Effects of bigleaf maple on the growth and morphology of mature conifers in the southern coastal forests of British Columbia.

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Abstract

The influence of bigleaf maple (*Acer macrophyllum*) on the growth of mature conifers in the coastal forests of British Columbia has not been previously assessed. I used a paired plot design to evaluate the influence of mature bigleaf maple on the growth and morphology of Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). Twelve conifer plots including bigleaf maple trees in the center (BLM) were paired with twelve plots that had only conifers present (DF). For the Douglas-fir and western hemlock growing in these plots, the diameter at breast height (DBH), height, age, volume, canopy morphology, site index, stand basal area, tree density and competition index were compared using paired-t tests between BLM and DF plots. Cores taken from Douglas-fir and western hemlock trees were used to assess growth chronologies; and radial growth rates and basal area increment (BAI) were compared between BLM and DF plots.

There were no significant differences in tree height, tree age, site index or competition index for both Douglas-fir and western hemlock, and DBH for Douglas-fir, when compared between BLM and DF plots. DBH was greater for western hemlock in BLM as compared to DF plots. Both Douglas-fir and western hemlock that were growing next to bigleaf maple had significantly higher radial growth rates and BAI than Douglas-fir and western hemlock surrounded by conifers only. BLM plots did not have a different standing wood volume (total or conifer-only) than DF plots. My findings suggest that the inclusion of bigleaf maple in conifer stands could enhance biodiversity without negatively affecting timber production.

Keywords: Bigleaf maple; Douglas-fir; western hemlock; growth model; competition; species influence.

Dedication

Dedicated to my dziadek Jerzy and babcia Jasia, Jamrozik for helping instill a love of nature and sparking my interest in forestry.

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List of Acronyms

AIC Akaike Information Criterion

BAI Basal area increment BC British Columbia

BLM Plots centered around a center bigleaf maple tree

C-N Ratio Carbon to nitrogen ratio

CV Crown volume

DF Plots centered around a center Douglas-fir tree

df Degrees of freedom

n Sample size

US United States of America

WAPA Weighted area potentially available

Chapter 1. Introduction

1.1. Research Rationale

Whether mixed-species forest stands can be more productive than monocultures of fast-growing species has been of interest to forest managers for some time (Kelty 1992). Currently, our understanding of each combination of tree species must be examined to specifically understand the most productive conditions for their growth (Pretzsch 2010). Within the productive coastal rainforests of western North America, information about the influence of mature bigleaf maple (Acer macrophyllum) on the growth of neighbouring conifers is lacking. Bigleaf maple is a large, broadleaf, angiosperm tree that grows together with conifers, including Douglas-fir (Pseudotsuga menziesii) and western hemlock (Tsuga heterophylla) (Peterson 1999). Research has demonstrated that soils in proximity to bigleaf maple have properties that may make them more fertile for neighbouring trees (Turk et al. 2008, Hamdan and Schmidt 2012). Resprouting bigleaf maple clumps can decrease the diameter at breast height (DBH) and height growth of Douglas-fir seedlings (Knowe 1995) and therefore herbicide treatments on bigleaf maple stumps following cutting is common. However, the influence of bigleaf maple on neighbouring conifers as they age is still unclear. This research attempts to fill in the gap of how the growth of mature conifers is affected by growing in proximity to mature bigleaf maple.

Bigleaf maple's range and frequency within that range are projected to increase significantly due to climate change (Hamann and Wang 2006). The potential increasing importance of bigleaf maple in the landscape makes it more pressing to know what effect bigleaf maple is likely to have on the growth of conifers that inhabit the same ecosystem.

1.2. Literature Review

1.2.1. Ecology of Bigleaf Maple

Bigleaf maple grows in the coastal forests of British Columbia (BC) and neighbouring parts of the United States (US). These forests are temperate evergreen rainforests that support a substantial forest industry (Raettig and Christensen 1999, *The State of British Columbia's Forests* 2010). In BC, bigleaf maple grows within the Coastal Western Hemlock and the Coastal Douglas-fir biogeoclimatic zones (Meidinger and Pojar 1991). These forests extend south along the border into the US. The corresponding climatic zones in the US are classified as the *Tsuga heterophylla* zone and the *Picea sitchensis* zone (Franklin and Dyrness 1973).

Bigleaf maple is the largest maple species growing on the west coast of North America. It attains a height of 15-30 m and commonly has a diameter up to 60 cm (Farrar 1995). The inability to tolerate frost means that it is concentrated along the Pacific Ocean's coast, its range not extending further than 300 km inland in Canada (Krajina et al. 1982). Bigleaf maple grows best on rich sites with a moisture regime from fresh to moist and is often found on fluvial deposits or at the base of colluvial slopes (Haeussler et al. 1990). Bigleaf maple's ability to occupy fairly wet sites is supported by its capacity to withstand temporary flooding of its root system (Krajina et al. 1982).

Bigleaf maple is considered moderately shade tolerant and is the most shade tolerant hardwood in its region (Packee 1976). However, the shade tolerance of bigleaf maple decreases with age (Haeussler et al. 1990). Bigleaf maple seeds germinate best in partially shaded canopy gaps. Fried and Tappeiner (1988) found that as a metric of sky opening changed from 5% to 20%, survival of bigleaf maple seedlings increased from 0% up to 60%. Bigleaf maple establishes best from seeds in conifer stands between the stem exclusion stage and before forbs and shrubs invade the understory (Fried and Tappeiner 1988). Limitations to the establishment of bigleaf maple are predation and browsing by mammals, and light availability. Planted bigleaf maple saplings are often browsed by deer and elk (McTaggart-Cowan 1945, Devereaux 1988).

The presence of bigleaf maple contributes to creating a more biodiverse forest community. The mass of epiphytes found on bigleaf maple is greater than on any other species in the same ecosystem (Nadkarni 1984). The use by birds of bigleaf maple includes cavity-nesting sites and day-time roosts for bald eagles (Stalmaster and Newman 2014). Bigleaf maple is often found in riparian areas and as such it contributes the most out of any hardwood in its ecosystem to the supply of coarse woody debris in rivers (Nakamura and Swanson 1994). Within natural environments, the generation of coarse woody debris in rivers has an impact on their hydrological and biological components (Wallace et al. 1995).

Bigleaf maple's traits make it ideal for developing in canopy gaps and reinvading highly disturbed areas (Peterson 1999). Bigleaf maple's large leaf size could be an adaptation to maximize photosynthetic potential within the long moist segments of the growing season. A positive moisture balance is correlated with a high specific leaf area, leaf diffuse conductance and mass-based photosynthetic capacity, meanwhile it is negatively related to leaf life-span (Reich et al. 1999). This is supported by a significant correlation between leaf size and leaf area index in the *Acer* genus (Ackerly and Donoghue 1998). The large leaf size may thus be useful for maximizing leaf area index and photosynthetic capacity, making bigleaf maple able to outgrow other tree species in canopy gaps and disturbed sites.

Bigleaf maple vigorously re-sprouts from epicormic buds along its stem if it is seriously damaged, most commonly by the cutting of mature trees and by fire. It has even been known to sprout prolifically from its root crown following disturbance by fire (Uchytil 1989). In an unshaded environment, stump-sprouts can grow to reach heights of 5 m to 6.5 m in a 3 year period (Minore and Zasada 1990). This can make it a strong competitor with shade intolerant conifer seedlings following clearcutting. Re-sprouting bigleaf maple, following a large scale fire disturbance or logging, is known to reduce the growth rates of neighbouring Douglas-fir seedlings (Knowe 1995). To reduce this effect, herbicide treatments on bigleaf maple stumps following cutting is common (Wagner and Rogozynski 1994).

1.2.2. Bigleaf Maple Nutrient Cycling

Bigleaf maple trees can have a noticeably positive impact on soil properties adjacent to them, in comparison with the soil properties found under conifers in the same forests. Fried et al (1990) showed that bigleaf maple had significantly higher litterfall than Douglas-fir growing in the same environment. Litterfall concentrations of N, Ca, Mg, K, Zn and Mo were greater under bigleaf maple than Douglas-fir (Fried et al. 1990). The mineral soils below bigleaf maple had higher levels of total N and higher organic matter content than under Douglas-fir but no significant differences were observed with other nutrients. The authors noted a higher concentration of nutrients in foliar litter and faster turnover time to be the biggest contributors to the difference in soil properties.

Turk et al. (2008) showed that soils adjacent to bigleaf maple have a higher level of organic matter content in the mineral horizons as well as higher pH, cation exchange capacity, concentrations of N as well as levels of exchangeable Ca, Mg and K and lower levels of exchangeable Al than soils without the influence of bigleaf maple. Another study in an old-growth forest in Oregon that involved bigleaf maple, Douglas-fir, western hemlock and western redcedar (*Thuja plicata*) found that bigleaf maple foliage had high levels of N, P, Ca, Mg, and K in relation to conifers (Cross and Perakis 2011). In this study, mineral soils sampled beneath bigleaf maple had significantly higher Ca and sum of cations (Ca + Mg + K) than soils beneath western hemlock. The overall influence of bigleaf maple on soils seems to demonstrate that bigleaf maple foliage is higher in N, Ca, Mg and K and influences mineral soil properties in a way to make them higher in organic matter, N and base cations. The soil conditions below bigleaf maple would create an environment that is beneficial for the growth of other plant species.

Bigleaf maple has a canopy that supports a large amount of canopy-dwelling epiphytes, which may contribute to the nutrient accumulation in the soils around bigleaf maple. The average epiphyte mass on trees found on the slopes of the Olympic Mountains was 35.5 kg (Nadkarni 1984). The accumulation of dead tree litter and epiphytic plants on the bigleaf maple's branches and in their bifurcations can lead to the development of arboreal soils, which are an important part of C and N pools in the forest (Haristoy et al. 2014). Precipitation-derived water running along the tree's bark, called stemflow, collects

dissolved nutrients from the tree's canopy and in the case of bigleaf maple had a higher pH and K concentration than that of adjacent conifers (Hamdan and Schmidt 2012).

The higher nutrient concentrations found in bigleaf maple foliage and stemflow likely contribute to a higher concentration of nutrients and a higher pH within the forest floor and mineral soil beneath bigleaf maple than neighbouring conifers. The spatial pattern of bigleaf maple's influence on soil properties is concentrated within 2.5 m of the trunk and litterfall was found to primarily fall directly below the extent of the canopy (Chandler et al. 2008). Reasons that the influence of bigleaf maple on forest soils is highly centered on the bole of the tree, include the low dispersal of litterfall and the noticeably nutrient enriched stemflow of bigleaf maple.

Tree litter that has higher concentrations of N, or lower C-N ratios, can be expected to have higher rates of N mineralization (Aber and Melillo 1980). Therefore, one would expect the addition of leaf litter with higher N concentrations, to mineralize faster and have a fertilization-like effect on trees, leading to higher growth rates of trees. It would be expected that the higher N content in bigleaf maple's foliage would have this fertilizer-like effect on Douglas-fir and western hemlock. Higher N mineralization rates have been correlated with higher site indices for Douglas-fir (Klinka and Carter 1990).

1.2.3. Ecology of Douglas-fir and Western Hemlock

Two of the most prominent conifer species native to the forests of the Coastal Western Hemlock and the Coastal Douglas-fir biogeoclimatic zones are Douglas-fir and western hemlock. Coastal Douglas-fir is an early seral tree species that grows quite quickly and is the preferred timber species in plantations in the coastal forests of North America (Minore 1979). Individual trees can attain a height of 60 m and a diameter of 2.0 m (Farrar 1995). Douglas-fir needs mostly full sun conditions to grow at its most productive rate. The silvicultural management of plantations of Douglas-fir favours even-aged stand management using the clear-cut silvicultural system and replanting with a smaller selection of species than are present initially (Curtis et al. 2004, *The State of British Columbia's Forests* 2006). The minimum size gap required for the regeneration of Douglas-fir on mesic sites is expected to be 750 – 1000 m² (Spies et al. 1990). Mature

Douglas-fir trees are resistant to low severity fires and are long lived, making them an early seral species that persists into the old-growth stage.

Western hemlock is a very shade tolerant species that occupies a climax position in the forest canopy as it is able to develop under the existing canopy and persist into old age (Minore 1979, Spies et al. 1990). Western hemlock can attain a height of 50 m and DBH of 1.2 m (Farrar 1995). It seldom grows in pure stands and is often mixed with Douglas-fir, western redcedar and species from the genus *Abies* (Franklin and Dyrness 1973). Western hemlock is intolerant of fire and is often killed during medium to high intensity fires and thrives in areas with higher moisture levels (Agee 1993, Pojar and Mackinnon 1994). The range of western hemlock extends along the Pacific coast of North America from central Alaska to California and in the wet western side of the Rocky Mountains from central British Columbia to Idaho (Pojar and Mackinnon 1994).

1.2.4. Stand Establishment and Development

The development of Douglas-fir stands is greatly dependent on how the stands are established. Forest stands in North America are generally reforested under a managed system. This provides a significant amount of control on how the stand is established and how it develops into the future. Reducing the planting density of stands can increase the growth rate of individual trees in the stand. In a dendrochronological study of old-growth Douglas-fir trees, the diameter of trees at 100, 200 and 300 years of age was strongly correlated with BAI at 50 years of age (Poage and Tappeiner 2002). Spacing trials also showed that trees planted with more space between individuals developed larger boles and crowns (Curtis and Reukema 1970, Oliver and Larson 1990).

There is evidence that natural Douglas-fir stands developed under densities lower than what current planting densities prescribe. Studies of the diameter growth of old-growth Douglas-fir trees in the Oregon Coast range were found to have higher growth rates beyond 50 years of age, the time Douglas-fir trees reach stem exclusion, than contemporary even-aged stands (Tappeiner et al. 1997). This is suggested by Tappeiner et al. (1997) to be the result of lower stand densities, of only one-fourth or one-fifth that of typical contemporary stands (100-120 vs. 500 trees/ha).

