

**Juvenile growth of subalpine fir (*Abies lasiocarpa*) in the  
Montane Spruce Ecological Zone of British Columbia Canada**

by

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## **Abstract**

Subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) is a widely distributed western North American conifer that can grow under a wide range of light environments, initial densities and site qualities. It can be a major component of stands found within the Thompson Dry Mild variant of the Montane Spruce ecological zone (MSdm2) in the southern interior of British Columbia, Canada. In chapter 2 of this dissertation, I examined the effects of light, moisture, nutrients and neighbor density on juvenile subalpine fir growth. This led me to conclude that: 1) light availability had the largest influence on juvenile tree growth; 2) Delta-13C was the second most important growth predictor; 3) tree size also improved growth predictions; 4) soil moisture was a weak growth predictor; 5) foliar N levels did not improve growth predictions; and 6) density, as expressed as stems/ha, improved growth predictions negligibly. The results from chapter 2 helped to determine the important predictor variables (light and tree size) that were used in investigating the importance of spatially explicit competition on the development of juvenile trees (chapter 3). The chosen spatial model utilized tree size and the crowding effect of neighbors to predict juvenile radial growth. This model was then incorporated into SORTIE-ND as a new juvenile growth behavior, “Juvenile NCI Growth”, and used to test whether juvenile or mature trees have a greater competitive influence on juvenile subalpine fir growth under three basal area classes. Here, I found that juvenile radial growth was faster under the canopy of mature trees than in the neighborhood of similar sized juveniles at the two lowest density classes, 7 and 20 m<sup>2</sup>/ha. This indicated that symmetric competition processes dominated. I also found that at the highest density class, there were no differences in juvenile radial growth between the two neighbor strata.

Chapter 4 was designed to test the influence of site series on growth predictions using SORTIE-ND. I found that site series did have an influence on the growth and development of the stand, as would be expected, which suggests that incorporating site quality into SORTIE-ND would improve growth and yield predictions.

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## **Chapter 1: Introduction**

Management of forest ecosystems for sustainable timber production and associated ecosystem services requires an understanding of the relative role of different resources on the growth and development of juvenile trees. Availability of light, nutrients and moisture plays an important role in the growth and mortality of seedlings and saplings. Of particular interest to researchers has been the role of light in the growth of juvenile trees because of its importance in physiological processes, such as photosynthesis (Canham 1988; Klinka et al. 1992; Chen et al. 1996; Williams et al. 1999; Duchesneau et al. 2001; Grassi and Giannini 2005). Although only a small fraction of solar energy is captured in photosynthesis, growth of juvenile trees is closely related to the amount of radiation absorbed in the absence of other limiting factors (Kozlowski 1991). In individual trees, light interception is influenced by the forest light environment, crown architecture, structural characteristics of branches, and leaf morphology (Messier 1999). Therefore, a species' ability to adapt morphologically and physiologically to changes in the forest light environment often determines its ability to grow and survive, particularly in low light conditions. This is often referred to as a species' shade tolerance, where generally more shade-tolerant species exhibit greater survival than less shade-tolerant species in light-limiting environments (Oliver and Larson 1990; Kobe and Coates 1997). Knowledge of the interspecific variation in shade tolerance of different tree species is often used to explain and predict patterns of forest succession.

Soil moisture also plays a significant role in the growth and distribution of juvenile trees. Drought and water deficits can cause stomates to close, thereby limiting transpiration and photosynthesis, which reduce growth and can eventually cause

mortality. Zanher (1968) reported that up to 80% of the variation in diameter growth of trees in humid areas (and up to 90% in arid areas) can be attributed to variations in moisture availability. The ability of trees to grow and survive in areas that suffer from moisture deficits depends upon their ability to maintain a positive water balance. Many tree species have developed adaptations to promote water homeostasis either by restricting water loss from the plant body or by increasing water absorption to replace losses by respiration (Kozlowski 2002). These interspecific differences in drought tolerance play an important role in the distribution of species along a moisture continuum.

Mineral nutrients play many roles in plants, functioning as constituents of plant tissues, regulators of osmotic potential, constituents of buffer systems, activators of enzymes, and regulators of membrane permeability (Kozlowski 1991). Of the mineral nutrients, nitrogen (N) is the nutrient that plants require in greatest quantity and that most frequently limits growth in natural systems (Chapin et al. 1987). Nitrogen is of particular importance to photosynthesis. Many studies have identified the strong link between leaf N concentration and maximum photosynthetic capacity (Reich 1995; Field and Mooney 1986). When N is in limited supply, trees often have difficulty synthesizing important enzymes such as Rubisco, resulting in reduced photosynthesis and tree growth.

There has been a great deal of research investigating the responses and adaptations of seedlings and saplings to a single resource (e.g., light), but it is likely that multiple resources interact simultaneously to limit or promote juvenile tree growth. For example, there is evidence that, for many tree species, addition of water and nutrients increases growth, but only above certain light thresholds (Canham et al. 1996; Drever and

Lertzman 2001). The relative importance of different resources for juvenile tree growth shifts across resource gradients, and it is therefore necessary to identify resource availability, interactions and thresholds to predict growth patterns. Identification of such interactions and thresholds may be further complicated by the fact that trees can adjust resource acquisition to capture the most limiting resource. When conducting multiple resource studies, the distribution of carbon (i.e., to shoots and roots) shifts across resource gradients, and therefore measures of total plant biomass may be better determinants of tree growth than individual stem or root measurements (Canham et al. 1996).

Competition is a negative interaction between two or more organisms that reduces the availability of resources to each other or other individuals (Chapin 2002). It can have a profound influence on the availability of light, moisture, and nutrients and subsequently juvenile tree growth. As a result of competitive interactions with other trees, seedlings and saplings often undergo morphological and physiological changes to compensate for the reduction in one or more resources (Takahashi 1996; Peterson 1997). The magnitude of these changes largely depends upon the number and size of immediate competitors and whether their resource requirements are proportional to their size (Weiner 1990).

Although it is well known that density of neighbors has an influence on tree growth (Harper 1977; Lavigne 1988), it is not well understood if the effect is equal either across single or multiple resource gradients.

Understanding growth and mortality is critical for predicting juvenile tree regeneration (Harcombe 1987) and therefore is key to the successful application of any silvicultural system (Smith 1986; Nyland 2002). Our social requirement to manage ecosystems sustainably is resulting in increased use of more complex silvicultural

systems than simply clearcutting. All-aged systems, such as variable retention, tend to promote multi-species stands that are both structurally and spatially heterogenous (Oliver and Larson 1990). There are many benefits to variable retention systems, including provision of an immediate growing stock, shading and sheltering of seedlings, cover for wildlife, and reduced risk of soil erosion (Kneeshaw et al. 2002). To successfully apply variable retention systems requires an understanding of how juvenile trees grow and survive across a range of canopy retention levels and site qualities. Furthermore, interspecific differences in shade tolerance and other autecological constraints result in interspecific variation in response to partial overstory removal.

The purpose of this dissertation was to examine the growth responses of juvenile subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) to variation in light availability, site quality, and crowding. The empirical relationships derived from the study were then used to develop a new juvenile tree spatial competition index. This model was then incorporated into SORTIE-ND (Canham 2002) as a new juvenile growth behavior, “Juvenile NCI Growth”. Using the modified SORTIE-ND model, I then conducted simulation experiments to test if juvenile or mature trees have a greater competitive influence on juvenile subalpine fir growth. I also investigated the influence of site series on stand growth predictions in SORTIE-ND to simulate a 100-year forecast of a subalpine fir stand. Site series, which classifies site quality based on soil moisture and nutrient availability (Meidinger and Pojar, 1991), is based on topographical and soil morphological properties as well as the presence or absence of key indicator species.

## **Literature review**

### **Influence of light availability on juvenile tree growth**

Light plays an important role in many physiological plant processes, particularly photosynthesis, and has a large influence on the morphological development of plants. During photosynthesis, light energy is trapped by chlorophyll and used to synthesize reduced carbon compounds from carbon dioxide and water. These carbon compounds are then used to support plant growth and maintenance. Light also drives transpiration and controls temperature, which in turn controls the rate at which many chemical reactions occur within plants. Light is also used by trees to trigger developmental events and mark the passage of time.

There are many factors controlling light availability in forest ecosystems, including the stage of forest development, spatial distribution of trees, density of trees, and tree species composition (Messier et al. 1998; Coomes and Grubb 2000). Light availability is often very low in young dense stands at the stem exclusion stage, for example, increasing slightly with stand maturity and canopy gap development. Light transmission to the understory also depends on species composition, increasing for example, with the proportion of broadleaf species in the canopy (Lieffers and Stadt 1994; Messier et al. 1996).

Attenuation of light through the forest canopy has important implications for tree growth. Forest canopies have a large influence on attenuation of light in the 400-700 nm waveband, which is used in photosynthesis. Tree canopies have much less effect on the longer far-red wavelengths (700-800 nm) than shorter wavelengths (400-700 nm), causing the red (655-665 nm) to far-red (725-735 nm) ratio (R:FR) to diminish (Messier

1996). The R:FR in the sub canopy can cause morphological changes in understory trees (Fløistad and Patil 2002).

