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The influence of forest structure on light and regeneration in complex coniferous stands

by

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Abstract

Quantification of the effects of residual forest structure on the understory light environment is needed to guide silvicultural strategies that facilitate regeneration. In this study I measured understory light using various methods in a dry, uneven-aged mixed conifer forest in British Columbia, Canada. These measurements were collected from an experiment established in 1994 where four residual basal area treatments ($8m^2/ha$, $16m^2/ha$, $24m^2/ha$ and uncut) effectively created a gradient of structure. Estimates of stand structure including density (N), basal area (G) and stand density index (SDI) explained 12 to 38% of the variability in understory light levels. Stand variables that heavily weighted the influence of larger trees on light attenuation were weak predictors of understory light. Incorporating variables describing the composition and size of trees in the overstory greatly increased the predictive power of the models. The abundance and growth of regeneration was strongly positively related to both light and understory vegetation.

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TABLE OF CONTENTS

List of Figures

List of Tables

Chapter 1: Introduction

1.1 General Introduction

Silvicultural systems that retain substantial amounts of forest structure are seeing increased use in an attempt to mitigate multiple land use conflicts and public pressure surrounding the long term effects of clear felling systems (Gilmore 1997, Emmingham 1998). These types of systems are generalized into the broad grouping of management approaches termed as 'continuous cover forestry' (Pommerening 2006). It is thought that frequent low severity harvesting practices that maintain continuous forest cover can emulate small scale disturbances, so as to keep the forest in a dynamic state while maintaining or creating complex or structurally diverse stands (Smith et al. 1997).

In the Douglas-fir (IDF) forests of British Columbia's southern interior, complex forest structures with mixed species and heterogeneous canopies are common (Hope et al. 1991, Arsenault and Klenner 2004). These stands occupy low to mid elevations which put them in close proximity to human communities allowing intensive forest operations to become feasible; while also increasing the importance of recreation and aesthetic values (Hope et al. 1991). This provides forest decision makers with an array of challenges related to multiple land use conflicts.

Retaining structure is thought to minimize the amount of understory vegetation that competes with regeneration (Harper et al. 2005), reduce incidence of frost injury (Sagar and Waterhouse 2010) and provide protection from high temperatures during long periods of drought (Tappeiner and Helms 1971). Retaining complex forest structure is also important for the maintenance of mule deer winter range habitat through increased snow interception and the role mature timber plays as a potential food source (Armleder et al. 1986).

While retaining structure has benefits, in the IDF the dynamics of these irregular or uneven-aged stands is much more complex relative to even-aged stands and thus the use of partial cutting is quite limited (~1.7% of harvested area used some form of selection harvesting in 2008). Foresters have been reluctant to utilize these silvicultural systems due to the risk associated with regenerating stands under the influence of residual forest structure in ways that comply with current regeneration standards. The response of natural regeneration in the IDF, under the influence of residual structure has been reported to range from highly dense to nonexistent (D'Anjou 1998, Statland 2008).

While many silvicultural systems utilize residual structure, selection systems provide for continuous maintenance of a broad range of tree sizes in perpetuity. This system relies on the successful establishment and growth of regeneration (Leak 1976) in order to ensure growing space is well occupied and that there is continual recruitment of trees into all size classes (Matthews 1989).

In general, when growing space is fully occupied, the amount of biomass in the overstory is inversely correlated with the amount of biomass in the understory (Cannell and Grace 1993, Constabel and Lieffers 1996). As a result, disturbance of the overstory canopy will be complemented by changes in the availability of resources to both tree regeneration and other vegetation in the understory (Emborg 1998, Coates and Burton 1999).

Openings in a forest canopy generally improve resource availability in the understory; though this effect is not consistent among sites and forest types (Pouslon and Platt 1989, Coates and Burton. 1997). In the dry, mixed conifer forests of the Sierra Nevada, Tappeiner and Helms (1971) have shown a slight increase in soil moisture under shaded conditions and reduced abundance of understory vegetation. Conversely, in mature coniferous forests of the Pacific Northwest, Gray et al. (2002) found gap centers to be generally wetter than the corresponding intact forest. Coates and Burton (1997) found that canopy heterogeneity influences understory microsites both within gaps and within the surrounding forest matrix and this concept has often been ignored by researchers.

In the understory, light is widely considered to be the major resource limiting or influencing establishment, growth and survival of tree seedlings (Emmingham and Waring 1973, Grant 1997, Kumar et al. 1997, Gray et al. 2002, Lieffers et al. 1999). Light availability is continuously changing as a stand develops and thus exposes regeneration to a range of various environmental conditions (Lieffers et al. 1999). In addition, conditions that favor early growth can differ from those required for older trees (Gerrish 1990, Messier 1996, Williams et al. 1999). The literature suggests that small tree seedlings are not able to survive extended periods of low light (ie. below 8 to 10% full sun) and as a result substantial mortality can occur (Carter and Klinka 1992, Chen and Klinka 1997, Chen and Klinka 1998). The morphological and developmental plasticity of a species will dictate its ability to acclimatize to variable light environments (Messier et al. 1999).

Past research has shown that environmental variables that influence regeneration can be altered to some extent by manipulating forest canopy structures (Parker 1995, Carlson and Groot 1997). In general, there is an inverse relationship between canopy closure and the amount of light reaching the understory (Comeau and Heineman 2003, Drever and Lertzman 2003). Specifically, Douglas-fir (*Pseudotsuga menziesii* var *glauca* (Beissn.) Franco) requires roughly 20% full sun to survive and 50% full sun to attain 60% of its maximum relative height growth (Chen and Klinka 1997) with the greatest height and diameter growth under 100% full sun conditions (Drever and Lertzman 2001).

Under certain circumstances, forest managers may want to sacrifice the growth rates of regenerating seedlings by reducing understory light availability in an attempt to protect regeneration from a variety of issues such as: competition with aggressive vegetation (Lieffers and Stadt 1994, Bailey et al. 1998, Peek et al. 2001, Maundrell and Hawkins 2004), growing season frosts (Groot and Carlson 1996, Pritchard and Comeau 2004, Sagar and Waterhouse 2010), and high rates of evapotranspiration (Tappeiner and Helms 1971). In a selection system this loss in understory growth rates may be compensated by increased growth of overstory trees (Matthews 1989).

Guidance to forest decision makers regarding appropriate residual densities and structures to retain under uneven-aged management is limited (Day 1998). Exploring relationships between stand structure and light availability can provide a biologically meaningful understanding of stand development that can aid in management.

Managing light availability can be a useful approach for meeting stand objectives related to site occupancy and growth (Lieffers et al. 1999, Messier et al. 1999); however this variable is not easily measured (Anderson 1966). The literature lacks information on how complex residual structure influences the understory light environment and subsequent success of small tree regeneration. Tools for quantifying the understory light environment in complex stands require either expensive sophisticated equipment or subjective ocular measurements; utilizing estimators of stand density and size density relationships to predict understory light availability provides a potential solution.

There is substantial interest in finding ways to utilize conventional stand data in the prediction of understory light levels. Based on relationships with tree size, leaf area and light penetration, stand variables such as basal area, stand density index (SDI, Reineke 1933) and relative density (RD) have been used by many authors to estimate light in the understory of coniferous (Kuusipalo 1985, Vales and Bunnell 1988, Sampson and Smith 1993, Palik et al. 1997, Hale 2003, Sonohat et al. 2004, Hale et al. 2009), deciduous (Comeau 2001, Pinno et al. 2001, Comeau and Heineman 2003, Comeau et al. 2006) and mixed species stands (Messier et al. 1998; DeLong et al. 2005). Previous examinations of relationships between stand structure and light have focused primarily on even-aged homogenous structured forests (eg. Hale et al. 2009) and early growth response of seedlings in relation to gaps (Messier et al. 1999). Only a few studies have looked at light availability in complex stands (Promis et al. 2009, Balandier et al. 2009).

Complex forests are characterized by multiple strata and mixed species composition that form irregular horizontal and vertical distributions of canopy gaps and biomass (Franklin and Van Pelt 2004). The relationship between understory light availability and stand structure in a homogenous even-aged canopy may differ substantially from what might be found in an uneven-aged heterogeneous canopy with the same leaf area (Van Pelt and Franklin 2000). Understory light levels in heterogeneous canopies are known to be highly variable at the microsite (10m x 10m) scale (Palik et al. 1997), while operational prescriptions are applied at the stand level. The relationship between measures of forest structure in heterogeneous canopies and understory light availability remains poorly developed.

In this thesis I will explore relationships between light availability and understory tree regeneration response, while examining the use of stand variables as surrogates for light availability or as direct predictors of understory tree regeneration response in dry, complex Douglas-fir forests. Recommendations surrounding methods of stand regulation and best predictors of light will be made.

1.2 Characteristics of Uneven-aged Douglas-fir Stands

1.2.1 Interior Douglas-fir

Douglas-fir (*Pseudotusga menziesii*) has is considered by many to be the world's most important and valued timber tree (Hermann and Lavender 1990). Its large economic impact and wide ecological amplitude contributes to the importance of this species for both timber (ex. tall and straight growth form) and non-timber values (ex. mule deer forage). Cold temperatures generally limit its northern range, while moisture limits the southern range; resulting in Douglas-fir being distributed from the mountains of central Mexico through the central interior of British Columbia (with discontinuities occurring south of Idaho) (Hermann and Lavender 1990).

In the interior of British Columbia this species (*Pseudotusga menziesii* var. *glauca* (Mirb.) Franco) occupies a broad range of sites within the interior Douglas-fir zone (IDF), which is one of 14 biogeoclimatic zones within the province and covers approximately 600,000 ha of area (Tisdale and McLean 1957). Douglas-fir also occurs in the Interior Cedar Hemlock Zone, the Montane spruce Zone, and parts of the Engelmann Spruce –Subalpine Fir Zone. Warm dry summers coupled with cool winters are indicative of the IDF and have subsequently resulted in the majority of its area being termed as the "dry-belt" region (Hope et al. 1991). The rainshadow formed in the lee of topographic barriers to the west (Cascade and Columbia Mountains) is the underlying factor controlling the climate of the IDF. The mean annual temperature ranges from 1.6 to 9.5°C; while mean annual precipitation ranges from 300 to 750 mm. Moisture deficits and growing season frosts are common limiting factors in the IDF, contributing to a host of ecological conditions (Hope et al. 1991).

Interior Douglas-fir can grow on all aspects and in most topographical situations within its wide elevational range (365- 2590 m) (Arno 1991). In dry regions of the IDF soils are characterized as infertile with shallow organic horizons that are at high risk to displacement and compaction (Mitchell and Green 1981 cited in Vyse et al. 1991, Braumandl and Curran 1992). The establishment of interior Douglas-fir has been shown to be sensitive to the amount of organic matter due to its high water holding capacity and availability of nutrients (Graham et al. 1991). Conversely, mineral soil has been shown to be closely associated with ectomycorrhizae, increased survivorship, improved water availability and subsequently increased rates of growth (Page-Dumroese et al. 1990, Heineman et al. 2003). According to Graham et al. (1991), the only substrate Douglas-fir has trouble establishing on is unconsolidated litter that does meet the moisture requirements of the seed or small germinants.

Moisture availability is an important factor for determining productivity and spatial structures of IDF forests (Lopushinsky 1991, Simpson 2000). Interior Douglas-fir has been classified as having a moderate resistance to drought with less resistance than lodgepole pine (*Pinus contorta* var *latifolia* Douglas ex Loudon) or Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) but more than western larch (*Larix occidentalis* Nuttall). The internal water storage of Douglas-fir is generally low when compared to other conifers (Lopushinsky 1991). On average sapwood comprises 51% of the total cross sectional area and heartwood conducts very little water contributing to a lower resistance to drought (Simpson 2000). However, Douglas-fir has a lower leaf water potential threshold for stomatal closure (-1.9 MPa), relative to lodgepole pine (-1.4 MPa) (Lopushinsky 1991). In a study by Drew and Ferrell (1979), Douglas-fir seedlings grown under low light levels were less drought resistant than those under full light regardless of soil moisture status. This is thought to result from a decrease in the proportion of carbon allocated to roots with decreasing light availability.

The crown morphology of interior Douglas-fir is indicative of a shade tolerant species (Barnes et al. 1998). In low light environments, lateral growth of the shoots becomes more predominant than apical growth (Williams et al. 1999). This suggests that this species has the ability to utilize sunflecks and adjust its crown architecture to harvest light. Douglas-fir has also been found to decrease its live crown depth in response to low light environments (Hermann and Lavender 1990). Although Douglas-fir has been found to survive in low light environments (< 5% full sun) (Williams et al. 1999), it responds well to release (Steen et al. 1987).

Following disturbance, interior Douglas-fir has the potential to become a prolific seed producer (1.95 million viable seed/ha), though seed rain can be infrequent (only 1000 viable seed/ha can be found in non seed years) (Schearer and Schmidt 1990, Burton et al. 2000). Lowry (1966) reports an abundant cone crop every 2 to 7 years, and correlates cone abundance with meteorological variables (eg. warm January in the same year, with a wet preceding year and a cool July two years before harvest). Most seeds fall within 300m of the parent tree, and are often screened by neighboring trees under dense conditions (Issac 1943).

Once established, seedlings can grow upwards of 9 cm per year and can consistently exceed 1 m in height after 8 years on good sites. The growth of seedlings in the first year can be increased under shaded conditions (Hermann and Lavender 1990). As a consequence of Douglas-fir being able to occupy an assortment of ecological conditions, the productivity of stands in the IDF can range from 2 m^3 ha^{-1} yr^{-1} to 9 m^3 ha^{-1} yr^{-1} (Bonner 1990). Arno (1991) reports studies in the IDF with growth of 0.7 to 1.4 m^3 ha^{-1} yr^{-1}. Marshall and Wang (1996) report growth to range from 3.3 to 4.4 m^3 ha^{-1} yr^{-1} in IDF stands with uneven-aged structures.

1.2.2 Stand Structure

IDF forests can have an array of structures, varying from pure even-aged stands to complex stands with multiple species and cohorts. The wide range of stand structures is attributed to the ability of Douglas-fir to take on successional roles of both tolerant and intolerant species (as defined in Barnes et al. 1998) depending on its environment (Schmidt 1991, Carter and Klinka 1992). On dry sites Douglas-fir acts as a climax species were it replaces seral occupants like trembling aspen and lodgepole pine. In moist areas (ie. in the Interior Cedar Hemlock Zone), the species is seral to the more shade-tolerant trees such as Western red-cedar (*Thuja plicata* Donn ex D. Don in Lambert) or Western hemlock (*Tsuga heterophylla* Rafinesque) (Arno 1991).

Pure Douglas-fir climax stands and mixed stands of Douglas-fir, lodgepole pine and western larch, are the primary constituents throughout much of the south-eastern IDF (Meidinger and Pojar 1991). The western larch component of these forests is highly important, as western larch is a fast growing, valued timber species that contributes both to aesthetics and species diversity.

Western larch is a long lived seral species that is very shade intolerant. Growth rates rival that of lodgepole pine and volumes of pure managed stands can range from 308 m^3/ha to 813 m^3/ha on poor to high quality sites, respectively (Schmidt and Shearer 1990). In natural stands wildfire is essential for the maintenance of western larch. Exposed mineral soil resulting from wildfire often produces the best height increments giving an advantage over competitors. In the IDF pure western larch stands are infrequent and most often develop as a dominant stratum in Douglas-fir stands following wildfire.

Although the IDF is dominated by a single species (Douglas-fir), regionally, IDF forests are denser and more productive in the central interior; while slow growing in drier portions of the southern interior (Huggard et al. 2005). Ecological associations in the very dry (southern) areas of the IDF include ponderosa pine (*Pinus ponderosa* Douglas ex Lawson) climax stands and grassland communities (Hope et al. 1991). While on higher elevation sites that receive more moisture, interior spruce forms transitional stands into the Montane Spruce biogeoclimatic zone (Meidinger and Pojar 1991).

Even–aged stands are generally found under wetter conditions and are often associated with a variety of different species; while uneven-aged stands are generally found under dryer conditions (Steen 1987, Vyse et al. 1991). This observation is a generality, as stand structure develops from a variety of interacting factors. Disturbances are fundamental to the development of stand structure, composition and the functioning of ecosystems (Coates and Burton 1997). Stands in the IDF are influenced by a mixed severity disturbance regime, ranging from low intensity gap forming disturbances operating at individual tree levels to large scale stand replacing disturbances (Arno 1991, Arsenault and Klenner 2004, Klenner et al. 2008).

Mature Douglas-fir and ponderosa pine have thick bark enabling them to survive low severity surface fires (Herman and Lavender 1990). The historic fire interval in the IDF is argued to range from 7 to 20 years but in more recent years most sites have not experienced fire for 30 to 90 years (Daigle 1996). The province of British Columbia (1995) estimates the regime for surface fires ranges from 4 to 50 years, while crown fires range from 150 to 200 year intervals. Fires influence ecological processes through the release of nutrients locked in carbon sinks, warming cold soils, reducing organic floor depth, influencing the floristics of a stand and creating seedbeds (Heinselman 1981). Fire is a natural stocking control agent that favors the removal of highly dense, diseased, fire susceptible trees (Braumandl et al. 1994).

Over time, repeated low severity fires lead to the development of uneven-aged stands (Daigle 1996, O’Hara 2009). Current management practices employ fire suppression, which can alter the natural structure within stands by increasing the incidence of small stems (Moore et al. 1999), causing species shifts (Stephenson 1999, O’Hara 2002, Zald et al. 2008), and lead to increased fuel loadings (Keane et al. 1990, Arsenault and Klenner 2004). This has put many IDF stands at risk for crown fires, different successional trajectories, different ‘natural’ structures and susceptibility to insect and disease attack.

Insects and disease generally cause small scale disturbances, but when populations surpass endemic stages the result can be catastrophic (ex. *Dendroctonus ponderosae*). Interior Douglas-fir and associated tree species in the IDF are commonly influenced by bark beetles (*Dendroctonus ponderosae* and *Dendroctonus pseudotsugae*), root disease (*Armillaria ostoyae*), western spruce budworm (*Christoneura occidentalis*) and mistletoes (*Arceuthobium* spp) (Hope et al. 1991). The mortality of a few trees causes the formation of gaps which are important because they keep the forest in dynamic state (Yamamoto 2000).

In some forest types, gaps may occur at greater frequency than large scale disturbances, as disturbances that cause mortality among many adjacent trees are less common (Spies et al. 1990, Coates and Burton 1997, Yamamoto 2000). In Douglas-fir/Western hemlock forests gap forming processes operate at intervals between 8 to 10 years with a majority of the gaps being over 25 years old (Spies et al. 1990). Runkle and Yetter (1987) estimated that gaps in temperate deciduous forests are formed at a rate of 1% of the stand area per year.

The nature of and importance of gaps may vary as a stand develops (Yamamoto 2000). Tyrell and Crow (1994) working in Hemlock-hardwood forests found a linear increase in gap size with stand age. During earlier stages of stand development gaps are generally filled in by lateral branch growth due to their smaller size (Spies et al. 1990). As the stand develops, crowns rise, mortality occurs and subsequently understory light increases. This results in generally larger gaps that may allow either shade intolerants to establish and /or shade tolerant species to be released. Means (1982), working in the central western Cascade Range of Oregon has shown that on dry sites Douglas-fir can establish and reach upper strata in relatively smaller gaps. Franklin and Dyrness (1973, cited in Spies and Franklin 1989) have found that Douglas-fir growing in the Coastal Western Hemlock Zone does not reach the canopy in gaps less than ~700 to 1000 m^2. Mailly and Kimmins (1997) suggest large gaps of 0.25 to 0.5 ha for coastal Douglas-fir. When sufficient sized gaps occur, survivorship and establishment may be hindered by the availability of suitable seedbed (Yamamoto 2000) and/or by competing herb/shrub or other juvenile trees (Spies and Franklin 1989).

Using silvicultural systems that form open canopies with high light levels may provide adequate resources for Douglas-fir growth but also favor the growth of grasses and shrubs which can compete for growing space and soil moisture (Vyse et al. 2006). Royo and Carson (2006) explain that a site utilization issue or balance between vegetation response and understory tree response is created when the understory is rich in light. Harper et al. (2005) working in clearcuts in the wet warm IDF found that when total vegetation cover was < 25% substantial volume gains were observed. Many studies recommend some form of site preparation to alleviate moisture limitations from competing native grasses (ex. Nicholson 1989, Fleming et al. 1996, Simard et al. 1998, Heineman et al. 2003). As well as competing for soil moisture, dense layers of grass also contribute to a greater risk for frost injury by trapping cold air and limiting soil warming (Steen et al. 1990), which is already an issue in large openings (Stathers et al. 1990, Simard et al. 2003). Conversely, more closed canopies can favor early Douglas-fir survival but may reduce the establishment and growth rates for advance tree regeneration, which can limit recruitment and the long term development of the stand.

1.2.3 Regeneration of Interior Doulas-fir

In the IDF natural regeneration is often used to meet stocking standards (Kaipainen et al. 1998), especially following partial cutting prescriptions on hot, dry sites (Vyse et al. 1991). Douglas-fir is expected to regenerate naturally following partial harvesting and provide a well stocked understory (Weetman and Vyse 1990). However, natural regeneration is often clumpy, irregularly spaced (Klenner and Vyse 1998, Huggard et al. 2005, Statland 2008), slow growing (Vyse et al. 1991), highly dense (Day 1998) or nonexistent (D’Anjou 1998).

Regenerative patterns of small trees in any forested ecosystem are influenced by many processes that interact at a variety of scales (Kneeshaw and Bergeron 1996). According to Simard et al. (1998), failure to regenerate trees in the IDF are due to an insufficient seed supply, winter temperature extremes, early frost, summer drought, and competition for resources (namely water and light).

Newsome et al. (1990), states that seedling mortality is directly influenced by frost, seasonal drought, cattle damage and competition from graminoids.

Establishment, composition and abundance of natural tree regeneration first depend on a presence and distance to a seed source (Kneeshaw and Bergeron 1996). Ferguson and Carlson (1991) observed that distance to a seed source is more important in drier habitat types because more seeds may be needed to successfully establish a seedling. Herman and Lavender (1990) found that the majority of Douglas-fir seed falls within 100 m. Huggard et al. (2005) suggest that a contributor to the patchiness of Douglas-fir natural regeneration was the irregularity of seed fall, with seed being abundant in 2 years and nearly absent in 3 years over the 8 years of monitoring.

The consumption of seeds has also been found to be a limiting factor for the establishment of natural regeneration with consumption rates being as great as 95% (Burton et al. 2000, Doney and Lloyd 2001 as cited in Huggard et al. 2005). Huggard and Arsenault (2009), working in the IDFxh and IDFdk found the most important seed predators were deer mice (*Peromyscus maniculatus*) that were estimated to consume 24 000 to 336 000 seeds ha^{-1} year^{-1} in uncut forests and between 96 000 to > 1 000 000 seeds ha^{-1} year^{-1} in openings. The presence of coarse woody debris was found to have little effect on small mammal populations and these authors suggest that removal won’t decrease seed loss but may have adverse effects on seedlings due to increased trampling of seedlings by cattle (Huggard and Arsenault 2009).

The IDF provides most of the forested summer range for the cattle industry (Hope et al. 1991). The principal forage species in this region is *Calamagrostis rubescens* Buckl., though cattle and native ungulates are known to browse and trample regenerating seedlings. Mitigating livestock effects on small regenerating trees is largely dependant on cattle management via limiting overgrazing (Newsome et al. 1990). When vegetation becomes scarce (<100kg/ha) browsing mortality drastically increases (Newman et al. 1998). Although cattle trampling can constitute a large amount of mortality, Mclean and Clark (1980) suggest that this mortality can be negligible compared to mortality from competition or reduced availability of appropriate microsites.

While a supply of seed is a necessity for establishing trees, the microsite on which the seed lands provides the conditions for regeneration success (Geier-Hayes 1991). According to Graham et al. (1991), the only substrate Douglas-fir has difficulties establishing on is unconsolidated litter that does meet the moisture requirements of the seed.

Temperature of the surrounding air can be an important limitation to seedling survival and growth on frost prone IDF sites (Heineman et al. 2003). The dry air of the IDF cools and heats quickly. In the absence of wind, air temperatures at seedling height can be many degrees cooler than the corresponding air above (Steen et al. 1990). These conditions can lead to development of radiative frosts which can occur in any month of the growing season. Frost damage to seedlings is usually in the form of damage to the current year's foliage with the risk being highest soon after budburst and before buds harden off in the late summer. Conversely, high temperatures (1 to 4.7º C above monthly normal) followed by severe cold temperatures (-30º C) during the winter can cause widespread winter injury to seedlings that are not protected by snow cover (Van Der Kamp and Worral 1990). During the summer, high temperatures can put seedlings outside the optimal range for physiological processes (15-25ºC) and indirectly cause growth declines when exacerbated by low soil water potentials (Tappeiner and Helms 1971).

Some authors suggest that water is the most important factor limiting seedling growth and establishment in the IDF (Lopushinsky 1991, Simpson 2000, LeMay et al. 2009). Water deficits affect every aspect of plant growth, modifying anatomy, morphology, physiology and biochemistry. Trees are smaller on drier sites, their leaves are usually smaller, thicker and more heavily cutinized, vessel diameter of early wood is smaller and cell walls are thicker and more lignified, with greater root growth relative to shoot growth (Kozlowsky and Pallardy 1997). Drought susceptibility is amplified when soils are colder as the viscosity of water increases and subsequently permeability of root membranes decrease (Lopushinsky and Kaufmann 1984).

Many studies indicate that below ground resource competition has a strong influence on understory productivity in dry climates (Coomes and Grubb 2000, Devine and Harrington 2008, Coates et al. 2009, Devine and Harrington 2009). Studies that have included trenching or site preparation have shown positive results in terms of increased water availability (Mclean and Clark 1980, Nicholson 1989, Fleming et al. 1996, Harper et al. 2005, Huggard et al. 2005). Heineman et al. (2003) found that mechanical and chemical site preparation increased soil water availability and increased air temperatures during the night through the reduction of pinegrass. Harper et al. (2005), working in the IDFww found that herbicide treatments (i.e. glyphosate and hexazinone) reduced competing vegetation and resulted in greater growth rates. Simard et al. (1998), found increased survivorship when large patches of pinegrass were removed. It is generally accepted that some form of seedbed disturbance that exposes mineral soil will provide suitable conditions for Douglas-fir establishment and seedling development (Newsome 1998, Simard et al. 1998, Vyse et al. 2006).

Competition has been shown to switch to facilitation under conditions of high abiotic stress (Maestre et al. 2009). Studies have shown that vegetation and overstory trees can increase establishment and germination on hot, dry sites (Haig 1936 as cited in Ferguson and Carlson 1990, Helgerson 1990, Geier-Hayes et al. 1991, Oester 2008) through protection from radiative frost, insolation and reduced competition from graminoids. However, as the stand develops the same vegetation and overstory trees can hinder growth and development (Devine and Harrington 2008). For instance, in some cases Douglas-fir establishment has been found to be negatively correlated with light, while the growth response was generally best only in the largest gaps (Steele and Geier-Hayes 1989, Gray and Spies 1997). Managing the amount of light reaching the understory through controlling the amount, position and type of intercepting vegetation can provide the benefits of suppressing competitors and the protection needed during establishment (Lieffers et al. 1999).