Donato et al. (2012) propose that early-successional complexity can persist with long-lived species, like Douglas-fir and western hemlock, to become a source of late-successional complexity if canopy-closure and competitive exclusion are not dominant forces in a stand. The creation of complex young stands can thus be of importance in creating future complex stand structure and the incorporation of young sparsely stocked stands may be key for this to succeed. Tepley et al. (2013) created a theoretical model with multiple pathways for the establishment of stands in Douglas-fir/western hemlock forests. This model was able to fit into it the many previous pathways for old growth characteristics to develop in stands. It includes both stands that establish at high densities as well as low densities, and in both cases, how stand structure is influenced by the occurrence of, severity, and frequency of disturbance events.

The inclusion of a more diverse set of initial tree species in a stand, like bigleaf maple, may be a means of reducing stand density of the restocked tree species and creating a more diverse stand. Through competition for resources, bigleaf maple stump sprouts can reduce the growth of Douglas-fir seedlings within 15m of the sprouts (Knowe 1995). By reducing the growth of Douglas-fir seedlings, and causing the mortality of some others, the bigleaf maple sprouts can reduce the density of Douglas-fir stems in the early stages of stand development. Shading by trees or shrubs can also help facilitate the establishment of shade-tolerant tree species among the shade-intolerant ones (Zavitkovski and Newton 1968). The space provided by bigleaf maple sprouts could later be occupied by more shade tolerant tree species, such as western hemlock and western red cedar. These factors would reduce the competitive advantage of Douglas-fir and would create a more diverse and open stand

1.2.5. The influence of tree species diversity on forest productivity

Theoretical ecology can help explain the occurrence of higher productivity in assemblages of multiple tree species than in monocultures. The ecological niche consists of the conditions necessary to support the vital activities of a type of organism (Alley 1982). Organisms seek out the necessary resources and conditions for their survival and if their niches overlap, competitive interaction is the result. Competition is the resource-related form of interaction between two or more organisms (Birch 1957). Genetic similarity is often

associated with niche overlap (den Boer 1980). The more genetically similar a population of individuals is, the higher the likelihood it will experience higher intraspecific competition than interspecific competition (Schoener 1977). From this it would also follow that an assemblage of genetically similar individuals vying for the same limited resources, in the same way, is likely to experience a higher level of competition than an assemblage of dissimilar individuals.

There are two types of positive interactions between tree species that can result in multiple species improving their biological fitness. The first one, called niche complementarity, is when species occupy different niches in the same geographic space. Niche complementarity relies on interspecific competition to be less than intraspecific competition (Chen et al. 2003). The second type of positive interaction is facilitation which occurs when one species modifies the conditions in its environment in a way that is beneficial for another species. One of the most common examples of facilitation is the creation of nutrient rich soil conditions by one plant species that benefit another plant species. This is especially true of plants that fix nitrogen (Rothe and Binkley 2001).

The relationships in a stand between tree species can be competitive or can be beneficial, either through niche complementarity or facilitation. These relationships can change as stand development progresses (Cavard et al. 2011) and can be dependent on environmental stresses (Pugnaire and Luque 2001). Competition, niche complementarity and facilitation are all interactions between plant species that may be observed when bigleaf maple grows in conjunction with conifers in a stand.

Experimental observation of how plant community diversity relates to overall productivity can help explain the different relationships bigleaf maple can have with adjacent conifers. The foundational studies on this subject focused on herbaceous species, especially grasslands, which display logarithmic increases in productivity in relation to increased species diversity (Hector et al. 1999, Loreau et al. 2001). The connection between species diversity and productivity in forest ecosystems has been harder to establish (Kelty 1992, Chen et al. 2003). The results seem to be more dependent on the species in question and the environment they inhabit.

There are some examples of silvicultural integration of multiple species being more productive than monocultures at the stand scale. A review of much recent research on multispecies assemblages in Europe found Fagus sylvatica and Picea abies stands to be more productive together than in monoculture (Pretzsch 2005). A study by Amoroso and Turnblom (2006) also demonstrated that, at high densities, plantations of Douglas-fir mixed with western hemlock were more productive than Douglas-fir alone. Mixing of a shade-intolerant and shade-tolerant species to promote crown stratification and aboveground resource partitioning continues to be one of the most recommended multispecies tree assemblages (Chen et al. 2003). Even-aged stands of Douglas-fir and western hemlock were found to stratify after 20 years with Douglas-fir overtopping and suppressing the hemlock (Wierman and Oliver 1979). Another analysis of forest inventory data from across much of the US found that successional diversity in stands, defined as a mix of early and late successional species, was correlated with productivity (Caspersen and Pacala 2001). Forest tree species composition can also influence how disease and pests affect the stand and this can subsequently influence stand growth performance. Meta-analysis of studies documenting the difference in growth performance, windthrow damage and pest and disease damage between single species and multi-species stands found that mixed species stands had higher growth performance and lower incidence of damage (Jactel and Brockerhoff 2007, Griess and Knoke 2011).

There are also cases where multi-species stands are less productive. In the Interior Cedar Hemlock (ICH) and Interior Douglas-fir (IDF) zones of BC any presence of paper birch (*Betula papyrifera*), a second shade-intolerant species, with Douglas-fir reduced the rates of the shade-intolerant conifer's growth likely due to competition for light (Simard 1990). Long and Shaw (2010) could not find evidence for increased overall biomass production with increased tree diversity in ponderosa pine (*Pinus ponderosa*) stands across its range.

A specific analysis of growth of Douglas-fir and western hemlock in the presence and absence of bigleaf maple may determine if competition in stands is stronger or weaker with the presence of bigleaf maple. There are theoretical ways bigleaf maple could be a lesser competitor than previously thought and actually increase overall wood production in a stand. Along with other vegetation in natural stands, bigleaf maple could contribute to

reduced stocking levels of Douglas-fir by shading out newly-germinated Douglas-fir seedlings to a level where intraspecific competitive exclusion is minimized between Douglas-fir individuals. Furthermore, the establishment of bigleaf maple in existing canopy gaps could add to the overall wood that is produced in a stand without significantly decreasing the growth rate of surrounding conifers. Lastly the impact that bigleaf maple has on soil properties might be able to create sites more conducive to conifer growth which could potentially be a form of facilitation.

1.3. Research Goal and Hypotheses

My overall research goal was to determine the influence of mature bigleaf maple on the growth of mature adjacent conifers. To do this methodically, the following hypotheses were used:1) mature Douglas-fir trees growing next to bigleaf maple have higher growth rates than those that are only surrounded by conifers due to the increased nutrient-rich conditions created by bigleaf maple and decreased competitive effect of having bigleaf maple in the stand; 2) mature western hemlocks growing next to bigleaf maple have higher growth rates than those that are only surrounded by conifers due to the increased nutrient-rich conditions created by bigleaf maple and decreased competitive effect of having bigleaf maple in the stand; 3) a stand of conifers with a component of bigleaf maple has more standing wood than one without bigleaf maple due to the increased growth rates of the conifers adjacent to bigleaf maple and better resource partitioning among different species; and 4) site quality as measured by site index for Douglas-fir and western hemlock will be higher in plots containing bigleaf maple due to bigleaf maple's effect on creating more nutrient rich site conditions.

Chapter 2. Methodology

2.1. Study Area

The fieldwork for this study was conducted in The University of British Columbia's Malcolm Knapp Research Forest (49°15'48.69"N, 122°34'20.25"W). The Research Forest is located northeast of Vancouver, BC, Canada. The study area lies in the dry maritime subzone of the Coastal Western Hemlock biogeoclimatic zone (Meidinger and Pojar 1991). The area receives 1827 mm of precipitation that falls mainly between the months of October to March and the average annual temperature is 9.8°C. The forest stands used in the study were located at approximately 150 m above sea level.

The main tree species located in the study site are coastal Douglas-fir, western hemlock, western redcedar, bigleaf maple and black cottonwood (*Populus balsamifera ssp. trichocarpa*). The main understory vegetation is dominated by red huckleberry (*Vaccinium parvifolium*), vine maple (*Acer circinatum*) and swordfern (*Polystichum munitum*).

The soils within the study area were formed from morainal and colluvial parent materials and are reported to be sandy loam Gleyed Dystric Brunisols (Soil Classification Working Group 1998). The soils have a compacted layer at a depth of approximately 40 cm.

2.2. Sampling Design

Two mature conifer stands with a component of mature bigleaf maple were located within the study area (Figure 2.1). These stands will be referred to as stand A (in the north) and stand B (in the south). The stands are composed of multiple cohorts of trees thus making them uneven-aged with dominant and codominant trees ranging in age from 70-140 years. A preliminary assessment of tree ages in the stands was carried out by coring the trees using an increment borer at 1.3 m above the ground level and counting the number of rings that the trees had accumulated. Tree ages were later verified by using a more rigorous methodology described later in the site chronologies section.

Within the two stands, 12 plots were located that were centered on a bigleaf maple tree and these plots were paired with plots centered on a Douglas-fir tree. The plot center trees were chosen to have no major scars or growth deformities and they were dominants or co-dominants. The bigleaf maple-centered plots will be called BLM plots and the Douglas-fir centered plots will be called DF plots. There were 4 paired plots in stand A (Figure. 2.2) and 8 paired plots in stand B (Figure. 2.3). The paired plots were chosen to be as similar as possible in abiotic and biotic factors. The pairing process was carried out once all the site data were gathered, but while selecting sites, care was taken not to include areas that were noticeably different. The site characteristics that were considered in pairing the plots were: proximity, degree of slope, aspect, humus form, moisture regime, nutrient regime, site series, and tree species composition (Table 2.1). In addition plots were selected such that there were no other deciduous trees within 15 m of the plot center trees. The only exception to this allowed for multiple bigleaf maples in the bigleaf maple plots.

Proximity meant that the paired plots were in the same stand. A stand in this study is a contiguous community of trees sufficiently uniform in composition, structure, age and size class distribution, spatial arrangement, site quality, condition, or location to distinguish it from adjacent communities (Nyland 1996). Mean distance between paired plots was 80 m with a minimum distance of 20 m and a maximum of 210 m. Initially it was attempted to locate pairs of plots within 20 m of each other, but it was necessary to increase this distance in order to find paired plots with similar site characteristics. Slope was measured

with a clinometer and aspect was determined with a compass. Humus form was assessed (Klinka and Green 1981) for 2 forest floor samples that were collected randomly from within 2 m of each plot center tree. Moisture regime, nutrient regime and site series were determined using the tables in Klinka et al. (1995). Species composition was assessed by recording the species of the trees that were adjacent to the center tree in each plot. The paired plots included 3 paired plots that had Douglas-fir but no western hemlock surrounding the center trees, 2 paired plots that had only western hemlock but no Douglas-fir surrounding the center trees and 7 paired plots that had both Douglas-fir and western hemlock surrounding the center trees. Thus there were 10 paired plots that had Douglas-fir trees surrounding the center trees and 9 paired plots that included western hemlock surrounding the center trees.

To characterise the soil conditions for the 2 stands, four soil pits were excavated, 2 in stand A (Pits 3 and 4) and 2 in stand B (Pits 1 and 2) with one soil pit located in the north end and one in the south end of each of the 2 stands (Figures. 2.2 and 2.3). For each horizon in each pit, the following were recorded: horizon designation, horizon depth, soil textural class, coarse fragment content, structure, and colour (Table 2.2). Each soil profile was classified using the Canadian System of Soil Classification (Soil Classification Working Group 1998). Pits 1 and 3 were classified as Orthic Humo-Ferric Podzols, while pits 2 and 4 were Orthic Dystric Brunisols. Pit 2 had a buried Orthic Humo-Ferric Podzol that appeared to have been buried in a mass movement.

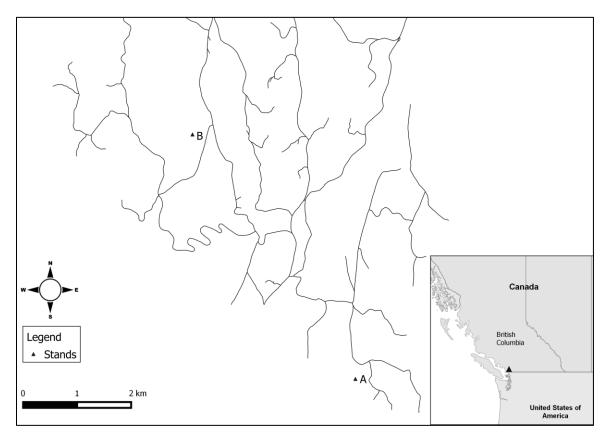


Figure 2.1 Map of study stands in Malcolm Knapp Research Forest, near Vancouver, BC Canada. The lines on this map represent the road network within the forest area.

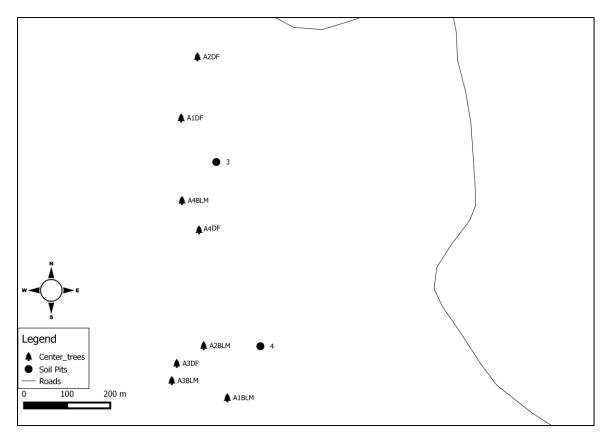


Figure 2.2 Map of the paired plots in stand A in Malcolm Knapp Research Forest. Plots are paired so that each pair of plots contains one plot with a bigleaf maple (BLM) and one plot with a Douglas-fir (DF) at its center.