The morphological response of juvenile trees to light availability varies among tree species (Carter and Klinka 1992; King 1997; Messier et al. 1999; Williams et al. 1999). These morphological responses can include changes in crown architecture, shoot growth and needle morphology. Crown morphology changes more among shade-tolerant than intolerant species across a light gradient (Williams et al. 1999). As light availability decreases, shade-tolerant conifers decrease height growth in favor of lateral branch growth, decrease the number of whorl and inter-whorl branches, decrease their live crown ratio, and increase their specific leaf area (Carter and Smith 1985; Klinka et al. 1992; King 1996). Shade-intolerant conifers, such as pine (*Pinus* spp.), appear unable to make large modifications to their crown morphology, and therefore retain a conical crown form, even in low light conditions (Williams et al. 1999). Research suggests that tree species able to modify their crown morphology are more likely to survive in low-light conditions (Messier et al. 1999; Duchesneau et al 2001). Many tree species have also developed adaptations in needle morphology that allow them to grow and survive in shady understories. For species able to grow in low-light conditions, their shade leaves are thinner, have reduced stomatal density, have a greater specific leaf area, have more chlorophyll per unit fresh weight, and have a lower leaf photosynthetic compensation point and rate at saturation ( $P_{max}$ ) (Kosłowski et al. 1991).

### **Moisture availability and juvenile tree growth**

Water has many important functions in the growth and development of juvenile trees. An adequate water supply is just as essential to the successful growth of trees as

photosynthesis and other biochemical processes involved in the synthesis of carbohydrates and proteins, and their transformation into new tissues (Kramer and Kozlowski 1979). One of the most important functions of water in tree growth is the maintenance of turgidity, which is necessary for cell enlargement, stomatal opening, and for maintaining the form of many plant tissues. Water is also an essential component of the protoplasm, constituting at least 50 percent of the fresh weight of woody plants (Kramer 1969). It is essential for transporting gases, minerals and other solutes throughout plant tissues. Water is also a necessary reagent in photosynthesis and hydrolytic processes such as starch digestion.

Climate, topography, soil texture, aspect, and forest cover all influence soil moisture availability and therefore juvenile tree growth. Climate affects the quantity and phase (rain, snow, hail, sleet or fog) of precipitation falling upon a particular site, and thus is a major determinant of moisture availability. In the case of rain, the amount of precipitation available for infiltration is largely dependent upon the duration of the precipitation event. For all types of precipitation, interception by vegetation can be a major determinant as to how much water reaches the soil. Tree crowns and ground vegetation can intercept large quantities of precipitation that is subject to evaporation (Aston 1979; Klaassen et al. 1998).

Site topography influences soil depth and texture, which in turn influence soil moisture availability. Soils in depressions and on lower slopes commonly have finer soil textures and higher moisture contents than mid-slopes and ridge-tops. The texture of a soil, the proportion of different sized soil particles, is a major determinant of the rate of water infiltration. Coarse textured sandy soils tend to have a high rate of infiltration in

comparison to fine textured soils consisting of silt and clay. However, fine textured soils have large surface areas due to the small particle sizes, resulting in greater water-holding capacity and soil water potential. Under intermediate levels of rainfall, sandy soils tend to be more xeric than finer textured soils (Chapin et al. 2002).

The aspect of a slope influences solar input, which plays an important role in evaporation and transpiration. Water losses due to evaporation, transpiration and sub-surface flow have a significant influence on soil moisture availability. Evaporation refers to the loss of liquid water to the atmosphere. This process requires energy from the sun and an upward flow of water from lower in the soil. Evaporation increases as humidity decreases and temperature increases; wind also hastens evaporation. Transpiration is the loss of water from stomates in plant tissues to the atmosphere due to vaporization. As plants grow, water is absorbed by the roots and translocated up the stem to the leaves. Solar radiation causes moisture to evaporate on the outside of the leaf creating a moisture deficit within the leaf cells, triggering the movement of water from the roots. The resulting moisture gradient around the plant root causes water to move from the soil to the root. This process can have a significant influence on moisture availability depending upon transpiration rates and the amount of surrounding vegetation.

In forest ecosystems where moisture deficits and drought are common, trees adapt to maintain a positive water balance and avoid moisture stress. Many desiccation-avoidance adaptations of woody plants have been identified in leaves (shedding; small or few needles; small, few, and sunken stomata; rapid stomatal closure during drought; abundant leaf waxes; strong development of palisade mesophyll), in stems (twig and stem photosynthesis; low resistance to water flow in vascular plants), and in roots (extensive

root growth; high root:shoot ratios; high root regenerating potential after transplanting) (Kozlowski 2002).

Periods of tree moisture stress can be determined by examining the isotopic composition of plant tissues (Dupouey et al. 1993). During photosynthesis, C3 plants discriminate against the heavier  $^{13}\text{C}$  isotope of atmospheric  $\text{CO}_2$  (Farquar et al. 1982). When trees experience moisture stress, they reduce water loss by closing their stomates, which reduces  $\text{CO}_2$  diffusion between the pore and the atmosphere. The reduction in  $\text{CO}_2$  concentrations within the leaf causes the tree to discriminate less against  $^{13}\text{C}$ , resulting in higher tissue  $^{13}\text{C}$  concentrations (less negative  $\delta^{13}\text{C}$ ). Although moisture availability appears to have a very strong influence on the  $\delta^{13}\text{C}$  of C3 plant tissues (Farquar et al. 1989), other environmental factors such as irradiance and soil nutrient status may also have an influence. The variable light environment in the understory alone, for example, has been shown to cause substantial variation in leaf  $\delta^{13}\text{C}$  values (by approximately 3‰) (Percy and Pfitsch 1991). Warren et al. (2001) found that an increase in irradiance from thinning in pine stands resulted in more efficient uptake of  $^{13}\text{C}$  and higher tissue  $^{13}\text{C}$  concentrations. Increases in soil nutrient status, particularly N availability, have also been found to decrease  $^{13}\text{C}$  discrimination (Sparks and Ehleringer 1997; Livingston et al. 1998). Stable C isotope concentrations may also be influenced by respired  $\text{CO}_2$  below the forest canopy (Sternberg et al. 1989). Berry et al. (1997) found there was no significant difference between the daily mean  $\delta^{13}\text{C}$  values at 15 m ( $-7.77\text{‰}$ ) and 3 m ( $-7.89\text{‰}$ ), but atmospheric  $\text{CO}_2$  was significantly depleted in  $^{13}\text{C}$  closer to the ground surface due to soil respiration, with daily average  $\delta^{13}\text{C}$  values of  $-8.85\text{‰}$  at 5 cm above

ground. The depletion of  $\delta^{13}\text{C}$  near the ground surface may cause leaves sampled near the forest floor to have lower  $\delta^{13}\text{C}$  concentrations regardless of soil moisture availability.

### **Nitrogen plays an important role in juvenile tree growth**

Nitrogen compounds make up a small percentage of the dry weight of woody plants, but are very important in biochemical and physiological processes. Nitrogen is the mineral nutrient that plants require in the greatest quantity and it most frequently limits growth in both agricultural and natural systems (Chapin 1987). Large amounts of N occur in amides, amino acids, nucleic acids, nucleotides, hormones, vitamins, and alkaloids (Kramer and Kozlowski 1979). A major function of N in plants is in the production of proteins, in particular the structural proteins that form the protoplasm. Nitrogen is also a major component of photosynthetic enzymes such as Rubisco, which can account for as much as 25% of total leaf N (Chapin et al. 2002). As a result, photosynthetic capacity correlates strongly with leaf tissue N concentrations (Field and Mooney 1986).

In forest ecosystems, the N utilized by trees largely comes from the decomposition of plant litter and soil organic matter (Chapin et al. 2002). Other possible N sources are biological fixation and atmospheric deposition. Although many forms of N occur in forest ecosystems, trees generally utilize only the inorganic forms, ammonium and nitrate, of which ammonium is commonly preferred because it is already reduced. Factors influencing the N availability for tree growth include: rates of biological N fixation, atmospheric inputs, decomposition rates, nitrogen immobilization, and losses of N due to leaching. Since most inorganic nitrogen in forest ecosystems comes from decomposition, any factor affecting decomposition rates has a large influence on N

availability. The decomposition of litter commonly varies with forest type, nutrient conditions of the soil, aeration, moisture conditions, and temperature (Kramer and Kozloski 1979). Compared with conifer stands, forest floors of broadleaf stands have lower C:N ratios, higher N contents, and less organic matter accumulation (Prescott et al. 2000). Generally, soils that are nutrient-rich have higher decomposition rates, partly because of larger fixed carbon inputs that support a greater abundance of soil microorganisms (Chapin et al 2002). Soil aeration and mixing often cause bursts of microbial activity due to the exposure of previously unavailable organic material (Van Veen and Kuikman 1990). Moisture availability is particularly important to soil microbial activity, and hence N availability. Haynes (1986) found that decomposition rates declined at soil moisture contents below 30-50%. The influence of moisture and temperature on decomposition rates is often most evident following forest harvesting. Harvesting generally increases both soil moisture and soil temperature, and hence microbial activity and decomposition rates (Yin et al. 1989). However, extreme temperatures or desiccation at the soil surface can reduce decomposition rates of surface litter (Prescott et al. 2000).