Many researchers have studied the response of seedlings growing under the influence of residual overstory across gradients of light in thinned Douglas-fir stands (Table 1-1). Williams et al. (1999), found Douglas-fir persisting for over 50 years in light environments less than 5% full sun in the B.C, interior. Drever and Lertzman (2003) estimate that >20% full sun is needed to ensure survival in Douglas-fir stands in the Coastal Western Hemlock Zone. Growth has been shown to be compromised at light levels less than 40% full sun (Drever and Lertzman 2001). Although these studies suggest Douglas-fir may be managed between 20 and > 40% full sun to insure a well established forest, these levels may change in drier ecosystems. For instance, while Douglas-fir is classed as being moderately shade tolerant; there is evidence that this species has higher shade tolerance under drier conditions (Carter and Klinka 1992). Likewise, the effect of understory competition on seedlings may be underestimated given the limited availability of water experienced in IDF forests.

Table 1-1 A summary of published information on effects of light environment on Douglas-fir growth and survival.

Author	Overstory density or light level	Region
Williams et al. (1999)	5% of PPFD survived 50 years and reached 3m	Interior B.C.
Brandeis (2001)	< 20 m^2/ha BA to grow	W. Cascades, Oregon
Carter and Klinka (1992)	>30-40% Percent above canopy light (PACL): other factors influenced relative height growth	Coastal B.C.
Chen and Klinka (1997)	>7.4% full sun: sunflecks contribute 32.4% of daily total	Interior Douglas-fir Zone, B.C.
DeLong et al. (2005)	>5% full sunlight to survive or < 21-25 m^2/ha BA	Interior Cedar Hemlock Zone, B.C.
Drever and Lertzman (2001 & 2003)	20% full sun to ensure survival 40% full sun to grow at max	Coastal B.C.
Harrington (2006)	> 3.8 Relative Density (Curtis 1982) severely limit stem volume growth (SVI)	W. Cascades, Washington
Chruchill (2005)	125-150 SDI to produce economic volumes, 150-275 SDI to promote recruits in upper strata	W. Cascades, Washington
Mailly and Kimmins (1997)	>20% RLI (relative light intensity) to ensure survival; >40% RLI to obtain optimum growth	Coastal B.C.

1.3 Management of Uneven-aged Douglas-fir Stands

Historically, the interior Douglas-fir forests of western Canada have been an important source of high quality structural wood products (Corrao 1990, Keegan 1990, Simpson 2000). Various forest products include lumber, plywood, pulp, paper, particle board, fiberboard, house logs, posts and poles, and fuel wood (Keegan 1990). Douglas-fir and western larch make up 12.5% and 5.6%, respectively, of the total harvested volume in the Rocky Mountain Forest District of B.C. (2008) and are commonly sold under the Douglas-fir/Larch grade (Blatner and Govett 1990). In the western United States, interior Douglas-fir accounts for 31 billion cubic feet of growing stock (VanHooser et al. 1990) and Keegan (1990) estimates the sales value between 1984 and 1988 has exceeded $1.1 billion annually in 1998 dollars.

While management for fiber guides many management decisions, interest in uneven-aged management is increasing as a result of public dislike for clearcuts (Guldin 1996) and by the potential to reduce costs associated with regenerating trees. Between 2008 and 2009, over 1,466 ha were harvested across British Columbia using some form of selection harvesting (B.C. Min. For. 2009). In the IDF, retaining a variety of structure provides a host of benefits such as; protective cover, snow interception and food (mature Douglas-fir needles) for mule deer during the winter (Armleder et al. 1986), protection from frost injury, reduced transpiration demand and vegetation competition; while maintaining mycorrhizal associations (Teste and Simard 2008), aesthetics, and mature tree inventory; the potential to reduce tree regeneration costs and not be limited by adjacency requirements (retaining more than 40% basal area of the initial stand).

Forest management prescriptions have historically recognized the need to retain structure by emulating the natural disturbance regimes via partial cutting systems (Coates and Burton 1997, Vyse et al. 2006). Selective harvesting (diameter limit ‘highgrading’) of high quality, valuable trees in the IDF was the norm in the earlier part of the century and continued in to the 60’s (Day 1998).

This era in IDF forest management coupled with fire suppression has left many stands degraded with poor, unattractive and un-productive structures.

These past management prescriptions have generally failed to incorporate the importance of stand structure regulation and stocking control and this has resulted in hesitation and reluctance to utilize these systems (Becker 1995). Martin et al. (2005) suggest that these failures can be attributed to the historical policy guiding stocking and site occupancy in managed uneven aged forests.

Selection systems offer an attractive alternative as the quality of the residual stand is important in determining the success of the system. Single tree selection systems have the potential to meet diverse management objectives, as forest structures provide a range of habitat and forest products. Generally, selection systems which utilize frequent low intensity harvesting schedules and retain trees in a variety of size classes have been used to form and maintain uneven-aged structures (Smith et al. 1997). These systems can alleviate problems for regenerating trees that are seen by clear-cutting while increasing future silvicultural options (Guldin 1996).

An important attribute of selection systems is the reliance on the continued growth, establishment and recruitment of natural regeneration (Leak 1976). In the IDF many stands managed under selection regimes have inadequate quantities of natural regeneration, open canopies, and low recruitment into upper canopy strata which has ultimately lead to a loss of stand vigor (Simpson 2000). This has resulted in forested stands with uneven ages and sizes with irregularly spaced overstory and clumped understory trees that are susceptible to fire, insect and disease (Day 1998, Simpson 2000). Inadequacies in achieving desired forest structure have caused foresters to be reluctant in incorporating selection systems into operational management.

The basic components of a selection system rely on developing forest structures that ensure a continuous surge of seedlings and recruitment after each entry, commitment to stand tending, control of stocking in each size (or age) class using a form of stocking regulation (i.e. BDq see pg 19) and a viable system of tree selection (Becker 1995, O’Hara 1996, O’Hara and Gersonde 2004).

The complexity of these systems is increased when managing mixed-species stands. The response of established trees to light availability is species specific (Chen 1997); as are tolerances to extremes in microclimate and rates of acclimation. In general, shade intolerant species have a higher light compensation point and thus require a greater amount of light relative to shade tolerant species (Kozlowski and Pallardy 1997). This has created much debate about whether or not Douglas-fir or shade intolerant species can be successfully regenerated using single tree selection systems or whether group selection systems (which create small gaps) are required (Coates and Burton 1997, Smith et al. 1997, Malcolm et al. 2001). If single tree selection systems are to be used with mid-shade tolerant or shade intolerant species, understory light levels and thus residual overstory densities need to be well managed.

Guidance to decision makers regarding appropriate levels of residual overstory is limited. Two common approaches to stand density regulation are the BDq method and the Check method. The BDq approach is comprised of three parameters: the basal area to be retained (B), the maximum diameter to be retained (D) and the ratio between successive diameter classes (q). Although the selection of each parameter is influenced by management objectives, the purpose of the approach is to set a target diameter distribution. (B.C. Ministry of Forests 2003). The Check method distributes the forest into three classes (small, medium and large) that are to be inventoried successively to acquire information between diameter increment and growing stock, planning of fellings, and to fix the yield for the next period. Cutting entries work toward the normal distribution of size classes (Matthews 1989). While stand regulation provides a foundation for implementing uneven-aged management, current approaches still have their disadvantages. Exploring relationships between stand structure and light availability can provide a biologically meaningful understanding of stand development that can aid in management.

A few studies present information on relationships between light transmittance in the understory, residual overstory basal area and understory growth in thinned coniferous stands (e.g. Carter and Klinka 1992; Williams et al.

1999; Drever and Lertzman 2001; Brandeis 2001; Drever and Lertzman 2003; DeLong et al. 2005, Harrington 2006). Most of these studies have included thresholds for Douglas-fir's survival (5% Photosynthetic photon flux density (PPFD)) or growth as defined by potential to reach upper strata (40% full sun or less than 20 m^2/ha) or potential for release (20% full sun or less than 21 to 25 m^2/ha) when under the influence of residual overstory in thinned even-aged systems or coastal Douglas-fir ecosystems. A better understanding of the effect of residual stand structure on the abundance, survival, and development of tree regeneration is needed to support uneven-aged management of interior Douglas-fir in B.C. and Alberta.

Quantifying the impacts of residual overstory on competition and understory light can provide a greater understanding of the development of uneven-aged stands in response to selection systems. Traditionally, basal area has been used to quantify structure as it is easily measured, though it is not totally justified because depending on the tree size, basal area can vary within equally dense stands (Ziede 2005).

Reineke's (1933) Stand Density Index (SDI), which is the number of trees per hectare calculated as if the quadratic mean diameter of the stand were 25 cm has been used in the United States to control stocking (Shaw 2006). SDI is developed from theories pertaining to site occupancy like the -3/2 self thinning constant (Long 1995) and is closely related to periodic annual increment (Innes et al. 2005) and light capture (Vales and Bunnell 1988)). Zeide (2005) recommends the use of SDI in place of basal area or trees per hectare as an ecologically meaningful measure of density.

1.4 Study Rationale

Partial harvesting is becoming an increasingly appealing stand level prescription due to public pressure and concerns about the adaptability of clearcutting systems. Benefits of partial harvesting in the IDF include the protection of frost susceptible species, reduced transpiration rates, winter range habitat for mule deer, maintenance of aesthetic and recreational values, alleviation of adjacency requirements and reduced costs associated with planting. The IDF is especially a good candidate for prescriptions that involve partial cutting due to the climate, species and previous disturbance regime which naturally maintain an uneven-aged structure.

The IDF is a unique forest type that makes up a considerable portion of the B.C. interior land base. The dry climate and history of past disturbances create stand conditions that challenge simplistic assumptions related to hierarchal competition and basic growth dynamics. Previous studies have examined effects of light on the growth of planted Douglas-fir seedlings in pine dominated stands or in even-aged systems (Chen 1997, Williams et al. 1999, Balster and Marshall 2000, Vyse et al. 2006). However, few studies have looked at how residual structure affects light availably and resulting growth in dry uneven-aged interior Douglas-fir systems. The literature also lacks information on the appropriate level of overstory density and subsequent light level that is required by species growing in dry environments (Carter and Klinka 1992, Brandeis 2001, Drever and Lertzman 2001, Harrington 2002). Quantifying the impacts of residual overstory on competition and understory light will provide a better understanding of the development of uneven-aged stands in response to selection systems.

Many forested areas in B.C. have uneven-aged stand structures resulting from salvage operations occurring in mountain pine beetle disturbed stands, and past histories of selective logging. Evaluating the adequacy of seedling and sapling stocking in these stands has led to development of a multi storied assessment system (Martin et al. 2005). The multi-storied assessment system is currently based on a number of very simplistic assumptions about light availability that need to be evaluated and perhaps even modified for IDF forests. Policy surrounding uneven-aged stocking standards using estimators of site utilization and theories pertaining to resource competition are of substantial interest.

1.5 Objectives

The objectives of this thesis are to investigate relationships between residual forest structure and light availability for natural tree regeneration. Relationships between light availability and regeneration of Douglas-fir have been previously studied; though the majority of literature pertains to even-aged systems (which are fairly well understood and have an extensive history of stand modeling) or other forest types (ex. coastal Douglas-fir) that have different resource levels. Methods for estimating the light environment and its effects on natural tree regeneration and vegetation in dry uneven-aged stands remains poorly understood. The following are a list of objectives this study will address in order to shed some light on this topic.

(1) What is the effect of light availability created from residual structure on (a) the growth, (b) the abundance and (c) the vegetation response in dry uneven aged mixed conifer forests?

    i) How does light influence the growth and the abundance of various sized regenerating trees?
    ii) What types (layers) of vegetation are responding to light availability?
    iii) Do residual basal area treatments differ in terms of light, vegetation, or abundance of seedlings 14 years after harvesting?

(2) Can light availability, abundance or growth of natural tree regeneration be predicted from overstory density estimators?

i) Do different overstory species play the same role in light attenuation?

ii) Which layer of overstory has the strongest influence on light attenuation?

iii) Which overstory density estimators (if any) are the best predictors of light or growth or abundance of natural tree regeneration?

My research will use a study that was initiated in 1994 near the St. Mary's River near Cranbrook, B.C. The forest is a mixture of Douglas-fir, western larch, lodgepole pine and ponderosa pine with a variety of sizes and age classes. Due to the preference in harvesting pine and the recent outbreak of Mountain Pine beetle (*Dendroctonus ponderosae*) the resultant stand structures are similar to salvaged logged mixed conifer stands. The purpose of the trial was to evaluate the operational feasibility of single tree selection systems in dry uneven-aged mixed conifer forests.

1.6 Thesis Outline

This thesis will be structured as a single scientific paper by combining the two major objectives. The first chapter is an introduction to the study, the second chapter describes the study site and methods used for this study, the third chapter presents the results, the fourth chapter provides the discussion and the final chapter (5) provides conclusions and recommendations. Table 1-2 provides a list of the tree species found throughout the thesis.

Table 1-2 Tree species and their abbreviations used throughout the thesis. † Ranking from most tolerant (1) to least tolerant (6) (Burns and Honkala 1990)

Species			Tolerance Ranking†	
Scientific Name	Common Name	Code	Shade	Frost
Pseudotusga menziesii var. *glauca* (Beissn.) Franco	Douglas-fir (interior)	Fd	2	4
Larix occidentalis Nut.	western larch	Lw	6	5
Pinus contorta var *latifolia* Dougl. ex Loud.	lodgepole pine	Pl	3	1
Picea glauca (Moench) Voss. x *Picea engelmannii* Parry ex Engelm.	interior spruce	Sx	1	2
Populus tremuloides Michx.	trembling aspen	At	5	3
Pinus ponderosa Dougl. ex Laws.	Ponderosa pine	Pp	4	6

Chapter 2: Methods

2.1 Site Description

This study was conducted at the St Mary River Research Trial (49°37’10’’ N, 115°58’20’’W), which is approximately 25 kilometers North West of the town of Cranbrook. The study site is in the IDF dry mild Kootenay biogeoclimatic variant and has a site series of 01 with less than a hectare of site series 04 (edatropic grid 3-4/C) according the British Columbia biogeoclimatic (BEC) ecosystem classification system (Meidinger and Pojar 1991). The stands on this site are dominated by Douglas-fir, western larch and lodgepole pine with scattered components of interior spruce, Ponderosa pine and aspen. Pre-treatment basal area was 37 m^2/ha for all live standing trees (greater then 4cm. dbh), with Douglas-fir reported as the most common species in the understory (Refer to Table. 2-1).

The ground cover of the study site is dominated by pinegrass (*Calamagrostis rubescens* Buckl.), kinnikinnick (*Arctostaphylos uva-ursi* Spreng.), and bunchberry (*Cornus Canadensis* L.) with shrub communities primarily consisting of common juniper (*Juniperus communis* L.), tall Oregon grape (*Mahonia aquifolium* (Pursh) Nutt.), soopolallie (*Sheperdia Canadensis* (L.) Nutt.), Saskatoon berry (*Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roem.) and snowberry (*Symphoricarpos albus* (L.) S.F. Blake).

According to estimates of site index based on the BEC site series (SIBEC, Mah and Nigh 2003) the site $index_{50}$ for Douglas-fir on 01 sites in the IDFdm2 is 19.3, western larch has a site $index_{50}$ of 18 while lodgepole pine has a site $index_{50}$ of 19.9, allowing the site to be classified as medium in terms of its growth class. The productivity of this site series is deemed low. However, due to site specific variation there is some variation in this management interpretation (Braumandl and Curran 1992). Productivity is largely limited by soil moisture and occurrence of growing season frost. Hope et al. (1991) reports that mean annual precipitation can range from 300 mm to 750 mm across the zone.

The elevation of the St. Mary’s River Research Trial ranges between 935 – 975 m, with slight microtopographical variation occurring across the area. Soils consist of Orthic Gray Luvisols and Brunisolic Gray Luvisols with silty-loams and silty-clay-loam textures and an absence of coarse fragments. Table 2-2 provides a summary of two representative soil profiles on this site. Soil compaction is evident from the previous logging history and forest displacement risk is considered high (Braumandl and Curran 1992).

Previous disturbance history consists of partial harvesting since the 1880’s and large fires occurring approximately 120 years ago (Waterhouse et al. 2008) which appear to have left a component of western larch which is now approximately 200 years old. This large scale disturbance was supplemented by a number of low severity ground fires, resulting in an uneven-aged structure. The age class distribution has at least four distinct classes among the three major species.

Table 2-1 Pre-harvest (1994) structural attributes for live trees in the St. Mary’s River Research Trial. (from Waterhouse et al. 2008)

Species	Basal Area (m2/ha)		Density (Stems/ha)	
	> 4 cm dbh	>12 cm dbh	> 4 cm dbh	>12 cm dbh
Douglas-fir	12.8	9.2	2144	311
western larch	12.2	11.2	805	361
lodgepole pine	11.9	9.2	1259	614

Table 2-2 Soil profile descriptions for pits excavated in two plots near soil water potential sensors.

Horizon	Site 11 (Medium)			Site 8 (Control)		
	Depth (cm)	Texture	Structure	Depth (cm)	Texture	Structure
L	4-3			1-2		
F	3-0.5			0.5-1		
H	0.5			0.-0.5		
Ae	0.11	SiL	Med. Blocky	0-3	SiL	Med. Blocky
Bt_1	11-29	SiCL	Med. Blocky	.		
Bt_2	29-54	CL	Med. Blocky	.		
Bm_1	.			3-25	SiL	Med. Blocky
Bm_2	.			25-50	SiCL	Med. Blocky
C	54+	SiCL		.		
C (Bt?)				50+	SiCL	

Comments: Rooting depth 60cm, Clay skins present, 0% coarse fragments.
Completed by Dr. Phil Comeau

2.2 Study Design

The St. Mary River Trial follows a randomized complete block design with replication and subsampling. Sixteen treatment units (100m x 100m) were established in 1994 and randomly assigned to one of four residual basal area treatments (making 4 replicates of the 4 treatments) with target basal areas retaining 8 m^2/ha, 16 m^2/ha and 24 m^2/ha and un-harvested or ~36 m^2/ha, which are denoted as light, medium, heavy and control treatments, respectively (Table 2-3). Treatment units were evenly segregated into two locations, which act like statistical blocks. Each treatment unit was delineated into a 10 m x 10 m square grid, where each square represents a subplot. Out of the 100 subplots, 16 subplots of the inner 64 were randomly selected by row for sampling. Within each subplot a 3.99 m radius regeneration plot was established (Fig. 2-1). Treatment units and subplots were established before harvesting.

Harvesting took place between November and December of 1994. Trees > 17.5 cm dbh were marked to leave, to meet the residual basal area of the assigned treatment. Tree selection for harvest was initiated in order of species preference, with lodgepole pine > western larch >> Douglas-fir, the majority of trees selected for harvest were lodgepole pine (to mitigate risk from mountain pine beetle). Logging staff were instructed to protect regenerating understory (trees < 17.5 cm dbh or future crop trees). All trees were hand-felled then skidded using either a 1987 Komatsu 37E crawler tractor or 1993 John Deer rubber tire line skidder. Skidding was restricted to skidder trails (4m wide), though off-trail random skidding was permitted under some circumstances.

Table 2-3 Random assignment of treatments to Treatment units

Treatment	Target Basal Area (m^2/ha)	Current Basal Area (15 years post harvest)	Corresponding Treatment Units (TU)
C	Unharvested (~37)	37.3	3, 8, 12, 14
H	24	24.3	2, 6, 9, 16
M	16	23.4	1, 5, 11, 15
L	8	22.7	4, 7, 10, 13

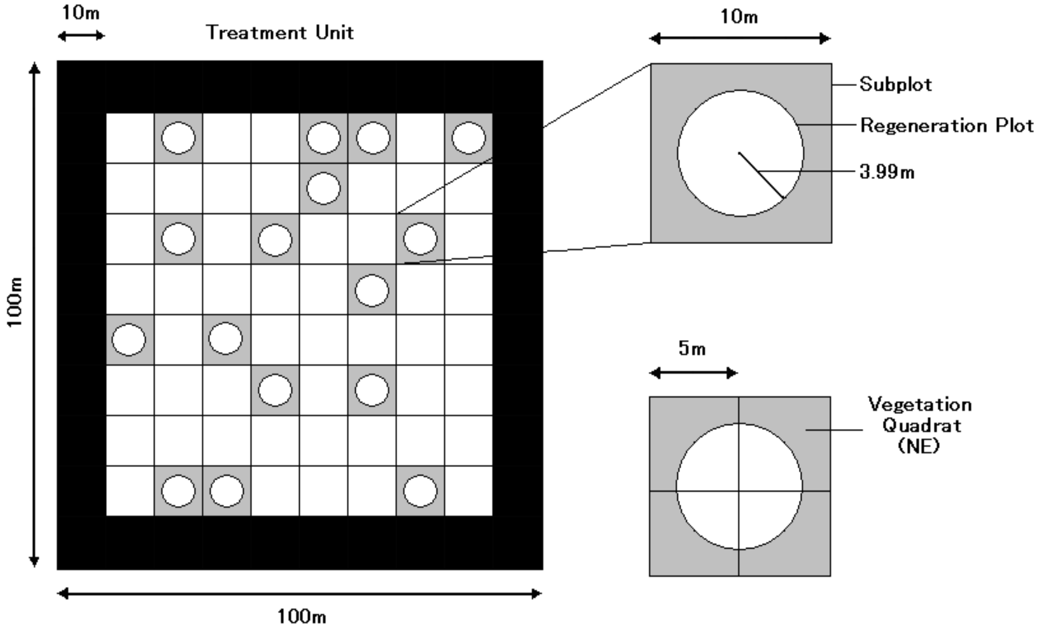

Figure 2-1 Hypothetical layout of a one hectare treatment unit. Black border represents the treated buffer between treatments. Grey squares represent randomly selected subplots with corresponding regeneration plots.

2.3 Data Collection

2.3.1 Overstory Data

During the 2008 growing season, the B.C. Ministry of Forests and Range (MOFR) contracted data collection in the St. Mary River Research Trial site. Data was collected according to the Resources Information Committee Standards (RISC) found in 'Forest Inventory and Monitoring Program: Growth and Yield Standards and Procedures Version 1.0' (RISC 2003). Trees were measured by species for diameter at breast height (DBH), top height, height to live crown, crown class, as well as indicators of vigor and health. In all subplots an ocular estimate of crown closure was recorded. Various stand density estimators were calculated using the formulas in table 2-4.

Table 2-4 Overstory density estimators used as predictor variables and their corresponding formulas

Overstory Density Estimator	Formula	Variable Definitions
Trees per hectare (N)	$\sum n_i$	n_i is an individual tree
Stand density index (Reineke 1933) (SDI)	$N*(D_q/25)^{1.6}$	N is trees per hectare, D_q is the quadratic mean diameter
Basal area (G)	$(\sum (л * (d_i/200)^2))$	d_i is diameter at breast height (1.3m) in m
Relative Density (Curtis) (RD)	$G / D_q^{-0.5}$	G is the basal area per hectare and D_q is the quadratic mean diameter
Quadratic mean diameter (D_q)	$\surd (\sum d_i^2)/n$	d_i is diameter at breast height (1.3m) and n is the number of trees
Sum of height (sumHt)	$\sum HT_i$	HT_i is the top height of an individual tree
Sum of Diameter (sumDBH)	$\sum d_i$	d_i is diameter at breast height (1.3m) in cm
Sum of natural log transformed diameter (LnDBH)	$\sum \log_e(d_i)$	d_i is diameter at breast height (1.3m) in cm

2.3.2 Understory Data

2.3.2.1 Understory Tree Regeneration

Understory trees were assessed (in 2008) within each 10m x 10m subplot. Variables were measured on the tallest and most vigourous trees present in each size class. Measurements included root collar diameter, DBH, height to top of bud, height to base of live crown, crown width, vigor and a complete damage assessment (leader, foliage, stem and subsequent cause). Crown width measurements were used to calculated crown surface area. Using the area of an ellipse, crown surface area (CSA) was calculated by,

$$CSA_i = \pi r^2 + \pi rs$$

Where, r is the crown radius taken as an average of the north-south and east-west diameters and s is the length of the crown from the top of the tree to the drip line.

A subset of previously measured Douglas-fir regeneration (from the contracted data) was selected for re-measurement in mid October 2009. In four subplots (10m x 10m) of each treatment unit (1.0 ha), three previously tagged trees were selected, representing: 1) the tallest and or most vigourous tree in the 80cm to < 4 cm dbh class; 2) 30 cm to 80cm class; and, 3) 15 cm to 30 cm class. These trees were measured for top height (using a height pole), root collar diameter (using calipers or dbh tape) and dbh (using dbh tape). When all three size classes were not represented in the subplot, additional subplots were added to the subset.

In addition to the re-measured growth variables, internode length was measured retrospectively for each of the previous 5 years to provide data on height growth. Trees sampled for 5 year height growth were less than 2 meters in height to reduce error associated with measuring false internodes and sampling time. The internodes were averaged over the five years, starting from the end of the 2009 growing season.

Growth of Douglas-fir regeneration was calculated as stem volume increment (SVI) over the period of two growing seasons (2008 and 2009). Stem volume (SV) was calculated using the volume of a cone (in cm);

$$SV = ⅓ * \pi\, r^2 * h$$

Where r is the radius of the tree at root collar (d/2) and h is the height of the tree in the referenced year. SVI was calculated as the difference between SV in 2009 and 2008. This variable was transformed using the natural logarithm to stabilize the variance, due to indications that variance was increasing with tree size. Within each regeneration subplot (3.99 m radius) the density of tree regeneration was recorded for each species and layer (4= 15 cm to 1.3 m tall and 3 = over 1.3 m tall to 3.9 cm DBH) present.

2.3.2.2 Vegetation

In all subplots ($n = 256$) percent cover of understory vegetation was estimated in four quadrats measuring 5m x 5m in each of the four cardinal directions (NE, SE, SW and NW) (Fig 2-1). Percent cover was measured as the vertical leaf area projection of each of the vegetation layers. Cover was recorded by vegetation layer for each of grass, forb, low shrub (<1.3m), tall shrub (>1.3m), moss, coarse wood debris, non-vegetative, natural tree regeneration (<1.3m) and advanced tree regeneration (>1.3m) layers. The four quadrats were then averaged to obtain percent cover for the subplot.

2.3.3 Light Data

Light in the understory is influenced by the interaction of the forest canopy with the path of the sun, elevation, time of year and weather conditions and is thus inherently heterogeneous. Three methods were used to measure light transmittance in order to capture this variability: photodiodes (direct), hemispherical photography (indirect), and LICOR LAI-2000 Plant canopy Analyzers (direct estimate of diffuse, LICOR Inc, Lincoln NE). Each method has its own advantage and disadvantage when estimating light transmittance.

Photodiodes provide a continuous measure of Photosynthetic Photon Flux Density (PPFD) which is the flow of Photosynthetic Active Radiation (PAR) or the amount of photons between 400 nm and 700 nm striking a surface and is thus represented as moles per unit area per unit time. When a photodiode sensor is set under an open sky and another is set under a forest canopy, the ratio of the two can be expressed as a percentage of above canopy PPFD (percent above canopy light, PACL).

A total of 8 light sensors (one in the open) were installed over a range of light conditions and treatments to provide a measure of total PPFD (sum of PPFD of the growing season). Five understory light sensors (custom Gallium Arsenide-Phosphide Photodiode based sensors, Fielder and Comeau 2000) were connected to CR1000 data loggers and programmed to measure light every 15 seconds and store the data as an hourly average. Three additional light sensors were connected to HOBO micro station data logger to increase the range of light levels that were sampled. Photodiodes give a direct estimate of light to which the two indirect but less time consuming (and cheaper) methods can be evaluated.