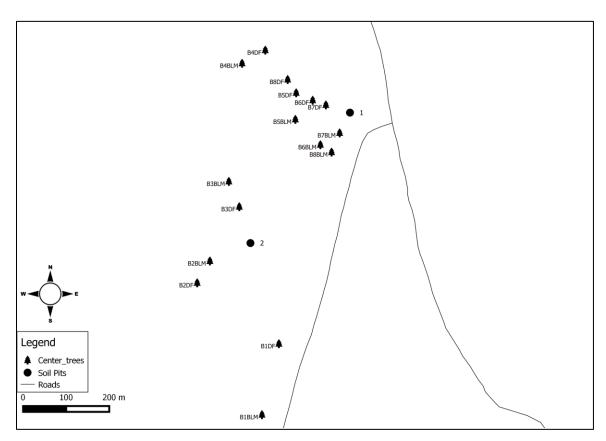


Figure 2.3 Map of the paired plots in stand B in Malcolm Knapp Research Forest. Plots are paired so that each pair of plots contains one plot with a bigleaf maple (BLM) and one plot with a Douglas-fir (DF) at its center.

Table 2.1. Site characteristics of paired-plots (see footnotes on next page)

Plot Name	Site Series	Humus Form ³ Sample 1	Sample 2	Slope (°)	Aspect	Moisture Regime ⁴	Nutrient Regime ⁴	Tree Species Composition ⁵
A1BLM	05	Mullmoder	Mullmoder	6	East	fresh	rich	Cw, Hw, Mb
A1DF	05	Mormoder	Mormoder	14	East	fresh	rich	Cw, Fd, Hw
A2BLM	05	Mormoder	Mormoder	6	East	fresh	rich	Hw, Mb
A2DF	05	Mormoder	Mormoder	12	East	fresh	rich	Cw, Fd, Hw
A3BLM	05	Vermimull	Rhizomull	7	East	fresh	rich	Fd, Hw, Mb
A3DF	05	Hemihumimor	Hemimor	13	East	fresh	rich	Cw, Fd, Hw
A4BLM	05	Mormoder	Mullmoder	6	East	fresh	rich	Cw, Fd, Hw, Mb
A4DF	05	Mormoder	Hemimor	14	East	fresh	rich	Cw, Fd, Hw
B1BLM	05	Mormoder	Vermimull	24	West	fresh	rich	Cw, Fd, Mb
B1DF	05	Mormoder	Velmor	24	West	fresh	rich	Cw, Fd, Hw
B2BLM	05	Mullmoder	Mullmoder	26	West	fresh	rich	Cw, Fd, Hw, Mb
B2DF	01	Mor	Humimor	21	West	fresh	medium	Cw, Fd, Hw
B3BLM	05	Mormoder	Mormoder	23	West	fresh	rich	Cw, Fd, Hw, Mb
B3DF	05	Mormoder	Mormoder	24	West	fresh	rich	Cw, Fd, Hw
B4BLM	03	Rhizomull	Mormoder	9	West	moderately dry	medium	Cw, Fd, Hw, Mb
B4DF	03	Mormoder	Mormoder	10	West	moderately dry	medium	Cw, Fd
B5BLM	05	Mullmoder	Mullmoder	10	West	semi dry	rich	Cw, Fd, Hw, Mb
B5DF	05	Hemimor	Amphimormoder	10	West	semi dry	rich	Cw, Fd, Hw
B6BLM	05	Rhizomull	Rhizomull	13	West	semi dry	rich	Cw. Mb
B6DF	05	Mormoder	Mormoder	10	West	semi dry	rich	Cw, Fd, Hw
B7BLM	05	Hemimor	Mormoder	10	West	semi dry	rich	Cw, Fd. Hw, Mb
B7DF	05	Mormoder	Mormoder	10	West	semi dry	rich	Cw, Fd, Hw
B8BLM	05	Vermimull	Vermimull	10	West	semi dry	rich	Cw, Fd, Hw, Mb
B8DF	05	Orthimormoder	Humimor	10	West	semi dry	rich	Cw, Fd, Hw

(Continued from previous page)

- ¹ The plot naming follows this protocol. The first character refers to whether the plot is located in the A or B stand. The second character refers to which set of paired plots within each stand the particular plot is located in. There are 4 pairs in stand A and 8 in stand B. The final characters refer to whether the plot has a bigleaf maple (BLM) or Douglas-fir (DF) at its center.
- ² 01 Hw Flat moss, 03 FdHw Salal, 05 Cw Sword fern
- ³ (Klinka and Green 1981)
- ⁴ (Klinka et al. 1995)
- ⁵ Cw: western redcédar, Fd: Douglas-fir, Hw: western hemlock, Mb: bigleaf maple

Table 2.2 Soil Profile Descriptions

Pit #	Horizon	Depth (cm)	Textural Class	Coarse Fragment (%)	Structure	Colour
1	LF	3-0	N/A	N/A	N/A	
	Ahe	0-3	sandy loam		single grain	2.5YR 7/1 light reddish grey
	Bf	3-18	sandy loam	10	single grain	7.5YR 5/8 strong brown
	Bm	18-75	sandy clay loam	25	subangular blocky	7.5YR 6/3 light brown
	BC	75-95	sandy loam	30	single grain	5YR 8/4 reddish yellow
	С	95-113+	sandy loam	30	single grain	10YR 7/1 light grey
2	LFH	9-0	N/A	N/A	N/A	
	Bm	0-5	sandy clay loam	15	subangular blocky	7.5YR 6/3 light brown
	С	5-9	sandy clay loam	15	subangular blocky	10YR 7/2 very pale brown
	Charcoal	9-25				
	Aeb	25-27	N/A	8	single grain	10YR 8/1 white
	Bmb	27-80	sandy loam	40	single grain	10YR 6/6 yellowish brown
	BC	80-97	sand	30	single grain	10YR 6/4 light pinkish brown
	С	97-100+	sandy clay loam	25	angular blocky	2.5Y 8/8 yellow
3	LFH	16-0	N/A	N/A	N/A	
	Ae	0-2	N/A	20	single grain	2.5YR 7/1 light whitish grey
	Bf	2-21	sandy loam	25	single grain	5YR 6/6 light reddish brown
	ВС	21-47	loam	25	subangular blocky	7.5YR 8/2 pinkish white
4	LFH	20-0	N/A	N/A	N/A	
	Bm	0-25	loam	20	single grain	7.5YR 6/4 light brown
	ВС	25-47	loam	35	single grain	10YR 8/4 very pale brown

2.3. Tree Morphology

To investigate the influence of bigleaf maple on the growth characteristics of surrounding trees, morphological characteristics of the trees in the vicinity of the plot's center trees were recorded. Measurements were taken of i) the 24 center trees, ii) the trees that were adjacent to those trees, and iii) trees adjacent to the adjacent trees, for a total of two tiers of trees around each plot center tree. Trees were deemed adjacent to each other if their crowns touched, intersected or were near enough that no sizeable gap existed between them. If it was unclear whether a sizeable gap existed between the trees, we included the tree and measured all of its characteristics rather than remove it from the analysis.

For each center tree, the species of tree was identified, and DBH, height, crown radius, and crown depth, were measured. Tree heights and crown depths were obtained by standing at a point where one could see the top of the tree, measuring the distance to the base of the crown and of the tree and measuring the angles to the top and bottom of the tree and the bottom of the crown using a clinometer. Trigonometric functions were then applied to the distance and angles to obtain the tree's height and crown depth. Crown radius was measured by walking out to the edge of the tree's canopy and looking directly up, which was verified using a clinometer, and measuring a horizontal distance from the edge of the tree's canopy to the trunk of the tree. Two crown radii measurements were made in a random direction and then the mean of those values was used for further comparison. The location of each center tree was collected using a global positioning system (GPS).

For trees adjacent to the center trees, tree height, DBH and species name were measured and recorded in the same way as for the center trees. Canopy radius was separated into a 180-degree arc that faced towards the center tree and a 180-degree arc that faced away from the center tree. Two measurements of canopy radius were measured for each towards and away direction in the same way they were for the center trees and then those values were averaged to provide a towards and away crown radius measurement. The second tier of trees had their DBH, height and crown radius measured in the same way that center trees did. The first and second tier of trees were only recorded

if their DBH was greater than 10 cm. The locations of the first and second tier trees were determined relative to the center trees by measuring the angle to the center tree using a compass and measuring the horizontal distance from the center tree to the tree being measured using a tape measure.

Crown volume was calculated for each tree by using the average of the crown radius values to determine the base radius of the volume of a cone, with the crown depth serving as the height. Merchantable wood volume was also calculated for Douglas-fir and western hemlock trees in all plots using volume equations for Douglas-fir (British Columbia Forest Service 1976) and for western hemlock (Embry and Haack 1965).

The canopy area of bigleaf maple in a plot was used as a metric of bigleaf maple influence. Larger tree canopies tend to create more litterfall (Maguire 1994) and potentially can create more shade. The canopy area of bigleaf maple was calculated in each of the plots centered on a bigleaf maple tree. This was done by adding together the area of each bigleaf maple within a 10 m radial distance from the center maple tree, including the plot center maple tree. The canopy area of each bigleaf maple tree was calculated by assuming a circular area based on two radial measurements of each tree's canopy.

For each plot, the average tree characteristics were determined by averaging the values for up to 3 randomly selected dominant or codominant trees of a set species. All of the data analysis was carried out using R software (R Development Core Team 2012). Paired t-tests and Wilcoxon signed-rank tests (Mendenhall et al. 2006) were used to determine if there was a difference between the average properties of the trees that were in each pair of BLM and DF plots. The trees were divided by species and then the averages for each species' attributes for each plot were calculated and used in the tests. The attributes that were tested were: tree age, DBH, tree BA, height, crown radius, crown depth, crown volume, bigleaf maple canopy diameter as well as volume of bole. This was done both for the Douglas-fir and the western hemlock datasets. To test whether the tree morphological characteristics' datasets were normally distributed, a Kolmogorov-Smirnov test was used to compare against a randomly generated normal distribution with the same mean and standard deviation as the dataset. BLM and DF datasets were tested for

normality separately. When the data were normally distributed, parametric tests were utilized, whereas when the data were not normally distributed, data transformations were attempted and only when those did not work were non-parametric tests used, as would be advised by the principle of Ockham's razor (Legendre and Legendre 2012).

The paired t-tests and the Wilcoxon signed-rank tests were conducted using an alpha level of 0.1 because of the small sample sizes (n= 9, 10 or 12) that were used for these tests. The tests for normality were conducted using an alpha level of 0.05.

2.4. Site Chronologies

Two increment cores were collected from all adjacent trees as well as each center tree in each plot. Increment cores were collected along topographic contours so that reaction wood was avoided. Cores were sampled on opposite sides of each tree at breast height (1.3 m), unless one side was rotten, in which case two cores were taken from the same side of the tree. The cores were then mounted onto wooden boards and sanded. Coring and handling of cores followed the procedures in Speer (2010).

A Velmex tree ring measuring device ("Velmex Inc." 2014) was used in conjunction with a stereo microscope to measure the annual radial increment of wood growth of each core. The Velmex tree ring measuring device was connected to a digital encoder, which was connected to a computer running Measure J2X, thus storing the information of each radial increment series. To estimate the age of trees for which the coring procedure had missed the pith of the tree, a geometric model for estimating the missing radius was used (Duncan 1989).

The dendrochronology program library in R (R Development Core Team 2012) was used to form chronologies from the raw data of annual increment growth and to cross-date the cores to analyze accuracy of measurement and determine if rings had been missed in the process (Bunn 2010). Cross-dating was possible and successful with the Douglas-fir cores. There were much larger discrepancies in the western hemlock cores and cross-dating was not possible. This is likely due to the fact that western hemlock

develops in the understory of other trees and is thus more influenced by neighbouring trees than climatic or stand-level variables.

For the remainder of the study, I chose to focus on the years 1960-2010 as the timeframe for which to compare growth rates of the trees. The 50-year period is likely a long enough period to cancel out minor fluctuations in growth rates that are anomalous and yet short enough that I was able to find enough stands in which bigleaf maple has been around in a mature form for the majority of this time period.

Several ways of interpreting the growth rates of the trees I had cored were used. The first and simplest method was to present the unaltered radial growth for each year. From the radial growth and the tree's DBH, the basal area increment (BAI) was determined. The BAI is a measure of how much area in wood is accumulated each year in the tree's stem on a cross-section plane located at breast height (1.3 m). This was calculated by subtracting the known radial increment from the present, back to the year 1960 from the current total tree radius and calculating the tree basal area in 1960. From that basal area in 1960 I added each year's BAI as derived from radial growth. Once the BAI was known, differences in BAI were recorded, and the accumulation of BA from 1960-2010 was assessed.

A second method was used to determine if the radial growth series and BAI increment series of Douglas-fir and western hemlock were significantly different in BLM plots than DF plots. Difference chronologies were constructed and tested against a normal distribution with a mean of zero. First, the radial growth series of each tree was detrended using a negative exponential equation so that the age of the trees did not have an effect on the observed radial increment (Bunn 2008, 2010). To form the difference chronologies, the yearly DF mean plot radial increment values were subtracted from their paired BLM mean plot values. This mean difference chronology was tested against a normal distribution with a mean of zero, using a Kolmogorov-Smirnov test, to see if the difference was significantly different from zero. This was done separately for Douglas-fir and western hemlock. The same steps were taken with the yearly BAI series, with the exception that the BAI values did not have to be detrended before the difference chronology was calculated and subsequently tested.

