Growth and establishment of species with a range of shade tolerance within a strip shelterwood in the Interior Cedar Hemlock Zone of British Columbia

by

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Abstract

Strip or group shelterwood and other continuous cover forestry practices are commonly advocated for managing mixed species forests of Interior-Cedar Hemlock (ICH) Biogeoclimatic zone in British Columbia. In strip-shelterwood systems, narrow openings are created in the canopy to facilitate regeneration of a mixture of species. Successful regeneration of mixed species stands using the shelterwood method requires knowledge of how the various component species respond to the range in light levels created as a function of opening size and location within openings. However, the effectiveness of these silvicultural systems in regenerating mixed species stands for various forest ecosystems, particularly for the ICH are not well investigated. Available information suggests that for several species with different shade tolerances to coexist in a forest stand, species must show evidence of growing at different rates along the light gradient (niche partitioning). In particular, to achieve a competitive hierarchy, shade intolerant species need to grow faster than tolerant species in areas with high light levels.

To address this issue, I conducted this study in two small (50 m × 150 m) clearings in a mixed stand of the interior cedar hemlock zone of southern British Columbia.

Obtaining reliable estimates of the light gradient within shelterwood strips was an essential part of this study. Thus, in the first study, I evaluated several commonly used light estimation techniques including: 1) hemispherical photography; 2) LAI-2000 plant canopy analyzer; and, 3) midday measurements of % photosynthetic photon flux density (hourly average PPFD) under sunny and overcast skies. The core finding of this chapter was that light indices that integrated direct beam contribution gave the best characterization of the existing light gradient. On the other hand, indices that accounted primarily for diffuse light were poorly correlated with the growing season light. Canopy conditions (degree of heterogeneity), stand orientation and gap sizes are important considerations in selecting any indirect light index for studies, especially in high latitude forests.

In the second study, I compared growth rates of nine species with varying shade tolerance along the light gradients within the strip-shelterwood. I also examined how gap-position influences vary between species and draw inferences on the sensitivity of each species to edge proximity. I found evidence of species' niche partitioning along the light gradient, and also for changing positions toward the north – south direction (separation into different clusters and niches not occurring at the same position within the gap). Two highly shade intolerant species (Ponderosa pine and lodgepole pine) exhibited the highest growth rates along the light gradient and achieved a discrete growth hierarchy by separating from the other species. In general, the overlapping species were mostly close in shade tolerance. Furthermore, shade tolerant species were relatively less sensitive to changes in gap position than intolerant species. Therefore, my conclusion from this chapter is, to maximize the potential of mixed species establishment, species also need to be matched to their suitable niches within strip-shelterwood gaps.

As an extension to my second study I investigated how shade tolerant and intolerant species differ in distribution of height and diameter growth during the growing season across gap environments, and if differences in growth distribution would confer competitive advantages to certain species. In general, shade intolerant species adopted a competitive strategy (higher height surge at the beginning of the growing season followed by sustained diameter growth in the later season) across all gap environments. Between the two moderately tolerant species (Douglas-fir and white pine), white pine appears to have adopted a more conservative growth strategy across the gap due to continuity in its diameter investment throughout the growing season. Douglas fir, Engelmann spruce and subalpine fir appear to have adopted a growth strategy that is gap-environment specific. Finally, the range of light conditions created by strip-shelterwood harvesting combined with differences between shade tolerant and intolerant species in resource exploitation strategies suggests that regenerating a diverse mixture of species through strip-shelterwood systems is a viable option in Interior Cedar Hemlock forests.

Preface

The dissertation is my original work. I have received contribution from my supervisor (Dr. Phil Comeau) in the forms of critique, questions, suggestions, and editing. I decided on the sampling protocol in consultation with my supervisor. Data collection, organization, analyses, interpretations and manuscript structuring and writing was done by me. A final version of chapter 2 has been published as:

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The final structure of chapter 2 was thus shaped to some extent by the suggestions made by two anonymous reviewers during the peer-reviewing process with the Journal.

Publication of chapters 3 and 4 in peer reviewed journals is planned.

Dedicated to:

My beloved Parents, Mr. Hossain (late) and Mrs. Khatun

And

My lovely son, Yasir Kazi

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1 Chapter 1: Introduction

1.1 Background and rationale

During the past 3 decades, there has been a renewed word-wide interest in the use of continuous cover systems (CCF) in forest management (Lähde et al., 1999; Malcolm et al., 2001; Mason, 2003; Puettmann et al., 2015; Bianchi et al., 2020). The main reason leading to increased interest toward CCF is its potential to reduce the negative impacts of clear-cutting on forested landscapes (Rojo and Orois, 2005; Mason, 2015). While the main aim of forestry practice still remains low-cost timber production, timber production in CCF can also be economically viable in the long term, as this system can maintain the flow of good quality timber through various cutting cycles (Peura et al., 2018; also see Eggers et al., 2019). Moreover, CCF meets social values better than clear-cutting as social views on clear-cutting are often not favorable (Rojo and Orois, 2005). However, in addition to timber harvesting, studies have also reported a higher potential of CCF methods to provide ecological, social, aesthetics and recreational benefits from managed forests than that from conventional clear-cutting systems (Puettmann et al., 2015; Lundqvist, 2017; Bianchi et al., 2020).

The Interior Cedar Hemlock Biogeoclimatic zone (ICH) in British Columbia (B.C.) harbors the most productive and diverse forests in the southern interior (Newsome et al., 2010). These forests are valued for their high species diversity, wildlife habitat and water yield. These forests occur at valley bottom to mid elevation, making visual quality important to managing these forests (DeLong et al., 2005). Interest in non-timber benefits from these forests has generated interest in continuous cover forestry practices that can be implemented across British Columbia (Newsome et al., 2010; Day et al., 2011). Partial harvesting systems, such as shelterwood or selection systems can offer greater potential to preserve the natural complexity of ICH forests

(Newsome et al., 2010). However, the effectiveness of shelterwood or other forms of partial harvesting systems has not been fully evaluated in British Columbia.

In the shelterwood method of regeneration, the old stand is gradually removed in a series of cuttings to promote the establishment of a new even aged stand under the partial shade of the existing forest canopy. Shelterwood methods generally involve two or more cuttings (Hannah, 1988; Matthews, 1989). Trees are removed in successive cuttings while the largest, most vigorous and best formed individual of the desirable species are normally retained until the final cutting (Matthews, 1989). These healthy, vigorous retained trees, in addition to acting as a seed source, provide protection to the young seedlings. In time, the shelter becomes a hindrance rather than a benefit to the growth of the seedlings and the remaining older trees are then removed to give the new crop an opportunity to fully utilize the growing space and resources of the stand.

There are several variations in shelterwood methods. In a uniform shelterwood method, trees that are retained to provide shelter are more or less uniformly distributed throughout the block. In strip shelterwood methods, harvesting occurs in linear strips across the stand. Each strip is oriented to use the side shade from adjacent intact stand, as well as shelter from trees retained in the strip and maximize sunlight penetration. Patches are opened in the stand in group shelterwood systems so that the surrounding edges of the uncut timber shelter the new regeneration. The group sizes can be enlarged until all groups converge to allow regeneration of the entire stand. In the irregular shelterwood method, the regeneration period is extended longer than the normal 20% of the rotational length. As a result, there is subsequent variation in tree height in the new stand created using the irregular shelterwood method. The advantage with this method is that one can grow small overwood trees to a size class of greater value, add high value increment to large overwood trees, or retain some large trees for a longer period to meet aesthetic objectives (Hannah, 1988).

Shelterwood systems can be effectively employed in places where it is difficult to regenerate due to harsh environmental conditions such as frost or high temperature events. In practice, shelterwood systems should be designed in such a way that they create a favorable microclimate (light, air temperature, soil temperature and moisture) at or near the ground to favor seed germination, growth and survival of new regeneration of the desirable species.

Several studies report the influence of overstory removal on the understory microclimate and regeneration in different forest ecosystems. Gap studies (i.e., Coates, 2000; Stathers and Newsome, 2001; Prevost and Raymond, 2012) clearly show effects of opening sizes in group shelterwood on patterns of availability in growth resources (light, air temperature, soil temperature and moisture). Light levels increase with increases in opening size and south sides of openings are typically shaded by the adjacent stands, resulting in lower amounts of direct sunlight near the southern edge compared to the northern edge (Messier, 1996; Coates, 2000; Delong et al., 2000). Air and soil temperatures also tend to increase with opening size and are higher at the north edge of openings than at the south edge due to higher inputs of direct sunlight (Gray et al., 2002; Huggard and Vyse, 2002; Spittlehouse et al., 2004). Air and soil temperatures may also increase for a short distance under the intact stand to the north of large openings. Numerous studies indicate reductions in soil moisture near the edge of openings relative to the center of large openings due to higher competition from the edge trees (Coates, 2000; Gray et al., 2002; Spittlehouse et al., 2004). These spatial patterns in microclimate can influence the growth and establishment of the regeneration within a gap and studies have shown that this largely depends on the requirements and tolerances of the species to the existing microclimate (light, air temperature, soil temperature and moisture) in various parts of openings (Wright et al., 1998; Coates, 2002; Kern et al., 2017). Studies also indicate that patterns of tree growth in relation to light levels, gap size and location in gaps strongly reflects the shade tolerance of the species (Valladares and Niinemets, 2008). Coates (2000) reported that among the five species he examined (western redcedar, western hemlock, subalpine fir, hybrid spruce and lodgepole pine), all showed asymptotic increases in rates of height and diameter growth with increasing gap size. At the largest gaps, tree sizes at young age declined with increasing shade tolerance. However, these differences diminished as the gap sizes decreased. DeLong et al. (2005) also found highly variable height growth responses, with shade tolerant western hemlock performing significantly better than less tolerant Ponderosa pine and Douglas-fir. Competition from the surrounding stand edges also influenced the growth performance of the regeneration. Coates (2000) observed that the advantages of increased light at the north edge of large gaps were negated by competition for soil moisture from the surrounding edge. He also reported that the influence of the adjacent stand can extend 10 m into the gap from the dripline. Similar findings were also reported by York et al. (2003).

Shade tolerance is an ecological concept, which has been widely used to explain species coexistence, community structure and dynamics, and succession (Valladares and Niinemets, 2008;Valladares et al., 2016; Bianchi et al., 2018). Shade tolerance expresses a relationship between light availability (percent above-canopy light or canopy transmission) and the survival, growth, allometry, leaf and physiological characteristics of the tree species. It is primarily concerned with light-growth relationships and intimately associated with light compensation and saturation points of species (Chen, 1997;Givnish, 1988). Simply defined, shade tolerance illustrates the ability of trees to survive and maximize carbon gain in the light limited understory environment (Kimmins, 2004). Others have interpreted shade tolerance as the function of the degree of morphological and physiological plasticity in the face of environmental change (Carter and Klinka, 1992; Mailly and Kimmins, 1997; Claveau et al., 2002).

Shade tolerant tree species adapt morphologically to low light by reducing their height/diameter, root/shoot ratio to maintain a balance between photosynthetic to non-photosynthetic tissues (Chen et al., 1996; Givnish, 1988; Valladares and Niinemets, 2008). For this reason, advanced regeneration of shade-tolerant species in a low light environment is often flat-topped, with little or no leader dominance and lateral branch growth exceeding terminal shoot growth. In contrast, shade-intolerant species show little plasticity in their patterns of growth allocation, resulting in tall, thin and spindly regeneration under low light (Chen, 1997; Canham,1988; Claveau et al., 2002).

Shade-tolerant species have a lower height: diameter ratio, higher lateral branch growth, and a higher lateral: terminal increment ratio than shade-intolerant species in low light conditions (Chen, 1997; Canham,1988). Shade intolerant species allocate much of their photosynthate to height growth to reach or penetrate the canopy while shade tolerant species allocate more resources in lateral growth to harvest more photosynthetic active radiation. With regard to growth response to changing light levels, shade tolerant species exhibit strong height growth response to an increase in light at low-light levels but usually achieve a much lower asymptote than shade intolerant species at high light (Carter and Klinka, 1992; Wright et al., 1998; Valladares et al., 2016; Avalos, 2019). In contrast, these studies report weaker growth responses of shade intolerant species to increases at low light but had the highest growth rates at high light.

The ability of understory plants to grow and survive in the partial or complete shade of an overstory depends on the complex interactions between leaf and plant-level responses to temperature, light, and nutrient and water availability (Walters et al., 2006; Valladares and Niinemets, 2008; Avalos, 2019). Since shade tolerance is a complex attribute (Valladares and Niinemets, 2008), ranking of tree species into different tolerance classes (very tolerant, intermediate tolerant, intolerant and very intolerant) based on only a light response curve is incomplete (McCree and Troughton, 1966) and highly subjective (Carter and Klinka, 1992). Moreover, light compensation point varies with season with light compensation point of a shade plant during leaf development in the spring being considerably higher than that for the same foliage in summer due to different respiration rates (Unsworth, 1987).

1.2 The problems being addressed

Broadly, research presented in this thesis aims at understanding if the differences (as reviewed above) between shade tolerant and intolerant tree species in adapting to different understory light conditions can predict the development of mixed species regeneration within a strip-shelterwood. This study was conducted on a mesic site located in the Columbia-Shuswap variant of the Interior Cedar-Hemlock moist warm biogeoclimatic subzone (ICHmw2), near Nakusp, B.C.

Since light is the principal factor governing tree growth and survival within a gap (Denslow, 1987; Lieffers et al., 1999; Bianchi et al., 2018; Avalos, 2019), examination of the growth responses of various shade tolerant species along the light gradient may generate vital information that can help explain species' coexistence within small gaps and shelterwood strips. However, as evidence also suggests that multiple environmental factors and their complex interactions can influence tree growth and survival (Carter and Klinka, 1992; York et al., 2003;

Prévost and Raymond, 2012; Valladares et al., 2016), I also examine species' growth responses in relation to changing locations within the strip-shelterwood in this study using gap location acting as a surrogate of dynamic environmental factors. Furthermore, I expect gap position should capture effects of below ground competition from the north and south edges.

More specifically, this study attempts to address the following issues:

1. Studies have shown that small gaps have light conditions that favor regeneration of shade tolerant species rather than intolerant species (Busing and White, 1997; Brokaw and Busing, 2000; Avalos, 2019), but it is unclear whether microclimatic conditions found within strip-shelterwood gaps can support mixed regeneration of shade tolerant and intolerant species. Thus, I first focus on characterizing the light conditions within the strip-shelterwood (Chapter 2). In doing so, it was necessary that I evaluate light estimation methods and identify methods that are appropriate for characterizing light gradients within gaps.

2. Second, I test whether the theory of species' partitioning of the light gradient can explain coexistence of multiple species with different light requirements or tolerances to shade in two strip shelterwood gaps (Chapter 3). Here, I model the growth responses of nine species representing a wide range in shade tolerance (very intolerant to very tolerant) along the existing light gradient and compare growth rates between the species. Moreover, growth responses are also examined in relation to distance from the south edge. This approach is expected to help identify edge effects and provide a more comprehensive understanding of the influence of gap environment on species growth performance.

3. Since shade intolerant species are better at exploiting temporal variation in understory light than tolerant species, these species are expected to realize a larger portion of their annual growth during the early part of the growing season, whereas relatively more shade tolerant species may distribute growth more evenly throughout the growing season (Ameztegui and Coll, 2011; Paquette et al., 2012; Rozendaal et al., 2015; Ameztegui et al., 2017; Noyer et al., 2019) within gaps. Thus, to gain a better understanding of the growth strategy of shade tolerant and intolerant species and how this relates to specific gap environments, I examine the seasonal patterns of height and diameter growth of five species across the shelterwood gaps (Chapter 4).

1.3 Thesis structure

In chapter two**,** I begin with the evaluation of several light estimation techniques to provide a reliable estimate of light in a strip-cut shelterwood system of the study site. The methods I evaluated were: i) hemispherical photography indices; ii) LAI-2000 sensor measurements of DIFN; and iii) Mid-summer sunny and cloudy day midday %PPFD.

Within a strip shelterwood, the distribution of light is influenced by various factors including, but not limited to, tree heights and canopy density in the surrounding unharvested stand and the size, shape and orientation of the opening (Lieffers et al., 1999). Moreover, as is the case for any openings in northern temperate forests, light within a strip-opening is distributed along a north-south gradient. Along that axis, the northern portions of the gap usually experience higher light levels than southern portions (Gendreau-Berthiaume and Kneeshaw, 2009). Light at any particular location within a strip can also vary with season (Lieffers et al., 1999), with the change in solar elevation (Prévost and Raymond, 2012), and with sky conditions (Gendron et al., 2001).

Within overcast days, most light penetrates into the understory as diffuse light, which depends primarily on sky-view fraction (Canham et al., 1990; Gendron et al., 1998). Due to such variability in light, and differences in species' growth potential, different species may occupy different locations within a gap (see Valladares et al., 2016). Therefore, to understand why particular species dominate a gap location over other species, accurate characterization of the existing light environment is necessary.

However, precise characterization of understory light over the growing season is cumbersome; it requires continuous hourly measurements usually obtained with fixed sensors and dataloggers. Installation of sensors and dataloggers required to obtain continuous hourly measurements is expensive and time consuming and also requires substantial technical expertise. Therefore, this task is commonly accomplished through measuring light in indirect ways using portable sensors or hemispherical photographs. These indirect methods are more efficient and less expensive based on measurements taken at one point in time during the growing season (Lieffers et al., 1999).

The two most popular hemispherical methods are canopy photography and the LAI-2000 plant canopy analyzer (Fotis and Curtis, 2017). Both methods provide an estimate of light through measuring the gap geometry of the canopy for the location of the photograph or where the sensor is used. Portable PAR sensors can also be used to obtain measurement of light (Parent and Messier, 1996) and overcome some of the theoretical and practical limitations of the hemispherical methods (see Gendron et al., 1998). However, there are disagreements regarding to what extent different factors i.e., sky conditions (sunny versus overcast), measurement durations, and timing of measurements during the day can influence the reliability of these methods. Moreover, these light estimation methods vary in accuracy from one silvicultural system to another, due to differences in stand or gap characteristics (Battaglia et al., 2003; Rozenbergar et al., 2011). Battaglia et al. (2003) found that hemispherical photography performed better (higher R^2 and less bias) than the overcast day method for an open-canopy woodland forest ecosystem. In a study conducted in a mixedwood temperate forest, Gendreau-Berthiaume and Kneeshaw (2009) found that estimates from both hemispherical photographs and instantaneous measurements on sunny days gave similar patterns of light distribution along the north-south axis of circular gaps. Therefore, it is necessary to evaluate the effectiveness of these methods for their accuracy in case of a strip-cut shelterwood system in a mixed Interior Cedar-Hemlock zone forest ecosystem of southern interior, British Columbia. I believe accurate information on the existing light environment and how it varies spatially and temporally within a strip-shelterwood can be helpful in developing or refining shelterwood prescriptions.

Light is a major growth limiting factor controlling the dynamics of understory regeneration (Canham, 1988; Coates and Burton, 1999; Lieffers et al., 1999; Philipson et al., 2012). Therefore, characterization of its pattern is important. After characterizing the light gradient within the strip-shelterwood, in the third chapter**,** I investigate if the range of light conditions created with a strip-opening is sufficient to facilitate regeneration of a diverse mixture of species differing in shade tolerance, and to what extent, species' growth performance can be influenced by the proximity toward the edges (north versus south).

In theory, several species can coexist within a gap through occupying different positions when various species grow at different rates based on their light requirement along an existing light gradient within gaps. Thus, species coexistence within a gap is strongly related to understanding linkages between shade tolerance rank and performance along the light gradient. This mechanism is termed gap partitioning by species. Under the gap partitioning theory, shade tolerant species will grow faster in shaded gap positions than shade intolerant species, but the opposite is true in high light environments (Sack and Grubb, 2001; Van Couwenberghe et al., 2013; Valladares et al., 2016). However, not all ecologists agree with this theory and some propose an alternative theory that shade intolerant species perform consistently better than shade tolerant species at all light environments in a gap (Coates and Burton, 1999; Kitajima and Bolker, 2003). In addition, there are possibilities that species may overlap to a considerable degree in their growth response along a light gradient, particularly in species-rich ecosystems (DeLong et al., 2005; Valladares et al., 2016). Therefore, it is unclear how species rich ecosystems where this study site is located (in the Interior Cedar Hemlock Biogeoclimatic zone of British Columbia) will respond to light gradients created by a strip-shelterwood system. Furthermore, relating species to gap-position is important to avoid early mortality and to maximize growth of the desired species (Bradshaw, 1992; York et al., 2003; Zdors and Donis, 2017). Research related to the influence of edges can increase ability to predict regeneration performance based on the location within the gap. Thus, in chapter three, I also attempt to quantify the nature of edge influence (north versus south) on the growth of regenerating trees as it relates to their shade tolerance.

Several studies emphasize the need to examine seasonal patterns in environmental resources and their subsequent influence on species height and radial growth responses to identify growth limiting factors, and regeneration's competition and facilitation dynamics within a forest ecosystem (Kikvidze et al., 2006; Swemmer et al., 2007; Drew and Downes, 2018). This is important since multiple species with different abilities to utilize temporal resources (i.e.

competitiveness) can successfully regenerate and occupy various positions within a gap (Kobe, 1999; Valladares et al., 2016; Álvarez-Yépiz et al., 2017; Avalos, 2019) and thereby can coexist within a small gap. Therefore, in chapter four, I investigate if shade tolerant and intolerant species exhibit different growth strategies in relation to variations in seasonal patterns of height and diameter growth across gap micro-environments. More specifically, I examine whether these species exhibit similar or different patterns in their seasonal investments toward height or diameter growth within changing light conditions inside the gap.

In the case of a strip shelterwood in southern British Columbia, seasonal distribution of resources and its influence on seasonal growth patterns are unknown. Important questions in this regard are whether seasonal microclimatic patterns (i.e., primarily light) are related to seasonal growth patterns for various shade and drought tolerant species, and whether seasonal shifts in growth of trees may occur in response to different seasonal patterns in limiting factors at different locations within gaps. I expect that the north edge of a large gap will benefit from higher radiation (light and temperature) and these higher levels of radiation may be beneficial in spring and early summer but may be detrimental and may induce stronger soil moisture deficits in mid and late summer. Understanding seasonal shifts in limiting environmental factors and their relationship to tree growth will help us to better understand facilitative and competitive effect from the edges over the growing season. Such understanding can be fundamental to developing successful silvicultural prescriptions (Wright et al., 1998; Coates, 2002).

To conclude, in chapter five I summarize major findings and present conclusions and future recommendations.

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2 Chapter 2: Characterizing light across a strip shelterwood in a mixed conifer forest

2.1 Introduction

Clearcutting with artificial regeneration is the leading silvicultural practice in North America (Raymond and Bedard, 2017). However, this method may fail to achieve biodiversity, wildlife and recreational objectives. Thus, silvicultural strategies like shelterwoods or various other forms of partial cutting are increasingly advocated or practiced in many regions around the world as well as in British Columbia (DeLong et al., 2005; Day et al., 2011).

In a shelterwood, the old stand is removed in 2 or more cuttings to promote the establishment of a new even aged stand under the shelter of a forest canopy (Hannah, 1988). In a strip shelterwood, a small or medium sized opening is created in the canopy. Inside that opening, various factors can influence the distribution of light, including tree heights and canopy density in the surrounding unharvested stand and the size, shape and orientation of the opening (Lieffers et al., 1999). In northern temperate forests, light is distributed along a north-south gradient. Along that axis, the northern portions of the gap usually experiences higher light levels than southern portions (Gendreau-Berthiaume and Kneeshaw, 2009).

Light levels at any particular location within a strip can also vary with season (see Lieffers et al., 1999). Prévost and Raymond (2012) found differences in light level between center, south and north locations of an opening were less in June but became more pronounced going from June to September. Due to such variability in light, and differences in species' growth potential, different species may occupy different locations within a gap (see Valladares et al., 2016). Therefore, to understand why particular species dominate a gap location over other species, accurate characterization of the existing light environment is necessary. Knowledge of the light environment and how it varies spatially and temporally can help in developing or refining shelterwood prescriptions.

Precise characterization of understory light requires continuous hourly measurement of photosynthetically actively active radiation (PAR) over an entire growing season. Obtaining these direct measurements is usually accomplished through installing light sensors and connecting them to dataloggers. However, installation of sensors and dataloggers is expensive and time consuming and also requires substantial technical expertise. Due to high spatial variability in understory light, direct methods require collection of a large number of samples in the field, which further adds to its expense. In contrast, indirect methods involving the use of portable sensors or cameras that are more efficient and less expensive are commonly used to estimate growing season transmittance based on measurements taken at one point in time during the growing season (Lieffers et al., 1999).

Hemispherical methods such as canopy photography and the LAI-2000 plant canopy analyzer are two indirect techniques frequently used in forestry research (Fotis and Curtis, 2017). Hemispherical photography measures the gap geometry of the canopy to estimate direct and diffuse radiation for the location of the photograph. Several studies indicate that this technique effectively estimates understory light for a number of forest types (Comeau et al., 1998; Gendron et al., 1998). The LAI-2000 hemispherical sensor works on similar principles to photography, but it only measures diffuse transmittance (Diffuse non-interceptance, DIFN) in the blue spectrum (<490 nm wavelength). Studies have reported strong relationships between DIFN and understory PAR for many forest types, including deeply shaded conifer dominated (Machado and Reich, 1999), and young deciduous and paper birch dominated mixedwood forests (Comeau et al., 1998).

Use of portable PAR sensors to obtain measurement of light are popular (Parent and Messier, 1996) and overcome some of the theoretical and practical limitations of the hemispherical methods (see Gendron et al., 1998). These estimates have been found to correlate well with growing season PPFD (photosynthetic photon flux density, Messier and Puttonen, 1995), however, there are disagreements on the general sampling approach; for example, sky conditions (sunny versus overcast), measurement durations, and timing of measurements during the day.

One single measurement on an overcast day was found to be very effective in estimating the mean % daily PPFD for a range of sky conditions (Messier and Puttonen, 1995). Upon further testing of this method for a range of gap sizes and heterogeneous canopies, Gendron et al. (1998) also reported similar findings. However, Battaglia et al. (2003) found that hemispherical photography performed better (higher R^2 and less bias) than the overcast day method for an open-canopy woodland forest ecosystem. In a study conducted in a mixedwood temperate forest, Gendreau-Berthiaume and Kneeshaw (2009) found that estimates from both hemispherical photographs and instantaneous measurements on sunny days gave similar patterns of light distribution along the north-south axis of circular gaps. Light estimation methods have also been found to vary in accuracy from one silvicultural system to another, due to differences in stand structure (Battaglia et al., 2003; Rozenbergar et al., 2011). In response to concerns regarding effectiveness of the various methods, this study aims to evaluate several light estimation techniques for their accuracy in a strip-cut shelterwood system in a mixed Interior Cedar-Hemlock zone forest ecosystem of southern interior, British Columbia. The methods I evaluated were: i) hemispherical photography indices; ii) LAI-2000 sensor measurements of DIFN; and iii) Mid-summer sunny and cloudy day midday %PPFD. Assessment was done in two medium (0.75 ha) sized experimental gaps (Figure 2.1).

The study site is in the northern hemisphere; therefore, the southern portion of the strip will receive most light as diffuse radiation from the northern portion of the sky. In contrast, the northern edge of the gap will receive both direct and diffuse light (Canham et al., 1990). Consequently, the relative contribution of diffuse and direct light to total is expected to vary going across the strips from south to north. I hypothesize that indirect methods based solely on diffuse light (e.g. the overcast days method) will yield poor estimates of the growing season light environments in this strip-cut situation. Alternatively, indirect indices accounting for both diffuse and direct components will provide better estimates. I also asked the following questions:

1. Can hemispherical techniques characterize growing season transmittance within the strip?
2. Do sky conditions (sunny versus overcast) influence the relationship between midday PAR sensor light indices and growing season transmittance in the opening?
3. Can month to month variations (May to September) in growing season transmittance be predicted by these light indices?

2.2 Methods

2.2.1 Study site

A strip shelterwood experimental project (EP 1191) was initiated in 1994 by Nelson Forest Region's Forest Science division. The site is located 50 km south of Nakusp, British Columbia (Lat. 49 57'N, Long. 117 53'W). The site is on a level area with a mesic soil moisture regime (MacKillop and Ehman, 2016) in the Columbia-Shuswap variant of the Interior Cedar-Hemlock moist warm Biogeoclimatic subzone (ICHmw2). The site is occupied by an even-aged mature mixed stand consisting of 53% Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franc.), 25% western redcedar (*Thuja plicata* Donn ex D. Don in Lamb), 15% larch (*Larix occidentalis* Nutt.), and 5% pine (*Pinus* L. spp.) and birch (*Betula papyrifera* Marsh) with other species (including trembling aspen [*Populus tremuloides* Michx.], balsam poplar [*Populus balsamifera* L. subsp. trichocarpa (T.&G. ex Hook.], and western white pine [*Pinus monticola* Dougl.]) comprising the remainder. The dominant species are about 35 m tall and the stand density is approximately 650 stems/ha (Delong et al., 2000).

The ICHmw2 has a climate with cool winters (mean temperature: -8 - -5° C), warm summers (12.5 - 14.5° C) and mild springs (2.5 to 5° C). While spring and summer months are moist (mean precipitation ranges from 150-250 mm), fall is dry (MacKillop and Ehman, 2016). Based on 1961-1990 normals obtained from ClimateNA (Wang et al., 2016), solar radiation intensity for the site is typically higher in spring (15.6 MJ m^{-2} d^{-1}) and summer (21.1 MJ m^{-2} d^{-1}) than fall (8.4 MJ m^{-2} d^{-1}). With regard to local atmospheric conditions, open sky PPFD data collected near the site for a 6-week period from June 10 to July 23, 2009 show that sky conditions can vary throughout the growing season; for example, I found 50% of days were sunny, 34% were variable, 11% were cloudy, and another 5% were cloudy with occasional sunny breaks.

2.2.2 Experimental design

During the winter of 1994/95, two 0.75 ha openings were created in the mixed conifer stand. Each opening was 50 m wide and 150 m long, with the long axis oriented east-west (Figure 2.1). Due to the size and orientation of the openings, a gradient in light levels exists as reported in many other gap studies (Canham et al., 1990).

In the spring of 1995, the openings were planted with seedlings of ten species common in the ICH, viz.,Douglas-fir, western larch, Engelmann spruce (*Picea engelmannii* Parry ex Engelmann), western redcedar, western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), white pine (*Pinus monticola* Dougl. ex D. Don.), Ponderosa pine (*Pinus ponderosa* (Dougl. ex P. & C. Lawson), lodgepole pine (*Pinus contorta* Dougl. ex Loud. var.latifolia Engelm. Ex S. Wats.), subalpine fir (*Abies lasiocarpa* (Hook) Nutt.), and paper birch. Three replicate rows were established for each species and species were assigned randomly to rows. Rows are oriented north-south across each block. Each row is 90 m long extending 20 m into the uncut stand south and north of each block. The spacing was 2.6 m between rows and within each row seedlings were planted at 3 m spacing. A 20-m wide unplanted buffer was maintained on both the east and west sides of each block (Figure 2.1).

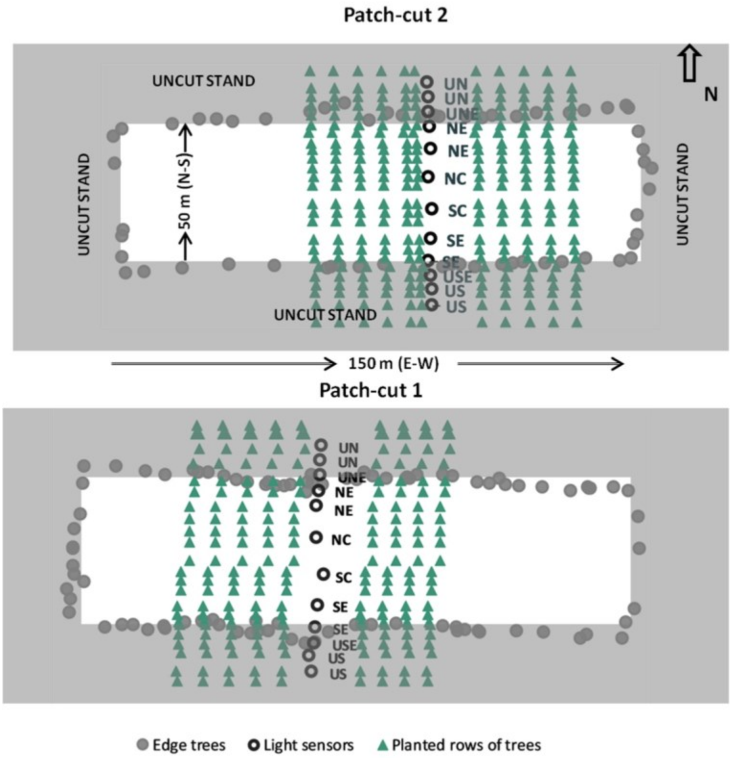

Figure 2.1. An illustration of the experimental layout for each patch cut. Gap environments are: UN - under north canopy; UNE - north edge under canopy; NE - north edge inside opening; NC - north of the centre; SC - south of the centre; SE - south edge inside opening; USE - south edge under canopy; US - under south canopy.

2.2.3 Light measurement

2.2.3.1 Fixed sensor

Direct and continuous measurement of PPFD was achieved using sensors as described by (Fielder and Comeau, 2000) based on GaAsP photodiodes (Gallium arsenide Phosphide-Hamamatsu Corp.1995) housed in a protective casing of aluminum and acrylic, and with a translucent acrylic diffuser to protect the photodiode and to provide for cosine correction. These photodiode-based sensors are not only cost effective for obtaining a large number of samples but provide a very good (nearly linear) spectral response (over the 400 - 700 nm range). They are almost insensitive to temperature change and resistant to moisture. In addition, the sensor packages are sturdy, easy to level, and capable of preventing the accumulation of rainwater during the wet season. Photodiodes used in this study were calibrated against quantum sensors (model LI-190S, LI-COR, Lincoln, NE, USA) and output (milli-volt) was converted to PPFD. A detailed description of the procedures can be found in Fielder and Comeau (2000) and Gendron et al. (1998).