LAI-2000 Plant Canopy Analyzers can be used to measure diffuse transmittance (DIFN) in most sky conditions as long as the sun is not within the sensor view. The LAI-2000 has an optical light sensor that detects open sky light from five concentric rings that form five angles in the sky (portions). Two types of readings are taken: (1) in an open area and (2) at the sample point. The ratio of the two measurements provides a percentage of overstory diffuse light (DIFN) which has been shown to be highly correlated with the total light transmitted over the growing season (Gendron et al. 1998, Comeau et al. 1998). Indirect light under the canopy is extremely uniform and relatively easy to measure (Reifsnyder et al. 1972). The open unit and unit used at the sample point were merged and analyzed using C2000 software (supplied with the instrument) by interpolating (linearly) the overstory sky conditions at the time of the sample reading.

At the plot center of the 256 (16 treatment units with 16 subplots) 10 m x 10 m subplots, LAI 2000 Plant Canopy Analyzers were used to measure DIFN (masking ring 5) (Comeau et al. 1998). Measurements were taken at four heights; ground level (amount of light reaching the forest floor), above the shrub or herb layer (20-40 cm), 130 cm (the amount of light reaching the Douglas-fir regeneration layer) and at 250 cm (the amount of light reaching the upper strata of the understory). DIFN measurements were also taken at the midcrown (drip line) of the pre-selected Douglas-fir regeneration used for growth measurements. All DIFN readings (using 180º restrictors) were taken in two directions: east in the afternoon and west in morning. The two measurements taken at each point were then averaged to get a 360º estimate of light availability for the plot. LAI-2000 measurements were taken in early July, to get the maximum leaf area obtained within each plot.

To provide a comparison to other studies, hemispherical photographs were taken at 1.3m meters at subplot centers where corresponding natural Douglas-fir regeneration growth re-measurements were taken. A Nikon coolpix 990 camera with a fisheye lens adaptor (185º view) was used to take photographs when the sun was low enough in the horizon to avoid uneven exposure of photographs. The photographs were then analyzed using SLIM software (Comeau et al. 2009) to determine gap fraction, transmittance and contribution of beam and diffuse components to understory light. The Nobis and Hunziker automatic threshold method (Nobis and Hunziker 2005) was used during the batch process and manual thresholding was used as needed with poorly contrasted photographs.

2.3.4 Microclimate

In 2008 sensors were installed in one representative replicate of each treatment to provide information on diurnal and seasonal patterns of soil and air temperature, soil moisture. Soil and air temperature were measured using unshielded chromel-constantan thermocouples at 30cm and 100 cm, respectively. Although unshielded probes may be influenced by direct sunlight, the objective was to sense minimum temperature events using a sensor of similar size and exchange properties to a tree needle, so, that radiative cooling may be detected.

Soil moisture was measured using Campbell Scientific Model 227 gypsum soil moisture blocks at both 15 cm and 30 cm. Gypsum blocks measure soil water potential in kPa by detecting changes in electrical resistance in the gypsum block as it absorbs water. Lopushinsky and Klock (1974), studied transpiration rates of five North American conifers under greenhouse settings, found a decline in transpiration rates at soil water potentials lower than -200 kPa. In a study by Nilsson and Orlander (1995) on drought damage of Norway spruce seedlings, soil water potentials of -100 kPa (10cm below soil surface) were thresholds for seedling drought stress. Orlander and Due (1986), working with seedlings of

Scots Pine showed that when water potential decreased to -100 kPa transpiration rates were 25% of the maximum. Based on these results, I used a conservative threshold of -200 kPa to determine drought stress of the various regenerating species. It is noted that plants will continue to absorb some water from the soil until bulk soil Ψ_w reaches the plant $\Psi_{\pi.}$ This can occur at values of -1500 kPa to -700 kPa (Kozlowski and Pallardy 1997).

All microclimatic measurements were taken at two locations on opposite sides of the sampling area (subplot). Temperature measurements were taken every five minutes and hourly average values were stored using Campbell Scientific CR1000. Soil moisture measurements were collected once per hour and stored in the datalogger. There are no replicates of microclimatic data by treatment and thus analysis is limited to describing the microclimate for one selected plot in each treatment.

2.4 Statistical Analysis

Differences in stand structure, growth, light, vegetation and abundance among treatments used analysis of variance based on a randomized complete block with 2 replicates within each block and subsampling design. The following is the model used to test for treatment differences;

$$Y_{ijk} = \mu\ldots + T_j + B_k + TB_{jk} + \varepsilon_{i(jk)}$$

where μ is the grand mean, T_j is the j^{th} treatment ($j = 1 \ldots 4$), B_k is the k^{th} block ($k = 1,2$), TB is their interaction due to replication of treatments within blocks and $\varepsilon_{i(jk)}$ is the sampling error or the variation between i^{th} subsamples nested within the j^{th} treatment of the k^{th} block ($i = 1 \ldots 16$) (Kutner et al. 2005). When data could not be transformed (as in species counts), non-parametric ANOVA (Kruskal-Wallis test) was used to detect treatment differences without including random effects. Multiple comparisons using a Tukey adjustment (HSD) complimented the two way ANOVA ($\alpha = 0.05$). Planned linear contrasts were used to estimate differences between harvested and unharvested treatments ($\alpha = 0.05$).

Preliminary exploratory data analysis indicated that the count of the number of trees violated the assumptions of general linear models and defining characteristics of continuous variables (ex. Fig. 3-15). In other words, the count data is highly skewed to the right with an inflation of zero's occurring in the Lw, Pl and At sample populations. Generalized linear models (GLM) were used to determine the effect of light, stand variables (Table 2-4) and vegetation on tree regeneration abundance (15cm to 1.3 m) since they can be used to model response variables with skewed distributions and also when relationships between the response and explanatory variables are unique (Zuur et al. 2009). Douglas-fir regeneration abundance was modeled as function of the light environment, a seed source or the presence of the regenerating species being in the overstory, site occupancy or the number of competing species the regenerating area (the total number had to be used because size metrics were not taken for every regeneration tree) and the influence of surrounding vegetation. The following base model was used:

$$\boldsymbol{\mu}_i = e^{b0 + b1*DIFN + b2*Over + b3*Other + b4*Vegetation}$$

Where the response variable (tally) follows an exponential family of distributions (Fig. 2-12), and uses a log link function to relate the linear predictors to the mean response (this way the model will not predict a negative number). The explanatory linear predictors include: *DIFN* which is the light environment above the regenerating layer, *Over*, a binary variable indicating the presence (1) or absence (0) of an overstory seed source within a 10m x 10m area, *Other* which is the number of other species that are within the regenerating layer, *Vegetation* which will have specific coefficients for various types of vegetation cover (eg. low shrubs, grass, etc) calculated as a percentage of the establishing seedbed.

The Poisson distribution was originally used to model Douglas-fir abundance, but provided an inadequate fit when compared to the negative binomial distribution ($x^2 = 2003.4$, $p < 0.0001$). Since the negative binomial model allows for a dispersion parameter (theta), the assumption of the mean equating to the variance (required with Poisson models) can be violated (allowing for overdispersion).

Because the abundance of aspen, larch and pine shows an excess number of zero counts (Fig. 2-12) a zero inflated mixture model was used. This mixture model uses logistic regression to determine the probability of a false zero. A false zero occurs due to measurement error (i.e. a tree was present but was not tallied), design error (i.e. a tree was just outside of the sampling area) or because of random circumstances (i.e. the tree isn't there but the establishing area is well suited to the species). Thus, a "zero" model using a binomial distribution and logit link function will be used to model the probability of false zero's and a "count" model using either a Poisson or a negative binomial distribution with a log link function will model "true zero's" and the counts. The following models are defined using the Poisson distribution:

$$\boldsymbol{f}(y_i = 0) \qquad = \boldsymbol{\pi}_i + (1 - \boldsymbol{\pi}_i) \times e^{-\mu_i}$$

$$\boldsymbol{f}(Y_i = y_i \mid y_i > 0) \qquad = (1 - \boldsymbol{\pi}_i) \times \frac{\boldsymbol{\mu}^{y_i} \times e^{-\mu_i}}{y_i\,!}$$

where,

$$\boldsymbol{\mu}_i = e^{b0 + b1*rDIFN + b2*Over + b3*Other + b4*Vegetation}$$

and

$$\boldsymbol{\pi}_i = \frac{e^{b0 + b1*Over + b2*Other + b4*Vegetation}}{1 + e^{b0 + b1*Over + b2*Other + b4*Vegetation}}$$

The $\mathbf{E}(\mathbf{Y_i}) = \boldsymbol{\mu_i} \times (1 - \boldsymbol{\pi}_i)$ with the Var $(\mathbf{Y_i}) = (1 - \boldsymbol{\pi}_i) \times (\boldsymbol{\mu}_i + \boldsymbol{\mu}i^2/k) + \boldsymbol{\mu}^{\mathbf{2}}_{\mathbf{i}} \times (\boldsymbol{\pi}^{\mathbf{2}}_i + \boldsymbol{\pi}_i)$, k is the dispersion parameter (theta) within the negative binomial model and assumed to be one for the Poisson distribution. For western larch the negative binomial distribution was found to best fit the count process as determined by likelihood ratio tests and comparison of AIC. For pine the zero inflated model with a fitted with a Poisson distribution to model the count process provides a better fit than the negative binomial model using a likelihood ratio test and comparison of AIC (Zuur et al. 2009, Kutner et al. 2005).

The R version 2.10.1 (R Development Core Team 2009) system for statistical computing was used to model the GLM's. The MASS package (Venables and Ripley 2002) was used to fit negative binomial GLM's using the glm.nb() function. The pscl package (Zeileis et al. 2008) was used to model zero inflated negative binomial models and the lmtest package (Zeileis and Hothorn 2002) was used in concordance with the previous two to utilize the likelihood ratio (LR) test denoted by 'lrtest' which tests differences in the log likelihood between nested models. Model selection required eliminating highly correlated predictor variables, followed by removal of predictor variables with high p-values and supplemented with a comparison of Akaike Information Criterion (AIC) values and LR tests to find the most parsimonious model. Model validation was supported by Pearson residuals and Chi-Square test (where the deviance divided by the degrees of freedom is approximately asymptotically chi-squared distributed) (Zuur et al. 2009).

Regression analysis was used to assess relationships between (a) light or stand variables with growth and (b) light and stand variables. Simple linear and non-linear regression models were fit using PROC NLIN and PROC NLMIXED in SAS version 9.1. Explanatory variables included overstory stand variables found in Table 2-4 and DIFN. Dependant variables included DIFN, 5 year average leader length and stem volume increment (assuming the change in volume of a cone).

Explanatory variables used in each equation were determined to be independent of each other based on correlation analysis and variance inflation factor (VIF) estimates. A VIF greater than 10 was assumed to be significant evidence for multicollinearity (Kutner et al. 2005). While multicollinearity does not bias the prediction of the model, standard errors of correlated predictor variables tend to be inflated (Kutner et al. 2005). Model selection was achieved using a step wise selection process when multiple stand variables were included in the regression model. Methods used to evaluate regression goodness of fit included r^2 (for linear models), i^2 for non linear models (without an intercept) and root mean square error (RMSE). AIC was used to compare models that were estimated using maximum likelihood techniques. Visual examination of residual plots was used to evaluate model fit and homogeneity of variance.

$$\mathrm{RMSE} = \sqrt{\frac{1}{n}\sum_{j=1}^{n}(\hat{Y}_i - \bar{Y})^2} \;\; ; \;\; \mathrm{VIF} = \frac{1}{1 - R_i^2}$$

$$\mathrm{R}^2 = \frac{\sum(\hat{Y}_i - \bar{Y})^2}{\sum(Y_i - \bar{Y})^2} \;\; ; \;\; \mathrm{I}^2 = 1 - \frac{\sum(Y_i - \hat{Y}'_i)^2}{\sum(Y_i - \bar{Y})^2}$$

Where Y_i is the individual observation or sampling unit, $\hat{Y}_i$ is the estimate predicted from the model , $\bar{Y}$ is the grand mean and R_i^2 is the coefficient of determination from auxiliary ordinary least squares regression that has X_i as a function of other explanatory variables (Kutner et al. 2005). Parameters were either compared using t-tests to test if slopes or intercepts were significantly different from zero or using 95% confidence intervals.

Models used to explain the effects of either stand variables or light availability on growth variables were fit to various curves based on biological underpinnings from a curve fitting catalogue (Sit and Poulin-Costello 1994). They took the following form:

$$Y = f(\beta X) * HT^d$$

Where $f(\beta X)$ is a nonlinear equation explaining the effect of light availability or stand variables, HT^d is a function equation with initial height (HT) and fitted parameter (d) to adjust the growth response for a given observation. The closer d is to zero the less effect initial height has on the growth response. Previous studies indicate similar relationships (Comeau et al. 1993, Filipescu and Comeau 2007, Cortini and Comeau 2008).

Nonlinear models were used to explore the relationships between light and stand variables, as they provided the best fit to the data as suggested by model statistics and residual plots. All structural based light models used an exponential equation or its linearized version which is similar to Beers law ($I_f/I_o = e^{-kz}$). While using the linearized version of the exponential model may introduce bias (multiplicative) in the errors, its use is necessary for estimating collinearity between predictor variables and enables the use of linear regression techniques (Miller 1984). Other studies evaluating the use of stand parameters as explanatory variables of light availability have used similar models (Vales and Bunnell 1988; Drever and Lertzman 2003; Hale et al. 2009). When estimates of variance inflation factors were needed, PROC REG was used with a linearized version of the exponential model ($\mathrm{Ln}(Y) = \beta_0 + \beta_1 X_1$).

Chapter 3: Results

3.1 Microclimate

The results of microclimate monitoring are intended to provide general and descriptive background relating to the microclimate that seedlings are experiencing. Since air and soil temperature and soil moisture were only measured in one plot for each treatment - statistical analysis and testing for treatment effects is not possible. Given the lack of replicates, inferences about treatment differences must be made with caution.

3.1.1 Air Temperature

During the 13 month period between September 2008 and September 2009 air temperatures at one meter height ranged from -30.5 to 36 °C (across all treatments) (Fig. 3-1). Above freezing temperatures began to occur in mid March, while below freezing temperatures began to occur in late September. Maximum air temperatures occurred between mid-July and early August. During these summer months prolonged periods (July 16th to 24th) of +30 °C temperatures occurred. Winters were characterized by several severe cold temperature events (-20 to -30 °C) followed by warming periods of 0 to +3 °C air temperatures.

Substantial diurnal variation occurred throughout the growing season, allowing summer temperatures to drop by more than 20 °C during the night, with maximum temperatures occurring between 15:00:00 and 17:00:00 hours. Spring time air temperatures (after vernal equinox) dropped below zero degrees potentially exposing seedlings to frost injury. During 2009, frosts occurred up to June 7th, 2009.

Reduction in the residual basal area resulted in greater variability in air temperature at 1.0 m height (Figure 3-2). Minimum air temperatures at one meter were 2.7 °C colder in a light residual basal area treatment unit relative to a control treatment unit during both early spring and summer, though the number of frost events was the same in each treatment unit. The heavy treatment unit was within 1.08 °C of the minimum control temperature throughout the growing season, while the medium treatment unit was within 1.8°C. Maximum air temperatures showed a similar trend, with the light treatment unit being warmer (within 3 °C) then control treatment unit.

Growing degree hours (May 1st to September 30th) were calculated by subtracting threshold temperatures (5°C or 0°C) from hourly temperatures and then calculated as the sum of the values. At both 5°C and 0°C thresholds, the light treatment unit had the greatest number of hours below the two thresholds (320 hrs below 5°C and 42 hrs below 0°C) (Table 3-1). The heavy and medium treatment units had roughly the same number of hours below 0°C, but the medium treatment unit had more hours below the 5°C threshold. The control treatment unit had the greatest number of hours above the thresholds (3398 hours above 5°C and 3348 hours above 0°C) (Table 3-1).

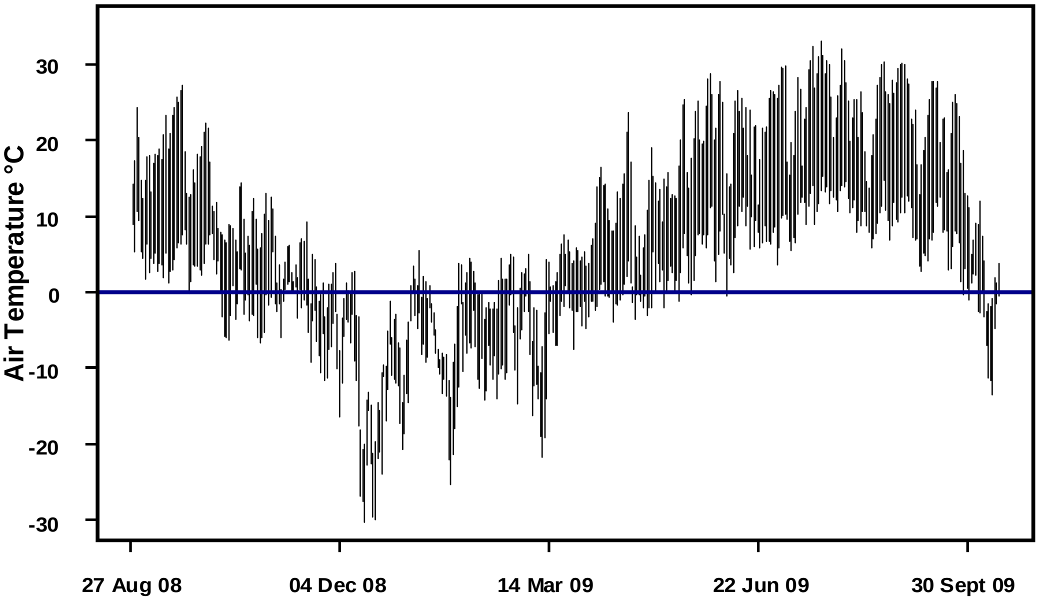

Figure 3-1 Air temperature at 1.0 m height in the uncut control treatment (TU8) during the 2009 growing season. Vertical bars representing the daily maximum and minimum air temperatures .

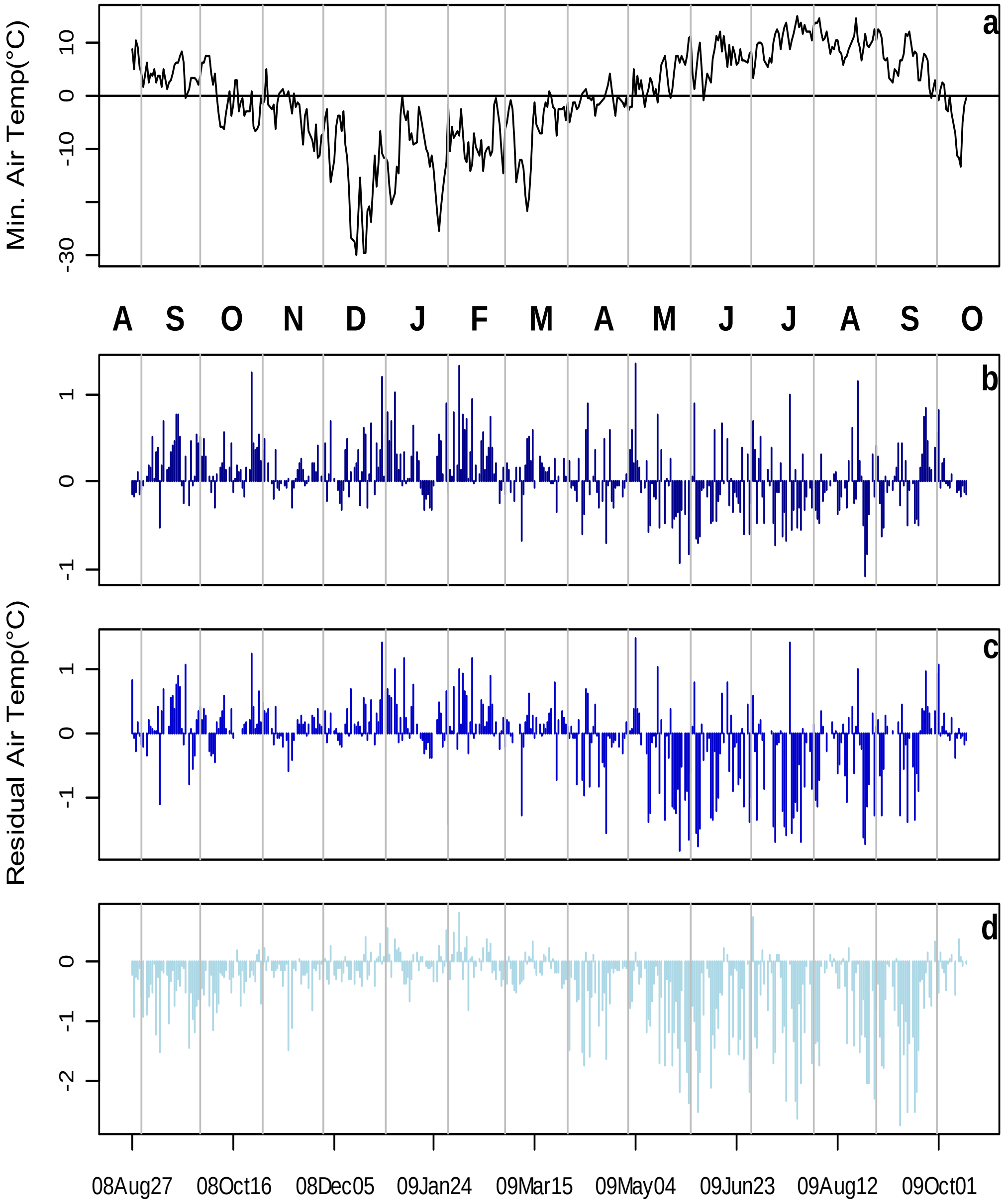

Figure 3-2 Minimum air temperature at 1.0 m height in uncut control (a). Residual minimum air temperature compared to control for Heavy (b), Medium (c) and Light (d) treatment units. X-axis represents the time stamp**.**

Table 3-1 Growing degree hours (number of hours referenced to the indicated threshold values) for air temperatures (1.0 m in height) during the growing season (May 1st to September 30th, 2009))

Treatment	**Growing Degree Hours (Air temperature)**			
	Above 5°C	*Below 5°C*	*Above 0°C*	*Below 0°C*
Control	3398	274	3648	24
Heavy	3395	277	3646	26
Medium	3378	294	3647	25
Light	3352	320	3630	42

3.1.2 Soil Temperature

Seasonal trends in soil temperature (at 30 cm) are shown in figure 3-3. The warmest soil temperatures occurred during mid-summer and ranged from 10 to 25°C. Winter soil temperatures ranged from 0.4 to -2.4 °C. The light treatment unit had an earlier warming date and higher diurnal variability in soil temperature (1 to 2 °C) than the other treatment units (Fig. 3-3). These results may be a function of sensor malfunction or as a result of the sensor being exposed (pulled out of the ground). Soil temperatures peaked at their seasonal maximum in early August and were below 0°C in late November. In mid-January, soil temperature across all treatments experienced a warming event with temperatures rising close to 0°C.

The light treatment unit was generally warmer as it had the highest number if hours above 10°C (2963) and 5°C (3610). The heavy treatment unit had the coldest soil with 201 hours below 5°C and 972 hours below 10°C (Table 3-2).

Table 3-2 Growing degree hours (number of hours referenced to the indicated threshold values) for soil temperature (30 cm below the surface) during the growing season (May 1st to September 30th, 2009)

Treatment	Growing Degree Hours (Soil temperature)			
	Above 10°C	*Below 10°C*	*Above5°C*	*Below 5°C*
Control	2948	724	3588	84
Heavy	2700	972	3471	201
Medium	2924	748	3606	66
Light	2963	709	3610	62

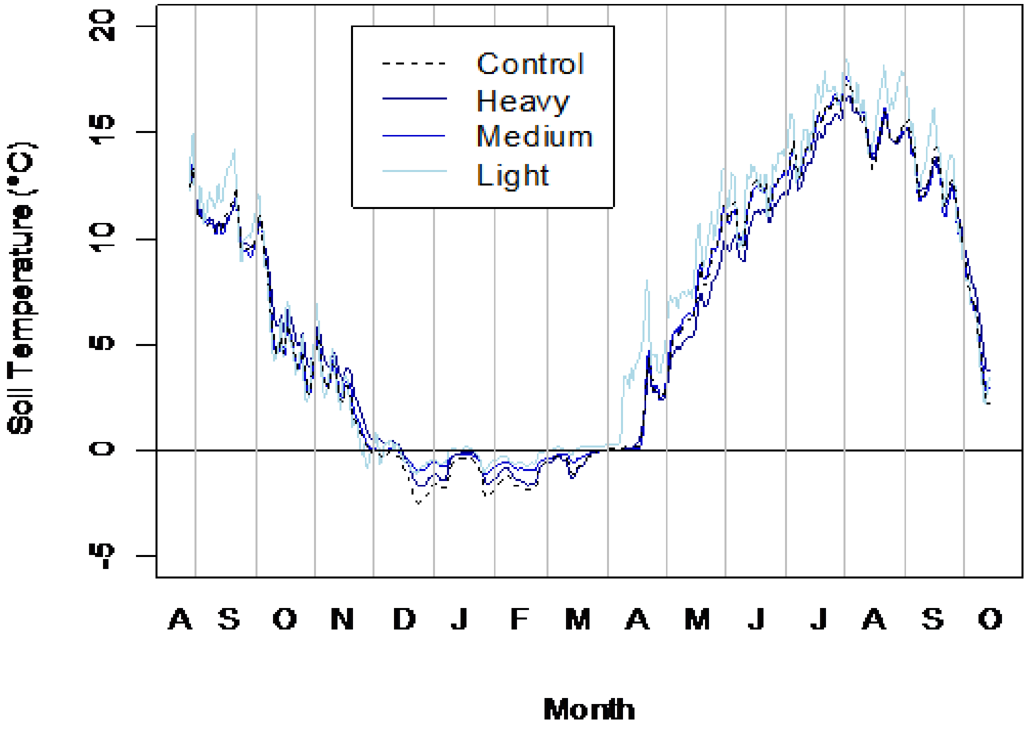

Figure 3-3 Daily average soil temperature at 30 cm below the surface for each treatment.

3.1.3 Soil Moisture

Soil water potential (Ψ_{soil}) was measured at two depths throughout the growing season and trends are shown in figure 3-4. Increases in soil water potentials were closely related to precipitation events recorded at the Cranbrook airport. The total precipitation was ~250 mm over the growing season. Soil water potentials drastically declined after May at both depths with various precipitation events occurring from May to mid-August that resulted in increases in soil moisture. The light and heavy treatment units reached lower Ψ_{soil} sooner and had the most number of hours below -200 kPa relative to the control and medium treatment units at 15 cm depth (Fig 3-4).

After mid-August (19th to 23rd), soil water potentials remained at -1000 kPa at 15 cm depth which is the minimum Ψ_{soil} detected (the range of a gypsum block is approximately 0 to -1000 kPa) and signified a prolonged drought period. At -1000 kPa Douglas-fir experiences stomatal closure which can reduce leaf conductance to 0.02 cm/s and transpiration to 40% of their maximum (Lopushinsky and Klock 1974, Drew and Ferrell 1979).