In the third method, the growth rates of the trees in BLM and DF plots were also compared for each decade between 1960 and 2010. For each decade growth rates for trees in each BLM plot were tested against those in the DF plot using a Wilcoxon signed-rank test because the values were not normally distributed.

To determine the relative size of the trees at the beginning of the period we were studying, the DBH of trees in 1960 was calculated. This was done by subtracting the known radial growth in the study period (1960-2010) from the DBH of trees in 2010.

2.5. Site Index, Competition Index, Basal Area and Tree Density

Site index is used to assess site quality by estimating tree height, at an index age, of a select species of tree (Skovsgaard and Vanclay 2008). Site index at 50 years of age was calculated for each plot by using the height and age and calculating the average of three (or less when three were not available), randomly selected, healthy and mature conifers of each species used in this study. The SiteTools version 3.3 software was used to determine site index ("SiteTools" 2004). A paired t-test was also used to test for a difference in site index between BLM and DF plots and this dataset was tested for normality.

As a proxy for a measure of actual use of resources by trees and their neighbours, competition indices are used to estimate the relative competition between trees that occurs in a site. For instance, the measurement of a tree's canopy volume can be used as an index of how much photosynthetic potential it has. Most of these indices are used as predictors of growth. Generally, the more resources an individual tree is able to acquire, the more potential it has to grow and would therefore be able to outcompete its neighbours. There are a lot of different competition indices that have been developed and no one index is best suited for all environments (Burkhart and Tomé 2012). For example, distance-dependant tree growth models sometimes provide only small increases in the ability to predict a tree's growth (Biging and Dobbertin 1995), while at other times they provide significant increases in predictive ability (Mailly et al. 2003).

A slightly modified version of the weighted area potentially available (WAPA) competition index was chosen to determine potential growing space for each tree (Moore and Schlesinger 1973). WAPA was determined by dividing the area within the stand into polygons centered on each tree and weighting by the size of the tree. This metric was calculated using a weighted Voronoi polygon function in the ArcGIS environment (Dong 2008). The DBHs of all of the trees, including bigleaf maple, were used as the weighting variable. This function uses the midpoints between trees to create bisector lines that divide the ground area of a stand equally and then weights these midpoints by the DBH of the tree. This ground area is then partitioned out based on what ground area falls between the bisecting lines and the nearest tree. The trees that are comparatively larger in diameter are partitioned a greater extent of the ground area of the stand than their smaller neighbours. WAPA has been used successfully as a competition index in Douglas-fir and western hemlock forests (Wardman and Schmidt 1998) and other studies have found distance-dependent competition indices superior to distance-independent ones in this ecosystem (Wimberly and Bare 1996). Area potentially available competition indices also performed well against many traditional and contemporary competition indices in a recent study (Shi and Zhang 2003)

Several measures were calculated of how the productivity of the trees in the plots can be measured on a broader scale. To extrapolate the basal area of each plot to a perhectare scale, mean site basal area (BA) was calculated. The plot mean BA was divided by the plot mean WAPA value, which is representative of the ground area each tree uses as its growing space, to determine the mean site BA. To compare the productivity of each plot over the last 50 years, site BA productivity was calculated by dividing the mean plot BAI from 1960-2010 by the plot mean WAPA value and also by the number of years of growth.

I used circular fixed area plots with a radius of 10 m that originated from the center of the center tree within each plot to determine whether bigleaf maple affects stand-level characteristics, such as total wood volume and tree density. The BA by species and the standing merchantable wood volume were determined for each fixed radius plot. For those trees that were partially within the 10 m radius, the proportion of basal area in the plot was used to estimate the proportion of the tree's volume within the plot. Species-specific taper

equations were used to estimate the volume of wood in the bole of each tree. The volume equations used for Douglas-fir were derived from BC Forest Service (1976). The volume equation used for western hemlock was from Embry and Haack (1965). The bigleaf maple bole volume was estimated from Snell and Little (1983). Western redcedar wood volume estimates came from an equation from Farr and LaBau (1971). Using the fixed radius plots, I estimated the density of trees growing per hectare. For plots that included bigleaf maple, a calculation without the maples was carried out to determine if the presence of bigleaf maple decreased the density of conifers.

To see if there were any noticeable differences in tree mortality between paired plots, the basal area of standing dead trees, also known as snags, were calculated within a 10 m radius of each plot's center tree. This was done to see if the presence of bigleaf maple was leading to an increase in tree mortality in the plots, since increased mortality could have a major impact on wood volume yield.

All of the values of stand productivity including site BA, current basal area productivity, the stand metrics from the fixed area plots and the snag datasets were tested for normality and paired t-tests were conducted to determine if significant differences existed between values in BLM and DF plots.

2.6. Individual-tree radial growth models

A pooled sample was made of all the Douglas-fir, greater than 10 cm DBH, adjacent to and including the center trees used for the paired plot analysis of Douglas-fir (A3,A4,B1,B2,B3,B4,B5,B6,B7,B8). This was also done with western hemlock trees but only in the plots that were used for the western hemlock paired plot analysis (A1,A2,A3,A4,B2,B3,B5,B7,B8). For each tree species a Pearson product-moment correlation coefficient was used to test for correlations between crown volume, BAI, WAPA and bigleaf maple canopy area. This was done separately for all trees in BLM plots and DF plots. The p-values for these tests were adjusted using the Bonferonni method (Wright 1992) due to a greater chance of type I error occurring with performing multiple tests on the same data set. The reason for testing whether these variables are correlated is to assess whether they share a linked relationship. For instance, if a higher crown volume is

correlated with a higher BAI we might be able to infer that the increased BAI was related to greater photosynthetic potential of the tree.

A series of linear regression models were fitted to the data obtained from the two conifer species to determine which factors were related to the basal area increment observed in 49 Douglas-fir and 44 western hemlock trees. These were the same trees used in the correlation analysis. For each of the two conifer species whose growth rates are being studied, a series of three hierarchical models was developed. The first model (1) used the 50-year basal area increment from 1960-2010 (BAI) as the dependent variable and the site factors as independent variables. The factors that were tested were DBH, the height of the tree (H), the WAPA index used previously in this study, and bigleaf maple canopy area (BLM). The second model (2) was similar to the first but rather than using the bigleaf maple canopy variable, it used a binary dummy variable of bigleaf maple presence or absence (BLM0). If bigleaf maple was present a value of one was assigned and zero if it was absent. The third model (3) was fitted to only those trees that were adjacent to bigleaf maple but otherwise used the same format as the first model.

$$BAI = DBH + H + WAPA + BLM \tag{1}$$

$$BAI = DBH + H + WAPA + BLMO$$
 (2)

$$BAI = DBH + H + WAPA + BLM$$
 (3)

Though site index could have been used as another variable, it was found to correlate too strongly with height and DBH values and was thus likely interfering with the strength of representation of those variables in the model. The models were visually tested for the assumptions of homoscedasticity, linearity and independence of errors. When it was necessary, data transformations were utilized to meet the assumptions of a regression model and to best fit the model to the data. Box-Cox transformations were used to determine how to best transform the independent variable. The dependent variable was transformed and visually tested to see which model better fit the assumptions of a linear regression.

The model selection process that was used to find the most parsimonious model was the backwards stepwise elimination process. To fit the simplest model that would account for the largest variation in the data, the combination of the adjusted coefficient of variation (Adj. R²) and the Akaike information criterion (AIC) were used (Crawley 2007).

Chapter 3. Results

First I will present the differences in plot and tree characteristics that were derived from the paired plot analyses. Then I will show the radial growth chronologies and their derivatives from the measurement of tree cores. Next I will present the measures of site quality and finally the results of the regression models.

3.1. Tree morphology

The area of bigleaf maple canopy in each plot in a 10 m radius from the center tree ranged from 95 m² to 994 m² with a mean of 361 m² (Figure 3.1). The values were normally distributed around the mean. The plots in stand A had a much lower canopy area of bigleaf maple in comparison to the plots that were in stand B. This partially had to do with the age of the trees (Table 3.1) as well as the number of individuals in each stand.

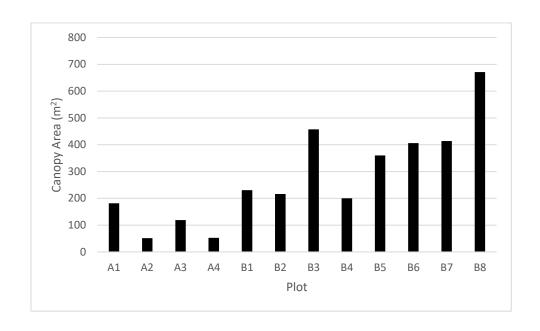


Figure 3.1. Area of bigleaf maple canopy within a 10 m radius of plot center for each bigleaf maple-centered plot. The plots in stand B generally had higher areas of bigleaf maple.

Table 3.1. Age at breast height and DBH of center bigleaf maple in each plot

Plot	A1	A2	A3	A4	B1	B2	В3	B4	B5	B6	B7	B8
Age (years)	58	74	63	61	82	106	96	107	104	91	100	115
DBH (cm)	31.0	41.2	41.4	30.7	125.3	50.0	30.5	67.0	63.6	114.2	57.7	75.2

To be able to compare the growth rates between paired plots it was important to discern if the trees were approximately the same age and had a similar age structure. There was no significant difference in ages of the trees between paired plots (Table 3.2) though the trees in the Douglas-fir plots were slightly older. The age of the Douglas-firs in the BLM and DF plots were normally distributed around their mean (BLM = 109.6, DF = 106.7; Figure 3.2). The Douglas-firs were mostly part of a cohort that regenerated between 91 and 150 years ago. A few trees were younger than that and likely grew into larger gaps that formed in the forest. There was no discernible difference in the distribution of age classes of Douglas-fir between BLM and DF plots. The stands are composed of multiple cohorts of trees thus making them uneven-aged with dominant and codominant trees

ranging in age from 70-150 years. The trees in stand A are generally younger and have regenerated following a fire in 1880 (Hamdan and Schmidt 2012). The trees in stand B are older and have regenerated following a fire in 1868.



Figure 3.2. Distribution of breast-height age by class for center Douglas-fir trees and adjacent Douglas-firs greater than 10cm DBH. Trees in both BLM and DF share a similarly shaped age distribution. Trees that are 141-150 years old are present in DF plots but lacking in BLM plots.

The western hemlocks were generally younger than the Douglas-firs encountered in the plots. There was no significant difference between the breast-height age distribution of western hemlock between BLM and DF plots (Figure 3.3, Table 3.3). The trees regenerated between 61 and 130 years ago. One noticeable difference between the BLM and DF plots is the presence of a couple of very old (120-130 years) western hemlock individuals that are only present in the DF plots.



Figure 3.3. Distribution of breast-height age for western hemlock that were adjacent to the plot center trees and greater than 10cm DBH. The ages show somewhat of a normal distribution with a small amount of trees in the 81-90 year range. Only DF plots have trees that are in the 121-130 range.

There were no significant differences in the DBH, BA, tree height, crown depth, crown volume, breast height age and volume of bole of Douglas-firs in BLM plots as compared to those in DF plots. (Table 3.2) The crown radius of Douglas-firs in BLM plots was significantly greater than those in the DF plots (Table 3.2). There was no significant difference between the canopy radius facing towards the bigleaf maple and the canopy radius facing away from the maple for Douglas-fir trees adjacent to the plot center bigleaf maple trees (Figure 3.4).

Table 3.2. Characteristics of Douglas-fir in BLM or DF centered plots that are plot center trees or adjacent to the center trees (n = 10).

	BLM	DF	BLM:DF	p-values
DBH (cm)	80.6 ± 18.7	74.3 ± 19.6	1.08	0.28*
Tree BA (m ²)	0.53 ± 0.26	0.46 ± 0.23	1.16	0.37
Tree height (m)	50.0 ± 11.0	51.5 ± 9.1	0.97	0.78
Crown radius (m)	5.2 ± 1.3	4.1 ± 0.9	1.27	0.063
Crown depth (m)	24.3 ± 9.3	28.0 ± 8.0	0.87	0.41
Crown volume (m³)	203 ± 157	140 ± 71	1.45	0.25
Breast height age (years)	107 ± 24	110 ± 24	0.97	0.41
Volume of bole (m³)	9.0 ± 6.1	8.0 ± 4.4	1.13	0.69*

^{*} used Wilcoxon signed-rank test

There were no significant differences in tree height, crown radius, crown depth, crown volume, breast height age and volume of bole for western hemlock in BLM plots as compared to DF plots. The DBH and BA of western hemlock were greater in BLM plots compared to DF plots (Table 3.3). There was no difference in crown radius measurements for western hemlock facing towards the plot center and away from the plot center (Figure 3.5).

Table 3.3. Characteristics of western hemlock in BLM and DF centered plots that are adjacent to the plot center trees (n = 9).

	BLM	DF	BLM:DF	p-values
DBH (cm)	43.0 ± 9.2	36.5 ± 7.1	1.18	0.07*
Tree BA (m ²)	0.16 ± 0.07	0.11 ± 0.04	1.43	0.10
Tree height (m)	35.9 ± 8.1	33.8 ± 8.2	1.06	0.61
Crown radius (m)	3.5 ± 1.5	3.7 ± 1.0	0.94	0.68
Crown depth (m)	19.9 ± 7.9	18.3 ± 3.6	1.09	0.61
Crown volume (m³)	95 ± 104	79 ± 42	1.21	0.55
Breast height age (years)	86 ± 13	87 ± 15	0.99	0.87
Volume of bole (m³)	2.4 ± 1.3	1.6 ± 0.9	1.47	0.17

^{*} used Wilcoxon signed-rank test

A comparison of the DBH of species used in the study showed that bigleaf maple was significantly smaller than Douglas-fir but significantly larger than western hemlock and western redcedar (Table 3.4). Bigleaf maple tree height was not significantly different than the height of adjacent western hemlock or western redcedar, but was significantly less than the height of adjacent Douglas-fir (Table 3.5).