Nitrogen deficiencies can cause chlorosis or mottling due to impaired synthesis of chlorophyll (Kramer and Kozlowski 1979), which reduces photosynthesis and tree growth. Nitrogen availability can also have a significant influence on biomass allocation and needle morphology. Lowered soil N availability commonly results in higher root:shoot ratios (Wilson 1988; Ingestad 1991; Thomas et al. 1994; Canham et al. 1996; Jose et al. 2002) and changes in crown morphology of juvenile trees. Jose et al. (2002) found that elevated levels of soil N increased total and specific leaf area of longleaf pine (*Pinus palustris* Mill.) seedlings. Their study also suggests that biomass allocation to roots is

more strongly affected by N availability than soil moisture availability, supporting the findings of Canham et al. (1996).

Determining soil nutrient status can be difficult and expensive. Soil sampling is one method commonly used to determine the availability of important macro-nutrients such as nitrogen. However, due to the variability of mineral nutrients in soils, it can be difficult to get a representative sample of soil nutrient status. As a result, foliar nutrient status is often used as an alternative method in determining the availability of important micro and macro-nutrients (Brockley 2001). This sampling technique is based on the concept that the nutrient status of a tree's foliage is a better indicator of the soil nutrients available to that tree. Foliar sampling is generally less expensive than soil sampling and it may provide some insight into the photosynthetic capacity of a tree, since leaf N levels and photosynthesis are positively correlated. However, there are some issues to be aware of when using this technique, particularly when used as an index of soil N availability. Of greatest concern is the variation in leaf nitrogen across light gradients, particularly at low light (Mitchell et al. 1999, Lusk and Reich 2000). Under low light conditions, trees often maintain lower leaf protein levels due to the high respiratory costs of maintaining high tissue protein levels (Chapin et al. 2002). The reduction in leaf protein level helps maintain a positive carbon balance but it may also result in lower leaf N levels, resulting in an underestimation of soil N availability.

### **The influence of competition on resource availability and juvenile tree growth**

Many definitions of resource competition have been suggested but simply stated competition can be thought of as the interactions among plants using the same limited resources. Grime (1973) defined resource competition as “the tendency of neighboring

plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space” and Tilman (1987) stated that his approach is “essentially identical to that stated in Grime’s definition”. However, Grime and Tilman do have different theories regarding the effects of competition on species coexistence and community composition across environmental gradients. In highly productive environments, Grime (1977) suggested that competition is more intense due to having many neighbors and competitors who exhibit rapid growth rates will dominate. Grime also suggests that competition is unimportant in less productive areas and a species ability to tolerate stress determines its overall success. Alternatively, Tilman (1987) argued that competition is important at all productivity levels and what changes are the resources plants compete for: soil resources in unproductive environments and light on more productive sites. Tilman further suggested that in unproductive environments superior competitive ability depends on the ability to drawdown resources to some critical level not tolerated by neighbors.

Competition for limited resources is a major determinant in the successional development of forest ecosystems. Trees often experience different mechanisms and intensities of competition through forest stand development. Weiner (1990) suggests that competition may be symmetrical, where competitors share limited resources in direct proportion to their relative sizes (resource depletion), or it may be asymmetrical, where larger sized competitors acquire a greater portion of limited resources than smaller competitors (resource pre-emption; Weiner 1990). Symmetrical competition is thought to involve competition for soil water or soil nutrients, whereas asymmetrical competition involves competition for light (Newton and Jolliffe 1998).

Since light comes directionally from above, overstory trees can have a suppressive effect on smaller ones by shading (Mori and Takeda 2003). The effect of overstory neighbors on the understory light regime depends upon stand age, stand structure, stand density, and species composition. Generally speaking, multi-storied stands transmit less light to the understory than even aged stands due to the many layers of leaves (Kozlowski 1991). As mentioned previously, species composition of a stand also plays an important role in the amount and type of radiation penetrating the canopy. Some studies have found that light transmission to the understory increases with an increase in the proportion of broadleaves in the canopy. Lieffers and Stadt (1994) found that in west central Alberta, Canada, hardwood-dominated overstories transmitted between 14 and 40% of incoming light while conifer canopies consisting of white spruce (*Picea. glauca* Moench(Voss)) transmitted between 5 and 11% of light.

Competition for mineral nutrients is common in forest stands, and is evident in many thinning experiments where soil and foliar nutrients increased in response to reduced tree density. Thibodeau (2000) found that thinning young balsam fir (*Abies balsamea* (L.) Mill.) stands from 14,400 stems/ha (control) to 3,000 stems/ha increased foliar nitrogen (N) concentrations from 10.2 g/kg N and 15 g/kg N. Similar thinning effects on soil moisture availability have also been observed. Many studies have found that a reduction in tree density resulted in increased soil moisture availability (Aussenac and Granier 1988; Thibodeau 2000). This increase in water availability may only be temporary, however, because thinning can also increase abundance of understory shrubs and herbs (Harrington 2006). Additional evidence of water competition comes from soil

trenching experiments, where reduced root competition resulted in increased soil moisture availability (Harrington et al. 2003; Lindh et al. 2003).

Trees commonly undergo a variety of morphological changes in response to competition. Many sources indicate that, for dominant and co-dominant trees in particular, radial growth increases with reduced tree density while height growth is relatively insensitive to density for most species (Sjolte-Jorgenson 1967; Lanner 1985; Smith 1986; Nyland 2002; Simard et al. 2004). Reductions in tree density also cause tree crowns to expand in width and slow in crown rise (Peterson et al. 1997; Baldwin et al. 2000; Makinon and Isomaki 2004). However, average density on its own may not provide an accurate characterization of the competitive environment. Average density does not adequately describe important factors such as type of neighbors, proximity or spatial arrangement of neighbors, or the size of neighbors. For this reason various competition indices have been used to take these factors into account, in addition to density, when trying to explain the effects of competition on tree morphology (Takahashi 1996; Duchesneau et al. 2001; Grassi and Giannini 2005). Duchesneau et al. (2001) studied the effects of light and intraspecific competition on the growth and crown morphology of balsam fir (*Abies balsamea* (L.) Mill.), and found that these traits were best predicted by a competition index that accounted for the size of the target tree and the percent cover, height and distance to competing vegetation. They found that interspecific competition did not significantly affect growth and crown morphology of saplings receiving less than 25% full sunlight, but it negatively affected relative height growth, relative radial growth and apical dominance ratio for those receiving more than 25% full light. Grassi and Giannini (2005) also found no significant effects of competition on the

morphology of Norway spruce (*Picea abies*) or silver fir (*Abies alba*) saplings growing at light levels below 32%.

### **Silvics of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.)**

Subalpine fir was chosen as the species of interest in this study because of its ability to grow under a wide range of light environments, initial densities and site qualities in the study area. Subalpine fir is a widely distributed western North American conifer, occurring from the Yukon Territory in Canada to Arizona and New Mexico in the United States. In British Columbia (BC), subalpine fir occurs in wet cool temperate, wet montane boreal, and continental subalpine boreal climates (Krajina 1969). Within my study area, subalpine fir typically co-occurs with hybrid white spruce (*Picea glauca* x *Picea engelmannii* [Moench] Voss), lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. Ex Loud) and to a lesser extent trembling aspen (*Populus tremuloides* Michx.) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca* Mirb. Franco). It can germinate and survive on a wide variety of seedbeds, including exposed mineral soil, decaying logs, and undisturbed forest floor. It can also establish on very harsh sites where the soils are shallow, dry, and nutrient poor. Subalpine fir can grow under nearly the full range of natural light intensities, but establishment and early survival are usually favored by shade (Burns and Honkala, 1990). Cui and Smith (1991) found mortality as high as 90% for naturally regenerated 1 year-old seedlings in open sun-exposed sites.

Subalpine fir exhibits a high degree of shade tolerance and it survives better under closed-forest conditions than moderately shade tolerant hybrid white spruce and shade intolerant lodgepole pine. In general, the *Abies* species are more plastic in their shoot and crown morphology in relation to light availability than either spruce or pine

(Dueshesneau et al. 2001). Many studies also report that *Abies* species are better able to curtail height growth and grow laterally at very low light levels, resulting in umbrella shaped crowns (Kohyama 1980; Klinka et al. 1992; Parent and Messier 1995; King 1997). This adaptation increases assimilative capacity and the probability of survival under closed canopy conditions. Differences in shape between the umbrella crowns of low-light saplings and the conical crowns of high-light saplings is particularly noticeable in *Abies* (Kohyama 1980).

Subalpine fir grows in a wide range of densities. On recently disturbed sites with a nearby viable seed source, densities of juvenile subalpine fir have been recorded as high as 70,000 stems/ha. Subalpine fir will also grow across a wide range of site qualities, and is frequently found growing on soils that are too wet or too dry for its common associates. Good growth occurs on lower slopes, alluvial floodplains, and glacial moraines, and at high elevations on well drained, fine- to medium-textured sand and silt loams that developed primarily from basalt, andesite, and shale (Burns and Honkala, 1990). Growth is poor on shallow and coarse-textured soils developed from granitic and schistic rock, conglomerates, and coarse sandstones, and on saturated soils, but subalpine fir also establishes on severe sites, such as lava beds, tallus slopes, and avalanche tracks, before any of its common associates (Burns and Honkala, 1990). Its ability to grow across such a wide range of sites is partially due to its high degree of morphological plasticity.

