EFFECTS OF RED ALDER DENSITY ON GROWTH OF

DOUGLAS-FIR AND WESTERN REDCEDAR

by

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Abstract

Red alder (*Alnus rubra* [Bong.]), is the most common hardwood species along the Pacific Northwest coast and is widely distributed as a component of mixed stands with conifers on highly productive sites. It is also a strong competitor in young conifer stands and rapidly overtops associated juvenile conifers, often making it challenging to meet free-growing obligations under current standards in Southwestern British Columbia (BC). Presently, many forest managers err on the side of caution and expend resources to control red alder to meet free-growing requirements. Due to a lack of scientific data, we are unable to determine whether these expenditures are warranted. The goal of this study was to provide information to assist in improving policies and practices around free-growing relating to alder in coastal conifer stands.

Data from mixed red alder-conifer plantations established by the BC Ministry of Forests in 1992 and 1994 were used to examine: 1) the effects of differing initial densities of red alder (*Alnus rubra* [Bong.]) on the growth of Douglas-fir (*Pseudotsuga menziessi* (Mirb.) Franco) and western redcedar (*Thuja plicata* Donn.), at both individual tree level and plot level; 2) the competitive effects of red alder on conifers, and the effectiveness of various distance dependent and independent competition indices for predicting conifer growth, including both additive and replacement experiment series; and, 3) the influence of light and nitrogen on conifer growth.

Current standards for free-growing in B.C. do not accept alder within 1 m radius of conifers. While one alder within a 1 m radius may be indicative of densities approaching 10,000 alder per hectare, our results suggest that densities of up to 400 alder per hectare may be acceptable and possibly desirable on some sites. The growth of Douglas-fir may be enhanced when red alder density is relatively low during the first 25 years after establishment. We found that the competitive effects of red alder were consistently lower than that of conifers, and Douglas-fir height was largest in the highest density treatment (400 tph) from age 7 to age 15, and same for alder height growth. 200 alder per hectare gave the largest Douglas-fir height and diameter at age 20. As also expected due to western redcedar's greater shade tolerance, it showed less sensitivity to the presence of red alder than Douglas-fir. 100 alder/ha gave the best growth of redcedar. These findings suggest the current free-growing assessment standards may be overestimating red alder competition, that alder density up to 400 stems/ha are not having negative effects on Douglas-fir or western redcedar on mesic sites and the use of larger radius plots should be considered.

Preface

This thesis is an original work by Chengdong Fang. No part of this thesis has been previously published.

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1. Introduction

1.1 Red alder and associated conifers

Red alder (Alnus rubra [Bong.]), the most common hardwood species along the Pacific Northwest coast (Fig. 1.1), is a relatively short-lived deciduous tree species with rapid juvenile growth. It occurs primarily as a lowland species (Coastal Western Hemlock zone) and generally grows within 200 km of the seacoast at elevations below 750 m (Johnson 1968). Red alder grows best on deep alluvial soils and often regenerates on exposed mineral soils with high light levels after burning or harvesting. It can tolerate poor drainage conditions while its growth is limited by low winter temperatures and lack of soil moisture (Deal and Harrington 2006). Rapid height growth of young alder helps it to escape browsing which is typically encountered by conifers (Newton and Cole 1994). Also, it forms a deciduous canopy with high light penetration, which allows more understory vegetation compared to pure conifer stands (Peterson et al. 1996). Red alder has root nodules to fix atmospheric nitrogen into usable forms and in consequences, improves the site fertility (Binkley 1983, Comeau and Sachs 1992). The levels of Ca, Mg, K, and P are also reported to be increased within alder stands (Bormann et al. 1994). Studies showed that red alder improves biodiversity by providing soil nitrogen, habitat, and organic matter for understory plants and wildlife such as songbirds and invertebrates (Hanley et al. 2006, Wipfli et al. 2003 and 2004, Hibbs et al. 1994, McComb 1994).



Fig.1. 1 Native distribution of species for red alder (*Alnus rubra* (Bong.)), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), and western redcedar (*Thuja plicata* Don. ex D. Don) (Modified from Deal et al. 2017).

Red alder is not only ecologically important but also economically important. In recent years, its commercial value has increased substantially and has become the major commercial hardwood tree species in the Pacific Northwest (Deal and Harrington 2006). Red alder has excellent gluing, staining, and finishing properties and it can be used to make furniture, cabinets, veneer, plywood,

and paper (Harrington 1984, Meier 2008). However, there is a lack of available information on red alder growth and yield from managed stands or plantations. On good sites, alder trees can reach 24 m tall by age 20 and achieve mean annual increment of 14 m³/ha volume growth in sawlog rotations of 30 to 32 years (Smith 1968, DeBell et al. 1978). Red alder grows rapidly at young ages but grows considerably slower after age 20 (Harrington 1990). Red alder growth is influenced by initial stand density, site factors (soil, moisture, and nutrients) and management regimes (thinning and vegetation control) (Hibbs et al. 1994, Deal 2006). In particular, stand density appears to have an important effect on stand growth with most rapid growth in stands of moderate to moderately high densities of red alder (Bormann and Gordon 1984, DeBell and Giordano 1994, Knowe and Hibbs 1996).

Red alder is widely distributed both in pure stands and mixed stands with conifers (Harrington et al. 1994). However, it is much more common as a component of mixed stands with conifers in most North Pacific forest cover types (Fig. 1.1, Eyre 1980, Deal and Harrington 2006). The main conifer species associated with red alder in the Pacific Northwest region are Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), Sitka spruce (*Picea sitchensis* [Bong.] Carr), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), grand fir (*Abies grandis* [Dougl. ex Don] Lindl.), and western redcedar (*Thuja plicata* Don. ex D. Don). As conventional timber tree species, conifers have a slower initial growth but greater longevity than red alder (Burns and Honkala 1990). Their presence and survival in mixed stands depends on their shade tolerance, from a medium high (Douglas-fir), high (Sitka spruce, grand fir), to very high (western hemlock, western redcedar) (Puettmann and Hibbs 1996). Differences in species silvics such as growth rate and shade tolerance influence the mixed red alder-conifer stands spatially and temporally. In addition, conifers are less adapted to extended flooding but are more resistant to summer drought

(i.e., Douglas-fir) compared to red alder (Puettmann and Hibbs 1996).

1.2 Why mixed red alder-conifer stands?

Red alder has impressive juvenile growth rates, and the recent increase in alder prices has resulted in increased interest in managing alder. Growing red alder together with conifers may have advantages. Firstly, growing alder with conifers in a plantation can give more options for providing periodic income throughout the different rotations associated with their differential growth rates and maximize wood volume production (Kelty 2006). Secondly, alder can improve site productivity through fixing nitrogen with nitrogen-fixing actinomycetes in root nodules (Frankia spp.). It has been reported that the fixation rates in mixed stands can be $80-125 \text{ kg}^{-1}$. ha⁻¹ · vear⁻¹ (Miller and Murray 1978; Binkley et al. 1994). Studies from nitrogen-deficient mixed alder-Douglas-fir stands have shown significant increases in stand growth with overall wood production nearly double that of adjacent pure Douglas-fir stands with Douglas-fir site index also being increased by an average of 6.4 m (Tarrant 1961, Tarrant and Miller 1963, Miller and Murray 1978). In addition, alder produces more aboveground litterfall than conifers, and the litterfall has high nutrient concentrations and rapid decomposition rates. Roots also have high nitrogen contents and their turnover may be another pathway to improve nutrient cycling and trees. Thus, the improved nutrient cycling would contribute to higher stand productivity including increases in conifer growth. Even if alder will be shaded out and dies off in a mixed stand over the long term, it may make substantial contributions to soil nitrogen and conifer growth (Berg and Doerksen 1975, Tarrant and Miller 1963). Thirdly, alder is resistant to two widespread diseases afflicting conifers in the Pacific Northewest region including laminated root rot (Phellinus weirii) and Swiss needle cast (Nelson et al. 1978, Deal and Harrington 2006). Studies have found that red alder can mitigate pest and pathogen infections of conifer species in the mixed stands (Harrington et al. 1994; McLean 1989, Hibbs and DeBell 1994, McComb 1994). For example, alder may serve as a biological control for laminated root rot and help to mitigate conifer growth losses (Trappe 1972; Harrington et al. 1994). Other potential benefits include enhanced complexity and ecological functions (Piccolo and Wipfli 2002, Deal et al. 2004, Deal 2007) as well as adaptation to climate change through increased forest health and resilience (Cortini et al. 2012).

1.3 Tradeoffs associated with managing alder with conifers

Red alder can also be a strong competitor in young conifer stands due to its rapid juvenile height growth, leading to detrimental effects of alder on light availability for understory conifers when it is present at sufficient densities. An understanding of both the competitive and beneficial effects of red alder in mixture with conifers is fundamental to making sustainable management decisions for complex forests. Stand density determines the utilization of available growing space. Data from 70-year-old mixed wood plantations suggests that the facilitative effects of red alder depend on site conditions, particularly nitrogen availability (Binkley 2003) with beneficial effects being found predominantly on sites where nitrogen deficiencies limits conifer growth. The growth of Douglas-fir or other conifers may be enhanced when red alder density is low (Miller and Murray 1978, Comeau and Sachs 1992, Comeau et al. 1997). However, when red alder densities are maintained at low levels, resulting red alder can have poor wood quality (large knots, lots of branches). Therefore, in these situations alder is only there for ecological and productivity reasons. Comeau and Sachs (1992) suggested that the optimal density for red alder in mixture with 1000 Douglas-fir per hectare should be 100-200 trees per hectare on low-quality

sites and less than 100 trees per hectare on –higher-quality sites. And several studies showed the yield in mixed stands was not higher than in pure stands under such circumstance (Cole and Newton 1986, Newton and Cole 1986). In general, sites with low to moderate moisture limitations (adequate, but somewhat limiting alder growth) and moderate to high nitrogen deficiency appear to be good candidates for alder-conifer mixtures (Peterson et al. 1996).

Shainsky and Radosevich (1992) found that initial size differences and red alder's rapid juvenile growth played a role in determining the competitive hierarchy. Because of alder's ability to grow faster and produce copious leaves, it is able to obtain resources such as light and soil moisture, and thus impact Douglas-fir growth negatively. However, alder's sensitivity to drought contributes to Douglas-fir's competitive ability on moisture-limited sites since Douglas-fir is generally more drought tolerant. In addition, species shade-tolerance characteristics vary within conifer species, which means Douglas-fir will be more affected by competition than western redcedar (Peterson et al. 1996, Harrington 2006).

As mentioned, mixed species stands provide increases in productivity and biodiversity, and improve forest health (Comeau 1996, Chen et al. 2003, Man and Lieffers 1999). However, there is still debate and discussion relating to the desirability of admixing broadleaved species into conifer stands due to the lack of clear information on the outcomes and optimum arrangements (Knoke et al. 2008). For foresters to embrace and adopt mixedwood management, complex processes and interactions (both positive and negative interactions) within mixed stands and their outcomes must be better understood and demonstrated (Grover and Fast 2007).

1.4 Light and nitrogen availability

The success of establishment, subsequent growth and survival of tree seedlings is strongly influenced by light and nitrogen availabilities, which are also key factors involved in the tree interactions and stand development. Light use efficiency, which reflects the ability of plants to translate available light energy (by absorbing radiation energy) into biomass (Monteith 1972, 1977), varies with plant properties and stand conditions. A stratified mixed canopy with a shadeintolerant tree in the upper canopy and a more shade-tolerant tree below is likely to use a greater proportion of available light than a monoculture of shade-intolerant trees since shade-tolerant trees can effectively capture light transmitted to the understory (Kelty 1992). In our study, three tree species in mixed stands vary in their shade tolerance, from intolerant (red alder) to moderately tolerant (Douglas-fir), and very tolerant (western redcedar) (Niinemets and Valadares 2006). The amount of light reaching the understory of mixed-species stands can be estimated using stand variables such as basal area, stand density index and relative density based on relationships with tree size, leaf area and light penetration (Messier et al. 1998; Comeau 2000; Comeau et al. 2006). In general, light levels under stands of red alder decrease exponentially with increasing alder basal area.

Red alder has positive effects on various soil characteristics including nitrogen availability and nutrient cycling. Binkley and Greene (1983) noted that mixed red alder-Douglas-fir stands appear to have higher ecosystem production than pure Douglas-fir stands on N-limited sites. One main factor is that red alder has the nitrogen-fixing capacity with root symbionts that can transform atmospheric N into usable form, and contribute to the growth of both tree species (Binkley et al. 1994). It has been reported that the fixation rates in mixed stands can be 80-125 Kg⁻¹ ha ⁻¹ year ⁻¹ (Miller and Murray 1978; Binkley et al. 1994). Red alder is a deciduous tree

species with more aboveground litterfall production than conifers (Waring and Schlesinger 1985), and the litter contains higher nutrients (Zavitkowski and Newton 1968; Gessel and Turner 1974; Cole and Newton 1986). Studies indicate that red alder litter, as well as other litter mixed with red alder litter show increased litter decomposition rates (Neal et al. 1965; Bormann and Sidle 1990). Faster decomposition will improve nutrient cycling and lead to enhanced nutrient availability for the plants.

1.5 Competition indices

Competition indices are useful for quantifying and interpreting the competitive effects of neighboring trees on subject tree growth, and have been widely used to measure competition in form of tree growth responses. Typically, competition indices can be divided into two categories: 1) distance-dependent indices, which incorporate tree size information with relative distance of neighboring trees to subject trees within a given stand or plot (Hegyi 1974); and 2) distanceindependent indices, which aggregate non-spatial information such as tree size and number of competitors (Lorimer 1983). In relatively uniform and well stocked stands, distance-independent indices work well to predict the effects of competition. While in stands with more complex structure and relative-low density competitors, distance-dependent indices may work better (Comeau et al. 2003). Numerous studies have compared indices to assess their effectiveness as predictors of growth for several species and forest conditions (Hegyi 1974, Biging and Dobbertin 1992, Comeau et al. 2003, Pukkala 1989, Daniels 1976, Ledermann 2010). Biging and Dobbertin (1992) found that distance-independent indices based on crown measures (crown cross-sectional area, crown volume, and crown surface area) performed better than distance-dependent indices. In contrast, Daniels et al. (1986) found that distance-dependent indices produced slightly

improved basal area growth models than the best distance-independent indices for loblolly pine (*Pinus taeda* L.). Semi-distance-independent competition indices were also compared with several distance-dependent indices by Ledermann (2010), and he found that the best indices of both types could explain similar levels of variation in basal area increment. These study results indicate that no single type of index performs consistently better than others under various conditions, because their performance varies with tree species, forest conditions and sites (Lorimer 1983, Biging and Dobbertin 1992).

For red alder at low densities, the distance to associated conifers would be expected to be important in accounting for competition, which suggests that we should use distance-dependent indices for better prediction of competitive effects. On the other hand, results vary depending on both the broadleaf and conifer species. Previous studies show that two distance-independent indices (Diameter's Sum and Crown Surface Area) had the highest correlations with Douglas-fir stem volume growth, while for western redcedar the best indices were distance-dependent (Cortini and Comeau 2008). In addition, Cortini and Comeau (2008) found simple indices such as height factor, total number of competitors, and competitor basal area performed well in their study. Selection of the ideal competition index is complicated due to the simultaneous beneficial and negative effects of red alder with both effects being dependent on site, soil and other factors. Therefore, it is necessary to evaluate a range of distance-dependent and distance-independent indices and select ideal ones, which are most effective for predicting radial growth of conifers growing in mixture with low to moderate densities of red alder, in order to provide better suggestions for free growing standards for conifer species.