I established a transect going north-south across the centre of each patch-cut and installed photodiode based sensors at 5, 15, 22.5, 27.5, 32.5 and 37.5 m north and south of the gap center (see Figure 2.1 for sensor locations). Sensors were installed at 1.5 m height above the ground on a 10 cm ×10 cm plexiglass plate mounted on a 1.5 m tall steel post. Sensors were leveled and connected to CR 10x dataloggers (Campbell Scientific Inc., Logan, Utah). Dataloggers were housed in plastic boxes (Pelicases) with a desiccant and grounded. To protect dataloggers from animals, a large aluminum washtub was inverted over the case and anchored to the ground using bent steel rebar stakes. PPFD (Photosynthetically active Photon Flux Density) at each location was sampled every 60 seconds, with average PPFD recorded on an hourly basis for the period of this study (May15th - September 30th, 2009*)*. From the hourly average PPFD (μmol m^{-2} s^{-1}), hourly total PPFD was calculated through multiplication by 3600 (number of seconds within an hour), which was summed over the growing season to provide the growing season total PPFD (μmol m^{-2} gs^{-1}; gs=growing season). Here, I report the total growing season PPFD in moles rather than micro-moles (1 mole = 10^6 μmol). This growing season total PPFD was then divided into their monthly PPFD values (μmol m^{-2} mo^{-1}; mo=month), as May (15 - 31), June (1 - 30), July (1 - 31), August (1 - 31) and September (1 - 30). Such monthly subdivisions were created as a basis for examining how light distribution changed over the growing season at various microsites inside the strip. I also obtained open sky PPFD readings using a smart PAR sensor (S-

LIA-M003) attached to an Onset HOBO® datalogger (Onset Computer Corporation, 2001-2011) installed in a nearby clearing. This datalogger ran for a 6-week period (June 10th to July 23rd, 2009).

2.2.3.2 Optical instrument

2.2.3.2.1 LAI-2000 Plant Canopy Analyzer

LAI-2000 measurements were taken from July 25-28, 2008 beside each photodiode at 1.5 m above the ground. Before measurement, the sensor was oriented in the appropriate direction and leveled. Sampling days were mostly clear and sunny. I used a 180° view cap on the lens and recorded data twice a day in two compass directions. In the morning, measurements were taken between 10.00 - 11.30 AM local time with the sensor pointed west and, in the afternoon, sensors were oriented to the East and readings were taken between 3.30 and 6.00 PM local time. The above canopy sensor was installed on a tripod, in a nearby clearing and the datalogger was programmed to automatically record data every 15 seconds. Configuration, synchronization and matching of both above and below canopy sensors were done following instructions outlined in the operating manual (Li-Cor, 1992).

FV2000 software was used for data downloading and pairing of above and below canopy readings. During data processing, I turned the 5th detector ring (68° zenith angle) off since previous studies indicate that including data from this ring weakens estimates of transmittance (Comeau et al., 1998). After DIFN was calculated for the east and west azimuth, I averaged them to obtain single value of DIFN at each photodiode location.

2.2.3.2.2 Hemispherical photographs

2.2.3.2.2.1 Image acquisition

I used a digital camera (Olympus CAMEDIA C-5050ZOOM) and a hemispherical lens (Raynox fisheye converter DCR-CF185PRO) to take the photographs beside each photodiode location at 1.5 m height. The camera was leveled on a tripod with the top of the camera aligned due north. I used maximum resolution and auto exposure but turned off the auto-flash. The majority of the photographs were taken in August 2007 (full leaf on); however, photographs inside the opening were retaken in August 2008 due to presence of sun-glare on few of them. This time, photographs were taken in the evening when the sun was no longer visible in the sky, but the sky was not dark. This was done to avoid issues related to presence of glare on the images and also to ensure that sky was somewhat uniformly illuminated at the time of photography.

This study was conducted in a mature conifer forest, therefore, from practical standpoint, gap fraction for the locations inside the gap is not expected to change from one year to the other and, therefore, acquiring photographs in two different years (2007 and 2008) and their subsequent use to predict radiation regimes in 2009, is not problematic, although it may introduce some error. The same reasoning is assumed for LAI-2000 measurements taken in 2008. All photographs and LAI-2000 measurements reflect a period when stands have full leaf development and maximum leaf area, they do not, however, represent the spring, autumn or winter periods when some species (western larch, paper rich, aspen, and black cottonwood) are lacking or have only a portion of their midsummer leaf area.

2.2.3.2.2.2 Image analysis

Images were analyzed using the Gap Light Analyzer (GLA) version 2.0, Frazer et al., 1999). I used a blue color plane first to enhance the contrast between the canopy structures and the sky and then selected a thresholding value that gave a reasonable representation of the canopy in the registered image. Light indices were computed using the default model parameter settings in GLA. In brief, I selected a sky division based on 36 azimuth and 9 zenith angles, a uniform overcast sky (UOC) model for the diffuse light distribution, and 2-minute intervals for computation of the sun's position. Furthermore, beam fraction and clear sky transmission were set at 0.5 and 0.65, respectively, as recommended by Canham et al. (1994). Photographic light indices were computed for the entire growing season (May 15th to September 30th) as well as for the duration of each month (for May: 15 - 31; June: 1 - 30; July: 1 - 31; August: 1 - 31 and September: 1 - 30) in order to evaluate if variability in seasonal light level in the understorey can be predicted by hemispherical photography.

2.2.3.3 PAR sensors indices

To test the use of a single measurement under either overcast or sunny conditions, I selected a sunny (July 16th) and a uniform overcast (June 22nd) day. Figure 2.2 shows the diurnal distribution of the open sky PPFD for the sunny and the overcast day.

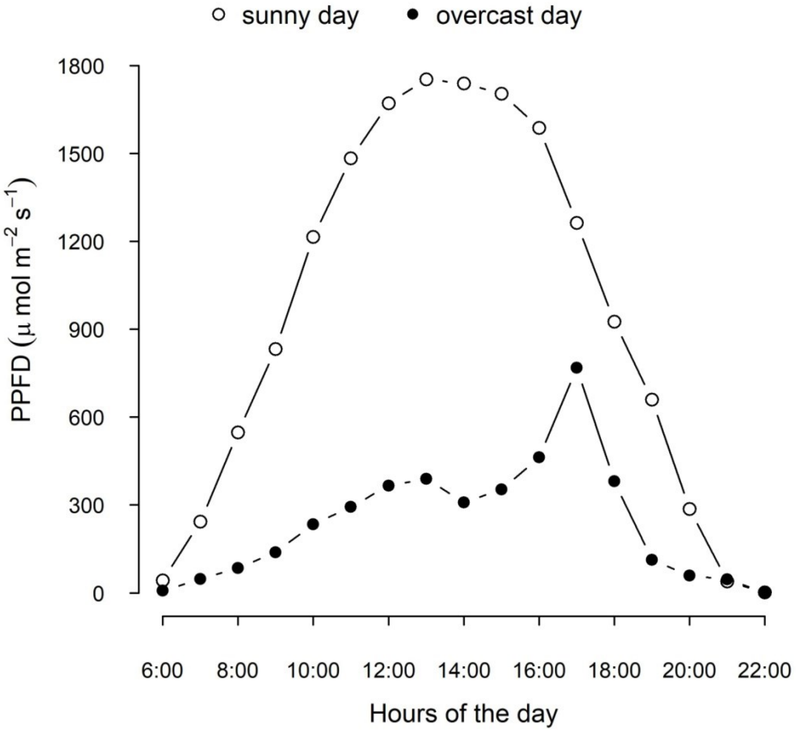

Figure 2.2. Diurnal patterns of above canopy PPFD (hourly average) for a sunny and an overcast day.

Mid-summer, midday %PPFD (transmittance) was calculated for the sunny and the overcast day by dividing hourly average PPFD recorded at each photodiode below the canopy (for example, hourly average midday PPFD means the average of 60 readings recorded between 13:00 and 14:00 hour by photodiodes) by their corresponding hourly average open sky PPFD. % PPFD was then averaged for different durations or different times within the day as indicated in Table 2.1. To calculate a new index (mixed sky midday index), I selected two additional sunny and overcast (near overcast) days. Then I calculated the indices by averaging % PPFD recorded at mid-day (13:00 hour) for various combinations of sunny and overcast skies as described in Table 2.2.

Table 2.1. Comparison of midday (13:00 h) point estimates (average transmittance of various durations/at different times) in predicting growing season transmittance (% PPFD).

Method	**Intercept**	**Slope**	**rmse***	**R^2**	**N**
Sunny day					
1-hour (13:00-14:00 hours)	**9.15** (3.98)	**0.58** (0.08)	9.55	0.81	15
2-hour (12:00-14:00 hours)	**8.31** (3.81)	**0.67** (0.08)	9.01	0.83	15
3-hour (11:00-14:00 hours)	**9.28** (3.58)	**0.72** (0.09)	8.73	0.84	15
4-hour (11:00-15:00 hours)	**6.90** (3.02)	**0.72** (0.07)	7.07	0.90	15
5-hour (10:00-15:00 hours)	**7.30** (3.30)	**0.80** (0.08)	7.75	0.87	15
6-hour (10:00-16:00 hours)	4.84 (2.58)	**0.83** (0.06)	5.82	0.93	15
At 10:00,13:00, and 16:00 hour	**3.99** (1.71)	0.95 (0.05)	3.83	0.97	15
Overcast day					
1-hour (13:00-14:00 hours)	3.87 (6.46)	1.20 (0.24)	12.62	0.67	15
2-hour (12:00-14:00 hours)	3.16 (6.46)	1.20 (0.23)	12.45	0.68	15
3-hour (11:00-14:00 hours)	3.12 (6.26)	1.24 (0.23)	12.16	0.69	15
4-hour (11:00-15:00 hours)	3.23 (6.52)	1.19 (0.23)	12.55	0.67	15
5-hour (10:00-15:00 hours)	3.62 (6.43)	1.22 (0.24)	12.52	0.67	15
6-hour (10:00-16:00 hours)	4.76 (6.69)	1.19 (0.25)	13.16	0.64	15
At 10:00,13:00, and 16:00 hour	4.32 (6.58)	1.05 (0.21)	12.91	0.65	15

Note: All regression models are highly significant ($P < 0.001$). Standard errors are in parenthesis. Model estimates and fit statistics were obtained through OLS parameterization of the regression models. Intercepts that are significantly different from zero ($P < 0.05$) are bolded. Slopes that differed significantly from 1:1 line are also bolded to indicate significance. * Root mean square error.

Table 2.2. Regression coefficients for comparison of different mixed sky midday indices used to predict the growing season transmittance (% PPFD).

Midday index for the following sky conditions	**Intercept**	**Slope**	**rmse***	**R^2**	**N**
Single sunny day	**9.15** (3.98)	**0.58** (0.08)	9.55	0.81	15
1 sunny and 1 overcast	3.79 (3.57)	0.90 (0.09)	7.68	0.88	15
1 sunny and 2 overcast	3.37 (3.62)	0.87 (0.09)	7.70	0.88	15
1 sunny and 3 overcast	2.20 (3.86)	0.96 (0.10)	7.97	0.87	15
Single overcast day	3.87 (6.46)	1.20 (0.24)	12.62	0.67	15
1 overcast and 1 sunny	3.79 (3.57)	0.90 (0.09)	7.68	0.88	15
1 overcast and 2 sunny	4.68 (3.32)	**0.77** (0.08)	7.33	0.89	15
1 overcast and 3 sunny	6.12 (3.40)	**0.71** (0.07)	7.74	0.87	15

Note: All regression models are highly significant ($P < 0.001$). Standard errors are in parenthesis. Model estimates and fit statistics were obtained through OLS parameterization of the regression models. Bold indicates a significant intercept. Slopes that differed significantly from 1:1 line are also bolded to indicate significance. *Root mean square error.

2.2.4 Data analysis

Open sky light data were available for a 6-week period (from June 10th and July 23rd, 2009), which allowed me to calculate canopy transmittance for that 6-week period by dividing the total below canopy PPFD with their corresponding total above canopy PPFD. However, as below canopy PPFD were continuously recorded for the entirety of the growing season (May 15 to September 30), and most other studies report their findings in transmittance, I developed a conversion between total growing season (May 15 to September 30) below canopy PPFD (mol m^{-2} gs^{-1}) and the 6-week transmittance (% PPFD), by the use of a regression equation (see Figure 2.3). The regression line explained 95% of the variation in transmittance ($R^2 = 0.95$) with a root mean square error of 5.03. Since this is a linear transformation of the total below canopy PPFD, the expected north-south pattern in light across the strip remained the same, regardless of whether data were expressed in their absolute values or as calculated transmittance values. However, since unexplained variability resulting from transformations based on the use of a regression equation can obscure subtle differences in monthly light levels between below canopy microsites, I describe month to month variation in growing season transmittance using the below canopy light levels in their actual units, which is mol m^{-2} mo^{-1}.

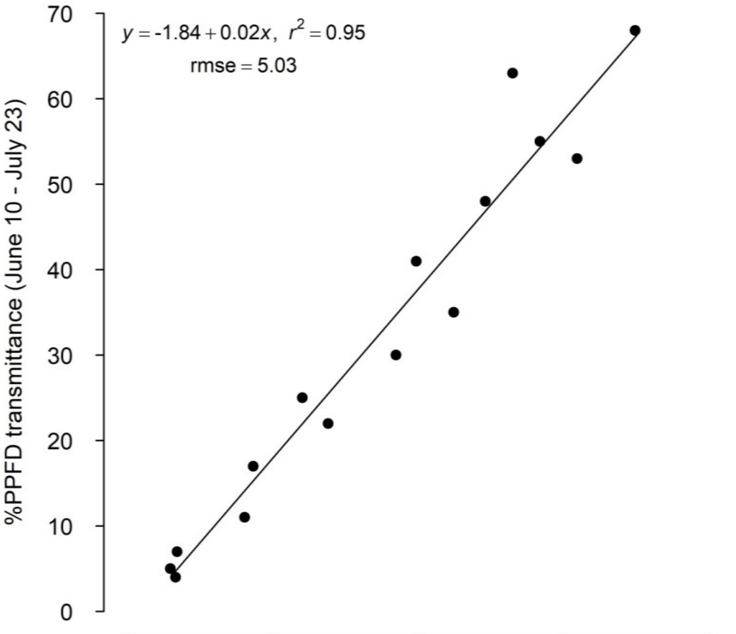

Figure 2.3. Regression line to convert actual PPFD values (mol m^{-2} gs^{-1}; gs=growing season) to their corresponding % transmittance for the entire growing season (May 15 to September 30).

Linear regression analysis was used to examine the relationship between the calculated growing season transmittance (% PPFD as dependent variable) and various surrogate indices of light (independent variables). As I further investigated prediction of seasonal variability in growing season transmittance by these one-time, instantaneous mid-summer indices, I examined the best indices for their correlation with total monthly below canopy PPFD (mol m^{-2} mo^{-1}). Fit statistics such as, R^2 and root mean square error (rmse) were used to compare among the regression models. Slopes of the regression lines were also tested to see if they differed significantly from unity. All analyses were completed using R statistical software (R Core Team, 2019).

2.3 Results

2.3.1 Growing season transmittance estimation

2.3.1.1 Hemispherical method

Two widely used hemispherical techniques investigated in this study were: a) LAI-2000 hemispherical sensor and b) fisheye canopy photograph. Although all hemispherical indices (LAI-2000 and photographs) gave a linear and statistically significant ($P < 0.001$) relationship, with intercepts not significantly different from zero ($P > 0.05$, Table 2.3), indices varied on how well they correlated with growing season transmittance. For example, LAI-2000's measure of diffuse transmittance (DIFN) gave stronger correlation ($R^2 = 0.68$) and less variability (rmse = 12.45) as compared to both diffuse ($R^2 = 0.57$, rmse = 14.28) and gap fraction indices ($R^2 = 0.58$, rmse = 14.11) from the photographs. On the other hand, direct beam index obtained from photographs gave stronger correlation ($R^2 = 0.87$) with growing season transmittance, followed by its total light estimate ($R^2 = 0.82$). However, all photographic indices consistently overestimated actual light levels (Figure 2.4 B - D; Table 2.3), and among them, the bias estimated from direct beam light was significant (slope significantly different than 1). DIFN

(LAI-2000) overestimated actual light level above 25% transmittance, but below this point, it correlated well with growing season transmittance (Figure 2.4 A; Table 2.3).

Table 2.3. Summary of linear regression models for predicting growing season transmittance (% PPFD) from two hemispherical light estimation techniques (sensor vs. image) (% PPFD = a +bX).

Method	**Output**	**Intercept**	**Slope**	**rmse**[*]	**R^2**	**N**
LAI-2000	DIFN180	2.81 (6.52)	0.80 (0.15)	12.45	0.68	15
Hemispherical photograph	Diffuse (%)	-3.13 (9.25)	0.76 (0.18)	14.28	0.57	15
	Direct (%)	-3.95 (4.44)	**0.70** (0.08)	7.97	0.87	15
	Total (%)	-8.27 (5.77)	0.82 (0.11)	9.24	0.82	15
	Gap Fraction (GF)	-5.00 (9.48)	1.08 (0.25)	14.11	0.58	15

All regression models are highly significant ($P < 0.001$). Standard errors are reported in parenthesis. Model parameters and fit statistics were calculated using OLS (ordinary least squares). None of the intercepts are significant. Slope of direct light differed significantly from 1:1 line and is bolded to indicate significance. [*] Root mean square error.

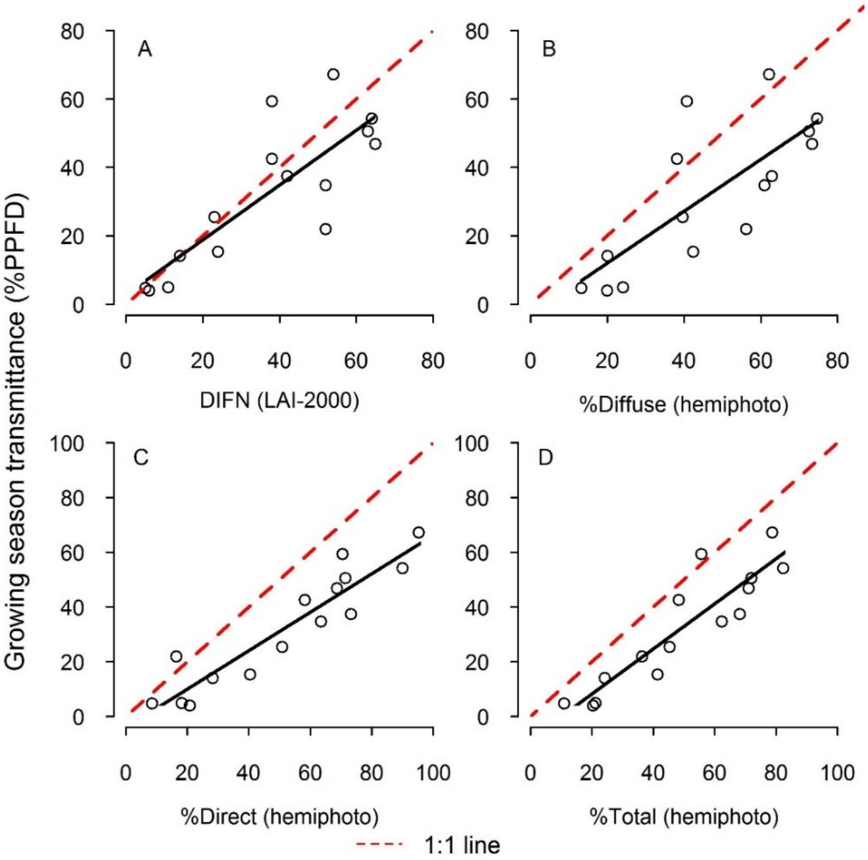

Figure 2.4. Relationships between growing season transmittance and hemispherical light estimation. Graph A = Diffuse (DIFN) transmittance from LAI-2000; Graphs B – D = Diffuse, direct and total (diffuse + direct) transmittance estimated from hemispherical photograph, respectively. See Table 2.3 for regression estimates.

2.3.1.2 PAR sensor indices

2.3.1.2.1 Sunny and Overcast sky light measurements

On a sunny day, one midday (13:00 h) light measurement showed higher variability (a high rmse) in the relationship with growing season transmittance than measuring light continuously for 4 - 6-hour duration or at different times within the day (Figure 2.5 A - D; Table 2.1). Measuring light at different times (morning, noon, and afternoon) gave slightly better results (R^2 = 0.97) than that for 4 - 6 hours continuous duration (R^2 = 0.87 - 0.93). Moreover, with this method, the data points also fell close to 1:1 line, and the slope did not differ significantly from 1 (Figure 2.5 D). Although the intercept term was still significant (P ≈ 0.04), the standard error of the intercept (1.71) and the root mean square error (3.83) for this method were the lowest. The intercept was not significant when light was continuously measured for a 6-hour duration (Table 2.1) but was significantly different from 0 for other durations.

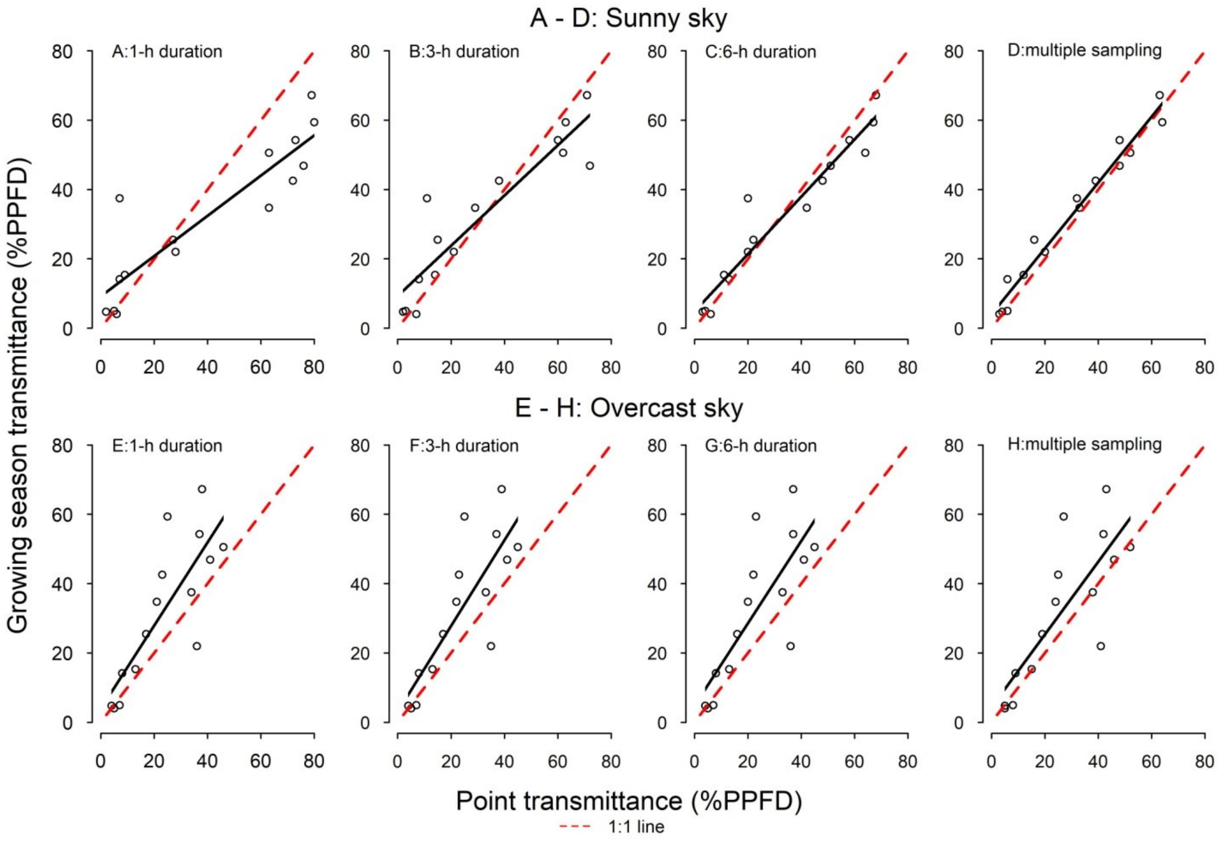

Figure 2.5. Relationships between growing season transmittance (% PPFD) and midday point estimates for sunny (graphs A - D) and overcast (graphs E - H) sky conditions. See Table 2.1 for regression estimates and description.

Contrary to the findings reported by several studies that a single light measurement on overcast days strongly correlates with growing season transmittance (Parent and Messier, 1996; Comeau et al., 1998; Gendron et al., 1998), in this study, I found that this approach provided a weaker correlation and had higher variability (the higher rmse) than results from sunny day measurements. Moreover, measuring light continuously for longer duration or at different time intervals within an overcast day did not improve R^2 values, and in some cases resulted in reductions in R^2 values (Table 2.1). Furthermore, the overcast day method consistently underestimated actual light (Figure 2.5 E - H).

2.3.1.2.2 A mixed sky midday index

Taking midday measurements under multiple days with a mix of sunny and overcast (near overcast) skies provided a better estimate of growing season transmittance ($R^2 = 0.87 - 0.89$) and a lower bias than obtained from a solitary midday measurement under either a sunny (0.81) or an overcast day (0.67). Combining midday averages from one sunny day with midday averages from multiple overcast days only increased R^2 slightly (from 0.81 to 0.88) but had less bias (a non-significant slope of 1) (Figure 2.6 A - D). Conversely, the midday average of one overcast day to multiple sunny days resulted in an increase in R^2 (to 0.89) but added significant bias (slope was significantly different than 1) (Figure 2.6 G - H). The best result was obtained by averaging midday transmittance (% PPFD) of one sunny and one overcast day. This gave a non-significant intercept and an R^2 (0.88) similar to that obtained by measuring light continuously for 4 - 6 hours on a sunny day (0.87 - 0.93). The bias was also not significant for this method (Figure 2.6 B or F).

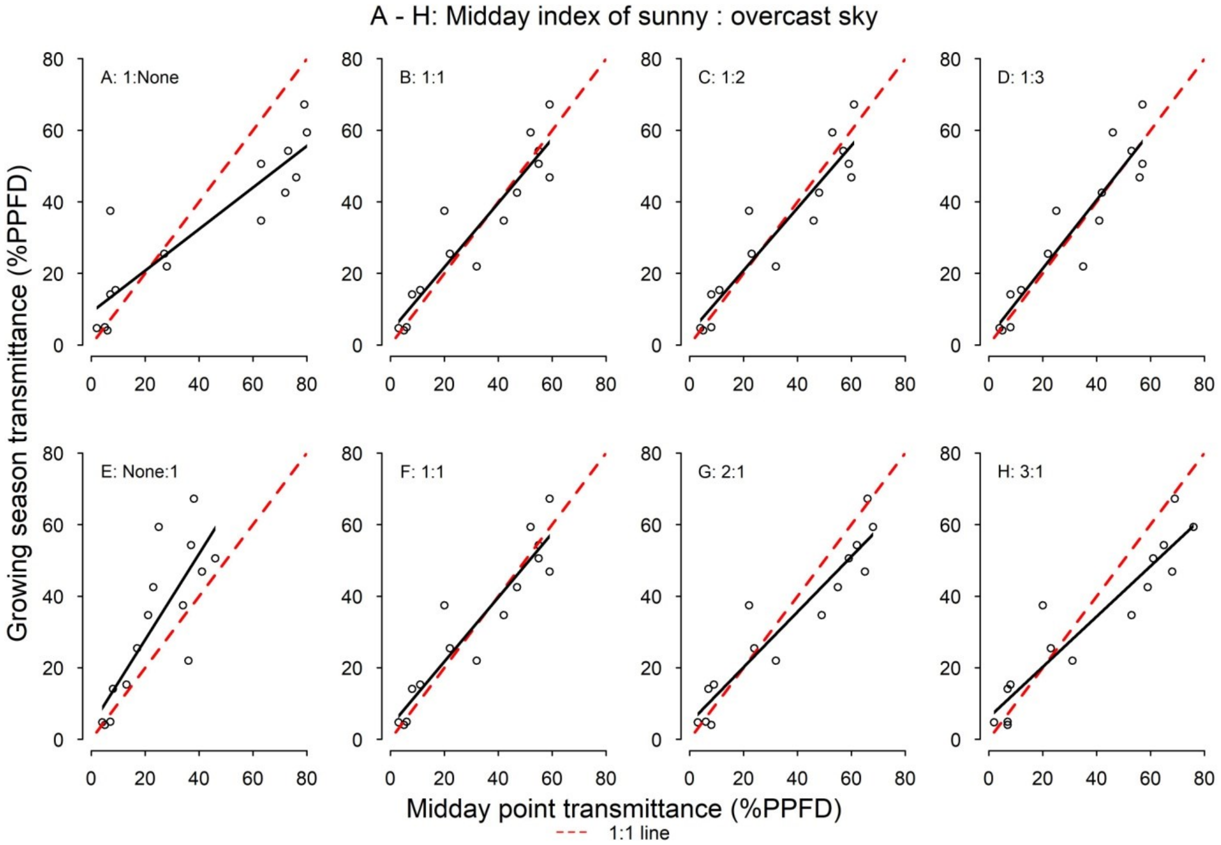

Figure 2.6. Relationships between mixed sky midday indices and growing season transmittance (% PPFD). Graph A represents midday light transmittance of a sunny day; Graphs B - D represent average midday transmittance of one sunny day to increasing number of overcast days (up to 3). Graph E represents the same for one overcast day and F - H represent the same for one overcast day to increasing number of sunny days (up to 3). See Table 2.2 for regression estimates.

Table 2.4. Summary of linear regression estimates for predicting seasonal below canopy total PPFD (mol m^{-2} mo^{-1}; mo=month) for four selected indirect light estimation techniques.

Method	**Intercept**	**Slope**	**rmse***	**R^2**	**N**
May					
Photograph (total light)	-53.28 (41.43)	6.64 (0.76)	67.61	0.86	15
Overcast day midday % PPFD	35.85 (48.23)	10.14 (1.76)	94.23	0.72	15
Mixed sky midday index[1]	54.92 (37.20)	6.96 (0.97)	80.05	0.80	15
Sunny day multiple measurements[2]	**52.13** (22.87)	7.52 (0.63)	51.18	0.92	15
June					
Photograph (total light)	-104.12 (78.93)	10.91 (1.43)	129.30	0.82	15
Overcast day midday % PPFD	11.57 (70.05)	18.16 (2.56)	136.80	0.80	15
Mixed sky midday index[1]	59.98 (59.70)	12.02 (1.56)	128.5	0.82	15
Sunny day multiple measurements[2]	58.16 (36.13)	12.89 (0.99)	80.85	0.93	15
July					
Photograph (total light)	-101.41 (81.83)	10.83 (1.49)	133.90	0.80	15
Overcast day midday % PPFD	24.63 (78.85)	17.42 (2.88)	154.00	0.74	15
Mixed sky midday index[1]	43.78 (48.78)	12.39 (1.28)	105	0.88	15
Sunny day multiple measurements[2]	49.37 (27.61)	13.03 (0.76)	61.78	0.96	15
August					
Photograph (total light)	-46.16 (67.57)	8.09 (1.24)	109.80	0.77	15
Overcast day midday % PPFD	104.65 (84.15)	10.49 (3.07)	164.40	0.47	15
Mixed sky midday index[1]	64.57 (42.72)	9.09 (1.12)	91.94	0.84	15
Sunny day multiple measurements[2]	75.66 (36.97)	9.32 (1.02)	82.73	0.87	15
September					
Photograph (total light)	-12.53 (65.37)	4.94 (1.24)	93.44	0.57	14
Overcast day midday % PPFD	144.86 (74.68)	3.36 (2.64)	133.70	0.12	14
Mixed sky midday index[1]	80.03 (52.00)	4.42 (1.32)	102.4	0.48	14
Sunny day multiple measurements[2]	76.70 (44.87)	4.82 (1.19)	92.59	0.58	14

Note: All regression models are highly significant ($P < 0.001$), except for overcast index in September. Standard errors are shown in parenthesis. Bold indicates a significant intercept. [1] Average of two-midday % PPFD of one sunny and one overcast day; [2] measurements taken at 10:00, 13:00, 16:00-hour. [*] Root mean square error.

2.3.2 Seasonal light (PPFD) estimation

I evaluated four light indices to predict monthly variation in growing season light. These are: a) total transmittance from hemispherical photograph; (b) overcast day midday % PPFD; c) mixed sky midday index (one sunny and one overcast day); and, d) sunny day multiple measurements at different time intervals within the day. Of these four indices, multiple measurements on a sunny day best predicted the monthly variation in growing season light. Other than the intercept being significant in May ($P \approx 0.04$), this method predicted monthly variations in light from spring to the end of summer. However, in fall, I observed a sharp decline in R^2 and the highest variability around the regression line compared to other months of the growing season (Figure 2.7 A - E; Table 2.4).

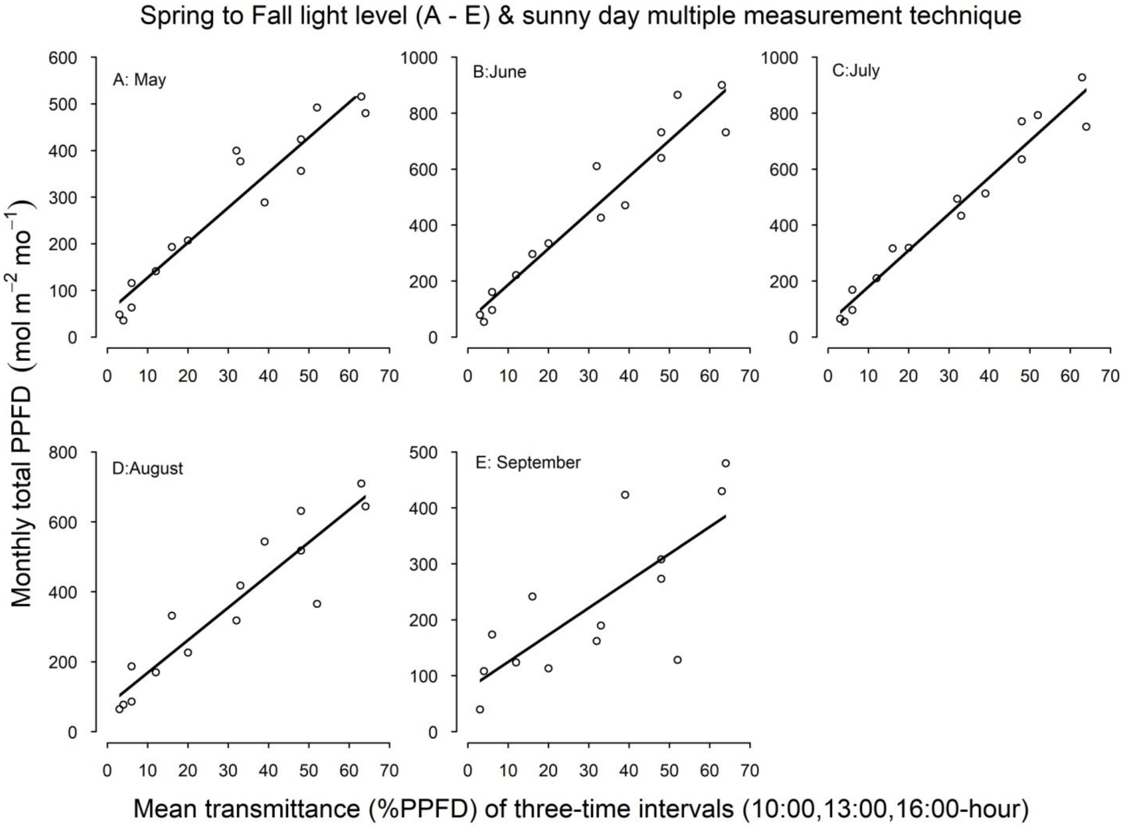

Figure 2.7. Seasonal light level (mol m^{-2} mo^{-1}; mo = month) as predicted by the best light estimation method, i.e. multiple measurements on a sunny day at three-time intervals. Panels A - E represent various light environments within the growing season, namely, A = spring; B - D = mid-summer months; and E = Fall. See Table 2.4 for detail.