### **Development of SORTIE-ND**

The SORTIE model was originally developed as a small scale disturbance model in the early 1990's (Pacala et al. 1993; 1996). More recently, the model has been modified, now referred to as SORTIE-ND, and re-parameterized to make population

dynamic forecasts for northern interior mixed species stands (Kobe and Coates 1997; Wright et al. 1998; Canham et al. 1999; LePage et al. 2000; Astrup 2006). Initial development of the model focused on the light-growth relationship for juvenile trees (<10cm diameter at breast height of 1.3 m above ground, dbh), since light has been shown to be predictive of juvenile tree growth (Klinka et al. 1992; Pacala et al. 1994; Wang et al. 1994; Kayahara et al. 1996; Chen 1997; 1998; Coates and Burton 1999; Claveau et al. 2002), and is the resource most easily manipulated by silvicultural interventions. Once juvenile tree light-growth functions were developed, efforts were redirected to determine if there was a relationship between juvenile tree growth and mortality. Kobe and Coates (1997) sampled eight tree species and determined the minimum annual growth increment (for the last 4 yrs.) for each species to stay alive. The growth-mortality functions they developed were consistent with previous categorizations of species into shade-tolerance classes. More recent efforts to develop the SORTIE-ND model have focused on predicting the growth of adult trees (>5 cm dbh) as a function of their competitive environment. In British Columbia, parameter files have been created and tested for “medium” site series in the Interior Cedar-Hemlock and Sub-boreal Spruce ecological zones (Canham et al. 2004; Coates et al. 2008; Thorpe et al. 2010).

## **Overview of the dissertation**

The overall objectives of this dissertation were to: 1) determine the effects of multiple resources (light, water, nutrients) on subalpine fir juvenile tree growth across gradients of canopy retention and site quality, and determine whether the density-growth relationship varied across a range of site qualities (Chapter 2); 2) develop and incorporate

a spatially explicit subalpine fir juvenile growth model into SORTIE-ND and to test if juvenile or mature trees have a greater competitive influence on juvenile subalpine fir growth (Chapter 3); and 3) parameterize the “Logistic growth with size dependent asymptote” juvenile tree growth behavior in SORTIE-ND for juvenile subalpine trees growing in dry, medium and wet site series and to use SORTIE-ND simulations to examine the effects of site series on the growth and development of a subalpine fir stand (Chapter 4). Chapter 2 was designed to examine the growth responses of juvenile subalpine fir to variation in light availability, site quality, and crowding. In Chapter 3, I used the empirical relationships derived from Chapter 2 to develop a new juvenile tree spatial competition index. This model was then incorporated into SORTIE-ND as a new juvenile growth behavior, “Juvenile NCI Growth”, which was then used to examine if juvenile or mature trees have a greater competitive influence on juvenile subalpine fir growth. In my final research chapter, Chapter 4, I investigated the influence of site series on stand growth predictions in SORTIE-ND. Three separate parameter files were developed using the “Logistic growth with size dependent asymptote” juvenile tree growth behavior in SORTIE-ND. The three parameter files were parameterized using juvenile tree data collected from dry, medium and wet sites. The three parameter files were then used to run simulations in SORTIE-ND testing the effects of site series on the growth and development of a subalpine fir stand over 100 years.

## **Chapter 2: Juvenile subalpine fir responses to light, site quality and crowding**

### **Introduction**

Gaining a better understanding of multiple resource limitations on the growth and development of juvenile trees is an important goal of forest dynamics research and underlies design of forest management practices. Factors such as light, nutrients and moisture each play an important role in the growth and mortality of seedlings and saplings. Of particular interest to researchers has been the role of light in the growth of juvenile trees because of its importance in physiological processes, such as photosynthesis, and its influence on tree morphology (Canham 1988; Klinka et al. 1992; Chen et al. 1996; Williams et al. 1999; Duchesneau et al. 2001; Grassi and Giannini 2005). Research suggests that tree species that are able to modify their crown morphology are more shade-tolerant and therefore more likely to survive in low-light conditions (Messier et al. 1999; Duchesneau et al. 2001). This knowledge of the interspecific variation in shade tolerance of different species is often used to explain and predict patterns of stand development.

In addition to light, mineral nutrients such as N play an important role in the growth and development of juvenile trees. According to Chapin et al. (1987), N is the nutrient that plants require in greatest quantity and that most frequently limits growth in natural systems. Nitrogen is a major component of photosynthetic enzymes such as Rubisco, which can account for as much as 25% of total leaf N (Chapin et al. 2002). As a result, photosynthetic capacity correlates strongly with leaf tissue N concentrations (Field and Mooney 1986). Despite the body of scientific research showing that N can limit the growth rate of juvenile trees, very few studies have investigated how natural variation of

N affects tree growth, particularly in conjunction with other resources such as light and moisture availability (Finzi and Canham 2000; Kobe 2006; Walters et al. 2006; Bigelow et al. 2009). Some of these studies have found no significant effects of N availability on juvenile tree growth (Finzi and Canham 2000; Bigelow et al. 2009) while others have found that N influences growth at high but not low light intensity (Kobe 2006).

The growth and survival of juvenile trees is also influenced by soil water availability. Water deficits can cause stomates to close, limiting transpiration and photosynthesis, and reducing growth (Zanher 1968). Soil water is an important determinant in the availability of many nutrients, particularly soil N, where it plays an important role in nitrogen fixation, mineralization, denitrification and leaching. Although soil water deficits can occur at any light level, they are more common at higher light levels where juvenile tree water demand is highest (Canham et al. 1996; Sack and Grubb 2002). Periods of tree water stress can be determined by examining the isotopic composition of plant tissues (Dupouey et al 1993). During photosynthesis, C3 plants discriminate against the heavier  $^{13}\text{C}$  isotope of atmospheric  $\text{CO}_2$  (Farquar et al. 1982). When trees experience soil water stress, they reduce water loss by closing their stomates, which in turn reduces  $\text{CO}_2$  diffusion between the pore and the atmosphere. The closure of stomata and reduction in  $\text{CO}_2$  concentrations within the leaf reduce discrimination less against  $^{13}\text{C}$ , resulting in higher tissue  $^{13}\text{C}$  concentrations (less negative  $\delta^{13}\text{C}$ ). Although soil water availability has a strong influence on the  $\delta^{13}\text{C}$  of C3 plant tissues (Farquar et al. 1989), other environmental factors such as irradiance and soil nutrient status may also be important.

It is well known that the density of neighbors has an influence on juvenile tree growth (Harper 1977; Lavigne 1988). Many studies indicate that, for dominant and co-dominant trees in particular, radial growth increases with reduced neighbor density while height growth is relatively insensitive to density for most species (Sjolte-Jorgenson 1967; Lanner 1985; Smith 1986; Nyland 2002; Simard et al. 2004). Reductions in tree density also cause tree crowns to expand in width and slow in crown rise (Peterson et al. 1997; Baldwin et al. 2000; Makinon and Isomaki 2004).

It is less clear how competition from neighbors effects tree growth across resource gradients. Grime (1977) suggested that competition from neighbors is unimportant in unproductive environments and a species ability to tolerate stress determines its overall success. In contrast, Tillman (1987) suggested that competition is important at all productivity levels and what changes are the resources plants compete for: soil resources in unproductive environments and light on more productive sites.

The density of neighbor trees may be of particular importance to the growth and development of juvenile subalpine fir (*Abies lasiocarpa* [Hook] Nutt.) because of its ability to regenerate at very high densities (Burns and Honkala, 1990). Juvenile subalpine fir was chosen as the species of interest in this study because of its ability to grow under a wide range of light environments, initial densities and site qualities. Subalpine fir is very shade-tolerant (Wright et al. 1998) and can germinate and survive on a wide variety of seedbeds, including exposed mineral soil, decaying logs, and undisturbed forest floor. It can also establish on very harsh sites where the soils are shallow, dry, and nutrient poor. Subalpine fir can grow under nearly the full range of natural light intensities, but establishment and early survival are usually favored by shade

(Burns and Honkala, 1990). In this study, I examined the effects of light, site quality and neighbor density on juvenile subalpine fir growth.

The first objective of this study was to determine the effects of multiple resources (light, water, nutrients) on juvenile tree growth across gradients of canopy retention and site quality. I hypothesized that juvenile tree growth responses to one resource depended on surpassing thresholds in availability of the other resources based on conjectures by Sprengel (1828). The second objective was to determine whether the density-growth relationship varied across a range of site qualities. I hypothesized that neighborhood density effects would be greatest on dry sites where belowground resources are in limited supply.

## **Methods**

### **Study area**

This study was conducted in the southern interior of British Columbia, Canada, near Kamloops (50°40'N, 120°20'W). All samples were collected within the Thompson variant of the Dry Mild subzone of the Montane Spruce biogeoclimatic zone (MSdm2). The MSdm2 is characterized by cold winters and moderately short, warm summers. The mean annual temperature is 0.5-4.7°C (Meidinger and Pojar, 1991). This variant commonly receives 523-669 mm of precipitation annually of which 40-50% falls as snow (Lloyd et al., 1990). The study area is characterized by mid-elevation plateaus and gently rolling slopes. The elevation range of the sample sites was 1250-1500 m.