Soil water potentials at 30 cm depth showed a similar trend (Fig 3-4). Soil water potentials reached their minimum at around -500 kPa for the majority of the summer with the heavy treatment unit reaching this potential earlier than any of the other treatment units. The heavy treatment unit did not have any days with Ψ_{soil} above -200 kPa after June 1st (Table 3-3). The control and medium treatment units had the greatest percentage of days with Ψ_{soil} greater than -200 kPa. Significant precipitation events that can recharge the soil were generally over by late July with drought stress conditions continuing into September. This provided evidence that the spring snow melt and a few precipitation events provide the majority of growing season moisture at this site.

Table 3.3 Number of hours in each month with drought conditions (<-200 kPa) for various treatments

Month	Treatment (number of hours < -200 kPa at 15 cm)			
	Control	Heavy	Medium	Light
May	0	41	0	0
June	449	578	145	563
July	494	744	627	686
August	733	744	744	744
September	720	720	720	720
Total	2396	2827	2236	2713

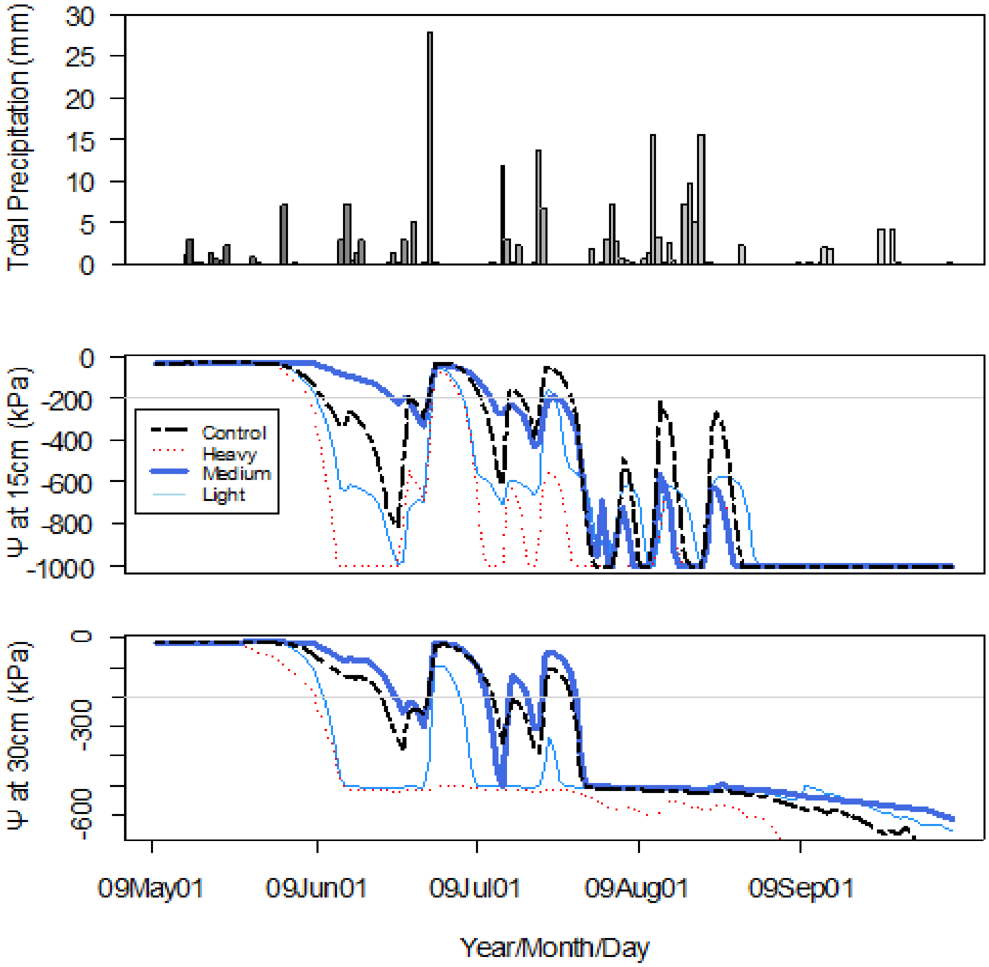

Figure 3-4 Variation in Soil water potential at 15cm and 30cmdepth over growing season (May 1st, 2009 to September 30th, 2009). Y-axis is on a scale of increasing negative numbers. -200 kPa is selected as a threshold for the onset of drought stress.

3.2 Stand Structure and Composition

Across the study site residual densities ranged from 481 to 2212 trees per hectare and basal area ranged from 19.0 to 42.4 m^2/ha across treatments fifteen years post harvest (Table 3-4). Douglas-fir and western larch make up the majority of stand basal area with scattered minor components of lodgepole pine (Fig. 3-5, 3-6, 3-7, 3-8). Douglas-fir had the greatest number of stems > 4 cm dbh, with the exception of treatment unit 7 (Light). Aspen, ponderosa pine, subalpine fir, paper birch and interior spruce were found in less than 3% of sample plots.

In un-harvested treatment units, Douglas-fir comprised the majority of sapling sized (1.3 m to < 4 cm DBH) trees with densities ranging from 137.5 to 1287.5/ha (Table 3-1, Fig. 3-8). Shade intolerant species were not generally found in the seedling or sapling size layers within un-harvested stands. There is substantial variability in structure and composition between un-harvested stands as shown by diameter distributions (Fig. 3-8).

Fifteen years post-harvest, the control (untreated) treatment has significantly more basal area, summed height, SDI and trees per hectare (>4 cm DBH), than the rest of the treatments ($p<0.05$). There were generally more stems in layer one (>12.5 cm dbh) which were contributing to the majority of the basal area, SDI and summed height. There was no significant difference in stand variables between harvested treatments.

Another contributor to variation within treatments was tree mortality. Mountain pine beetle was the main mortality agent for lodgepole pine in these stands and caused a substantial reduction in the pine component (50-70%). For lodgepole pine, mortality was concentrated in the larger diameter classes with 90% of the dead or dying trees being between 10 and 30 cm dbh. In contrast, the majority of Douglas-fir mortality (82%) was found between 6 and 16 cm dbh, while Western larch has 67% of dead or dying trees between 4 and 14 cm dbh. The overall percentage of dead trees for Fd varied between 4 and 6%; with the predominant cause being either windthrow or vegetation press. Lw constituted between 5 to 20% of the trees being dead either from abiotic (low light) or fungal pathogens.

Table 3-4 A summary of stand structural attributes for each treatment unit and grouped by treatment. C = unharvested, H=high residual density (24 m2/ha), M=medium residual density (16m2/ha) and L=light residual density (8 m2/ha). N 1.3 to 4 is the number of trees/ha between 1.3 m to 4 cm DBH, N > 4 is the number of trees/ha greater than 4 cm DBH, G is the basal area using tress > 4 cm dbh, Dead N > 4 is the number of dead trees/ha greater than 4and S_{CrL} is the sum of crown lengths (m/ha). Parenthesis includes standard error.

TU/ Treatment		N 1.3 to 4 (trees/ha)			N > 4 (trees/ha)			G > 4 (m^2/ha)			Dead N > 4 (trees/ha)			S_{CrL} (m/ha)
		Fd	**Pl**	**Lw**	**Fd**	**Pl**	**Lw**	**Fd**	**Pl**	**Lw**	**Fd**	**Pl**	**Lw**	
3	C	1287.5	0	0	1762.5	250.0	200.0	23.0	4.8	2.7	106.3	637.5	56.25	97.7 (8.2)
8	C	550	0	25	1387.5	50.0	156.3	19.1	2.0	21.3	62.5	112.5	6.25	93.6 (8.7)
12	C	137.5	0	0	475.0	56.3	125.0	25.0	2.8	9.0	62.5	118.8	43.75	52.9 (5.1)
14	C	212.5	0	0	531.3	37.5	468.8	14.0	1.4	22.4	12.5	193.8	168.8	73.4 (7.5)
2	H	750	62.5	37.5	1137.5	187.5	225.0	13.1	6.5	6.8	43.75	206.3	31.25	80.1 (7.5)
6	H	425	25	0	112.5	168.8	200.0	6.0	4.4	11.7	0	125	6.25	44.1 (4.1)
9	H	812.5	0	312.5	843.8	31.3	125.0	13.1	1.2	13.2	87.5	56.25	6.25	61.5 (6.1)
16	H	787.5	25	37.5	431.3	43.8	212.5	8.5	1.0	9.7	31.25	206.3	12.5	44.7 (6.1)
4	M	626.6	0	133.3	840.0	140.0	713.3	7.4	3.3	11.9	37.5	150	43.75	84.7 (9.3)
7	M	226.6	253.3	93.3	156.3	56.3	262.5	7.6	2.3	8.7	31.25	93.75	31.25	37.7 (5.6)
10	M	137.5	25	12.5	566.7	33.3	93.3	21.8	1.1	6.9	50	93.75	18.75	59.8 (7.5)
13	M	812.5	0	0	1181.3	100.0	100.0	14.2	2.9	4.6	112.5	0	0	71.4 (7.4)
1	L	925	175	125	1250.0	150.0	256.3	14.4	4.3	4.7	26.7	166.7	33.3	76.8 (7.4)
5	L	325	0	25	643.8	37.5	181.3	11.7	1.1	6.8	0	137.5	12.5	60.8 (7.5)
11	L	475	112.5	100	812.5	131.3	212.5	13.4	4.0	6.7	87.5	12.5	12.5	63.9 (7.7)
15	L	337.5	12.5	87.5	562.5	0.0	75.0	16.0	0.0	7.1	87.5	181.25	18.75	43.5 (5.0)

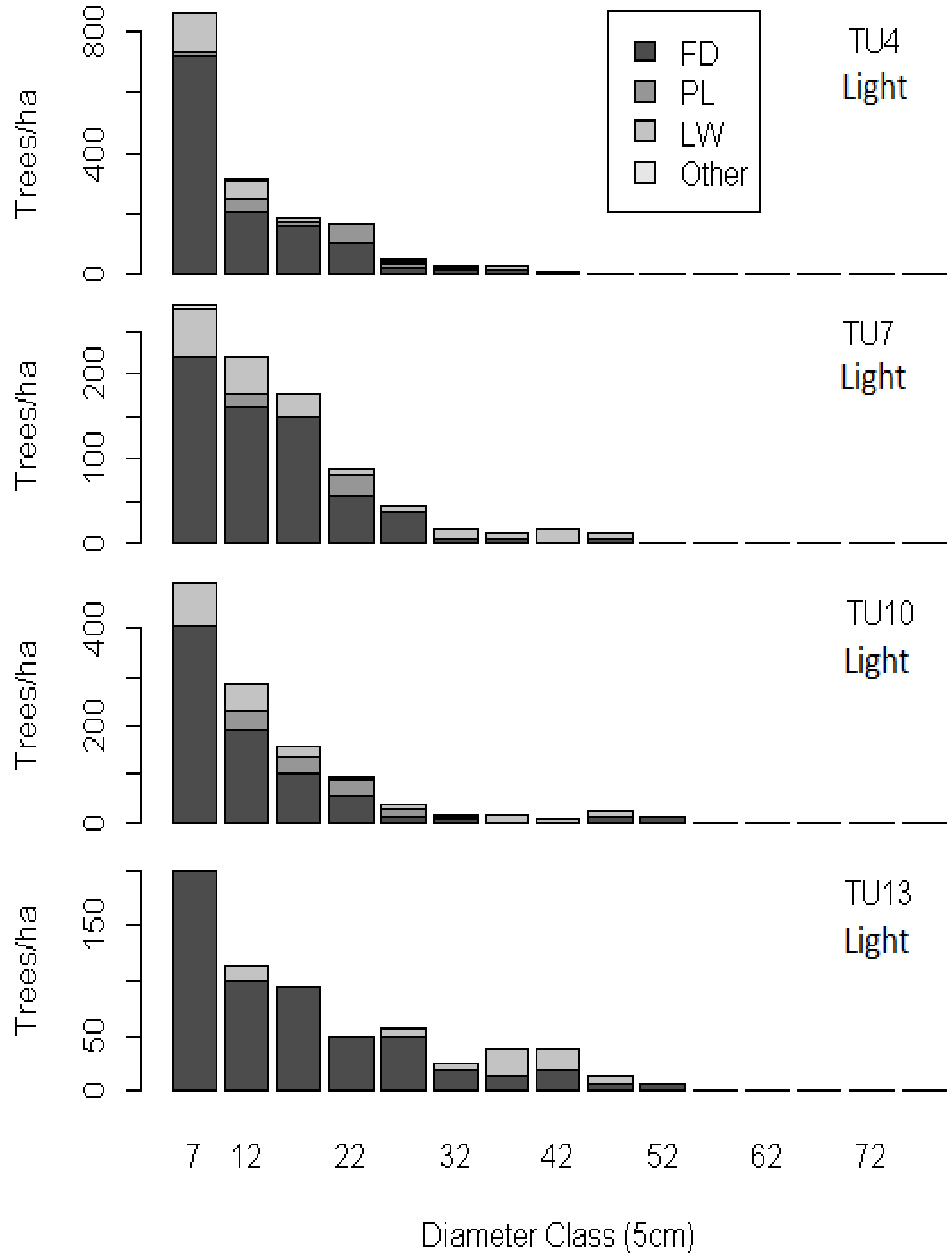

Figure 3-5 Diameter distributions by major species for light residual basal area treatments (8 m^2/ha). Various colors show species composition, with dark = Douglas-fir (FD), medium dark = lodgepole pine (PL), medium light = western larch (LW) and light = remaining species (Other). Refer to table 3-4 for estimated stand structural variables.

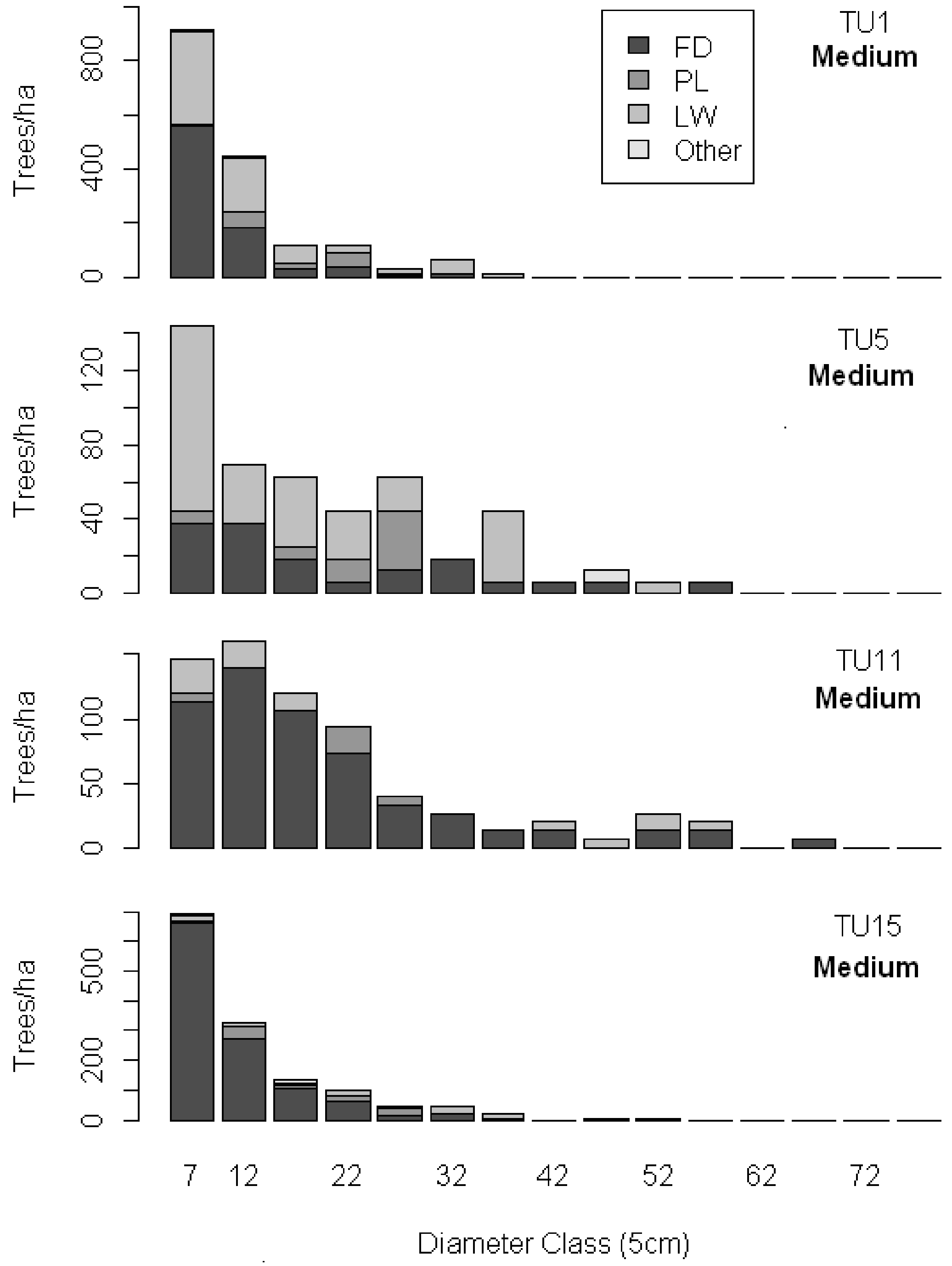

Figure 3-6 Diameter distributions by major species for medium residual basal area treatments (16 m^2/ha). Various colors show species composition, with dark = Douglas-fir (FD), medium dark = lodgepole pine (PL), medium light = western larch (LW) and light = remaining species (Other). Refer to table 3-4 for estimated stand structural variables.

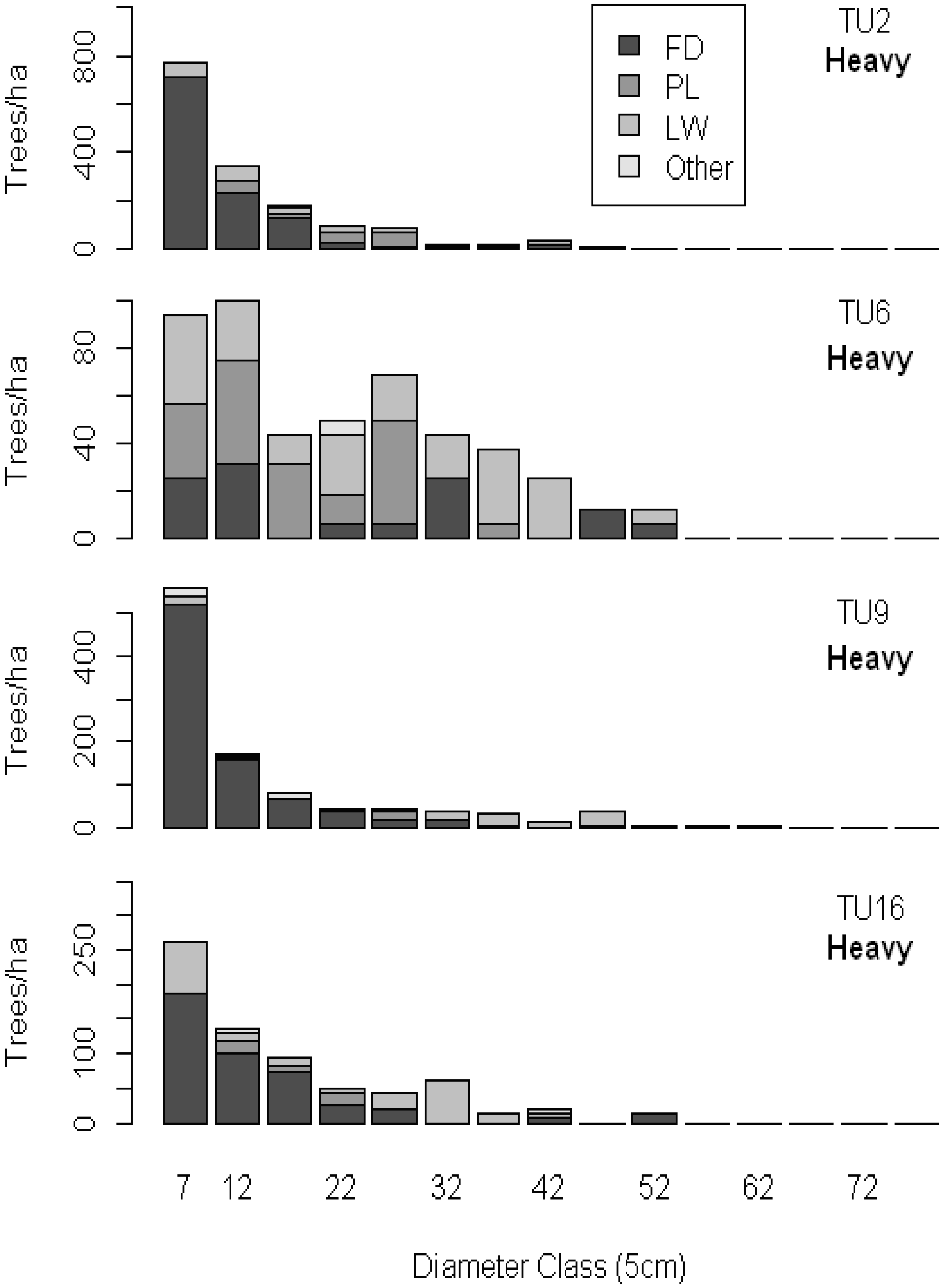

Figure 3-7 Diameter distributions by major species for heavy residual basal area treatments (24 m^2/ha). Various colors show species composition, with dark = Douglas-fir (FD), medium dark = lodgepole pine (PL), medium light = western larch (LW) and light = remaining species (Other). Refer to table 3-4 for estimated stand structural variables.

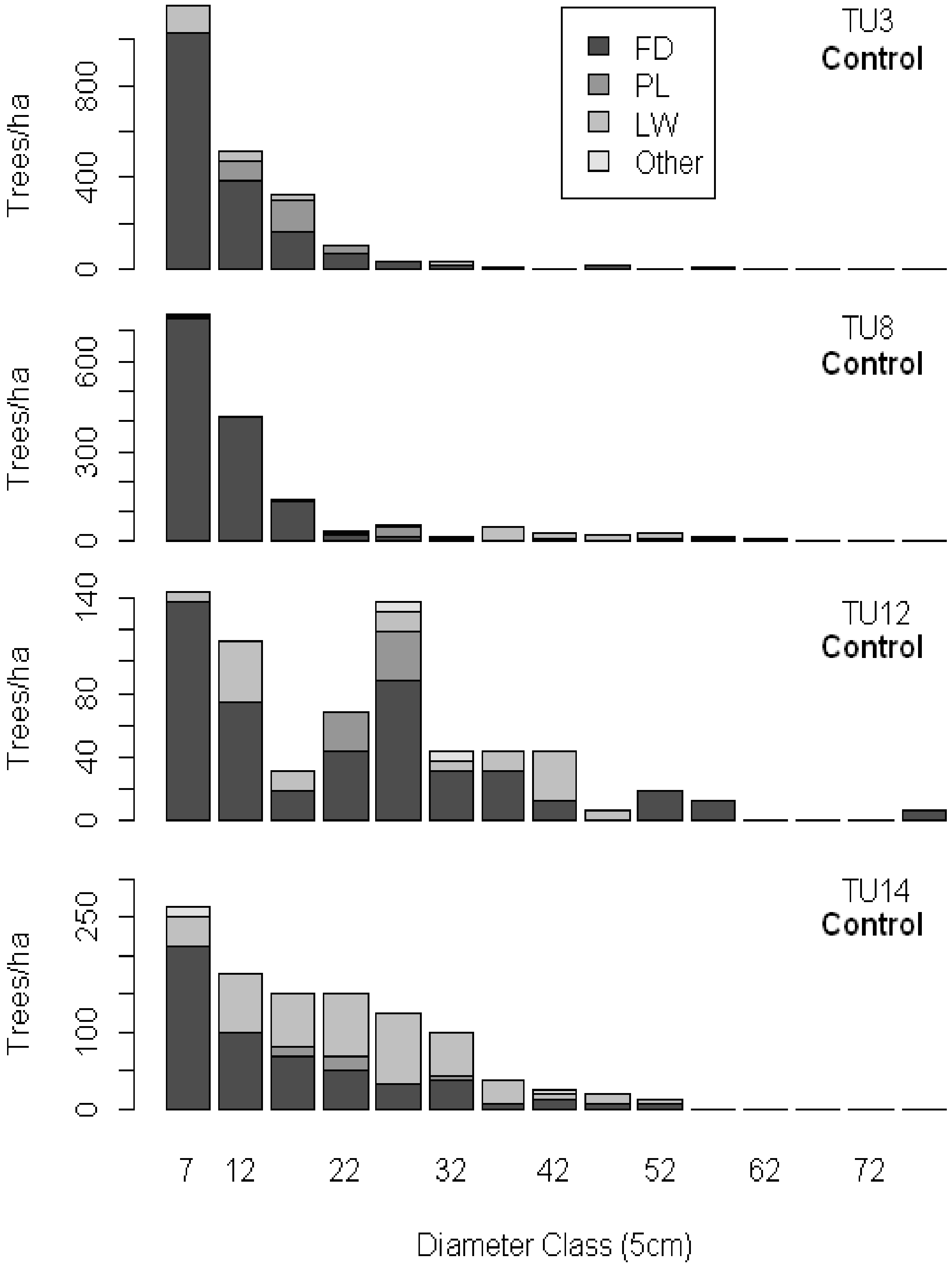

Figure 3-8 Diameter distributions by major species for unharvested treatments (~36 m^2/ha). Various colors show species composition, with dark = Douglas-fir (FD), medium dark = lodgepole pine (PL), medium light = western larch (LW) and light = remaining species (Other) Refer to table 3-4 for estimated stand structural variables.

3.3 Light Availability

Total PPFD over the growing season ranged from 140697 to 606621 µmol m^{-2} across treatments. Growing season % PPFD was only measured from June 5th to June 12th because of technical problems with the open sensor (sensor malfunction). Gendron et al. (1998) showed that mean daily %PPFD was fairly stable throughout the growing season and most variable during the beginning and end of the season.

A comparison of DIFN (diffuse non interceptance as a percentage) taken from LAI 2000 Plant Canopy Analyzers and estimates of diffuse light taken from hemispherical photographs showed a significant positive relationship. DIFN explained 63.1% of the variation in percentage of diffuse (Diffuse) (r^2 =0.631, p<0.0001) with the intercept of the model was not being significantly different from 0 (t_{63}=0.20, p=0.845) and the slope not being significantly different from 1 (t_{63}=1.18, p=0.24). A comparison of DIFN and gap fraction (GFR) estimated from hemispherical photography using SLIM (scope = 60º) showed a relatively better relationship, with 65.97 % of the variation of GFR being explained by DIFN (r^2=65.97, p<0.0001). The intercept for the model with DIFN and GFR was not significantly different from 0 (t_{63}=0.39, p=0.699) and the slope was not significantly different from 1 (t_{63}=1.976, p=0.052). This suggests hemispherical photographs and LAI-2000 measurements of DIFN were giving similar estimates. It should be noted that above 0.3 (DIFN) the relationship to hemispherical photography estimates diminishes (Fig. 3-9). The linear model relating direct light to DIFN was also significant (r^2=0.245, p <0.0001).