A midday light measurement on an overcast day, on the contrary, gave the least precise (highest rmse) estimate of the monthly light levels. This method performed well only for the spring (May; $R^2 = 0.72$) and two mid-summer months - June ($R^2 = 0.80$) and July ($R^2 = 0.74$), however, the relationship was much weaker ($R^2 = 0.47$) for August, and it failed to correlate significantly with September light level ($P > 0.05$, Table 2.4). Photographic estimates of seasonal transmittance gave relatively better correlation (higher R^2) than the overcast day method, particularly for August ($R^2 = 0.77$) and September ($R^2 = 0.57$). This method also performed better than the mixed sky midday index for the beginning (May) and end of the growing season (September) while for the rest of the mid-summer months (June - August), the mixed sky midday index gave a more precise estimate (lower rmse). In general, all light indices correlated poorly with September light level where R^2 values dropped about 20-40% compared to rest of the months of the growing season (Table 2.4).

2.4 Discussion

2.4.1 Estimating growing season transmittance (% PPFD)

2.4.1.1 Hemispherical methods

I used two hemispherical techniques- hemispherical photography and LAI-2000-on several points along the N-S transect to quantify change in sky-view (gap fraction) between locations within the harvested strip (Figure 2.8). Due to the orientation of the stand, each location within the gap will receive varying amount of direct beam radiation (Stadt et al., 1997). Gap fraction, on the other hand, only provides unobstructed percentage of sky for reference locations without considering their azimuth. Therefore, where stand orientation influences the magnitude of the light gradient, gap fraction index cannot represent the existing light environment in the understory, though in the past, studies have reported gap fraction to be a reliable index for certain types of canopy condition, such in case of small gaps or homogenous canopies (Tobin and Reich, 2009; Rozenbergar et al., 2011).

North of the gap center (A) **North edge (C)** **Under north canopy (E)**

South of the gap center (B) **South edge (D)** **Under south canopy (F)**

Figure 2.8. Change in sky-view from the center towards the north and south canopy within the opening.

Gap fraction typically correlates strongly with the diffuse fraction of light (Table 2.3, also see Chazdon and Field, 1987). Hence, it is not surprising that in this strip shelterwood study, either gap fraction (Table 2.3) or diffuse estimates showed more variability around regression lines (Figure 2.4 A - B). However, between LAI-2000 and the photograph, diffuse estimates from the LAI-2000 showed less variability (Figure 2.4 A vs. B; Table 2.3), which is in agreement with Machado and Reich (1999) and Rozenbergar et al. (2011), who also found that LAI-2000 performed better than hemispherical photography in a deeply shaded forest structure (transmittance level < 20%). Comeau et al. (1998) also reported similar finding, but for a sparse deciduous forest structure with a much wider range of light conditions (4-65% transmittance).

Nevertheless, the increased variability observed at higher transmittance with diffuse light can be explained by the fact that diffuse measurements ignore the influence of stand orientation on total light received by each microsite, whereas microsites within a gap would receive varying amount of direct beam radiation depending on their location (Canham et al., 1990; Tobin and Reich, 2009). For instance, gap fraction between northern and southern side of the gap can be roughly similar, but total light received between the two locations can be markedly different. For this reason, gap fraction or diffuse light has been observed to show increased variability at higher transmittance.

Due to its higher resolution, hemispherical photography records canopy openings in greater detail than LAI-2000. Therefore, when used in conjunction with the solar track, photographs generally gives a better outcome (Rhoads et al., 2004) than LAI-2000. In this study, direct beam index from photographs provided stronger correlation ($R^2 = 0.87$; Figure 2.4 C) than its other outputs, but it showed a significant bias. On the other hand, photographic total light index gave a slightly weaker correlation than its direct beam index ($R^2 = 0.82$), but the bias was not significant this time (Figure 2.4 D; Table 2.3). This results clearly indicate that inclusion of the direct beam component in the hemispherical model was an important consideration for this site and stand condition (see Canham et al., 1990).

Due to absence of local open sky PPFD or weather data for the entire growing season, hemispherical indices were computed based on several constants used in GLA. These constants may not accurately represent diurnal and seasonal variations in sky conditions and consequently contribute to unexplained variance. The use of on-site weather and open-sky PPFD data could reduce this variance. Moreover, photographic indices consistently overestimated growing season transmittance as reported by other studies (Comeau et al., 1998; Ferment et al., 2001; Kobe and Hogarth, 2007). Such overestimation is common with digital photograph due to their higher sensitivity to changing light condition (Hale and Edwards, 2002; Nobis and Hunziker, 2005). In addition, the thresholding process applied to separate the white (sky) pixels from the black (canopy) can also contribute to overestimation. However, such bias from the use of hemispherical photographs can be corrected by calibrating photographs with direct measures of light from PAR sensors (Rich et al., 1993).

2.4.1.2 PAR sensor indices

2.4.1.2.1 Sunny sky and overcast sky measurements

This study is in disagreement with a number of studies that suggested sunny day, around midday instantaneous light measurement method is less reliable in characterizing growing season transmittance than overcast days % PPFD (Messier and Puttonen, 1995; Parent and Messier,1996; Gendron et al., 1998; Battaglia et al., 2003; Tobin and Reich, 2009). In this study, overcast day % PPFD provided a relatively weak correlation ($R^2 = 0.67 - 0.68$) with growing season transmittance, with a much higher scatter above 30% transmittance (Figure 2.5 E - H). Moreover, when measurements were taken over longer periods, from 1 hour to up to 5 hours, there was no improvement in the relationship between overcast day % PPFD and growing season transmittance. This reinforces the findings of other studies that on an overcast day, % PPFD can be sampled any time during the day (Parent and Messier, 1996) or any day within the growing season (early, mid or late) as long as canopy remains static (Gendron et al., 1998). Diffuse light varies between microsites primarily as a function of sky-view (Figure 2.8), therefore, spatial orientation of microsite is typically disregarded in this method (north vs south, see Stadt et al., 1997), which might explain the weak correlation found in this study between this method and the growing season transmittance.

For this study site, midday, sunny day % PPFD (1-hourly average) provided higher correlation than midday overcast day % PPFD and correlation became stronger (lower rmse and higher R^2) when measurements were taken over a 4 - 6-hour period (Figure 2.5 A - D; Table 2.1), which is in agreement with Comeau et al. (1998), who also found that measuring light for 3 - 6 hours duration on a sunny day increased R^2 and reduced root mean square error values. Based on this, they suggested that measuring light on a sunny day can also be a potentially useful technique in estimating growing season transmittance. The dispute surrounding collection of light either on sunny days or overcast days as observed between this study and others (Messier and Puttonen, 1995; Parent and Messier, 1996; Comeau et al., 1998; Gendron et al., 1998; Battaglia et al., 2003) can be attributed to differences in stand conditions, with most studies dealing with stands with a homogenous canopy or very small gaps. In addition, this computation of light indices used hourly averages of % PPFD, whereas in other studies 5 to 10-minutes averages were used.

It is not surprising that sunny day indices will perform better in open-canopied forests due to its accounting for direct beam radiation (but see Battaglia et al., 2003; Gendreau-Berthiaume and Kneeshaw, 2009). Moreover, sunny day indices account for transmitted or scattered radiation, both of which are expected to be much higher under clear than overcast conditions. However, I observed a significant y-intercept for most sunny day indices, which was also noted by Engelbrecht and Herz (2001). Due to this, they cautioned on the use of this method for predictive purposes. In this study, the intercept became non-significant with a substantial increase in R^2 (from 0.81 to 0.93) when light was measured for longer duration (6-hour). Throughout the day, direct beam contribution varies as a function of time (Anderson, 1970). By averaging light for longer durations, integration of direct beam contribution from different angles resulted in an increase in R^2 and the intercept becoming non-significant.

While measuring light for 6-hour durations on a sunny day provided a stronger correlation ($R^2 = 0.93$) and a non-significant intercept, taking light measurements at different times (morning, noon and afternoon) within the day was found to provide the strongest correlation with growing season PPFD ($R^2 = 0.97$). However, in this approach, the y-intercept was still significant ($P \approx 0.04$). Moreover, actual light was slightly underestimated at the lower end of transmission. Apart from this, the regression line fell close to a 1:1 line which reflected that a non-significant bias can be achieved by this method (Table 2.1). The significant y intercept may be due to the lowest standard error observed amongst all other indices (Table 2.1). And the reason for higher correlation between this method and growing season transmittance may be due to its ability to integrate changes in direct beam contribution between gap microsites during the day (Figure 2.5 D). Bias and scatter in the relationship was much less as well. Gendron et al. (1998) also found average of two 10-min light transmittance recorded at two different times (10:00 and 14:00) of a sunny day gave better correlation than taking an instantaneous light measurement around noon.

2.4.1.2.2 Mixed sky

Since, on sunny days, a midday % PPFD measurement gives a good approximation of the maximum light levels in gaps (Gendreau-Berthiaume and Kneeshaw, 2009), it is assumed to be a biased estimate of the overall growing season transmittance (Gendron et al., 1998). However, on overcast days, % PPFD measurements underestimate growing season transmittance since they ignore the contribution of direct light or sunflecks to total light. Therefore, sampling only once at mid-day under a sunny or an overcast sky may not represent the total light environment for the growing season. Given this experimental condition, I found an average of two-midday % PPFD under a sunny and an overcast sky gave better correlation and an unbiased estimate of growing season transmittance. Increasing the proportion of sunny days used to determine the average decreased the scatter in the relationship but introduced bias (Figure 2.6 E - H). In contrast, increasing the proportion of overcast skies used to determine the average reduced the bias but caused a decrease in R^2 (Figure 2.6 A - D; Table 2.2). Hence, I conclude that rather than exclusively sampling under sunny or overcast conditions, midday indices should be calculated based on a mixture of sky conditions in situations that are similar to this study. Averaging measurements taken under both sky conditions accounts for contributions of diffuse and direct components in large gaps, where the contribution to light received in each gap microsite depends on their spatial orientation and cannot be ignored (Stadt et al., 1997).

2.4.2 Seasonal light (PPFD) estimation

Since seasonal variations in light can influence the survival and growth of the regeneration, I evaluated several of the light indices to predict monthly variations in growing season transmittance. Results indicate that several indices correlate well with seasonal light levels, at least for the spring (May) and the summer months (June - August). These results differ from those of Rich et al. (1993) who indicate that one-time instantaneous measurements taken at any time during the year may not represent the highly variable light environments between days and months found in medium or large gaps for the whole growing season.

I observed the relationship between diffuse index (overcast day % PPFD) and hemispherical index (total light) with monthly light levels becoming weak going from the beginning (May) to the end of the season (September); in fact, the relationship of the diffuse index to September light level was not even significant ($P > 0.05$). Machado and Reich (1999) also observed a weakening relationship between LAI-2000 (DIFN) and mean daily PPFD going from June to September and in case of hemispherical photography, Nunez and de Gouvenain (2015) found it did not give reliable estimates of seasonal light transmittance for the highly fragmented forests in Southern New England that they studied. This is not surprising since the assumption of static canopy conditions is an inherent weakness in hemispherical models (see Frazer et al., 1999). Photographs taken in mid-summer (June to August) may not adequately capture canopy effects on the radiation regime for the full length of the growing season, particularly when deciduous species are present. Consequently, several studies suggest that hemispherical methods should be used in conjunction with other direct measurements of light, like PAR sensors (Gendron et al., 1998; Nunez and de Gouvenain, 2015). However, in this study, hemispherical photograph provided reasonable estimates of seasonal light levels for the majority of the growing season length (May - August). This is because the canopy of this mature conifer forest remains more or less stable during the summer period; as a result, photographs taken in mid-summer accounted the canopy conditions for a good segment of the growing season. However, the difference between this study and Nunez and de Gouvenain (2015) may be due to the differences in location (41° N and 72° W versus 49° N and 118° W), stand characteristics (oak-hickory highly fragmented forest versus mixed conifer forest) and duration of the season under question. They tested hemispherical photographs against winter (October - April) versus summer (May - September) seasons, whereas I tested them to detect the monthly differences within the duration of the growing season (May - September).

In general, all indices evaluated for predicting seasonal light levels showed a much weaker relationship to September light levels (Figure 2.7 E; Table 2.4). Indirect indices are usually sampled around mid-summer, when the mature overstory remains stable. But in September the canopy of temperate forests that include deciduous broadleaves (e.g. Balsam poplar, paper birch) and deciduous conifers (e.g. Western larch) is changing. Moreover, solar elevation angle becomes much lower in September and results in increased light interception by tall surrounding edge trees (see Prévost and Raymond, 2012). Therefore, the September light environment inside an opening is most likely to be dominated by scattered light. Consequently, it is not surprising that mid-summer light indices are not the best predictors of September light conditions in these experimental gaps. In addition, since the light environment during September is likely to be different than the rest of the summer months (June to August), to capture the influence of the change in canopy and the lower solar elevation angle, I suggest taking additional light measurements with PAR sensors during mid-September.

2.5 Conclusions

Results corroborate the finding that hemispherical photography can be a useful tool in providing reliable light estimates for open canopied system (Battaglia et al., 2003). Photographic methods provided estimates of growing season transmittance, with an R^2 value of 0.82. This study also reveals that diffuse estimates, either measured using LAI-2000 (DIFN), or using a PAR sensor on an overcast day or from hemispherical photography, gave higher variability when transmittance was high, due to these methods ignoring spatial differences in the contribution of the direct fraction between northern and southern sides of canopy openings.

Results also indicate that sky conditions (sunny versus overcast) under which instantaneous measurements should be collected must be given consideration, but this might also depend on the geographic location, stand structure and opening sizes. In this study, midday 1-hour light measurement on a sunny day performed better than measuring light on an overcast day. In addition, measuring light continuously over 4 - 6 hours duration or taking multiple measurements at different times within the day (morning, noon and late afternoon) improved R^2 on a sunny day, but similar approaches on an overcast day did not. Moreover, taking the average of two-midday 1-hour light measurement for one sunny and one overcast day (mixed sky index) exhibited better correlation and less bias than the midday light measurement of either sunny or overcast days, separately.

Of the four methods evaluated, except % PPFD on an overcast day, all indirect methods were very effective in predicting seasonal light levels for the period of May to August ($R^2 = 0.77$ - 0.96). All indices correlated poorly with September light levels, suggesting mid-summer light indices will not be as effective in characterizing the light gradient at the end of the growing season (September) (i.e. measurements will need to be taken in September in order to characterize its light levels). Overall, from the findings of this study, I conclude that, in characterizing the light environment under heterogeneous canopy conditions or inside medium or large gaps, accounting for the contribution of direct beam is an important consideration, which should not be ignored as suggested by Stadt et al. (1997). Therefore, for higher latitude forests, given the stand orientation and gap sizes, indices that integrate such contribution should be considered.

2.6 Limitations

It was difficult to find a large opening near the site location to install LAI-2000's open unit and a PAR sensor to collect open sky PPFD data. The site is located near the bottom of a valley; therefore, I had to install those units into a clearing located on top of a mountain, which might not have always reflected the exact sky condition for the above and below canopy sensors, particularly when sky conditions were variable. This likely contributed to some uncontrolled errors in this study. In addition, use of a smart sensor (S-LIA-M003) to collect the open sky light readings may have contributed to some differences and errors compared to the GaAsP photodiodes used for on-site measurements.

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3 Chapter 3: Light-growth responses of nine tree species in a strip shelterwood

3.1 Introduction

Interior Cedar Hemlock (ICH) forests in British Columbia are well known for their complex stand structure and high species diversity. These forests can support up to 14 commercial tree species in a single stand, including a wide range of shade tolerant conifers (ranging from very tolerant western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) to the least tolerant lodgepole pine (*Pinus contorta* Dougl. ex Loud. var.latifolia Engelm. Ex S. Wats.) and western larch [*Larix occidentalis* Nutt.]) and several broadleaf species (e.g. paper birch (*Betula papyrifera* Marsh) and trembling aspen [*Populus tremuloides* Michx.]). The vast majority of these forests are naturally occuring at valley bottom to mid elevation, hence these forests are greatly valued by the surrounding local communities for aesthetics and recreation in addition to them serving as a souce of readily accessible lumber (DeLong et al., 2005; Newsome et al., 2010).

Over the past four decades, forest management paradigms have been shifting toward a more holistic sustainable management approach, where multiple economic, ecological and social objectives are considered simultaneously. Under this approach, in addition to timber harvesting, other non-timber forest management objectives such as biodiversity (Tullus et al., 2018), wildlife (Escobar et al., 2015), watershed and recreation (Pukkala et al., 2016; Peura et al., 2018) are included in forest management planning. Moreover, this approach seeks to preserve the natural complexity and structure of forests and their biodiversity and visual quality. Shelterwood systems can improve visual quality over clear-cutting, and can often resolve conflicting ecological and economic objectives (Kern et al., 2017). However, uncertainty exists whether regeneration of a mix of shade intolerant, moderately tolerant and highly tolerant species would be successful under this system.

Shelterwood systems are usually applied to facilitate regeneration of even-aged stands through removing overstory canopies uniformly in a stand or in strips or groups. If trees are uniformly removed using the uniform shelterwood method, conditions for regeneration of intolerant and moderately tolerant tree species may not be suitable due to the moderate levels of shade cast by the retained canopy (Newsome et al., 2010). However, group or strip shelterwood methods can be used to create conditions that are suitable for moderately tolerant and intolerant species (York et al., 2003; Kern et al., 2017; Shabaga et al., 2019). In group or strip shelterwood methods, a small clear-cut is created in the canopy which leads to increased light levels in the understory.

Light is a principal growth limiting factor controlling the dynamics of understory regeneration in these forests (Canham, 1988; Coates and Burton, 1999; Lieffers et al., 1999; Philipson et al., 2012). In northern hemisphere forests, due to the southerly location of the sun during most of the year, light usually is distributed along the north-south axis within openings, but light received by microsites varies in magnitude depending on size, shape and orientation of the gaps and location within the gap. In general, the northern section of a gap experiences more direct beam radiation than its southern portion, where light is primarily diffuse; the southern portion of a gap remains under the influence of shade for the much of the growing season (Canham et al., 1990; Hossain and Comeau, 2019; Chapter 2).

Thus, when the varying contribution of diffuse and direct beam light in the understory follows a gradient, it is expected that various species will grow at different rates based on their light requirements or shade tolerance. In order to predict regeneration performance for different positions within gaps, a sound understanding of the mechanisms of shade tolerance in required. Shade tolerance is an ecological concept primarily derived from the relationship between light and growth or survival of species; however, such simplification of shade tolerance is still a matter of controversy (Kimmins, 2004; Bianchi et al., 2018; Avalos, 2019) and thus, many ecologists have proposed other inherent physiological and morphological characteristics as criteria to quantify and appropriately rank the shade tolerance of tree species (Mailly and Kimmins, 1997; Kneeshaw et al., 2006; Lusk and Jorgensen, 2013; Ameztegui et al., 2017).

Shade-tolerant and intolerant species often have different morphological and physiological adaptation strategies for dealing with low light levels (Daniel et al. 1979; Chmura et al., 2017). The two most important mechanisms enabling shade tolerant species to survive at low light are: a) reduction of the respiration rate leading to a lowering light compensation point and a slower growth rate; and, b) increase in specific leaf area to facilitate harvest of more photosynthetically active radiation in light limited environments.

In terms of plasticity, shade tolerant species show more crown plasticity when responding to understory light heterogeneity than shade intolerant species. Shade tolerant species modify their crown shape to be more efficient in capturing light at low light environment. These species show more lateral than vertical expansion (Williams et al., 1999; Claveau et al., 2002). Height: diameter or lateral branch: terminal shoot increment ratios are often used to describe such crown architecture or shape. Appearance-wise, shade tolerant species are generally flat-topped in low light environments, whereas shade intolerant species are thin, tall and spindly (Valladares and Niinemets, 2008).

Shade intolerant species are early successional species with ecological traits that can support high leaf level carbon gain at high light levels, and as a result, they typically grow faster than shade tolerant species. In contrast, shade tolerant species, due to their characteristic morphological and physiological adaptations, are more efficient in light capturing and utilization in shaded understory than shade intolerant species (see Valladares and Niinemets, 2008; Avalos, 2019), due to which, shade tolerant species can often grow faster than shade intolerant species in light limited environments. This trade-off in growth rates across the light gradient has been widely accepted as one of the mechanisms of species coexistence for many temperate and tropical forests (Sack and Grubb, 2001; Van Couwenberghe et al., 2013; Valladares et al., 2016). However, it has been also observed that not all shade intolerant species grow poorly at low light conditions, rather they may grow consistently better at all light environments within a gap (Coates and Burton, 1999; Kitajima and Bolker, 2003; Valladares and Niinemets, 2008). Based on these findings, many ecologists often times have abandoned the low versus high light growth trade-off hypothesis and supported the alternative hypothesis of survival versus growth trade-off between low and high light (Kobe et al., 1995; Kobe and Coates, 1997); although, evidence in favor of both hypotheses were found in certain forests ecosystems (see Lin et al. 2002).

The ICH is a species-rich ecosystem; hence, in developing silvicultural prescription, both ecological and silvicultural issues must be considered. For the maintenance of species diversity, forest scientists need a comprehensive understanding of niche-based theory, including the uncertainties in its predictions for mixed species regeneration within natural and artificially created gaps. However, there is limited understanding of how species rich ecosystems respond to light gradients created by strip-shelterwood and other silvicultural systems. Furthermore, there is debate surrounding the mechanisms driving species coexistence. A fundamental question is whether species coexistence is driven by niche specialization (niche theory) or by intraspecific variability within the population (neutral theory, see Hubbell, 2001) or both (see reivews by Avalos, 2019; Valladares et al., 2016). Although niche-partitioning is commonly recognized as the primary mechanism (see Molino and Sabatier, 2001 and their intermediate disturbance hypothesis), significant overlapping of niches is evident in gaps in diverse ICH forests. In this case, within a large species pool, a few species may be subject to competitive exclusion by other species; for example, highly shade tolerant species may outcompete moderately shade tolerant or highly shade intolerant species or even within the cohort of shade tolerant species, relatively less shade tolerating species may die due to intense competition from more shade tolerating species.

While it is important to test if data generated in this experiment support species' coexistence theory, it is also important to fill information gaps regarding species' performance at various positions within gaps, in relation to their south/north edges (edge effect). Relating species to their suitable gap-position is important to avoid early mortality and to maximize growth of the desired species (Bradshaw, 1992; York et al., 2003; Zdors and Donis, 2017). Research on this topic is timely since it will advance understanding of the influence of edges and will increase the ability to predict regeneration performance based on the location within the gap. Thus, this study also attempts to quantify edge influence (north versus south) on the growth of regenerating trees as it relates to their shade tolerance.

Overall, this research aims to answer the following broad question: Do the variations in growth rates among species support the mechanism of species coexistence in strip-shelterwood gap and thereby, facilitate mixed species regeneration in the Interior Cedar Hemlock zone (ICH) forests?

However, in the same context, I also ask the following specific questions,

1. How does the growth rate of 9 species of differing shade tolerances (Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franc.), Engelmann spruce (*Picea engelmannii* Parry ex

Engelmann), western redcedar (*Thuja plicata* Donn ex D. Don in Lamb), western hemlock, western white pine (*Pinus monticola* Dougl. ex D. Don.), Ponderosa pine (*Pinus ponderosa* (Dougl. ex P. & C. Lawson), lodgepole pine, subalpine fir (*Abies lasiocarpa* (Hook) Nutt.), and paper birch) vary along light gradients within the strip-shelterwood?

2. Can species' light (i.e., niche) partitioning be further elucidated through their response to changing positions within gap?
3. How do the northern and southern edges of the strip-shelterwood affect species' growth performance and is this associated with the differentiation in shade tolerance?

I expect to see that species will differentiate into discrete niches or clusters following their shade tolerance ranking due to differences in growth rates along the light gradient. I expect to see at least 3 distinct patterns in light-growth relationship between species in the following order: highly shade intolerant > moderately shade tolerant > shade tolerant. I also expect to see niche overlap, particularly within each tolerance cohort. For edge effects, shade tolerant species are expected to suffer less growth reductions at the south edge of openings than shade intolerant or moderately shade intolerant species, but the reverse is expected at the north edge proximities.

3.2 Methods

3.2.1 Study area

The study site is located on a level area in a valley bottom, 50 km south of Nakusp, British Columbia (Lat. 49 57'N, Long. 117 53'W) in the Columbia-Shuswap variant of the Interior Cedar-Hemlock moist warm Biogeoclimatic subzone (ICHmw2). Situated 550 m above sea level, the site has a mesic soil moisture and a medium nutrient regime (MacKillop and Ehman, 2016). Site soil is sandy loam with 35% course fragments, therefore, well drained. The surface organic layer is fairly thin (<5 cm) and due to lack of organic matter content in the upper mineral soil layers, soil water holding capacity is low. The rooting depth of the soil is about 40 cm.

The forest found on site is an even-aged mature mixed species stand consisting of 53% Douglas-fir, 25% western redcedar, 15% western larch, and 5% lodgepole pine and birch with other species (including trembling aspen, balsam poplar [*Populus balsamifera* L. subsp. trichocarpa (T.&G. ex Hook.], and western white pine) comprising the remainder. The dominant species are about 35 m tall and the stand density is approximately 650 stems/ha (Delong et al., 2000).

The climate of ICHmw2 is characterized by warm moist summers (12.5-14.5° C and 150-200 mm) and cool (-8 - 5° C) to mild (-5 - 1° C) moist winters (300 – 450 mm). Snowfall is moderate. Snow generally remains on the ground from December to March/April. Snowpacks are moderately deep (< 150 cm, but multiple weeks of > 150 cm snowpack can occur), with rainfall on the snowpack happening quite frequently. A relative mild climate and presence of continuous snowpack prevents soils from freezing to any significant depth (MacKillop and Ehman, 2016). At the study site, mean annual temperature is 7.1°C, mean annual precipitation is 738 mm, mean summer precipitation is 287 mm, precipitation as snow is 134 mm, with summers typically experiencing drought as indicated by a summer (June-August) climate moisture index (CMI) value of -16.22 mm. Negative CMI values for all months between May and September indicates greater evapotranspiration over precipitation during the growing season, though the annual value remains positive (13.1 mm) on the site (1981-2010 Climate Normals from ClimateNA v6.3; Wang et al., 2016).

3.2.2 Experimental design

Two small openings (< 1 ha) were created in the mixed conifer stand during the winter of 1994/95. The size of each opening was 50 m × 150 m, with the long axis oriented east - west (Figure 3.1)

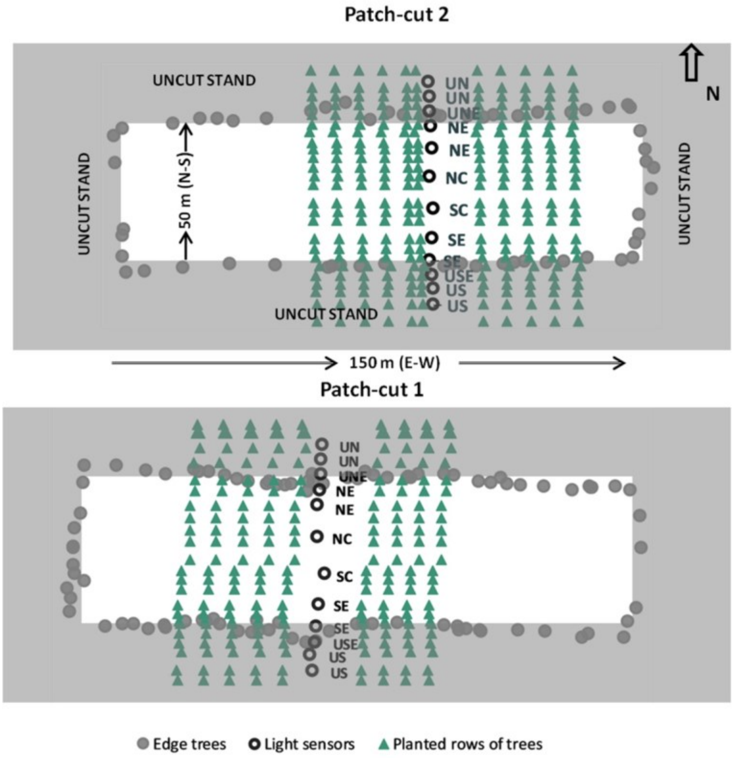

Figure 3.1. An illustration of the experimental layout for each patch cut. Gap environments are: UN - under north canopy; UNE - north edge under canopy; NE - north edge inside opening; NC - north of the centre; SC - south of the centre; SE - south edge inside opening; USE - south edge under canopy; US - under south canopy (adopted from chapter-2).

In the spring of 1995, the openings were planted with seedlings of ten species common in the ICH, viz., Douglas-fir, western larch, Engelmann spruce, western redcedar, western hemlock, white pine, Ponderosa pine, lodgepole pine, subalpine fir, and paper birch in three replicate rows with species being randomly assigned to rows. Table 3.1 summarizes the shade tolerance of these species and describes selected silvical characteristics.

Table 3.1. Comparative tolerance to main stress factors and key silvics of the 9 Interior Cedar Hemlock (ICH) tree species planted in strip-shelterwood experiment.

Tree species[1]	**Tolerance ranking[2]**			**Silvical Characteristics[3]**					
	Shade	**Drought**	**Water-logging**	**Reprod capacity**	**Seed dissemination capacity**	**Potential for natural regen. at low light**	**Potential for natural regen. in the open**	**Suitability for SW system**	**Suitability for selection system**
PL	1.48	4.21	2	H	L	L	H	M	L
EP	1.54	2.02	1.25	H	H	L	H	L	L
PY	1.64	4.32	1.02	H	L	L	H	M	L-H
FD	2.78	2.62	1.79	H	H	L-H	H	L-H	L-H
PW	2.97	2.42	1.02	M	L	H	L	M	L-M
SE	4.53	2.58	1.02	M	M	L	H	M	M
CW	4.73	2.23	1.01	H	M	M	H	M	H
BL	4.83	2.02	0.97	M	L	H	L	M	H
HW	4.96	1.17	0.95	H	H	H	H	M	H

Note: [1]PL= lodgepole pine; EP = paper birch; PY = Ponderosa pine; FD = Douglas-fir; PW = western white pine; SE = Engelmann spruce; CW = western redcedar; BL = subalpine fir; HW = western hemlock.

[2]Numeric quantification of stress tolerance on the scale of 0 (no tolerance) to 5 (high tolerance) after (Niinemets and Valladares, 2006). [3]Silvical characteristics are taken from (Klinka and Chourmouzis, 2005). Silvical characteristics of paper birch are from (Weetman and Vyse, 1990) and (Haeussler et al., 1990). The interpretative classes are, L= low, M = intermediate, and H = high.

Planting rows were oriented north to south across each block. Each row is 90 m long extending 20 m into the uncut stand south and north of each block. Row to row spacing was 2.6 m and within each row seedlings were planted at 3 m spacing. A 20-m wide unplanted buffer was maintained on both the east and west sides of each block (Figure 3.1).

3.2.3 Data collection and preparation

3.2.3.1 Characterization of the light gradient

To capture the north-south light gradient a transect going from north to south across the centre of each opening was established at the end of June, 2007 with photodiode based sensors installed at 5, 15, 22.5, 27.5, 32.5 and 37.5 m north and south of the gap center (see Figure 3.1 for sensor locations). The sensors were GaAsP photodiodes (Gallium arsenide Phosphide-Hamamatsu Corp. 1995) based, housed in a protective casing of aluminum and acrylic, and with a translucent acrylic diffuser to protect the photodiode and to provide for cosine correction. A detailed description of the sensors can be found in Fielder and Comeau (2000). Sensors were installed at 1.5 m height above the ground and were connected to CR 10x dataloggers (Campbell Scientific Inc., Logan, Utah) for continuous measurement of light (Photosynthetically active Photon Flux Density or PPFD). Below canopy light (PPFD in mol m^{-2} $hour^{-1}$) was continuously recorded from July 1st to September 30th, 2007, and later converted to % transmittance based on results described in Hossain and Comeau (2019) and in chapter 2 of this thesis. Although light was measured for 3 subsequent years (2007-2009), some sensors failed in 2008 and 2009 resulting in the loss of data for some gap locations. Furthermore, no significant canopy disturbances occurred during the period of 2007-2009, thus light levels measured in 2007 provide a reasonable representation of the existing north-south light conditions within the gap. Consequently, due to its extensive coverage of the gap locations, I decided to characterize the light gradient based on 2007 data only.

3.2.3.2 Tree measurement

All live trees were measured (stem diameter or D5, i.e., diameter at 5 cm above the ground, dbh, height and leader length) in June of 2007. Trees were remeasured in late September of 2007 2008, and 2009. Trees that were in poor condition (lean or animal damaged or of poor vigor or diseased or insect infested) were excluded from data analysis to reduce the influence of extraneous factors. All live trees and light sensor locations were mapped and distance of each individual tree and light measurement point were calculated from the furthest point under the south canopy. Stand edges were mapped to provide an exact demarcation of the openings' boundaries so that each individual tree can be related to the surrounding north and south edges of the cutblocks.

3.2.3.3 Tree volume estimation

In 2007, a sample of 24 trees (2 trees randomly selected within approximately 5 m of each of the 12 light sensor locations) of each species were selected in each of the two blocks for measurement to provide a total of 48 trees of each species. These sampled trees were used in developing equations for estimating stem volume (SV cm^3) from stem diameter at 5 cm height (D5, cm) and height (Ht, cm). Actual stem volume of these trees was determined by measuring diameter at 5 cm and at 25 cm intervals up the stem (for trees taller than 2 m, measurements were taken at 50 cm intervals up the stem). Independent of 2007 sampling, the 4 largest trees of each species were sampled and measured in late August 2009 to ensure that stem volume equations applied across the full range of tree sizes present on site. For estimating stem volume (cm^3) for each species, an adaptation of Honer’s equation was selected as it best described the data (Honer et al., 1983; Pitt et al., 2004)

$$SV=\frac{D5^{a}}{b+(c/HT)} \qquad 3.1$$

a, b and c are regression parameters and Table 3.2 shows the parameter-estimates and fit statistics by species. Using these species-specific equations, I estimated the total stem volume of each tree since planting from stem diameter (D5 cm) and height in 2009. In this chapter, total volume is considered to represent growth since planting; however, a lack of information on initial tree sizes is a possible source of unaccounted error. Blocks were planted at the same time; therefore, though the stock type varied between species, it is safe to assume that initial size differences were small and will have very minimal effect on the outcome of the analyses.

Table 3.2. Regression equations for estimating stem volume for the 9 tree species commonly found in ICH.