In the MSdm2, forests located on zonal sites (medium soil moisture regime) commonly consist of mixed stands of subalpine fir, hybrid white spruce and, to a lesser extent, lodgepole pine. The understory is often mossy with a shrub layer composed of

falsebox (*Paxistima myrsinites*), black huckleberry (*Vaccinium membranaceum*) and grouseberry (*Vaccinium scoparium*). The dry sites in the MSdm2 are usually found on ridge crests and areas with shallow soils. Lodgepole pine on these sites is the predominant tree species with a small component of Douglas-fir and subalpine fir. These stands tend to be open with a poorly developed understory consisting of common juniper (*Juniperus communis*) and pinegrass (*Calamagrostis rubescens*). The wet sites support climax stands of hybrid white spruce and subalpine fir. The understory has a patchy shrub layer, composed of black gooseberry (*Ribes lacustre*), birch-leaved spirea (*Spirea betulifolia*) and black twinberry (*Lonicera involucrata*), and a well-developed herb layer. The soils in the MSdm2 are Humo-Ferric Podzols or Dystric Brunisols (Agriculture Canada Expert Committee on Soil Survey, 1987).

### **Field sampling**

To examine the growth responses of juvenile subalpine fir to variation in light availability, site quality, and crowding (neighbor densities), I destructively sampled 304 subalpine fir saplings growing across a resource gradient. To ensure saplings were sampled across different levels of neighborhood crowding, residual canopy over-story, and site quality, I created a 27 cell matrix, consisting of three density classes (low, medium, and high), three light classes (low, intermediate, and high), and three site series. The three neighbor density classes, low (0-20 neighbors), medium (21-80 neighbors) and high (more than 80 neighbors), were used to ensure I had a continuous range of neighbor density data. The same approach was applied to light availability where low (0-33 % full sunlight), intermediate (34%-66% full sunlight) and high (more than 67% full sunlight) light classes were used. The three MSdm2 site series I sampled represent dry (03), medium (01,04), and wet soil moisture regimes (05) as defined by Lloyd et al. (1990).

Site series is an index of site quality based on soil moisture and nutrient availability (Meidinger and Pojar, 1991), and is based on topographical and soil morphological properties as well as the presence or absence of key indicator species. In my study area, soil moisture regime is strongly positively correlated with soil nutrient regime, and hence it was appropriate to represent site series by soil moisture regime alone (Lloyd et al. 1990).

On each site series, seedlings were selectively sampled across a light gradient from fully open to fully closed canopy conditions. Across the light gradient, selected sample trees were subjected to varying levels of neighborhood crowding (densities). Sample trees, hereafter referred to as target trees, were located in the understory of mature stands, canopy gaps, regenerating burns or associated mature remnants, and partially cut and clearcut areas. Areas that had been disturbed within the last eight years were avoided to ensure the measured growth rates were a reflection of the current environmental conditions and not a recent release or suppression event. All field sampling was conducted during the summers of 2004, 2005 and 2006.

The target trees were 1-3m in height (Table 2.1), at least 25m apart (to ensure independence of samples) and were free of defects (forks, crooks, scars, broken leaders, etc.). Each target tree was assessed for total height, root collar diameter (10cm above the ground), dbh and leader increment (1999-2003). To determine total tree age, radial growth and years to 100cm, stem disks were collected at ground level, 10cm and 100cm, respectively. In the lab, a Velmex™ micrometer combined with a Nikon™ dissecting scope was used to measure five years (1999-2003) of radial growth along the shortest and longest axis found between the pith and outermost growth ring; these values were then

averaged per tree. The target tree also served as the center of a fixed 3.99m radius plot, where all neighboring trees (>50cm tall) were spatially mapped using an Impulse Laser™ with Mapstar™ attachment. Neighborhood trees were assessed for species, basal diameter (10cm), dbh and total tree height. Total fixed plot density (stems/ha) was calculated by summing all of the stems greater than 50 cm in height in the 3.99m plot and adjusting that count to a per/ha basis.

To quantify light availability, hemispherical canopy photos were taken at a height equal to 70 percent of the target tree height. Hemispherical canopy photographs allow characterization of the amount of photosynthetically active radiation at a given location (Canham 1988; Frazer et al. 2000). Photos were taken directly over the target tree stump using a tripod mounted Nikon™ Coolpix 5000 digital camera with a Nikon™ FC-E8 0.21x fish-eye lens. GLI, an index of whole growing season light availability, was then computed from each photograph using the GLA 2.0 software (Frazer et al. 2000). This index integrates the seasonal and diurnal distribution of solar radiation transmitted through the canopy into a single index of available light in units of percent of full sun.

To assess soil water and soil nutrient availability, I collected site series, soil volumetric water content, foliar nutrient concentration, and natural abundance  $\delta^{13}\text{C}$  data. Target tree foliage was sampled for C and N concentrations, and these measures were used as indicators of soil nitrogen availability. Soil nitrogen availability has previously been shown as the nutrient best correlated with soil nutrient regime in BC (Klinka et al. 2000). Foliar samples were collected from the top ½ to ¼ of the target tree crowns. Foliar sampling and nutrient analysis were carried out using the procedures described in Ballard and Carter (1985). A Hydrosense™ soil moisture probe was used to estimate

volumetric water content (VWC) around the drip line of each target tree at 0, 120 and 240 degrees and then averaged. The measurements were collected 10-20cm below the surface of the mineral soil horizon. This information was collected for all 304 target trees but due to budget constraints, it was only collected on a single occasion at the end of a dry week in the month of August. I collected continuous soil moisture and available N data rather than using the categorical variables, soil moisture regime and soil nutrient regime. Although this approach may not be as useful for management purposes, my overall objective was to understand the ecological basis of the resource interactions and their relationships with tree growth.

I collected stem wood samples for determining natural abundance  $\delta^{13}\text{C}$  data; this was used as an indicator of water stress experienced by the target trees relative to their growing conditions. This method provides a more direct, less expensive, and more integrated measure of soil water availability to saplings over entire growing seasons than commonly used methods, such as soil water content or xylem water potential measurements. From each stem disc, the growth rings corresponding to the 1999-2003 growing seasons were removed and powdered using a fine metal file. Approximately 2-3 mg of the mixed samples were sent to the Davis Stable Isotope Facility at the University of California for combustion and analysis of carbon content on a ANCA-GSL elemental analyser interfaced to PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK).

## **Analysis**

I developed and tested 12 candidate models that represented the relationship between radial growth and the following variables: 1) size (target tree root collar diameter); 2) site series (dry, medium, and wet soil moisture regimes represented by

dummy variables); 3) light availability (% full sun); 4) nitrogen availability (foliar N (% mass)); 5) soil water availability (soil volumetric water content (%)); 6) neighbor density (stems/ha); and 7)  $\delta^{13}\text{C}$  (‰). Model 1 (Table 2.2) used a basic power function to predict radial growth as a function of target tree size (root collar diameter). Tree diameter accounts for changes in radial increment due to increased circumference as well as accounting for changes in time using dbh as a proxy for age. Therefore, tree size is an important predictor of radial growth (Canham *et al.* 2004, Astrup 2006, MacFarlane and Kobe 2006), and it was included as a predictor variable in all subsequent candidate models. In Model 2, the parameter “a” of Model 1 was allowed to vary by site series (i.e., a factor in R), and both parameters “a” and “b” of Model 1 were allowed to vary by site series for Model 3.

In Models 4, 5 and 6, radial growth was predicted as a function of light (% full sun),  $\delta^{13}\text{C}$  (‰), and neighbor density (stems/ha), respectively. Model 7 predicted radial growth as a function of light and neighbor density. To test whether soil N availability influenced radial growth, a nitrogen term was included in Model 8. A similar approach was taken to test the influence of soil water availability on radial growth (Model 9).

Model 10 included changes in parameter “c” for different site series. This same approach was used in Model 11 to test whether site quality influenced the  $\delta^{13}\text{C}$ -growth curves. Model 12 predicted radial growth as a function of site series, tree size, light and  $\delta^{13}\text{C}$ .

The analysis was conducted using the R language and environment (R Development Core Team, 2006) using a package developed by Canham (2002). For all models, the error terms followed a normal distribution. However, since error variances

were not equal, a variance function where the error variance was a power of the predicted radial growth was included for all models. Maximum likelihood estimates of all model parameters were obtained using simulated annealing (a global optimization algorithm) (Goffe et al., 1994). Akaike's Information Criteria ( $AIC_c$ ) appropriate for small sample sizes (Hurvich and Tsai 1989; Burnham and Anderson 2002) was used to distinguish different functional forms of the model. Using these criteria, models with minimum  $AIC_c$  have the greatest empirical support; models that are within 2  $AIC_c$  units have similar levels of support (Burnham and Anderson 2002).