1.6 Free-growing standards

There may be challenges and costs associated with meeting current free growing obligations. Current free growing assessment procedures accept the presence of a deciduous tree within one quadrant of a 1.0 m radius assessment circle in British Columbia, and such allowance is considered as free growing for the crop tree (B.C. Ministry of Forests. 2000). The quadrant method is used to determine whether the crop tree is free growing. The cylinder on the left illustrates one quadrant with vegetation taller than the crop tree is considered as free growing while the right is not free growing (Fig. 1.1). However, this approach may be overestimating the current and future levels of competition on conifer growth, and may not effectively predict either problems to tree growth or their absence (Lieffers et al. 2002). Due to a lack of information on the optimum stand density and spatial arrangement of mixtures, and of clear information on when alder is beneficial and when it is not, many licensees err on the side of caution and eliminate red alder to meet the current free-growing requirements. As well, the increased harvest of mature alder has led to concerns that the current inventory of red alder will not meet projected demands (Tarrant et al. 1994). Therefore, better information on the effects of red alder on Y is needed to support evaluation and revision of methods employed for assessing free-growing status.



Fig.1. 2 Assessing free growing using the quadrant method. The cylinder on the left illustrates one quadrant with vegetation taller than the crop tree. The cylinder on the right shows two quadrants with vegetation taller than the crop tree (from "Establishment to free growing guidebook. Vancouver Forest Region." B.C. Ministry of Forests. 2000.

Research questions

Three key research questions are addressed in this study:

- What are the effects of initial density of red alder on growth of Douglas-fir and western redcedar?
- 2) Do distance-dependent competition indices work better than distance-independent indices in red alder-conifer mixtures? Which competition indices work best?
- 3) Does red alder density influence light levels (diffuse non-intercepted light) and soil and foliar nitrogen?

Research objectives

To improve our understanding of the competitive effects of different amounts and spatial arrangements of red alder, and how these effects are influenced by factors such as site quality, conifer species, and stand-age, long-term studies of mixed alder-conifer plantings were established in 1992, 1994, and 1999 using both additive and replacement series designs as described by Comeau et al. (1997) (MOF EP1121.01). The main objectives of this study are to use the data to:

1) Examine the effects of differing initial densities and proportions of red alder on the

survival and growth of Douglas-fir and western redcedar;

- 2) Assess relationships between growth of conifers and red alder densities at both the individual tree and plot level;
- 3) Evaluate the effectiveness of various distance-dependent and distance-independent competition indices, as well as the influence of assessment plot radius;
- 4) Explore the relationships between light levels and alder density;
- 5) Analyze the effects of alder density on soil and foliage nitrogen content.

2. Methods and Analysis

2.1 Site description



Fig. 2.1 The research study area of southwest British Columbia, Canada. The study sites including all the installations of EP1121.01 are indicated in the labeled region.

This study is part of the long-term Experimental Project (EP) 1121.01 established in British Columbia by the BC Ministry of Forests at five installation sites (Table 2.1) (Comeau et al. 1997; Thomas et al. 2005). All sites are located in the Coastal Western Hemlock (CWH) zone, but vary from dry maritime to very wet maritime subzones. The CWH zone typically has a cool mesothermal climate with cool summers (although hot dry spells can be frequent) and mild winters. Mean annual temperature is about 8°C and ranges from 5.2 to 10.5°C among the CWH subzones. The soil moisture regime ranges from slightly dry to very wet, and soil nutrient regime ranges from medium to rich with relatively larger amounts of available N and other nutrients,

and rapid turnover of organic matter (Green and Klinka 1994). The Gough Creek installation has the highest elevation (425 m) and a westerly aspect with a middle slope (10%).

Table 2. I Field instantations established in D.C. for additive and replacement series experiments							
Installation (Site No.)	District	Subzone ^a	Soil Moisture Regime	Soil Nutrient Regime	Year Established	Species planted ^b	
Additive Series							
Waterloo Creek (1)	South Island	CWHdm	3	c	1992	Fd, Cw, Dr	
Gough Creek (2)	Sunshine Coast	CWHdm	3	c	1992	Fd, Cw, Dr	
Holt Creek (4)	South Island	CWHxm	5	d	1994	Fd, Cw, Dr	
Malcolm Knapp Research Forest (6)	Chilliwack	CWHvm	6	d	1999	Fd, Cw, Dr	
Replacement Series							
East Wilson Creek (3)	Sunshine Coast	CWHdm	3	c	1992	Fd, Dr	
Holt Creek (5)	South Island	CWHxm	5	d	1994	Fd, Dr	

 Table 2. 1 Field installations established in B.C. for additive and replacement series experiments

^a CWHdm=Dry maritime, CWHxm=Very dry maritime, CWHvm=Very wet maritime; ^bFd: Douglas-fir, Cw: Western redcedar, Dr: Red alder. Relative soil moisture regime uses eight classes to rank the relatively driest soil (0) to the relatively wettest soil (7) within a particular biogeoclimatic subzone or variant. Soil nutrient regime, five classes are recognized, ranging from very poor with low amounts of available N and other nutrients and slow turnover of organic matter; to very rich with relatively large amounts of available N and other nutrients, and rapid turnover of organic matter. C stands for median, d rich and e very rich (Green and Klinka 1994).

2.2 Experimental design

This study includes two major experiments: 1) additive series field experiment, which planted different amounts of broadleaves into a conifer plantation, and is used to test the effects of red alder at varying densities on the production of Douglas-fir or western redcedar with a fixed density (Kelty and Cameron 1995); and, 2) replacement series field experiment, which involved planting Douglas-fir and red alder in different proportions while keeping the total density constant, and is used to identify the nature of interactions between two species and how they change as the proportion of each species changes (Radosevich 1987). Data available from Additive and Replacement experiments of mixed alder-conifer plantings in five installations:

Waterloo Creek (near Courtenay), Gough Creek (near Gibsons), East Wilson Creek (near Gibsons), and Holt Creek (near Duncan) and Malcolm Knapp Research Forest, focus on both short-term and long-term effects of red alder densities on conifer growth and stand development (Comeau et al. 1997). Each installation contains 5-8 plots (Thomas et al. 2005). Nursery grown seedlings were planted for all 3 species in the year of establishment. Douglas-fir and western redcedar were 1 year old nursery grown planting stock, and they were all grown at the Cowichan Lake Research Station or at the BC Ministry of Forests Surrey Nursery. Trees were grown the previous summer, stored frozen over the winter, and planted in the spring. Red alder were 1 year old container grown (PSB 416 or 615) stock grown at Cowichan Lake Research Station. They were lifted from containers in early spring for planting.

The additive experiments were established at four locations (Fig. 2.1). By design (Table 2.2), all plots have the same total density (1100 tph) of conifers with equal proportions of Douglas-fir and western redcedar. At each location one of five "broadleaf" densities [0, 50, 100, 200 and 400 red alders per hectare] was randomly assigned to a single plot. Experimental units (treatment plot) are 0.36 ha (60 m x 60 m) at Holt Creek and Malcolm Knapp, and 0.49 ha (70 m x 70 m) at Waterloo Creek and Gough Creek. Each treatment was randomly assigned to one plot within each installation. This study utilizes a randomized block design with the blocks located at different sites, and with one replicate of each treatment established in each block.

	1	11	1
Treatment	Species planted	Number of trees/ha	Square spacing (m)
1	-	0	-
2	Red alder	50	14.2×14.1
3	Red alder	100	10.0×10.0
4	Red alder	200	7.1×7.1
5	Red alder	400	5.0×5.0

 Table 2. 2 Description of the five treatments applied in the additive experiment series

The replacement series experiments (Table 2.3) involved establishing mixtures of Douglas-fir and red alder in five proportions at a total density of 742 tph (3.67 m spacing) following an experimental design protocol developed by the Oregon State University Hardwood Silviculture Cooperative (http://hsc.forestry.oregonstate.edu/). Canadian installations (each having one replicate of each of the five treatments) are located at Holt Creek (South Island District; planted in 1994) and East Wilson Creek (Sunshine Coast District; planted in 1992), and experimental units (treatment plots) are 0.36 ha (60 m x 60 m) and 0.49 ha (70 m x 70 m) respectively. Measurements taken in year 22 are available for both of these installations (as well as previous measurements).

Treatment	Proportion alder	Proportion Douglas-fir	Total trees/ha	Spacing (m)
1	1.0	0	742	3.67
2	0.5	0.5	742	3.67
3	0.25	0.75	742	3.67
4	0.11	0.89	742	3.67
5	0	1.0	742	3.67

 Table 2. 3 A description of the five treatments established for the replacement series study

2.3 Data collection

2.3.1 Vegetation measurements

Both experiments established 0.1 ha (17.54 m radius) permanent measurement plots in the center of each treatment plot, and numbered tags were attached to all trees in the measurement plot. Root collar diameter, diameter at 1.3 m (DBH, when trees are >2 m tall), height, height to crown base, crown radius (in four cardinal directions: north, east, south, and west), and crown length have been measured periodically since the time of establishment. Measurement years for each installation are shown in Table 2.4. In each plot the location of all trees in these measurement

plots was mapped within 10 cm accuracy to provide spatial data for analysis and to assist with locating trees during re-measurement.

Veen of Trees		А	dditive Series	5	Replacemen	t Series
Year of Tree -	Holt	Waterloo	Gough	Malcolm Knapp	East Wilson	Holt
Data Measurement	Creek	Creek	Creek	Research Forest	Creek	Creek
1992		Е	Е		Е	•
1993		2	2		2	
1994	Е	3	3		3	Е
1995	2	4	4		4	2
1996	3	5	5		5	3
1997	4				6	4
1998	5	7	7			
1999				Е		6
2000	7			2	9	
2001		10	10	3		
2002				4		9
2003					12	
2004	11	13	13			11
2005				7		12
2006		15	15			
2008	15			10	17	
2010						17
2011		20	20			
2013	20			15	22	
2015						22

Table 2. 4 Timeline of available tree data in measurement year

E represents establishment year, numbers are timeline of the tree data collected in each experiment plot, "." represents no data.

2.3.2 Light Measurements

Diffuse non-intercepted light levels were measured at 1.5 m above the ground during midsummer 2017 using LAI-2000 plant canopy analyzers (Li-Cor Inc., Lincoln NE) (Comeau et al. 1998). The LAI-2000 measurements at 3 oldest additive installations (Waterloo, Holt and Gough Creek) and at 2 replacement series installations (Holt and East Wilson Creek). The measurements were taken at 5 locations in each plot: plot center as well as 9 m north, south, east and west of plot center. Measurements were taken at each point with the sensor "pointing" west in the morning and east in the afternoon, with a 180-degree view restrictor on the sensor. A matching sensor was placed in a nearby opening and set to record readings at 5 minute intervals. Additional data from fish eye photos, ceptometer, photo diode sensor array was also available from previous measurements for some plots (Table 2.5).

Light was also measured for selected trees in 2004 at Holt, Waterloo, Gough and East Wilson Creek. In the additive plots containing 50, 100, 200 and 400 alder per hectare, 6 western redcedar and 6 Douglas-fir were randomly chosen from each plot and measured. In the replacement plots (all except the 100% alder) ten Douglas-fir were randomly selected. Readings were taken with the sensor pointing east (90 degrees) in the afternoon and west (270 degrees) of the tree in the morning using the LAI-2000 plant canopy analyzers (Li-Cor Inc., Lincoln NE) at mid-crown using the 180 degree views on the lens. A telescoping pole was used to position the sensors at mid-crown height. The open sky readings were set up in open areas so that the sensor had a clear view of the sky above about 25 degrees from the horizontal.

2.3.3 Nutrients

Soil samples were collected from 10 systematically selected locations in each plot at 3 depths (LFH, 0-10 cm, 10-20 cm, 20-40 cm) in 2010. Forest floor samples were collected using a 15 cm x 15 cm metal frame, forest floor thickness was recorded, and dry weight of forest floor samples was determined in the lab for use in calculation of forest floor dry weight and nitrogen content. Volumetric samples of mineral soil were collected for each depth to determine bulk density and fine fraction density to use in calculation of soil nitrogen content. Mineralizable N was determined for soil samples following methods outlined by Waring and Bremner (1964). Soil samples were analyzed by the B.C. Ministry of Forests and Range Research Branch laboratory.

Foliage samples were collected (dormant season) in 2011 from a subsample of 10 Douglas-fir in each of the 3 selected plots at each of the 6 installations, 2 trees were selected near plot center and 2 moving towards plot edges along each of 4 cardinal directions. Nitrogen concentration in these foliage samples was determined using a Leco Truspec NC Elemental Analyzer, which involves high-temperature combustion of a small sample followed by measurement of the amount of gaseous nitrogen oxides emitted (Miller 1998). Foliar samples were analyzed by the B.C. Ministry of Forests and Range Research Branch laboratory.

London	Installation Type	Dl.4	Alder density	Conifer density
Location	Installation Type	Plot	(tph)	(tph)
East Wilson (HSC4302)	Replacement Series	1	371	371
East Wilson (HSC4302)	Replacement Series	2	0	742
East Wilson (HSC4302)	Replacement Series	4	186	556
Holt Creek (HSC4303)	Replacement Series	9	186	556
Holt Creek (HSC4303)	Replacement Series	11	371	371
Holt Creek (HSC4303)	Replacement Series	12	0	742
Holt Creek	Additive	1	400	1100
Holt Creek	Additive	2	200	1100
Holt Creek	Additive	5	0	1100
Gough Creek	Additive	4	200	1100
Gough Creek	Additive	5	400	1100
Gough Creek	Additive	8	0	1100
Waterloo	Additive	5	0	1100
Waterloo	Additive	6	200	1100
Waterloo	Additive	7	400	1100
MKRF	Additive	3	200	1100
MKRF	Additive	4	400	1100
MKRF	Additive	5	0	1100

Table 2. 5 EP1121 – Soil and foliar (Douglas-fir only) sampling completed for BC sites in 2010 and 2011 (3 plots sampled at each location. Soil samples collected at 10 points in each plot sampled).

2.4 Tree data processing

The principles for manipulating the raw data are: 1) only tagged and live trees were analyzed, 2)

data was filtered to remove trees that have been affected by snow press, damage agents and that are nearly dead (but due to small sample size of red alder, red alder that had partial damage, lean, or sweep were retained), 3) replanted or sprouted trees were removed as they are not representative of the trees that were planted originally.

2.4.1 Stem mapping

The map data was translated into UTM coordinates using Traverse PC software version 6.0 (windows), then exported as CSV files. The distance from plot center to each tagged tree was calculated using the *euclidean* distance function in ArcGIS (10.4). For the missing plot centers, the Mean Center tool in ArcGIS was used to locate the midpoint of the associate plot. All stem maps were plotted in ArcMap for the purpose of verification.