All independent variables were highly significant predictors of total PPFD. Measurements of GFR, DIFN, and Diffuse were the best predictors of total PPFD, while direct light explained the least amount of variability in total PPFD (Table 3-5). Total transmittance (as a percentage from above canopy), estimated from hemispherical photographs was the best predictor of total light. None of the models have an intercept significantly different from zero.

There were no significant differences between means of GFR, Direct and Diffuse at 1.3 m height across treatments (p=0.61, p=0.95, p=0.58, respectively). DIFN measured above the regenerating tree layer (1.3m) ranged from 0.083 to 0.58 in the uncut control to 0.081 to 0.68 across harvested treatments. There were no significant differences between treatment means for DIFN being measured at the ground, above the grass layer or at 1.3 m. Above the upper boundary of the understory (~2.5m) the control is significantly darker than the medium treatment (p=0.044) (Table 3-6). The amount of plot to plot variability within treatments is the highest source of variability which is due to gaps, mortality of the pine component, and branch elongation over the 15 year period since treatments were applied.

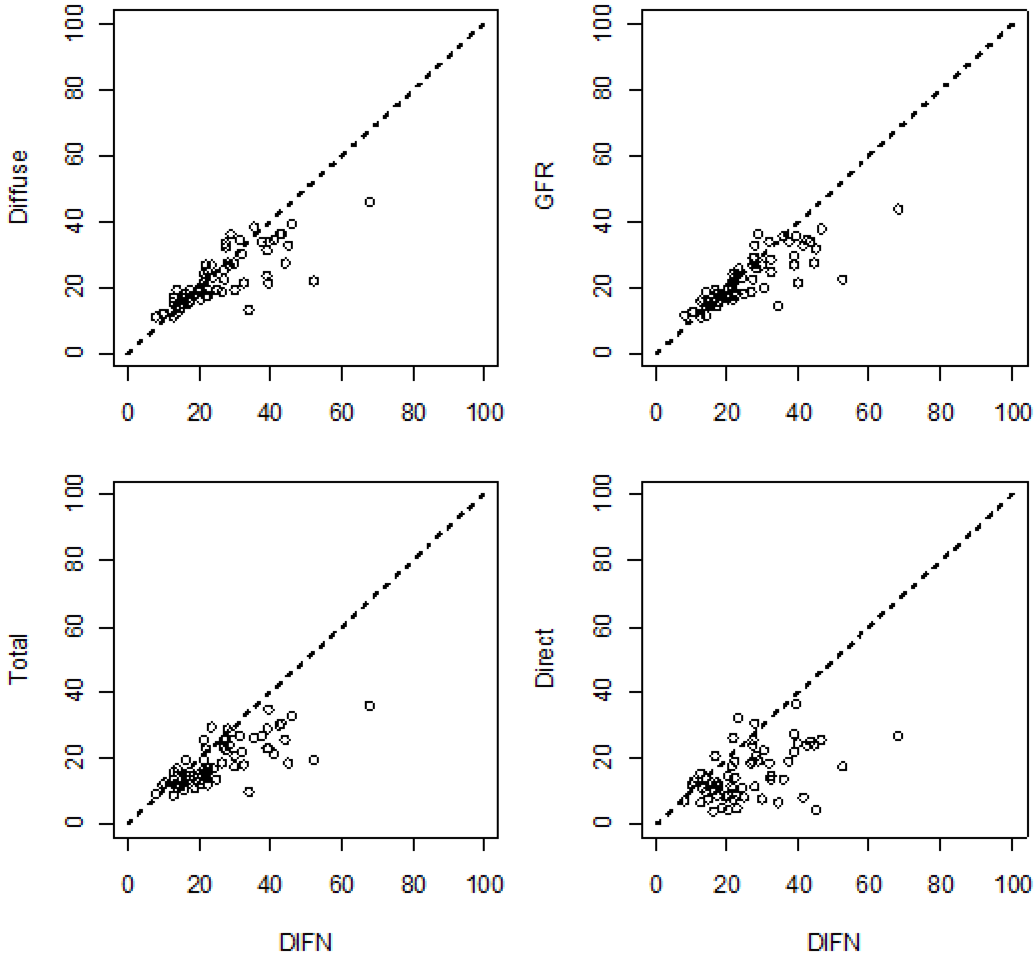

Figure 3-9 Relationships between estimates of transmittance based on DIFN and hemispherical photography estimates. The dashed line on each graph shows a 1:1 relationship.

Table 3-5 Simple linear regression models predicting total growing season PPFD (June 5th to October 15th) µmol m^{-2} from LAI 2000 Plant Canopy Analyzers (DIFN) and hemispherical photography (Gap fraction (GFR), Diffuse, Direct and Total estimates of light). Bolded parameters are significantly different than 0 at alpha =0.05.

Model (SLR)	***n***	**β_1 (StdErr)**	**β_2 (StdErr)**	**RMSE**	**$_{adj}$ R^2**
Total PPFD= $\beta_1 + \beta_2$DIFN	*6*	-84375 (51760)	**175117** (233220)	48144	0.917
Total PPFD= $\beta_1 + \beta_2$GFR	*6*	-200471 (80160)	**16265** (2614)	57432	0.883
Total PPFD= $\beta_1 + \beta_2$Diffuse	*6*	-174139 (69456)	**19349** (2835)	52782	0.901
Total PPFD= $\beta_1 + \beta_2$Direct	*6*	77011 (53960)	**12416** (2750)	76011	0.795
Total PPFD = $\beta_1 + \beta_2$TotHemi	*6*	-43473 (40371)	**16223** (1855)	41839	0.937

Table 3-6 The comparison of DIFN (fractional diffuse transmittance) among residual basal area treatments (C =control, H= heavy, M= medium and L= light) at different vertical light environments (Forest floor is 0 height, herb layer ~30cm, layer 4 = 1.3m and upper layer ~2.5m . Different letters within each row indicate significant differences between treatment means indicated by Tukey's HSD (α =0.05).

Light Location	C	H	M	L
Forest Floor	0.16 (0.0166)	0.17 (0.0166)	0.199 (0.0166)	0.226 (0.0166)
Herb layer	0.20 (0.019)	0.25 (0.019)	0.289 (0.019)	0.3119 (0.019)
layer 4	0.22 (0.026)	0.28 (0.026)	0.277 (0.026)	0.318 (0.026)
Upper layer 4	0.18 a (0.023)	0.31 ab (0.023)	0.334 b (0.023)	0.306 ab (0.023)

3.4 Predicting Light Availability from Selected Stand Variables

Stand variables were better correlated with light measured at 1.3 meters rather than light measured at the ground level, above the herbaceous vegetation or at ~2.5 meters. Since all light measurement techniques provided similar results models discussed in the balance of this chapter will use DIFN measured at 1.3m (tree regeneration height). The following analysis will start with determining the usefulness of single stand variables then progress to complex models using different estimates of stand structure (horizontal and vertical structure) as estimates of light availability.

The exponential model (analogous to Beer's law) was found to have the best fit, relative to simple linear or power models, as judged by residuals, root mean square error (RMSE) and coefficient of determination. Of the stand variables used, models that separated structure by species gave the best results (Table 3-7).

$$\mathrm{DIFN} = \beta_0\, e^{(\beta_1 \mathrm{FD} + \beta_2 \mathrm{LW} + \beta_3 \mathrm{PL})}$$

Where DIFN is diffuse transmittance, FD, LW, and PL are calculated stand variables for Douglas-fir, western larch and lodgepole pine, respectively. $\beta 1$, $\beta 2$, $\beta 3$, are species specific coefficients taking into account overstory composition differences in light attenuation. Table 3-7 provides statistics related to selected models. Figure 3-10 provides a visual representation of the fitted models taking species differences into account.

Using this model with various stand variables as the independent variable, the sum of height (>4cm DBH) provided the best fit and basal area (G) the worst. A unit increase in Fd trees per hectare provides a 0.43% decrease in light levels, while increases in either Lw or Pl trees per hectare did not significantly reduce light levels given the range of densities. Dead trees per hectare was not a significant predictor ($p = 0.16$) and was excluded from the models.

Stand variables that include some measure of tree size (SDI/ha and G/ha) provide evidence that both Fd and Pl were significantly reducing light levels. There was no difference between Fd and Pl in reducing light levels with these models. Lw was not significantly affecting light availability in any of the models. The relatively low amount of variation being explained by the models (i^2<0.38) suggests models for predicting light availability in uneven aged stands needs to incorporate other factors affecting light availability.

Table 3-7 Various stand density estimators (N = density, G= basal area, SDI = stand density index, sum of height) were used as predictors of light availability and separated by species. The following model was developed for the stand variables not separated by species (Total) DIFN= a*e(b*Xi), where Xi is the stand variable of interest. The following model was developed for species separated stand variables (Spp) DIFN= a*e(b*x_1 + c*x_2 + d*x_3) , where x_1 is the effect of FD, x_2 is the effect of LW and x_3 is the effect of PL. For all models n =254. Bolded parameters are significantly different than 0 at alpha =0.05.

Stand Variable	Total/ Spp model	a	b	c	d	i^2	RMSE
N	Total	**0.3961** **(0.0136)**	**-0.0335** **(0.00345)**	.	.	0.331	0.0908
	Spp	**0.3862** **(0.0126)**	**-0.0427** **(0.00404)**	-0.00720 (0.0081)	-0.00177 (0.0157)	0.376	0.0876
G	Total	**0.3407** **(0.0171)**	**-0.7393** **(0.1827)**	.	.	0.064	0.107
	Spp	**0.3536** **(0.0168)**	**-1.2939** **(0.2397)**	-0.2060 (0.2196)	**-1.4172** **(0.5846**)	0.120	0.104
SDI	Total	**0.3819** **(0.0187)**	**-0.0525** **(0.00832)**	.	.	0.144	0.102
	Spp	**0.3824** **(0.0174)**	**-0.0781** **(0.0105)**	-0.0143 (0.011)	**-0.0633** **(0.0253)**	0.204	0.0990
Sum of Height	Total	**0.4081** **(0.0163)**	**-0.0029** **(0.00032)**	.	.	0.285	0.0933
	Spp	**0.4048** **(0.0145)**	**-0.00448** **(0.00040)**	-0.00054 (0.0004)	-0.00115 (0.00081)	0.381	0.0873

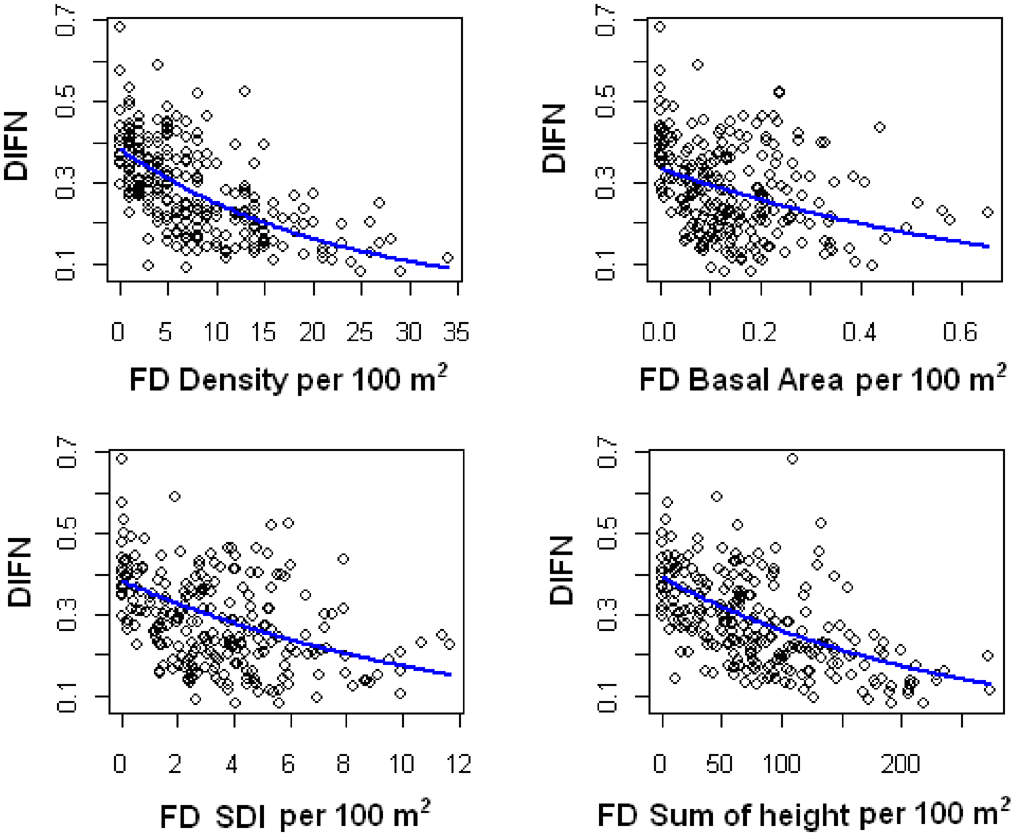

Figure 3-10 Scatter plot showing the relationships between understory light and selected stand variables. The fitted line (blue) represents the effect when species composition is taken into account with non-significant variables held constant at their average. See table 3-7 for statistical description.

While it was impractical to measure every tree within the stand, an average estimate of stand density using the average of all subplots sampled within the plot was used to assess the effects of structure of the surrounding stand. In general, stand level estimates of structure were significant and increased the amount of DIFN variation being explained by 1 to 4% (Fig. 3-11, Table 3-8). When stand structure estimated at the plot scale included some measure of size and density (ie. SDI, G, and RD) either the average N per stand or average sum of heights per stand was selected as predictors via stepwise regression. When stand structure estimated at the plot level included only density, stand level estimates that included both size and density were selected into the model; with G being the best predictor.

Previous studies (Hale et al. 2009) suggest that a combination of stand variables may account for unexplained variation in light availability. Various models were tested to investigate the use of combinations of stand variables in multiple linear regressions. My results suggest that while adding more than one stand variable increases the amount of variation being explained by the model and lowers the root mean square error; gains were marginal (Table 3-8). The inclusion of N and all other selected stand variables resulted in other stand variables being insignificant and thus dropped from the model. Incorporating various stand variables with either G or SDI resulted in either G or SDI being insignificant and thus removed from the models.

Including metrics with height and crown length resulted in marginal increases in the predictive power of the models. The use of multiple stand variables was restricted due to issues with multicollinearity (VIF>10). For instance Douglas-fir density was highly correlated with summed Douglas-fir height ($r = 0.92$, $p < 0.0001$, $n=254$), Douglas-fir LnDBH ($r=0.989$, $p<0.0001$, $n=254$), and summed Douglas-fir diameter ($r=0.88$, $p < 0.0001$, $n=254$). Similarly, G was highly correlated with SDI ($r = 0.96$, $p<.0001$, $n=254$) and relative density ($r=0.94$, $p < 0.0001$, $n = 254$).

Combining density (N) with quadratic mean diameter (Dq) and the height of the tallest tree resulted in a marginal increase in predictive power (Model 5, Fig. 3-11, Table 3-8). Interestingly D_q was positively related to light availability - suggesting that plots with larger stems were associated with higher light levels in the understory (Fig. 3-11). The density of smaller stems (1.3m to < 4 cm DBH) was significantly negatively correlated with light ($r= - 0.271$, $p < 0.0001$, $n = 255$), but was not a significant variable when included with the best predictors of light, such as Douglas-fir N or summed height.

Incorporating a measure of the vertical or horizontal variation in stand structure into these models may encompass the effect of light filtering. Skewness of the size distribution was added to the model as a proxy for differential size effects (Sterba and Monserud 1993). Skewness measures the degree and direction of asymmetry in the distribution of the variable of interest. A value of zero indicates a normal distribution or a theoretical even-aged stand, a negative number indicates a negatively skewed distribution with a greater tendency towards larger trees (taller), a positive number indicates a positively skewed distributed distribution with a greater tendency towards smaller trees (shorter). Skewness of the height distribution was a significant predictor variable which was negatively related to light availability and selected over the skewness of diameters; suggesting the importance of vertical structure (Fig. 3-11, Table 3-8).

The best model explained 43% of the variation in DIFN and included N, sum of Fd heights, skewness of the height distribution and a stand level estimate of basal area (Model 15, Table 3-8).

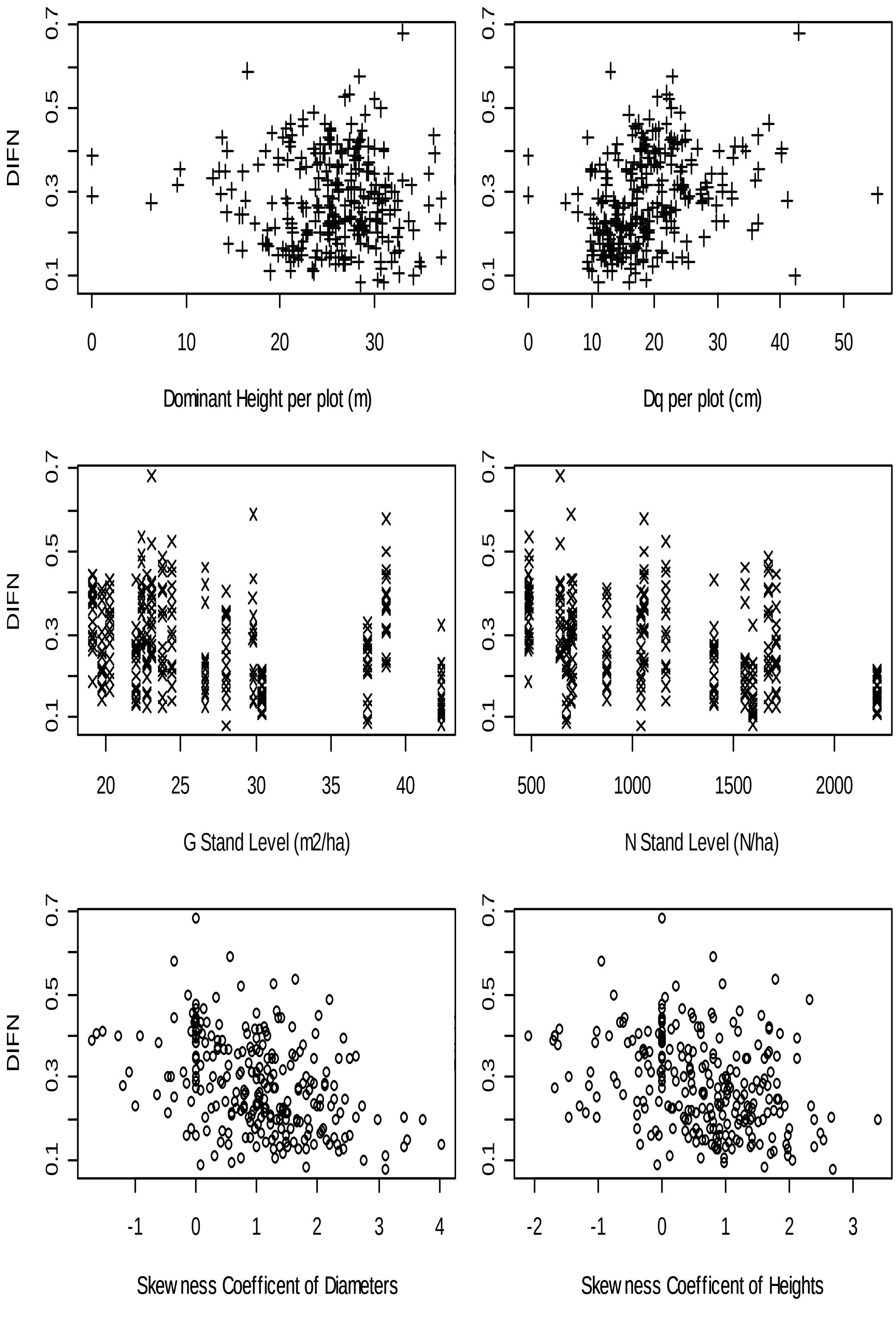

Figure 3-11 Scatter plots of various variables used as covariates in structural based light models. G stand level and N stand level are calculated as an average of the 16 subplots measured in each plot, while other covariates are calculated at the subplot level ($100m^2$).

Table 3-8 Relationships between DIFN and various combinations of stand variables (DBH >4cm) calculated at the subplot scale. Gstand and Nstand are calculated at the stand level scale (hectares). Bolded parameters are significantly different from 0 at alpha =0.05.

No.	Model	RMSE	$_{adj}R^2$
1	**-1.03 - 0.0358** N_{Fd}	0.333	0.372
2	**-0.757 - 0.0337** N_{Fd} **-1.095** G_{stand}	0.324	0.407
3	**-0.758 - 0.0341** N_{Fd} + 0.0625 $G_{Fd\ Pl}$ **- 1.119** G_{stand}	0.328	0.395
4	**-0.737 - 0.0304** N_{Fd} **-0.059** SK_{height} **- 1.136** G_{stand}	0.320	0.422
5	**-0.863 - 0.0306** N_{Fd} **-0.0169**Ht_{max}**+ 0.0113** D_q	0.326	0.400
6	**-1.17 - 1.06** $G_{Fd\ Pl}$	0.401	0.089
7	**-0.858 - 0.816** $G_{Fd\ Pl}$ **-0.0315** N_{stand}	0.371	0.224
8	**-0.845 - 0.901** $G_{Fd\ Pl}$ **-0.119** SK_{height} **- 0.0245** N_{stand}	0.355	0.291
9	**-1.073 - 0.0684** $SDI_{Fd\ Pl}$	0.381	0.175
10	**-0.749 - 0.0486** $SDI_{Fd\ Pl}$ **-0.00294** Ht_{stand}	0.361	0.262
11	**-0.740 -0.0478** $SDI_{Fd\ Pl}$ **– 0.119** SK_{height} **-0.0025** Ht_{stand}	0.345	0.331
12	**-1.00 - 0.00427** Ht_{Fd}	0.339	0.349
13	**-0.904 - 0.0037** Ht_{Fd} **- 0.0129** N_{stand}	0.335	0.367
14	**-0.759- 0.00196** Ht_{Fd} **- 0.01808** N **-0.85861** G_{stand}	0.324	0.408
15	**-0.737 - 0.0019** Ht_{Fd} **- 0.0155** N **- 0.0699** SK_{height} **- 0.908** G_{stand}	0.319	0.430
16	**-0.961 -0.0145** $LnDBH_{Fd}$	0.341	0.341
17	**-0.717 -0.0158** $LnDBH_{Fd}$ **-0.0621** SK_{height} **-1.123** G_{stand}	0.323	0.411

Variables: N_{Fd} = number of Fd trees per plot, G_{stand} = basal area averaged among subplots, SK_{hieght} = Skewness coefficient in the height distribution, Ht_{max} = height of tallest tree, D_q = quadratic mean diameter, $G_{Fd\ Pl}$ = basal area of Fd and Pl, N_{stand} = number of trees averaged among plots, $SDI_{Fd\ Pl}$ = stand density index of Fd and Pl, Ht_{Fd} = sum of Fd heights, N= number of trees, $LnDBH_{Fd}$ = the sum of natural log transformed diameter at breast height.

Although single estimates of stand structure explained between 12.2 to 38.2 % of the variability in DIFN, the effect of sub-canopy layers within plots has not been taken into account. The significance of the skewness coefficient suggests that the distribution of size was an important attribute of light attenuation.

To further explore the effects of size distributions, a multiple linear regression model was used to determine the influence of different sized trees on light availability in the understory. The basal area and number of trees per height class were used as predictor variables for light as they represent two commonly used stand variables. The coefficient for each size class describes the effect for that class. The dependant variable had to be transformed to deal with heteroscedasticity and thus the following model was used

$$\mathrm{Log}_e\mathrm{DIFN} = b_0 + \Sigma\, b_i{*}X_i + e$$

Where DIFN is diffuse transmittance, b_i are the coefficients for the effect of each size class, X_i is the amount of basal area or number of trees within height classes within a 2 meter interval starting at 2 meters and diameter classes (5 cm width).

Multiple linear regressions using the basal area and number of trees per height class explained 42.6% and 45.8% of the variation in light availability, respectively (Table 3-9 and Table 3-10). Various predictor variables showed no evidence of being linearly correlated with one another and thus the model does not indicate problems with multicollinearity. Figure 3-12 and Figure 3-13 provide graphical representations of the effect each height class has on light availability. The changes in slope (bi) indicate that basal area in smaller classes had a stronger negative effect on light availability than did basal areas in larger classes (Fig. 3-12). When a tree per 100m2 was used, the number of trees in the taller classes was having a greater negative effect on light attenuation relative to trees in the smaller classes (Fig. 3-13).

Table 3-9 Estimates from a multiple regression using basal area (per $100m^2$) in each 2 m height class as the independent variable. Ln (DIFN) = b0 + b1*Ba_{2-4} + b2*Ba_{4-6} + b3*Ba_{6-8} . . . + b18*Ba_{36-38}. R^2=0.426, RMSE = 0.33, n= 252. Bolded p-values reject the null hypothesis that estimates are not different from zero at alpha = 0.05.

Parameter (Height Class)	Estimate (Standard Error)	Pr > |t|	Partial R^2	Variance Inflation Factor
Intercept	-0.90734 (0.05285)	**<.0001**	.	0
2-4	36.6238 (15.40601)	**0.0183**	0.014	1.47136
4-6	-13.7059 (4.79617)	**0.0047**	0.1276	1.86049
6-8	-7.63942 (2.98542)	**0.0111**	0.0686	1.68765
8-10	-9.24744 (2.26967)	**<.0001**	0.0579	1.49332
10-12	-3.60255 (1.71451)	**0.0367**	0.02618	1.39142
12-14	-3.02289 (1.33406)	**0.0244**	0.01786	1.15293
14-16	0.48526 (0.65278)	0.458	0.000956	1.1502
16-18	-3.12376 (1.08096)	**0.0042**	0.01272	1.13138
18-20	-2.41078 (0.90973)	**0.0086**	0.01615	1.16549
20-22	-0.288 (0.40502)	0.4777	0.000242	1.11122
22-24	0.15855 (0.35788)	0.6581	0.00411	1.12205
24-26	-0.185 (0.52009)	0.7224	0.00014	1.06274
26-28	-1.98974 (0.77425)	**0.0108**	0.00744	1.13076
28-30	-0.36267 (0.37883)	0.3394	0.00146	1.0816
30-32	-1.27878 (0.4074)	**0.0019**	0.01708	1.173
32-34	-1.1734 (0.39559)	**0.0033**	0.03102	1.15234
34-36	-1.38478 (0.46493)	**0.0032**	0.0219	1.05838
36-38	-0.27886 (0.58131)	0.6319	0.000567	1.18509

Table 3-10 Estimates from a multiple regression using number of trees per 100m^2 in each 2 m height class as the independent variable. Ln (DIFN) = $b_0 + b_1 * t_{2-4} + b_2 * t_{4-6} + b_3 * t_{6-8} \ldots + b_{18} * t_{36-38}$. R^2=0.458, RMSE = 0.32, n= 252. Bolded p-values reject the null hypothesis that estimates are not different from zero at alpha =0.05.