Species	**Parameters**						**N**	**rmse**	**Pseudo R^2**
	a	**a.SE**	**b**	**b.SE**	**c**	**c.SE**			
PL	1.31298	0.12185	**0.00018**	0.00016	0.59657	0.12560	34	1918	0.99
EP	1.57787	0.19878	**0.00034**	0.00074	1.72439	0.46233	28	1071	0.98
PY	1.59171	0.06847	0.00044	0.00020	0.96892	0.12108	31	986	1.00
FD	1.65375	0.18429	**0.00078**	0.00101	1.34523	0.19355	49	986	0.99
PW	1.23624	0.11280	-0.00028	0.00005	0.90676	0.18760	37	302	1.00
SE	1.87280	0.05660	0.00327	0.00081	1.66031	0.13767	44	286	1.00
CW	0.84679	0.21457	-0.00024	0.00007	0.49315	0.16000	37	775	0.98
BL	1.32727	0.29233	**0.00130**	0.00114	0.18494	0.09916	32	1757	0.90
HW	1.17487	0.14961	-0.00083	0.00017	1.09372	0.29852	45	686	0.99

Species are: PL= lodgepole pine; EP = paper birch; PY = Ponderosa pine; FD = Douglas-fir; PW = western white pine; SE = Engelmann spruce; CW = western redcedar; BL = subalpine fir; HW = western hemlock. Rmse = Root mean square error and N = sample size. Here, bold indicates statistical non-significance.

3.2.4 Data analysis

To estimate light at each seedling, a non-linear peak function was fitted to describe the relationship between % PPFD and distances of the sensors from the south end of the transect (Figure 3.2). Growth of each tree measured as total volume (cm^3) was then regressed against light calculated from the non-linear peak function to examine light-growth relationships for each of the 9 selected species.

A Gaussian peak function provided the best fit of the data (see Figure 3.2 for the fit).

$$ae^{-0.5\left(\frac{x-b}{c}\right)^2} \qquad 3.2$$

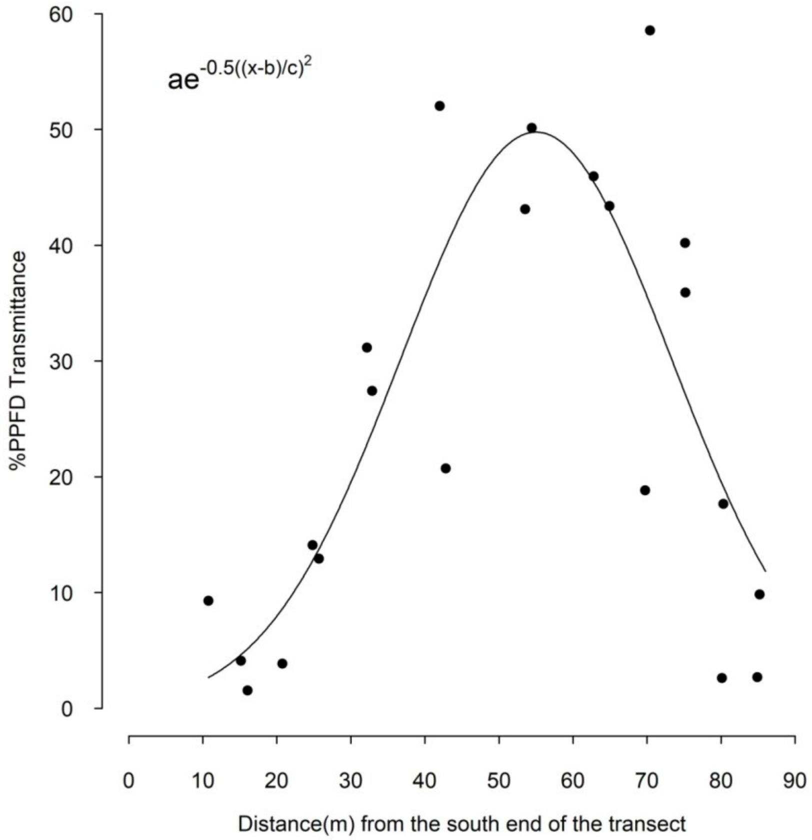

Figure 3.2. Non-linear curve describing light transmittance as a function of distance from the furthest point under the south canopy. Here, N = 22, rmse (root mean square error) = 10.89, Pseudo $R^2 = 0.69$. All parameters (a = 49.78, b = 55.02, c = 18.29) are highly significant ($P < 0.001$).

To address my first question (between species differences in relationships between stem volume and light), it is necessary to determine if slopes of the light-growth relationships were statistically different between species. To do this, an interaction term was included in the regression model (light-species). The model took the following form:

$$\text{Log (volume)} \sim \text{intercept} + \log(\text{light}) + \text{species} + \log(\text{light})*\text{species} + \text{error} \qquad 3.3$$

To address question 2 (Can species' light partitioning be further elucidated through their response to changing positions within gap?) and question 3 (How do the northern and southern edges of the strip-shelterwood affect species' growth performance and is this associated with the differentiation in shade tolerance (see Table 3.1 for the ranking of shade tolerance), the north-south trend in growth was modeled for each species, using a quadratic function of the relative distance from the southern edge including species-distance interaction with both linear and quadratic terms.

The model form:

$$\text{Log (volume)} \sim \text{intercept} + \text{species} + \text{distance} + \text{species}*\text{distance} + \text{species}*\text{distance}^2 + \text{error} \qquad 3.4$$

This allowed me to examine interspecific variation in edge to edge growth response between 9 species.

Quadratic relationships between growth and distance were used to explore the influence of stand edges on volume growth of each species. Post-hoc comparisons of the marginal means at several gap-positions with Tukey adjusted P values were used to differentiate between species that showed significant growth differences across gap locations (Lenth et al., 2019). Edge influence (south versus north) was quantified for each species based on growth reductions toward both the north and south edges (5 m into the opening from the physical boundary of both edges), as compared to that for the location of their respective peak (optimum niche). Log transformation of total volume was applied to meet the assumptions of normality and equality of variance and for linearization of the relationships. All analyses were completed using R statistical software (R Core Team, 2019) .

3.3 Results

3.3.1 Species-specific light-growth response

The growth rates of all tree species increased without any horizontal asymptote as light level increased (Figure 3.3).

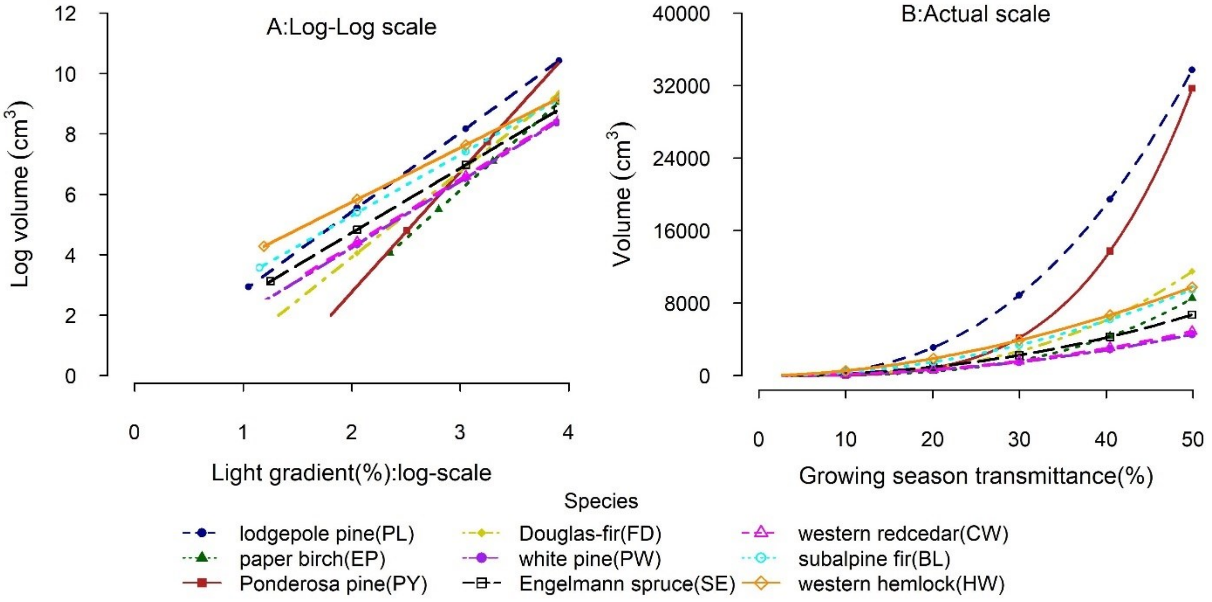

Figure 3.3. Growth responses of the 9 species to the light gradient. See Table 3.3 and Table 3.4 for parameter estimates, Equation 3.3 is back transformed to original scale (Figure 3.3 B).

Since the primarily focus of this study was to detect if there are interspecific differences in species' light-growth responses, the significance of the interaction term in the light growth model (see Equation 3.3) was of interest. In log-log scale, the model reveals a highly significant interaction ($P < 0.001$; Figure 3.3 A), which implies that among all the species, at least one had a different growth response (see Table 3.3).

Table 3.3. Analysis of variance table (Type III) of the linear regression model (See Equation 3.3) for describing the effect of light on growth responses for the 9 species (log-log scale). Parameter estimates are provided in Table 3.4.

Parameters	**Sums of Square**	**DF**	**F value**	**P value**
Intercept	5.11	1	2.72	0.10
Log (Light)	130.09	1	69.11	< 0.001
Species	91.80	8	6.10	< 0.001
log (Light) × species	84.85	8	5.63	< 0.001
Residuals	1221.72	649		

Further examination of the log-log model also indicates several species, such as paper birch, Douglas-fir, and Ponderosa pine which differed in their responses to the light gradient as compared to the reference species, subalpine fir (see Table 3.4). Moreover, visually a cross-over pattern in growth response among species was also evident, an indication that rank reversal in growth performance occurred along the light gradient, for example, see light response curves of lodgepole pine, Ponderosa pine, Douglas-fir and western hemlock. At the same time, several species such as, white pine, Engelmann spruce, western redcedar and subalpine-fir responded with parallel slopes with the changing light conditions within the strip (Figure 3.3 A).

Following back-transformation of the data into their original units, two highly shade intolerant species lodgepole pine and Ponderosa pine diverge from the other species into a distinct group, with these two species responding with a higher magnitude of growth than the others, above 15-25% of transmittance. The growth rates of these two species are consistent with their current designation as highly shade intolerant. In contrast, paper birch (another shade intolerant) and Douglas-fir (moderately shade tolerant) did not respond in a manner consistent with their shade tolerance; these two species mostly clustered with the other more shade tolerating species (Figure 3.3 B).

Variability in species' growth response also generally increased with the increase in transmittance (see Figure 3.4). Below 20% light level, in general, light adequately described the variation in growth for all species except lodgepole pine. For lodgepole pine, at light levels above 10%, the scatter around the regression line increases. In the log-log model, light explains 46-68% of the variation in volume in this study (Table 3.5), while at a higher light level, other factors such as soil moisture, nutrient availability or temperature are expected to affect this relationship (Carter and Klinka, 1992; Klinka et al., 1992). In a field study it is difficult to separate the effects of several confounding factors. In such instances, gap-position itself can be used as an effective predictor variable to model the growth variations among species inside a gap since each gap position will represent a complex dynamic gap-environment, where multiple resource factors are constantly interacting (see Gray and Spies, 1996; Coates, 2000; York et al., 2003; Zdors and Donis, 2017). Furthermore, using gap-position as a predictor variable helps in quantifying edge influence on regenerating trees (Table 3.5 and Figure 3.4) in ways that forest managers can easily relate to and subsequently, use in selecting suitable species for strip shelterwood.

Table 3.4. Details of the light-growth model (Equation 3.3) describing log-volume growth as a function of log-light and species (9); species represent varying degree of shade tolerance.

Coefficients	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
Intercept	1.25	0.76	1.65	0.100
log (Light)	2.02	0.24	8.31	< 0.001
PL	-1.06	1.21	-0.88	0.380
EP	-4.71	1.47	-3.21	0.001
PY	-6.44	1.37	-4.7	< 0.001
FD	-3.03	1.02	-2.97	0.003
PW	-1.4	1.03	-1.36	0.174
SE	-0.80	0.99	-0.81	0.420
CW	-1.32	0.97	-1.35	0.177
HW	0.88	1	0.89	0.375
log (Light) × PL	0.60	0.37	1.60	0.109
log (Light) × EP	1.18	0.43	2.72	0.007
log (Light) × PY	1.95	0.43	4.59	< 0.001
log (Light) × FD	0.82	0.32	2.59	0.010
log (Light) × PW	0.17	0.34	0.50	0.629
log (Light) × SE	0.12	0.32	0.36	0.718
log (Light) × CW	0.17	0.31	0.54	0.590
log (Light) × HW	-0.22	0.32	-0.69	0.492

Here, N = 667; rmse (root mean square error) = 1.37; Adj.R^2 = 0.63; $P < 0.001$. Species are: PL= lodgepole pine; EP = paper birch; PY = Ponderosa pine; FD = Douglas-fir; PW = western white pine; SE = Engelmann spruce; CW = western redcedar; BL = subalpine fir; HW = western hemlock.

Table 3.5. Regression equations and fit statistics for volume growth of 9 species along the gradient of light within a strip-shelterwood (see Equation 3.3 and Table 3.3).

Species	**Equation**	**rmse**	**Adj-R^2**	**N**	**P**
PL	Log (Volume) = 0.18 + 2.62 × log (Light)	1.55	0.51	66	< 0.001
EP	Log (Volume) = **-3.47** + 3.20 × log (Light)	1.22	0.58	73	< 0.001
PY	Log (Volume) = **-5.19** + 3.98 × log (Light)	1.61	0.68	45	< 0.001
FD	Log (Volume) = **-1.78** + 2.85 × log (Light)	1.37	0.65	104	< 0.001
PW	Log (Volume) = -0.15 + 2.19 × log (Light)	1.47	0.58	53	< 0.001
SE	Log (Volume) = 0.44 + 2.14 × log (Light)	1.27	0.61	78	< 0.001
CW	Log (Volume) = -0.07 + 2.19 × log (Light)	1.34	0.59	100	< 0.001
BL	Log (Volume) = 1.25 + 2.02 × log (Light)	1.14	0.60	66	< 0.001
HW	Log (Volume) = **2.13** + 1.80 × log (Light)	1.44	0.46	82	< 0.001
Note: Light is growing season transmittance (%). Bold indicates a significant intercept. Species are: PL= lodgepole pine; EP = paper birch; PY = Ponderosa pine; FD = Douglas-fir; PW = western white pine; SE = Engelmann spruce; CW = western redcedar; BL = subalpine fir; HW = western hemlock. Rmse = Root mean square error and N = sample size.					

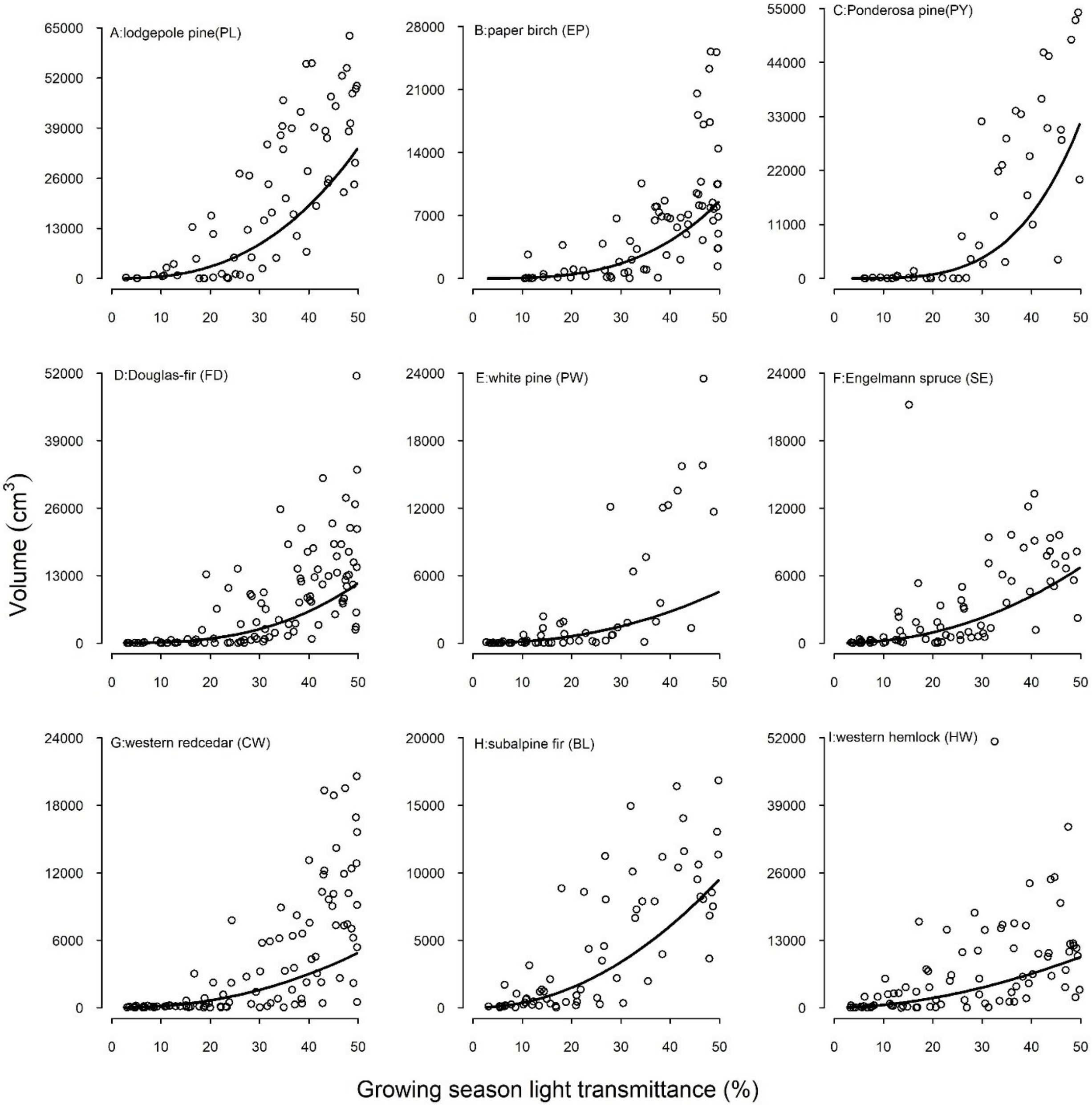

Figure 3.4. Scatter-graph of volume growth in response to growing season light transmittance (%) for 9 species. See Table 3.5 for parameter estimates and P values. Graphs are shown in original scale after back transformation of Equation 3.3.

3.3.2 Growth response in relation to gap-positions

All species exhibited a unimodal pattern of growth response along the north-south axis of the gap with a quadratic equation fitted to the data providing a satisfactory description of this pattern (See Figure 3.5). The influence of the gap position was statistically significant for all species ($P \sim 0.005$ to < 0.001), though the variability explained differed widely (R^2 ranged from 36-82%) between species (Table 3.6). For the three shade tolerant species, white pine, Engelmann spruce and western hemlock, gap-position explained only 36-45% of the variability in growth, while for others it ranged from 58-82%. The influence of gap position (distance from the south edge) differed between species in both linear and quadratic terms (the interaction term of the distance-growth model is highly significant, $P < 0.001$; see Table 3.7), suggesting differences in the location of the peak along with differences in their magnitude (see Table 3.6).

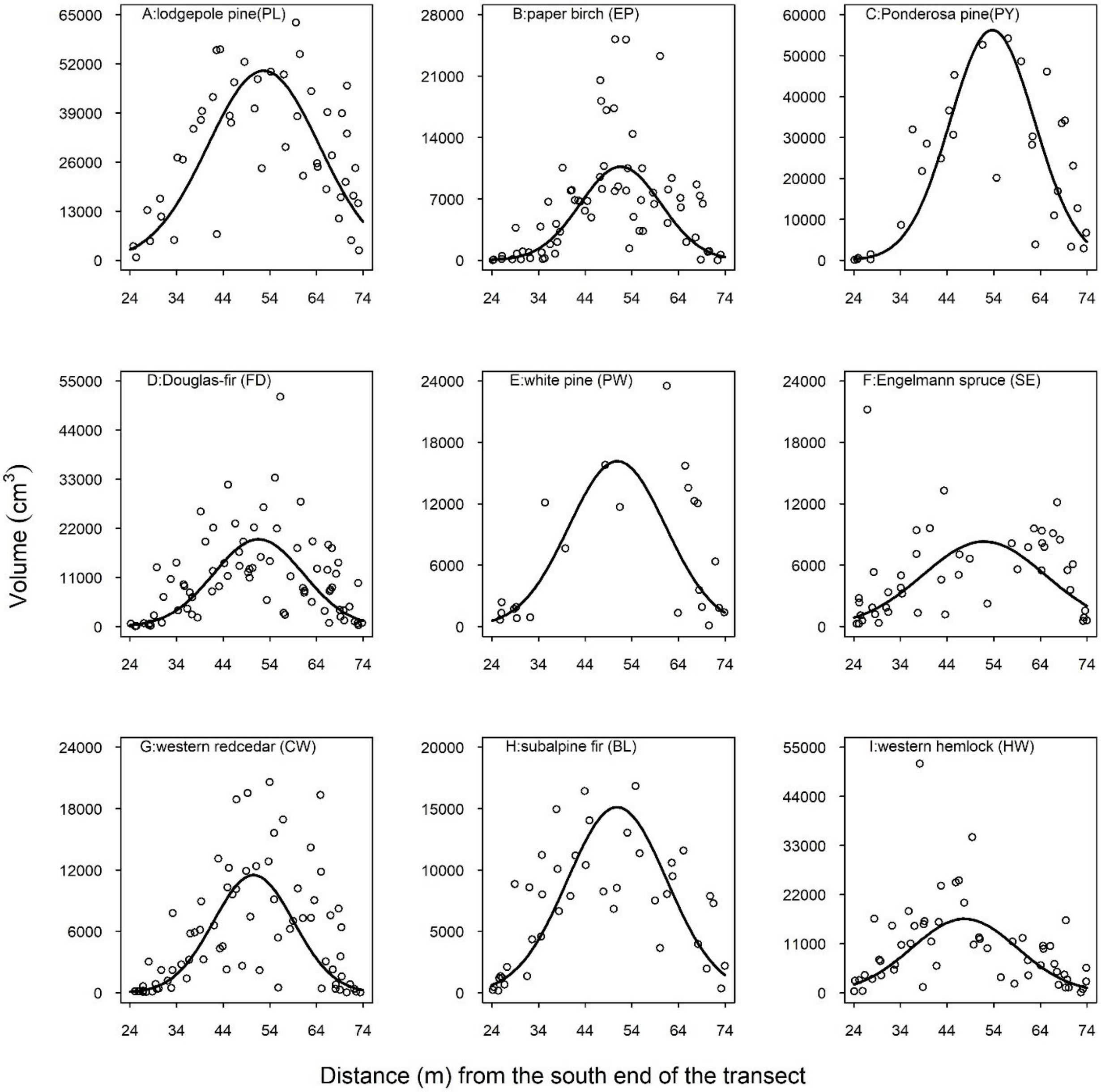

Figure 3.5. Scatter-graphs describing the growth responses of 9 species to changing positions along the north-south axis within the strip-cut. South and north edges are at 24 m and 74 m, respectively. Table 3.6 provides parameter estimates and statistical information for the polynomial equations shown in Figure 3.5. Graphs are shown in original scale after back transformation of Equation 3.4.

Table 3.6. Coefficients and statistics for the quadratic relationship between growth and distance from the south edge of the opening for 9 species.

Species	**Equation**	**rmse**	**Adj-R^2**	**N**	**P**	**Maxima**
PL	$\text{Log (Vol)} = 1.11 + 0.37 \times D - 0.004 \times D^2$	0.62	0.58	47	< 0.001	53
EP	$\text{Log (Vol)} = \mathbf{-8.59} + 0.69 \times D - 0.007 \times D^2$	1.00	0.65	68	< 0.001	52
PY	$\text{Log (Vol)} = \mathbf{-6.71} + 0.66 \times D - 0.006 \times D^2$	0.78	0.82	30	< 0.001	54
FD	$\text{Log (Vol)} = \mathbf{-4.52} + 0.56 \times D - 0.005 \times D^2$	0.87	0.60	77	< 0.001	52
PW	$\text{Log (Vol)} = -2.36 + 0.47 \times D - 0.005 \times D^2$	1.08	0.41	23	0.005	51
SE	$\text{Log (Vol)} = 1.22 + 0.30 \times D - 0.003 \times D^2$	0.90	0.36	46	< 0.001	52
CW	$\text{Log (Vol)} \mathbf{= -7.98} + 0.69 \times D - 0.007 \times D^2$	1.03	0.62	72	< 0.001	50
BL	$\text{Log (Vol)} = -1.73 + 0.45 \times D - 0.004 \times D^2$	0.71	0.68	41	< 0.001	51
HW	$\text{Log (Vol)} = 0.86 + 0.37 \times D - 0.004 \times D^2$	0.91	0.45	55	< 0.001	48

Here, Vol represents volume in cm^3 and D represents gap-position (distance (m) from the south endpoint of transect). Bold indicates a significant intercept. Species are: PL= lodgepole pine; EP = paper birch; PY = Ponderosa pine; FD = Douglas-fir; PW = western white pine; SE = Engelmann spruce; CW = western redcedar; BL = subalpine fir; HW = western hemlock.

Table 3.7. ANOVA table for Equation 3.4 for species growth (log-volume) response to changing gap environments. Parameter estimates are shown in Table 3.8.

Parameters	**SS**	**DF**	**F value**	**P value**
Intercept	1.17	1	1.45	0.23
Species	47.85	8	7.45	< 0.001
gap-position	37.74	1	47.02	< 0.001
gap-position^2	34.23	1	42.64	<0.001
Species × gap-position	35.45	8	5.52	< 0.001
Species × gap-position^2	31.76	8	4.95	< 0.001
Residuals	346.79	432		

Table 3.8. Regression parameters for the distance-growth (log-volume) model (Equation 3.4), describing the interaction between species and the changes in growth as a function of gap-position.

Coefficients	**Estimate**	**Std. Error**	**t value**	**Pr (>|t|)**
Intercept	-1.734	1.438	-1.206	0.23
PL	2.848	2.211	1.288	0.20
EP	-6.855	1.985	-3.454	<0.001
PY	-4.977	2.269	-2.193	0.03
FD	-2.786	1.928	-1.445	0.15
PW	-0.622	2.745	-0.227	0.82
SE	2.955	2.028	1.457	0.15
CW	-6.250	1.947	-3.209	0.001
HW	2.590	1.993	1.299	0.19
gap-position	0.447	0.065	6.857	<0.001
gap-position^2	-0.004	0.001	-6.53	<0.001
PL × gap-position	-0.078	0.096	-0.812	0.42
EP × gap-position	0.246	0.088	2.799	0.005
PY × gap-position	0.211	0.101	2.086	0.04
FD × gap-position	0.112	0.085	1.316	0.19
PW × gap-position	0.027	0.126	0.212	0.83
SE × gap-position	-0.146	0.092	-1.584	0.11
CW × gap-position	0.240	0.087	2.771	0.006
HW × gap-position	-0.075	0.089	-0.848	0.40
PL × gap-position^2	0.001	0.001	0.924	0.36
EP × gap-position^2	-0.002	0.001	-2.574	0.01
PY × gap-position^2	-0.002	0.001	-1.684	0.09
FD × gap-position^2	-0.001	0.001	-1.184	0.24
PW × Gap-position^2	0.000	0.001	-0.202	0.84
SE × gap-position^2	0.001	0.001	1.584	0.11
CW × gap-position^2	-0.002	0.001	-2.719	0.007
HW × gap-position^2	0.001	0.001	0.553	0.58

Here, N = 459; rmse (root mean square error) = 0.90; Adj. R^2 = 0.66; $P < 0.001$. Species are: PL= lodgepole pine; EP = paper birch; PY = Ponderosa pine; FD = Douglas-fir; PW = western white pine; SE = Engelmann spruce; CW = western redcedar; BL = subalpine fir; HW = western hemlock.

Further examination of the regression coefficients also confirms that at least three of the species, lodgepole pine, Ponderosa pine, and Douglas-fir differed from the reference species, subalpine fir in their growth responses (in terms of peak and the magnitude, see Table 3.8). Visual examination of species' distance-growth response reveals more information, location of the maximum growth did not necessarily occur at the physical centre of the gap (~ 49 m). In fact, considering the maxima of the curves (Table 3.6), several patterns can be generalized. First, two highly shade intolerant species peak around 54 m, close to the location of the maximum light level (or ecological centre of the gap, light level peaked at 55 m). Then highly shade tolerant species, western hemlock's, maximum growth occurred at 48 m. For the rest of the species, peak of their growth or optimum niche occurred between 50-52 m. Furthermore, considering the overall shape of the curves, a few distinct clusters can be separated, visually. First, two highly shade intolerant species, lodgepole pine and Ponderosa pine can be distinguished from the other species by their superior growth response (first cluster). While for rest, species are closely packing in their growth responses, a group of species can be identified within them as a second cluster (Figure 3.6). For example, Douglas-fir, white pine and subalpine fir and western hemlock can be separated as a 2nd cluster from western redcedar, paper birch and Engelmann spruce, forming the third cluster. In the second cluster, western hemlock and Douglas-fir growth responses can be separated as distinct in terms of their peaks and spread of the curve (Figure 3.6 B).

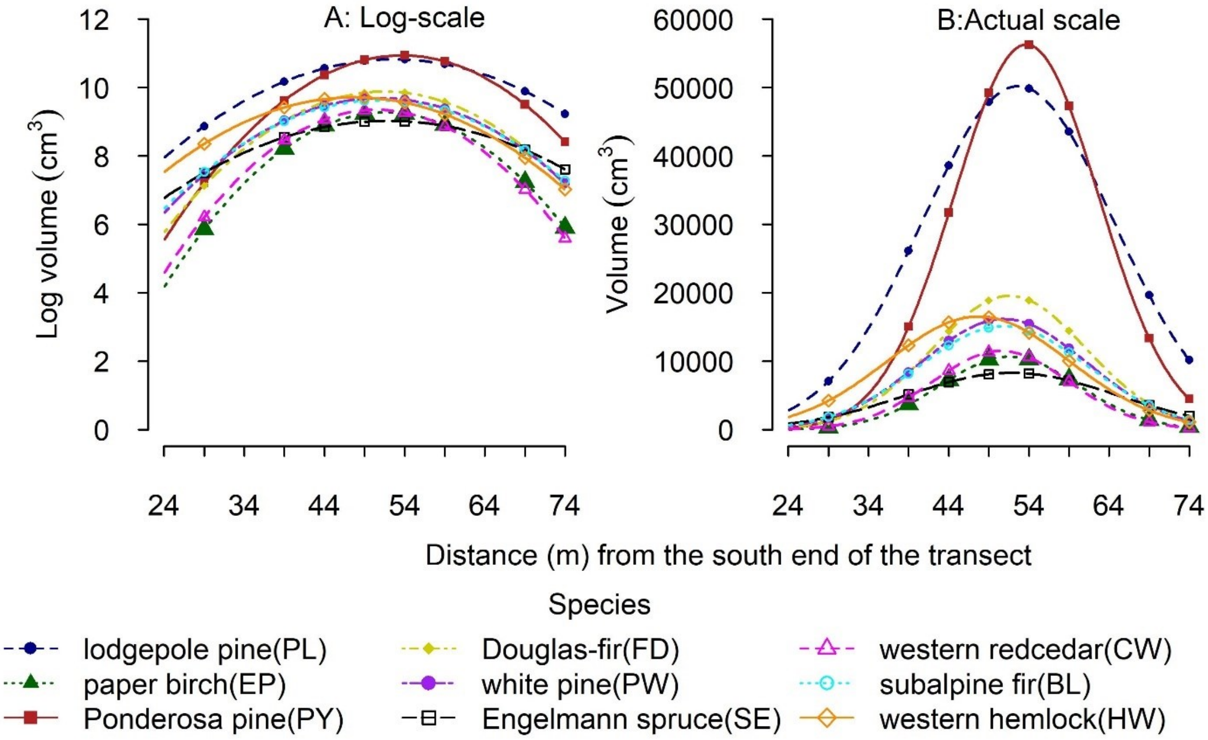

Figure 3.6. Fitted growth-gap positions regression curves using quadratic term in the model. South edge is located at 24 m, centre at 49 m and north edge at 74 m. All the fits are statistically significant (P < 0.001). Equation 3.4 is back transformed to original scale (Figure 3.6 B).

3.3.3 Edge influence

All species suffered growth reduction at edge proximities but at different magnitudes. For instance, a strong south edge influence was observed for two highly shade intolerant species, paper birch and Ponderosa pine, log-volume reductions were 31% and 34%, respectively. In contrary, south edge influence on lodgepole pine, the least in shade tolerant ranking, was unexpectedly lower in magnitude (17% log-volume reduction-Table 3.9).

Table 3.9. Edge influence on log-growth of each species within the 50 m wide shelterwood openings. Edge influence is quantified as percent growth reduction from centre to edge proximities. North and south of the peak locations were calculated as 50% of the distance between the edges and location of each species' respective peak.

Species	**South Edge (%)**	**South of the peak (%)**	**North of the peak (%)**	**North Edge (%)**
lodgepole pine (PL)	17	4	2	9
paper birch (EP)	34	8	6	22
Ponderosa pine (PY)	31	8	3	13
Douglas-fir (FD)	25	6	4	17
white pine (PW)	21	5	4	16
Engelmann spruce (SE)	15	4	2	9
western redcedar (CW)	31	8	6	25
subalpine fir (BL)	20	5	4	15
western hemlock (HW)	13	3	5	18
Light level (%)	18	36	48	37

Shade tolerant species on the other hand are expected to be less impacted by south edge proximity due to their adaptation to shade. Only two shade tolerant species Engelmann spruce and western hemlock, showed such response; these two species had only 13 - 15% reduction in their growth (log-volume) at the south edge, again few expectations were also observed. Western redcedar, approximately similar to Engelmann spruce in shade tolerance was negatively impacted by south edge proximity (31% volume loss in log-scale). Species like subalpine fir (20% growth reduction), which has similar shade tolerance to western hemlock, had approximately similar growth reduction to two moderately shade tolerant species, like Douglas-fir (25%) and white pine (21%).

In comparison to south edge, north edge exerted a very week influence on shade intolerant species, such as lodgepole and Ponderosa pine (9 and 13% growth reduction respectively), with paper birch being an exception. Despite being highly shade intolerant, this species, compared to others, suffered a higher growth reduction (22%) at the north edge. For shade tolerant species, north edge influence varied from low (Engelmann spruce -9% reduction) to high (western redcedar-25% reduction). Besides Engelmann spruce and western redcedar, the other two highly shade tolerant species, subalpine fir and western hemlock, were subject to moderate influence at the north edge (log-growth reduction, 15-18%). Another interesting finding in this study was that western hemlock suffered greater growth reduction at the north (18%) compared to south edge gap environment (13%). As usual, growth reduction in two moderately shade tolerant species, Douglas-fir and white pine, at the northern edge was in between the range observed for all other species (16-17% growth reduction, see Table 3.9).