2.4.2 Periodic annual increment

The periodic increment of height (HT, m/year), basal area (BA, cm²/year), and stem volume (VOL, cm³/year) was calculated for a period of 8 years. The 8-year period is between 1998 and 2006 for Waterloo and Gough Creek, 2000 and 2008 for Holt Creek additive experiment and East Wilson Creek, 2005 and 2013 for MKRF, 2002 and 2010 for Holt Creek replacement experiment, as follows:

$$PAI_{HT,BA,VOL} = \frac{T_{t_8} - T_{t_1}}{t_8 - t_1}$$
(Equation 2.4.2),

where T is the tree data of HT, BA, and VOL. t is the measurement year. Initial tree size was determined as the first growing season of the eight years' period in 1998. Stem volume was calculated using the New Volume Equations developed by Nigh (2016). The general equation is:

$v = e^{b_0} \times dbh^{b_1} \times ht^{b_2}$ (Equation 2.4.3),

where v is the tree volume (m³), dbh is the diameter at breast height (cm), and ht is total height (m). These volume equations predict total volume and merchantable volume by species and region and by species and biogeoclimatic zone. The parameters to calculate the actual stem volume of the measured conifers are listed in the Table 2.7.

Table 2. 6 Results of the total volume equation fitting by species and zone. Shown are the estimates of the total volume equation parameters and their standard errors (below in parentheses) and the estimates of the error parameters δ and σ^2 (Nigh 2016).

Species	Zone	b_0	<i>b</i> ₁	b ₂	δ	σ^2
Dr	CWH	-10.167	1.867	1.101	2.046	0.007
		(0.031)	(0.012)	(0.018)		
Fd	CWH	-9.985	1.712	1.155	2.068	0.012
		(0.026)	(0.011)	(0.017)		
Cw	CWH	-9.492	1.726	1.023	2.081	0.012
		(0.017)	(0.009)	(0.012)		

2.4.3 Competition indices

Douglas-fir and western redcedar trees within 12 m from the plot center were selected as subject trees, and the distance between each subject tree and all their neighbor trees was used to calculate distance dependent competition indices (CI) (Fig. 2.2). A function (appendices) was built in the R statistical program (R core team 2017) to calculate the distances from all subject trees to their neighbor trees within a 5.64 m search radius. Lorimer (1983) shows in his study that the variance in tree growth explained by competition increases sharply until the search radius of competition exceeds a size of about 2 to 3 times the mean crown size of overstory trees in the stand, after that point it starts to level off. A search radius of 5.64 m for coniferous trees was at least 2 to 3 times the mean crown radius in our stands and hence sufficient for measuring

coniferous competition. Thirteen competition indices were calculated (Table 2.8) for coniferous and deciduous (red alder only) trees separately using dplyr packages (Hadley et al. 2017) available in R. For subject trees with no red alder competition, the values have been set to 0.0001 to account for the absence of the broadleaf competition while allowing for analysis using non-zero values.

Competition indices CI	Formula	Values
Distance independent		
BA: basal area sum	$BA = \sum BA_j$	BA_j = competitor basal area (RCD ²)
Bal: basal area larger	$BAl = \sum_{j=1}^{n} BA_{j(larger t)}$	$BA_j = $ competitor ba larger
DI: Lorimers' index	$DI = \sum_{j=1}^{n} \frac{DBH_j}{DBH_i}$	$DBH_i = DBH$ subject tree, $DBH_j = DBH$ competitor
HF: height factor	$HF = \sum \frac{Ht_j}{Ht_i}$	Ht_j = competitor height; Ht_i = selected species ht
DS: diameter sum	$DS = \sum D_j$	$D_j = $ competitor diameter (RCD)
DSL: diameter Larger	$DSL = \sum D_{j(larger t)}$	D_j = competitor diameter larger (RCD)
TN: tree number	$TN = \sum N_j$	$N_j = $ competitor number
CSAs: crown surface area	$CSA = \sum CSA_j$	CSA_j = competitor projected crown area
Distance dependent		
DDR : diameter distance ratio	$DDR = \sum \frac{D_j}{dist_{ij}}$	$dist_{ij}$ = distance; D_j = competitor diameter
SFI: spacing factor index	$SFI = \sum \frac{dist_{ij}}{htdiff_{ij}}$	$dist_{ij}$ = distance; $htdif f_{ij}$ = differential ht (competitor – selected species)
DWS : distance weighted size ratios	$DWS = \sum \frac{D_j / D_i}{dist_{ij}}$	D_j = competitor diameter (RCD); D_i = subject tree diameter (RCD); $dist_{ii}$ = distance
MBH : modified Braathe index of height difference	$MBH = \sum \frac{htdiff_{ij}}{dist_{ij}}$	$dist_{ij}$ = distance; $htdiff_{ij}$ = differential ht between subject tree and competitor
MBD : modified Braathe index of diameter difference	$\text{MBD} = \sum \frac{DBHdiff_{ij}}{dist_{ij}}$	$dist_{ij}$ = distance; $DBHdiff_{ij}$ = differential DBH between subject tree and competitor
Hegyi's index	$Hegy is = \sum \frac{DBH_j}{(DBH_i)dist_{ij}}$	$dist_{ij}$ = distance; DBH_i = DBH subject tree, DBH_j = DBH competitor

Table 2. 7 Competition indices and formulas used for their calculation for this study.


Fig. 2. 1 Schematic of a sample measurement plot with three selected subject trees (solid dots) with neighbors (open dots) within their respective competition plots.

2.4.4 Light

FV2000 software (LiCor Inc., Lincoln, Nebraska) was used to determine diffuse non interceptance (DIFN) values. As per Comeau et al. (1998, 2006), readings from the outer rings (4 and 5) of the LAI 2000 sensor were not included in the DIFN determination. DIFN data collected in 2004 were also used for the subject trees with available increment data.

2.5 Statistical analysis

Statistical analyses were performed in R Studio (2017) based on R version 3.3.2 (R Core team 2016). The functions used to perform calculations and statistical analyses were from packages included in the base R installation, and installed packages "Ismeans" (Lenth 2016) and "ggplot2" (Wickham 2009). The general and versatile method implemented in non-linear mixed effects

model (nlme) by Pinheiro and Bates (2000) was also used. Both linear and non-linear models used in the study were checked for the distributional assumptions and model adequacy: 1) scatter plots of standardized residuals versus fitted values for checking heteroscedasticity using the *plot* method, 2) the normal probability plots of estimated random effects for checking marginal normality and identifying outliers using the *qqnorm* method, 3) A plot of the empirical autocorrelation obtained by the *ACF* method to check correlation structures of the model, 4) the normal plot of the normalized residuals to check normality, 5) the plot of the observations against the within-group fitted values to attest the model adequacy, 6) the plot of the augmented predictions to check the adequacy of the mixed-effects model using *plot* and *augPred* methods. As a final assessment, both the population predictions (corresponding to random effects) are displayed in the plot of augmented predictions for comparison and to show how individual effects are accounted for in the models (Pinheiro and Bates 2000).

2.5.1 Effects of red alder density treatments on growth of coniferous trees

The linear mixed effects model (lme) with red alder density and growth year as two explanatory variables was formulated to evaluate treatment effects on coniferous trees across available time series. Age 4, 7, 10, 15, 20 since stand establishment were selected and treated as factorial variables. The linear model used for each species was as follows:

$$Y_{ij} = \mu + X_i + T_j + XT_{ij} + B_{ij} + \varepsilon_{ij}, i = 1, ..., 5, j = 1, ..., 4, \varepsilon_{ij} \sim N(0, \sigma^2)$$
 (Equation 2.5.1)

where Y_{ij} is the response; μ is the overall mean, X_i is the red alder density treatment; T_j is tree age; B_{ij} is the random effects of the j_{th} replication nested within installation; i indexes the red

alder density or proportion treatment and j the installation. Several response variables such as tree height, diameter at breast height (DBH), height to diameter ratio (HDR) and stem volume at both individual tree level and plot level from four installations were calculated and entered into the model separately, and Type II sum of squares in Anova (R, car package) was used to test the significance of main effects (red alder density and growth year) and their interactions. Post-hoc multiple comparisons with Least Squares Means were used to obtain the average, standard errors, 95% confidence intervals, and pair-wise contrasts for each treatment. If the lme indicated significant treatment effects, then Tukey's Studentized Range (HSD) Test was used for multiple comparisons among treatments and a significance level of α =0.05 was used for all response variables.

2.5.2 Effects of competition on growth of coniferous trees

The effects of competition and initial subject tree size on conifer growth were evaluated using a non-linear mixed effects model (nlme). A combination of exponential competition and power of initial size as used in Comeau et al. (2003) and Cortini and Comeau (2008) (Equation 2.5.2) was used in the models.

$$PAI_{ij} = a + b_1 * e^{\left(b_2 * CI_{conif_{ij}} + b_3 * CI_{decid_{ij}}\right)} * in. BA_{ij}^c + \varepsilon_{ij}, \quad \varepsilon_{ij} \sim N(0, \sigma^2) \text{ (Equation 2.5.2)},$$

where PAI_{ij} is the ith PAI_{BA} or PAI_{VOL} of each subject tree i within site j. CI_{conif} and CI_{decid} are the competition indices for coniferous and deciduous species for each neighbor tree relative to their subject tree, and in. BA is the initial basal area in the year of 1998 for Waterloo and Gough and 2000 for Holt Creek. ε_{ij} is the residual standard error with parameters a, b_1 , b_2 , b_3 , and c to be estimated. All parameters in the model were first to be considered mixed as both fixed and random (as suggested in Bates and Pinheiro 1998), then the AIC was used to compare models with alternative sets of fixed-effects and covariance parameters. Also, the inclusion of a Power Variance Function on initial size for each separate site was used for improving the model fit. The best fitting models were determined by comparing the AIC values using the ML method. Diagnostic plots of standardized residuals versus fitted values and normality of random effects were conducted to test model fit (Pinheiro and Bates, 2000).

2.5.3 Light and nitrogen responses to density treatments and competition

The average light levels for each treatment plot were analyzed as responses to tree basal area. Non-linear mixed models were built considering installation sites as random factors:

$$Y = a + b_1 X_1 + b_2 X_2 + b_3 X_3 + \varepsilon$$
(equation 2.5.3),

where Y is the average diffuse non-intercepted light (DIFN) for each plot within each site, X_1, X_2, X_3 are the basal area per hectare of red alder, Douglas-fir, and western redcedar respectively in the associated plot of each site. In comparison, light levels as responses to basal area of each species were analyzed separately to compare species light interception contributions and model fits.

The average light levels measured for selected subject trees within each plot were analyzed using non-linear mixed models with basal area and initial crown surface area as two explanatory variables. Preliminary analysis tested various linear and non-linear regressions to explore relationships between light and growth responses as well as competition. Power functions provided the best models relating conifer growth to DIFN and initial crown surface area (CSAi):

$$Y = a + b_1 X^{b2} CSAi^c + \varepsilon$$
(equation 2.5.4),

where Y is the conifer stem volume or basal area growth, X is DIFN and the other independent variable is CSAi. The relationship between DIFN and competition indices were also analyzed using non-linear mixed model:

$$Y = a + b_1 e^{b_2 C I_{conif} + b_3 C I_{dr}} + \varepsilon$$
(equation 2.5.5),

where Y is the DIFN for the subject trees, CI_{conif} and CI_{dr} are the competition indices for conifers and red alder respectively.

Relationships between broadleaf density and N concentration (in soil, lfh, and foliage) were evaluated using a multiple quadratic polynomial regression model:

$$Y = a + b_1 X + b_2 X^2$$
 (equation 2.5.6),

where Y is the percent of nitrogen or total mineral N, X is the red alder density (tph) or basal area per hectare.

3. Results

3.1 Effects of red alder density on growth of Douglas-fir and western redcedar

3.1.1 Mean tree size relative to red alder density and growth year on each site

Fig. 3.1, 3.2, and 3.3 show the mean height, DBH, and volume (including stem volume and stand volume), at all available measurement years from age 4 to 20, calculated for each tree species of each density treatment plot on four installation sites (additive experiments). Replacement experiments were not analyzed for the effects of red alder proportion on conifer growth, due to a lack of replications. Changes in each species density (stems per hectare, sph) with age for each installation site are illustrated in Fig. 3.4 Douglas-fir and western redcedar started with an average density of 550 sph (except for MKRF that has plantations of 570 sph), however, high mortality occurred during the first growing season, especially for western redcedar in Gough and Holt Creek (Fig. 3.4).

density ◆ 0 ▲ 50 - 100 + 200 · 🛛 400



Fig. 3. 1 Mean height of Fd, Cw, and Dr after establishment (years) with red alder density treatments at Waterloo Creek, Gough Creek, Holt Creek, and Malcolm Knapp Research Forest (MKRF).

density → 0 🔺 50 🚽 100 + 200 🖄 400



Fig. 3. 2 Mean diameter at breast height (DBH) of Fd, Cw, and Dr after establishment (years) with red alder density treatments at Waterloo Creek, Gough Creek, Holt Creek, and Malcolm Knapp Research Forest (MKRF).



Fig. 3. 3 Stand volume of Fd, Cw, and Dr after establishment (years) with red alder density treatments at Waterloo Creek, Gough Creek, Holt Creek, and Malcolm Knapp Research Forest (MKRF).



Fig. 3. 4 Stems per hectare changes with installation, treatment, and age. Initial density for CW and FD in Gough, Holt and Waterloo is 1100tph, in MKRF is 1150tph.

3.1.2 Tree growth in relation to red alder density and growth year

Table 3. 1 P values from Mixed-effects model ANOVA results ($\alpha = 0.05$) for Fd, Cw, and Dr, testing differences in tree responses including HT (m), DBH (cm), HDR, BA (cm²/tree), and VOL (cm³/tree) and plot responses including mean BA (cm²/ha) and VOL (cm³/ha) by density treatment at selected measurement years

	~ -	Tree res	ponses		Plot responses			
Species	Source	HT (m)	DBH (cm)	Ln HDR	BA (cm ²)	VOL (cm ³)	BA (cm ² /ha)	VOL (cm ³ /ha)
Fd	density	<.0001	<.0001	<.0001	0.0013	0.0448	0.1439	0.9775
	year	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
	density:year	<.0001	0.2037	0.0237	0.0142	0.0039	0.9915	0.9908
Cw	density	<.0001	<.0001	<.0001	0.0307	0.0062	0.8836	0.9044
	year	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
	density:year	<.0001	<.0001	<.0001	<.0001	<.0001	0.9659	0.9413
Dr	density	<.0001	0.1329	<.0001	<.0001	<.0001	<.0001	0.0034
	year	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
	density:year	0.0049	0.1437	0.2269	0.2346	0.0534	<.0001	<.0001

Note: P values are based on analysis of variance (ANOVA), Boldface values are significant at $P \le 0.05$, Dr DBH was tested using analysis of deviance type II tests. The insignificant interactive values with lines crossed off indicate the associated response variables will be analyzed at an averaged age.

The results of the mixed model ANOVA using tree level response variables show significant (α

= 0.05, P < .0001) effects of density on height, DBH, lnHDR (log height to diameter ratio), basal area, and volume of all three species (Table 3.1). No significant density effects were found on the growth of either Douglas-fir or western redcedar using plot level response variables. Most of red alder's response variables except for its DBH show significant density effects (P < .0001; Table 3.1) at either tree level or plot level. Significant interactions between density effects and growth year (P < 0.05; Table 3.1) are evident in coniferous tree responses and red alder's height. Therefore, a pairwise comparison of least-squares means (Ismean) using Tukey's method was conducted at each selected age. Table 3.2 shows the Ismean of height, DBH, InHDR, basal area, and volume, at age 4, 7, 10, 15, and 20 respectively, calculated for each density treatment with grouping letters. The response variables without significant interactions with growth year were averaged over year levels by density treatment (Table 3.3). Slight differences in red alder density treatments were evident for Douglas-fir DBH and red alder lnHDR, basal area, and volume.