## Results

As noted, target tree size (i.e., root collar diameter) is an important predictor of radial growth (Model 1, Pseudo- $R^2=0.276$ , Table 2.2). However, this simple power function had the highest  $AIC_c$  (729.1) and was the least predictive model. Models incorporating site series were an improvement over using size alone (Models 2 and 3). For Model 2, parameter 'a' was allowed to vary with site series. Model 2 suggests that radial growth was fastest on medium sites and slowest on dry sites, with little difference between medium and wet sites (Figure 2.1a). To determine whether the impacts of tree size were different across sites, parameter 'b' was also allowed to vary with site series (Model 3). This model improved radial growth predictions over Models 1 and 2 with an  $AIC_c$  of 711.7 (Table 2.2). According to Figure 2.1b, Model 3 showed that saplings responded differently to changes in tree size for different site series. Radial growth was similar for all three site series until trees reached a root collar diameter of approximately 2cm. At that size, the growth curves diverged, with much slower growth occurring on the

dry sites. On the wet sites, radial growth was linear and on the medium sites, radial growth was greater for trees larger than 3cm root collar diameter. Since tree size accounted for approximately 30% of the variation in radial growth, it was incorporated into all subsequent growth models. Although Model 3 provided slightly improved predictions, it was more difficult to modify for other factors impacting growth; as a result, Model 2 was used as the base model and other factors were added to this model.

Of all variables tested, light availability resulted in the greatest improvement over using size and site series (Model 4 versus Model 2); also, light availability was the most predictive of juvenile subalpine fir radial growth (Pseudo  $R^2$ -values improved from 0.301 to 0.742, Table 2.1). Model 4 was modified to test if trees were responding differently to light availability on the three site qualities by allowing parameter 'c' of Model 4 to vary with site series (Model 10). In comparison to Model 4, this resulted in lower  $AIC_c$  values and improved model performance (Table 2.1). Model 10 predicted little difference in the radial growth of juvenile subalpine fir among the three site series at light levels below 30% (Figure 2.2). However, at light levels greater than 30%, radial growth rates on the dry sites were slower than those on the wet and medium sites. Radial growth differed little between the wet and medium sites below 60% light availability. For these juvenile trees, there were no clear signs of a plateau in the light-growth relationship for any of the site series.

To determine whether N availability influenced the light-growth curve, nitrogen was added by allowing parameter 'c' of Model 4 to vary with nitrogen (Model 8). This model did not perform better than Model 4, the simpler light+size+site series-growth model (i.e.,  $AIC_c$ s of Model 4 versus 8 were within 2 AIC units). Thus, inclusion of the

nitrogen-term did not improve model performance. This may be explained by the similarity in mean foliar N levels across site series (1.03% on wet sites; 1.04% on medium sites; 0.99% on wet sites) (Table 2.1). Similarly, soil water availability was added to Model 4; this model (Model 9) did perform better than Model 4 with an AIC<sub>c</sub> of 423.8, indicating that soil water availability affected radial growth. According to Figure 2.3, Model 9 predicts greater radial growth on sites with low volumetric water content. Mean volumetric soil moisture content was considerably lower on the dry (4.4%) and medium (8.44%) sites than on the wet sites (30.75%) (Table 2.1). At all light levels, an increase in soil volumetric water content resulted in slower radial growth rates.

Models that included neighbor density as a factor did little to improve radial growth predictions. In Model 6, neighbor density (stems/ha) was combined with target tree size and site series, resulting in an AIC<sub>c</sub> of 703.7. However, the gain in model performance was much less than the gains from other factors, particularly light availability. Using Model 6, Figure 2.4 shows the trend of decreasing radial growth with increasing neighbor density. Using both density and light as modifiers for Model 7 resulted in a slightly poorer model than adding light only (Model 7 versus Model 4, AICs of 429.6 and 426.1, respectively). Overall, in comparison to light availability, neighborhood density did little in helping determine how the local environment affected resource-growth relationships.

After light,  $\delta^{13}\text{C}$  was the next most predictive variable of juvenile tree radial growth, given size and site series. Using a simple tree size and site series, augmented with  $\delta^{13}\text{C}$  model (Model 5), an additional 35% of variation in radial growth was accounted for relative to Model 2. Figure 2.5 shows that radial growth increased with

higher (less negative)  $\delta^{13}\text{C}$  values. Model 11 was designed to test whether site quality affected the parameter 'g' associated with  $\delta^{13}\text{C}$  in Model 5; the result was a higher AICc (577.8) than Model 5 (573.5) indicating that this more complex model was less precise. There was a wide range of  $\delta^{13}\text{C}$  values (-31 to -24‰) on wet and medium sites but  $\delta^{13}\text{C}$  was consistently greater than -28.9‰ on dry sites (Figure 2.6). Figure 2.6a shows that  $\delta^{13}\text{C}$  values generally increased with light availability across all site qualities. The lower  $\delta^{13}\text{C}$  values (below -29‰) observed on the wet and medium sites occurred at light levels below 37% full sunlight (Figure 2.6a). Figures 2.6a and 2.6b show there was no correlation between foliar N or soil volumetric water content.

The most complex model, Model 12, predicted radial growth from tree size, site series, light availability and  $\delta^{13}\text{C}$ . This model had the lowest AICc (414.8) and accounted for 76% of radial growth variation (Table 2.2). Figure 7 confirms that subalpine fir radial growth was fastest on medium sites. It also shows that faster growth rates were associated with higher  $\delta^{13}\text{C}$  values, and this was true regardless of the level of light availability. The slowest radial growth rates occurred on the dry sites.

## **Discussion**

Of the growth factors investigated in this study, light availability was the best predictor of juvenile subalpine fir radial growth. In a simple growth model consisting of tree size, site series, and light, light availability explained an additional 44% of the variation in radial growth. As others have observed, I found threshold levels of light below which site quality had little influence on radial growth (Carter and Klinka 1992; Canham et al. 1996; Drever and Lertzman 2001; Kobe 2006). This supports the

hypothesis that juvenile tree responses to one resource depend on surpassing thresholds in availability of the other resources. I found that below 30% light availability, site quality had no influence on radial growth. Carter and Klinka (1992) found a similar 30% light threshold for Douglas-fir and western red cedar (*Thuja plicata* Donn. Ex D. Don in Lamb) and Drever and Lertzman (2001) found light was the primary determinant of Douglas-fir growth below 43% sunlight. Many leaf-level studies of species of similar shade tolerance as subalpine fir indicated that the light saturation point (maximum photosynthesis) is reached between 30-40% full sunlight (Koppenaar et al. 1995; Mitchell and Arnott 1995; Man and Lieffers 1997). Klinka et al. (1992) found that changes in subalpine fir morphology begins at light levels above 34%, whereby height increment exceeds lateral increment resulting in increased leaf area. It is thus possible that juvenile subalpine fir growth patterns above 30-40% light may be attributed to changes in morphology and leaf area.

Radial growth rates on dry sites were slower than those on the medium and wet sites at light levels above 30% (Figure 2.2). This is most likely attributed to the low volumetric moisture content on the dry sites given that I was unable to find clear differences in foliar N levels among the three site qualities (Table 2.1). It could also be due to shallow rooting, which may limit the ability of trees to acquire moisture and nutrients on the dry sites. Subalpine fir has a shallow root system, particularly on dry or shallow sites where the depth of root penetration is limited; under more favorable site conditions, subalpine fir develops a relatively deep lateral root system (Burns and Honkala 1990). Slower radial growth on the dry sites may also be attributed to increased carbon allocation to the lateral roots. Many studies have found that water stressed

seedlings have higher root to shoot ratios (Kolb et al. 1990; Canham 1996; Runion et al. 1999; Jose et al. 2003).

The light-growth curves (i.e., Model 4) for wet and medium sites diverged at 60% light with better growth performance on medium sites. Above 60% light, it appears the wet sites were too wet for optimal subalpine fir growth. Even so, subalpine fir is frequently found growing on soils that are too wet or too dry for its common associates and grows best on well drained fine to medium textured sand and silt loams (Burns and Honkala 1990). On wet sites, Carter and Klinka (1992) found that Douglas-fir, western red cedar and western hemlock height increment was restricted unless above-canopy light levels were high. On all three site qualities, there were no signs of a plateau in the subalpine fir light-growth curves, agreeing with several other field studies examining growth as a function of light (Klinka et al. 1992; Wright et al. 1998; Coates and Burton 1999; Drever and Lertzman 2001).

Delta-<sup>13</sup>C was the second most important factor predicting juvenile subalpine fir radial growth and it provided insight into the relative importance of light, water and nutrients in limiting growth. In contrast to soil volumetric content and foliar N, I found a very strong relationship between light and  $\delta^{13}\text{C}$ , which further supports the overall importance of light as a growth regulating factor for juvenile subalpine fir. As found by Kranabetter et al. (2009), my results show a distinct plateau in  $\delta^{13}\text{C}$  at approximately 40% light availability. This plateau once again coincides with the 30-40% light saturation point in leaf-level studies (Koppenaar et al. 1995; Mitchell and Arnott 1995; Man and Lieffers 1997) and supports the possibility that gains in radial growth above 40% light can be attributed to changes in leaf morphology and leaf area as well as leaf physiology.