Table 3.4 Comparison of bigleaf maple tree DBH at center of plot with the DBH of either western hemlocks, Douglas-firs, or western redcedars adjacent to them.

	Mean center bigleaf maple DBH (cm)	Mean conifer DBH (cm)	Ratio of maple to conifer DBH	p-value	n
Western hemlock	46.8 ± 16.0	36.5 ± 7.1	1.3	0.09	9
Douglas-fir	55.3 ± 31.4	74.3 ± 19.6	0.7	0.10	10
Western redcedar	53.2 ± 8.5	36.3 ± 13.1	1.3	0.01	8

Table 3.5 Comparison of bigleaf maple tree height at center of plot with the height of either western hemlocks, Douglas-firs, or western redcedars adjacent to them.

	Mean center bigleaf maple height (m)	Mean conifer height (m)	Ratio of maple to conifer height	p-value	n
Western hemlock	32.9 ± 9.1	35.9 ± 8.1	0.92	0.40	9
Douglas-fir	33.7 ± 9.5	50.1 ± 11.0	0.67	0.02*	10
Western redcedar	30.1 ± 9.4	26.0 ± 7.5	1.15	0.42	8

^{*} used Wilcoxon signed-rank test

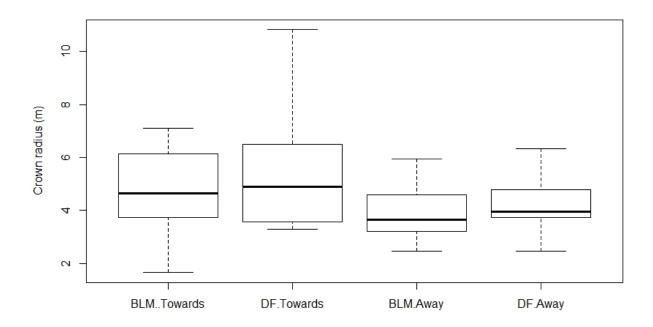


Figure 3.4 Crown radius of Douglas-fir in BLM and DF centered plots. Also differentiated by whether facing towards or away from the plot's center tree (n = 10). The boxplots show no difference in the crown radius size for BLM and DF plots, towards and away from the center of the plots. The away values seem to have a much smaller variance than the towards values.

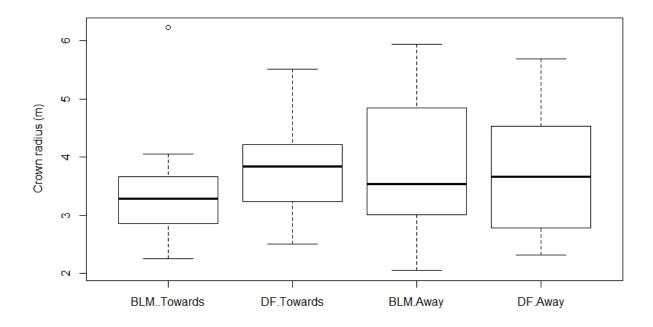
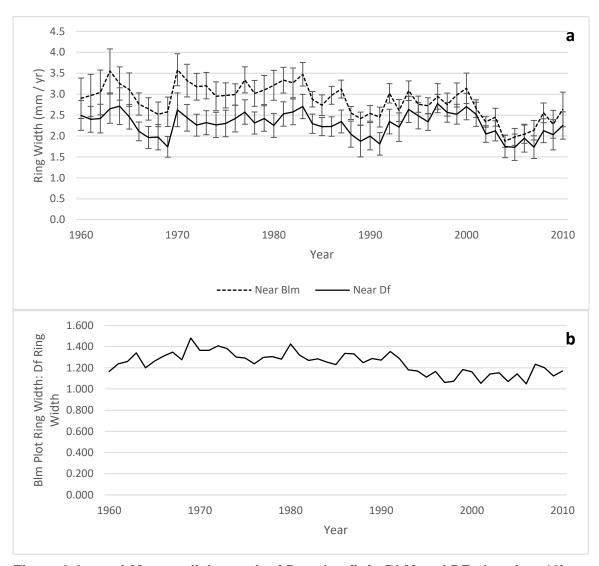


Figure 3.5. Crown radius of western hemlock in BLM and DF centered plots. Also differentiated by whether facing towards or away from the plot's center tree, (n = 9). There is no visible difference in these values but the towards values seem to have less variance than the away values.

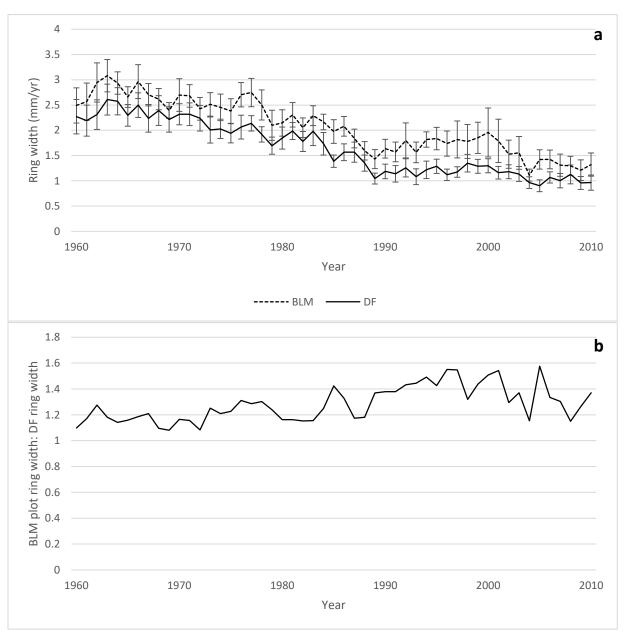
3.2. Site Chronologies

In the fifty-year time period between 1960 and 2010, Douglas-fir growing in BLM plots had more radial growth than Douglas-fir in DF plots (p < 0.01, Figure 3.6). Even when controlled for age and size, a significant difference was observed when the difference chronology for detrended radial growth for 1960-2010 was tested against a normal distribution with a mean of zero (p < 0.01). The higher radial increments for Douglas-fir in BLM plots resulted in a higher accumulation of basal area in the period from 1960-2010 (Table 3.8). There was a significant difference between the difference chronology for BAI for 1960-2010 and a normal distribution with a mean of zero (p < 0.01). For Douglas-fir, BLM decadal BAIs were greater than DF decadal BAIs only in the 1970s and 1980s [1960-1969 (p = 0.38), 1970-1979 (p = 0.06), 1980-1989 (p = 0.03), 1990-1999 (p = 0.32), and 2000-2009 (p = 0.27) (Figure 3.10)]. There was no clear difference in the cumulative BA for Douglas-fir in BLM and DF plots (Figure 3.12). The DBH of Douglas-fir in 1960 was not significantly different between BLM and DF plots (Table 3.6).

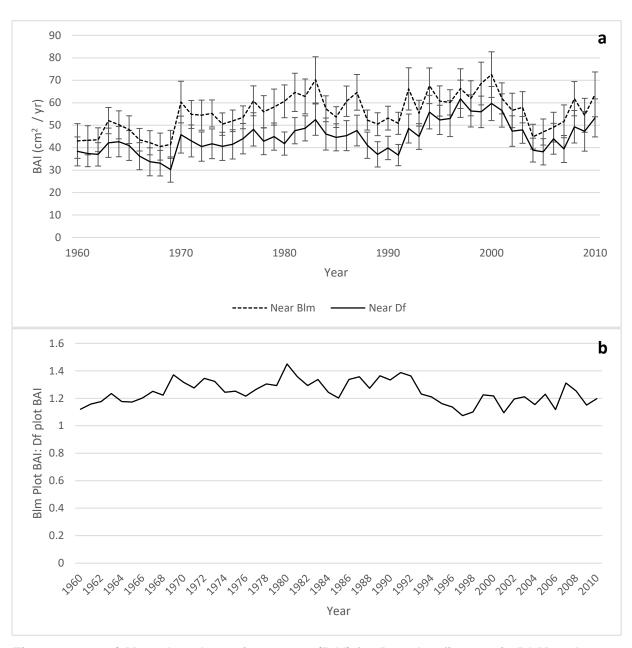
For the 1960-2010 time period, the growth rates of western hemlock in BLM plots were also higher than in DF plots. The radial growth rates were higher in every year for BLM plots (Figure 3.7). A significant difference existed when the difference chronology for detrended radial growth for 1960-2010 in western hemlocks was tested against a normal distribution with a mean of zero (p < 0.01). The higher radial increments for western hemlock in BLM plots resulted in a higher accumulation of basal area in the period from 1960-2010 (Table 3.7). There was a significant difference for BAI for the years 1960-2010 and a normal distribution with a mean of zero (p < 0.01, Figure 3.9). For western hemlock BLM decadal BAIs were significantly greater than DF decadal BAIs only in the last two decades: [1960-1969 (p = 0.25), 1970-1970 (p = 0.20), 1980-1989 (p = 0.13), 1990-1999(p = 0.03), and 2000-2009 (p = 0.07) (Figure 3.11)]. The significance of the difference increased with each decade. The cumulative BA of the western hemlock plots was very similar between BLM and DF plots in 1960 but the higher BAI of hemlock in BLM plots meant the cumulative BA diverged quickly and the difference continued to increase (Figure 3.13). The DBH of western hemlocks in 1960 was not significantly different between BLM and DF plots (Table 3.7).



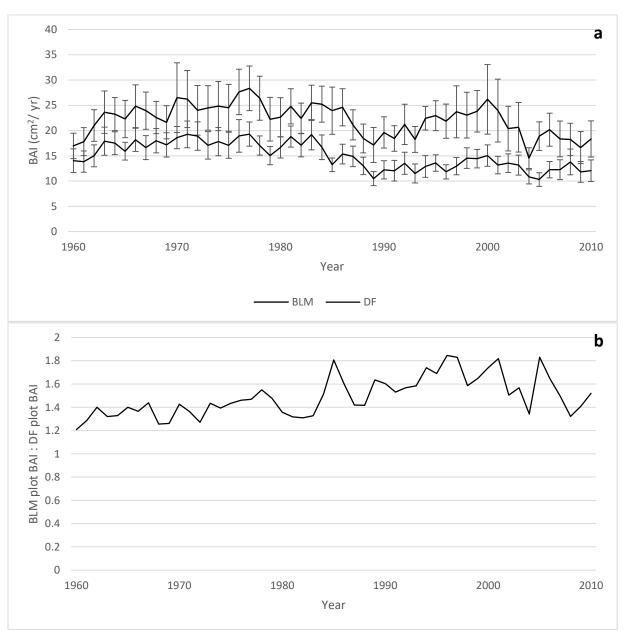
a) Mean radial growth of Douglas-fir in BLM and DF plots (n = 10) and b) the ratio of Douglas-fir radial growth in BLM plots to the radial growth in DF plots. The BLM values appear to be higher than the DF values though that trend becomes less clear after the year 1990.



a) Mean radial growth of western hemlock in BLM and DF plots (n = 9) and b) the ratio of western hemlock radial growth in BLM plots to the radial growth in DF plots. The BLM radial growth values are noticeably higher than the DF values for the whole series.



a) Mean basal area increment (BAI) for Douglas-fir trees in BLM and DF plots between 1960 and 2010 (n = 10). b) The ratio between the mean BAI for Douglas-fir trees in BLM and DF plots. The BLM values are higher overall than the DF values, but this trend is most clear between 1980 and 1990.



a) Mean basal area increment (BAI) for western hemlock trees in bigleaf maple (BLM) and conifer (DF) centered plots between 1960 and 2010 (n = 9). b) The ratio between the mean BAI for western hemlocks in BLM and DF plots. The BLM BAI values are clearly much higher than the DF values.

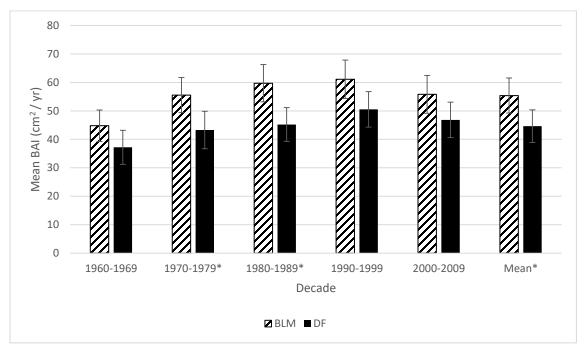


Figure 3.10. a) Mean annual BAI for Douglas-fir in the last 5 decades (n = 10). BLM plots had overall higher mean BAI and this was most clear in the two decades between the years 1980 and 2000.

* Indicates difference between BLM and DF where p < 0.1.

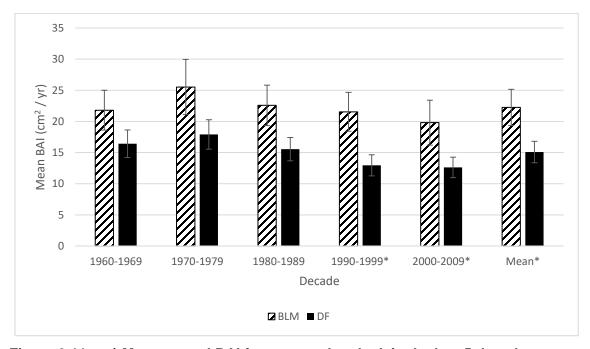


Figure 3.11. a) Mean annual BAI for western hemlock in the last 5 decades (n = 9). BLM plots had consistently higher mean BAI in all decades.

* Indicates difference between BLM and DF where p < 0.1.