Holt Creek; year 15 for MKRF at 2013). (Years 4, 7, 10 and 15 include data from all 4 locations, while results for year 20 include data from 3 locations).										
Variable	Treatment (stems/ha)	Year 4	Year 7	Year 10	Year 15	Year 20				
Fd										
Height (m)	0	1.89a	3.26a	5.42a	8.92ab	13.8ab				
	50	1.68a	3.06a	5.26a	8.72a	12.76a				
	100	1.77a	3.27a	5.69ab	9.51bc	13.85ab				
	200	1.82a	3.28a	5.65a	9.59bc	14.37b				

3.58b

-2.2a

-2.19ab

-2.19ab

-2.08c

-2.12bc

6.13b

-2.49a

-2.43ab

-2.44ab

-2.38bc

-2.33c

9.9c

-2.59a

-2.55ab

-2.53b

-2.52bc

-2.45c

14.2b

-2.59a

-2.5b

-2.48b

-2.5b

-2.47b

1.85a

-1.61a

-1.54a

-1.64a

-1.58a

-1.57a

400

0

50

100

200

400

LnHDR

Table 3. 2 Lsmean tree size by density treatment from year 4 (1995: Waterloo and Gough Creek; 1997: Holt Creek; 2002: MKRF) to year 20 (2011: Waterloo and Gough Creek; 2013:

Variable (cont.)	Treatment (stems/ha)	Year 4	Year 7	Year 10	Year 15	Year 20
Basal Area (cm ² /tree)	0	1.24a	10.62a	44.85a	145.39a	318.56b
	50	0.95a	8.5a	40.78a	129.28a	254.92a
	100	0.93a	9.61a	43.19a	135.31a	271.24ab
	200	1.00a	8.79a	40.42a	137.3a	310.84b
	400	1.02a	9.91a	41.23a	124.82a	273.27ab
Stem volume (cm ³ /tree)	0	160.8a	2026.57b	12168.19a	57375.45a	170346.08b
	50	127.77a	1509.15a	11106.25a	49768.27a	135682.78a
	100	123.29a	1816.57ab	12343.07a	57355.84a	152123.57ab
	200	135.98a	1797.87ab	11996.36a	59064.47a	182564.28b
	400	139.39a	2094.23b	13124.68a	56298.07a	158749.84ab
Stand basal area (m ² /ha)	0	0.0349a	0.5219a	2.2056a	7.1202a	14.6473a
	50	0.0273a	0.3832a	1.8854a	5.7693a	10.9579a
	100	0.0265a	0.4209a	1.9092a	6.1890a	12.1083a
	200	0.0276a	0.3850a	1.8403a	6.2394a	15.0150a
	400	0.0325a	0.4842a	1.8867a	5.5203a	13.3825a
Stand volume (m ³ /ha)	0	0.0434a	1.0096a	5.9833a	28.1014a	78.3375a
	50	0.0308a	0.6913a	5.1306a	22.2115a	58.3241a
	100	0.0389a	0.8164a	5.4615a	26.2410a	67.9348a
	200	0.0419a	0.8279a	5.4963a	26.8808a	88.2412a
	400	0.0462a	1.0340a	5.9958a	24.9086a	77.7798a
Cw						
Height (m)	0	1.33a	2.27a	3.55b	6.14bc	7.39a
	50	1.25a	2.24a	3.17a	5.25a	7.76a
	100	1.58b	2.45a	3.94c	6.57c	8.78b
	200	1.45ab	2.39a	3.65bc	5.93b	7.45a
	400	1.25a	2.44a	3.87c	6.13bc	8.07ab
Diameter (cm)	0		1.53a	3.5ab	8.83bc	10.95a
	50		1.51a	3.03a	7.08a	11.74a
	100		1.72a	4.16c	9.43c	13.73b
	200		1.67a	3.59b	7.97ab	10.63a
	400		1.67a	3.91bc	8.08ab	11.68a
LnHDR	0	-0.76a	-1.57bc	-2.07bc	-2.56a	-2.69ab
	50	-0.79a	-1.42c	-2.05c	-2.52a	-2.7ab
	100	-0.53a	-1.63ab	-2.24a	-2.58a	-2.72a
	200	-0.55a	-1.59abc	-2.12bc	-2.51a	-2.61b
	400	-0.69a	-1.72a	-2.17ab	-2.5a	-2.63ab
Basal Area (cm ² /tree)	0		2.77a	13.42b	77.86bc	105.49a
	50		2.86ab	9.12a	46.99a	123.76a
	100		3.33b	17.37b	82.75c	163.96b
	200		3.17ab	13.36b	61.61ab	104.51a
	400		3 16ab	17 44b	63 95h	128 48ab

Variable (cont.)	Treatment (stems/ha)	Year 4	Year 7	Year 10	Year 15	Year 20
Stem volume (cm ³ /tree)	0	39.21a	670.07b	4615.49b	32299.77bc	45594.01a
	50	23.07a	398.79a	3165.67a	16863.18a	54861.24ab
	100	21.94a	655.62b	5934.1bc	33783.91c	76320.06b
	200	17.03a	578.89ab	4463.15ab	24921.89b	47675.47a
	400	24.57a	822.62b	6502.54c	26860.54bc	62701.15ab
Stand basal area (m ² /ha)	0	0.0033a	0.1059a	0.6931a	3.3364a	3.5186a
	50	0.0023a	0.0575a	0.5038a	1.9005a	4.6087a
	100	0.0016a	0.1220a	0.9361a	3.9584a	6.5027a
	200	0.0020a	0.0841a	0.6346a	2.6780a	3.3577a
	400	0.0030a	0.1244a	0.8713a	2.8985a	4.9566a
Stand volume (m ³ /ha)	0	0.0061a	0.2575a	2.1592a	13.6472a	15.1993a
	50	0.0038a	0.1281a	1.3990a	6.6911a	20.4804a
	100	0.0033a	0.2923a	2.8813a	15.9637a	30.2732a
	200	0.0035a	0.2005a	1.9227a	10.5939a	15.1004a
	400	0.0059a	0.3017a	2.8011a	11.8223a	23.8306a
Dr						
Height (m)	50	4.22a	5.77ab	7.02a	8.52a	10.8a
	100	3.96a	5.87a	7.65ab	9.87ab	11.49a
	200	4.05a	6.1a	7.7a	9.95b	12.9b
	400	4.36a	6.57b	8.33b	10.85c	12.46ab
Stand basal area (m ² /ha)	50	0.1974a	0.2594a	0.2559a	0.5485a	0.6980a
	100	0.2425ab	0.5591ab	1.1090b	1.8782b	2.0077b
	200	0.3115ab	1.1500bc	2.3656c	4.2813c	6.1813c
	400	0.4697b	2.1513c	4.4538c	7.1110c	7.9967c
Stand volume (m ³ /ha)	50	0.2662a	0.9981a	1.6148a	3.1440a	4.3260a
	100	0.2749a	1.4962a	3.9601ab	8.1273a	10.8865a
	200	0.6447a	3.6983ab	8.9135bc	20.0657b	35.8970b
	400	1.0505a	6.9647b	17.7234c	35.2922b	46.3187b

Note: Values with different letters within the given year are significantly different according to Tukey's pairwise comparisons. Height to diameter ratio is given on the log (not the response) scale. Confidence level used: 0.95.

Table 3. 3 Averaged tree size over year levels by red alder density treatments

Variabla	Density treatment (stems/ha)									
v al lable	Dr 0	Dr 50	Dr 100	Dr 200	Dr 400					
Fd DBH (cm)	8.4583b	8.1855a	8.3245ab	8.2577a	8.3262ab					
Dr lnHDR		-2.61a	-2.57a	-2.56a	-2.48b					
$Dr BA (cm^2)$		136.68ab	134.9a	135.29a	137.95b					
Dr VOL (cm ³)		64041.61ab	64061.66a	64124.09a	64870.38b					

Note: Interactive term was removed since no significance was found, so results are averaged over the levels of: year. Values with different letters within the given year are significantly different according to Tukey's pairwise comparisons. Height to diameter ratio given on the log (not the response) scale. Confidence level used: 0.95.

Fig. 3.5, 3.6, 3.7, and 3.8 illustrated that density effects varied with tree age and tree species. Fig. 3.5 shows lsmean of height for each tree species relating to alder density treatments and growth year. There were slight variations among treatment effects from age 4 to age 20, and with some of the differences between treatments becoming larger over time. While statistically significant Douglas-fir height was largest in the highest density treatment (400 tph) from age 7 to age 15, and same for red alder height growth. For western redcedar height, which showed significant treatment effects, 200 tph surpassed 400 tph effects at older ages resulting in the highest tree height. While treatment effects on DBH were not statistically significant for red alder, 100 tph seems to have the highest constant DBH growth for western redcedar, and 0 tph for Douglas-fir (Fig. 3.6). For Douglas-fir, differences between treatments for DBH or volume growth trends are negligible at young ages, but 200 tph has the highest stem volume responses at older ages (Fig. 3.6 and 3.7). Stem volume and basal area responses to density treatments for western redcedar indicate that 100 tph is highest for western redcedar (Fig. 3.7). As for lnHDR, it showed similar responses compared to other variables. Fig. 3.7 displayed that lnHDR is constantly the lowest in 100 tph treatment for western redcedar and 0 tph treatment for Douglas-fir across all ages. For red alder, both tree level and stand level volumes and basal area increase significantly with alder density (Table 3.1). The total stand volume which summed volumes of all three tree species was not significantly affected by density treatments.



Fig. 3. 5 Lsmean height of Fd, Cw, and Dr after establishment (years) as response to red alder density treatments (stems per hectare).



Fig. 3. 6 Lsmean diameter at breast height of Cw (a, significant interactions between density treatments and growth year) and Fd (b, no significant interactions) after establishment (years) as response to red alder density treatments (stems per hectare).



Fig. 3. 7 Lsmean stem volume, basal area, and height to diameter ratio (log transformed) of Cw and Fd at each year as response to red alder density treatments (stems per hectare), significant interactions between density treatments and growth year were found.



Fig. 3. 8 Lsmean basal area, height diameter ratio (log transformed), and stem volume of red alder at an averaged year as responses to density treatments, no significant interactions were found between treatments and year.

3.1.3 Tree growth relative to red alder density at age 15

Table 3.4 presents the Ismean for HT (height), DBH, HDR (height diameter ratio), BA (basal area), VOL (volume), and CSA (crown surface area), at age 15. Mixed model ANOVA indicated that there was red alder treatment had a significant effect on HT and HDR for all three species, and HT and HDR were largest in the highest density treatment (400 tph) at age 15 for Douglas-fir and red alder ($P \le .001$, Table 3.4). For DBH and VOL, only western redcedar responded significantly to the treatment effects (P < .0001; Table 3.4). For BA and CSA there were significant treatment effects on both Douglas-fir and western redcedar (P < 0.05) but no effects on red alder itself. Tukey's pairwise comparisons indicated the difference between treatment groups for Douglas-fir was not apparent. However for western redcedar, 100 tph treatment constantly had greatest effects on all the variables we tested (Table 3.4). The significant treatment effects on height and HDR of all three species are also illustrated in Fig. 3.9, and Fig. 3.10.

Spp	Treatment density	HT (m)	DBH (cm)	InHDR	BA (cm ²)	VOL (cm ³)	CSA (cm ²)
Fd	P-value	<.0001	0.1719	<.0001	0.0275	0.0961	0.0106
	Dr 0	8.88ab	12.68	-2.59a	145.94b	58594.64	58.27ab
	Dr 50	8.62a	11.69	-2.55ab	121.3ab	47494.93	51.63a
	Dr 100	9.53bc	12.37	-2.53ab	135.95ab	57443.35	61.04b
	Dr 200	9.59bc	12.31	-2.52b	136.02ab	58835.45	61.54b
	Dr 400	9.89c	11.8	-2.45c	121.32a	54803.68	59.79ab
Cw	P-value	0.007	<.0001	0.0003	<.0001	0.0015	0.0004
	Dr 0	6.18ab	8.90ab	-2.57ab	74.54ab	28278.78ab	30.04ab
	Dr 50	5.81a	8.14a	-2.49b	61.76a	23905.95a	27.39a
	Dr 100	6.55b	9.36b	-2.6a	79.38b	31429.64b	34.28c
	Dr 200	5.99a	8.09a	-2.53b	62.54a	24995.52a	30.4abc
	Dr 400	6.18ab	8.29a	-2.51b	63.69a	25170.26a	32bc
Dr	P-value	0.0001	0.3129	<.0001	0.9326	0.2171	0.9900
	Dr 50	8.94a	15.65	-2.81a	194.64	85744.11	4.29
	Dr 100	9.73ab	15.33	-2.75a	199.25	85550.44	4.3
	Dr 200	10.14bc	16.38	-2.74a	210.14	101598.73	4.3
	Dr 400	10.72c	15.29	-2.62b	205.86	100834.8	4.27

Table 3. 4 Summary of *P*-values and treatment means for tree size of Douglas-fir, western redcedar, and red alder by treatment at age 15

Note: red alder CSA shown on log scale.



Fig. 3.9. Lsmean height of Fd, Cw, and Dr at age 15, as responses to red alder density treatments.



Fig. 3.10. Lsmean lnHDR of Fd, Cw, and Dr at age 15, as responses to red alder density treatments. Higher the lnHDR, higher HDR, and indicates higher slenderness.

3.2 Effects of competition on growth of Douglas-fir and western redcedar

Periodic annual increment (PAI) of three response variables including stem volume, basal area and height were calculated during 8 years of growing seasons for selected subject conifers. To investigate growth response of Douglas-fir and western redcedar to competition, 14 competition indices (CI) were tested against these growth variables using the best predictive non-linear mixed model as suggested in Comeau et al. (2003) and Cortini and Comeau (2008). Figure 3.9 indicates overall good fit of the model I used. The residuals are normal and evenly distributed and random effects are within one straight line in the Q-Q plot. Additional scatterplots used to assess these models are provided in Appendix 6. The xyplots of predictions versus the primary covariates (basal area and height growth) for both coniferous species are also included in Appendix 4 and 5.