Delta-<sup>13</sup>C values for juvenile subalpine fir ranged from -30.98‰ to -24.56‰. I found the lowest  $\delta^{13}\text{C}$  values ( $< -28.9\text{‰}$ ) associated with trees growing on wet and medium sites with light levels below 37%. The low  $\delta^{13}\text{C}$  values of these juvenile trees can likely be attributed to lower evaporative demands and transpiration in the low light environment and higher soil moisture availability. Increases in canopy cover generally result in lower understory light levels thereby reducing daytime temperatures and often increasing relative humidity (Chen et al. 1995; Heithecker and Halpern, 2007; Rambo and North, 2009; Robson et al. 2009). Although a fraction of the reduction in  $\delta^{13}\text{C}$  values may also be due to soil  $\text{CO}_2$ , the small height range of my sample trees reduced this possibility, and much of the decrease in isotopic composition was thus likely to be associated with stomatal and photosynthetic effects (Farquhar et al. 1989). Kaufmann (1982) found that stomatal conductance of subalpine fir growing at low light increased with increasing relative humidity, but it is also common for photosynthetic capacity to decline in low light environments (Hodges and Scott, 1968; Chapin et al. 2002; Robson et al. 2009). This suggests that the low  $\delta^{13}\text{C}$  values on wet and medium sites reflected low water use efficiency, but also decreased photosynthetic capacity and relatively high stomatal conductance in the low light environment. These results are supported by other studies that have also found a greater depletion of  $\delta^{13}\text{C}$  in the understory than in gaps (Kranabetter 2008; Robson et al. 2009). The lack of trees with  $\delta^{13}\text{C}$  values below -28.9‰ on dry sites could simply mean that subalpine fir with a low water use efficiency was unable to survive on dry sites. Juvenile trees growing at high light generally had higher  $\delta^{13}\text{C}$  values and therefore higher water use efficiency. According to the linear relationship presented by Farquhar et al. (1982), water use efficiency can increase either

by an increase in photosynthetic capacity, a decrease in stomatal conductance, or a decrease in both with larger declines in stomatal conductance than photosynthetic capacity. In this study, it is likely that trees with higher water use efficiency (higher  $\delta^{13}\text{C}$ ) values had greater photosynthetic capacity at higher light.

On each site quality, faster growth rates were associated with higher  $\delta^{13}\text{C}$  values regardless of light availability. Nguyen-Queyrens et al. (1998) related  $\delta^{13}\text{C}$  values to height growth performance of maritime pine (*Pinus pinaster* Ait.) and found that tree vigor was correlated with high  $\delta^{13}\text{C}$  values. Bigelow et al. (2009) also found higher  $\delta^{13}\text{C}$  values in faster growing conifers. The fastest radial growth rates in this study occurred in trees with high  $\delta^{13}\text{C}$  values growing on medium sites. In comparison to the other sites, the superior growth of these trees can likely be attributed to higher photosynthetic capacity. The slower radial growth rates observed on the wet sites may partially be due to periodic flooding. It is possible that some of the wet sites in this study experience short term seasonal flooding, which could decrease photosynthetic rates and growth (Zaerr 1983; Kozlowski 1984). The slowest radial growth rates occurred on dry sites, where volumetric soil water content was very low. Low soil moisture content often results in decreased photosynthetic capacity, explaining the slow radial growth rates. It is also possible that more carbon is allocated to root systems of juvenile subalpine fir on sites with low volumetric moisture content (Kolb et al. 1990; Canham 1996; Runion et al. 1999; Coomes and Grubb 2000; Jose et al. 2003).

Tree size was an important predictor of radial growth, as expected, both due to the decline in radial increment with increasing circumference, and also because tree size acts as a proxy for age. Many other studies have also indicated the importance of tree size in

modeling annual radial growth (Williams et al. 1999; Duchesneau et al. 2001; Claveau et al. 2002; Astrup 2006; MacFarlane and Kobe 2006, Bigelow et al. 2009; Martin et al. 2010). For this study, the simple size model accounted for 28% of the variation in radial growth. Size models modified by allowing parameters to change with site series (Models 2 and 3) showed that juvenile trees greater than 2cm responded differently on the three site qualities. For trees larger than 2cm, radial growth was fastest on the medium sites and slowest on the dry sites. The slower radial growth rates observed among larger trees on the dry sites could be attributed to decreased photosynthetic capacity, increased carbon allocation to the roots, or a combination of both.

The effect of soil water availability (as measured by volumetric water content) on juvenile tree radial growth was weak. A model that included soil water availability as a predictor performed only marginally better than a simpler light-growth model. Nevertheless, this model suggested that growth was fastest on sites with low volumetric soil moisture content, and that increases in soil volumetric water content marginally reduced radial growth rates at all light levels (Figure 2.3). Here, trees growing slowly under excessive water levels may be driving this weak relationship. Pacala et al. (1994) also failed to observe a significant effect of soil moisture availability when they modeled sapling growth as a function of resources in a northern temperate forest. Rather than these results providing evidence that water was not limiting, the authors suspected that saplings experienced more variation in light than in water availability. When Kobe (2006) modeled sapling growth as a function of resource availability in northern Michigan, USA, he found that soil water availability was a weak predictor of radial growth for two out of four species of hardwoods. In my study, the weak effect of soil

moisture availability on radial growth may be partly attributed to the single soil moisture measurement. Even though I observed distinct difference in soil volumetric water content between site series, it is likely that additional measurements throughout the growing season would have provided a better metric of soil water availability.

Natural variation in foliar N availability did not play a role in juvenile subalpine fir radial growth. Foliar N was collected as a measure of forest nutrition since a number of studies have found a positive correlation between foliar nitrogen and soil fertility (Radwan and Harrington 1986; Wang and Klinka 1997; Kranabetter et al. 2003; Kranabetter 2008). However, the amount of variation in sapling growth explained did not increase when a nitrogen term was added to the light-growth curve. Other resource-growth studies have also found that variation in N availability played little or no role in sapling growth (Finzi and Canham 2000; Bigelow et al. 2009). One possible explanation suggested by Finzi and Canham (2000), which may be applicable here, is that the natural range of variation in N availability is smaller than the potential range of a species growth response.

Models that included neighbor density resulted in small gains in radial growth predictability. I hypothesized that neighborhood density effects would be greatest on dry sites where belowground resources are in limited supply; however, modifying the parameter with density for site series differences did not result in a better model. The model with density did perform slightly better than the simpler size/site series-growth model, with radial growth tending to decrease at higher neighbor densities. When a density term was combined with tree size, site series, and light availability; however, the model performed worse than the simpler tree size, site series, and light model. Other

studies investigating the combined effects of neighbor density and resource availability, such as light and site quality, also found a poor relationship between neighbor density and juvenile tree growth. Fahlvik and Nystrom (2006) modeled the diameter growth of juvenile trees as a function of tree size, site characteristics and stand density and found variables representing tree density and competition were not significant. Duchesneau et al. (2001) examined the combined effects of light, intraspecific competition and size on the growth of balsam fir saplings and also found no significant effect of intraspecific competition on relative growth when they used their entire data set. However, when they divided their data they found intraspecific competition was important to saplings growing above 25% photosynthetic photon flux density.

## **Conclusions**

Light had the largest influence on juvenile subalpine fir growth. Below 30% light availability, site quality had no influence on radial growth, but above 30%, radial growth was fastest on the medium sites and slowest on the dry sites. There was no clear light saturation point on any site quality. Delta-<sup>13</sup>C was also important in predicting radial growth and it provided insight into the relative importance of light, water and nutrients. I found a strong relationship between light and  $\delta^{13}\text{C}$ , which further supports the overall importance of light as a growth regulating factor for juvenile subalpine fir. Delta-<sup>13</sup>C values for juvenile subalpine fir ranged from -30.98‰ to -24.56‰, with the lowest  $\delta^{13}\text{C}$  values (< -28.9‰) on wet and medium sites at light levels below 37%. These low  $\delta^{13}\text{C}$  values may be attributed to lower evapo-transpirational demands in the low light and high soil moisture environment. Higher  $\delta^{13}\text{C}$  values were associated with faster growth rates

regardless of light availability and were most likely due to higher photosynthetic capacity. As expected, tree size was also an important predictor of radial growth, accounting for 28% of the variation in subalpine fir radial growth. The effect of soil water availability (as measured by volumetric water content) on juvenile tree radial growth was weak. A model that included soil water availability as a predictor suggested that radial growth was fastest on sites with low volumetric soil moisture content. However, this model performed only marginally better than a simpler light-growth model. Rather than providing evidence that water was not limiting, these results may indicate that saplings experienced more variation in light than in water availability. Despite the known importance of N in many BC forest ecosystems, natural variation in foliar N availability did not play a role in juvenile subalpine fir radial growth. It is possible that the natural range of variation in N availability was smaller than the potential range of subalpine fir growth response. Lastly, models that included neighbor density only resulted in small gains in radial growth predictability. A model including density did perform slightly better than a simpler size/site series-growth model showing a decrease in radial growth at higher neighbor densities.