Parameter (Height Class)	Estimate Standard Error	Pr > |t|	Partial r^2	Variance Inflation Factor
Intercept	-0.97542 (0.04445)	**<.0001**	.	0
2-4	0.04317 (0.02553)	0.0921	0.01741	1.39238
4-6	-0.03821 (0.01252)	**0.0025**	0.18253	2.04367
6-8	-0.03633 (0.01338)	**0.0071**	0.09534	2.14391
8-10	-0.03322 (0.01677)	**0.0489**	0.02987	1.91053
10-12	-0.02905 (0.02001)	0.1478	0.01682	1.79557
12-14	-0.04498 (0.02231)	**0.045**	0.01612	1.38379
14-16	-0.05684 (0.02402)	**0.0188**	0.00747	1.20712
16-18	-0.06074 (0.02668)	**0.0237**	0.00941	1.30145
18-20	-0.04253 (0.02577)	0.1002	0.00155	1.24008
20-22	0.03456 (0.02915)	0.237	0.00751	1.17138
22-24	0.000798 (0.03313)	0.9808	0.000066	1.09059
24-26	-0.01635 (0.03435)	0.6346	0.000023	1.08398
26-28	0.01304 (0.03869)	0.7364	0.00146	1.10448
28-30	-0.05455 (0.04716)	0.2486	0.00387	1.07769
30-32	-0.20803 (0.05817)	**0.0004**	0.02603	1.13542
32-34	-0.17919 (0.07064)	**0.0118**	0.02157	1.17868
34-36	-0.3147 (0.10628)	**0.0034**	0.02046	1.06528
36-38	0.01035 (0.15889)	0.9481	0.000011	1.19718

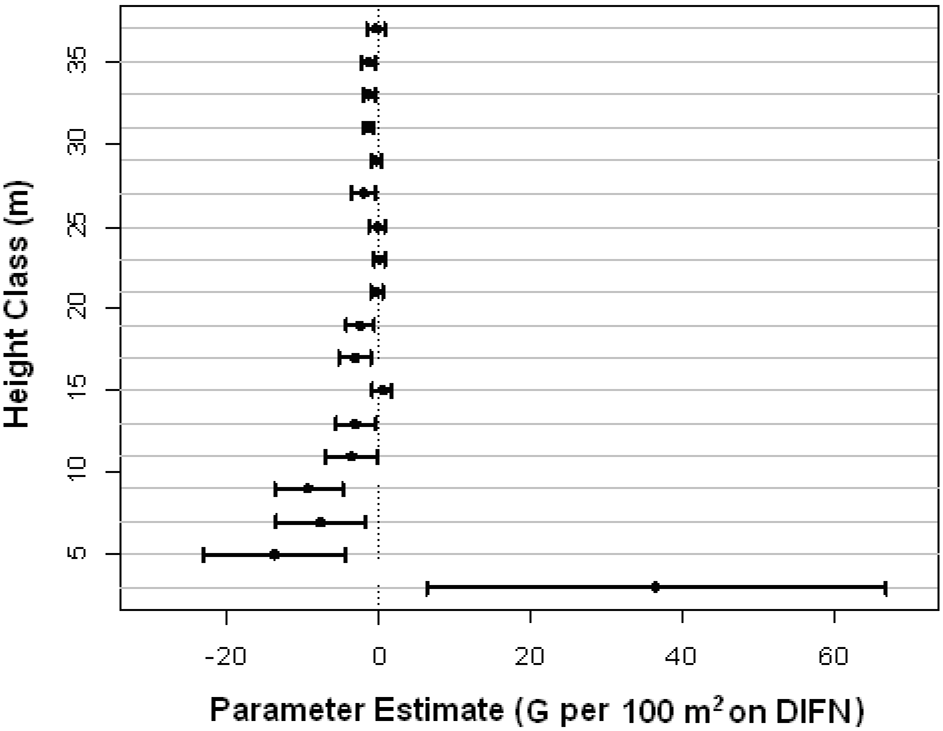

Figure 3-12 Effects of height class on parameter estimates from the regression model for the effect of basal area (m^2 /$100m^2$) on DIFN for each height class. Error bars are 95% confidence intervals of the estimate. See table 3-9.

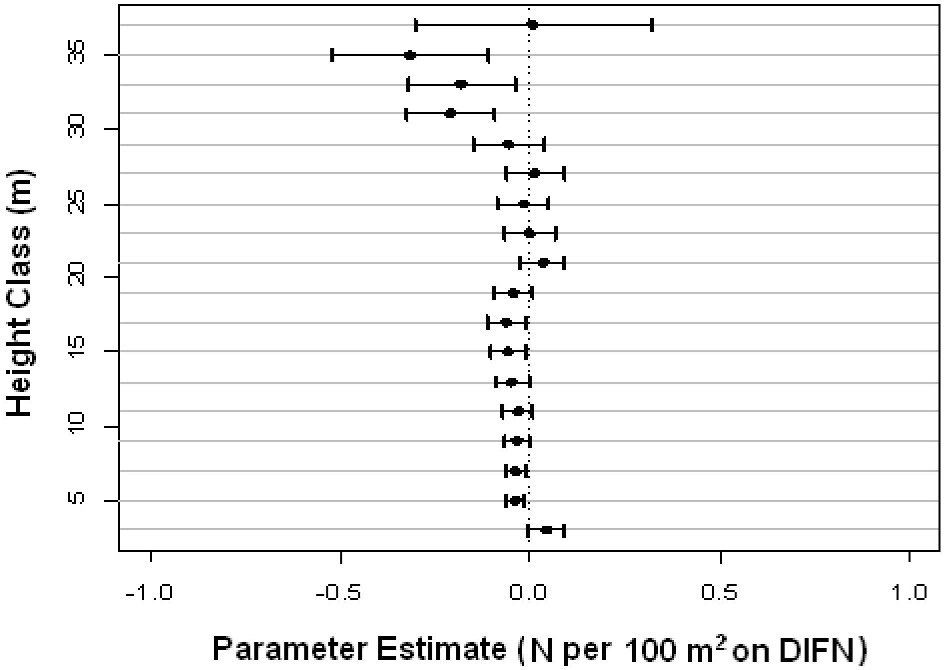

Figure 3-13 Effects of height class on parameter estimates from the regression model for the effect of density (N/$100m^2$) on DIFN for each height class. Error bars are 95% confidence intervals of the estimate. See table 3-10.

Investigation into the effect various size classes have on light availability indicates that different strata should be weighted differently. While including a detailed regression of many size classes provided fair results (42-45% of the variation was explained), accumulating the effect of size into a smaller number of classes can provide a more realistic or parsimonious model for practical use. It was also useful to test whether the observed effects of size were confounded by size class width or an issue with sample size. Size classes whose effect was approximately the same (consecutively not significantly different) were combined into a single stratum to create a total of three size strata; small (4 to 10 meters height or 5 to 10 cm DBH), medium (10.1 to 20 meters or 10.1 to 22 cm DBH) and large (>20.1 meters or >22.1 cm DBH). These strata were then included in the top three models developed in table 3-8 (Models 4, 15, 17).

19. $\text{Log}_e\ DIFN_{1.3} = b_0 + b_1\ N_{Fd\ small} + b_2\ N_{Fd\ medium} + b_3\ N_{Fd\ large} + b_4\ SK_{height} + b_5\ G_{stand}$

Where, model ${}_{adj}R^2$ =0.461, 0.462, RMSE = 0.311, 0.310, b_0 = -0.746, -0.7178, b_1 = -0.0302, -0.0305, b_2 = -0.0542, -0.068, b_3 =-0.0322, -0.0274, b_4 = -0.053, -0.0448, b_5 =-1.0546, -1.116, for strata estimated using height and diameter classes respectively. $N_{Fd\ small,}$ $N_{Fd\ medium,}$ $N_{Fd\ large}$, are number of Douglas-fir(per plot) in each small, medium and large strata, respectively.

20. $\text{Log}_e\ DIFN_{1.3} = b_0 + b_1\ Ht_{Fdsmall} + b_2\ Ht_{Fdmedium} + b_3\ Ht_{Fd\ large} + b_4\ N + b_5\ SK_{height} + b_6\ G_{stand}$

Where model ${}_{adj}R^2$ = 0.469, 0.471, RMSE =0.309, 0.308, b0=-0.723, -0.711, b1 =-0.00344, -0.00235, b2 =-0.00351, -0.00421, b3 =-0.00136, -0.00131, b4=-0.00604, -0.00938, b5=-0.0644, -0.0681, b6=-1.033, -1.019, for strata estimated using height and diameter classes respectively. $Ht_{Fd\ small,}$ $Ht_{Fd\ medium,}$ $Ht_{Fd\ large}$, are sum of Douglas-fir heights (per plot) in each small, medium and large stratum, respectively.

21 $\text{Log}_e\ \text{DIFN}_{1.3} = b_0 + b_1\ \text{LnDBH}_{small} + b_2\ \text{LnDBH}_{medium} + b_3\ \text{LnDBH}_{large} + b_4\ \text{SK}_{height} + b_5\ \text{G}_{stand}$

Where ${}_{adj}R^2$ =0.442, 0.460, RMSE = 0.316, 0.311, b_0 =-0.742, -0.715, b_1 =-0.0168, -0.0162, b_2 =-0.0206, -0.0252, b_3= -0.00936, -0.0081, b_4=-0.0676, -0.0475, b_5=-1.086, -1.117, for strata estimated using height and diameter classes respectively. $\text{LnDBH}_{Fd\ small}$, $\text{LnDBH}_{Fd\ medium}$, $\text{LnDBH}_{Fd\ large}$, are the sum of Douglas-fir log transformed dbh (per plot) in each small, medium and large stratum, respectively.

The best model (20) explained 47.1 % of the variation in DIFN indicating no loss in explanatory power compared with using 2 m height classes. This suggests other factors need to be incorporated that are not accounted for by structural variables used in this study

3.5 Predicting Growth of Douglas-fir Regeneration from Light and Stand Variables

Average 5 year leader length equaled 2.3 cm (SD=1.2), 3.6cm (SD=1.69) and 6.8cm (SD=4.25) for small, medium and large size Douglas-fir regeneration. Average diameter increment across treatments equaled 0.78cm/yr (SD=1.53), 0.85 cm/yr (SD=1.61) and 0.98 cm/yr (SD=1.56) between two growing seasons for small, medium and large size Douglas-fir regeneration.

Stem volume increment between 2008 and 2009 did not differ among treatments for small (p=0.47), medium (p=0.56) and large (p=0.36) size classes. The same result was found when using average 5 year height and diameter increment. Although the greatest height increments were found within the light treatments and lowest height increments were found within the control treatments the amount of variation within treatments was sufficient to mask differences among treatments (alpha =0.05).

Simple linear models were first used to explore relationships between growth of Douglas-fir regeneration and light. The residuals under this linear model showed signs of heteroscedasticity and thus a logarithmic transformation (with a one being added due to observations with zero) was applied to the dependant variable, SVI.

Power models were found to best explain the relationship between SVI and light once initial size (height in 2008) was included. Adding a covariate to account for variation in initial size greatly increased the i^2 value and reduced the RMSE (Table 3-11). Initial height acted approximately the same as the covariate crown surface area; as judged by a minute difference in i^2, RMSE and AICc values. DIFN explained 84% of the variation in log transformed stem volume increment after accounting for initial size.

While various types of models were fit to the relationship between SVI and stand variables, those that took the form of the best models used to predict light explained the most variation in log transformed SVI (77.7 to 82.3%). The top three models predicting SVI used either Douglas-fir density (N_{Fd}), sum of Douglas-fir log transformed diameter ($LnDBH_{Fd}$) or summed Douglas-fir height as explanatory variables, the worst models of SVI used either Douglas-fir basal area, SDI or RD as explanatory variables. The combination of different stand variables resulted in a marginal increase in the predictive power of the model. The skewness coefficient for either diameter or height distributions were not significant and were therefore excluded from the models (Table 3-11).

Table 3-11 Results from selected models predicting growth (Ln of stem volume increment +1) of Douglas-fir regeneration using and light or various stand variables described below.*n*=218. Bolded parameters are significantly different from 0 at alpha =0.05.

No.	Model	${}_{adj}R^2$	RMSE
1	0.36+ **8.23** DIFN	0.120	1.910
2	**1.28**+ 15.43 DIFN$^{\mathbf{1.965}}$	0.140	1.900
3	**-0.675**+ **0.151** DIFN$^{\mathbf{0.2565}}$ CSA$_i^{\mathbf{0.3569}}$	0.830	0.840
4	**-1.844**+ **0.867***DIFN$^{\mathbf{0.3342}}$ *HT$_i^{\mathbf{0.4468}}$	0.840	0.830
5	(**0.0906** **-0.0012** N$_{Fd}$ **-0.000819** G$_{stand}$)*Ht$_i^{\mathbf{0.7905}}$	0.800	0.929
6	(**0.0787** **– 0.00015** Ht$_{Fd}$ **-0.000503** G$_{stand}$)*Ht$_i^{\mathbf{0.8107}}$	0.812	0.901
7	(**0.0964** **-0.00055** LnDBH **-0.000848** G$_{stand}$)*Ht$_i^{\mathbf{0.788}}$	0.805	0.918
8	(**0.104** **-0.0286** G$_{Fd\ Pl}$ **-0.00217** N$_{stand}$)*Ht$_i^{\mathbf{0.7417}}$	0.777	0.981
9	(**0.0951** **-0.00266** SDI$_{Fd\ Pl}$ **-0.0000166** N$_{stand}$)*Ht$_i^{\mathbf{0.7620}}$	0.793	0.947
10	(**0.0837** **-0.001** N$_{Fd\ small}$ **-0.00247** N$_{Fd\ medium}$**-0.00393** N$_{Fd\ large}$ **-0.000609** G$_{stand}$)*Ht$_i^{\mathbf{0.8046}}$	0.801	0.914
11	(**0.0866** **-0.000156** Ht$_{Fd\ small}$ **-0.00059** Ht$_{Fd\ medium}$ **-0.00122** Ht$_{Fd\ large}$ **-0.0097** N **- 0.000672**G$_{stand}$)*Ht$_i^{\mathbf{0.8183}}$	0.823	0.876
12	(**0.0837** **-0.00052** LnDBH$_{small}$ **-0.00098** LnDBH$_{medium}$ **-0.0011** LnDBH$_{large}$ **-0.000596** G$_{stand}$)*Ht$_i^{\mathbf{0.804}}$	0.810	0.912

Variables: N$_{Fd}$ = number of Fd trees per plot, G$_{stand}$ = basal area/ha averaged among plots, G$_{Fd\ Pl}$ = basal area/plot of Fd and Pl, N$_{stand}$ = number of trees averaged among plots, SDI$_{Fd\ Pl}$ = stand density index of Fd and Pl, Ht$_{Fd}$ = sum of Fd heights, N= number of trees, LnDBH$_{Fd}$ = the sum of natural log transformed diameter at breast height.

The initial size of Douglas-fir regeneration was an important attribute when modeling growth and thus the relationship between stand variables or light and growth of different sized Douglas-fir regeneration (as it relates to regeneration standards) will be explored. For small sized Douglas-fir regeneration N, DIFN and LnDBH were the best predictors of 5 year average height growth, explaining 43.1, 43.4 and 45% of the variation, respectively (Table 3-12). Stand variables other than N and LnDBH were not significant ($p>0.05$) for trees less than 30 cm. The number of regenerating trees (15 cm and 1.3 m) and initial size were the most significant variables in the models predicting 5 year average leader length in trees less than 30 cm (Table 3-12).

The density of layer 3 stems (1.3 m to < 4cm DBH) was not a significant predictor in any of the regression models for either trees between 30 and 80 cm or greater than 80 cm in height and was thus omitted from the models. DIFN and all selected stand variables were significant and negatively related to 5 year average leader length in trees between 30 and 80 cm in height. The best models included DIFN, N and LnDBH which explained 63.1, 53.0 and 50.7 %, respectively of the variation in 5 year average leader length (Fig. 3-14). The worst models included G, SDI and RD; which explained 35.6, 41.9, and 43.5% of the variation in 5 year average leader length, respectively (Table 3-12). Differentiating the stand variables by species increased the predictive power of the models constructed for trees between 30 and 80 cm.

For Douglas-fir trees taller than 80cm stand density variables and light availability were significant in models predicting 5 year average leader length. Initial size was insignificant and was excluded from the models ($p=0.50$). N was found to be the best predictor, explaining 63.3% of the variation, followed by LnDBH (63.0%) and summed height (57.9%) (Fig. 3-14).

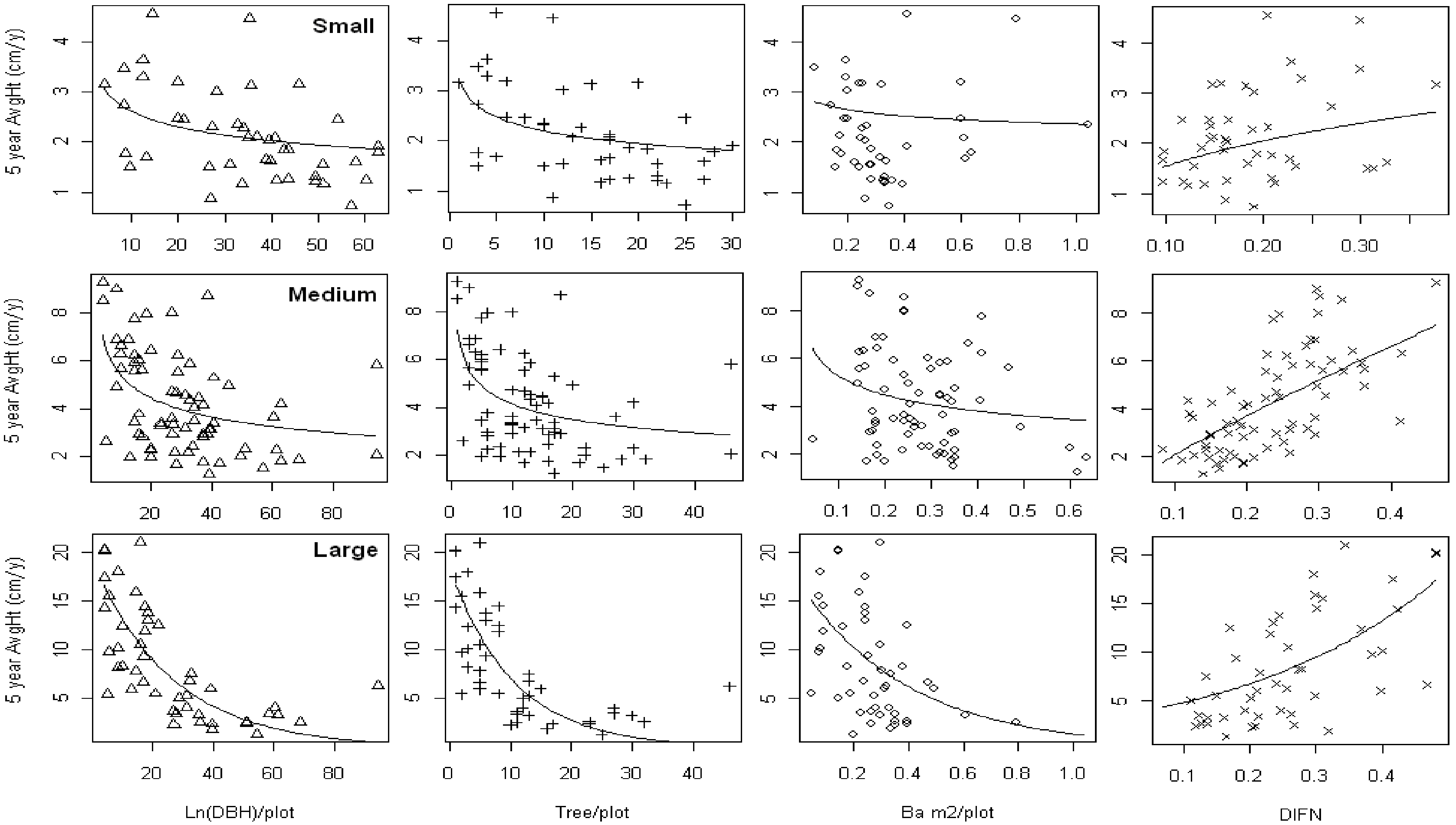

Figure 3-14 Relationships between selected stand variables and growth taken as an average of 5 year leader lengths for small medium and large size Douglas-fir regeneration. Statistical information for the fitted curves is found in table 3-12.

Table 3-12 Statistical information for the relationships between various stand variables and growth of three different size classes of Douglas-fir regeneration using the model average 5 year height increment $= (a*\text{Estimator}^{b})*Ht_i^{c} + d*N_{Layer3}$ See table 2-4 for definition of estimators. N_{layer3} = the number of trees 1.3m in height to < 4 cm DBH. Bolded parameters are significantly different than 0 at alpha =0.05.

Size	Estimator	a	b	c	d	I^2	RMSE
Small <30 (*n*=43)	N	0.4544 (0.401)	**-0.1456** (0.0544)	**0.6607** (0.2802)	**-0.1216** (0.0486)	0.450	0.698
	G	0.4291 (0.385)	0.0579 (0.0855)	**0.6081** (0.2808)	**-0.1670** (0.0393)	0.356	0.756
	LnDBH	0.5591 (0.5037)	**-0.155** (0.0656)	**0.6505** (0.2829)	**-0.1270** (0.0392)	0.431	0.711
	Sum of Height	-0.1289 (0.0725)	-0.1289 (0.0735)	**0.6416** (0.2857)	**-0.138** (0.0400)	0.397	0.732
	SDI	0.4185 (0.3813)	-0.0274 (0.0953)	**0.6076** (0.2849)	**-0.1595** (0.0406)	0.351	0.759
	RD	0.3443 (0.3273)	-0.0512 (0.0957)	**0.608** (0.2857)	**-0.1560** (0.0409)	0.354	0.757
	DIFN	0.4156 (0.3322)	**0.3372** (0.1393)	**0.7341** (0.2616)	**-0.1159** (0.0392)	0.434	0.702
Medium 30-80 (*n*=71)	N	0.2124 (0.144)	**-0.2431** (0.0409)	**0.8999** (0.1643)	.	0.530	1.45
	G	0.0558 (0.0427)	**-0.2334** (0.1034)	**1.0215** (0.1862)	.	0.354	1.69
	LnDBH	0.282 (0.1993)	**-0.2800** (0.0498)	**0.9157** (0.1665)	.	0.507	1.48
	Sum of Height	0.4745 (0.3647)	**-0.3029** (0.0591)	**0.9294** (0.1693)	.	0.487	1.50
	SDI	0.1388 (0.102)	**-0.327** (0.090)	**1.0163** (0.1775)	.	0.419	1.60
	RD	0.0306 (0.0227)	**-0.3390** (0.0858)	**1.0101** (0.1753)	.	0.435	1.57
	DIFN	0.5557 (0.3382)	**0.8308** (0.1124)	**0.8248** (0.1412)	.	0.631	1.275
Large >80 (*n*=46)	N	**18.38** (1.76)	**-0.0954** (0.017)	.	.	0.633	3.86
	G	**16.85** (3.17)	**-2.511** (0.839)	.	.	0.319	5.26
	LnDBH	**19.272** (1.98)	**-0.0383** (0.0067)	.	.	0.630	3.88
	Sum of Height	**19.405** (2.30)	**-0.0071** (0.00139)	.	.	0.579	4.13
	SDI	**19.82** (3.079)	**-0.147** (0.0346)	.	.	0.472	4.63
	RD	**20.26** (2.99)	**-15.218** (3.34)	.	.	0.505	4.49
	DIFN	**3.457** (0.959)	**3.368** (0.771)	.	.	0.412	4.89

3.6 Predicting Abundance of Understory Regeneration from Light and Stand Variables

The total count of Douglas-fir regeneration (< 1.3 m) per $50m^2$ was compared among treatments using a mixed model ANOVA on the log transformed dependant variable total tally (log (x +1)) (Table 3-13). Harvesting significantly increased the number of trees less than 1.3 meters in height ($F_{1,3} = 48.5$, $p = 0.006$). The control treatment had the lowest log (tally+1) and was significantly smaller than the light ($p= 0.0002$) and medium treatments ($p=0.0439$). The heavy treatment was significantly smaller than the light ($p=0.019$) and medium treatments ($p= 0.0025$). The variation between treatments was the greatest source of variation. Table 3-13 provides a comparison of least square means of the log values.

The density of Douglas-fir regeneration (<1.3m) was also analyzed using a mixed model as the positive number of counts allowed the data set to be normalized using a logarithmic transformation. Comparing the amount of Douglas-fir regeneration, there was a significant difference in log (tally +1) among treatments ($F_{3,3} = 9.71$, $p = 0.047$). The control treatment had a significantly smaller log (tally +1) than the light treatment ($p=0.041$) while the remaining treatments did not differ significantly after using a Tukey adjustment (Table 3-13).

The rest of the species failed to meet the assumptions of ANOVA even after various transformations and thus it was necessary to use a non parametric ANOVA (Kruskal-Wallis test) to determine if the sample comes from different populations among treatments (after averaging the subplots to avoid pseudo-replication). Western larch and lodgepole pine were found to be absent in the control treatment with no difference between harvested treatments ($X^2 = 1.49$, $p =0.68$, $X^2 = 1.9$, $p=0.59$). Aspen was found within all the treatment with their being no difference among treatments ($X^2 = 1.87$, $p = 0.598$).

Table 3-13 Least square means for tree regeneration abundance (#trees /50m^2) for all species combined and for just Douglas-fir (Fd) across treatments. Different letters signify the means were significantly different based on analysis using Tukey's HSD (α= 0.05)

Treatment	Total Tally		Fd Tally	
	LSMEAN (log+1) scale	Standard Error	LSMEAN (log+1) scale	Standard Error
C	1.7834a	0.3585	1.6960a	0.3594
H	2.0344a	0.3570	2.0402ab	0.3594
M	2.3128b	0.3511	1.8673ab	0.3606
L	2.7080b	0.3500	2.4867b	0.3594

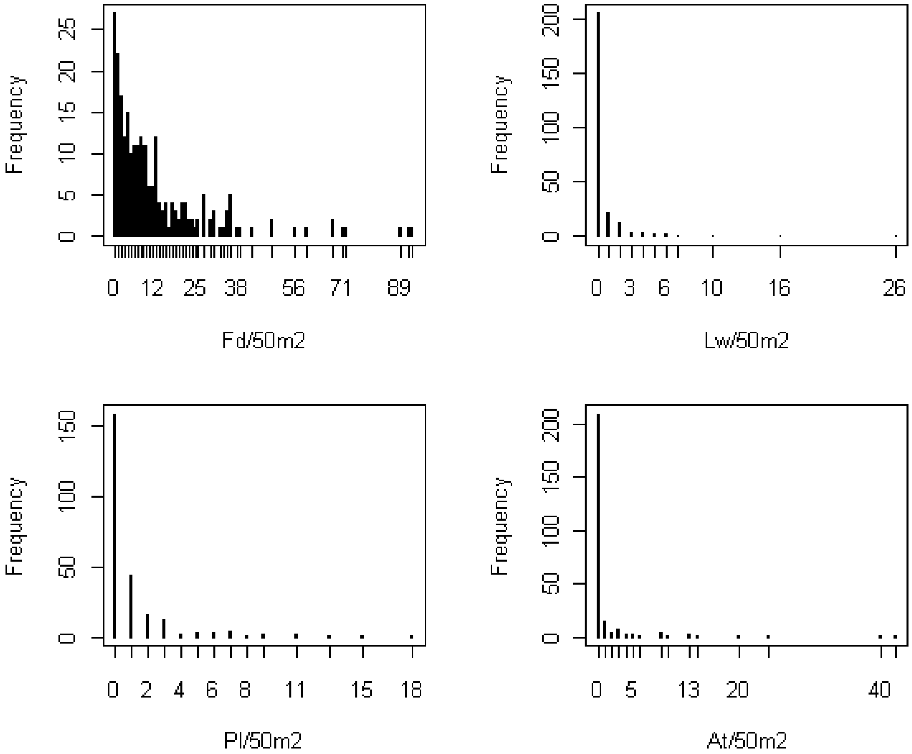

Figure 3-15 Frequency distributions of counts for trees <1.3 m for the four species being modeling using GLM's.