Models	CI	Obs. #	Adj- <i>R</i> ²	RMSE	AIC	а	<i>b</i> ₁	b ₂	<i>b</i> ₃	С
PAI VOI	L									
	BAs	372	0.827	2750.20	6770.69	552.5569	1306.7607	0.0000	-0.0001	0.6993
	BAl	372	0.833	2721.21	6761.95	852.4309	1478.1172	-0.0002	-0.0002	0.6639
	DI	372	0.930	2685.08	6500.16	293.2576	3527.6668	-0.0768	-0.0594	0.3982
	HF	372	0.932	2607.66	6510.71	423.3126	3301.9845	-0.0925	-0.0723	0.4248
	DS	323	0.909	2832.47	5840.85	-183.1791	2711.9093	-0.0013	-0.0038	0.5067
	DSL	323	0.926	2972.74	5782.15	-724.8487	4043.2773	-0.0041	-0.0043	0.3882
	TN	372	0.925	2611.12	6555.77	377.9900	3157.8841	-0.1050	-0.0920	0.4464
	CSA	323	0.924	2972.74	5795.85	-864.2562	4016.2179	-0.0007	-0.0007	0.3898
	DDR	372	0.916	2720.92	6574.79	296.2751	2878.5687	-0.0219	-0.0155	0.4782
	SFI	372	0.893	2650.61	6687.29	531.5950	1532.8792	0.0002	0.0008	0.6221
	MBH	372	0.941	2569.95	6468.74	303.9651	3108.5918	-0.1799	-0.0662	0.4187
	Hegyi's	372	0.931	2670.39	6481.29	232.3343	3503.6981	-0.2917	-0.1545	0.3971
	DWS	372	0.931	2694.23	6470.64	251.0979	3599.5557	-0.2985	-0.1636	0.3874
	MBD	372	0.923	2763.15	6770.69	102.6054	3298.3301	-0.0725	-0.0310	0.4046

Table 3. 5 Parameter values and statistical information for non-linear models of Douglas-fir growth

Models	CI	Oba #	Ad: D^2	DMSE	AIC	a	h	h	h	c
(cont.)	CI	ODS. #	Ац-л	KNISE	AIC	u	D ₁	<i>b</i> ₂	<i>D</i> ₃	ι
PAI BA	BAs	372	0.865	5.3258	2076.46	1.3327	5.4428	-0.0001	-0.0002	0.4943
	BAl	372	0.881	5.2720	2034.60	0.6730	7.3063	-0.0003	-0.0002	0.4050
	DI	372	0.911	4.7435	1905.43	1.1121	9.8358	-0.0708	-0.0512	0.2975
	HF	372	0.903	4.9119	1962.95	1.3699	8.6793	-0.0757	-0.0525	0.3354
	DS	372	0.867	5.2431	2070.88	1.2818	5.7496	-0.0016	-0.0036	0.4883
	DSL	372	0.890	5.0681	2004.68	0.3315	8.6477	-0.0046	-0.0036	0.3589
	TN	372	0.898	4.7879	1978.50	0.6132	9.1178	-0.0851	-0.0671	0.3365
	CSA	372	0.888	5.0681	2017.06	0.4175	8.2493	-0.0008	-0.0006	0.3702
	DDR	372	0.808	5.0854	2101.81	1.3106	6.0310	-0.0174	-0.0110	0.4770
	SFI	372	0.859	5.2483	2092.02	1.4780	4.7428	-0.0001	0.0001	0.4945
	MBH	372	0.902	4.7268	1954.63	1.2642	7.8083	-0.1337	-0.0427	0.3504
	Hegyi's	372	0.913	4.7072	1882.00	0.9985	9.9075	-0.2768	-0.1272	0.2922
	DWS	372	0.914	4.7249	1878.69	1.1332	9.9551	-0.2873	-0.1329	0.2889
	MBD	372	0.915	4.8390	1886.06	0.4669	9.7798	-0.0745	-0.0243	0.2917
PAI HT	BAl	372	0.681	0.1521	-413.89	1.1189	-0.3670	0.0003	0.0004	-0.1968
	DI	372	0.737	0.1412	-477.05	-0.0108	0.8817	-0.0262	-0.0375	0.0271
	HF	372	0.769	0.1357	-521.36	-0.1624	1.0652	-0.0300	-0.0429	0.0176
	DS	372	0.656	0.1530	-391.51	1.2839	-0.5897	0.0005	0.0028	-0.1512
	DSL	372	0.702	0.1480	-436.50	1.1513	-0.3565	0.0043	0.0053	-0.1511
	TN	372	0.627	0.1441	-408.49	2.3987	-1.6363	0.0169	0.0114	-0.0381
	CSA	372	0.687	0.1480	-421.01	1.1568	-0.3881	0.0007	0.0009	-0.1624
	DDR	372	0.718	0.1448	-456.59	1.1578	-0.3614	0.0166	0.0153	-0.1464
	SFI	372	0.575	0.1544	-363.15	3.3959	-2.7862	-0.0001	-0.0004	-0.0337
	MBH	372	0.821	0.1319	-605.17	0.2032	0.7502	-0.1177	-0.0648	-0.0086
	Hegyi's	372	0.747	0.1394	-492.32	0.0328	0.8351	-0.1049	-0.1156	0.0282
	DWS	372	0.747	0.1394	-492.32	0.0331	0.8347	-0.1050	-0.1157	0.0282
	MBD	372	0.714	0.1439	-413.89	2.5679	-1.7868	0.0081	0.0069	-0.0244

Note: the number of observations (obs. #), model AIC, and equation parameters $(a, b_1, b_2b_3 \text{ and } c)$, where b_2 is related to conifers and b_3 to red alder for the competition indexes. Significant parameter values are shown in bold type. The model used for relationships with competition indexes is: $Y = a + b_1 e^{b_2 CI_{conif} + b_3 CI_d r} BAi^c + \epsilon$.



Fig. 3. 11 Douglas-fir: Scatter plots of standardized residuals against fitted PAI VOL values, histograms of the normalized residuals and Q-Q plot of random effects for the best fitting PAI VOL model during the period of 1998 to 2006 (MBH).



Fig. 3. 12 The responses of Periodic Annual Increment (PAI) stem volume of Douglas-fir subject trees as affected by the amount of conifers (MBH of conifers) and the amount of red alder (Dr MBI) competition at each installation site.



Fig. 3. 13 The responses of PAI stem volume of Douglas-fir subject trees as response to MBH coniferous competition, MBH red alder competition, and initial basal area in each plot at all installation sites. Fixed effects (population level) in blue, site effects in pink, and plot effects (stand level) in green.



Fig. 3. 14 Relationships between PAI stem volume of Douglas-fir and the modified Braathe index (MBH) of conifers (solid red line) and red alder (dashed blue line) and initial basal area of Douglas-fir subject trees (right plot). The curves are calculated using the mean value of MBH of each species and mean value of initial BA respectively. The model and parameter values are provided in table 3.5.



Fig. 3. 15 Relationships between PAI basal area of Douglas-fir and the DWS of conifers (solid red line) and red alder (dashed blue line) and initial basal area of Douglas-fir subject trees (right plot). The curves are calculated using the mean value of DWS of each species and mean value of initial BA respectively. The model and parameter values are provided in Table 3.5.



Fig. 3.16 Relationships between PAI height of Douglas-fir and the MBH of conifers (solid red line) and red alder (dashed blue line) and initial basal area of Douglas-fir subject trees (right plot). The curves are calculated using the mean value of MBH of each species and mean value of initial BA respectively. The model and parameter values are provided in Table 3.5.

Table 3.5 shows the parameter values and statistical information for non-linear models, which was used to examine competition effects on Douglas-fir growth and compare the effectiveness of 14 competition indices. For Douglas-fir, the competition measure with the highest adjusted R^2 and more significant parameters was the modified Braathe index (MBH, height differences between subject tree and neighbors weighted by the distance) for stem volume (adjusted $R^2 = 0.941$, n = 372) (Table 3.5). The height factor (HF, adjusted $R^2 = 0.932$, n = 372) ranked in second place of all indices tested for Douglas-fir PAI stem volume. For Douglas-fir PAI basal area, the distance weighted size ratio (DWS, adjusted $R^2 = 0.914$, n = 372) has the highest adjusted R^2 with all the parameters in the model being significant (Table 3.5). The modified Braathe index (MBD, diameter differences between subject tree and neighbors weighted by distance) had a slightly higher adjusted R^2 but less significant parameters than DWS for basal area. For Douglas-fir PAI height, the competition measure with the highest adjusted R^2 was MBH (adjusted $R^2 = 0.821$, n = 372), followed by DWS and Hegyi's index (adjusted $R^2 = 0.747$, n = 372).

Relationships between western redcedar growth and competition indices are presented in Table 3.6. Both Lorimers' index (DI) and DWS had the highest adjusted R^2 . However, with consideration of the highest adjusted R^2 , lowest RMSE and AIC, and more parameters to be significant, Lorimer's index was considered as the best index for both stem volume (adjusted $R^2 = 0.792$, n = 261) and basal area (adjusted $R^2 = 0.819$, n = 268) of western redcedar. For PAI height, MBH had the highest adjusted R^2 with 68.3% of the variations can be explained by the model (n = 260). The distribution of the residuals and the random effects confirm good overall model fit (Fig. 3.16).

Response	CI	Obs. #	Adj- <i>R</i> ²	RMSE	AIC	а	b_1	b ₂	b_3	С
PAI _{vol}	BAs	261	0.660	1425.85	4525.63	941.6475	2112.9176	-0.0001	-0.0004	0.6419
	BAl	261	0.689	1377.15	4498.98	523.8870	3281.2088	-0.0004	-0.0004	0.4907
	DI	261	0.792	1146.12	4333.83	137.7647	5506.8447	-0.0841	-0.0511	0.2362
	HF	261	0.776	1184.75	4377.76	111.2197	5462.4361	-0.0885	-0.0462	0.2621
	DS	261	0.668	1419.53	4524.84	963.4578	2256.8379	-0.0024	-0.0054	0.6402
	DSL	261	0.718	1336.75	4470.31	40.3820	4523.0136	-0.0065	-0.0045	0.3572
	TN	261	0.746	1266.73	4429.12	-614.7307	5990.3418	-0.1033	-0.0589	0.2340
	CSA	261	0.708	1336.75	4485.67	256.0905	3874.0555	-0.0012	-0.0008	0.4070
	DDR	261	0.738	1351.06	4461.17	-63.9029	4428.9780	-0.0213	-0.0090	0.3466
	SFI	255	0.683	1481.60	4416.92	907.8027	1792.9347	-0.0062	0.0220	0.5992
	MBH	260	0.752	1230.57	4400.05	213.8318	4503.0967	-0.1037	-0.0529	0.3129
	Hegyi's	260	0.787	1183.11	4338.39	180.2367	5129.7567	-0.2811	-0.0980	0.2677
	DWS	261	0.792	1179.02	4336.80	128.3964	5183.8860	-0.2784	-0.0959	0.2506
	MBD	261	0.771	1187.91	4354.94	428.0120	4307.7324	-0.0714	-0.0473	0.3269
PAI _{BA}	BAs	268	0.650	1425.85	1376.70	2.4878	5.4745	0.0000	-0.0004	0.5413
	BAl	268	0.687	1377.15	1340.92	2.4736	7.2410	-0.0004	-0.0004	0.5048
	DI	268	0.819	1146.12	1208.53	1.5339	12.1017	-0.0864	-0.0481	0.2549
	HF	268	0.786	1184.75	1260.32	1.8117	11.0105	-0.0860	-0.0519	0.3152
	DS	268	0.654	1419.53	1375.92	2.5404	5.7508	-0.0012	-0.0054	0.5464
	DSL	268	0.732	1336.75	1323.13	2.1710	8.4089	-0.0069	-0.0048	0.4498
	TN	268	0.765	1266.73	1286.87	1.8730	10.1291	-0.1187	-0.0781	0.3680
	CSA	268	0.718	1336.75	1334.27	2.2865	7.7312	-0.0013	-0.0009	0.4757
	DDR	268	0.740	1351.06	1312.93	1.7158	8.9016	-0.0218	-0.0116	0.4146
	SFI	268	0.643	1481.60	1389.30	2.3364	4.9448	-0.0007	0.0031	0.5114
	MBH	267	0.759	1230.57	1275.39	1.6606	9.4726	-0.0936	-0.0598	0.3439
	Hegyi's	267	0.818	1183.11	1201.16	1.3370	11.8949	-0.2842	-0.0981	0.2552
	DWS	267	0.818	1179.02	1201.06	1.3575	11.8776	-0.2849	-0.0986	0.2559
	MBD	267	0.814	1187.91	1223.02	1.7374	9.9153	-0.0721	-0.0391	0.3096

Table 3. 6 Parameter values and statistical information for non-linear models of Western redcedar growth.

Response	CI	Obs. #	Adj- <i>R</i> ²	RMSE	AIC	а	<i>b</i> ₁	b ₂	b ₃	С
(cont.)			Ū				-	-	U U	
PAI _{HT}	BAs	261	0.513	1425.85	-432.57	0.2539	0.2680	0.0000	-0.0001	0.1783
	BAl	261	0.546	1377.15	-435.91	0.3174	0.2477	-0.0003	-0.0002	0.2340
	DI	261	0.662	1146.12	-507.43	-0.3906	1.0398	-0.0155	-0.0069	0.0208
	HF	261	0.591	1184.75	-492.26	-0.1253	0.7793	-0.0235	-0.0132	0.0408
	DS	261	0.523	1419.53	-425.18	0.3565	0.1770	-0.0011	-0.0018	0.3095
	DSL	261	0.569	1336.75	-445.39	0.2321	0.3643	-0.0037	-0.0012	0.1423
	TN	261	0.603	1266.73	-463.72	-0.3018	0.9286	-0.0257	-0.0050	0.0376
	CSA	261	0.557	1336.75	-439.19	0.2660	0.3124	-0.0007	-0.0002	0.1716
	DDR	260	0.482	1351.06	-429.79	0.3029	0.2728	-0.0101	-0.0091	0.2093
	SFI	259	0.542	1481.60	-428.75	0.3375	0.1678	0.0004	0.0190	0.2666
	MBH	260	0.683	1230.57	-539.83	0.1203	0.5346	-0.0561	-0.0248	0.0635
	Hegyi's	260	0.657	1183.11	-502.16	-0.2097	0.8532	-0.0646	-0.0185	0.0292
	DWS	260	0.563	1179.02	-473.90	0.0210	0.6110	-0.0809	-0.0375	0.0513
	MBD	260	0.632	1187.91	-484.26	0.0836	0.5312	-0.0243	-0.0121	0.0649

Note: the number of observations (obs. #), model AIC, and equation parameters (a, b_1 , b_2b_3 and c), where b_2 is related to conifers and b_3 to red alder for the competition indexes. Significant parameter values are shown in bold type. The model used for relationships with competition indexes is: $Y = a + b_1 e^{b_2 CI_{conif} + b_3 CI_{d}r} BAi^c + \epsilon$.

The results indicate that the best fitting model was consistently obtained from the combination of coniferous and deciduous competition with initial subject tree basal area, and with most of the parameters in the models being significant for conifer growth (Table 3.5 and 3.6). For Douglas-fir and western redcedar, parameter values for coniferous competition were larger than those for red alder, indicating that conifers were having stronger competition effects (per unit of competition index) than red alder. Furthermore, competition was having a stronger effect on Douglas-fir than western redcedar, as indicated by the higher parameter values of Douglas-fir than those for western redcedar (Table 3.5 and 3.6).

After preliminary model testing, the best model fit appeared to include installation sites and plots as random effects, and with all the parameters being fixed as well as intercept and parameter c

being random (see the equation formation in the appendix). Fig. 3.11 shows all levels of the model effects including population level as fixed effects together with stratified random effects: site level (six installation sites) and plot level (five plots each site). The observations of conifer growth in relation to competition were illustrated in Fig. 3.10 (Fd) and Fig. 15 (Cw). Substantial variations were evident among the installation sites. There are small numbers of observations at some sites due to poor tree survival and poor site conditions. However, conifer growth followed the expected negative trend, decreasing with increasing competition (Fig. 3.11). The negative relationship was also evident with red alder competition. A stronger negative impact of coniferous competition than red alder was indicated by the higher negative parameter estimate of b₂ compared to b₃ in the models (Table 3.5 and 3.6). Such stronger effects can also be seen from the steeper slopes in coniferous competition relative to red alder competition against conifer growth (Fig. 3.12, 3.13, and 3.14). The positive correlations between initial basal area and conifer growth are shown in the figures mentioned above for each plot separately. This strong relationship was reflected in the large parameter estimates of c in Table 3.5 and 3.6. Generally, the plot level curve fit more closely to the observations compared to other level fits. As all the model fits showed significant deviation from each other, this makes inclusion of site and plot as random factors necessary. Similar trends are also evident in the responses of western redcedar to competition (Fig. 3.18, 3.19, and 3.20).