A Tukey adjusted post-hoc means comparison tests on the growth data (log-volume) collected at the locations south and north of the peak (50% of the distance between the edge and the location of the peak) shows that the difference in volume growth between two locations are not statistically significant for all species, regardless of their differences in shade tolerance, although Ponderosa pine came close to being significant (P ~ 0.08, see Figure 3.7).

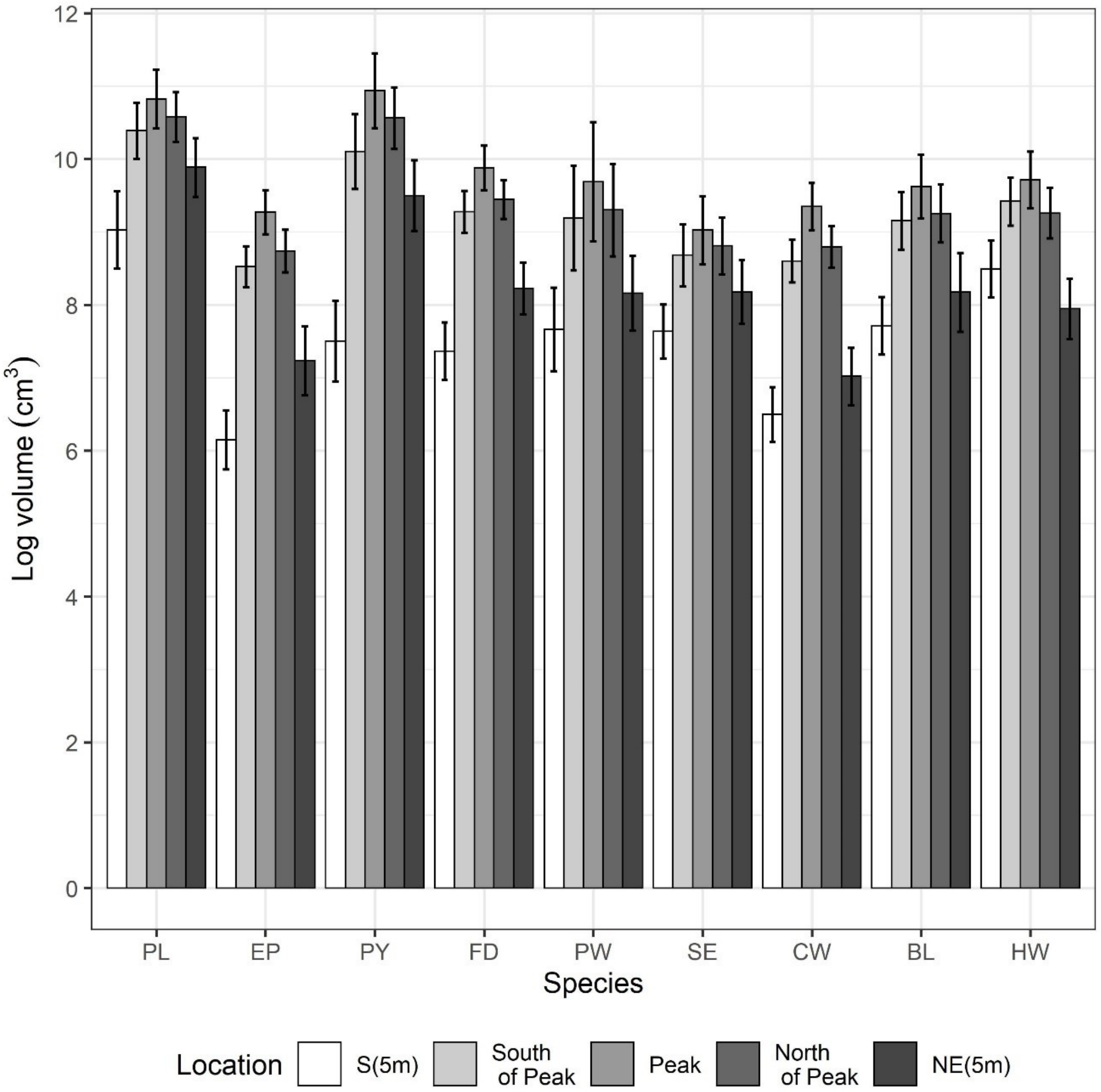

Figure 3.7. Trends in growth of each species across five gap environments. Species are: PL= lodgepole pine; EP = paper birch; PY = Ponderosa pine; FD = Douglas-fir; PW = western white pine; SE = Engelmann spruce; CW = western redcedar; BL = subalpine fir; HW = western hemlock. Boxes indicate the least-squares mean. Error bars indicate the 95% confidence interval around the least-squares mean.

Further examination also reveals that for two shade intolerant species, paper birch and Ponderosa pine and for moderately shade tolerant Douglas-fir, the growth response (log-volume) differed between the two edges (north versus south, $P < 0.05$). Though highly shade intolerant lodgepole pine was not significant, its P value was close to 0.05, $P \sim 0.09$). On the other hand, no significant differences ($P > 0.05$) were found for relatively more shade tolerating species (White pine, Engelmann spruce, western redcedar, subalpine fir and western hemlock).

3.4 Discussion

3.4.1 Regeneration of a mixture of shade tolerant and intolerant species within strip-cut openings

The key question being addressed in this study is whether or not strip-shelterwood harvesting can facilitate mixed species regeneration in the Interior Cedar Hemlock zone (ICH) forests. The theory of a trade-off in growth rate along the light gradient between shade tolerant and intolerant species has been frequently used to explain coexistence of a large number of species in various forest ecosystems (Grubb, 1977; Lin et al., 2002; Gravel et al., 2010; Valladares et al., 2016). According to this theory, shade tolerant species may have higher survival rates than shade intolerant species in low light environments (i.e. closed canopy conditions), but at higher light levels (i.e., open canopy condition) shade intolerant species can grow more rapidly than shade tolerant species. Due to this contrasting strategy between shade tolerant and intolerant species, species segregate into distinct regeneration niches along the light gradient within a gap.

Inside the openings created by strip shelterwood treatments, there is clear evidence of a strong north to south light gradient ($P < 0.001$; See Figure 3.2); therefore, the possibility for coexistence of species of various levels of shade tolerance (shade tolerant, moderately tolerant and intolerant) will largely depend on whether these species grow at different rates, and segregate into discrete growth hierarchies along the light gradient. The expectation was that segregation would occur in the order of species' shade tolerance ranking, such as shade intolerant > moderately shade tolerant > shade tolerant. Partial support in favor of this hypothesis can be found in this study.

First, evidence from this study shows changes in species' rank in growth along the light gradient. Moreover, two highly shade intolerant species, Ponderosa pine and lodgepole pine, showed a clear separation in growth hierarchy from other species, including one shade intolerant (paper birch), two moderately tolerant species (Douglas-fir and white pine) and four shade tolerant species (Engelmann spruce, subalpine fir, western redcedar and western hemlock). These species appear to cluster together, although Douglas-fir deviated slightly at light levels above 30% (Figure 3.6). It is not surprising that when a large number of species are growing in intimate mixtures within a narrow range of light (2.5-49%) that they will overlap in their growth responses. Previous studies reported similar results (Pacala et al., 1994; Wright et al., 1998; Van Couwenberghe et al., 2013). However, given the fact that there is evidence of a few species achieving distinct growth hierarchy, the question remains if this can be taken as sufficient evidence in support of mixed species regeneration within strip-shelterwood opening. Results from this study are consistent with observations from other studies that indicate that if opportunities are provided for shade intolerant species to grow in some portions of the opening, it is very likely that tolerant species will grow in mixture with the intolerants (Holgén and Hånell, 2000; York et al., 2003; Gravel et al., 2010; De Montigny and Smith, 2017; Kern et al., 2017; Shabaga et al., 2019).

In this experiment, growth measurements were taken for 3 consecutive years, 13 years after planting. After 13 years, the species show limited niche separation based on growth rates (performance optima are not distinct along the light gradient). All species are performing best at the higher light levels near the center/north of the centre of the opening indicating niche sharing between species. Latham (1992) proposed the competitive hierarchy theory to explain species' coexistence in circumstances where species are exhibiting niche sharing. According to this theory, many co-occurring species having inclusive niches can still continue to coexist, through changing their performance (i.e., growth) ranks (See Latham, 1992; Lin et al., 2002). The higher growth rates exhibited by the two highly shade intolerant species (Ponderosa pine and lodgepole pine) in this experiment is consistent with this theory, since these two species will reach the canopy sooner than others (Claveau et al., 2002) and thus it is increasingly likely that these two species can grow in intimate mixtures with other more shade tolerating species. The likelihood of shade intolerant species growing in intimate mixtures with shade tolerant species increases with canopy disturbance and with faster growth of shade intolerant species at high light while the likelihood decreases when the growth rate of shade tolerant species surpasses the intolerant species. Furthermore, when growing in mixtures, a faster growing shade intolerant species cannot be competitively excluded by a slower growing shade tolerant species until the height of the shade tolerant species surpasses that of the shade intolerant (Gravel et al. 2010).

However, the unexpected light-growth response of highly shade intolerant paper birch is concerning. The silvics of this species also suggest that paper birch usually doesn't do well in shelterwood or in mixtures unless it dominates over the shade tolerant species (Burns and Honkala, 1990). In this study, at light levels exceeding 40%, this species did surpass the growth of two shade tolerant species (western redcedar or white pine) and is similar to growth responses of highly shade tolerant species such as western hemlock or subalpine fir. Thus, to maintain paper birch in mixtures with other species in this 50 m wide strip-cut, it is of paramount importance that this species is to be planted in its appropriate growth niche, i.e., mostly in areas of high light.

The range of light conditions (2.5-49%) that existed within the strip-shelterwood can support moderately shade tolerant species, such as Douglas-fir and white pine. At least 20% of light can ensure survival of Douglas-fir, and at least 40% of light can support adequate growth of Douglas-fir under partial harvesting systems (Mailly and Kimmins, 1997; Drever and Lertzman, 2001). Moreover, in this study Douglas-fir was observed to surpass the growth of the other more shade tolerant species (western hemlock, western redcedar, subalpine fir and Engelmann spruce) at light levels above 40%. In a group selection study De Montigny and Smith (2017) noted that the minimum gap-size requirement for adequate height growth of Douglas-fir was between 0.24 to 0.33 ha and gap-diameter to dominant tree height ratio of 1.5-2.2. Thus, given that paper birch is planted in the high light area within the gap, and based on the existing research on Douglas-fir, it is likely that both paper birch and Douglas-fir can establish in the mixtures to regenerate within strip-shelterwoods in the Interior Cedar Hemlock zone of B.C.

3.4.2 Within-gap partitioning and edge effect

In the first part of this study, I mainly focused on investigating patterns of growth rates along the light gradient. Results show that species such as lodgepole pine, ponderosa pine, Douglas-fir and western hemlock, did change their performance ranks along the light gradient, thus exhibiting a cross-over pattern in light-growth responses (Figure 3.3). However, evidence of species responding with parallel slopes was also present. When growth responses were examined for changes in gap-position, evidence of species' clustering into distinct groups also emerges (Figure 3.6 B). In appearance, the dominant clusters and few single species' response within the a certain cluster could provide evidence of niche partitioning to some degree, hereby supporting the assumption of the hypothesis that species will segregate into distinct niches based on the differences in competitive ability for light, or in shade tolerance. However, it is true that species similar in their competitive ability or having smaller differences in shade tolerance may provide week evidence of niche partitioning in an ecosystem. This is particularly true for species-rich ecosystems like ICH where many species are supported together (Wright et al., 2000; DeLong et al., 2005; Lilles et al., 2014; Valladares et al., 2016). Weak evidence of niche partitioning might mean competitive exclusion of species, and lack of coexistence in the community. However, an alternative theory has been suggested (neutral theory by Hubbell, 2001), where all species are assumed equivalent in their competitive ability; according to this theory, species' coexistence within a local stand can be explained by the demography of the neighboring community. A species lost due to random death at a local scale, will be replaced by the migration of propagule from the surrounding community, limited by dispersal or recruitment (Molino and Sabatier, 2001; Gravel et al., 2006; Nishimura et al., 2010; Valladares et al., 2015).

I argue that data in this study provide more support toward coexistence of species within strip-cut gaps based on niche-theory rather than neutral theory. However, both mechanisms may work simultaneously to promote species coexistence. In particular, species that are ecologically similar (i.e., similar shade tolerance), may persist through neutral processes described above (see Gravel et al., 2006). However, niche separation is necessary to maintain mixtures of shade tolerant and intolerant species; because, through this process, shade intolerant species may avoid competitive exclusion by more shade tolerating species.

Certain gap-locations favor certain species, while imposing severe limitations on others, and this species-gap-position interaction is believed to be related to species' shade tolerance (Bradshaw, 1992; Wright et al., 2000). Shade tolerant species are usually less sensitive to variations between microsites than intolerant species (Messier and Puttonen, 1995; Annighöfer, 2018; Lu et al., 2018). As a result of this difference, different positions within the gap support different species (see Bradshaw, 1992; Wright et al., 2000).

Results from this study are consistent with the assumption that variability in growth rates declines with increasing shade tolerance. Shade tolerant Engelmann spruce showed the least sensitive response to changing gap positions whereas the two highly shade intolerant species, Ponderosa pine and lodgepole pine, showed the most sensitive response (Figure 3.6). Moreover, in relation to the influence of gap environment on species' growth performance, this study contradicted Coates (2000) but was in partial agreement with Coates and Burton (1999) and others (Kitajima and Bolker, 2003; Valladares and Niinemets, 2008). With the exception of lodgepole pine, a highly shade intolerant species, Coates (2000) found all of his species performing best at the centre location, but not showing significant differences between the sunny-north and shaded south-edge. He recorded poor lodgepole pine growth at the south edge. In my study, however, lodgepole pine's growth did not differ between the two edges (north vs. south; P ~0.09), though other shade intolerant species in this study such as paper birch, and Ponderosa pine showed difference between north and south edges (see Figure 3.7). A moderately shade tolerant species, Douglas-fir also showed difference in growth between the two edges.

Most gap studies emphasize quantifying edge influences, particularly in the case of shade intolerant species, since these species might not benefit from gap creation due to pronounced competition from trees in the surrounding edges (York et al., 2003; Zdors and Donis, 2017). I quantified edge influence as percent growth reduction between the centre and the edges for each species. As expected, the two highly shade intolerant species (Ponderosa pine and lodgepole pine) show a strong south edge influence, while north edge influences on these two species were weak. North edge influence was also weaker than south edge influence for the moderately tolerant species (Douglas-fir and white pine). The two pine species are well known for their deep root systems, and higher drought tolerance, which enables them to maintain higher photosynthesis rates than other species (see also Wright et al, 1998; Coates and Burton, 1999; Sherich et al., 2007). Although Douglas-fir is less tolerant to drought than Ponderosa pine (Niinemets and Valladares, 2006), both species belong to drier forest ecosystems. Western white pine is known as a moderately drought tolerant species (Niinemets and Valladares, 2006). Consequently, Douglas-fir, Ponderosa pine and western white pine are able to grow well at the north edge in contrast to other species that are less drought tolerant but more shade tolerant (Sherich et al., 2007). The study site is well drained, with negative CMI value (-16-22) for the months of May to September; an indication that summer drought conditions are prevalent on the site (ClimateNA v6.3, Wang et al., 2016). In addition, the north edge is subject to intense radiation received directly from sun; consequently, creating a warmer and drier microhabitat within the gap. The general pattern of growth reductions at edge proximities observed in this study, (i.e., comparatively less shade tolerant species are suffering less growth reduction at the dry north edge than shade tolerant species) indicate support for a trade-off between shade and drought tolerance (Sack, 2004; Niinemets and Valladares, 2006). However, such a trade-off might also pose a limitation on niche differentiation between coexisting species, as suggested by Sack (2004). This might explain the limited niche differentiation observed in this study. A rigorous examination of species' tolerance to multiple abiotic stresses, is required as a basis for fully understanding the underlying mechanisms that influence species' coexistence in small shelterwood gaps (Laanisto and Niinemets, 2015).

Paper birch and western redcedar were strongly influenced by both north and south edges. Paper birch as an early successional species failed to respond like Ponderosa or lodgepole pine, in contrast, it responded like western redcedar. Both species are shallow rooted species with no defined tap root system and fine-roots mostly confining to the top 60 cm, thus these two species are easily outcompeted by the close proximity of their neighboring mature edge trees. As data are lacking, I am unable to identify any definite process like competition for water, nutrients or allelopathy or root architectural limitations that might be responsible for suppressing the growth of these trees at the edges. Moreover, for birch, biotic factors, like insect damage from birch leaf miner (*Fenusa pusilla* (Lepeletier)) can be an important factor limiting its growth. Ontogenetic effects on the shade tolerance of birch have been reported in the literature with birch being tolerant when young and intolerant when mature (Kitajima and Bolker, 2003; Kneeshaw et al., 2006).

Western redcedar is classified as a highly shade tolerant species and compared to its other associate, western hemlock, the limited growth response of this species at the light limited south edge may be perceived as perplexing. Wang et al. (1994) and Kobe and Coates (1997) investigated the growth response of this species along a light gradient and concluded that this species can survive at very low light, but it is not a shade requiring species. It has been reported that when light is limiting, both above and below ground competition from the surrounding edge trees can severely limit growth of western redcedar (see Burns and Honkala, 1990; Klinka and

Brisco, 2009). This species is also subject to browsing damage by deer and other ungulates. At the north edge of the opening, western redcedar can also be subject to heat stress, as foliage of this species lacks cutin or wax layers making it more sensitive to heat and high transpiration rates (Klinka and Brisco, 2009).

Another highly shade tolerant species, subalpine fir was observed to suffer 20% and 15% growth reduction at the south and north edge, respectively. Considering its shade tolerance, and adaptation to cooler and higher elevation environments, I believe its lower growth at the south edge may be due to its slow shoot and root growth response at the early stages. Though subalpine fir usually forms a relatively deep root system in well-drained sites (like this study site), but this species is also highly susceptible to drought and is often damaged by spring frost (Burns and Honkala, 1990). I speculate, these factors might have contributed to its growth reduction at the north edge.

Compared to the south edge, most species in this study had higher growth at the northern edge, with the exception of western hemlock. At the north edge all species are subject to higher radiation load and increased competition for soil moisture from the trees located at the north edge (York et al., 2003). Despite these limitations, species were able to show higher growth potential at the north edge which may imply that these species were able to capitalize on the higher light level and warmer soil temperatures at the north edge. Western hemlock's reduced growth at the north edge may result from its higher specific leaf area, high shoot/root ratio and crown shape. Having higher specific leaf area and poor root development might have subjected this species to higher heat stress (transpiration loss) which resulted in less photosynthesis and thus reduced its overall growth potential (Carter and Klinka, 1992; Chen, 1997; Canham et al., 1988; Givnish, 1988).

3.5 Conclusions

As a mechanism of mixed species regeneration, I investigated whether separation between highly shade intolerant (Ponderosa pine, lodgepole pine, and paper birch), moderately tolerant (Douglas-fir and white pine) and highly shade tolerant (Engelmann spruce, western hemlock, western redcedar and subalpine fir) species are apparent. Results from this study do not indicate clear distinction into discrete shade tolerance related categories based on relationships between growth and light or between growth and gap location. Several species show overlapping growth responses with other species and a few species, for example, paper birch and western redcedar, exhibited a growth pattern contrary to their shade tolerance ranking. Despite these anomalies, results indicate that the strip-shelterwood method can be used to support mixed species regeneration based on the evidence that two highly shade intolerant species (Ponderosa pine and lodgepole pine) did grow at a faster growth rate than other species. Moreover, two moderately shade tolerant species (Douglas-fir and white pine) eventually surpassed the growth of other more shade tolerating species as the distance increased from the south edge. The superior growth rate of the two pine species provides a greater chance to reach the main canopy than shade tolerant species (Lu et al., 2018), thus, shade tolerant species may not competitively exclude shade intolerant species at the early stage of stand development. Busing and White (1997) in investigating how small-scale disturbances help maintain species coexistence reported that application of the gap partitioning hypothesis is more relevant to intolerant species than to tolerant species. Also, the overlaps observed in this study were mostly between species that are similar in shade tolerance ranking and should not be deemed as problematic in maintaining species coexistence.

Considering species' response to edge proximity, western redcedar, paper birch, Ponderosa pine, lodgepole pine, white pine and Douglas fir should not be planted along the southern edge location. Considering the best potential of species, Ponderosa pine, and lodgepole pine can be planted beginning from the centre to north edge location. Douglas-fir and white pine can be planted at the same gap locations, but considering their moderate shade tolerance, the planting location of these two species can be extended a little bit further towards the southern part of the gap. However, it is better to avoid planting Douglas-fir and white pine within 5 m of the north edge of openings. Paper birch should be planted within 10 m of the gap centre. Although western larch was not included in this study, it appears that this species will do well near the centers of gaps that are at least 50 m wide together with Ponderosa and lodgepole pine. Western redcedar, considering its sensitivity to both edges, can be planted starting from 10 m away from the south edge up to the center location. Other species (western hemlock, subalpine fir, and Engelmann spruce) can be planted anywhere in the gap due to their gradual growth response to increasing light. These species can also be planted in close proximity (within 10 m) to either the north or south edges.

Results from this study apply to rectangular canopy openings of similar sizes where the influence of the surrounding north or south edge extends up to one tree height. An increase in size in the direction of the north-south axis would mean less influence from south edge and more area under the influence of direct sunlight. As a result, the strong south edge influence observed for the shade intolerant species in this study will decline. Larger openings will also provide more open area for species such as western larch, Ponderosa pine and paper birch to be planted near the middle position of the gap. Furthermore, increasing the area represented by the south of the gap centre environment is expected to favor the establishment of Douglas-fir and western white pine. Above all, a stronger distinction between shade intolerant, moderately tolerant and tolerant species may emerge (with three distinct peaks) if the size of the opening is extended toward the north-south direction. Inversely, if gap size decreases, the range of light conditions will become shallower, resulting in openings primarily favoring the establishment and growth of shade tolerant species, to the exclusion of highly shade-intolerant species (Kobe et al., 1995; Kneeshaw and Bergeron, 1998; Catovsky and Bazzaz, 2000; De Montigny and Smith, 2017)**.**

3.6 Limitations

Some important limitations of this study include lack of tree level light data which could improve the light-growth relationships presented here. Both survival and growth rates of trees should be considered while discussing species differentiation in gaps based on shade tolerance (Valladares et al., 2016), however due to the limited time period of this study (3-growing season), long term survival data were missing. It is true that differential survival and growth response at low versus high light environments play an important role in maintaining species diversity during regeneration phase, but for juvenile trees, after their establishment, changes in growth hierarchies along the light or resource gradient due to differential growth rate between shade tolerant and intolerant species becomes much more important (Kobe, 1996; Van Couwenberghe et al., 2013; Valladares et al., 2016) and thus, this study was primarily predicated on patterns in growth rates along the spatial gradient of light. Intra-regeneration competition was not included in the light-growth models, though in this condition it would be hard to separate such effects from the competitive effect of the surrounding edge trees. Only one opening size was examined in this study, consequently this study cannot address potential impacts of different opening sizes.

The conclusions of this study are based on the growth potential of planted seedlings. However, forest management under continuous cover forestry practices often targets natural regeneration. In this instance, some of the species in this study, such as Douglas-fir, larch or pine species may still need to be planted, since these species either don't produce abundant seed, have limited seed dispersion ability or may require disturbed seedbed conditions for successful germination and establishment (Burns and Honkala, 1990).

3.7 Management implications

Results from this study indicate that strip shelterwood cuttings create a strong north-south light gradient, along which species with a wide range of shade tolerance can grow at different rates and thus coexist within the opening. If regeneration of a mixed species stand is the primary forest management objective, predictive models that link gap-position, light, and growth performance of species can be used as tools in designing shelterwood cutting. The distance-growth relationships provided by this study provide useful information regarding species sensitivity to edge environments which is useful in selecting suitable species for other gap-based silvicultural practices.

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4 Chapter 4: Seasonal growth patterns of five species with contrasting shade tolerant in relation to locations within a strip-shelterwood

4.1 Introduction

Spatial and temporal variability in light, air temperature, soil temperature and soil moisture can influence regeneration, survival and growth, and coexistence of multiple species in a gap (Messier and Puttonen, 1995; Lieffers et al., 1999; Coates, 2000; Ligot et al., 2014; Kern et al., 2017; Annighöfer et al., 2019). Interactions between the various environmental factors in an opening can create a range of growing conditions where multiple species with varying degrees of competitive ability can successfully regenerate and occupy various positions within a gap (Kobe, 1999; Valladares et al., 2016; Álvarez-Yépiz et al., 2017; Avalos, 2019).

Strip-shelterwood is a variant of the shelterwood silvicultural system designed to regenerate an even-aged forest structure (Matthews, 1989), where regenerating understories are protected from harsh environmental conditions such as frost or high radiation load by shelter from the standing edges. In this system, overhead canopies are completely removed within strips to allow for increased penetration of light to the understory (Groot, 1999; Day et al., 2011). As for any gap in higher latitude forests, microsites along a north-south transect receive both direct and diffuse light in varying amounts; microsites within the southern portion of a gap receive a greater fraction of light as diffuse due to shading by the southern edge, in contrast, microsites at the northern section receive both direct and diffuse light (Canham et al., 1994; Gendreau-Berthiaume and Kneeshaw, 2009; Hossain and Comeau, 2019 and also see chapter 3). Many factors such as solar position in the sky, sky conditions, leaf phenology, gap size, gap shape, canopy height, slope and aspect govern the amount of light received by each microsite within a gap (Baldocchi et al., 1984; Gendron et al., 2001; Beaudet and Messier, 2002).

Direct light originates from the solar disk and varies in intensity throughout the day and throughout the growing season. Thus, the potential amount of incident direct light varies temporally but is highest on clear-days. On cloudy-days, the incident light is largely diffuse. Since diffuse light is distributed across all parts of the sky, its seasonal variation is small (Gendron et al., 2001; Olpenda et al., 2018). On clear-days, heterogeneity in understory light largely depends on diurnal and seasonal changes in solar position and its interactions with the surrounding stand edges (height and density of the border trees; Canham et al., 1990; Comeau et al., 1998; Nunez and de Gouvenain, 2015). Early in the season (May-July), canopy development affects the distribution of light within an opening, but later in the season (July to September), it is mostly affected by changes in solar elevation (Canham et al., 1990; Gendron et al., 2001). In a study in eastern Quebec, Prévost and Raymond (2012) reported that, inside one hectare openings in a yellow birch-conifer stand, light transmittance was much lower in late-summer than in early summer. They attributed this to increased interception of light by the tree crowns as solar angle decreased from June to September. Moreover, differences in light level between microsites also changed with solar elevation; for example, differences in light level between gap-positions, e.g., the center, south and north, were less in June when solar elevation was higher, but became larger late in the season.

Plant to plant interaction or competition for resources can change from one time period to another, even within the relative short growing season observed in temperate regions. In one study, Kikvidze et al. (2006) found plant to plant interactions shifting from competition to faciliation with changing environmental conditions (from mesic to dry) within a single season. Kimberley and Richardson (2004) found that the effect of weed competition on the growth of radiata pine can be better understood through understanding seasonal patterns of resouce availability. Seasonal variation in light at forest edges was found to be associated with the survival of white pine seedlings in a study conducted in southern New England (Nunez and de Gouvenain, 2015).

Shade tolerance is an index which defines how well a species is able to survive and grow in low light environments (Chen, 1997; Valladares and Niinemets, 2008). Shade tolerant and intolerant species have different acclimation strategies for dealing with highly variable understory light environments (Carter and Klinka, 1992; Walters and Reich, 1996; Valladares and Niinemets, 2008; Valladares et al., 2016). Shade intolerant species show a rapid response in growth for increase in light level in high light environments but are usually less responsive to subtle changes in light level under shaded understory conditions. On the other hand, shade tolerant species can effectively utilize small increase in ambient light condition and thus, can survive or grow better under low light conditions than shade intolerant species (Sipe and Bazzaz, 1995; Valladares et al., 2016).

Shade tolerant and intolerant species also differ in their carbon allocation strategies (Kobe, 1997; Imaji and Seiwa, 2010; Seki et al., 2013). To better persist at low light conditions, shade tolerant species are known to adopt a conservative resource-use strategy (see Sanchez-Gomez et al., 2006); therefore, rather than incurring cost (i.e., growth), these species allocate more carbon (e.g., photosynthate) to defense (pathogens or herbivory) and storage (to overcome periods of stress). In contrary, shade intolerant species adopt a net carbon gain maximization strategy; consequently, these species tend to invest more resources in stem growth (e.g., height and diameter). In particularly, these species allocate more carbon to vertical growth than to diameter growth to gain a competitive advantage over other co-occurring species (above reviews and see also Sanchez-Gomez et al., 2006; Poorter and Kitajima, 2007); however, this strategy comes as a cost of maintaining higher respiration costs and, therefore, in low light environments (e.g., in the understory), survival of these species is usually low (Kobe and Coates, 1997).

Studies have reported that with increasing light level, tree species in temperate forests usually increase in both height and diameter growth simultaneously, suggesting that at the juvenile stage, stem height and diameter growth are likely to be strongly correlated (Canham, 1988; Beaudet et al., 2007; Lilles and Astrup, 2012). Nonetheless, a few other studies have also reported that investment in height and diameter growth can shift in response to heterogeneous environmental conditions (Bormann, 1965; Henry and Aarssen, 2001;see also Noyer et al., 2019). For example, at low light, allocation to height growth may take precedence over that of diameter growth, thus giving a high height-diameter ratio. For this reason, for juvenile trees responding to variable light conditions, height-diameter response may not be strongly correlated at all circumstances (Bormann, 1965; Rozendaal et al., 2015).

Numerous studies have been conducted on species' differential growth responses in relation to their shade tolerance within gaps of different sizes (Wright et al., 1998; Coates, 2000; Drever and Lertzman, 2001; York et al., 2004; Gravel et al., 2010; Newsome et al., 2016). However, these studies are based on species' annual growth response against a gradient in light and other resources. Such studies have not considered seasonal dynamics in resource availability and their link to location and growth. Seasonal studies are important since these studies can contribute in better understanding of how key growth limiting factors fluctuate seasonally, and how that can affect tree survival and growth, which may again lead to a better understanding of the effect of silvicultural practices on these growth limiting factor (e.g. light) or factors and their subsequent effect on the growth and survival of regeneration. Such understanding is fundamental to developing successful silvicultural prescriptions (Wright et al., 1998; Coates, 2002).

In this study, I test whether these species exhibit similar or different patterns in their seasonal investments toward height or diameter growth within changing light conditions inside the gap. For this purpose, five species were selected; the species ranked in order of increasing shade tolerance are: lodgepole pine, Douglas-fir, white pine, Engelmann spruce, and subalpine fir. Three gap-environments (south, centre and north) were also selected to represent 3 distinct light conditions (see chapter 2) and are subject to seasonal variations. Centre and north gap environments exhibit greater variation in light than the south and in response, shade tolerent and intolerant species are expected to vary seasonally between the 3 gap environments. An understanding of species-specific patterns in seasonal growth within a single growing season is expected to enhance understanding of species' responses to gap-position, and shed more light on their growth strategy. In particular, it is important that we understand if species adopt a different growth strategy (e.g., competitive or persistent) in different gap environments and if shade tolerance plays any role. To the best of my knowledge, there are no other studies relating to seasonal growth of trees in the context of a strip-shelterwood system.

Gap environments that are subject to strong seasonal variations in light (centre or north of the centre) will exhibit stronger seasonal influences on their growth. Shade intolerant species are believed to be better at exploiting temporal variations in understory light than tolerant species, therefore, shade tolerant and intolerant species may show different growth strategies related to different gap environments, and it is possible that a species' height growth strategy can differ from their diameter growth strategy. To understand species' acclimation strategy in different gap environments, it is also important to examine whether differences in growth strategy, and plasticity in strategies are related to species' shade tolerance.

Species selected for this study have determinate growth and usually complete most of their height growth (about 90% see Kobe, 1997, quoting from Ward, R.C., 1957a &b) within the early part of the growing season. Since tolerant and intolerant species may not actually differ in their height growth strategy, no significant influence of gap environment is expected for species' height growth strategies. However, the same might not be true for their diameter growth strategies. Determinate shade tolerant species, after a quick flush of leaves (height growth) in the early season, may allocate more growth either to diameter or to root-stem storage or defense for the remainder of the growing season. In contrast, shade intolerant species adopt a net carbon gain maximization strategy, and usually allocate carbon to maximize aboveground growth (height and diameter), at the expense of defense or storage (Kobe, 1997; Walters and Reich, 1999; Poorter and Kitajima, 2007). Therefore, I expect to see some degree of overlap between shade tolerant and intolerant determinate species in their diameter growth strategies, which I hypothesize, will be observed mostly for the high-light gap environments. However, despite similarity in growth strategies, shade tolerant and intolerant species will differ in their magnitude of investment, largely due to differences in their light utilization efficiency. For example, at the gap centre or north edge environments, shade tolerant species are expected to have a higher magnitude of seasonal difference (early versus late) in their diameter growth than shade intolerant species; thus the following pattern in species seasonal difference is expected at the two light abundant gap environments (in the order of highest to lowest): subalpine fir > Engelmann spruce > white pine > Douglas-fir > lodgepole pine. On the contrary, at the light limited south edge, shade tolerant and intolerant species may exhibit a different diameter investment strategy. At the south edge, shade tolerant species may continue to invest in their diameter growth till the end of the season, in contrast shade intolerant species may limit their period of diameter growth to the early part of the growing season. If this is true, then the following pattern of seasonal difference in diameter growth is expected at south edge (from high to low): lodgepole pine > Douglas-fir > white pine > Engelmann spruce > subalpine fir.

4.2 Methods

4.2.1 Site description

Data for this study come from a site located 50 km south of Nakusp, British Columbia (Lat. 49 57'N, Long. 117 53'W). The site is in the Columbia-Shuswap variant of the Interior Cedar-Hemlock moist warm Biogeoclimatic subzone (ICHmw2), with a mesic soil moisture regime (MacKillop and Ehman, 2016). The mature, even-aged, mixed species stand is located on a level area of a valley bottom and consists of 53% Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franc.), 25% western redcedar (*Thuja plicata* Donn ex D. Don in Lamb), 15% larch (*Larix occidentalis* Nutt.), and 5% pine (*Pinus* L. spp.) and birch (*Betula papyrifera* Marsh) with other species (including trembling aspen [*Populus tremuloides* Michx.], balsam poplar [*Populus balsamifera* L. subsp. trichocarpa (T.&G. ex Hook.], and western white pine [*Pinus monticola* Dougl.]) comprising the remainder. The dominant species are about 35 m tall and the stand density is approximately 650 stems/ha (Delong et al., 2000). For a detailed description of the climate and other information please refer to Chapter 2 and 3.

4.2.2 Experimental layout

The study design is as described in chapters 2 and 3. In brief, the experimental layout involves two small openings (< 1 ha) each 50 m × 150 m with the long axis oriented east-west created in the mixed conifer stand (see Figure 4.1, where only one strip-cut is shown) during the winter of 1994/95.