Generalized linear models (GLM) were used to explore relationships between understory tree abundance and light availability or stand variables from evidence that abundance populations highly skewed (Fig. 3.15). Since the abundance of tree regeneration is a count or non-integer that cannot be negative, the exponential family of distributions was better suited to the regression.

The negative binomial GLM was used to model the relationships between Douglas –fir regeneration abundance and light availability using the following linear predictors:

$$\boldsymbol{\mu}_i = \mathrm{EXP}(\ \beta_0 + \beta_1\mathrm{DIFN} + \beta_2\mathrm{Over} + \beta_3\mathrm{Other} + \beta_4\mathrm{DIFN}{*}\mathrm{Other} + \beta_5\mathrm{Grass} + \beta_6\mathrm{NonVegetative} + \beta_7\mathrm{LowShrub})$$

Where, DIFN is diffuse transmittance, Over is a dummy variable indicating the presence of an overstory seed source within a 10m x 10 m plot, Grass is the percent cover of grass, NonVegetative is the percent cover of non vegetative ground and LowShrub is the percent cover of low shrubs (<1.3m) within 10m x 10m plot.

The zero inflated negative binomial GLM was used to model the relationships between western larch regeneration abundance and light availability using the following linear predictors ($\mathbf{E}(\mathbf{Y}_\mathbf{i}) = \boldsymbol{\mu}_\mathbf{i}\ (1 - \boldsymbol{\pi}_i)$):

$$\boldsymbol{\mu}_i = \mathrm{EXP}(\ \beta_0 + \beta_1\mathrm{DIFN} + \beta_2\mathrm{Grass} + \beta_3\mathrm{NonVegetative} + \beta_4\mathrm{LowShrub} + \beta_5\mathrm{CWD} + \beta_6\mathrm{TallShrub})$$

$$\boldsymbol{\pi}_i = \frac{e^{\,b0 + b1{*}Over + b2{*}Other + b3{*}CWD}}{1\ +e^{\,b0 + b1{*}Over + b2{*}Other+ b3{*}CWD}}$$

Where, DIFN is diffuse transmittance, Over is a dummy variable indicating the presence of an overstory seed source, Other is the number of other competitors, Grass is the percent cover of grass, NonVegetative is the percent cover of non vegetative ground, CWD is the percent cover of coarse woody debris, TallShrub is the percent cover of tall shrubs (>1.3m) and LowShrub is the percent cover of low shrubs (<1.3m) within 10m x 10m plot.

The zero inflated negative Poisson GLM was to model the relationships between lodgepole pine regeneration abundance and light availability using the following linear predictors ($\mathbf{E}(\mathbf{Y_i}) = \boldsymbol{\mu}_\mathbf{i}\ (1 - \boldsymbol{\pi}_i)$):

$$\boldsymbol{\mu}_i = \mathrm{EXP}(\ \beta_0 + \beta_1\mathrm{DIFN} + \beta_2\mathrm{Over} + \beta_3\mathrm{NonVegetative} + \beta_4\mathrm{LowShrub})$$

$$\boldsymbol{\pi}_i = \frac{e^{\mathrm{b0 + b1*Over + b2*Other + b3*CWD}}}{1\ +e^{\mathrm{b0 + b1*Over + b2*Other + b3*CWD}}}$$

Where, DIFN is diffuse transmittance, Over is a dummy variable indicating the presence of an overstory seed source, Other is the number of other competitors, NonVegetative is the percent cover of non vegetative ground, CWD is the percent cover of coarse woody debris and LowShrub is the percent cover of low shrubs (<1.3m) within 10m x 10m plot.

Model validation required graphical exploration of the standardized residuals (Zuur et al. 2009). Residual plots are shown in figure 3-16. All graphs suggest no apparent trends within the residuals; with the exception of a few influential observations. The predicted response versus the standardized residuals suggests the model fits the data reasonably well, even though the amount of deviance explained by the model (Fd) was moderately low (16.6%). The Lw and At GLM's were influenced by a few large tallies, which was supported by the fact that there were already a low frequency of positive (true) counts within the two populations. The inferences based on these two species were to be taken with caution due to the limited sample size.

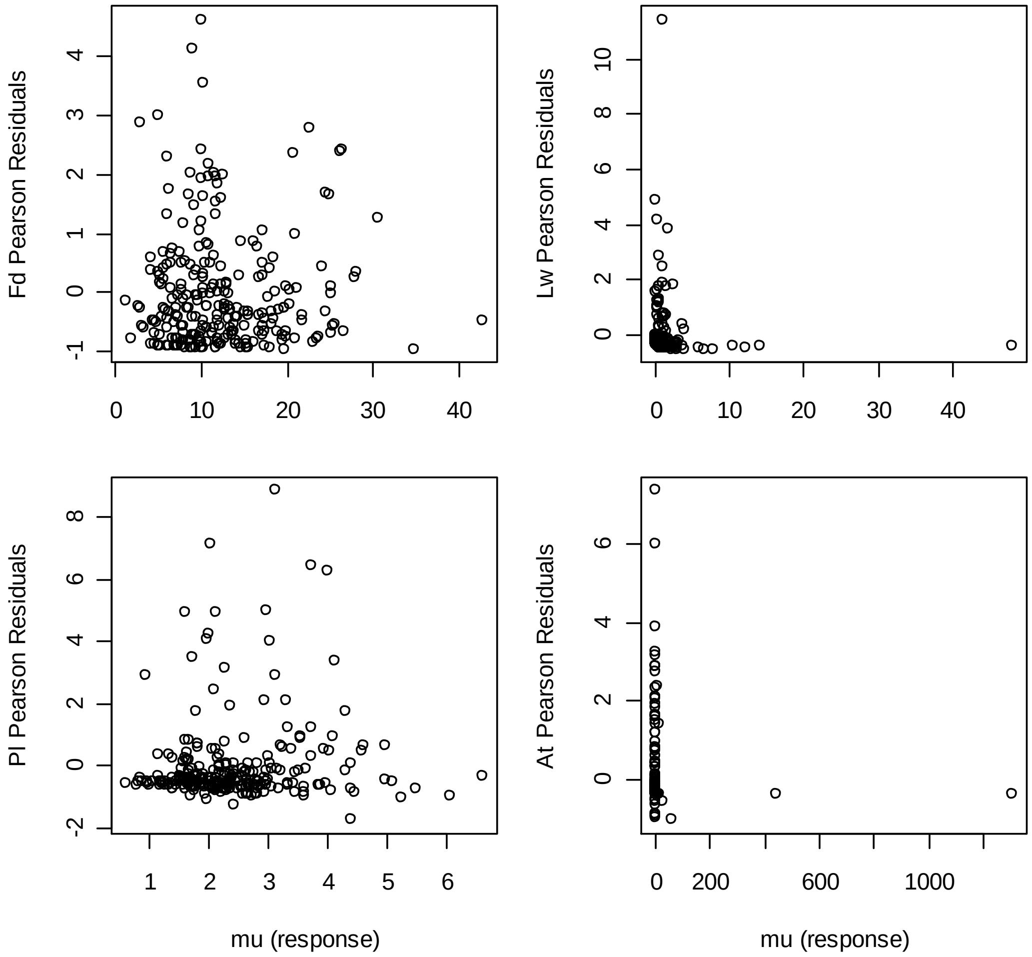

Figure 3-16 Pearson residuals vs. fitted values (on the response scale) for the negative binomial and zero inflated negative binomial models explaining the abundance of trees <1.3m by each species.

The negative binomial model for the abundance of Fd showed that the light environment (DIFN) has a highly positive and significant effect on abundance (Table 3-14). Estimates for the effect of light were significantly greater for Lw than Fd ($t=16.50$, $p < 0.0001$) or Pl ($t=13.71$, $p < 0.0001$). The positive intercept for the Fd model was a significant parameter within the model, which shows that zero counts have a low frequency under low light environments (Fig. 3-17). Figure 3-18 shows that for Fd the average of the predictor variables resulted in a low probability of a zero tally ($p<0.1$) and the probability decreases with increasing light levels.

The variable ‘Over’ suggests that having a seed source in the overstory will increase the abundance of tree regeneration. Having no overstory Fd increased the probability of zero tally by approximately 8% over the “Average” model (Fig. 3-18). The same effect also occurred for pine, with an increase in the probability of a zero tally by approximately 10% under low light conditions. Aspen was highly affected by the presence of a seed source under low light conditions, but after 0.30 DIFN the probability for a zero tally was the same as the average of the predictor variables. This affect was under the ‘zero’ (logistic) model, meaning the presence of aspen negatively influenced zero tallies.

The variable ‘Other*’* was highly significant and showed that having other regenerating trees in the sample area was associated with an increase in Douglas-fir regeneration but this variable has an interaction with light. The effect of having 20 competitors is shown in Figure 3-18. The interaction of DIFN and Other was negatively correlated and highly significant ($p<0.0019$).This interaction with DIFN showed that with greater light availability the probability of a zero tally increased in higher light environments when 20 other trees were within the plot area (Fig. 3-18). The percent cover of low shrubs was negatively related to the abundance of Fd ($p<0.0001$). Setting the low shrub parameter to the maximum amount of cover (67.7%) drastically increased the probability of a zero tally to 0.5 under low light conditions and with increasing levels of light the probability decreased moderately (Fig. 3-18).

The zero inflated negative binomial model for Lw provided evidence that light was the main driver of abundance for this species. Figure 3-17 (blue line) shows an exponential increase in Lw abundance at a DIFN of 0.4. Coarse woody debris and various types of vegetation were negatively affecting Lw abundance (Fig. 3-18). Coarse woody debris was correlated the highest with Lw abundance in both the count model and zero model. This suggested CWD both reduced positive tallies and increased the frequency of zero's within the data set.

The zero inflated models for Pl provided evidence that several factors were affecting this species abundance. Light was positively affecting the abundance of this species (Table 3-14); as well the presence of Pl in the overstory was a significant positive factor for an increased abundance of this species. The presence of other regenerating species was not significant. The increased presence of low shrubs provided evidence for a reduction in Pl abundance (Fig. 3-18). The increase in other tree regeneration and CWD increased the number of zero tallies.

The inferences on parameters for the At model should be interpreted with caution since the limited number of positive tallies makes it hard to analyze and interpret the data. The light environment did not directly effect of the abundance of At, though the interaction with other species in the plot area was significant. Other tree regeneration had a negative effect on At abundance under low light conditions, but under high light environments there was a positive effect of having competitors. Figure 3-18 shows how At abundance changes across light levels under no presence of competitors. The presence of an overstory aspen had a negative affect on the probability of false zero and no effect on the count process. In other words, having an aspen in the overstory reduced the probability of a zero tally but had no effect on number of tallies (Fig. 3-18).

Table 3-14 Parameter estimates for the negative binomial model of the number of trees <1.3. (Zi) is the parameters for the zero-inflated model. Over is a binary variable representing presence or absence of a seed source ($100m^2$), Other is the number of other competitors, remaining variables are percent covers.

Predictor	Fd		Lw		Pl		At	
	Estimate	Sig.	Estimate	Sig.	Estimate	Sig.	Estimate	Sig.
Intercept	2.382 (0.606)	<0.0001	2.44 (1.72)	0.156	0.497 (0.36)	0.17	1.12 (0.705)	0.11
DIFN	2.845 (0.823)	0.00055	7.58 (2.19)	0.0005	2.087 (0.694)	0.0026	-1.896 (2.09)	0.365
Over	0.684 (0.341)	0.0451	ns	.	0.500 (0.161)	0.0019	ns	.
Other	0.196 (0.0589)	0.00087	ns	.	ns	.	-0.251 (0.0604)	<0.0001
Other*DIFN	-0.480 (0.154)	0.0018	ns	.	ns	.	0.742 (0.164)	<0.0001
Grass	-0.0182 (0.0079)	0.0212	-0.058 (0.0257)	0.022	ns	.	ns	.
Non-vegetative	-0.0151(0.0073)	0.0396	-0.057 (0.0246)	0.0330	-0.0122(0.0067)	0.0669	ns	.
LowShrub	-0.052 (0.0071)	<0.0001	-0.0796 (0.0316)	0.0117	-0.0233 (0.009)	0.019	ns	.
CWD	ns	.	-0.083 (0.0448)	0.0627	ns	.	ns	.
TallShrub	ns	.	-0.133 (0.0603)	0.0265	ns	.	ns	.
Forb	ns	.	ns	.	ns	.	0.0349 (0.013)	0.0124
Intercept (Zi)	n/a	.	-6.646 (4.59)	0.148	-0.397 (0.406)	0.327	1.52 (0.272)	<0.0001
Other (Zi)	n/a	.	-0.063(0.067)	0.347	-0.0264 (0.012)	0.0297	0.000387 (0.0137)	0.977
Over (Zi)	n/a.	.	4.266 (4.17)	0.306	0.289 (0.372)	0.437	-2.883 (0.734)	0.0001
CWD (Zi)	n/a	.	0.216 (0.106)	0.041	0.0707 (0.023)	0.0019.	.	.

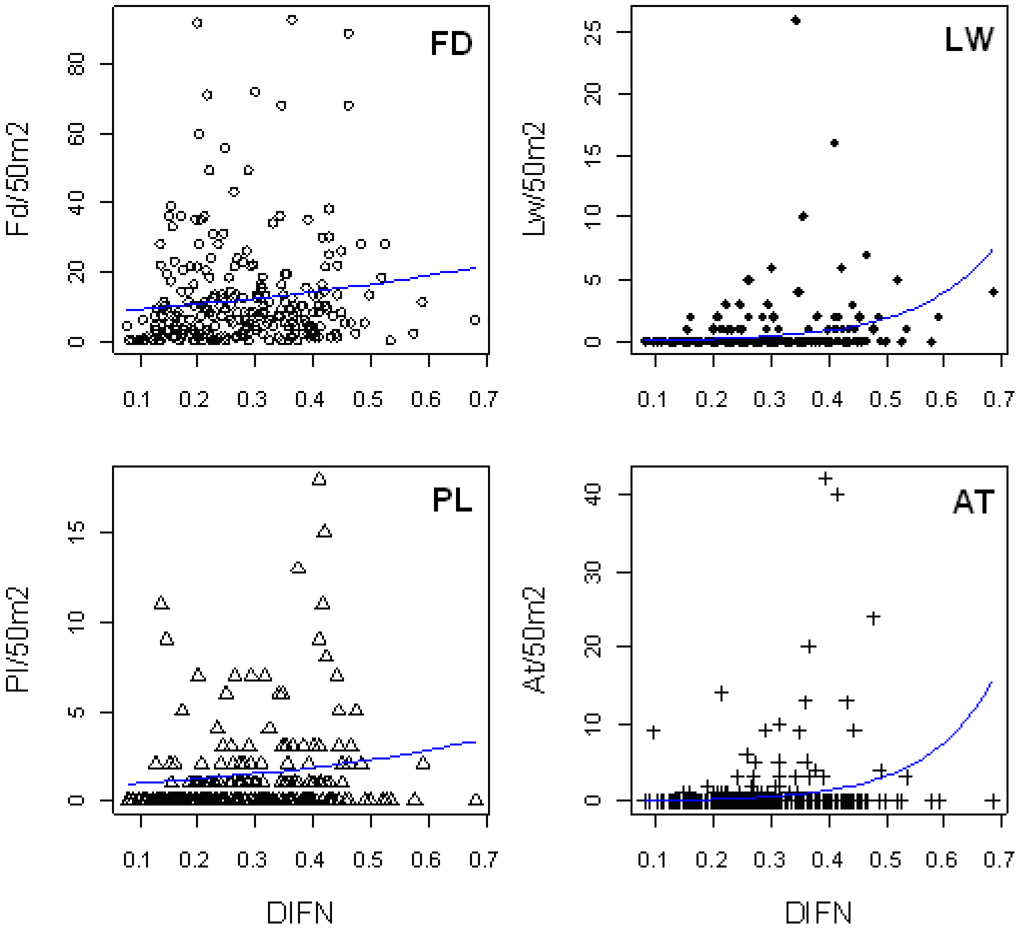

Figure 3-17 The relationship between the count of regeneration of the four species (<1.3m height) per 50m^2 and light availability (DIFN). DIFN is the light environment measured at 1.3m. Light blue line is the fitted curve using average values for all the other predictor variables in the model (Table 3-14).

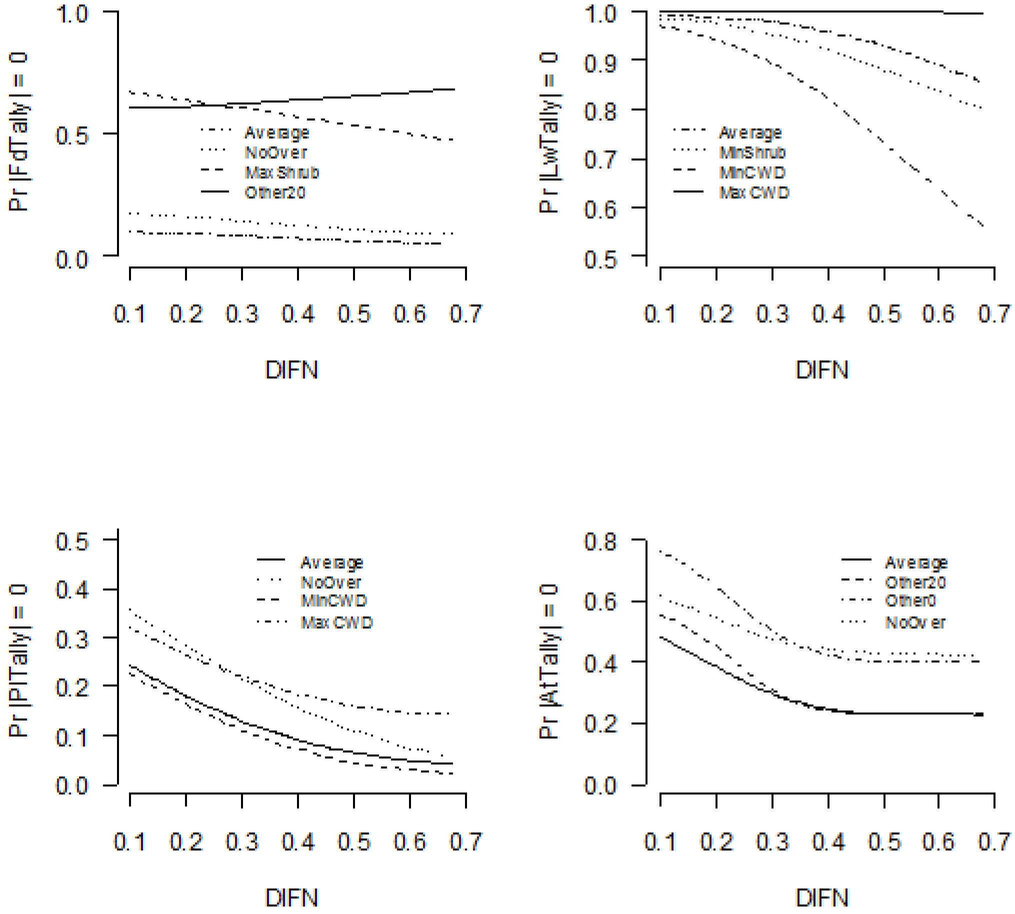

Figure 3-18 The predicted probability of observing a zero tally across a gradient of light availability. Average is the average value of all the other predictor variables used in the model. (Table 3-14). No Over and Over is either the absence or presence of an overstory seed source, respectively. Other20 and Other0 is when there are 20 and 0 other competitors, respectively, within the plot area. MaxShrub and MaxCWD are the maximum recorded percent covers for low shrub and coarse wood debris, respectively. MinShrub and MinCWD are the minimum recorded percent covers for low shrub and coarse wood debris, respectively.

While basal area (G) was the worst predictor of light it was one of the best predictors of small tree abundance. Table 3-15 shows the statistical information for the relationships between various stand estimators and small tree abundance. The sum of height was the best predictor of regeneration abundance as determined by the higher R^2_{pseudo} and low AIC value (Fig. 3-19). N was found to be the worst predictor of small tree abundance. Differentiating the stand estimators by species provided no gains in predictive capability.

The addition of a stand level variable to this model improved the model. Subplots with greater basal areas in the surrounding stand tended to have lower counts of of trees < 1.3m than in subplots with lower stand level basal areas as indicated by the sign and magnitude of the coefficient (Table 3-15). Adding the number of trees in layer 3 (1.3m to < 4cm DBH) to the models resulted in a significant positive relationship and increased the R^2_{pseudo} by 1%.

Table 3-15 Statistical information for the generalized linear model (using negative binomial distribution and log link) of the count of all trees <1.3 m in height, and using various stand variables. The model used is Abundance= exp(a+ b*Estimator + c*G_{stand}). Bolded parameters are significantly different than 0 at alpha =0.05. See table 2-4 for variables definitions.

Estimator	a	b	c	R^2_{pseudo}	AIC
N	**4.36** (0.2709)	**-0.020711** (0.00838)	**-5.31650** (0.9716)	0.105	1875.360
LnDBH	**4.4311** (0.2702)	**-0.01267** (0.00402)	**-5.2901** (0.9752)	0.1146	1872.315
G	**4.299** (0.2648)	**-1.6448** (0.5199)	**-4.4338** (1.0821)	0.1144	1872.376
Sum of Height	**4.4615** (0.2641)	**-0.003810** (0.000858)	**-4.7809** (0.9874)	0.1372	1864.891
SDI	**4.3500** (0.2654)	**-0.0767** (0.02446)	**-4.5269** (1.0695)	0.1146	1872.281
RD	**4.3597** (0.2658)	**-0.71588** (2.4183)	**-4.5783** (1.0628)	0.1143	1872.385

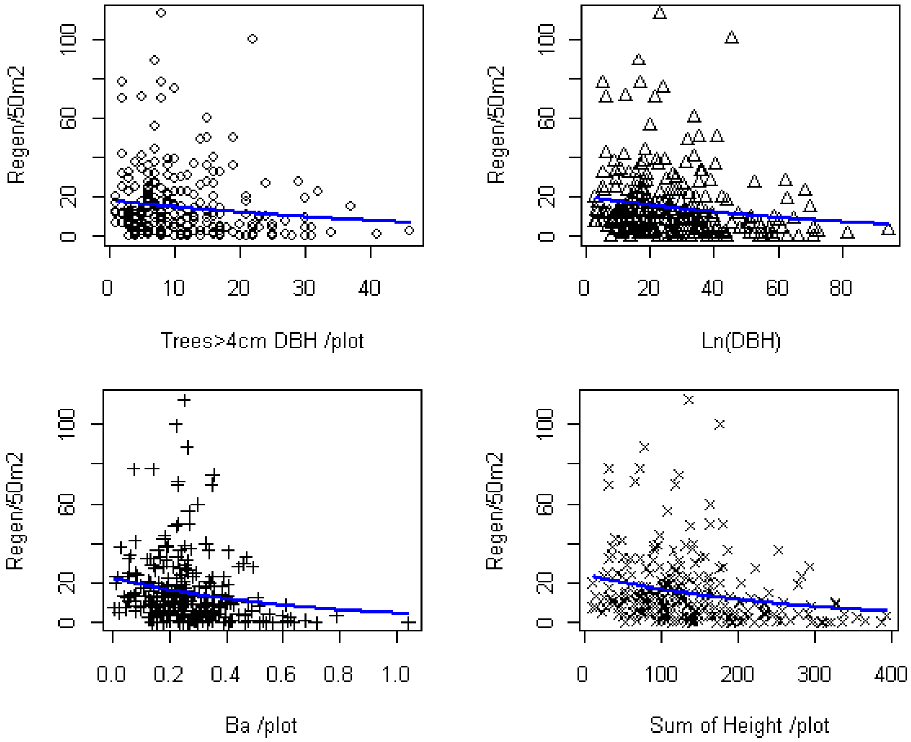

Figure 3-19 Relationship between the number of trees per plot (Regen/50m^2) and various stand variables (> 4cm DBH). Fitted curve includes the average of G_{stand} which is the average basal area of the treatment unit. Fitted curve includes the average of G_{Stand}. Statistical information is found in 3-15.

3.7 Vegetation Response to Light Availability

Total understory vegetation (the sum of low shrub, tall shrub, grass and forb) cover averaged 65% (ranging from 20 to 140 %) and was greater in treated plots than untreated plots (p=0.009). there were no differences among the treatments for the amount of cover of non-vegetative, forbs, tall shrub low shrub and advance tree regeneration (>1.3m) (p>0.05) (Table 3-16). Unharvested plots were found to have significantly more percent cover of coarse woody debris than harvested plots (p=0.0226). Harvesting increased grass cover (p=0.0148), with evidence that both medium (p=0.0475), and light (p=0.065) treatments had more grass cover than the control. Treated plots also had higher values of log (low shrub cover + 1) than untreated plots (p=0.0209). The control had significantly lower values of log (low shrub cover + 1) than the medium treatment (p=0.0426) (Table 3-16).

Untreated plots had less natural tree regeneration (<1.3m) cover than treated plots (p= 0.0115). There was a significant treatment effect on the cover of natural tree regeneration with the control having less cover than the light treatment (p=0.0149). The medium treatment had less cover than the light treatment (p=0.0323). The control treatment had less natural tree regeneration cover than the heavy treatment (p=0.0483) (control, medium < heavy, light).

Table 3-16 Least square means for % cover of the understory, like letters within each row indicate no significance difference between treatments (P>0.05) based on analysis using Tukey's HSD test. † Analysis was performed on log=transformed data.

Treatment	Least Square Means							
	Non-vegetative	CWD	Grass	Forbs	Tall shrub†	Low shrub†	Adv. Regen	Nat. Regen
Control	39.15 a (4.36)	15.598 a (2.214)	20.54 a (1.815)	17.03 a (3.089)	0.386 a (0.271)	1.7145 a (0.387)	5.183 a (1.523)	2.126 a (0.810)
Heavy	27.95 a (4.36)	11.17 a (2.214)	27.35 ab (1.815)	26.08 a (3.089)	0.479 a (0.271)	2.3661 a (0.387)	6.016 a (1.523)	5.096 b (0.810)
Medium	22.21 a (4.36)	10.13 a (2.214)	30.11 b (1.815)	25.08 a (3.089)	0.603 a (0.271)	2.5250 a (0.387)	3.531a (1.523)	3.018 a (0.810)
Light	30.79 a (4.36)	12.71 a (2.214)	28.73 ab (1.815)	22.69 a (3.089)	0.558 a (0.271)	1.9663 a (0.387)	5.678 a (1.523)	6.505 b (0.810)

A regression analysis was attempted to determine whether vegetation abundance had an effect on growth. All Douglas-fir regeneration size classes were showing a positive increase in stem volume with increasing percent cover of vegetation, but since total vegetation was well correlated with light this result appears to result from collinearity between the effect of light and vegetation. Thus, this analysis was abandoned and it was concluded that vegetation cover in of itself had no quantifiable effect on growth of established Douglas-fir given the variables used in this analysis.