Fig. 3. 17 The responses of PAI stem volume of western redcedar subject trees as affected by the amount of conifers (DI of conifers) and the amount of red alder (DI) competition at each installation site.

Scatterplot of Standardized Residuals vs. fitted values

Scatterplot of PAI_ht vs. fitted values



Fig. 3. 18 Western redcedar: scatter plots of standardized residuals against fitted PAI VOL values, histograms of the normalized residuals and Q-Q plot of random effects for the best fitting PAI VOL model during the period of 1998 to 2006 (DI).



Fig. 3. 19 The responses of PAI stem volume of western redcedar subject trees as response to DI coniferous competition, DI red alder competition, and initial basal area in each plot at all installation sites. Fixed effects (population level) in blue, site effects in pink, and plot effects (stand level) in green.



Fig. 3. 20 Relationships between PAI VOL of western redcedar and the DI of conifers (solid red line) and red alder (dashed blue line) and initial basal area of Douglas-fir subject trees (right figure). The curves are calculated using the mean value of DI of each species and mean value of initial BA respectively. The model and parameter values are provided in Table 3.6.



Fig. 3. 21 Relationships between PAI BA of western redcedar and the DI of conifers (solid red line) and red alder (dashed blue line) and initial basal area of Douglas-fir subject trees (right figure). The curves are calculated using the mean value of DI of each species and mean value of initial BA respectively. The model and parameter values are provided in Table 3.6.



Fig. 3. 22 Relationships between PAI HT of western redcedar and the MBH of conifers (solid red line) and red alder (dashed blue line) and initial basal area of Douglas-fir subject trees (right figure). The curves are calculated using the mean value of MBH of each species and mean value of initial BA respectively. The model and parameter values are provided in Table 3.6.

3.3 Light responses to red alder density treatments and competition effects

3.3.1 Total light measures in relation to red alder basal area

Fig. 3.23 illustrates the light level data distribution as response to the series of red alder density at three additive experiment sites in 2017. Gough and Holt Creek show similar responses while Waterloo Creek is substantially different from those two sites. Total light level of each plot was examined to test density effects using a non-linear mixed model. The light measures were log transformed to meet model assumptions and the measures from two replacement sites were not included in the analysis. The results revealed both density and basal area had negative correlations with understory light levels, and the parameters of the model were significant (Table 3.7). With consideration of both AIC and adjusted R^2 values, the model with basal area showed better model fit. Fig. 3.21 shows the relationship between DIFN and stand basal area of each

species and sum of all species' basal area, the light level variation explained by alder basal area was about 38.5%. The model with stand basal area of all three species included showed the best model fit compared to other individual model with only one species' basal area. And all the parameter values in M1 are significant. However, the variations explained by model M1 (*Adj*- R^2 =0.386) were slightly higher than the M2.



density 📋 0 🛱 50 🛱 100 🛱 200 🗰 400

Fig. 3. 23 Boxplot of DIFN values relative to red alder density at each installation site (additive experiment) in 2017.

Table 3. 7 Parameter values and determination of coefficients for non-linear mixed model of total light levels in relation to red alder basal area

Model	Basal area (cm ² ha ⁻¹)	Light response	Obs. #	Adj-R ²	RMSE	AIC	а	b1	b2	b3
M1	Dr+Fd+Cw	Ln(difn)	149	0.386	0.5642	264.6041	-2.4580	-0.0953	-0.05528	-0.1365
							(<.0001)	(<.0001)	(<.0001)	(<.0001)
M2	Dr	Ln(difn)	149	0.3851	0.6304	285.9608	-3.8324	-0.0919		
							(<.0001)	(0.084)		
M3	Fd	Ln(difn)	149	0.3147	0.6512	291.8723	-3.0256		-0.0809	
							(<.0001)		(0.0781)	
M3	Cw	Ln(difn)	149	0.1628	0.6587	294.0225	-3.5966			-0.1120
							(<.0001)			(<.0001)
M4	Sum	Ln(difn)	149	0.3850	0.5785	272.9619	-2.7271		-0.0671	
		× /					(<.0001)		(<.0001)	

Note: the number of observations (obs. #), model AIC, and equation parameters $(a, b_1, b_2 \text{ and } b_3)$, where b_1, b_2 , and b_3 relate to the basal area of red alder, Douglas-fir, and western redcedar respectively. P-values are shown in the


parentheses. The mixed model used for relationships between all species' basal area and light levels (DIFN) is: $Y = a + b_1X_1 + b_2X_2 + b_3X_3 + \epsilon$.

Fig. 3. 24 Relationship between DIFN (log transformed) and red alder stand basal area (m²/ha), the model is $Y = a + b\mathbf{1}X + \varepsilon$.



Fig. 3. 25 Scatter plots of standardized residuals against fitted values, histograms of the normalized residuals and Q-Q plot of random effects for the best fitting NLME, the light was measured in 2017.

3.3.2 Conifer growth relative to individual tree light levels

The light (DIFN) measures of subject trees in 2004 together with initial CSA as two explanatory variables were used to test the growth responses of two conifer species. The results from the non-linear mixed models shown in the Table 3.8 indicate that both independent variables had positive correlations with PAI stem volume (adjusted R^2 , Fd=0.835 and Cw=0.837) and basal area (adjusted R^2 , Fd=0.736 and Cw=0.797), where stem volume increments for both species had higher correlation with light than basal area increments. There were variations evident among the

installation sites particularly higher variations of conifer growth among sites (Fig.22 and 3.23, Fig.3.24 and 3.25). Initial CSA had bigger impacts on the growth responses compared to light levels (larger parameter values for initial CSA). As is also evident in Fig. 3.22, 3.23, 2.25 and 3.26, initial CSA tends to have much steeper slopes, which indicates stronger effects on conifer growth. Most of the parameters were significant in the model except for the intercept (Table 3.8). Fig.3.24 and Fig. 3.27 indicate overall good fit of the model of growth response to light. The residuals are normal and evenly distributed and random effects are within one straight line in the Q-Q plot.

Western redcedar growth response to DIFN										
	Response									
Species	Variable	Obs. #	Adj-R ²	RMSE	AIC	а	b ₁	b ₂	С	
Fd	PAI _{BA}	112	0.736	5.459	688.639	-7.4263	8.3451	0.1060	0.4628	
	PAI _{VOL}	112	0.835	2862.09	2082.39	-86.1981	997.03	0.0754	0.8571	
	PAI _{HT}	112	0.527	0.1523	-111.573	0.5832	0.1238	-0.1696	0.2962	
Cw	PAI _{BA}	53	0.797	2.7128	274.545	0.4186	2.1482	0.2255	0.9775	
	PAI _{VOL}	53	0.837	1141.36	910.382	243.6486	492.3209	0.2442	1.2494	

Table 3. 8 Parameter values and statistical information for non-linear mixed models of Douglas-fir and

 Western redcedar growth response to DIFN

Note: the number of observations (obs. #), *adjusted-R*², RMSE, model AIC, and equation parameters $(a, b_1, b_2 \text{ and } c)$, where b_2 is the power function of DIFN, c is the power function of initial crown surface area (CSAi). Significant parameter values are shown in bold type. The model used for relationships with competition indexes is: $Y = a + b_1 X^{b_2} CSAi^c + \varepsilon$.



Fig. 3. 26 The responses of PAI basal area of Douglas-fir subject trees as response to DIFN and initial basal area at each installation site. Fixed effects (population level) in blue, site effects (stand) in pink, the model is $Y = a + b_1 X^{b_2} CSAi^c + \varepsilon$. Parameter values and statistical information for the non-linear mixed effects model are provided in Table 3.8.



Fig. 3. 27 The responses of PAI stem volume of Douglas-fir subject trees as response to DIFN and initial basal area at each installation site. Fixed effects (population level) in blue, site effects (stand) in pink, the model is $Y = a + b_1 X^{b_2} CSAi^c + \varepsilon$. Parameter values and statistical information for the non-linear mixed effects model are provided in Table 3.8.

Scatterplot of Standardized Residuals vs. fitted values

Scatterplot of PAI_vol vs. fitted values



Fig. 3.28 Scatter plots of standardized residuals against fitted PAI VOL values of Douglas-fir, histograms of the normalized residuals and Q-Q plot of random effects for the best fitting PAI VOL model during the period of 1998 to 2006, the light was measured in 2004. Scatterplots of PAI BA were provided in the appendix.





Fig. 3. 29 The responses of PAI VOL of western redcedar of subject trees as response to DIFN and initial basal area at each installation site. Fixed effects (population level) in blue, site effects (stand) in pink, the model is $Y = a + b_1 X^{b_2} CSAi^c + \varepsilon$. Parameter values and statistical information for the non-linear mixed effects model are provided in Table 3.8.



Fig. 3. 30 The responses of PAI BA of western redcedar of subject trees as response to DIFN and initial basal area at each installation site. Fixed effects (population level) in blue, site effects (stand) in pink, the model is $Y = a + b_1 X^{b_2} CSAi^c + \varepsilon$. Parameter values and statistical information for the non-linear mixed effects model are provided in Table 3.8.

Scatterplot of Standardized Residuals vs. fitted values

Scatterplot of PAI_ht vs. fitted values



Fig. 3. 31 Scatter plots of standardized residuals against fitted PAI VOL values of western redcedar, histograms of the normalized residuals and Q-Q plot of random effects for the best fitting PAI VOL model during the period of 1998 to 2006, the light was measured in 2004. Scatterplots of PAI BA were provided in the appendix.

3.3.3 Individual tree light levels in relation to competition indices

Preliminary analysis indicated that the non-linear mixed model performed better in modeling light levels than a simple linear model. The individual tree light levels of Douglas-fir in 2004 were best predicted using basal area sum (BAs) with 80.0% of the variation explained (n = 112), and followed by basal area larger (BAl) (adjusted $R^2 = 0.7666$, n = 112) (Table 3.9).

Models	CI	Obs. #	Adj-R ²	RMSE	AIC	а	b_1	b ₂	b ₃	
DIFN Douglas-fir										
nlme1	BAs	112	0.8000	0.1330	-138.38	-2.9970	3.9237	0.0000	-0.0001	
nlme2	<mark>BA1</mark>	112	0.7666	0.1439	-136.40	0.2059	0.6995	0.0000	-0.0012	
nlme3	DI	112	0.5940	0.1557	-86.86	0.3638	0.5285	0.0148	-0.5199	
nlme4	HF	112	0.5198	0.1622	-81.69	0.4324	0.4545	0.0201	-0.7438	
nlme5	DS	112	0.6220	0.1439	-102.39	0.0801	0.8452	-0.0001	-0.0149	
nlme6	DSL	112	0.5597	0.1569	-98.85	0.3362	0.5762	-0.0001	-0.0265	
nlme7	TN	112	0.4742	0.1697	-111.55	0.5216	0.3677	0.0008	-0.7073	
nlme8	CSA	112	0.4870	0.1569	-111.48	0.5203	0.3759	-0.0001	-0.0080	
nlme9	<mark>DDR</mark>	112	0.4969	0.1660	-109.95	0.5057	0.3903	-0.0016	-0.1172	
nlme11	<mark>MBH</mark>	112	0.2334	0.2050	-86.31	0.1697	0.6826	-0.0210	-0.1417	
nlme12	Hegyi's	112	0.4607	0.1719	-107.50	0.5595	0.3246	0.0091	-1.8324	
nlme13	<mark>DWS</mark>	112	0.4607	0.1719	-107.50	0.5595	0.3246	0.0091	-1.8324	
nlme14	MBD	112	0.7515	0.1530	-135.10	0.4478	0.4478	-0.0047	-0.2901	
DIFN Western Redcedar										
nlme1	BAs	53	0.5544	0.2064	-7.3761	0.2053	0.7210	-0.0001	-0.0021	
nlme2	BAl	53	0.5790	0.2006	-8.0480	0.0938	0.8470	-0.0001	-0.0015	
nlme3	DI	53	0.6037	0.1946	-11.5225	0.1403	0.7630	-0.0054	-0.2249	
nlme4	HF	53	0.6052	0.1942	-12.6540	0.0391	0.9211	-0.0168	-0.1959	
nlme5	DS	53	0.5413	0.2094	-10.1557	0.1823	0.7827	-0.0015	-0.0270	
nlme6	DSL	53	0.5823	0.1998	-9.8834	-0.1969	1.2028	-0.0023	-0.0127	
nlme7	TN	53	0.5545	0.2063	-6.3790	-0.1609	1.1565	-0.0308	-0.2334	
nlme8	CSA	53	0.5792	0.1998	-4.3974	-1.3129	2.3228	-0.0003	-0.0010	
nlme9	DDR	53	0.6980	0.1768	-18.1257	0.1355	0.7797	-0.0043	-0.0810	
nlme11	MBH	53	0.6868	0.1730	-19.9694	0.1642	0.7446	-0.0132	-0.4050	
nlme12	Hegyi's	53	0.6642	0.1791	-18.2683	0.1723	0.7079	-0.0029	-0.8147	
nlme13	DWS	53	0.6899	0.1759	-18.3956	0.1830	0.6772	0.0042	-0.8223	
nlme14	MBD	53	0.7677	0.1711	-17.3232	0.2110	0.6492	-0.0007	-0.1905	

 Table 3. 9
 Parameter values and Coefficient of determinations for linear mixed models of mean light levels in relation to each selected competition indices

Note: the number of observations (obs. #), model AIC, and equation parameters (a, b_1, b_2b_3) , where b_2 is related to conifers and b_3 to red alder for the competition indexes. Significant parameter values are shown in bold type. The model used for relationships with competition indexes is: $Y = a + b_1 e^{b_2 CI_{conif} + b_3 CL_dr} + \varepsilon$, Y is the DIFN for the subject trees.

Although MBD ranked as the third best competition measure but the intercept and parameter b_1 in the model were significantly related to Douglas-fir light levels (adjusted $R^2 = 0.7515$, n = 112). Red alder competition had stronger influence on DIFN than coniferous competition, but the

parameter values related to conifers and red alder were not significantly related to DIFN. For western redcedar, DIFN had the highest correlations with the distance dependent competition index MBD (adjusted $R^2 = 0.7677$, n = 53), and second highest with diameter distance ratio (DDR, adjusted $R^2 = 0.698$, n = 53) (Table 3.9). Fig. 3.28 shows the relationship between DIFN and competition indices. The light levels decrease as competition increases, and red alder competition impacts were more significant than conifers. The distribution of the residuals and the random effects confirm good overall model fit (Fig. 3.29 and 3.30).



Fig. 3. 32 Relationships between DIFN and the MBH of conifers (red line) and red alder (blue line). The curves are calculated using the mean value of MBH of each species. The model and parameter values are provided in Table 3.2.2.



Fig. 3. 33 Scatter plots of standardized residuals against fitted DIFN values of Douglas-fir, histograms of the normalized residuals and Q-Q plot of random effects for the best fitting DIFN model in 2004.



Scatterplot of PAI_vol vs. fitted values



Fig. 3. 34 Scatter plots of standardized residuals against fitted DIFN values of western redcedar, histograms of the normalized residuals and Q-Q plot of random effects for the best fitting DIFN model in 2004.

3.4 Soil and foliage nitrogen

A non-linear mixed effects model with site variations as random terms was used to analyze mineralizable soil nitrogen and Douglas-fir foliar nitrogen. Red alder density showed better model fits than its basal area (Table 3.10). In general, increasing amounts of alder in the stand tends to be associated with higher soil nitrogen availability (Fig. 3.32). Foliar nitrogen of Douglas-fir seems to reach a peak at 250 alder per hectare and showed slight decrease as alder density increases beyond that point. Only the intercept of the model was found to be significant

among all the correlations (Table 3.10).