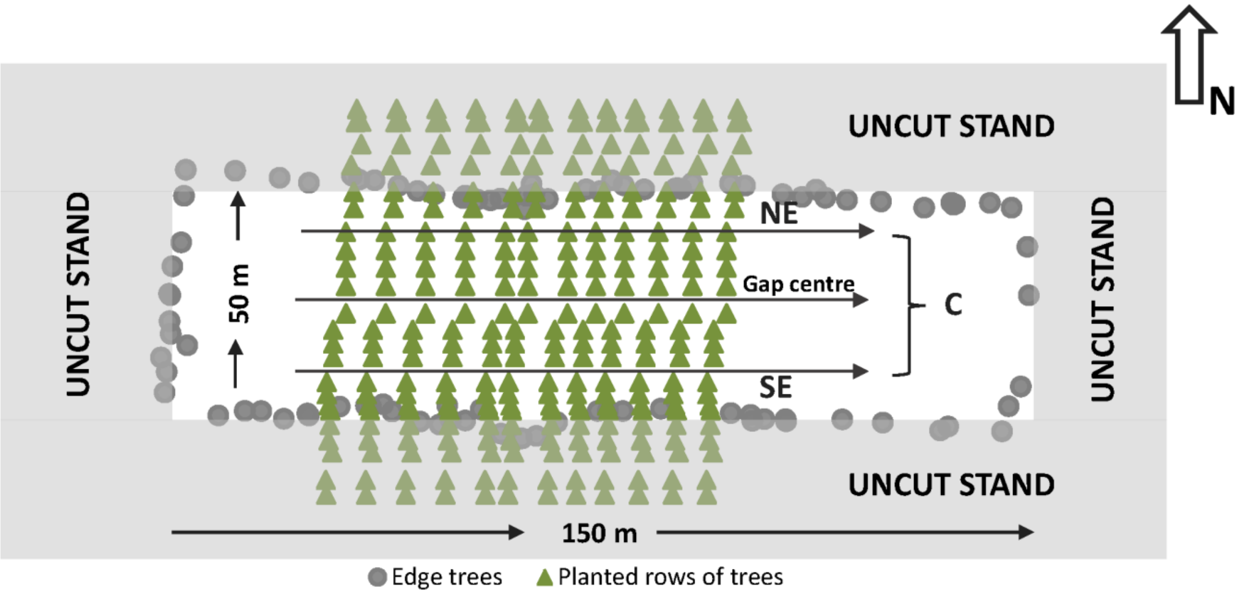

Figure 4.1. An illustration of the division of the 50 m wide cleared strips into the three gap environments used in this chapter. Gap environments were defined here as: NE = from north edge to 10 m inside opening; C = 15 m on either side of the opening centre; SE = from south edge to 10 m inside opening. See also Table 4.1.

In the spring of 1995, the two openings were planted with seedlings of ten species in three replicate rows, where species were assigned randomly to rows. The species selected all occur commonly in ICH zone forests in this area, viz., Douglas-fir, western larch, Engelmann spruce (*Picea engelmannii* Parry ex Engelmann), western redcedar, western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), white pine (*Pinus monticola* Dougl. ex D. Don.), Ponderosa pine (*Pinus ponderosa* (Dougl. ex P. & C. Lawson), lodgepole pine (*Pinus contorta* Dougl. ex Loud. var.latifolia Engelm. Ex S. Wats.), subalpine fir (*Abies lasiocarpa* (Hook) Nutt.), and paper birch. Rows are oriented north to south across each block and each row is 90 m long extending 20 m into the uncut stand south and north of each block. A row to row spacing of 2.6 m and plant to plant distance of 3 m within each row was maintained. A 20-m wide unplanted buffer was established on both the east and west sides of each block (Figure 4.1).

4.2.3 Sampling and data preparation

4.2.3.1 Characterizing of the seasonal light pattern

Light measurements were made directly and continuously with GaAsP (Gallium arsenide Phosphide) photodiodes connected to dataloggers. Sensors were installed at 1.5 m height on an established north-south transect running approximately across the centre of each strip-cut. A detailed description of the sensors, dataloggers and their installation and operation is provided in chapter 2.

In 2008, failure of several sensors resulted in incomplete coverage of microsites along the north-south transect; therefore, data from 2009 were used to characterize the seasonal light distribution within the strip-cuts. For the purpose of this study, the growing season (May–September) was divided into two portions: 1) early (mid-May to mid-July), and, 2) late (mid-July to mid-September). The rationale behind choosing the two-time segments for defining early and late seasons is to capture the effect of changes in solar elevation, as it interacts with the surrounding edges, on the light level received by microsites within the gap. In a study by Prévost and Raymond (2012) conducted inside one-hectare openings in a yellow birch-conifer stand, differences in light microenvironments were primarily associated with two portions of the growing season (early vs. late summer) with much lower light transmittance in late than in early summer. They attributed these differences in light level between microsites to the changes in solar elevation and its angular interaction with the standing edges.

4.2.3.2 Tree measurements

Since the objective of the study is to understand the seasonal distribution of growth (height and diameter) during the growing season for five tree species going from shaded south edge to sunny northern edge, trees planted under the north or southern canopy were excluded from analysis. In addition, along its north-south axis, the 50 m wide strip was divided into three gap environments: with each representing a distinct light condition. Using the light-distance relationship (Equation 3.2) presented in chapter 2, the estimated growing season transmittance in the southern (south edge), centre and north edge portions of the gap were 18, 49 and 37%, respectively (Table 4.1).

Table 4.1. General description of the three gap-positions and associated light level within the 50 m wide strip openings. Growing season light levels were predicted based on the light transmittance Equation 3.2, as described in chapter 3.

Gap-position	**Distance (m) from the south end of the transect**	**Description**	**Growing season total light transmittance (%)**	**Growing season diffuse fraction (%) (from hemispherical photo analysis)**
D1	> 24 - ≤ 34	South edge (SE)	18	63
D2	> 34 - ≤ 64	Gap-centre (C)	49	50
D3	> 64 - ≤ 74	North edge (NE)	37	53

In a separate but related study (see chapter 3), it has been observed that the growth responses of these species in the north and south edge locations (approximately 5 m away from both edges) differed significantly from that at roughly 12-14 m away from the two edge locations, into the opening (at 41 m and 60 m within the gap). Since the aim was to compare seasonal growth in contrasting environments, the two edge environments were restricted to 10 m wide bands located 10 m from the edges inside the opening (Figure 4.1).

Five species with determinate growth patterns were selected for analysis of seasonal growth responses to represent a range of shade tolerance: lodgepole pine, Douglas-fir, white pine, Engelmann spruce and subalpine fir. Within each gap environment of each block, up to 10 trees were randomly selected for each species (with fewer selected when 10 were not available) for measurement. In selecting trees, only healthy trees with good vigor were selected to control for the influence of extraneous factors. Stem diameter (D5, diameter at 5 cm height) and height were measured at roughly 30-day intervals between mid-May and mid-September of 2008 and 2009. Although data were collected at 30-day intervals in this experiment, results from Prévost and Raymond (2012) indicated that differences in light environments inside one hectare openings in a yellow birch-conifer stand were primarily associated with two portions of the growing season (early vs. late summer) with much lower light transmittance in late than in early summer. They attributed this differences in light level between microsites to the changes in solar elevation and its angular interaction with the standing edges, therefore, seasonal stem diameter (D5) and height growth in this study were calculated only based on these two time-lengths within each growing season (2008 & 2009) and expressed as the percent of annual growth (mid-May to mid-September). For example, % diameter increment for period 1= (mid-May to Mid-July) / (mid-May to mid-September) × 100 (see Table 4.2 for definition on the seasonal periods).

Table 4.2. Periodic growth estimation for two-time intervals within the growing season.

Period / Season	**Day - interval**	**Seasonal growth (%)**
P1 (early season)	Mid-May - mid-July	P1/A *100
P2 (late season)	Mid-July - mid-September	P2/A *100
A (Annual)	Mid-May - mid-September	

Since the purpose in this chapter is to examine patterns in seasonal investment in height and diameter across the gap, therefore, statistical analyses and their follow up discussions rely on percent scale data. Since some readers might be curious to know about the species' seasonal growth in actual scale, I also provide a summary of the raw data in Figure 4.2 and Figure 4.3.

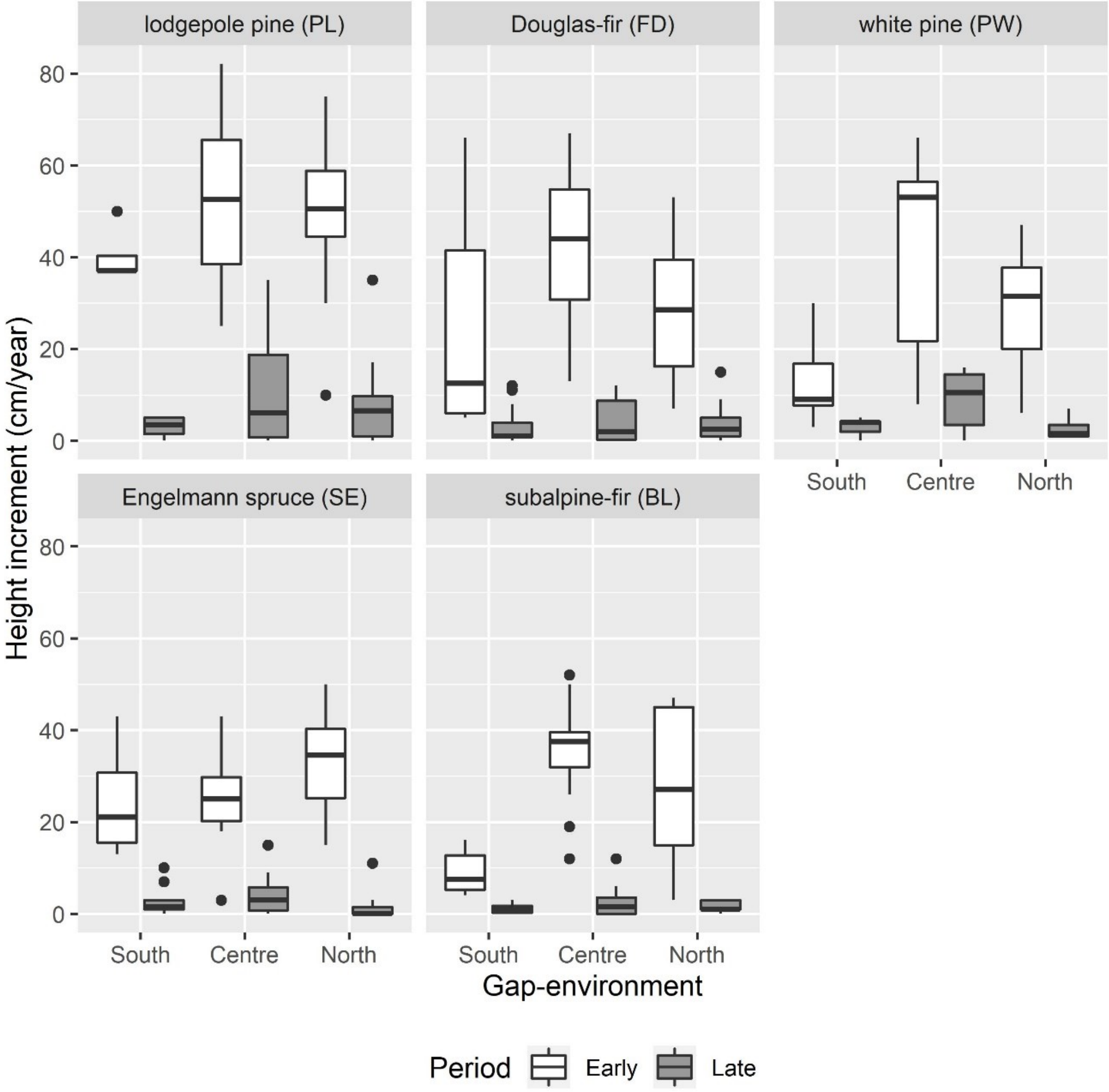

Figure 4.2. Seasonal mean height increment (cm) of species of various shade tolerance along changing positions within the 50 m strip-cut. Height data from 2008 and 2009 are combined. Early season = mid-May–mid-July and late season = mid-July–mid-September.

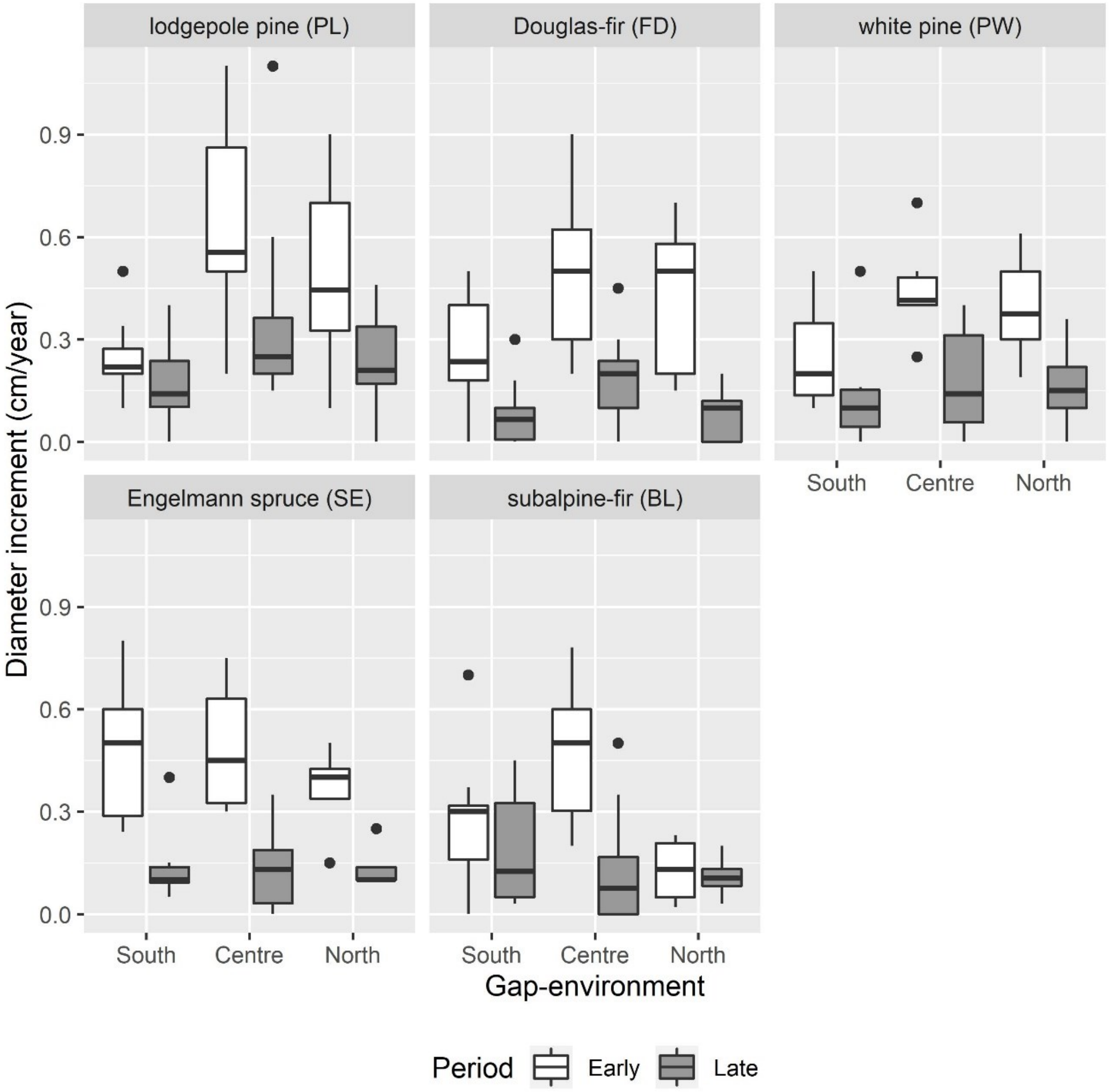

Figure 4.3. Seasonal mean diameter increment (cm) of species of various shade tolerance along changing positions within the 50 m strip-cut. Diameter data from 2008 and 2009 are combined. Early season = mid-May–mid-July and late season = mid-July–mid-September.

4.2.4 Statistical analyses

Light gradients in early and late seasons were characterized by a quadratic function of the changes in gap-position relative to the south edge (i.e., distance). To test if pattern in light differed between the two seasons, a dummy variable representing levels of seasonality was incorporated into the model and allowed to interact with the quadratic function of the distance. For example,

$$\text{Light} \sim \text{intercept} + \text{season} + \text{distance} + \text{season*distance} + \text{season*distance}^2 + \text{error} \qquad 4.1$$

A mixed model ANOVA, on the other hand, was used to test for differences between species, gap environment and period for periodic height and diameter growth applied.

$$\text{\% Height /Diameter} \sim \text{species*gap-environment*period, random} = \sim 1|\text{tree\_id/year} \qquad 4.2$$

Mixed model ANOVA can deal with data structures that involve nesting of trees within gap-environments, with trees growing close to each other and within each gap environment within a row being pseudo replicates or samples. Also, due to limited sample size within each year of data collection, data from the two consecutive years were pooled together to meet the requirement of minimum sample size and to increase sample size per gap-environment. In this case, year was used as a random factor to account for year to year variation since the aim was not to investigate differences between the two consecutive years. Post-hoc mean separation tests were performed on lsmeans with Tukey adjusted P values used to differentiate species that were showing significant seasonal differences in growth across gap locations. All analyses were completed using R statistical software (R Core Team, 2019).

4.3 Results

4.3.1 Seasonal pattern in light distribution across the strip-cut

Within the shelterwood gap, gap-position was a significant predictor of the light gradient in both early and late season ($P < 0.05$). In the early season maximum PPFD occurred at the gap centre and declined symmetrically going from the center towards the edges. The curve representing the late season is flatter with maximum PPFD shifting toward the north of the centre. Moreover, in the late season, the difference in light levels between north (higher light level) and south edges also becomes more evident (Figure 4.4).

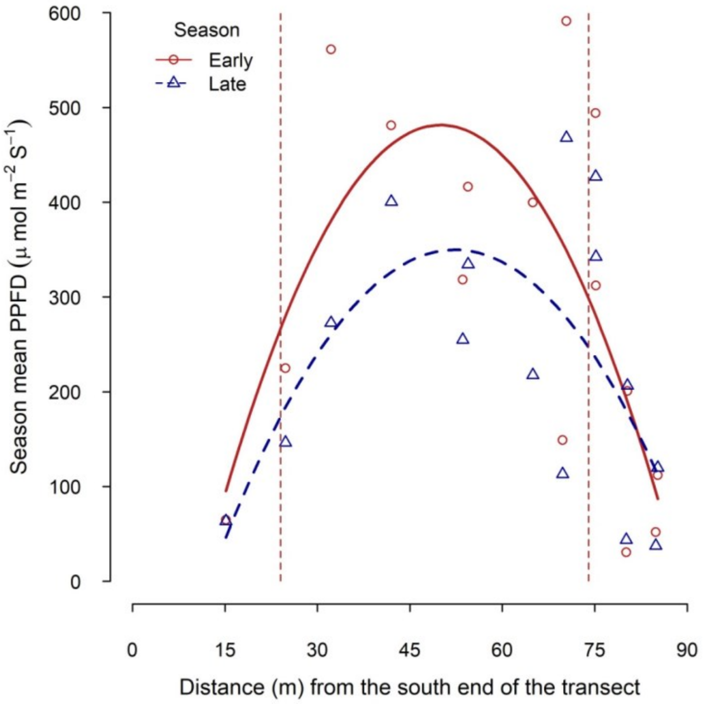

Figure 4.4. Quadratic regression fit to the data characterizes the seasonal distribution of growing season light within the strip opening in 2009 ($P = 0.003$, Adj. $R^2 = 0.40$ and rmse (root mean square error) = 130.4). Brown dashed lines indicate southern and northern boundaries of the openings.

The two seasonal patterns (early versus late) were not statistically different (P > 0.05) which is primarily due to large confidence intervals around their predicted lines. Nevertheless, visual interpretation of these patterns assists readers with interpretation and understanding of the seasonal growth pattern along the north–south axis of the gap.

4.3.2 Seasonal patterns in height growth response across gap locations

ANOVA showed a significant three way interaction, suggesting species' seasonal pattern in height investment (i.e., P ~ 0.002, Table 4.3) varied across the gap environments. Further examination of the ANOVA coefficients (Table 4.4) also supports these findings.

Table 4.3. Results from mixed model analysis of variance testing for effects of species, gap-position and season on % height growth increment (See Equation 4.2). For coefficients of the fixed effects, please see Table 4.4.

Factor	**numDF**	**denDF**	**F-value**	**P.value**
Intercept	1	130	299.15	< 0.001
Species	4	58	2.12	0.09
Gap-environment	2	58	0.68	0.51
Period	1	130	105.40	< 0.001
Species × gap-environment	8	58	1.62	0.14
Species × period	4	130	4.23	0.003
Gap-environment × period	2	130	1.35	0.26
Species × gap-environment × period	8	130	3.24	0.002

Levels of species with their codes are: lodgepole pine (PL); Douglas-fir (FD); western white pine (PW); Engelmann spruce (SE); subalpine fir (BL). Levels of gap-environments are: south edge (D1), centre (D2) and north edge (D3) and periods are defined as early (P1, mid-May-mid-July) and late (P2, mid-July-mid-September).

Table 4.4. Coefficients for the fixed effects of the mixed model assessing seasonal height growth with respect to gap-environment and species (See Equation 4.2).

Variable	**Coefficient**	**Std.Error**	**DF**	**t-value**	**P.value**
Intercept	86.17	5.26	130	16.38	< 0.001
PL	6.83	8.32	58	0.82	0.41
FD	0.21	6.17	58	0.03	0.97
PW	-9.67	6.96	58	-1.39	0.17
SE	5.73	6.66	58	0.86	0.39
D2	6.92	6.44	58	1.07	0.29
D3	3.03	7.8	58	0.39	0.70
P2	-72.33	7.44	130	-9.72	< 0.001
PL × D2	-14.92	9.84	58	-1.52	0.14
FD × D2	-3.08	7.99	58	-0.39	0.70
PW × D2	-4.42	9.49	58	-0.47	0.64
SE × D2	-15.07	8.48	58	-1.78	0.08
PL × D3	-10.2	10.78	58	-0.95	0.35
FD × D3	-1.74	9.23	58	-0.19	0.85
PW × D3	12.34	10.12	58	1.22	0.23
SE × D3	-0.31	9.91	58	-0.03	0.98
PL × P2	-13.67	11.77	130	-1.16	0.25
FD × P2	-0.42	8.73	130	-0.05	0.96
PW × P2	19.33	9.84	130	1.96	0.05
SE × P2	-11.47	9.41	130	-1.22	0.23
D2 × P2	-13.83	9.11	130	-1.52	0.13
D3 × P2	-6.07	11.04	130	-0.55	0.58
PL × D2 × P2	29.83	13.92	130	2.14	0.03
FD × D2 × P2	6.15	11.29	130	0.54	0.59
PW × D2 × P2	8.83	13.41	130	0.66	0.51
SE × D2 × P2	30.13	12	130	2.51	0.01
FD × D3 × P2	3.48	13.05	130	0.27	0.79
PL × D3 × P2	20.4	15.25	130	1.34	0.18
PW × D3 × P2	-24.68	14.31	130	-1.72	0.09
SE × D3 × P2	0.62	14.02	130	0.04	0.97

Levels of species with their codes are: lodgepole pine (PL); Douglas-fir (FD); western white pine (PW); Engelmann spruce (SE); subalpine fir (BL). Levels of gap-environments are: south edge (D1), centre (D2) and north edge (D3) and periods are defined as early (P1, mid-May-mid-July) and late (P2, mid-July-mid-September)

Regardless of differences in species' shade tolerance, a significant investment (more than 75%) in height growth occurred early in the season (mid-May-mid-July) for all gap environments (Tukey adjusted post-hoc mean separation test, Table 4.5). Species also showed difference in their pattern of investment (Figure 4.5); for example, in the early season, investment in height growth increased going from shaded south edge to light abundant, north edge for white pine, whereas the opposite trend was observed for highly shade intolerant species, lodgepole pine; for this species, early investment in height growth decreased going from south to north edge. Moderately shade tolerant Douglas-fir and highly shade tolerant subalpine fir exhibited a similar pattern in early seasonal height investment; these two species invested the highest in height growth at the centre gap location which then gradually decrease toward the edges. In comparison, shade tolerant species, Engelmann spruce showed a unique investment response, this species invested more heavily at the edges compared to the gap-centre (Figure 4.5).

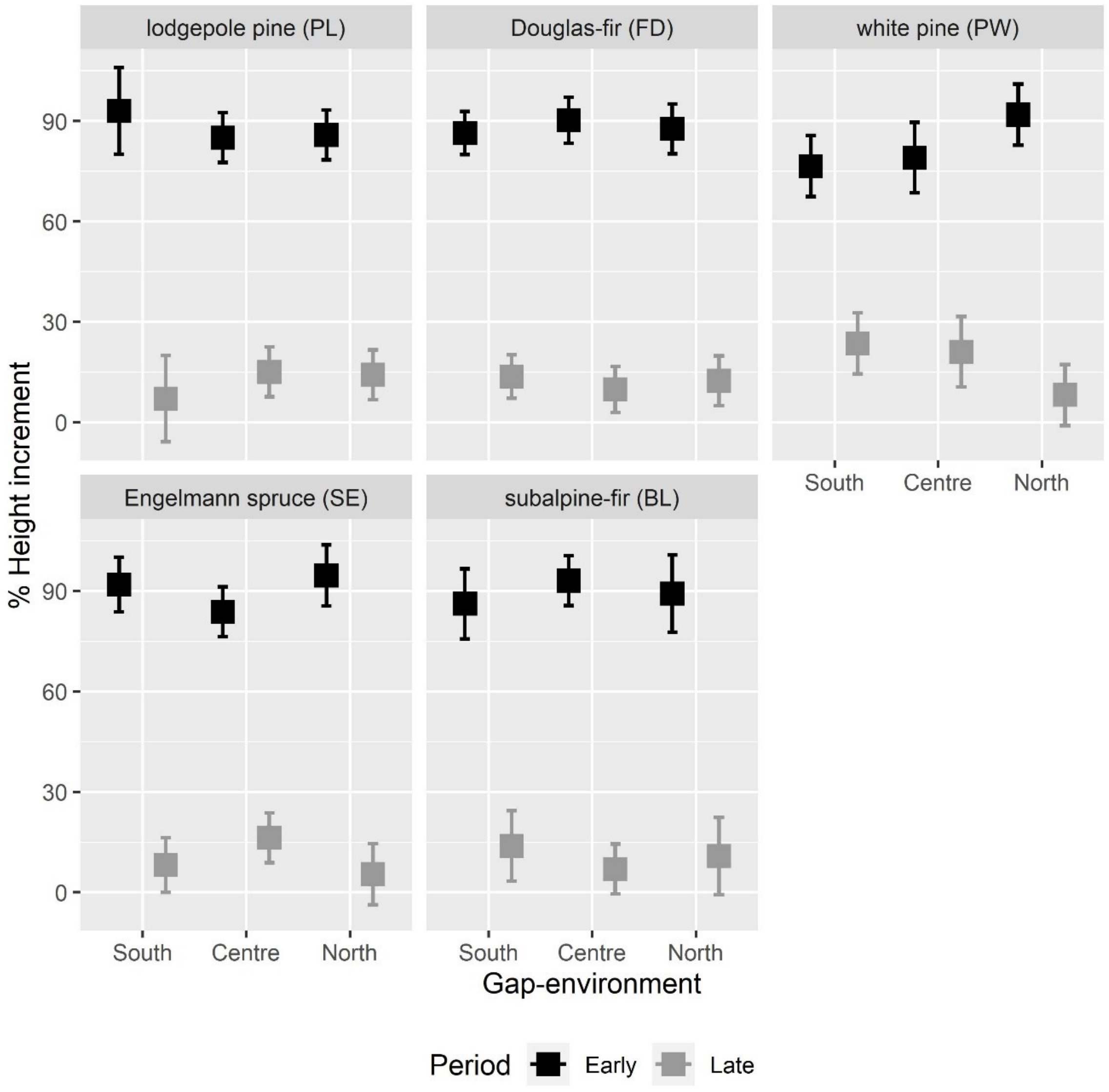

Figure 4.5. Seasonal distribution of annual height growth (May-September) with changing locations within the 50 m wide strip for species with differing shade tolerance. Levels of species with their codes are: lodgepole pine (PL); Douglas-fir (FD); western white pine (PW); Engelmann spruce (SE); subalpine fir (BL). Levels of gap-environments are: south edge (D1), centre (D2) and north edge (D3) and periods are defined as early (P1, mid-May-mid-July) and late (P2, mid-July-mid-September). Error bars are 95% confidence intervals around the mean height response.

Table 4.5. Seasonal differences (early versus late) in height growth response of five contrasting shade tolerant species within each gap-environment. Levels of species with their codes are: lodgepole pine (PL); Douglas-fir (FD); western white pine (PW); Engelmann spruce (SE); subalpine fir (BL). Levels of gap-environments are: south edge (D1), centre (D2) and north edge (D3) and periods are defined as early (P1, mid-May-mid-July) and late (P2, mid-July-mid-September).

Gap -env.[1]	**Comp**[2]	**PL**		**FD**		**PW**		**SE**		**BL**	
		Est[3]**.**	**P**	**Est.**	**P**	**Est.**	**P**	**Est.**	**P**	**Est.**	**P**
D1	P1-P2	86.00	< 0.001	72.75	<0 .001	53.00	< 0.001	83.80	< 0.001	72.33	< 0.001
D2	P1-P2	70.00	< 0.001	80.43	<0 .001	58.00	< 0.001	67.50	< 0.001	86.17	< 0.001
D3	P1-P2	71.67	< 0.001	75.33	< 0.001	83.75	< 0.001	89.25	< 0.001	78.4	< 0.001

[1] Gap-environment
[2] Comparison
[3] Estimate

The magnitude of seasonal differences (early versus late) in height growth investment was also examined for three gap environments. In the light limited south edge, species showed the following order (from highest to lowest): lodgepole pine > Engelmann spruce > Douglas-fir > subalpine fir > white pine. However, in the high-light gap centre, the rank order changed to: subalpine fir > Douglas-fir > lodgepole pine > Engelmann spruce > white pine; and finally, at the north edge, another light abundant environment which was also subject to heat or other associated stresses, the species ranked in the following order: Engelmann spruce > white pine > subalpine fir > Douglas-fir > lodgepole pine (Table 4.5).

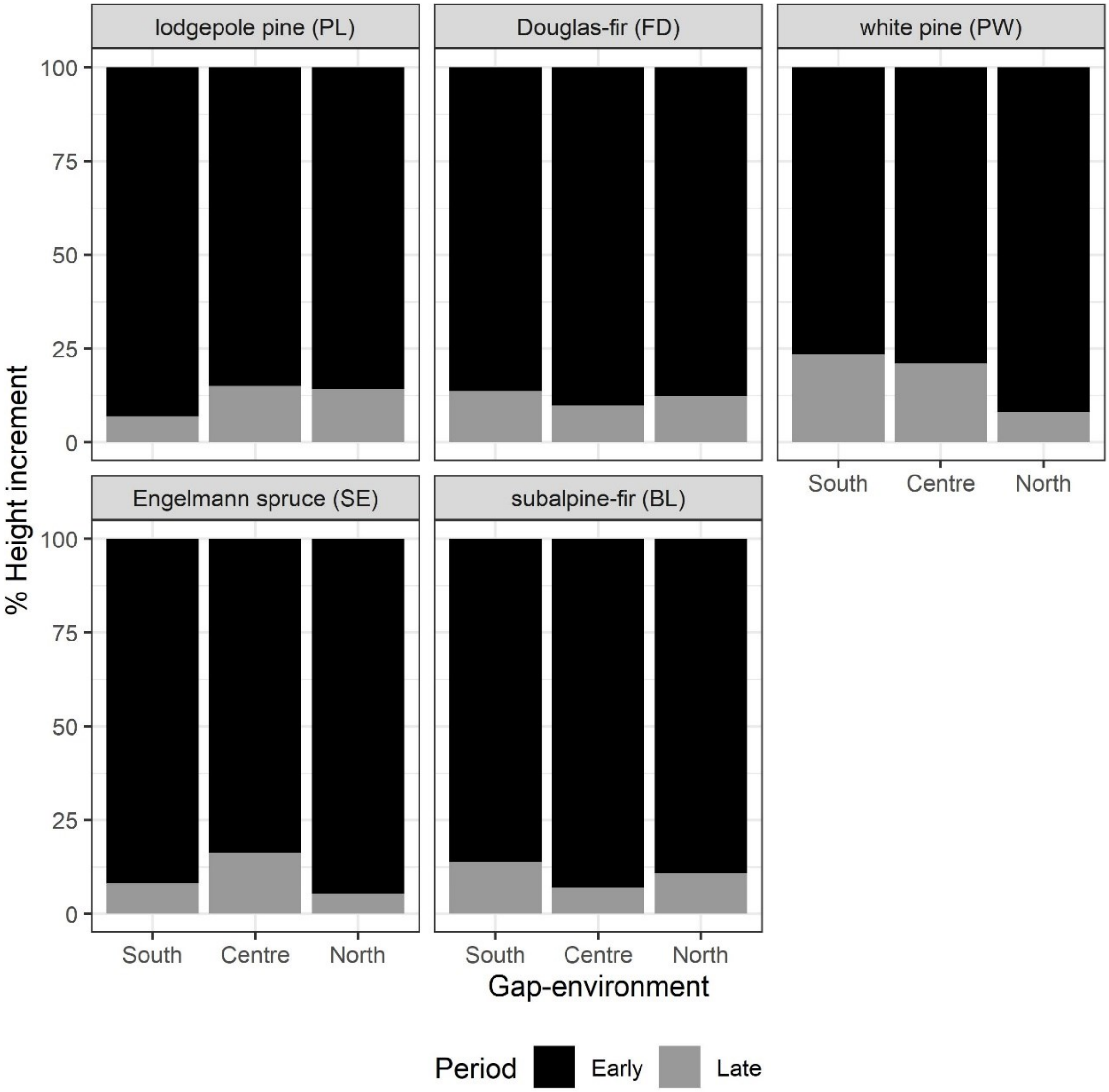

Figure 4.6. Seasonal contribution in height growth of five species with contrasting shade tolerance within the growing season. Levels of gap-environments are, south edge (D1), centre (D2) and north edge (D3) and periods are defined as early (P1, mid-May-mid-July) and late (P2, mid-July-mid-September).