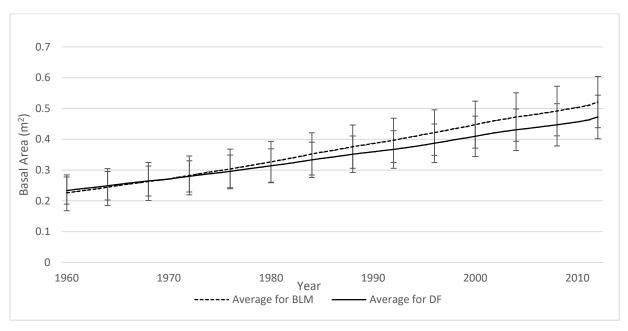


Figure 3.12. Mean cumulative basal area for Douglas-fir trees in BLM and DF plots (n = 10). The variance within the values makes it unclear whether the BLM values are actually higher than the DF values.

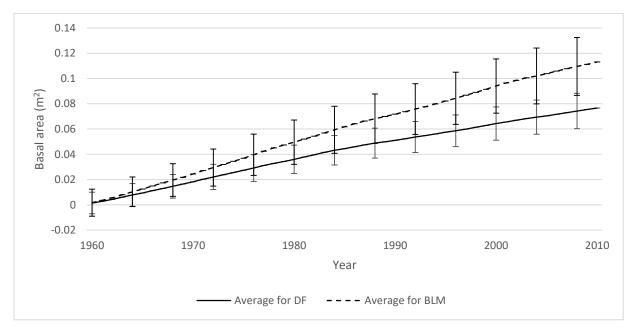


Figure 3.13. Mean cumulative basal area for western hemlock trees in BLM and DF plots (n = 9). There is a high standard error but the BLM plot values are higher and continue to increase faster than the DF values

Table 3.6 DBH and BAI of Douglas-fir in BLM and DF centered plots that are adjacent to the plot center trees (n = 10).

	BLM	DF	BLM:DF p-value
DBH in 2011 (cm)	80.6 ± 18.7	74.3 ± 19.6	1.08 0.28*
DBH in 1960 (cm)	28.2 ± 12.3	29.1 ± 11.2	0.97 0.80
Tree BAI 1960-2010 (m ²)	0.28 ±0.10	0.23 ± 0.09	1.24 0.12

^{*} used Wilcoxon signed-rank test

Table 3.7 DBH and BAI of western hemlock in BLM and DF centered plots that are adjacent to the plot center trees (n = 9).

	BLM	DF	BLM:DF	p-values
DBH in 2011 (cm)	43.0 ± 9.2	36.5 ± 7.1	1.18	0.07*
DBH in 1960 (cm)	13.1 ± 4.6	11.4 ± 3.5	1.14	0.36
Tree BAI 1960-2010 (m ²)	0.11 ± 0.04	0.07 ± 0.03	1.47	0.03

^{*} used Wilcoxon signed-rank test

3.3. Site Index, Competition Index, Basal Area and Tree Density

The mean site indices for Douglas-fir and for western hemlock were not significantly different between BLM and DF plots, however there was a weak trend of greater WAPA competition index for Douglas-fir (p = 0.17) and western hemlock (p = 0.24) in BLM as compared to DF plots (Table 3.8).

Table 3.8 Site index and WAPA values derived from paired plots of Douglas-fir and western hemlock (n = 10 for Douglas-fir and n = 9 for western hemlock)

	BLM	DF	BLM:DF	p-values
Douglas-fir site index (m)	36.6 ± 7.8	36.0 ± 8.5	1.02	0.72
Douglas-fir WAPA (m²)	91.1 ± 68.6	49.1 ± 25.4	1.85	0.17
Western hemlock site index (m)	26.1 ± 6.6	24.6 ± 7.8	1.06	0.63
Western hemlock WAPA (m²)	21.7 ± 11.9	15.4 ± 5.9	1.82	0.24

The mean site BA and the current BA productivity were not significantly different for Douglas-fir or western hemlock between BLM and DF plots (Table 3.9).

Table 3.9 Summary of the mean site BA and BA productivity (1960-2010) for Douglas-fir and western hemlock in conifer and bigleaf maple centered plots (n = 10 for Douglas-fir and n = 9 for western hemlock)

Basal Parameter	BLM plots	DF plots	Ratio of BLM:DF	P-value
Douglas-fir site BA (m² ha-1)	86.6 ± 49.0	102.8 ± 42.4	0.84	0.52
Douglas-fir BA productivity 1960- 2010 (m² ha-1 yr-1)	0.96 ± 0.57	1.0 ± 0.4	0.92	0.78
Western hemlock site BA (m² ha-1)	88.6 ± 45.9	75.4 ± 16.2	1.2	0.35
Western hemlock BA productivity 1960-2010 (m² ha-1 yr-1)	1.2 ± 0.6	1.0 ± 0.3	1.4	0.30

There were no significant differences in total BA, conifer-only BA and total wood in BLM and DF plots (Table 3.10). Tree density was not significantly different between BLM and DF plots, though there was a weak trend of greater density in DF plots (p=0.2). Conifer-only tree density was significantly different between plots with DF plots having significantly higher tree density than BLM plots.

The species contribution to BA in each plot was quite variable (Table 3.11). Douglas-fir had a greater contribution to BA values in the plots in stand B than the plots in stand A, whereas, western hemlock had a greater contribution in plots in stand A.

Table 3.10 Total BA, mean wood volume, and tree density for all trees within 10m fixed-radius plots (n = 12).

	BLM plots	DF plots	Ratio of BLM:DF	p-value
Mean total BA in 10m radial plots fixed on center tree (m² ha-1)	88.6 ± 36.8	84.1 ± 26.5	1.05	0.67
Mean conifer-only BA in 10m radial plots fixed on center tree (m ² ha ⁻¹)	72.8 ± 38.8	84.1 ± 26.5	0.86	0.38
Mean volume of wood (m ³ ha ⁻¹)	1349 ± 803	1293 ± 458	1.04	0.82
Mean volume of conifer-only wood (m ³ ha ⁻¹)	1166 ± 837	1293 ± 458	0.90	0.66
Tree density of all trees (stems ha-1)	409 ± 121	491 ± 149	0.83	0.21*
Conifer-only tree density (stems ha-1)	361± 123	491 ± 149	0.73	0.03*

Table 3.11. Basal area by species centered on and including each center tree based upon circular 10 m fixed radial plots.

Plot	Total Plot BA (m²/ha)	bigleaf maple BA (m²/ha)	Douglas-fir BA (m²/ha)	western redcedar BA (m²/ha)	western hemlock BA (m²/ha)
A1BLM	88	10.1	0.0	18.6	59.3
A1DF	65	0.0	6.3	27.8	31.1
A2BLM	48	4.2	0.0	0.0	43.7
A2DF	71	0.0	28.4	26.0	16.8
A3BLM	45	8.1	0.0	0.0	36.7
A3DF	51	0.0	14.2	13.0	23.7
A4BLM	46	2.4	0.4	9.7	33.9
A4DF	67	0.0	22.2	1.3	44.1
B1BLM	84	39.2	37.4	7.1	0.4
B1DF	134	0.0	110.0	18.6	5.7
B2BLM	89	6.3	71.1	7.6	4.0
B2DF	83	0.0	71.1	6.6	5.2
B3BLM	132	7.1	117.9	7.4	0.0
B3DF	62	0.0	29.4	23.5	9.0
B4BLM	66	11.2	40.4	14.2	0.2
B4DF	88	0.0	77.5	7.7	3.3
B5BLM	116	10.1	97.7	7.3	1.4
B5DF	64	0.0	46.9	5.7	11.1
B6BLM	80	32.6	0.0	47.8	0.0
B6DF	90	0.0	75.7	4.2	10.3
B7BLM	167	15.0	126.4	2.6	22.7
B7DF	127	0.0	99.6	21.9	5.8
B8BLM	101	54.8	14.4	25.6	6.2
B8DF	106	0.0	89.0	2.4	14.8

There was no significant difference in snag basal area between BLM and DF plots (Figure 3.14). The plots in stand A did have a noticeably higher number of snags than the plots in stand B that have older trees.

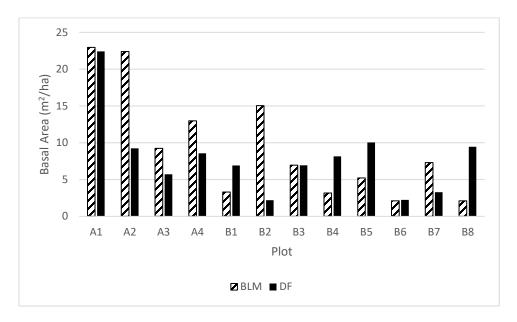


Figure 3.14. Snag basal area within a 10 m radius of plot centers

For Douglas-fir, DBH was strongly correlated with crown volume, BAI and WAPA (Table 3.12). WAPA and BAI also showed a correlation with each other. Tree DBH had a very strong relationship with BAI and also a fairly strong correlation with crown volume for the western hemlock trees studied (Table 3.13). BAI and crown volume also showed a correlation with each other. WAPA and bigleaf maple canopy area did not show a significant correlation with any other variable.

Table 3.12 Pearson correlation values of variables for Douglas-fir trees growing adjacent to plot center trees. Variables include: crown volume (CV), DBH, mean total basal area increment for 1960-2010 (BAI), WAPA, and maple canopy area. Values in parentheses are p-values adjusted using the Bonferroni method for multiple comparisons (n = 49).

	DBH	CV	BAI	WAPA
CV	0.62 (<0.01)			
BAI	0.63 (<0.01)	0.33 (0.15)		
WAPA	0.61 (<0.01)	0.27 (0.47)	0.54 (<0.01)	
Bigleaf Maple Canopy Area	0.86 (1.0)	0.76 (1.0)	-0.09 (1.0)	0.07 (1.0)

Table 3.13 Pearson correlation values of variables for western hemlock trees growing adjacent to plot center trees. Variables include: crown volume (CV), DBH, mean total basal area increment for 1960-2010 (BAI), WAPA, and maple canopy area. Values in parentheses are p-values adjusted using the Bonferroni method for multiple comparisons (n = 44).

	DBH	CV	BAI	WAPA
CV	0.59 (<0.01)			
BAI	0.96 (<0.01)	0.52 (<0.01)		
WAPA	0.18 (1.0)	0.02 (1.0)	0.19 (1.0)	
Bigleaf Maple Canopy Area	0.28 (1.0)	0.27 (0.79)	0.30 (0.34)	0.01 (0.69)

3.4. Individual-tree radial growth models

In the growth models developed for Douglas-fir the influence of bigleaf maple was generally negative. In the first model the canopy area was negatively correlated with BAI but that influence was not significant. This variable was retained because a larger AIC and Adj. R² were observed when this variable was included in the model. In the binary model the influence of bigleaf maple on BAI was significantly negative. Therefore, across these models bigleaf maple showed a generally negative influence on the BAI of Douglas-fir. The models for Douglas-fir point to multiple variables being related to cumulative BAI for the last 50 years. DBH and WAPA displayed positive correlation with BAI in all three models (Table 3.14).

For the models that were developed for western hemlock, the presence of bigleaf maple was only significant in the binary model of maple presence and the relationship observed was a positive one (Table 3.15). None of the other models demonstrated that the amount of bigleaf maple canopy area was significantly related to hemlock BAI. The model demonstrated a very high ability of DBH to predict the BAI of the trees studied. The WAPA variable had no significant influence on any of the models for western hemlock.

Table 3.14. Regression models of Douglas-fir BAI derived from a backward stepwise procedure using the variables BAI from 1960-2010, DBH, WAPA, and bigleaf maple crown area (BLM). The binary model uses a binary variable for the presence or absence of maple in the plot (BLM0) instead of BLM (n = 49 for the first two models and 24 for the model of only maple plots).

Standard model	Sqrt(BAI) = 0.24 + 0.003 DBH* + 0.0005 WAPA*- 0.00009 BLM	Adj $R^2 = 0.45$, $p < 0.001$
Model of binary maple presence	Sqrt(BAI) = 0.25 + 0.003 DBH* + 0.0007 WAPA*- 0.067 BLM0*	Adj $R^2 = 0.47$, $p < 0.001$
Model of only BLM plots	Sqrt(BAI) = 0.24 + 0.002 DBH + 0.001 WAPA*	Adj $R^2 = 0.51$, $p < 0.001$

^{: *} represent variables with p values of 0.05 or less.

Table 3.15. Regression models of western hemlock BAI derived from a backward stepwise procedure using the variables BAI from 1960-2010, DBH, WAPA, bigleaf maple crown area (BLM). The binary model uses a binary variable of the presence or absence of maple in the plot (BLM0) instead of BLM. (n = 44 for the first two models and 20 for the model of only maple plots).

Standard model	BAI = -0.06 + 0.004 DBH*	Adj R ² = 0.93, p < 0.001
Model of binary maple presence	BAI = -0.08 + 0.004 DBH* + 0.009 BLM0 *	Adj $R^2 = 0.93$, $p < 0.001$
Model of only BLM plots	BAI = -0.08 + 0.004 DBH*	Adj $R^2 = 0.97$, $p < 0.001$

^{*} represent variables with p values of 0.05 or less.

Chapter 4. Discussion

The discussion is organized in terms of the hypotheses that I proposed in the introduction. I will use the results that were presented to decide whether each hypothesis is supported or rejected and try to determine what factors may be responsible for unforeseen results.