Response	Explanatory	a	b1	b2	AIC	n
variable	variable					
Ln Mineralizable	DR Density	1209.2983	0.0021	-0.0013	218.76	14
nitrogen		(<.0001)	(0.4371)	(0.8680)		
	DR BA	1204.2248	65.3215	7.5359	221.38	14
		(<.0001)	(0.4499)	(0.5196)		
Foliar nitrogen	DR Density	1.2923	0.0015	-2.6e-6	0.79	15
		(<.0001)	(0.3168)	(0.4903)		
	DR BA	1.3074	0.0292	-4.6e-4	13.98	15
		(<.0001)	(0.6185)	(0.9477)		

Table 3. 10 Parameter values and statistical information for non-linear model of nitrogen availability

Note: the model used for the relationship between density or basal area and nitrogen is: $Y = a + b1X + b2X^2 + \varepsilon$, where Y is nitrogen availability and X is alder density (stems per hectare).



Fig. 3. 35 Relationships between nitrogen (both soil mineralizable and foliage nitrogen) and alder basal area. The line is described by a polynomial regression model: $Y = a + b1 X + b2 X^2 + \varepsilon$, where Y is nitrogen availability and X is alder density (trees per hectare). Parameter values and other statistical information can be found in Table 3.4.

4. Discussion

4.1 Effects of red alder density on growth of Douglas-fir and western redcedar

As tree age increases, larger differences in tree height, diameter, stem volume, and survival were evident among the alder density treatments that were applied at four additive experiment sites. However, there was also substantial variation in the responses of Douglas-fir and western redcedar to gradients in alder density between plots and between installations.

For Douglas-fir, there were positive correlations between tree height and the amount of red alder, and such correlations were getting stronger as trees grow. After age 4, the highest height and stem volume growth were found with the highest density treatments (except for stem volume which was highest with 200-tph treatment after age 10). This is consistent with observations of increased growth of Douglas-fir in mixture with red alder when growing on nitrogen deficient sites (Binkley 1983, Cortini and Comeau 2008). However, other response variables such as basal area and height to diameter ratio of Douglas-fir were largest with no red alder in the stand. For western redcedar, all response variables I tested seem to have more evident positive correlations with 100 tph red alder (stem volume was the highest with 100 tph after age 7). Positive effects (nitrogen availability) of alder might have outweighed the competitive effects on the cedar's growth in the moderate alder density stands. At the lower end of the density range benefits are small relative to variability between locations and plots. Higher alder densities result in competition becoming dominant over beneficial effects. This might have contributed to the nonsequential growth response across the range of density treatments. Another explanation might be that western redcedar is more shade tolerant than Douglas-fir, which may have also contributed to the less sensitive responses to red alder across the range of densities (Peterson et al. 1996, Harrington 2006). For red alder, moderate density contributes to higher tree size, which is not surprising.

Our study revealed similar height growth patterns for alder and conifers as reported in previous studies (Williamson 1968, Omule 1987, Green and Klinka, 1994). Significantly greater early growth of alder was apparent during the first 15 years compared with its conifer associates. Then the growth slowed considerably by age 20 and was surpassed by Douglas-fir height growth. Studies have shown that red alder approaches maximum total height before age 50, while both Douglas-fir and western redcedar continue to grow and eventually overtop the surrounding alder (DeBell et al. 1978, Omule 1987, Deal 2006). Longer-term succession and development for mixed alder-conifer stands has not been well documented and varies widely with tree species, initial stand density, site factors, disturbance and management practices (Deal et al. 2017). Since red alder is shade intolerant and relatively short-lived species, it is expected to eventually die out of these mixed stands within a few decades of being overtopped and suppressed by surrounding conifers. However it is unclear how long this exclusion will take. Some studies in the Pacific Northwest reported that most alder stands were breaking up by age 50, few remain intact beyond age 100, and all will succumb in less than 130 years (Chambers 1983, Newton and Cole 1994, Knowe et al. 1997). The highest alder density (400 tph) used in our study was only roughly 25 % of the stand composition, which showed no significant negative impacts on the conifer growth. Besides the wood production aspect, mixed alder-conifer stands also provide more ecosystem services and functions such as increasing biodiversity and improving wildlife habitat (Deal 2007, Hanley et al. 2006). Also, the mixed forest will benefit from the legacy of soil nitrogen inputs into the ecosystem by red alder even long after they have died and decayed. Retaining decadent or dead alder stems are very important for wildlife and biodiversity, especially cavity-nesting wildlife.

Results overall suggest that red alder densities of up to 400 stems per hectare have significant positive effects on tree height of all three species, but little or at most only small effects on diameter or volume of Douglas-fir or western redcedar. However, results are strongly affected by variation within and between study sites. The inconsistent alder density (caused by mortality mainly) contributed strongly to such variation. Consequently, stand basal area of red alder is likely to more accurately reflect the amount of alder. Additionally, stand age is a confounding factor that influences growth of mixed alder-conifer stands. Previous studies have suggested that stand age influences tree growth and interacts with competition (Wagner and Radosevich 1991). As expected, red alder height growth slowed down around the year 20 and with height of Douglas-fir often exceeding height of alder (Green 1994).

As mentioned above, there is substantial variation in survival of planted alder on the largely circum-mesic sites used for this study. The fact that small differences among alder density treatments were found may result from red alder not doing well on these sites in our study. All of the treatment plots above the road at East Wilson Creek, and the upper plots at Gough Creek were too dry (ie. submesic), so alder was not very competitive. Waterloo Creek was mesic with slightly wetter spots where alder grew well. Holt Creek had portions of plots and some entire plots with low areas where alder did well due to increased soil moisture availability. It is important to recognize that these are generally not good sites for red alder and as a result, their effects on Douglas-fir and western redcedar are not as large as they might be on better sites (wetter, subhygic and hygric) where alder can grow better. It is also difficult to fit tree growth data with respect to a wide time period into a mixed effects model that is linear in the parameters, as we can see a sigmoidal shape relative to growth years in Fig.3.7. It may be necessary to extend linear mixed-effects models to nonlinear forms in the future. Incorporating climate into

the growth models might also improve model fits. Due to the fact that observations for treatments were staggered through time, climate conditions may have differed (in addition to the different locations experiencing differing climatic conditions), and in consequence, may have influenced tree growth either directly or indirectly.

4.2 Effects of competition on growth of Douglas-fir and western redcedar

4.2.1 Non-linear mixed effects competition models

Initial tree size as an independent variable in non-linear mixed models examining relationships between growth and competition has been widely used in competition studies to account for effects of differences in subject tree height and leaf area on light capture (Morris and MacDonald 1991, Filipescu and Comeau 2007). For the two conifer species examined in this study, initial tree basal area during the period of 8 growth years (1998-2006) was a highly significant variable in all non-linear mixed models. Moreover, the combination of the power of initial basal area and exponential competition indices fitted the data well, which was supported by Comeau et al. (2003) and Cortini and Comeau (2008). Due to the fact that the inclusion of size in competition indices may result in strong collinearity between independent variables, the collinearity was tested through calculating the VIF values for the variables used in the model. For each competition index used in this study, VIF values were generally lower than 3, which indicates that there is no correlation among the variables.

4.2.2 Comparisons between competition indices

The 14 competition indices we tested in our study varied in their effectiveness for predicting conifer growth, and such effectiveness is also dependent upon the crop species. The modified

Braathe index of height difference (MBH) had the best model fit in predicting volume and height growth of Douglas-fir. The distance weighted size ratios of subject trees and competitors have the best performance for Douglas-fir basal area growth. However for western redcedar, the Lorimer's distance-independent index gave the best model fit for volume and basal area growth. In general, distance dependent indices have better model fits for predicting Douglas-fir growth, which indicates that it is beneficial to utilize the distance dependent measures of competition that incorporate subject Douglas-fir size in the calculation. This is consistent with the findings from Daniels et al. (1986) that distance dependent indices work better in stands with more complex structure and relative-low density of competitors. For smaller trees at the low densities of broadleaf trees found in this study (0-400 tph), the distance between crop tree and competitors appears to be important in accounting competition (Comeau et al. 2003). However in our study distance-independent indices worked better for western redcedar height and basal area growth even though there were slight differences between the best distance dependent and distance independent indices. The fact that the stands are well stocked with low densities of alder may have minimized the differences between the effectiveness of the distance-dependent or independent indices for western redcedar. The smaller size of western redcedar may also be important factors to the performance of competition measures (Simard and Sachs 2004, Cortini and Comeau 2008). The mean size of western redcedar is substantially shorter than both red alder and Douglas-fir after stand establishment. Western redcedar has also shown higher mortality and inconsistent densities, fewer observations can be selected as subject trees for the calculation of competition (observations, Fd = 372, Cw = 260).

My results are similar to findings from other studies which have compared the differences in effectiveness of distance-dependent and distance-independent indices where results have shown

small differences that are often not consistently better for any group of indices (Hegyi 1974, Daniels et al. 1986, Pukkala 1989, Biging and Dobbertin 1992, Comeau et al. 2003, Ledermann 2010). In fact, simple indices such as height factor and Lorimer's index also performed well in our study. No single type of index performs consistently better than others under various conditions, because their performance varies with tree species, forest conditions and sites (Lorimer 1983, Biging and Dobbertin 1992). Small differences are also evident in our study between the best competition indices (distance dependent) and the second best (distance-independent) such as Lorimer's index (DI) and height factor (HF), as indicated by adjusted R^2 . In our study, the limited range of densities and levels of red alder competition, and the interaction between the beneficial effects of red alder on nitrogen availability (or other factors which vary depending on site and microsite) and its negative effects on light levels may have contributed to the small differences and inconsistent results.

4.2.3 Competition effects of conifers and red alder and their responses to competition

With the comparison of parameter values for competition effects from red alder and conifers, red alder has smaller competition influences on conifer growth (stem volume, basal area, and height). This agrees with previous studies where deciduous competition had a lower impact on conifer growth compared to intraspecific competition (Stadt et al. 2007; Huang et al. 2013). When interspecific competition is weaker than intraspecific competition, competition reduction may occur due to interspecific differentiation in resource use (Forrester 2014). As has been shown by several other studies, Douglas-fir is more affected by competition than western redcedar since redcedar is shade-tolerant while Douglas-fir is intermediate in tolerance (Hermann and Lavender 1990, Carter and Klinka 1992, Peterson et al. 1996, Harrington 2006). However, care must be

exercised in the ranking of tolerance, since the increased mortality and reduced growth of redcedar associated with drought and deer browsing may have compressed the range of its growth responses. Carter and Klinka (1992) have classified Douglas-fir as tolerant on moderately dry sites and redcedar as less tolerant, which may lead to redcedar's weaker responses to competition. It has also been suggested by Simard and Sachs (2004) that tree size or sensitivity to drought or nutrient limitations may be associated with species responses to competition.

4.3 Light responses to red alder density treatments

4.3.1 Total light measures in relation to red alder basal area

As has been shown by several other studies, basal area of broadleaf competitors is effective for describing variation in light levels (Comeau et al. 1998, Comeau 2002, Comeau and Heineman 2003). Our results confirmed that basal area of red alder had a higher value of R^2 and better model fit compared to alder density. The model with all three species included has shown the best model fit with all the parameter values being significant. Although western redcedar is the most shade tolerant species in the mixed stand, cedar's basal area showed the strongest correlation with understory light levels compared to other two species. It is not surprising since the cedar grows underneath the other two tree species and it has denser canopy. Its height growth is the slowest among the three species, and Green and Klinka (1994) projected that it will take approximate 80 years to reach the same height as red alder. Douglas-fir's basal area showed the least correlation with light which may because of its dominance in the overstory canopy at the age of 25, followed by the overtopped or co-dominant red alder with relatively stronger responses to light since alder is the least shade tolerant species.

4.3.2 The correlation between light levels and competition indices

MacDonald et al. (1990) and Comeau et al. (2003 b) have shown that sum of basal area (BAs) has the best predictive results for understory light. However our study suggests that the modified Braathe index of diameter difference (MBD) has the best model fit for light levels of both conifer species. Although BAs has the highest correlations with light levels, all parameter values are insignificant and small, which indicates weaker relationships between light and BAs than MBD. Similar to the relationships between conifer growth and competition, light levels at individual Douglas-fir were more influenced by competition effects than that of western redcedar. This indicates that stronger competition effects thus have greater impacts on light and resulted in stronger growth responses. Moreover, Reed et al. (1983) suggested that Douglas-fir seedling growth is related to light and N concentration with light being a dominant factor.

The results also illustrate that the influences of conifers and red alder on light availability are different. The parameter values for the model of DIFN against the competition indices (calculated separately for conifers and red alder), are larger (steeper slope) for red alder compared to the ones for conifers themselves (Fig. 3.22 and 3.23). This indicates that red alder has a stronger competition effect on light levels during midsummer than conifers. This is not surprising because of larger crown size and leaf thickness of alder which makes it more capable of intercepting light (Cortini and Comeau 2008).

4.3.3 Conifer growth relative to light levels

By using the light data measured in 2004 for each selected subject tree, the relationship between conifer growth and light levels (DIFN) was also investigated. Previous studies have shown that

conifer growth is related to both initial tree size and light levels (Comeau et al. 1993, Comeau et al. 2003, Claveau et al. 2002), which was also demonstrated in the results. Stem volume of both Douglas-fir and redcedar were positively influenced by light. Similar to findings from Cortini and Comeau (2008), redcedar growth was more affected by light levels and crown surface area (CSA) than Douglas-fir. Steeper slope of the parameter associated with CSA also indicated its stronger influences on conifer growth compared to light effects. The more shade-tolerant western redcedar is mostly growing below the main broadleaf and Douglas-fir canopy and light availability appears to be the primary factor limiting growth, therefore the higher correlations with the DIFN values. In summary, species shade-tolerance characteristics, the size and crown surface area of the trees at the time of the measurements, and interactions between effects of competition for light and nitrogen additions by red alder were probably the factors that contributed to this outcome (Cortini and Comeau 2008).

4.4 Soil and foliage nitrogen

Studies have shown that red alder can fix 100- 200 kg⁻¹ ha⁻¹ year⁻¹ nitrogen (N) in pure stands and 50-100 kg kg⁻¹ ha⁻¹ year⁻¹ in mixed species stands (Binkley et al. 1992, 1994; Swanston and Myrold 1997). Our study has also shown that N availability (mineralizable N) in the soil increases with red alder density or basal area. In addition to alder's N fixation capacity, its litterfall productivity with higher litter decomposition rates and fine roots turnover with high N contents all contribute to site N availability and potentially enhance Douglas-fir's growth (Binkley 1983, Binkley 2003). Similar to the findings of Shainsky and Rose (1995), N concentrations in Douglas-fir foliage were positively correlated with red alder density in spite of the fact that the influence of red alder on N availability in the soil was much greater than in Douglas-fir foliage. The increasing trend of soil N was apparent as the increasing of the amount of red alder in the stand, however the trend for Douglas-fir foliar N declined after passing peak levels at 200 alder per hectare. Lower foliar N concentrations in treatments with high alder density may be the result of co-limitation by phosphorous (P). Generally, the limited sampling in our study provided low power to explain the benefits of the abundance of red alder to soil and foliar N as well as the different responses of conifer growth to N availability. Studies have also showed that systematic sampling shallower than 2.0 m produced significantly smaller estimates of total N and such shallow sampling could lead to biased results and misleading conclusions (James et al. 2015). But most fine roots (of trees) are located in the upper 40 cm, so this is the most active zone and may be not a limiting factor. Also, other nutrient elements such as P or potassium may be affecting the results since they play an important role in tree growth and nutrient cycling as well.

