Douglas-fir trees in stands of varying density. For. Ecol. Mgmt. 70: 41-53.

Melillo, J.M., Aber, J.D. and Muratore, J.F. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63: 621-626.

Nadkarni, N.M. 1984. Biomass and mineral capital of epiphytes in an *Acer-macrophyllum* community of a temperate moist coniferous forest, Olympic Peninsula, Washington Can. J. Bot. 62(11): 2223-2228.

Neary, A.J., and Gizyn, W.I. 1994. Throughfall and stemflow chemistry under deciduous and coniferous forest canopies in south-central Ontario. Can. J. For. Res. 24: 1089-1100.

Ogden, A.E. 1996. Soil characteristics of persistent canopy openings occupied by vine maple in a coastal western hemlock forest. M.Sc thesis, Department of Geography, Simon Fraser University. Burnaby, British Columbia.

Ogden, A.E., and Schmidt, M.G. 1997. Litterfall and soil characteristics in canopy gaps occupied by vine maple in a coastal western hemlock forest. Can. J. Soil Sci. 77: 703-711.

Parker, G.G. 1983. Throughfall and stemflow in the forest nutrient cycle. Adv. Ecol. Res. 13: 57-133.

Peech, M. 1965. Exchange acidity In Methods of soil analysis, Part 2. Edited By C.A. Black et al. Agronomy 9:905-913. Am. Soc. Of Agron., Inc. Madison, Wisconsin.

Perry, D.A. 1994. Forest Ecosystems. The Johns Hopkins University Press, Baltimore. 649 pp.

Peterson, E.B., Peterson, N.M., Comeau, P.G. and Thomas, K.D. 1999. Bigleaf maple managers' handbook for British Columbia. BC Ministry of Forests, Victoria. 54 pp.

Prescott, C.E. 2002. The influence of the forest canopy on nutrient cycling. Tree Physiology 22:1193-1200.

Prescott, C.E. 2005. Do rates of litter decomposition tell us anything we really need to know? Forest Ecology and Management 220:66-74.

Prescott, C.E., Taylor, B.R., Parson, W.F.J., Durall, D.M. and Parkinson, D. 1993. Nutrient release from decomposing litter in Rocky Mountain coniferous forests: influence of nutrient availability. Can J. For. Res. 23:1576-1586.

Prescott, C.E., Zabek, L.M., Staley, C.L. and Kabzems, R. 2000. Decomposition of broadleaf and needle litter in forests of British Columbia: influences of litter type, forest type, and litter mixtures. Can. J. For. Res. 30:1742-1750.

Prescott, C.E., Blevins, L. and Staley, C. 2004a. Litter decomposition in B.C. forests: controlling factors and influences of forestry activities. BC Journal of Ecosystems and Management 5(2):30-43.

Prescott, C.E., Vesterdal, L., Preston, C.M., and Simard, S.W. 2004b. Influence of initial chemistry on decomposition of foliar litter in contrasting forest types in British Columbia. Can. J. For. Res. 34: 1714-1729.

Qian, H., and Klinka, K. 1995. Spatial variability of humus forms in some coastal forest ecosystems of British Columbia. Ann. Sci. For. 52 (6): 653-666.

Rothe, A. and Binkley, D. 2001. Nutritional interactions in mixed species forests: a synthesis. Can. J. For. Res. 31:1855-1870.

Ryan, M.G., Melillo, J.M., and Ricca, A. 1990. A Comparison of methods for determining proximate carbon fractions of forest litter. Can. J. For. Res. 20:166-171.

Simard, S.W., Hagerman, S.M., Sachs, D.L., Heineman, J.L. and Mather, W.J. 2005. Can. J. For. Res. 35: 843-859.

Soulsby, C. 1997. Hydrochemical processes. *In* Contemporary hydrology. *Edited by* R.L. Wilby. John Wiley, Chichester, U.K. pp. 59-106.

Staley, C. 2004. UBC. Personal Communication.

Stockli, H. 1991. Influence of stemflow upon the decomposing system in two beech stands. Rev. Ecol. Biol. Sol. 28 (3): 265-286.

Tarrant, R.F., Isaac, L.A., and Chandler, R.F. Jr. 1951. Observations on litter fall and foliage nutrient content of some Pacific Northwest tree species. J. For. 49(12):914-915.

Tashe, N.C. 1998. The impact of vine maple on the biogeochemical nutrient cycle of conifer-dominated coastal forests in southwestern British Columbia. M.Sc thesis, Department of Geography, Simon Fraser University. Burnaby, British Columbia.

Tashe, N.C., and Schmidt, M.G. 2001. The impact of vine maple on site fertility of coastal temperate forests. For. Ecol. Manage. 147:263-279.

Taylor, B.R., Prescott, C.E., Parsons, W.J.F. and Parkinson, D. 1991. Substrate control of litter decomposition in four Rocky Mountain coniferous forests. Can. J. Bot. 69:2242-2250.

Thomas, K.D. 1999. The Ecology and Silviculture of bigleaf maple. BC Min. For. Extension Note 33.