Chapter 4: Discussion

Silvicultural strategies that promote the development of natural tree regeneration under the influence of residual structure rely on the concept that changes in forest canopy structure will be complemented by changes in resource availability for the understory (Grace 1993, Constabel and Lieffers 1996, Emborg 1998).

Openings in the forest canopy are known to increase the amount of solar radiation penetrating into the understory (Coates and Burton 1997). An influx of solar radiation interacts with the surface (albedo of understory vegetation) and potentially increases the amount of heat entering the soil profile (Stathers et al. 2001). Gray et al. (2002) have found soil temperature effects were closely correlated with direct light and air temperature for a variety of gap sizes.

In my study lower residual basal area treatments appear to have greater temporal variability in understory microclimate. A low residual basal area treatment unit had minimum air temperatures 3 degrees colder than unharvested treatment unit. In old growth Douglas-fir forests, Chen et al. (1993), found similar results where daily air temperature variation was lower in the intact forest, relative to large openings.

While larger openings can potentially increase light levels, incidence of frost becomes higher as minimum air temperatures are strongly correlated with the amount of sky being ‘seen’ (Groot et al. 1997). Sagar and Waterhouse (2010) have shown that retaining basal areas greater than 15 m^2/ha will lower risk of frost damage in Douglas-fir stands in the sub-boreal spruce zone. At St. Mary’s all treatments units have basal areas greater than 15m^2 fifteen years after harvest, with little evidence of frost damage being observed.

Managing understory light levels to achieve the desired overstory protection in mixed uneven-aged stands is complex. While understory light availability is known to decrease with increasing overstory density (Newsome et al. 2010), in stands with complex forest structure this relationship is not as simple.

4.1 Relationships Between Overstory Density and Understory Light Availability

Light availability in the understory is highly variable, with single stand variables capturing between 12 to 37.2% of this variation. Promis et al. (2009) working in uneven-aged *Nothofagus* forests of Chile found similar results. These results contrast with previously published studies relating stand characteristics to light transmittance under relatively uniform forest structures (Vales and Bunnell 1988, Comeau and Heineman 2003, Hale et al. 2003, Drever and Lertzman 2003, Soonohat et al. 2004, Hale et al. 2009).

Although density measures did not adequately explain light variability, no other estimate of structure explained light variability to the extent described in previous studies. Low coefficients of determination for such relationships in complex stands have been attributed to inadequate quantification of the distribution of leaf area (Franklin and Van Pelt 2004), interactions with various sized gaps, and the lack of spatial information (Canham et al. 1994, Brunner 1998, Courbaud et al. 2003, Sonohat et al. 2004). In addition, the use of small sample plot sizes in this study may also be problematic.

Complex stands have a considerable amount of spatial variation in forest structure (Maguire et al. 2007). Large gaps and clusters of trees surrounding plots may be influencing light levels at a variety of scales (Reifsnyder et al. 1971, Poulson and Platt 1989, Tinya et al. 2009) and clumped structure within and surrounding the area of the plot will lead to greater variability in transmittance (Canham et al. 1994).

The results from this study suggest that quantification of the light environment needs to incorporate stand structure beyond $100m^2$ (5 m radius) as suggested by the significance of a stand level estimate of structure. Tinya et al. (2009) found the correlation between DIFN and above canopy light to increase with increasing scales from 5 x 5m to 30 x 30m. Chen et al. (1995) report the influence of adjacent large openings on shortwave radiation can extend 30 to 60 m into the intact forest. As a general rule, assessment plots should have a radius at least equal to the height of the surrounding canopy except in very homogeneous stands where smaller plots may effectively characterize the entire stand (P. Comeau, pers. Comm. December 9, 2010).

In this study light levels ranged between 8 and 64 % full sky and represent a broad range for single tree selection (Drever and Lertzman 2003, Promis et al. 2009). The dry climate of the IDF influences leaf area relations of individual trees, as well as influencing the maximum LAI supported by the stand and may be a contributor to an increase in the amount of light transmittance over what has been observed in more humid climates (Grier and Running 1977, Barnes et al. 1997). Porous canopies and small gaps may be contributing to the range in light variability by allowing a substantial amount of light to penetrate through the canopy.

At the microsite scale some authors suggest that single estimates of stand structure are not sufficient for characterizing the light environment and more local variables should be considered (Balandier et al. 2009, Promis et al. 2009). This is largely due to a single stand parameter collected on a small plot not being able to encompass the influence of stand structure and species composition. However, when using multiple stand variables it is important to select variables which are not collinear.

Drever and Lertzman (2003) attribute the effectiveness of the summation of height as a stand variable explaining variation in understory light to the fact that the sum of height incorporates the number of stems as well as their height. Results from my study and others indicate that stand density is related to crown attributes such as radius and length (Krajicek et al. 1961, Beekhuis 1965, Putz et al. 1984, Innes et al. 2005). In my study, using a combination of non-correlated variables lowered the root mean square error (RMSE) but provided only a marginal increase in goodness of fit. Comeau and Heineman (2003) reported a lower RMSE when quadratic mean diameter was added to structural based light models. However, adding explanatory variables that average individual tree characteristic has limited use in multi-layered stands since the variability in these characteristics is large (Staudhammer and LeMay 2001).

Sonohat et al. (2004) found that adding covariates such as height, crown height, crown length/ total tree height, and height to the first green whorl provided only small improvements in the prediction of transmittance. In contrast, Promis et al. (2009) reported a substantial increase in the coefficient of determination when crown estimates (crown area, crown volume, average crown radius and stem volume) were used.

The relationship between understory light availability and stand variables can change with differences in canopy structure and composition (Barnes et al. 1998). Even-aged stands having similar sized trees and the majority of the foliage concentrated near the top of the canopy differ dramatically from tall, multilayered stands with the same amount of leaf area (Van Pelt and Franklin 2000). These complex stands have irregular distributions of leaf area within a vertical gradient (Barnes et al. 1998). Gersonde et al. (2004) show that when leaf area is concentrated in the upper canopy the majority of light is intercepted by dominant trees, while stands with irregular canopies provide more light resources to mid sized trees. Forest structures with irregular canopies tend to have a sigmoidal pattern in light transmittance within a vertical gradient; with the majority of leaf area in smaller trees while fully stocked even-aged stands have a skewed pattern in light transmittance with the majority of leaf area concentrated in similar sized trees within a single location (Barnes et al. 1998).

My results indicate that smaller trees (4-6 meters in height) have a greater relative effect on light extinction per unit of basal area than larger trees. Smaller trees are reducing light at a greater rate than larger trees per unit basal area for three reasons: (1) per unit of basal area, smaller trees have greater amounts of leaf area, (2) the crowns of smaller trees are closer to the point at which light is being measured and consequently obscure a larger fraction of the visible sky, and, (3) smaller trees generally occur in clumps.

The formation of large gaps has been known to support clumped or aggregated Douglas-fir regeneration (Armleder 1999). High density single cohort clumps of trees capitalize on the growing space created by large gaps when light, seedbed conditions and seed is abundant (Matthews 1989). Similarily, LeMay et al. (2009) have shown that smaller trees tend to occur in clusters in similar dry interior Douglas-fir forests. The aggregation of trees can be further exacerbated by harvesting operations.

The distance to foliage and the base of the live crown is important in determining the influence an individual tree has on light attenuation. Parker et al. (2002) reports that a single branch in the understory can reduce openness even under a large upper canopy gap. Past research has highlighted the importance of using canopy height in determining understory light transmittance (Brown and Parker 1994, Drever and Lertzman 2003, Parker et al. 2002). Vales and Bunnell (1988) suggest the height to live crown will influence the fit of structural based light models.

The height of a tree and its height to live crown base can incorporate allometric information such as sapwood taper, sapwood storage and potentially leaf area relationships (Dean and Long 1986, McDowell 2002). Comeau and Heineman (2003) found broadleaf top height was an important predictor in light transmittance models. While height and height to live crown base explained less than 40% of the variation in light availability in my study, these were highly significant variables. In complex stands, height to live crown is highly variable due to varying levels of light and competition interacting with differences in species composition. Results indicate that Douglas-fir (the most shade tolerant species on these sites) is the only significant contributor to light attenuation even though this species comprises 67% of the overstory composition. At this site the crown length of Douglas-fir is significantly longer than either western larch or lodgepole pine due to inherent differences in shade tolerance (Barnes et al. 1998), contributing to an increase in the amount of light attenuation.

My results contradict Sonohat et al. (2004) who showed that larch growing under even-aged management had the lowest light transmittance, but this may be related to stand age, which can also influence transmittance through effects on crown dimensions, crown density, leaf area index and other factors. The extinction coefficient of larch was found to increase with stand age then decrease in older stands (Sonohat et al. 2004). The majority of western larch stems in this study persist in the larger and older size classes.

Douglas-fir comprise the majority of trees in the sapling size class (1.3m to <4 cm dbh). These saplings have a wide and flat crown architecture which is indicative of a shade tolerant species (Barnes et al. 1998). In low light environments, lateral growth of the shoots becomes more predominant than apical growth (Williams et al. 1999). Douglas-fir has also been found to decrease its live crown depth in response to low light environments (Hermann and Lavender 1990).

The ‘pipe model’ theory proposes that a unit of leaf area is supplied with water from a constant number of conducting ‘pipes’ or area of sapwood (Shinozaki et al. 1964). However, relationships between leaf area and sapwood basal area can change with size and other factors. McDowell et al. (2002) have shown the ratio between leaf area and sapwood area declines as Douglas-fir trees become older and taller. The decline in the ratio between leaf area and sapwood area is thought to be influenced by the increased hydraulic path length exerting greater stress in drawing water from the soil (Midgley 2003). Larger trees may be sacrificing height and decreasing leaf area to sapwood area ratios in order to maintain hydraulic conductance (Becker et al. 2000, McDowell et al. 2002). The rate of decline has also been shown to change with species (Turner et al. 2000). Given that relationships between leaf area and sapwood area change with tree size and crown architecture, and that they will also change with basal area and diameter, it is not surprising that stand variables which account for the differential effects of smaller trees on light extinction tend to be more effective at predicting light at the microsite scale.

The stand structural variables that appear to provide appropriate weighting to differential size effects were density (number of stems), sum of height and the natural logarithm of the sum of raw diameters at breast height. These structural parameters performed the best because large trees are either treated as having the same effect as smaller trees or as only having slightly greater influence. However the number of stems per unit area does not discriminate among sizes and results in a failure to represent tree size.

The natural logarithm of the sum of raw diameters at breast height also provides a good estimate of light. Applying a logarithmic transformation effectively reduces the skewness of the distribution by limiting the degree of separation between large and small trees. Biologically, this seems to make sense when smaller trees are having a greater effect per unit basal area. Basal area is analogous to squaring the raw diameter which results in stronger weighting of large diameter trees. Consequently, basal area and other measures of stand density that square or weight larger diameter trees higher (such as quadratic mean diameter (Dq)) are generally poorer predictors of light availability under these stand conditions.

Stand density Index (Reineke 1933) and Curtis' relative density incorporate both size and the density of trees. Previous studies have shown SDI and RD work well to predict light in Douglas-fir dominated stands (Vales and Bunnell 1988, Smith 1991). Interestingly, neither SDI nor RD was effective at explaining the variation in light availability in the stands used in this study. Since these size-density metrics use either Dq or basal area, it is likely that size effects are being incorrectly estimated.

To conceptualize the differences between stand variables, formulas can be re-expressed using the following definitions:

[1] Trees ha^{-1} = number of stems $\cdot D_q^{\mathbf{0}}$

[2] Relative Density = Trees ha^{-1} $\cdot D_q^{\mathbf{1.5}} \cdot b_1$

[3] Stand Density Index = Trees ha^{-1} $\cdot D_q^{\mathbf{1.6}} \cdot b_2$

[4] Basal area ha^{-1} = Trees ha^{-1} $\cdot D_q^{\mathbf{2}} \cdot b_3$

Where D_q is the quadratic mean diameter, b1, b2, b3 are scaling coefficients taking into account differences in units and scale. As the exponents increase, more weight is given to larger trees while the predictive strength in determining light availability of these stand variables decreases.

If we assume light is good proxy for site occupancy, the results from this study suggest the slope of the maximum size-density line for these stands is much flatter than the constant determined by either Reineke (1933) or Yoda et al. (1963) in dry, uneven-aged stands as suggested by Sterba and Monserud (1993). This suggests that it would be useful to differentially weight size classes in size density relationships of uneven-aged stands and may at least partially explain why simple maximum size-density relationships do not hold in uneven-aged stands.

Sterba and Monserud (1993) have empirically shown that as a stand with a normal distribution of size classes (skewness =0) deviates into an uneven aged stand (skewness = - or +) the maximum number of trees per given unit area can have nearly any quadratic mean diameter. The skewness coefficient used in this study is negatively correlated with light suggesting that when structure deviates from an even aged stand to an uneven-aged stand there are increases in available light.

While structural indices such as N, G and SDI accounted for only a small portion of the variability in light, their use in practical models should not be ruled out entirely. RMSE values estimated in this study are comparable to studies that have reported high coefficients of determination. Comeau and Heineman (2003) working in paper birch stands have reported a RMSE of 0.33 and an R^2 of 0.86 for the linear relationship between log transformed DIFN and basal area. Vales and Bunnell (1988) working in the coastal western hemlock zone of British Columbia reported models explaining between 46 to 94% in the variation in diffuse light and RMSE ranges from 0.0917 to 0.2848 across subzones.

4.2 Overstory Effects on Growth of Douglas-fir Regeneration

Stand variables are useful in explaining variation in growth of small Douglas-fir; capturing 77.7 to 82.4 % of the variation after using initial height and a stand scale estimate of structure as covariates. Initial height was found to best represent the size of the individual, reflecting both the vertical position (Comeau et al. 1993), past history of growth (Morris et al. 1990), ability to conduct water (Waring et al. 1982) and amount of photosynthetic tissue (Gerrish 1990). Likewise, expected growth rates will change as a tree undergoes physiological changes with age and size (Gower et al. 1996). Wyckoff and Clark (2005), have shown size is a strong predictor of growth and often well correlated with an individual’s light environment.

Stand variables that were the best predictors of light were also the best predictors of growth; as DIFN explained 84% of the variation in growth (SVI). In dry climates, shading is often found to support the best growth rates for tree seedlings as diffuse light conditions ameliorate harsh conditions associated with direct light (Tappenier and Helms 1971, Hermann and Lavender 1990, Wayne and Bazzaz 1993). Past research has shown that survival of Douglas-fir regeneration is best when light levels exceed 20% of full sun (Drever and Lertzman 2003) with morphological development being negatively affected when light levels are below 40% full sun and the best growth rates when light is above 40% full sun (Carter and Klinka 1992, Mailly and Kimmins 1997, Drever and Lertzman 2001). The average light availability at tree regeneration height (1.3m) in my study ranged from 22 to 31.8% full sky across treatments which are within the range of light deprivation suggested by previous studies.

At my site, some of the Douglas-fir is growing and surviving in light environments less than 20% full sky. However, when light levels drop below 15% the variation in survival drops from 40% or less to 10% or less (Figure 3-13), suggesting that 15% full sunlight as a potential threshold value. This difference in the minimum light tolerance for Douglas-fir may be related to precipitation difference between studies (Carter and Klinka 1992) or to other factors. Most studies have examined coastal varieties of Douglas-fir (Table 1-1). Dry interior environments may be influencing leaf area relations (Grier and Running 1977, Spies et al. 1990) and increase resource allocation to roots, which may help seedlings survive in shade (Williams et al. 1999). In addition, differences in transmittance may be compensated for by differences in ambient PPFD as a result of differences in cloud cover. In dry climates there will be fewer cloudy days, which will result in higher levels of understory PPFD and the potential for better survival of seedlings.

Wright et al. (1998b) have found differences in species specific growth response curves across different climatic regions of north western British Columbia. Their results suggest species with intermediate shade tolerance may show different growth responses under both low light and high light environments under differing climates, whereas, shade tolerant species only show regional effects at low light and shade intolerant species only show regional effects at high light . Although Douglas-fir regeneration is surviving under low light, height growth is generally slow (2.3-6.8 cm across regeneration sizes), and not significantly different across treatments. This is consistent with the limited range in understory light levels observed in these stands 15 years post-harvest.

Results from this and other studies indicate that reducing overstory density can improve resource availability (Chen et al. 1993, Coates and Burton 1997, Carlson and Groot 1997, Wright et al.1998a, Stathers et al. 2001). While maintaining light levels (at 1.3m) above 30% full sun will allow newly established tree regeneration sufficient light for survival and growth, the density of small trees may also reduce growth rates. Gosler and Hasenuer (1997) have shown that competition among juvenile trees is important for predicting height growth in uneven-aged stands. Devine and Harrington (2008) concluded that while thinning treatments must achieve the requisite understory light environment, openings must be large enough to reduce root density which can severely limit sapling growth due to belowground competition.

Soil moisture is also a limiting factor in IDF forests (Simpson 2000); with prolonged drought conditions occurring after July. Given that my study site is much drier than other study sites, belowground competition for water may also be important. Although Douglas-fir seedlings can survive through summer long drought stress (Tappenier and Helms 1971, Hermann and Lavender 1990), reductions in the density of juvenile trees would likely allow for increased growth and provide space for other understory trees (Armleder 1999). Korol (1985), found reductions in canopy cover can increase soil moisture availability. In mature Douglas-fir stands Gray et al (2002) reported that soil water content was found to be higher in gaps 14m in diameter, relative to single tree gaps of 7 to 10m in diameter.

4.3 Overstory Effects on Abundance of Tree Regeneration

Abundance of tree regeneration and tree diversity was found to be greater in lower residual basal treatments. The abundance of understory trees is generally at acceptable levels and harvesting has lead to a well stocked understory. Removal of basal area has resulted in an array of microsites suitable for establishment for a variety of species. Other studies have found similar results where small gaps or thinning has increased the number of regenerating trees (Gray and Spies 1996, Waterhouse 1998, Bailey and Tappeiner 1998, Burton et al. 2000, Kuehne and Puettmann 2008). Conversely Spies et al. (1990) found Douglas-fir regeneration to be absent in small gaps (<250m^2) due to both lower levels of soil disturbance and low light levels in small gaps.

In the absence of harvesting, stands will likely develop into pure Douglas-fir stands, while partial harvesting which creates some gaps may result in a sustained mixed species forest. The results from this study suggest Douglas-fir can regenerate well under most light levels formed when selection harvesting created basal areas below 24 m^2/ha. Western larch and lodgepole pine abundance responded positively to light, with greater abundance of these 2 species occurring under the higher light levels found in medium and large sized gaps (~0.6 DIFN).

The response of abundance to light for the three species reflects their relative shade tolerance rankings. Western larch and lodgepole pine are disturbance adapted species and thus light levels that are indicative of larger disturbances will aid in their establishment (Schmidt and Shearer 1990, Shearer and Schmidt 1998, Coates and Burton 1999). Shade intolerant species reportedly reproduce in gaps 300 to 1000 m^2 (Runkle 1985, cited in Spies et al. 1990). Other studies have found partial cutting increases diversity (Poulson and Platt 1989, Kuehne and Puettmann 2008, Breckage et al. 2008). In a study conducted in a temperate deciduous forest with a heavy *Rhododendron* understory, Breckage et al. (2008) found understory tree diversity increased with both canopy and understory removal with shrub removal providing the greatest gains in terms of diversity.

While surrounding vegetation and light availability are important for successful tree establishment, other factors influence abundance (Bailey and Tappeiner 1998; Denslow and Guzman 2000). For instance, the presence of a seed source or an overstory tree is highly influential. Ferguson and Carlson (1991) state that the distance to a seed source is more important in drier than moist habitat types because more seeds may be needed to successfully establish a seedling. Likewise, seed predation by birds and rodents has been found to limit seed availability in interior Douglas-fir forests (Huggard and Arsenault 2009, Klenner and Sulivan 2009).

Results from my study suggest stand variables weakly account for the variation in abundance. While reducing the amount of overstory structure increases tree regeneration it is difficult to identify the specific factors controlling germination and establishment using data from my study. Sacenieks and Thompson (2000) found similar results where residual basal area had a weak effect on understory tree abundance. In a Douglas-fir forest in the Cascade Mountains, Van Pelt and Franklin (2000) found no difference between seedling density within gaps and around gaps. Spies et al. (1990) found more regenerating trees within gaps than the surrounding forest matrix, however Douglas-fir was absent in small gaps.

Models suggest total tree regeneration abundance is best under retention levels less than 24 m^2/ha with reduced shade intolerant species abundance over 16 m^2/ha. My study suggests that, while light is an important indicator for establishment, other factors such as seedbed, seed availability and abundance of understory vegetation will also contribute to the success of tree regeneration (Messier et al. 1999).

4.4 Understory Vegetation Response to Canopy Manipulation and its Effects on Tree Regeneration

Allowing an increase of light availability to the understory also has the potential to increase the abundance and LAI of understory vegetation (Royo and Carson 2006), which may compete with regenerating trees (Simard et al. 1998, Harrington 2006). In this study harvested treatments were found to have greater percent cover of vegetation than unharvested treatments. While no direct relationships between competing vegetation and growth were obtained, surrounding vegetation did influence the abundance of tree regeneration.

The collinearity between light and cover of various vegetation types limits the use of cover estimates as predictors. In my study, Douglas-fir was strongly influenced by low shrubs, likely due to their effects on light (Bartemucci et al. 2006), physical interactions with seedlings, competition for soil moisture and provision of protective cover for small mammals that can damage seedlings (Krauch 1945, Caccia and Ballare 1998).

Similarily, coarse woody debris (CWD) which is thought to be beneficial to seedling establishment through nutrient availability, increased conservation of soil water through reduced exposure (O'Connell et al. 2004), decreased summer soil temperatures (Devine and Harrington 2007) and shade effects (Heinemann et al. 2000), is negatively related to larch and pine abundance. The presence of coarse woody debris may provide unfavorable seedbed and microclimate conditions for these two species (Harrington and Schoenholtz 2010), or may be indirectly related to higher overstory densities (and control stands) in this study. Peterson and Leach (2008) have found the removal of coarse woody debris favors species that establish readily on mineral soil. Coarse woody debris not only takes up valuable growing space but also intercepts water (Sexton and Harmon 2009, Means et al. 1992) and allows moss layers to accrue which have been found to be detrimental to seedling establishment (Harmon and Franklin 1989). Heinemann and Kitzberger (2006) found course woody debris rapidly dries and does not provide a suitable microsite for seedlings growing on xeric sites.

Chapter 5: Conclusion

The implementation of a selection system relies on the assumption that changes in the overstory structure will be complemented by changes in resource levels of the understory environment. Continual growth and development of all strata is required to perpetuate complex forest structure into the future. Thus the successful application of selection systems depends on an understanding of the influence residual structure has on regenerating trees. However, since relationships between overstory structure, understory resource environments and tree regeneration performance (establishment, survival and growth) are complex, better quantitative information and tools are needed to aid in prescription development.

The goals of this thesis were to: (1) understand how residual structures influence understory tree performance; and, (2) determine if indirect methods can be developed to quantify the understory light environment in irregularly structured Interior Douglas-fir stands. This study was conducted in a Douglas-fir dominated mixed conifer forest in southeastern British Columbia, where management objectives and pre-harvest structure promote the use of selection harvesting. These forests are comprised of Douglas-fir, western larch and lodgepole pine with scattered components of aspen, and ponderosa pine.

The understory light environment was measured using hemispherical photography, LAI Plant canopy analyzers and directly using photodiodes. Overstory structure was quantified in 10m x 10m square plots and the growth and abundance of tree regeneration was measured in 3.99m radius plots. Nonlinear regression and linear regression was used with light availability and growth as dependant variables and stand variables and light availability as predictor variables. Generalized linear models were used to determine the influence of light, stand variables and other factors on the abundance of regenerating trees.

In these dry complex forests, light was found to be highly spatially variable in both harvested and non-harvested stands. While prolonged drought conditions and risk of frost are also limiting factors; light availability appears to be a key abiotic factor governing tree regeneration performance at this study site.

Selection harvesting has created a wide gradient of light levels as a consequence of the wide gradient of residual structures. Fifteen years after harvesting, stand level residual basal ranged from 19 to 42 m^2/ha which is above levels suggested for protection of Douglas-fir from frost injury (Sagar and Waterhouse 2010). Stand development has allowed differing residual basal area treatments to produce similar light levels after 15 years. Results from my study suggest that high levels of light in the understory can be achieved given a range of different residual basal areas and densities. In general, as the density of overstory (within $100m^2$) increased, light levels decreased in a nonlinear fashion; with surrounding estimates of structure (on the stand level) being significant and negatively influencing light availability.

However, no single stand variable could effectively account for much variation in understory light. Results from this study and other literature suggest that a 10 x 10 m plot is too small to effectively characterize the influence of the surrounding stand on light levels in these spatially variable stands. In addition, more detailed information regarding crown characteristics and spatial position of trees may be necessary to accurately estimate light levels.

Not surprisingly, the best predictors of light were generally the best predictors of growth. Strong relationships exist between the total number of trees per plot and growth of established trees (>30 cm height). These models suggest more than 10 overstory (>4cm dbh) Douglas-fir trees per $100m^2$ or a summed log transformed diameter of 30 will limit growth. Small tree regeneration is likely still being influenced by surrounding vegetation and microclimate that was influential during establishment. Abundance is negatively correlated with stand variables but the relationships are weak; likely due to a lack of spatial information and the use of small plots.

Large gaps allowing greater than 30% full sky are optimal for shade intolerant species such as lodgepole pine and western larch, whereas much smaller gaps allowing 15% full sky can provide for substantial regeneration and good survival of Douglas-fir. While light is an important characteristic for establishment, many other factors such as presence of a seed source, coarse woody debris, surrounding vegetation composition, and number of competing trees were found to highly influence regenerating tree abundance. These factors are likely indicating attributes of the seed supply, seedbed, and microclimate.

Understory vegetation was found to negatively influence abundance but not growth of Douglas-fir. This study has also shown that once seedlings become established (>30 cm in height) a positive linear relationship with light was observed. Management efforts that (1) lower the density of juvenile trees and (2) increase the availability of light will likely accelerate growth of understory trees into larger size classes.

My results indicate that natural tree regeneration is promoted when residual basal area is below 24 m^2/ha. While target light levels can be set at 15% of above canopy light for regeneration of Douglas-fir, target light levels should be set to no less than 30% full sky if a sustained species mixture is desired. In addition species harvesting preferences should be well justified as the retention of shade intolerant species can act as both a potential seed supply and as a weak light attenuator. Light attenuation by various strata should be incorporated into planning and tree marking guidelines, with greater weights to reducing the number of smaller stems if regeneration and growth are to be increased. The models developed in this study could be used to provide insight into how various combinations of structure influence light environments.

Future studies should utilize larger plots and should collect spatial information. In addition, experimental manipulation of understory vegetation would be useful for determining effects of vegetation on growth and regeneration and manipulation of densities of small trees (<4 cm DBH) would provide for better discrimination of effects of small tree densities. Size-density relationships should also be evaluated in stands with uneven-aged structure. This future work can then be used to modify existing policies surrounding stocking standards in partially cut or uneven-aged stands. At the present time, given the fact that residual basal area, stand density index, and density have limited utility in characterizing overstory influences on understory light availability, tree regeneration standards linked to these and similar measures of overstory density may have limited utility in uneven-aged stands.

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