4.5 Implications to free-growing standards

When growing in mixture with deciduous species that grow rapidly at young ages, a 1 m assessment radius is considered to be insufficient to characterize competitive environments for conifers (Lieffers et al. 2002, Cortini and Comeau 2007). Our results suggest that densities of up to 400 red alder per hectare (tph) may be acceptable at older ages. Herein highest height of all three species was found in the highest density treatments (400 tph) from age 7 to 20. Stem volume of Douglas-fir was found to be the highest in 400 tph from age 7 to 10, and 200 tph was best after age 10. Red alder density of 100 tph was consistently beneficial for western redcedar's size and growth. Also, densities of up to 400 tph tend to support better red alder growth. Due to the fact that red alder has been well recognized as an important timber species in the Pacific

Northwest region (Hibbs and DeBell 1994, Heebner and Bergener 1983), including red alder in conifer stands may be a win-win management practice. Current free-growing standards in B.C. do not accept red alder within a 1 m radius of conifers on coastal sites. While 1 alder within a 1 m radius may indicate that densities are sufficient to be problematic (approaching 10,000 alder per hectare), densities of 400 tph alder in our study would correspond to 1 alder in a 2.82 m radius plot (25m²), or up to 4 alder in a 5.64 m radius (100m²) plot. Therefore, the current assessment of free-growing status of subject trees may be overestimating red alder competition and the use of a larger radius plot should be considered for reducing expenditures on alder control and increasing stand productivity (Lieffers et al. 2002). However, my results are limited to mesic to sub-mesic sites which were sampled for this study where the effects of red alder are not as large as they might be on better sites where alder could grow well (wetter sites from subhygic to hygric). For natural stands and favorable site conditions for red alder, care should be taken in order to strike the balance between the competitive effects and facilitative effects. Application of spatial modeling incorporated with climate effects may have better estimation of future growth of the component tree species in alder-conifer mixed stands. Clearer treatment effects might be achieved through the use of actual density or basal area of red alder at associated ages in the growth mixed models instead of initial (i.e. treatment) density. Due to the fact that there was substantial tree mortality across the measurement years and that this varied between plots and locations. Future studies should explore effects of higher densities of red alder, a broader range of site conditions. In addition, ongoing measurement and evaluation of the plots used for my study are required to determine threshold values.

While results presented here come from artificially conditions where both conifers and red alder were planted, similar results are expected to apply where natural regeneration of red alder occurs at similar low densities in young conifer plantations. However, where red alder regenerates at higher densities, competitive effects would be expected to be much larger.

5. Conclusion

Our results indicate red alder density of 100 (redcedar) and 200 (Douglas-fir) tph has positive effects on the size of both Douglas-fir and western redcedar, especially height 4-7 years after planting of these species at four additive circum-mesic experiment sites. Stem volume of both conifer species were also improved by red alder (100 - 200 tph) at older ages (age 7 - 20). Consistent relationships between conifer growth and light levels at mid-crown height for both conifer species 4-6 years after stand establishment at both additive and replacement experiment sites were also found. While relationships between light and conifer growth were not influenced by sites, site to site variation was evident in effects of red alder density on size of these two conifer species. Higher alder density did increase nitrogen availability for the associated treatment plots. Basal area as the indicator of actual alder abundance in the associated year may have higher capability to predict either tree growth or light levels compared to initial alder density.

For predicting conifer growth, initial subject tree basal area (the first year of the growth period) was a highly significant explanatory variable along with various competition indices in nonlinear mixed models, and initial crown surface area was significant with light levels. No single competition index performed consistently better than the others in our study, with results varying by tree species and response variable. There were small differences between the best competition index and the second best, distance independent indices also performed nearly as well as distance dependent competition indices. The modified Braathe index of height difference (a distance dependent index) performed better than other competition indices for volume and height growth of Douglas-fir, while distance weighted size ratio was the best for Douglas-fir basal area growth. basal area growth of western redcedar. It is also worth noting that interspecific competition from red alder had weaker impacts on conifers than intraspecific competition from conifers themselves. As expected due to its greater shade tolerance, western redcedar showed less sensitivity to the presence of either red alder or conifer competition than Douglas-fir.

Limitations such as substantial site to site variation, inconsistent conifer survival, low alder densities, and lack of treatment replication at each site may have weakened the model fits and predictive abilities. Thus, more replications of treatment plots and higher densities of red alder should be considered to find an optimal density arrangement or threshold values. The limited number of plots sampled to determine soil and foliage nitrogen limited the ability to investigate relationships between nitrogen availability and tree growth or alder density. In addition, information on availability of phosphorus and other elements should be examined.

We found that current free-growing standards in B.C. are overestimating the competition from red alder. Our results thus recommend the use of larger plots or the application of stand level summaries of survey data, for evaluating red alder competition in coastal conifer plantations. Ongoing monitoring and measurement of the study installations, as well as quantifying the effects of climate, site, stand age and other factors are required to provide important information on long-term outcomes, including competitive and facilitative effects of red alder and their interactions on associated conifers and their yield and wood properties. The application of spatial models to calculate expected growth rates of the component tree species in a mixed species stand should also be considered when estimating future crop tree growth.

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Appendix

```
A.1 R code used for calculating distances between subject trees and competitors
```

```
Radius5.64 <- function(df){
 # df <- neighbor dataset
 df \leq -df[!is.na(df Syear), ]
 df <- df[!is.na(df$northing), ] # Remove the NA values
 plot id <- unique(df$plot)</pre>
year <- unique(df$year) # confirm NA values removed
                          # put the output in the dataframe
 output <- data.frame()
for(i in 1:length(plot id)){ # 1st loop locate each PLOT
  for(j in 1:length(year)){ # 2nd loop locate each year
   test <- subset(df, plot==plot id[i] & year==year[j])
   # Calculate the distance from the neighbor trees to all subject
   test id <- test[, c("tree", "northing", "easting")]
   test id <- test id %>% mutate(k = test[1, "tree"])
   # Set up a fake key to join on (a constant from each plot first row of tree number)
   test id <- test id %>%
    full join(test id, by = "k") \% > \%
    filter(tree.x != tree.y) \% > \% \# Calculate distance between all trees within each plot and same year
    mutate(dist = sqrt((northing.x - northing.y)^2 +
                  (easting.x - easting.y)^{2})) %>%
    select(-k)
   test sub <- subset(test, Distance<=12) # Select subject trees from df test
   tree ids <- test sub[, c('spp', 'tree', 'dbh', 'ht', 'year', 'Ba', 'CRSA', 'VOL')]
   test id sub <- test id[test id$tree.x %in% tree ids$tree, ] # Select subjects from test id
   test id sub <- subset(test id sub, dist<=5.64) # Select neighbor trees from df test id sub
   for(k in 1:length(tree ids$tree)){
     test neighbor <- test id sub[test id sub[test id sub[test]] == tree ids[tree[k], ]
     test nei <- left join(test neighbor, test, by = c("tree.y" = "tree"))
     # test[test$tree %in% test neighbor$tree.y, ]
     test nei$sub spp <- tree ids$spp[k]
     test nei$sub dbh <- tree ids$dbh[k]
     test neisub ht <- tree ids ht[k]
     test nei$sub year <- tree ids$year[k]
     test nei$sub Ba <- tree ids$Ba[k]
     test neisub CRSA \leq tree ids CRSA[k]
     test nei$sub VOL <- tree ids$VOL[k]
     output <- rbind(output, test nei)
   }#k
  } #j
 }#i
 return(output)
}# function
```
A.2 R code used for calculating competition indices

```
# Calculate subject tree PAI
sub inc <- sub %>%
 distinct(sub spp, tree.x, sub year, .keep all = TRUE) %>%
group by(plot, sub spp, tree.x) %>%
 mutate(PAI \ ht = abs(c(NA, diff(sub \ ht))/8), \# Calculate the PAI
     PAI ba = abs(c(NA, diff(sub Ba))/8),
     PAI crsa = abs(c(NA, diff(sub CRSA))/8),
     PAI vol = abs(c(NA, diff(sub VOL))/8)) \% > \%
na.omit()
# Calculate neighbor tree competition indices
CI DR \leq df \% > \%
                         # Red Alder Competition indexs
filter(year=='15' & spp=='DR') \% > \%
group_by(plot, sub_spp, tree.x) %>%
summarize(
  BAs=sum(Ba), \# sum of competitors ba
  BAl=sum(Ba/Ba > sub Ba), # sum of basal area of competitors with larger ba than subject trees
  DI=sum(dbh/sub_dbh), # Distance independent
  HF=sum(ht/sub_ht), # height factor
  DS=sum(dbh), # diameter's sum
  DSL=sum(dbh[dbh>sub_dbh]), # diameter's sum larger
  TN=n(), # total competitor number
  CSAs=sum(CRSA), # sum of competitor's crown surface area
  DDR=sum(dbh/dist), # diameter distance ratio
```

SFI=sum((dist/abs(ht-sub ht))[is.finite(dist/(ht-sub ht))]), # spacing factor index

DWS=sum(((dbh-sub dbh)/dist)[is.finite((dbh-sub dbh)/dist)]), # distance weighted size ratios MBI=sum(((ht-sub ht)/dist)[is.finite((ht-sub ht)/dist)]), # modified braathe index

Hegyi=sum(dbh/(sub dbh*dist)))

A.3 R code for the equations (Eqs.) used in the study

- R code for modeling red alder density effects on conifer tree size, Eqs. 2.5.1 (p. 24) *HT lme* <- *lme(ht~density * year, data=ep1121*, $random = \sim 1 | site,$ *weights=varPower(form=~1|site),*
 - *corr=corAR1(form=~1)*)
- *R* code for modeling competition effects on conifer growth, Eqs. 2.5.2 (p. 25) FdHt nlme <- nlme(PAI ht ~ a + b1 * exp(b2*BAs.x + b3*BAs.y) * sub ba^c, data=FD,

 $\begin{aligned} &fixed = a + b1 + b2 + b3 + c \sim 1, \\ &random = b1 \sim 1 | EP/Inst/plot, \\ &start = c(a = -30, b1 = 1000, b2 = -0.00001, b3 = 0, c = -0.01), \\ &weights = varPower()) \end{aligned}$

 R code for modeling total light levels as response to red alder basal area, Eqs. 2.5.3 (p. 26) DIFN_lme <- lme(DIFN ~ Baha, random = ~1|inst/plot,

weights=varPower(),
data = A DIFN avg)

 R code for modeling conifer growth as response to individual tree light levels, Eqs. 2.5.4 (p. 27) CWvol nlme <- nlme(PAI vol ~ a + (b1* difn^b2) * sub CRSA^c,

> $data=difn_grouped,$ fixed=a+b1+b2+c~1, random=a+c~1|inst, start=c(a=200,b1=400, b2=0.15,c=1.2),weights=varPower())

• *R* code for modeling the relationship between light and competition indices, Eqs. 2.5.5 (p. 27) *CwDIFN_nlme <- nlme(difn~a+ b1*exp(MBD.x*b2 + MBD.y*b3),*

> $data=CW_grouped,$ $fixed=a+b1+b2+b3\sim1,$ $random=a\sim1|inst/plot,$ start=c(a=1,b1=1, b2=-0.001,b3=-0.05), weights=varPower(), $correlation = corCAR1(form = \sim1))$

• *R* code for modeling soil nitrogen in relation to red alder basal area, Eqs. 2.5.6 (p. 27) DrBa.nlme <- nlme(MinrlN~a + b1*DrBa + b2*DrBa^2, data=soil,

 $fixed = a+b1+b2\sim 1$, $random = a+b1+b2\sim 1$ |site, start=c(a=11, b1=1, b2=-0.001))



A.4 PAI BA and HT of Douglas-fir as response to the best competition indices DWS and MBH respectively.

Fig. A. 1. The responses of PAI basal area (BA) of Douglas-fir subject trees as affected by the amount of conifers (DWS of conifers) and the amount of red alder (DWS) competition at each installation site.



Fig. A. 2. The responses of PAI basal area of Douglas-fir subject trees as response to DWS coniferous competition, DWS red alder competition, and initial basal area in each plot at all installation sites. Fixed effects (population level) in blue, experiment effects in pink, site effects in green, and plot effects (stand level) in red.



Fig. A. 3. Douglas-fir: Scatter plots of standardized residuals against fitted PAI BA values, histograms of the normalized residuals and Q-Q plot of random effects for the best fitting PAI BA model during the period of 1998 to 2006 (DWS).



Fig. A. 4. The responses of PAI HT of Douglas-fir subject trees as affected by the amount of conifers (MBH of conifers) and the amount of red alder (MBH) competition at each installation site.



Fig. A. 5. The responses of PAI height of Douglas-fir subject trees as response to MBH coniferous competition,MBH red alder competition, and initial basal area in each plot at all installation sites. Fixed effects (population level)in blue, experiment effects in pink, site effects in green, and plot effects (stand level) in red.



Fig. A. 6. Douglas-fir: Scatter plots of standardized residuals against fitted PAI HT values, histograms of the normalized residuals and Q-Q plot of random effects for the best fitting PAI HT model during the period of 1998 to 2006 (MBH).



A.5 PAI BA and HT of western redcedar as response to the best competition indices DI and MBH respectively.

Fig. A. 7. The responses of PAI basal area of western redcedar subject trees as affected by the amount of conifers (DI of conifers) and the amount of red alder (DI) competition at each installation site.



Fig. A. 8. The responses of PAI basal area of western redcedar subject trees as response to DI coniferous competition, DI red alder competition, and initial basal area in each plot at all installation sites. Fixed effects (population level) in blue, site effects in pink, and plot effects (stand level) in green.



Fig. A. 9. Western redcedar: Scatter plots of standardized residuals against fitted PAI BA values, histograms of the normalized residuals and Q-Q plot of random effects for the best fitting PAI BA model during the period of 1998 to 2006 (DI).



Fig. A. 10. The responses of PAI height of western redcedar subject trees as affected by the amount of conifers (MBH of conifers) and the amount of red alder (MBH) competition at each installation site.



Fig. A. 11. The responses of PAI height of western redcedar subject trees as response to MBH coniferous competition, MBH red alder competition, and initial basal area in each plot at all installation sites. Fixed effects (population level) in blue, site effects in pink, and plot effects (stand level) in green.



Fig. A. 12. Western redcedar: Scatter plots of standardized residuals against fitted PAI HT values, histograms of the normalized residuals and Q-Q plot of random effects for the best fitting PAI HT model during the period of 1998 to 2006 (MBH).



A.6 Validity of the underlying assumptions for the models and evaluation of model fit

Fig. A. 13 Scatter plots of standardized residuals against fitted PAI BA values of Douglas-fir, histograms of the normalized residuals and Q-Q plot of random effects for the best fitting PAI BA model during the period of 1998 to 2006, the light was measured in 2004.

Scatterplot of Standardized Residuals vs. fitted values

Scatterplot of PAI_ht vs. fitted values



Fig. A. 14 Scatter plots of standardized residuals against fitted PAI HT values of Douglas-fir, histograms of the normalized residuals and Q-Q plot of random effects for the best fitting PAI HT model during the period of 1998 to 2006, the light was measured in 2004.