I hypothesised that the presence of bigleaf maple would have a positive influence on the growth rates of adjacent Douglas-fir. My results showed that Douglas-fir trees growing next to bigleaf maple had higher growth rates than those that were only surrounded by conifers, as indicated by greater radial growth and BAI for Douglas-fir adjacent to bigleaf maple in the fifty-year period from 1960 to 2010. There is evidence that the BAI was higher for Douglas-fir in BLM plots. The difference chronology of BAI between BLM and DF plots was tested to be significantly different from a normal distribution with the same mean and standard deviation. The paired t-test result for the total BAI for this period found BLM plots had nearly significantly higher values. From this result it would be expected that Douglas fir would be larger in terms of BA and DBH than in BLM plots, however this was not the case. Douglas-fir in BLM plots did not have significantly higher BA or DBH than in DF plots. This may be partially explained by a weak trend towards DBHs of Douglas-fir in 1960 being smaller in BLM plots than in DF plots. This could be a result of the reduced growth rate of Douglas-fir near bigleaf maple in the conifer's establishment and early growth as observed by Knowe (1995). The initial reduction in growth might have left space for the Douglas-fir to expand into in the later years of growth as indicated by the higher BAIs in DF plots between 1960 and 2010. In the models that were developed for Douglas-fir BAI, the coefficients for both the presence of bigleaf maple and the amount of bigleaf maple in overall stands were negative, which suggested a possible negative correlation with the presence of bigleaf maple.

Whether these differences in the growth rate of Douglas-fir between BLM and DF plots are due to the effect of bigleaf maple on soil properties, to reduced competitive pressure, or a combination of both is not clear. A possible explanation for higher growth rates for Douglas-fir near bigleaf maple is that bigleaf maple may improve soil fertility in its vicinity. Turk et al. (2008) showed that bigleaf maple trees can have a noticeably

positive impact on soil properties. However if this were the main driving force of the difference in basal area growth, it would be expected that the bigleaf maple coefficient in the models developed would be positive.

The explanation for the conflicting results of a higher growth rate for Douglas-fir near bigleaf maple but a negative coefficient for maple presence in the regression models, may lie in the competition index values. Within these models, the WAPA index values were also incorporated and proved to be a positive predictor of BAI. The WAPA variable represents the competitive dominance, due to size, of the tree in the model in relation to its neighboring trees. The smaller DBH of bigleaf maple in relation to Douglas-fir is likely to be a factor that led to the observed higher radial and BAI growth rates of Douglas-fir in BLM plots. Even though the coefficients representing bigleaf maple variables in the models were negative, the coefficients for the WAPA variables were consistently positive for Douglas-fir.

The higher growth rates for Douglas-fir near bigleaf maple may be due to reduced competitive pressure related to the presence of bigleaf maple. This possibility is further supported by the findings that bigleaf maple was found to be significantly shorter than Douglas-fir in the study plots and the crown radius of Douglas-fir adjacent to bigleaf maple was found to be greater than for Douglas-fir adjacent to other conifers. This suggests that the space located above a bigleaf maple could be potential growing space that could be used by a Douglas-fir for crown expansion, thus improving the growth rate of the Douglas-fir adjacent to a bigleaf maple. The larger canopy radius that was observed for Douglas-fir in BLM plots is evidence that the Douglas-fir are using this space to generate more branch growth and expand their photosynthetic capacity. The higher BAI increment that is being observed in BLM plots may be partially a result of the smaller stature of the bigleaf maple trees, and the reduced competitive pressure for Douglas-fir, not the result of other species-specific factors.

Another reason Douglas-fir may have had larger radial growth adjacent to bigleaf maple is trees with low to moderate shade-tolerance tend to take advantage of available light, such as canopy gaps, more prominently than tolerant ones (Muth and Bazzaz 2002). Both bigleaf maple and Douglas-fir are less shade tolerant than the other conifers in the

stand, so it would be these two species that would be able to take advantage of canopy gaps and outcompete western hemlock and western redcedar for that space.

The higher growth rates experienced by Douglas-fir growing next to bigleaf maple thus are likely a result of niche complementarity rather than a facilitative relationship. An increase in growth due to niche complementarity would be similar to what Douglas-fir experiences when it grows in conjunction with western hemlock through the process of crown stratification (Wierman and Oliver 1979). Bigleaf maple is significantly shorter than Douglas-fir in these stands and thus is able to reduce the competitive effect on Douglas-fir. The stratification of tree crowns in stands that include both bigleaf maple and Douglas-fir occurs only after Douglas-fir is able to overtop the bigleaf maple. Before this occurs bigleaf maple has a more competitive relationship with Douglas-fir and reduces the conifer's growth (Knowe 1995).

Simard et al. (2006) found a similar change in the relationship with Sitka alder (*Alnus viridis* var. *sinuata*) and lodgepole pine (*Pinus contorta* var. *latifolia*) as the stand developed. The removal of Sitka alder significantly increased the growth of the pine at its early stages but it also had a negative impact on the long-term productivity of the stand. The pine and alder in this relationship are both relatively shade intolerant species that are in a slightly competitive relationship in the early stages of stand development. Once the pine is able to overtop the alder it is free from the shading caused by the alder, but the alder is also able to subsist in the understory and provide increased levels of nitrogen mineralization. Both the results of my study and the example of the relationship between alder and pine, support the proposal by Cavard et al. (2011) that relationships within a stand of trees can change throughout stand development from being competitive to beneficial. In the case of bigleaf maple and Douglas-fir it appears that the relationship does shift away from bigleaf maple having a significantly negative relationship on Douglas-fir seedlings, to the mature Douglas-firs having a neutral to positive relationship, in the higher basal area increment of Douglas-fir around bigleaf maple.

The hemlocks growing in BLM plots had significantly higher growth rates than their paired partners in the DF plots as measured by greater radial growth and BAI. The difference in the growth rates also seems to be staying the same or increasing as

supported by the increasing divergence between the cumulative basal area increment in Figure 3.13 and the fact that the difference in decadal BAI is stronger in the last two decades. The higher growth rates of western hemlock were large enough to significantly increase the DBH of those trees growing next to bigleaf maple as compared to those near only conifers even though there was no significant difference in the age of the trees. It is highly likely that the difference in western hemlock DBH between the plots, with and without bigleaf maple, will continue to increase because larger trees do continue to grow faster, due to an overall increasing leaf area (Stephenson et al. 2014).

Possible reasons for higher growth rates for hemlocks adjacent to bigleaf maple include reduced competition for trees near bigleaf maple and improved soil fertility near bigleaf maple. Reduced competition for hemlocks growing adjacent to bigleaf maple as compared to those growing adjacent to other conifers might be expected since bigleaf maple is generally shorter than Douglas-firs and thus may result in the hemlocks experiencing less competition for light. However, I did not find evidence that reduced competition near bigleaf maple was a reason for the higher levels of radial growth in hemlocks. The competition index was not a significant variable in any of the individualtree radial growth models. However, the competition index was based on tree DBH, so it did not necessarily take into consideration competition for light. The lack of competitor influence on western hemlock could be explained by its shade tolerance (Harrington 2006) resulting in the shading effect of larger competitors having less influence on it. This idea is supported by a study in which fast-growing paper birch (Betula papyrifera Marsh.) and red alder (Alnus rubra Bong.) had no significant effect on the growth of western hemlock when they were grown together at different densities (Cortini and Comeau 2008). In that study, no correlation was found between western hemlock growth and the competition measures that were tested.

It is possible that the increases in the growth of western hemlock adjacent to bigleaf maple may be due to the influence of bigleaf maple on soil properties. Turk et al. (2008) carried out a study in the same area as my study and found that plots that contained bigleaf maple, as compared to those with conifers only, had significantly higher pH, NO₃-N concentrations and contents and mineralizable N contents as well as significantly higher cation exchange capacity and concentrations of N (total, mineralizable and NO₃-N) and

exchangeable K, Ca and Mg in the mineral soil. Thus, the increased growth of hemlock growing adjacent to bigleaf maple, may be partially due to greater availability of nutrients, such as N, K, Ca and Mg, in the vicinity of bigleaf maple.

The existing literature does not make a clear relationship between the effects of fertilization with a positive growth response in western hemlock, but this could be related to the focus on single nutrient fertilization trials. The majority of studies have only used urea as a fertilizer and could be misinterpreting other nutrient deficiencies as a lack of growth response to fertilization (Gill 1981, Brown 2003). Furthermore, urea fertilization in coastal sites can increase the concentration of N in western hemlock foliage, but reduce the concentration of P, Ca, Mg, Mn, Fe, Al, and B (Gill and Lavender 1983). The authors suggest that the reduced uptake of nutrients caused by urea fertilization, as demonstrated by lower foliar nutrient concentrations, can exacerbate existing nutrient deficiencies that are unrelated to N. The addition of S and P in conjunction with N fertilization found that P deficiency was the cause of a lack of growth response to N fertilization in western hemlock on some sites (Radwan and Shumway 1983). Fertilization of western hemlock with both N and P on Vancouver Island also led to dramatic increases in western hemlock growth, whereas western redcedar experienced similar growth increases with N alone (Blevins et al. 2006).

Western hemlock growing next to bigleaf maple receives an increase in nutrients that is more balanced than direct urea fertilization and the stand structure in BLM plots may influence the effects of nutrient additions. It is possible that the mixed results of ureafertilized western hemlock would be more positive if a more complete fertilizer was used that included a mixture of plant micro and macronutrients (Brown 2003). I am suggesting that the increase in soil concentrations of N, K, Ca, Mg as well as overall increases CEC and pH found near bigleaf maple could address a greater range of nutrient deficiencies in western hemlock than urea could. The increased growth of western hemlock rates that I observed may be a result of the increase in multiple nutrients facilitated by the proximate bigleaf maple. It is also important to note that western hemlock has been shown to respond more positively to fertilization treatments when they are applied in conjunction with thinning treatments (Omule and Britton 1991). The decreased density of trees in BLM

stands would also likely enhance the positive effects of more nutrient rich soil properties in the BLM plots.

An additional explanation for increased growth of hemlock near bigleaf maple, is that bigleaf maple may decrease Al availability. Ryan et al. (1986) observed reduced growth and mortality of western hemlock grown in a nutrient solution with 175 ppm Al as compared to a nutrient solution without Al. A high enough concentration of soil Al appeared to decrease western hemlock growth. Turk et al. (2008) found significantly higher Al concentrations of 251 ppm in forest floor of conifer only plots compared to 109 ppm in bigleaf maple plots. The Al concentration found in this conifer forest floor is high enough to be detrimental to western hemlock growth, while the Al concentration of the bigleaf maple forest floor is significantly lower. High Al concentrations can have many negative impacts on plant health including: a reduced uptake of Ca and other divalent cations, dysfunction of cell division in the root meristem leading to abnormal root morphology, and decreased anion adsorption by roots due to increased position on adsorption sites (Foy 1974). The Al concentrations in conifer plots in this study may thus be high enough to have a negative effect on growth rates of western hemlock, and this may at least partly explain the higher growth rates near bigleaf maple.

The inputs of foliage of certain tree species can have a facilitative relationship on surrounding plants by creating fertilizer-like effects. The foliage of bigleaf maple has significantly higher concentrations of Ca than both western hemlock and Douglas-fir (Cross and Perakis 2011). Western red cedar is the only tree species that has comparable concentrations of foliar Ca to bigleaf maple in the same environment (Cross and Perakis 2011). It is possible that the higher Ca concentration in bigleaf maple's foliage is responsible for providing a source of Ca that is more easily available for hemlock uptake and at the same time decreases the reduction in divalent cations observed in soils with high Al concentrations.

An experiment that tested the addition of lime on western hemlock growth response found that a moderate application of lime did not have significant impact on western hemlock growth but a high application decreased growth (Heilman and Ekuan 1972). In the high application treatment the pH of the soil had been raised from 5.1 to 7.2.

The addition of lime also resulted in increased levels of N, Ca, and reduced Mn and Al in tree foliage. Typical mineral soils under bigleaf maple are around a pH of 4.9 (Turk et al. 2008). The pH of the soil in the high application of lime in this study is much higher than what would be found in mineral soils under bigleaf maple and in general coniferous forests in this geographic area. The high application of lime is likely creating conditions for tree growth that are far too high to be beneficial to western hemlock growth. The more moderate fertilizer-like effect of bigleaf may help explain the increased radial growth rates of western hemlock that I observed.

My third hypothesis postulated that a stand of only conifers has less standing wood biomass than one which also includes bigleaf maple. I observed no significant difference in basal area or wood volume of plots which included bigleaf maple compared to plots that did not include bigleaf maple. There was also no significant difference in the conifer-only basal area or wood volume between plots that included bigleaf maple and those that did not. Bigleaf maple did not make up the majority of the basal area of my plots but it did have a substantial contribution. The average percentage of basal area that was derived from bigleaf maple in our bigleaf maple plots was 19.3% (Table 3.11). When only conifer basal area and wood volume are considered, the subtraction of the bigleaf maple component, which has a mean of 13.6%, would not be substantial. Wood volume measured in my study falls within the range of standing tree volume observed in a 60-100 year old western hemlock forest in Oregon (700 to 1350 m³ ha⁻¹);(Acker et al. 1998). The older age of my stands could explain why my values are on the high end of the range of those observed in Oregon. The subtraction of the bigleaf maple component may be somewhat compensated by the faster growth that I observed in western hemlocks and Douglas-fir in BLM plots, as compared to DF plots.

Some limitations of my study influence how representative the results are to a larger area. One limitation is that the plot size I used was relatively small and thus did not include gaps. Thus the measured standing volume may be higher than the actual standing volume. One reason for this is that canopy gaps were left out of the study and would generally reduce the overall standing volume. This could possibly have been avoided if a more random sampling strategy had been employed. However, the number of potential sample plots was quite limited, as one of the criteria was to avoid other deciduous species.

It was challenging to find plots with bigleaf maple and no other deciduous species. The lack of plots that fit my requirements also led to a small sample size. Due to the small sample size, the trends we are observing are likely less clear than if a larger sample size were used. Another limitation of my study is that the plots were located in a small geographic area relative to the distribution of bigleaf maple. It is likely that the results from this study pertain to similar conditions as those of the study area, but not the entire region where bigleaf maple occurs together with Douglas-fir and western hemlock. A further limitation is that the ages of trees were only measured at breast height. The age it takes trees to grow to breast height age is not taken into consideration in this study, but it is recognized. Age to breast height can vary widely depending on the tree species and the level of competition from other vegetation (Stewart 1984).