In terms of seasonal contribution in percent, between 76% and 95% of annual height increment occurred at the beginning of the growing season, while the remaining 5-24% occurred late in the season (Figure 4.6). Of all the species, only moderately shade tolerant white pine had greater than 20% of growth (i.e., height) late in the season, which mostly occurred at the gap-centre

(21%) or south of the centre (24%) gap environments. For the other species, late season contributed less than or equal to 16% of their annual height increment (Figure 4.6)

4.3.3 Seasonal patterns in diameter growth response across gap locations

ANOVA results for diameter growth show a significant three-way interaction involving species, season and gap environment ($P < 0.001$; see Table 4.6), indicating species' seasonal diameter response should be interpreted separately for the levels of species and gap environment. Unlike height investment strategy, species' diameter investment varied between locations (from south-centre–north, $P < 0.001$, Table 4.7) within the gap. For example, the pattern of investment pattern for subalpine fir looks strikingly different than that of other species (Figure 4.7). This species makes a substantial early investment at the gap-center, followed by a sharp drop at the edges. In comparison, highly shade intolerant lodgepole pine invests more or less uniformly across the gap. Diameter investment strategy between the two moderately shade tolerant species, Douglas-fir and white pine also didn't match; while Douglas fir, showed a trend of increasing early investment from south to north edge, for white pine, it peaks at the centre and then gradually declines toward the edges. For highly shade tolerant Engelmann spruce, the trend in early diameter investment is opposite to that of Douglas-fir. Engelmann spruce starts with a lower investment at the north edge, which then increases toward the centre and remains the same at the south edge (Figure 4.7).

Table 4.6. Results from mixed model analysis of variance testing for effects of species, gap-position and season on % diameter growth increment (See Equation 4.2). See Table 4.7 for parameter estimates.

Factor	**numDF**	**denDF**	**F-value**	**P-value**
Intercept	1	142	84.32	< 0.001
Species	4	67	1.64	0.17
Gap-environment	2	67	9.63	< 0.001
Period	1	142	2.46	0.1200
Species × gap-environment	8	67	2.48	0.02
Species × period	4	142	3.28	0.01
Gap-environment × period	2	142	19.26	< 0.001
Species × gap-environment × period	8	142	4.97	< 0.001
Levels of species with their codes are: lodgepole pine (PL); Douglas-fir (FD); western white pine (PW); Engelmann spruce (SE); subalpine fir (BL). Levels of gap-environments are: south edge (D1), centre (D2) and north edge (D3) and periods are defined as early (P1, mid-May-mid-July) and late (P2, mid-July-mid-September).				

Table 4.7. Coefficients for the fixed effects variables of the mixed model assessing seasonal diameter growth with respect of gap-environment and species' shade tolerance (See Equation 4.2).

Variable	Coefficient Value	Std.Error	DF	t-value	P.value
Intercept	56.88	6.51	142	8.73	< 0.001
PL	6.25	9.21	67	0.68	0.50
FD	14.96	8.41	67	1.78	0.08
PW	13.75	9.21	67	1.49	0.14
SE	21.13	9.95	67	2.12	0.04
D2	25.63	7.83	67	3.27	< 0.001
D3	-7.88	11.28	67	-0.7	0.49
P2	-13.75	9.21	142	-1.49	0.14
PL × D2	-23.63	11.18	67	-2.11	0.04
FD × D2	-23.4	10.41	67	-2.25	0.03
PW × D2	-20.08	12.66	67	-1.59	0.12
SE × D2	-23.83	12.32	67	-1.93	0.06
PL × D3	9.75	13.92	67	0.7	0.49
FD × D3	21.04	13.48	67	1.56	0.12
PW × D3	7	14.07	67	0.5	0.62
SE × D3	0.13	16.39	67	0.01	0.99
PL × P2	-12.5	13.03	142	-0.96	0.34
FD × P2	-29.92	11.89	142	-2.52	0.01
PW × P2	-27.5	13.03	142	-2.11	0.04
SE × P2	-42.25	14.07	142	-3	< 0.001
D2 × P2	-51.25	11.07	142	-4.63	< 0.001
D3 × P2	15.75	15.95	142	0.99	0.33
PL× D2 × P2	47.25	15.8	142	2.99	< 0.001
FD × D2 × P2	46.81	14.72	142	3.18	< 0.001
PW × D2 × P2	40.17	17.9	142	2.24	0.03
SE × D2 × P2	47.65	17.42	142	2.74	0.01
PL× D3 × P2	-19.5	19.69	142	-0.99	0.32
FD × D3 × P2	-42.08	19.06	142	-2.21	0.03
PW × D3 × P2	-14	19.9	142	-0.7	0.48
SE × D3 × P2	-0.25	23.18	142	-0.01	0.99

Levels of species with their codes are: lodgepole pine (PL); Douglas-fir (FD); western white pine (PW); Engelmann spruce (SE); subalpine fir (BL); levels of gap-environments are: south edge (D1), centre (D2) and north edge (D3) and periods are defined as early (P1, mid-May-mid-July) and late (P2, mid-July-mid-September).

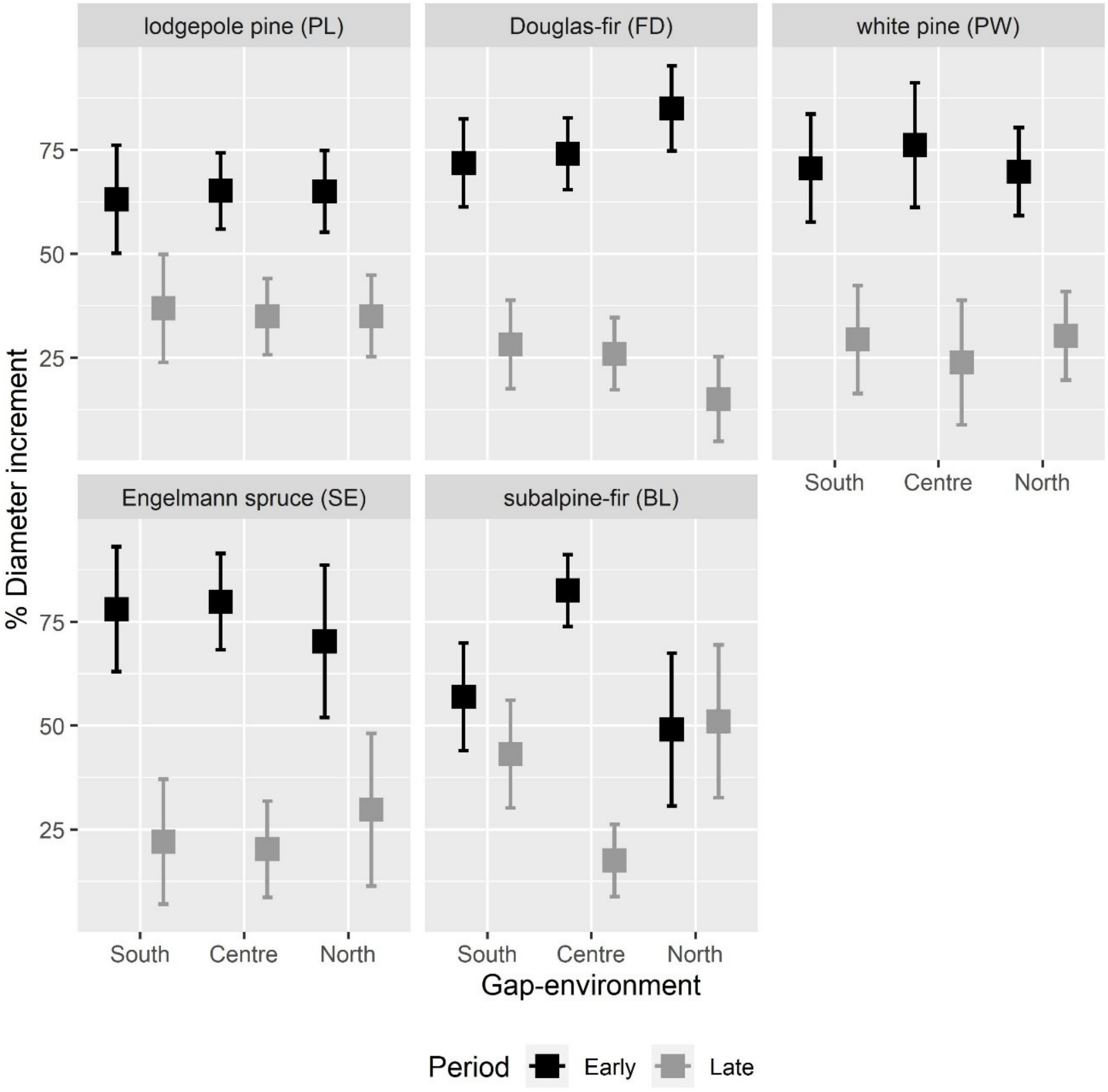

Figure 4.7. Seasonal distribution of annual diameter growth (May-September) with changing locations within the 50 m wide strip for five species with differing shade tolerance. Levels of gap-environments are: south edge (D1), centre (D2) and north edge (D3) and periods are defined as early (P1, mid-May-mid-July) and late (P2, mid-July-mid-September). Error bars indicate 95% confidence intervals around the mean diameter response.

Table 4.8. Seasonal differences (early versus late) in diameter growth response of five species with contrasting shade tolerance within each gap-environment. Levels of species with their codes are: lodgepole pine (PL); Douglas-fir (FD); western white pine (PW); Engelmann spruce (SE); subalpine fir (BL); Levels of gap-environments are: south edge (D1), centre (D2) and north edge (D3) and periods are defined as early (P1, mid-May-mid-July) and late (P2, mid-July-mid-September).

Gap-env.[1]	**Comp**[2]	**PL**		**FD**		**PW**		**SE**		**BL**	
		Est[3]**.**	**P**	**Est.**	**P**	**Est.**	**P**	**Est.**	**P**	**Est.**	**P**
D1	P1-P2	26.25	0.13	43.67	< 0.001	41.25	< 0.001	56.00	< 0.001	13.75	0.89
D2	P1-P2	30.25	< 0.001	48.11	< 0.001	52.33	< 0.001	59.60	< 0.001	65.00	< 0.001
D3	P1-P2	30.00	0.001	70.00	< 0.001	39.50	< 0.001	40.50	0.07	-2.00	1.00

[1] Gap-environment
[2] Comparison
[3] Estimate

The magnitude of seasonal differences (early versus late) in diameter response was also examined to see if the pattern can be related to differences in species' shade tolerance. In the light limited south edge (D1), species' can be ranked in the following order (from high to low): Engelmann spruce > Douglas-fir > white pine > lodgepole pine > subalpine fir; at the light abundant gap-centre (D2) the rank order changes to : subalpine fir > Engelmann spruce > white pine > Douglas-fir > lodgepole pine; and finally, in the north edge (D3) environment, the order changes to: Douglas-fir > Engelmann spruce > white pine > lodgepole pine > subalpine fir (Table 4.8).

In terms of seasonal contribution, unlike height (76-95%), diameter values varied widely; depending on gap position, the contribution in the early season varied from 49% to 85% (Figure 4.8). Further analysis revealed that seasonal effect on diameter growth was highly variable for highly shade tolerant subalpine fir. At the edges, its diameter growth continued to the end of the growing season, with late season contributing 43% to 51% at the south and north edge respectively. The gap-centre contributed only 18% in the late season for this species (Figure 4.8). Gap-position showed the least influence on the seasonal distribution of diameter growth for highly shade intolerant lodgepole pine. All gap positions contributed were similar for lodgepole pine diameter growth, with late seasonal contribution ranging from 35-37% within the gap. Classified as moderately shade tolerant Douglas-fir had the lowest late seasonal contribution for the north edge, but late season contributed more at the centre (26%) and south edge (28%). A similar pattern of seasonal contribution in diameter response is observed for moderately tolerant white pine and shade tolerant Engelmann spruce. Both species show higher late seasonal contribution to diameter growth for the edges than the gap-centre. Late in the season, white pine had about 29-30% diameter growth at the edges, and about 24% at the centre while for Engelmann spruce, it was about 22-30% at the edges, with north edge contributing 8% more than the south, and at the centre, the late seasonal contribution was about 18%.

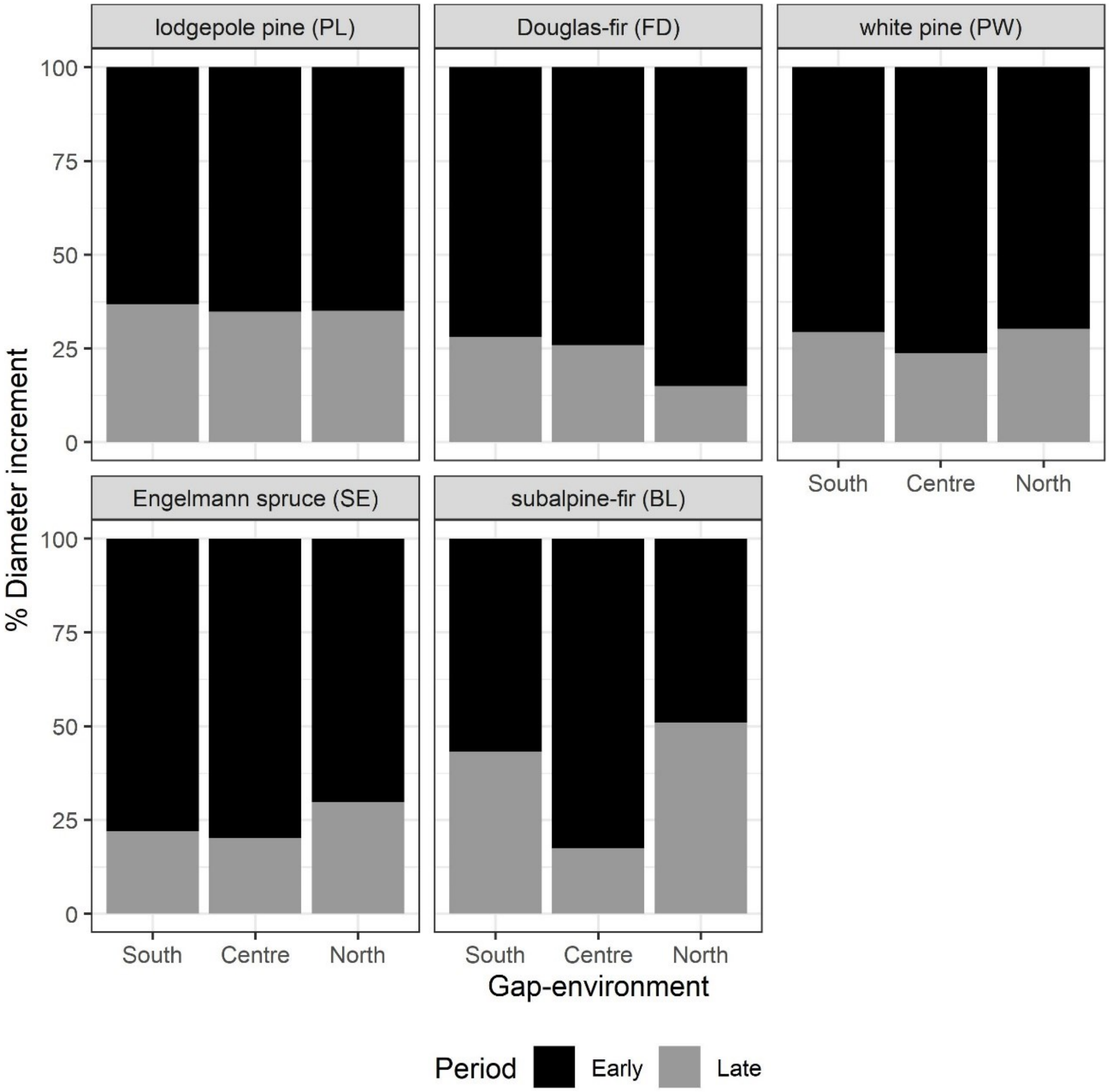

Figure 4.8. Seasonal contribution in diameter growth of five species with contrasting shade tolerance within the growing season. Levels of gap-environments are: south edge (D1), centre (D2) and north edge (D3) and periods are defined as early (P1, mid-May-mid-July) and late (P2, mid-July-mid-September).

4.4 Discussion

4.4.1 Seasonal light distribution pattern within strip-shelterwood gap

In northern latitude forests, the southerly position of the sun shifts the peak of the light availability slightly toward the north of gap centers (Canham et al., 1990; Hossain and Comeau, 2019; chapter 3); this pattern in light has been reported to also vary seasonally (Lieffers et al., 1999; Gendron et al., 2001; Prevost and Raymond, 2012). In this experiment, seasonal patterns (between early and late) in light availability were also apparent (Figure 4.4), thus confirming the findings of the previous studies. However, this study also reports that between the two seasonal patterns, no statistical difference was found due to the large confidence intervals around their predicted lines. Visual interpretation of these patterns confirms what has been reported by Prevost and Raymond (2012). Their study found light reaching the three locations (south, centre and north) within the gaps differed more late in season than early. Interactions between solar elevation angle and the crown of the standing trees at the southern edge cause this seasonality in light distribution within gaps (Canham, 1988; Gendron et al., 2001; Olpenda et al., 2018).

4.4.2 Seasonal dynamics in height growth response within strip-opening

My results confirm the expectation that, despite differences in shade tolerance all species exhibit an early height response (76-95 %) at all positions within the gap. In the early season, the higher light level (Figure 4.4) and timing of soil and air warming and achievement of critical heat sums for budbreak across the gap might have contributed to this. As solar elevation increased during the early season, light level increased at all gap locations due to less crown interception by standing trees of the southern edge, which benefited all species regardless of their shade tolerance (Easter and Spies, 1994; Van Pelt and Franklin, 1999; Gray et al., 2002). This increase in light and temperature at the beginning of the season can be associated with brisk spring bud break and afterwards, a surge in height growth in order to optimize light harvesting and to overcome shading by neighboring trees (Sumida et al., 1997; Franceschini and Schneider, 2014). Jackson et al. (1976) also present similar findings for radiata pine which showed rapid spring/summer growth followed by insignificant or slow growth for the balance of the growing season. Paquette et al. (2012) observed height growth in sugar maple ceasing near mid-summer in two understory light environments-understory (4.9%) and gap (21%), whereas more shade tolerant co-occurring Norway maple continued its extension growth into the late fall. In early summer, highly shade intolerant species in this study (lodgepole pine) also had about 86-93% of its annual growth in height occur in the early season for all light level across the gap. The earlier height growth surge in lodgepole pine was followed by less height growth in the late season (7-15%, Figure 4.5) may be suggestive of absence of polycyclic growth in this species, while for other species, it might be suggestive of diminishing activity in apical meristematic tissues as growing season approaches the end (Jackson et al., 1976).

However, this study also rejects the hypothesis that species will not vary in their pattern of height investment across the gap (all species showing similar spatial trend of height investment). Three-way ANOVA showed significant differences (P ~0.002), suggesting different investment patterns in height growth among species. However, such differences cannot be explained by shade tolerance rankings; for example, in the light limited south edge environment, highly shade intolerant lodgepole pine showed the highest magnitude of inter-seasonal difference (less growth in the late season, only 7% growth was recorded). On the other hand, two highly shade tolerant species, subalpine fir and Engelmann spruce had their highest growth investment early in the season at the centre and north edge location within the gap (93 and 95% respectively). In high light environments, due to their higher competitive ability faster growing species were expected to show a greater surge in height growth than slower growing species, but in low light environments, the reverse pattern was expected. But such patterns were not realized in my data and the reason can be many folds. First, I only examined species' growth responses within the opening (50 m wide strip-cuts), ignoring trees growing under the north and south canopy. Within the strip, growing season light transmittance ranged from 18% (at south edge) to 49% (at the gap centre). Light levels never dropped below a critical level of 2.5-5% at the south edge. Thus, I believe, effect of low light level on growth responses of these species was, therefore, never realized, which might explain the anomalies in height investment patterns observed between shade tolerant and intolerant species. Second, highly shade intolerant lodgepole pine often shows rapid growth at low light environments, as part of its shade avoidance strategy (Henry and Aarssen, 1997). For this reason, at south edge environment, this species might have not shown the expected magnitude of seasonal difference (early versus low) in height growth.

The higher than expected early seasonal height response of the slow growing species (Engelmann spruce, subalpine fir and white pine, on a comparative scale) is not surprising, considering the species selected for this study are all determinate conifers in terms of their height growth. These species generally cease growth around mid to late summer (August) and set their buds for the next growing season, as opposed to indeterminate tree species such as western hemlock or western redcedar. Indeterminate species tend to continue their height growth during the entire growing season; buds flush and shoot elongation of these species are more influenced by the existing microclimatic conditions (i.e., temperature and moisture) within the gap (see Kozlowski, 1964).

Despite the deterministic nature of the tree species examined in this study, as a result of the light distribution pattern I expected that intolerant species would extend their height growth a little longer than mid-summer, particularly in gap environments where light is not limiting. In addition, since the light distribution curve late in the season was flatter, with north edge receiving relatively more light than the south edge the expectation is that these species would extend the period of shoot growth beyond mid-summer. Van Pelt and Franklin (1999) found differences in the period of shoot elongation of one month due to the differences in the amount of light received by different gap environments. In my study, only white pine, a moderately tolerant species, partially meets this expectation for the gap centre location (21% of late seasonal growth). For the other species, late season contributed only 5-16% of their annual height growth in the two light abundant environments. Among all other species, moderately tolerant white pine also has the highest height growth at the south edge late in the season (24%). Other factors, that were not recorded, such as delayed snow melting or late soil warming that may have also impeded the early growth of this (and other) species at the south edge.

The fact that, of all the species, only two species, namely, moderately tolerant Douglas-fir and shade tolerant subalpine fir, showed a seasonal pattern in height response that closely matched to that of the pattern of light availability within the gap (i.e., a gradual decrease in height investment from the centre toward the edges, with north edge exhibiting the second highest height investment in the early season), may imply that only these two species are responsive to the seasonal fluctuations in light than other species. The rest of the species (lodgepole pine, white pine and Engelmann spruce) followed a complex pattern and its explanation requires consideration of other ecological factors besides shade tolerance, such as drought tolerance or tolerances to other stress factors (see the review by Valladares et al., 2016).

4.4.3 Seasonal dynamics in diameter growth response within strip-opening

As expected, a stronger influence of gap environment was detected for the patterns of diameter investment among species (gap environment itself and in a three way interaction is highly significant, $P < 0.001$, see Table 4.6), compared to that observed for height (gap environment alone isn't significant and P value of the three way interaction is 0.002, see Table 4.3). However, the expectation that, under high light environments within the gap (centre and north edge), shade tolerant and intolerant species will exhibit a similar growth strategy (e.g., diameter) but will differ in their magnitudes (of investment) was found only to be partially true. Moreover, the expectation that shade tolerant and intolerant species will differ in their growth strategy at the light limited environment, i.e., south edge, also turn out to be lacking support in my data.

The hypotheses I framed regarding diameter growth strategies are primarily based on species' differences in shade tolerance and their expected carbon allocation strategy, with changing light conditions. I expected that the pattern of diameter investment observed in the high-light environments (centre and north edge) would not match that in the low-light environment (south edge). However, observations from this study indicate the reverse. Furthermore, between the two light abundant environments - gap centre and the north edge - I also expected a fairly similar pattern of diameter investment. Only at the gap centre (highest light environment), the pattern of the intra-seasonal difference observed in the data met the hypothesized pattern (see Table 4.8 & Figure 4.7); but at the edges, it did not. At the south edge, lodgepole pine being a highly shade intolerant species unexpectedly continued its diameter growth till the end of the growing season (predicted response was an early diameter growth response due to increased irradiance level in the early season), and Engelmann spruce being a shade tolerant species exhibited a shorter period in diameter growth (as a shade tolerant species, expectation was a continuous diameter growth as part of allocation strategy of shade tolerance). At the north edge (high-light but prone to heat and drought stress), both moderately shade tolerant, Douglas-fir and highly shade tolerant, subalpine fir deviated from their expected pattern (a continuous investment was predicted, which was supposed to differ in magnitude). For subalpine fir, though this species met the general expectation of continuous growth, but magnitude-wise, this species had a much higher contribution from the late season than other relatively less shade tolerating species such as Douglas-fir, white pine and lodgepole pine. Moreover, for this species, contribution from late season exceeded that of the early season (see Table 4.8 & Figure 4.8). As for Douglas-fir, contrary to the expectation, this species received only15% contribution in diameter growth in the late season at the north edge.

In the previous study (chapter 3), I found that highly shade intolerant lodgepole pine was less impacted by the north and south edge proximities; in addition, this species also performed better across all gap environments, but it was not clear due to what growth strategy (either height or diameter or both) this species was performing better than other species. This species is known as a gap-species; therefore, it is not surprising that this species will exhibit a higher persistent capacity in utilizing available resources for a longer duration of the growing season than other species. A combination of factors, such as less tolerance of shade while also having higher drought tolerance (strong deep root system and lower specific leaf area) along with a greater height growth in early season (higher light harvesting opportunity), may have contributed to its higher investment in diameter growth late in the season. In particular, increased investment in diameter growth would mean greater stability and improved hydraulic conduction for this species. In the relatively drier north edge environment this strategy might convey additional competitive advantages for this species to reach and maintain a dominant position (Burns and

Honkala, 1990; Sherich et al., 2007) in the canopy. Moreover, its continuous diameter growth at the south edge also makes sense if the light level recorded at that edge is taken into consideration (18 %,), this probably allowed continuous support of aboveground growth, together with reduced allocation to roots or storage. Moreover, completing height growth within the early portion of the growing season and then maintaining continual diameter growth in absence of height growth after mid-summer through to the end of the growing season will contribute additional mechanical and hydraulic support (Wood et al., 2015).

Classified as moderately shade tolerant, but relatively less shade tolerant than white pine, Engelmann spruce and subalpine fir, Douglas-fir exhibited a different diameter growth strategy as it relates to gap environment. The magnitude of intra-seasonal difference (early versus late) in diameter response gradually increased going from the south to the north edge for this species. At the north edge, the early spike in diameter growth for this species makes it a less persistent user of growing season resources than lodgepole pine but may also suggest that higher thermal stress and soil moisture deficit late in the season might have impeded its diameter growth more than lodgepole pine. It has been seen in Figure 4.4 that, north edge is receiving a greater contribution of direct light, which can be a likely cause for sufficient tissue dehydration, which could have contributed to less diameter growth for this species late in the season (Kozlowski and Pallardy, 1997). In addition, higher temperatures at the north edge coupled with summer drought on this site and belowground competition from the roots of trees in the adjacent stand could lead to substantial drought stress in the north edge environment.

Moderately shade tolerant species are expected to persist under the light limited conditions but when exposed to higher light level are able to grow more than shade tolerant species, but less than intolerant species. Therefore, these species should have moderate response to fluctuating environmental conditions across the gap (not too extreme like shade intolerant species, and at the same time, not too gradual like shade tolerant species). in this study only white pine consistently exhibited such a pattern (See Figure 4.7 for its intra-seasonal pattern). This species, nearly as shade tolerant as Engelmann spruce, continued to invest in diameter growth, more or less uniformly until the end of the season across the gap (24-30% investment in diameter growth late in the season).

Engelmann spruce, as a shade tolerant species, was expected to perform similar to subalpine fir at the south edge, but this species had only 22% of its diameter growth in the late season at south edge and 30% growth at the north edge. This species is a high elevation species, adapted to cold and humid habitats, with low tolerance to high temperature and drought (Burns and Honkala, 1990). Shade tolerant species usually allocate growth to storage and defense and sacrifice growth under low light environments. After utilizing the initial increase in light during the early season, the reduced light level in the south edge environment late in the season might have prompted this species to adopt a survival strategy by investing into fall carbohydrate reserves that can be used for leaf flush the following spring. At the north edge, light is available for longer period of time and investing more in diameter growth (30% as oppose to 22% at south edge), might be part of the strategy of this species for coping with drought or thermal stresses at the north edge (Poorter and Kitajima, 2007; Imaji and Seiwa, 2010).

The strong influence of gap environment on subalpine fir’s diameter response was unexpected, considering its high shade tolerance. This may be due to its sensitivity to short-term variations in microsite conditions across the gap. In a mixed conifer forest Stephens et al. (2020) found a strong relationship between the establishment of subalpine fir and fine scale variation in environmental factors, with establishment and environment interacting in both space and time. Gap centre and north edge, particularly the centre, is prone to short-term fluctuations in light conditions (the light curves peak around that location with difference in magnitude between early and late season, see Figure 4.4). Such variations in light conditions can cause a shift in the allocation strategy with more carbon being allocated to height than diameter or vice-versa (Noyer et al., 2019). This might explain why this species had more than 80% of its total diameter growth in the early season at the gap centre. A surge in height growth followed by a shorter period of diameter growth may make this species less efficient hydraulically, which could make this species more susceptible to sudden heat or drought stress at the gap-centre. Subalpine fir is well adapted to cool climates and high elevation environments where length of the growing season is relatively short, which might also have prompted this species to adopt such an unexpected diameter growth strategy at the gap centre. In lower elevation ICH zone forests, it commonly grows in the understory of other species. In the south or north edge locations this species invested in diameter growth for a longer length of the growing season (Burns and Honkala, 1990; Klinka and Chourmouzis, 2005), which could have provided greater mechanical and hydraulic safety in these two gap locations, particularly at the north edge where this species has to combat high temperature and drought stress. This species is known to be highly susceptible to high temperature stress (Burns and Honkala, 1990). Thus, late snow melting in the early season at the south edge, and at the same time, higher temperature load at the centre or north edge, might have prompted this species to adopt different growth strategies moving across the gap.

While investment in height growth is strongly linked to species' ability to reach the canopy, investment in diameter growth is essential for providing mechanically stability and physiologically supporting the crown (Sumida et al., 1997; Strand et al., 2006; Franceschini and Schneider, 2014; Rozendaal et al., 2015). Investment in early height growth followed by continuous investment in diameter growth would be a prudent strategy for fast growing species to dominate a gap environment. In that regard, highly shade intolerant species lodgepole pine has a competitive advantage over all other species across the gap. Between the two moderately tolerant species (Douglas-fir and white pine), white pine appears to have adopted a more conservative growth strategy across the gap, showing continuity in its diameter investment throughout the growing season. Through its sustained use of temporally available light this species might be expected to survive and grow steadily within the gap if other factors such as diseases or insects are not limiting. Douglas fir, Engelmann spruce and subalpine fir appear to have adopted growth strategies that are specific to the gap-environment where they are growing. For example, both height and diameter growth early in the season by moderately tolerant Douglas-fir at the north edge may be interpreted as an acclimation strategy adopted by this species to better cope with thermal or drought stresses. Since competitive advantage gained in earlier season by this species in this gap environment might allow this drought tolerant species to allocate growth to roots for the remainder of the growing season. Engelmann spruce and subalpine fir adopted somewhat similar diameter growth strategies at the gap-centre and north edge locations but differed substantially at the south edge. Both of these species are close in shade tolerance and are the least in drought tolerance, therefore, continued investment in diameter growth at south edge can be taken as persistence strategy for both species. Higher diameter and height growth in the early season at the centre and south edge gap environments signals a more complex phenomenon which might require additional study and examination of effects of other growth limiting factors. Current year's height growth of determinate species is influenced by previous year's soil moisture conditions, while diameter growth is strongly related to current year's moisture condition (Collet et al., 2001). Future studies should consider acquiring data on soil and air temperature, vapor pressure deficit, soil moisture and other factors. Since patterns in diameter investment showed stronger responses to changes in gap environments along the north–south transect than height, I conclude that if shade tolerant and intolerant species are to coexist within a small opening like this strip-shelterwood, it will primarily be through their differences in diameter growth strategy.

4.5 Conclusions

Generalizations of the findings in this study are limited, as currently there are no similar studies that can be directly linked to this study. Moreover, data limitations limit the scope of this study to tree species that are only determinate and to this particular study site. A similar type of study involving a mix of determinate and indeterminate tree species with a wide range of shade tolerance could surely have shed more light on the adaptation strategies of tree species as it related to a certain gap environment. Despite such limitations, this study demonstrates differences between species in how they utilize the seasonal variations in light as it relates to specific gap environments. This study illustrates differences in growth strategies (competitive or conservative use of temporally available light) adopted by species of different shade tolerance growing in different gap environments and also illustrates the complexities of responses, even between species with similar shade tolerance ratings. Finally, the range of light conditions created by strip-shelterwood harvesting and the existing temporal variations combined with differences in exploitation by species of different shade tolerance clearly contribute to regenerating a diverse mixture of species in Interior Cedar Hemlock forests.

4.6 Limitations

This study investigated the seasonal distribution height and diameter in relation to light gradient (surrogate of gap-position) at a course scale (measurements were taken over a one-month interval). A finer scale investigation (i.e., hourly, daily or weekly measurements) coupled with physiological measurements (photosynthesis, chlorophyll fluorescence, transpiration) and different measures of biomass allocation to leaves, roots or branches could have shed more light on the differences in acclimation strategies between species, as it pertains to different environments within the gap. Also, light measurements should have been obtained at greater intensity over the space. Within each cutblock, at least 15 spots should have been sampled along the north-south transect. Light measurements were taken as hourly averages; instead, 5-10-minutes averages would have been more informative. Measurement of other environmental factors, including soil temperature, air temperature, vapor pressure deficit, soil moisture and nutrient availability would also be useful in understanding these responses.

The physical demarcation of the 3-gap-environments imposes limitations on the conclusions drawn from this study. I defined the edge environments (north and south) as 10 m distant from the either edges into the opening and the remaining 30 m distance between the two edge environments was defined as gap centre. By averaging growth responses of trees within the 30 m area (34–64 m see Figure 4.1), I am assuming that all trees from the gap centre to the edge environments' outer boundaries (10 m distance from north or south edge) are responding similarly; in fact, it may include samples from gap-environments that represent conditions somewhat in between the centre and the edge. To overcome this limitation, a different modeling approach should be considered like considering positions of the trees as a continuous variable, which I expect to further explore in future.

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5 Chapter 5: Conclusions and Recommendations

Although interest in continuous cover forestry, including shelterwoods or other partial harvesting methods, has been increasing in British Columbia (B.C) and around the world over the last few decades, critical information regarding the design and selection of suitable species for application in various forest ecosystems has not yet fully developed (Day et al., 2011; Mason, 2015; Puettmann et al., 2015; Pukkala et al., 2016; Peura et al., 2018; Bianchi et al., 2020). For example, while the Interior Cedar Hemlock (ICH) Biogeoclimatic zone in British Columbia is a highly diverse ecosystem, where forest stands support a large number of species varying in shade tolerance, there is still uncertainty regarding where mixed species regeneration can be possible with shelterwood systems. Among several variations, a strip shelterwood approach can be a potential option for forest managers to grow highly shade intolerant species in mixtures with highly shade tolerant ones, since in this system an opening is created in the canopy which can allow areas within the gap to receive sufficient light to support the growth of shade intolerant species. Moreover, it has been theorized that a range of light habitats can be created going across the opening leading to microenvironments that support both shade intolerant and moderately shade tolerant species. However, this has not been adequately tested in Interior Cedar Hemlock forests. This research makes an attempt to bridge this knowledge gap, at least partially. In addition, insightful interpretations of the research outcomes can provide a sound basis for managing other gap-based silvicultural systems (Kern et al., 2017), as group shelterwood or selection systems.