Overall wood production over time in a stand can be greatly reduced by tree mortality. The increase of tree growth with old age of trees does not apply at the stand level mostly due to mortality of individual trees (Stephenson et al. 2014). However, I did not observe any difference in tree mortality, represented by the incidence of snags in the 10 m fixed radius plots. It is therefore unlikely that mortality played a key role in the results I observed and that the increasing growth rates are associated with tree age and size. The lack of a difference in mortality does not mean that a more diverse stand that includes bigleaf maple may not reduce the incidence of damage and mortality from pests and disease as proposed by Jactel and Brockerhoff (2007). In this study's design I specifically looked for live trees that showed no incidence of major defects or disease and it is likely that nearby trees in the same stands were not affected by significant disease and insect damage. By looking for trees that appeared to be free of major defects I attempted to remove the impact of pest and disease damage from this study. The lack of a difference in tree mortality between BLM and DF plots validates that mortality was not responsible for a significant loss in stand wood production within this study.

Lastly, my results do not support the fourth hypothesis, which proposed that site index for Douglas-fir and western hemlock will be higher in plots containing bigleaf maple due to bigleaf maple's effect on creating more nutrient rich site conditions. I did not find any significant difference in site index values for Douglas-fir or western hemlock between BLM and DF sites. The lack of differences in site index suggest that the presence of

bigleaf maple may not have significantly increased site quality. The site indices were within the normal observable levels found for each tree species within this location (*Site Index Estimates By Site Series: Report by Region* 2013).

Of interest is the question as to why I might have observed higher radial growth rates and BAI in BLM plots but not higher height growth or site index values. Site index is predominantly used as an indicator of site quality in even aged stands (Skovsgaard and Vanclay 2008). The broad distribution of tree ages in the plots of this study means that site index might not be the best indicator of site quality to use. It was used because it is still the most convenient method and the best available means of looking at the site's productivity without logging and observing the growth of replanted tree stock.

Site index relies on the assumption that tree height is independent of stand density which is not always the case. There are several instances of stand density impacting height growth reported in the literature (Curtis and Reukema 1970, Mishra and Gupta 1993). The impact can be so large, that significantly different values in stand productivity can be observed in stands that are located on the same site but with different densities (MacFarlane et al. 2000). In Douglas-fir plantations thinning of denser stands can also, in the long term, increase the height growth of trees (Harrington and Reukema 1983). These examples demonstrate that the assumptions underlying site index as a tool are not foolproof and caution must be taken when using site index as an indicator of site quality.

Tree height is also an imprecise measurement to use with the methods I employed, especially with the large height of the trees in my stands. In this case the error in my measurements could be masking the actual difference in tree height between plots. My tree height measurements were directly used to determine site index, and so the site index measurements might also be imprecise.

Though not significant, there was a weak trend for BLM plots to have a lower stem density than DF plots (p=0.21). This difference in density is also represented in the WAPA index of both Douglas-fir and hemlock plots with a trend for more available space per tree in the BLM plots (p=0.17 and 0.24 respectively for BLM and DF plots). The presence of bigleaf maple in conifer stands may be important in creating more open, lower stem density, stands. Competition from resprouting broadleaf species following fire has been

suggested to add to competition that could lead to thinning of highly dense stands (Donato et al. 2009). Though often present in young or middle-aged stands, bigleaf maple does not have the same life-span as many of the conifers in these forests and thus may reduce stand density by being a competitor in young or middle-aged stands and subsequently reducing competition in mature stands through its own senescence.

Chapter 5. Conclusions

5.1. Summary of Findings

The study of the interactions of different tree species is important to further understand the dynamics of forests and to better manage them. My research set out to expand the understanding of how mature bigleaf maple affects the growth and morphology of proximate mature conifers that grow in the Pacific temperate rainforests of North America.

The influence of bigleaf maple on Douglas-fir in this study is mixed. Douglas-fir trees growing next to bigleaf maple had significantly greater radial increments in the 50 year period that was observed. The BAI for BLM plots was higher as evidenced by the difference chronology between BLM and DF. There was no significant difference in height between Douglas-fir in BLM and DF plots. Regression models of Douglas-fir BAI suggest that the presence of bigleaf maple may have led to higher growth rates as they were shorter than Douglas-fir and thus less competitive for light. Douglas-firs growing next to bigleaf maple had substantially larger overall crown radius, which is likely attributed to bigleaf maple being significantly shorter than the Douglas-firs that were located at the center of conifer-centered plots. When Douglas-fir grew next to smaller neighbors it was able to create larger canopies and grow faster.

Western hemlock had significantly higher basal area accumulation growing next to bigleaf maple as compared to just conifers. The higher growth rate was enough to significantly change the DBH of these hemlocks, as compared to hemlocks growing only next to other conifers. There was no observable difference in height between western hemlock in BLM and DF plots. It is possible, that more nutrient rich soil conditions around bigleaf maple contributed to western hemlock growing faster in BLM plots than western hemlock in sites that did not contain bigleaf maple.

I did not find evidence of an improvement in stand productivity due to bigleaf maple. Neither of the two conifer species experienced any significant difference in site index when growing next to bigleaf maple. There was no difference in overall site productivity in plots that contained bigleaf maple and those that did not. This is observed by differences occurring in basal area and stand volume for plots that contained bigleaf maple and ones that did not. This held true when both conifers and broadleaf tree productivity metrics were measured, and also when solely conifer tree area and volume were analyzed. One further finding of note is a trend towards stands that contain bigleaf maple having less tree stems per area when all trees are taken into account and this is significantly the case when only conifers are considered.

5.2. Suggestions for Future Research

Further research is needed concerning the role bigleaf maple plays in the development of low-density stands. There is also a need for the exploration of management strategies for bigleaf maple in short-rotation and longer-rotation plantations for bioenergy and fibre production.

More research is needed concerning how biodiversity can be maintained while providing a profitable timber supply in managed forests. This is especially true in early successional stages of stand development as many forests are affected by large-scale disturbance, where silviculture is central to stand regeneration because of obligations legislated by the government. How these types of stands may be spread out in a landscape context and how they can be best integrated into management alongside other uses of the forest is also important.

The impact of bigleaf maple on the growth rates western hemlock seedlings would further clarify the findings of this study. It could help establish whether western hemlock is benefited by the presence of bigleaf maple in the same stand. A confirmation of the negative effect of high Al concentrations on western hemlock conducted within forest plots is required. This may include experiments on the effect of western redcedar trees on growth rates of western hemlock because of high Ca foliar concentrations in cedar. Also, more research on the nutrient deficiencies of western hemlock stands would be helpful in identifying further fertilization trials that go beyond the regular application of N and P.

5.3. Management Implications

Bigleaf maple is a very versatile tree species that is able to establish and maintain itself within early, middle, and late developmental stages of stands (Peterson 1999). It does this by establishing itself aggressively in stands and withstanding many types of disturbance while also being a minimal competitor and even facilitating the growth of species like western hemlock.

With the knowledge gathered in this research, the effect that bigleaf maple has on conifer growth is clearer. It appears that the inclusion of bigleaf maple does not have a negative influence on wood volume in mature conifer stands and it potentially has a positive influence on conifer growth. These results suggest that it would be beneficial to include a component of bigleaf maple in conifer forests within the range that bigleaf maple occurs. The following are some ideas on how to effectively incorporate bigleaf maple into stand management.

1) Retention and integration of bigleaf maple in states and provinces bordering the Pacific Ocean can play a role in creating more biodiverse communities that are more resistant and resilient to disturbance without compromising timber production.

It has been suggested that to be better able to deal with unforeseen perturbations, forests should be managed as complex adaptive systems (Puettmann et al. 2009). One suggested method emphasizes creating stands of diverse density and species makeup within a set ecozone, on a landscape scale, whose average is similar to what currently would be a set density, or species makeup, imposed on each stand within that landscape. It may also be in the economic interest to diversify stands as it is likely to provide a more steady timber supply in the long term (Dymond 2014). Climate change is already creating an environment with more frequent and larger disturbances and this trend will continue into the foreseeable future (IPCC 2014). Models projecting climate change shifts in suitable habitat for bigleaf maple predict an increase of 216% in area and a frequency increase of 97% by 2085 (Hamann and Wang 2006). Bigleaf maple is likely to do well if disturbance frequency increases so it is important that we understand the impact of bigleaf maple on forest stands and learn to integrate it into silvicultural systems. As discussed in chapter 1, bigleaf maple has many roles in maintaining animal biodiversity by providing

food for large ungulates and small rodents, providing shelter for nesting birds and also contributing coarse woody debris to riparian areas (Peterson 1999). Maintenance of its biodiversity values can only be accomplished by maintaining bigleaf maple as a component of stands where it already grows.

A less direct method that can be used to minimize the competitive effects of bigleaf maples on newly planted conifer seedlings without removing the bigleaf maples from developing stands exists. It would be practical to leave bigleaf maple standing but epicormic and basal sprouting occurs from cut trees as well as residual standing bigleaf maples. This is presumably due to damage to the tree's canopy caused by the falling of surrounding trees (Tappeiner 1996). To counteract this action, a successful method is to cut the bigleaf maples a year or two prior to the cutting of the rest of the conifers in the stand, and making the cut low to the ground, so as to minimize the number of stem-based epicormic buds that germinate (Tappeiner 1996). This method minimizes the resprouting of the bigleaf maples by causing the sprouting to occur under the shaded canopy of the existing conifers. The bigleaf maples will likely survive, but planted or naturally regenerating conifers will have a better chance to become established in the stand with lessened competitive effects of resprouting bigleaf maple.

Bigleaf maple can also be managed as concentrated, pure stands that exist within the mosaic of different stand types. There is the possibility of managing clumps for short-rotation fibre production and fuel, or hardwood sawlogs (Harper et al. 2012). This can be especially useful in cases where *Armillaria* root disease is present in an area because bigleaf maple is more resistant to infection than most commercial conifers (Peterson 1999).

The management of bigleaf maple in mixed stands with conifers and as pure stands are both effective ways of keeping bigleaf maple as an integral component of the timber-producing landscape and perpetuating the ways in which it serves as a structural basis for aspects of animal and plant diversity.

2) Bigleaf maple retention could help create a diversification of early seral stands necessary in the development of a diversity of stand types.

Though this may not be the best means of establishing highly stocked forests, recent literature indicates that many of the old growth stands that are still around today developed under lower stand densities (Franklin et al. 2002, Winter et al. 2002, Donato et al. 2012). The cause of lower tree densities include a lack of seed source and competition from subcanopy vegetation, that can supress and stratify tree sapling growth (Donato et al. 2012). Bigleaf maple clump sprouts can have the effect of suppressing and stratifying sapling growth (Knowe 1995) and so can contribute to the process of creating less dense early seral stands. The importance of diverse early seral stands is emphasized by more than half of conservation-listed species in California, Oregon, and Washington being facultative or partial users of early seral stands (Swanson et al. 2014). Old growth stands are key to maintaining resilience in the forest landscape (Norden et al. 2009) and therefore the recreation of these types of stands is in our interest.

Structural components of a stand are key in restoring and preserving old growth characteristics (Freund et al. 2015). Stands that are more productive are able to restore large structural components more quickly (Larson et al. 2008). By creating less dense early seral stands we can help speed up the development of stands of trees with densities seen in the lower density old growth stands that exist in the Pacific Northwest today. By maintaining the competitive effect of bigleaf maple in young stands, less dense stands can develop and lead to faster growing individual trees. Less dense stands can also be established by thinning of younger Douglas-fir stands and underplanting with Douglas-fir and western hemlock seedlings (Chan and Larson 2006). This is a more labour intensive way of speeding up the formation of old-growth characteristics in Douglas-fir forests but it does provide a revenue stream and provides jobs in the process of rehabilitating forest stand structure.

Currently management practices in both the US and BC favours creating dense early seral stands of conifers that have rotation ages shorter than natural disturbance would create (McComb et al. 1993, Burton et al. 1999). In BC, following harvesting, stands are replanted and returned to a "free growing" condition. By definition of the Forest and Range Practices Act a, "free growing stand means a stand of healthy trees of a commercially valuable species, the growth of which is not impeded by competition from plants, shrubs or other trees" (*Forest and Range Practices Act* 2002). This same act

requires each cut stand to be returned to a free growing condition by the tenure holder. The US has similar legislation in the National Forest Management Act of 1976, which pronounces that each federal forest land have targets and strategies to replant logged over landscapes to maintain forest cover (*National Forest Management Act Of 1976* 1976, Freund et al. 2014).

The requirement to establish free to grow stands detracts from creating a diversity of stands within a forest landscape. As Donato (2012) discussed, stands are established at different tree densities which may persist and contribute to structural heterogeneity as the stand ages. The absolute requisite to meet free to grow standards, by planting a certain density of trees, creates a more uniform forest landscape than what would have been seen on the landscape in the past. A free to grow stand of trees is generally uniform in structure and lacks competition from other vegetation. This lack of direct competition as part of free to grow status may be in direct contradiction with the development of stands with diverse structure, which are needed to maintain the habitat for a diversity of species. Adjustments may need to be made to the free to grow requirements of stands so that the historical range of landscape-level diversity of stands is maintained in BC and the rest of the Pacific Northwest.

This study supports bigleaf maple's ability to maintain multiple ecosystem values without detracting from the economic timber values in a forest when it grows in conjunction with Douglas-fir and western hemlock. On a stand level scale the maintenance of complex stand structure that includes deciduous tree species can often be achieved within the setting of a productive commercial forest.

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