To answer the broad question in this research, I primarily applied the concept of niche-based hypothesis, however, also explored the possibility of explaining outcomes in the light of Hubbell's neutral theory (Hubbell, 2001). The niche-based hypothesis has been successfully applied in explaining species coexistence for many forest ecosystems, including temperate forests (see the comprehensive reviews by Valladares et al., 2016 and Avalos, 2019). According to this hypothesis, structure and dynamics of forests are driven by performance trade-offs (e.g., growth rates/survival) along light gradients. Species exhibit trade-offs in growth along the light gradient due to their differences in competition for light and in shade tolerance (Valladares and Niinemets, 2008). Openings created in northern latitude forests usually encompass a range of light conditions, but the magnitude of the range largely depends on the geometry (size, shape and orientation) of the gaps. As species exhibit different competitive ability along that light gradient owing to their differences in shade tolerance, species show specialization for certain portion of the light gradient, i.e., light partitioning. Shade intolerant species are gap colonizers and capable of rapid growth in high light, on the other hand, shade tolerant species are usually late successional species mostly capable of sustained growth (through slow growth) in low light conditions of the understory. In a rich-forest ecosystem, where many species are co-occurring, several species with similar or close competitive ability can overlap in their growth responses along the light gradient. These species may exhibit a considerable degree of niche-overlap and, therefore, might be subject to competitive exclusion.

In the species rich Interior Cedar-Hemlock biogeoclimatic zone in B.C. a larger number of species with a wide range of shade tolerance are found to be naturally co-occurring (Newsome et al., 2010). It is believed that these species coexist due differences in their utilization of resources during the growing season. Shade tolerant species are known to be less competitive in utilizing growing season resources than shade intolerant species (Sumida et al., 1997; Strand et al., 2006; Franceschini and Schneider, 2014; Rozendaal et al., 2015). Shade tolerant and intolerant species also differ in their allocation strategies, tolerant species usually allocate carbon to plant traits that will enhance their chance of survival, on the other hand, shade intolerant species may allocate photosynthates to new growth to gain competitive advantage (Jackson et al., 1976; Pacala et al., 1994; Paquette et al., 2012; Valladares and Niinemets, 2008). These differences in growth strategy between the two tolerant groups need to be explored to improve the understanding of mechanisms underlying species' coexistence within gaps of different sizes, including strip-shelterwood gaps, but so far only a few researches have addressed this issue, particularly in the context of shelterwood gaps in ICH forest ecosystems.

To fill this knowledge gap, I explored three main areas in this study:

1. Since existence of a strong light gradient is fundamental to supporting a mixture of shade tolerant and intolerant species within a gap, its reliable characterization was necessary. Therefore, I began with an examination of ways to characterize the light gradient as accurately and effectively possible (Chapter 2).
2. In chapter 3, as a mechanism of coexistence, I investigated whether separation in growth rate between highly shade intolerant (lodgepole pine, paper birch and Ponderosa pine), moderately tolerant (Douglas-fir and white pine) and highly shade tolerant (Engelmann spruce, western redcedar, subalpine fir and western hemlock,) species becomes apparent in this study, i.e., testing of niche-partitioning hypothesis (Chapter 3).
3. In chapter 4, I investigated whether species' coexistence can be further elucidated through differences in growth strategy between shade tolerant and intolerant species and how it relates to different gap environments. A selected number of shade tolerant and intolerant species were examined for their difference in utilizing the length of the growing season for their respective height and diameter growth across the gap, and if

such differences in growth strategy would translate into giving one species competitive advantage over another, within certain gap environments (Chapter 4).

In Chapter 2, of the methods selected (i.e., hemispherical photographs, LAI-2000, instantaneous estimate of light under sunny and overcast sky condition), studies have reported inconsistent results regarding their ability to characterize light accurately going from one forest ecosystem to the other and finally suggesting that there is no single best method that can work universally across various forest conditions. However, one method that gained the most attention is the use of a diffuse light estimate. Forest understory light conditions are difficult to characterize due to high spatial and temporal heterogeneity. The degree to which understory light varies is affected by different factors such as sky conditions (sunny versus cloudy), seasonal changes in solar angle, canopy conditions (closed/open), gap geometry etc. Since on an overcast day, above canopy light conditions remain fairly stable, with little intra-seasonal change, a diffuse estimate on an overcast day is expected to provide a reliable estimate of the growing season light in the understory. Diffuse estimates derived from other methods such as, LAI-2000 or hemispherical photographic diffuse index, are also expected to provide results similar to the overcast day method in a forest ecosystem. But I argue that since overcast day methods (e.g., diffuse method) do not account for the influence of gap geometry, canopy conditions or sun' seasonal movement (Gendron et al., 2001; Hale and Edwards, 2002) on understory light distribution, in certain forest conditions, this method might not be as effective. For example, the experimental design of this study was subject to a specific geometric orientation (rectangular, long axis going east–west), therefore, a reliable index for this system needs to incorporate the changes in the above canopy light conditions including both sunny days and overcast days, diurnal as well as seasonal changes of solar position and its interaction with the existing canopy (i.e., height and density). In brief, a method that will account for differences in direct beam contribution between microsites (direct beam originates directly from solar disk) will be needed.

Data in this chapter revealed that diffuse indices from hemispherical methods (LAI-2000 and photograph) performed poorly, but direct and total indices (photograph) gave lower variability (lower rmse) and stronger correlations (higher R^2) with growing season transmittance. Photographic methods provided estimates of growing season transmittance, with an R^2 value of 0.82. Sky conditions under which light measurements were recorded by photosynthetically active radiation (PAR) sensors influenced the relationships between PAR sensor indices and growing season transmittance. For example, measuring light around midday on a sunny day provided stronger correlation with growing season transmittance than overcast day measurements. Moreover, rather than using one midday light measurement on a sunny or an overcast day, an average of two measurements increased R^2 and reduced bias while measuring light three times on a sunny day (morning, noon and afternoon) gave the highest R^2 and the lowest variability. Several indices also correlated strongly with monthly light levels, measured from May-September.

Results regarding hemispherical photography corroborate the finding that this method can be a useful tool in providing reliable light estimates in gaps and medium to small openings (Battaglia et al., 2003). This study regarding diffuse estimates, either measured using LAI-2000 (DIFN), or using a PAR sensor on an overcast day or from hemispherical photography, providing higher variability when transmittance was high, indicates that these methods largely ignore the spatial differences in the contribution of the direct fraction between northern and southern sides of canopy openings, as reported by Stadt et al. (1997). Findings regarding sky conditions (sunny versus overcast) affecting the relationship between PAR instantaneous measurements and growing season transmittance emphasize the importance of considering the influence of geographic location, stand structure and opening sizes before selecting a light estimation method. In terms of predicting variability in seasonal light transmittance (for the period of May to August), of the four methods evaluated, except % PPFD on an overcast day, all indirect methods were very effective ($R^2 = 0.77-0.96$). All indices correlated poorly with September light levels, suggesting mid-summer light indices will not be as effective in characterizing the light gradient at the end of the growing season (September) (i.e. measurements will need to be taken in September in order to characterize its light levels). All of the findings in this chapter confirmed my assumption that the overcast day method, despite its simplicity and ease in data collection, may not be adequate for an open canopied system like mine, but may work for closed, homogenous canopy systems where influence of direct beam in minimum. For the strip-shelterwood silvicultural system, I suggest that a light index that incorporates both direct beam and scattered beam light is needed.

Though findings in Chapter 2 contribute valuable information on the reliability of conventional light estimation methods for non-homogenous canopies, I believe, in future expanding this research into the following direction would be beneficial. These light estimation methods should be evaluated across a broader range of gap sizes, shapes, and orientations. In addition, evaluation of effects of latitude, species composition and regional weather conditions should be studied more extensively. The new approach of averaging midday (13:00 h) light measurements for an array of sky conditions distributed across the growing season (mixed sky midday index) should be explored over the full length of the growing season (April - October). I also recommend further evaluation of PPFD measurements taken over a short time period using various available portable handheld sensors (see Jarzyna et al., 2018).

A reliable characterization of the light gradient was fundamental in testing species' niche specialization hypothesis. Therefore, in Chapter 3, the north–south light gradient was characterized using data from the most accurate method, that is data recorded directly and continuously for the entire duration of the growing season on a fixed sensor (Gallium arsenide Phosphide photodiodes, Chapter 2). Measuring light in this way accounted for the varying contribution of diffuse and direct beam light across the gap, and thus should provide reliable characterization of the range of existing light habitats created within strip-shelterwood gaps. To test my hypothesis, growth data for nine species with a wide range of shade tolerance were regressed again the characterized light gradient. The current classification of shade tolerance of the species selected in this experiment are as follows: highly shade intolerant: lodgepole pine, paper birch, and Ponderosa pine; moderately tolerant: Douglas-fir and white pine; and highly shade tolerant: Engelmann spruce, western redcedar, subalpine fir and western hemlock (Niinemets and Valladares, 2006). A trade-off in growth rates between these species along the gradient of light is supposed to promote coexistence of these species, and in Chapter 3, I aim at finding such evidence of trade-off. Moreover, I also investigated species' niche separation in terms of their changing positions along the north–south transect of the gap.

ANOVA analyses provided evidence of trade-offs in species' growth rates along the light gradient ($P < 0.001$). Species' responding to the changes in gap positions along the north–south transect also gave similar results ($P < 0.001$). However, the species' light response curve failed to indicate distinct separation of species into expected clusters of similar shade tolerance. While a few species did separate into a separate cluster along the light gradient, many of the species grew with a parallel slope or showed only subtle differences. However, species' distance (gap-position)-growth model provided more information and more clusters could be identified visually. First, this model revealed that species growth maxima didn't occur at the same gap location. Second, a few distinct clusters could be identified, among them two highly shade intolerant species, lodgepole pine and Ponderosa pine were distinct due to their superior growth response. Douglas-fir, white pine, subalpine fir and western hemlock can be separated as a 2nd cluster from western redcedar, paper birch and Engelmann spruce, forming the third cluster. In the second cluster, western hemlock and Douglas-fir growth responses can be separated as distinct in terms of their peaks and spread of the curve. However, this model also revealed several species with overlapping growth responses and a few species, for example, paper birch and western redcedar, which exhibited a growth pattern contrary to their shade tolerance ranking.

In addition to species separating into a few distinct clusters, a few individual species within clusters also responded in a certain manner which provides further evidence of within gap-partitioning. For example, growth responses of western hemlock and Douglas-fir in the second cluster (see result section and also Figure 3.6 B). Peak and spread of the curve of these two species were different than that of the others. Based on these findings, I conclude that niche partitioning is occurring within strip-shelterwood gaps, to some degree. Two-highly shade intolerant species separating into a cluster distinct from others is the evidence that this within gap-partitioning process is largely driven by species' differences in their competitive ability for light.

However, co-occurrence of species with similar competitive ability and shade tolerance may provide no evidence of niche partitioning in an ecosystem. This is particularly true for species-rich ecosystems like ICH where many species are supported together (Wright et al., 2003; DeLong et al., 2005; Lilles et al., 2014; Valladares et al., 2016). Weak evidence of niche partitioning might mean competitive exclusion of species, and lack of coexistence in the community. However, neutral theory (Hubbell, 2001), where all species are assumed equivalent in their competitive ability, explains species' coexistence within a local stand based on demography and dynamics of the neighboring community. A tree lost due to death at a local scale, will be replaced by the migration of propagules from the surrounding community, limited by dispersal or recruitment (Molino and Sabatier, 2001; Gravel et al., 2006; Nishimura et al., 2010; Valladares et al., 2015). However, tree species in this study are all planted, and data suggest evidence of niche-partitioning; yet, the possibility that both mechanisms are working simultaneously cannot be ruled out. Particularly, species that are ecologically similar (shade tolerance), may still maintain their presence at a local stand through neutral processes as described previously (see Gravel et al., 2006). In addition, niche-specialization is the process by which shade intolerant species can avoid competitive exclusion by more shade tolerating species.

Despite a few anomalies, results in this chapter indicate that the strip-shelterwood method can support mixed species regeneration based on the following: 1) two highly shade intolerant species (Ponderosa pine and lodgepole pine) did grow at a faster growth rate than other species; 2) two moderately shade tolerant species (Douglas-fir and white pine) eventually surpassed the growth of other more shade tolerating species as the distance increased from the south edge; and, 3) the overlaps in species growth responses observed in this study were mostly between species that are similar in shade tolerance ranking and should not be deemed as problematic in maintaining species coexistence. Moreover, this study revealed more information on how to match species to their suitable location within the gap and thus minimize species' mortality. With this information, species can be planted in their suitable locations within the strip-cut opening.

In future, I recommend this study (Chapter 3) should be expanded in the following direction: the competition or facilitation effect on the regenerating trees from the surrounding north and south edges should be examined; proper quantification of edge influence on species growth is also something that can have profound consequences in terms of maintaining species composition and projecting growth and yield of the stand. Thus, rather than drawing a general conclusion from a short-term study, it is important to monitor changes in edge influences over time. Moreover, effects of diseases (root disease such as *Armillaria ostoyae* are prevalent in this area) and their influence on mortality should be examined in future research.

Findings in chapter 3 clearly indicate that gaps of the size and shape used in this experiment have the potential to support mixed species regeneration. Gap environments are spatially and temporally heterogeneous; at a certain portion within the gap, ecological conditions may be conducive for certain species to maximize their growth potential, but in other areas, severe conditions (high temperature, soil moisture deficit etc.) may adversely affect their growth. In response, species must alter their growth strategy (i.e., height or diameter) to overcome such adversity (Givnish, 1988; Motallebi and Kangur, 2016). Therefore, in chapter 4, the focus of my investigation was how shade tolerant and intolerant species differ in how they utilize the growing season for their respective height and diameter growth across the gap, and if such differences in growth strategy would translate into giving one species a competitive advantage over another, at least within certain gap environments.

For the purpose of this experiment, I selected five species (chapter 4) of determinate growth habit but varied widely in their shade tolerance (highly shade intolerant lodgepole pine, moderately tolerant Douglas-fir and white pine, and highly shade tolerant Engelmann spruce and subalpine fir). Though species differed in their height investment pattern spatially, all species were similar in exhibiting an early surge in height growth. In contrast, gap environment exerted a strong influence in species diameter investment strategy (a much smaller P value from ANOVA analysis in case of diameter than height growth), an indication that species' coexistence within strip-shelterwood may be driven by the differences in their diameter growth strategy. However, considering the fact that investment in height growth is strongly linked to species' ability to reach the canopy, investment in diameter growth is essential for providing mechanically stability and physiologically supporting the crown (Sumida et al., 1997; Strand et al., 2006; Franceschini and Schneider, 2014; Rozendaal et al., 2015), a heavy investment in early height growth followed by a continuous investment in diameter growth would be a prudent strategy for fast growing species to dominate a gap environment. In that regard, highly shade intolerant species lodgepole pine will have the competitive advantage over all other species across the gap. Between the two moderately tolerant species (Douglas-fir and white pine), white pine appears to have adopted a more conservative growth strategy across the gap, due to continuity in its diameter investment throughout the growing season. This species, through its sustained use of temporally available light, might be expected to survive and grow steadily within the gap, if other factors such as diseases or insects are not limiting. Douglas fir, Engelmann spruce and subalpine fir appear to have adopted a growth strategy that is more gap-environment specific, and subject to complex interpretation. For example, both height and diameter growth early in the season by moderately tolerant Douglas-fir at the north edge may be interpreted as an acclimation strategy adopted by this species to better cope with thermal or drought stresses.

Engelmann spruce and subalpine fir adopted similar diameter growth strategies at the gap-centre and north edge locations but at the south edge, their diameter growth strategies differed substantially. Both species are close in shade tolerance and have low drought tolerance; therefore, continued investment in diameter growth at the south edge can be taken as a strategy of persistence for both species. However, their surge in both diameter and height in the early season at the centre and south edge gap environments signals a more complex response which indicates a need for longer term observation and data on other growth limiting factors. A better understanding of gradients in soil moisture deficit along the north–south transect within the strip-cut gaps would be useful. This should include examination of growing conditions in preceding years, as it has been reported that height growth of determinate species is influenced by previous year's growing conditions, including soil moisture deficits; in contrast, diameter growth is related to current year's microclimatic conditions (Collet et al., 2001).

Differences in acclimation strategies (competitive or conservative use of temporally available light) adopted by species of different shade tolerance at different gap environments are evident in these results which also illustrate the complexities of responses, even between species with similar shade tolerance ratings. Finally, the range of light conditions created by strip-shelterwood harvesting and the existing temporal variations combined with differences in exploitation by species of different shade tolerance reinforces my conclusions from chapter 3 that regenerating a diverse mixture of species in Interior Cedar Hemlock forests through strip-shelterwood systems is a viable option.

Along with reporting the core findings of chapter four, I also want to mention the possible areas that can be further explored in future to shed more light on species' acclimation strategies within small and medium sized openings. Without examining the eco-physiological behavior of species of different shade tolerance, and linking their physiological responses such as photosynthesis, respiration, transpiration etc. to their annual growth and seasonal growth patterns, the conclusion drawn from chapter four might not be complete. Therefore, future research in this area should consider eco-physiological modeling of these species encompassing other environmental variables besides light, such as soil moisture, relative humidity, air and soil temperature, key soil nutrients etc. A parsimonious model integrating key atmospheric (light and air temperature) and edaphic factors (soil temperature, moisture, and vital nutrients etc.) would certainly increase our understanding of species establishment and growth in various locations within strip-shelterwood openings.

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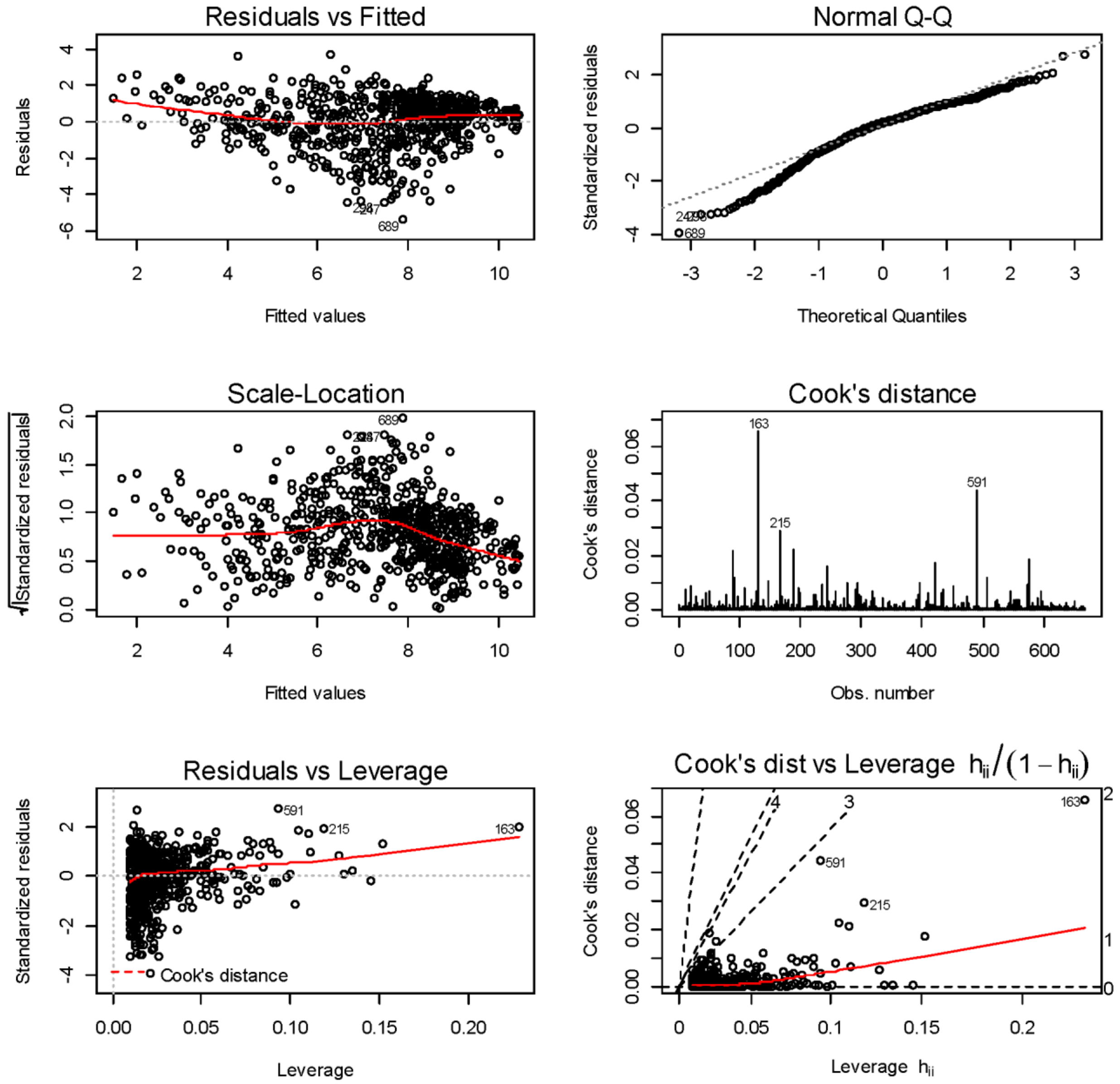
Appendices

Appendix A: Chapter 3 model assessment plots

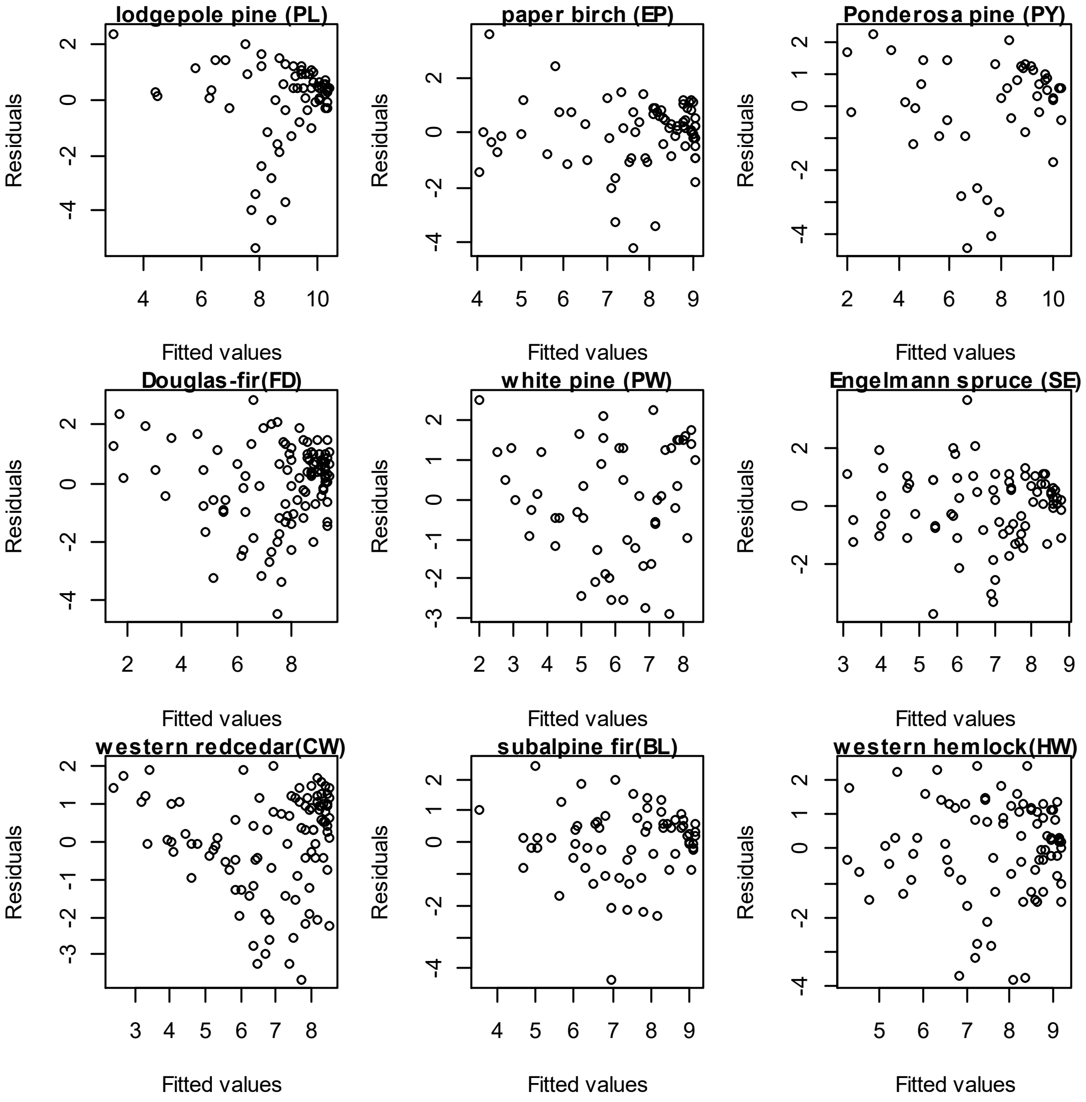
Residual plot of Equation 3.3

Log (volume) ~ intercept + log (light) + species + log (light)*species + error 3.3



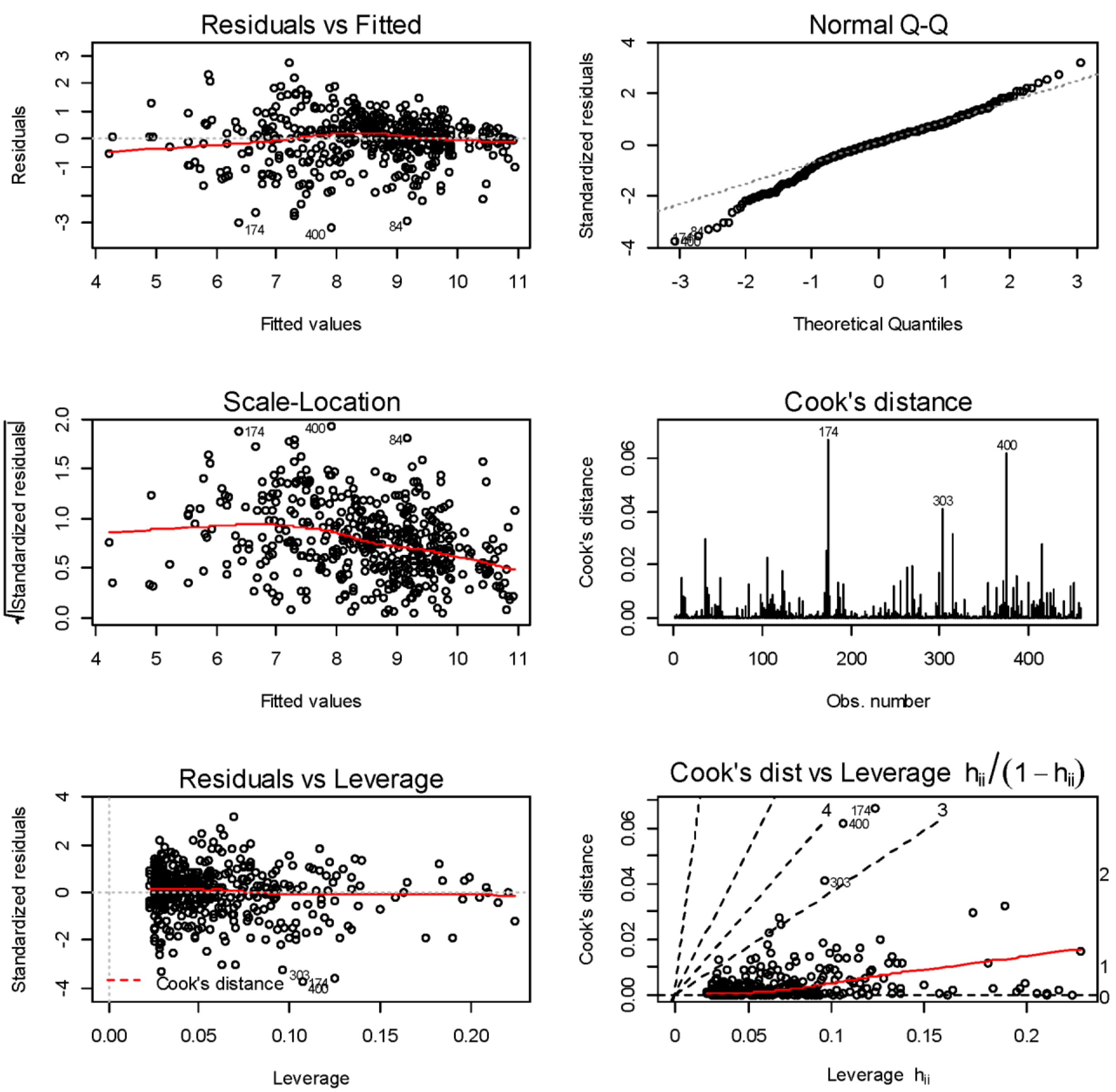
Residual plots of Figure 3.4 (for individual species)

Model: Log (volume) ~ intercept + log (light) + error



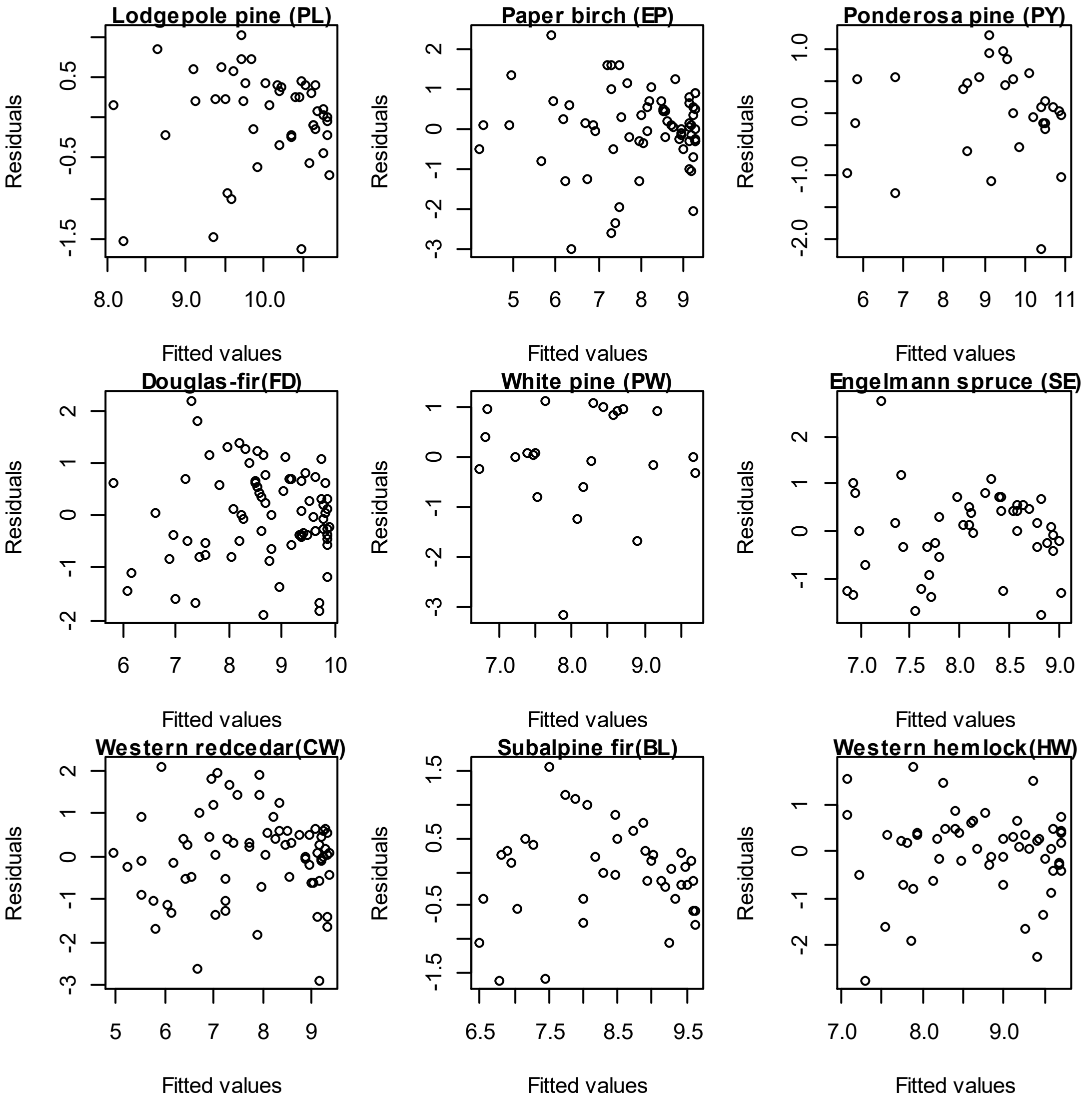
Residual plot of Equation 3.4

Log (volume) ~ intercept + species + distance + species*distance + species*distance^2 + error 3.4



Residual plots of Figure 3.5 (for individual species)

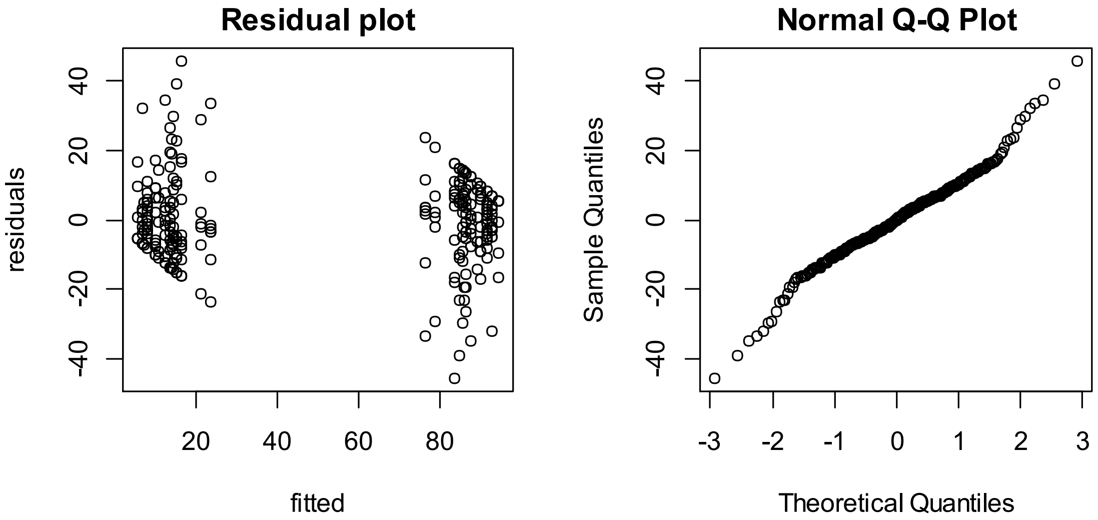
Model: Log (volume) ~ intercept + distance + distance^2 + error



Appendix B: Chapter 4 model assessment plots

Residual plot of Equation 4.2 (Height model)

% Height ~ species*gap-environment*period, random = ~1|tree_id/year 4.2



Residual plot of Equation 4.2 (Diameter model)

% Diameter ~ species*gap-environment*period, random = ~1|tree_id/year 4.2