The results of this study provide information on the growth responses of juvenile subalpine fir to variation in light availability, site quality, and crowding. This information can aid in the development of silvicultural strategies for subalpine fir growing under a wide range of conditions. This may be of particular use to practitioners developing partial retention harvesting prescriptions or dealing with the after-effects of the mountain pine beetle epidemic where a partial over-story remains. Subalpine fir is a shade-tolerant species making it suitable for fill-planting both natural and post-harvest

regenerated stands affected by the mountain pine beetle (*Dendroctonus ponderosae*), or for under-planting of declining stands. This research suggests that below 60% light availability there is no discernible difference between radial growth on medium and wet sites and below 30% light availability site quality becomes irrelevant. The absence of light saturation points suggests that any reduction in light availability will result in a decrease in radial growth regardless of site quality. The research also suggests that neighbor density was not a strong driver of juvenile tree growth which questions whether density should be managed to increase growth. Maintaining higher initial stand densities benefits tree quality characteristics and helps ensure sufficient stocking in the event of possible increased mortality due to climate changes. Finally, the data collected from this study will form the basis for the development of juvenile subalpine fir growth behaviours for SORTIE-ND, a resource-mediated, spatially explicit, mixed-species forest model.

Table 2.1 Mean, standard deviation (SD), minimum (Min.) and maximum (Max.) statistics for the variables collected for this study.

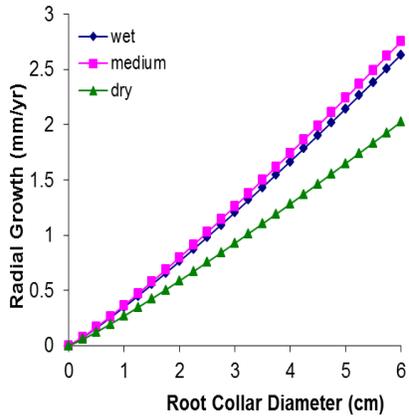
Site series	<i>n</i>		RCD (cm)	dbh (cm)	Height (cm)	Soil water (VWC)	Foliar N (% mass)	$\delta^{13}\text{C}$ (‰)	Light (% full sun)	Radial growth. (mm/yr)	Neighbor Density (stems/ha)	Total Age
wet	103	Mean	3.58	1.99	202.98	30.75	1.03	-28.07	41.30	0.79	7309	44
		SD	1.00	0.84	48.24	23.36	0.15	1.56	23.90	0.52	6082	19
		Min.	1.6	0.2	102	2	0.741	-30.98	8.7	0.0391	200	12
		Max.	5.9	3.9	305	87	1.361	-24.56	94.15	2.1581	26600	102
medium	129	Mean	3.18	1.94	190.85	8.44	1.04	-28.30	35.11	0.66	11929	45
		SD	1.04	0.86	50.74	4.90	0.18	1.46	24.28	0.58	14165	23
		Min.	1.2	0.3	98	3	0.586	-30.89	7.24	0.0397	200	11
		Max.	5.7	4.3	307	30	1.585	-24.58	92.95	2.4437	74200	96
dry	72	Mean	3.39	1.63	182.40	4.40	0.99	-27.34	35.88	0.54	4872	47
		SD	0.93	0.87	50.33	2.03	0.17	0.89	17.78	0.34	4788	22
		Min.	1.1	0.3	93	0	0.568	-28.91	11.33	0.0142	400	15
		Max.	5.2	4	318	11	1.491	-24.74	98.03	1.7061	31200	128

Variable description: *n* = number of target trees, RCD (root collar diameter at 10cm), dbh (diameter at breast height, 130cm), Soil water (VWC = Volumetric Water Content %), Foliar N (% mass),  $\delta^{13}\text{C}$  (‰), Light availability (% full sun), Neighbor density (stems/ha), Total age (years).

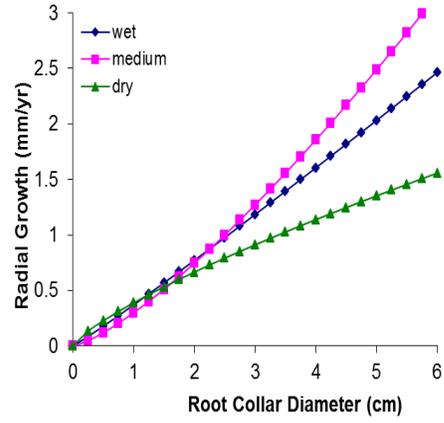
Table 2.2 Candidate growth models. Ranked from least precise (Rank = 12) to most precise (Rank = 1)

<i>No</i>	<b>Model</b>	<b>AIC<sub>c</sub></b>	<b>ΔAIC<sub>c</sub></b>	<b>Pseudo-R<sup>2</sup></b>	<b>Rank</b>
1	$RG=a*size^b$	729.1	314.2	0.276	12
2	$RG=a[site\ series]*size^b$	714.3	299.4	0.301	11
3	$RG=a[site\ series]*size^b_{[site\ series]}$	711.7	296.8	0.297	10
4	$RG=(a[site\ series]*size^b) * (1-\exp(-c*light^d))$	426.1	11.3	0.742	5
5	$RG=(a[site\ series]*size^b) * (g*\delta^{13}C^h)$	573.5	158.7	0.649	7
6	$RG=(a[site\ series]*size^b) * (\exp(-i*density^j))$	703.7	288.9	0.296	9
7	$RG=(a[site\ series]*size^b) * (1-\exp(-c*light^d)) * (\exp(-i*density^j))$	429.6	14.8	0.744	6
8	$RG=(a[site\ series]*size^b) * (1 - \exp(-1.0*(c + d*nitrogen)*light))$	424.5	9.6	0.745	4
9	$RG=(a[site\ series]*size^b) * (1 - \exp(-1.0*(c + d*moisture)*light))$	423.8	8.9	0.747	3
10	$RG=(a[site\ series]*size^b) * (1-\exp(-1.0*c[site\ series]*light))$	420.9	6.0	0.750	2
11	$RG=(a[site\ series]*size^b) * (g[site\ series]*\delta^{13}C^h)$	577.8	162.9	0.649	8
12	$RG=(a[site\ series]*size^b) * (1-\exp(-1.0*c[site\ series]*light)) * (g[site\ series]*\delta^{13}C^h)$	414.8	0.0	0.756	1

Variable description: 1) RG, 5 year average 1999-2003 (radial growth mm/yr); 2) size (target tree root collar diameter at 10cm above the ground); 3) site series (dry, medium, and wet soil moisture regimes); 4) light (% full sun); 5) N (foliar N (% mass)); 6) soil water (VWC); 7) density (neighbor density (stems/ha)); and (8)  $\delta^{13}C$  (‰). Parameters *a* through *j* were estimated using maximum likelihood.

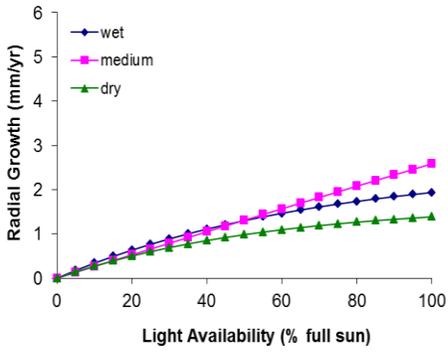


**a**

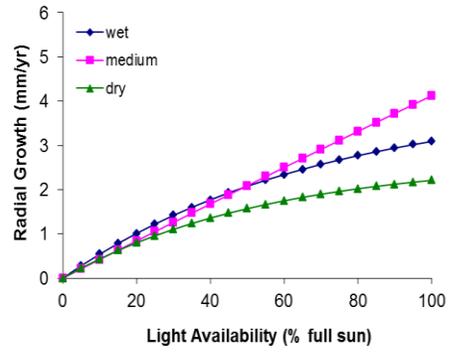


**b**

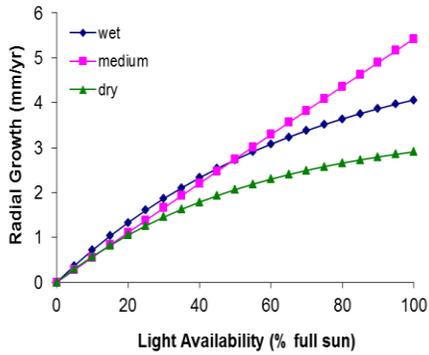
Figure 2.1 Predicted radial growth (RG; mm/yr) as a function of size (root collar diameter at 10cm) for: a) Model 2 ( $RG=a[\text{site series}]*\text{size}^b$ ); and b) Model 3 ( $RG=a[\text{site series}]*\text{size}^b$  [site series]).



**a**

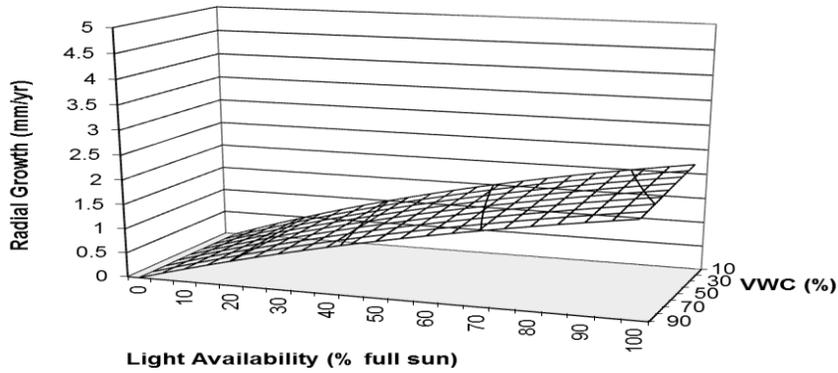


**b**

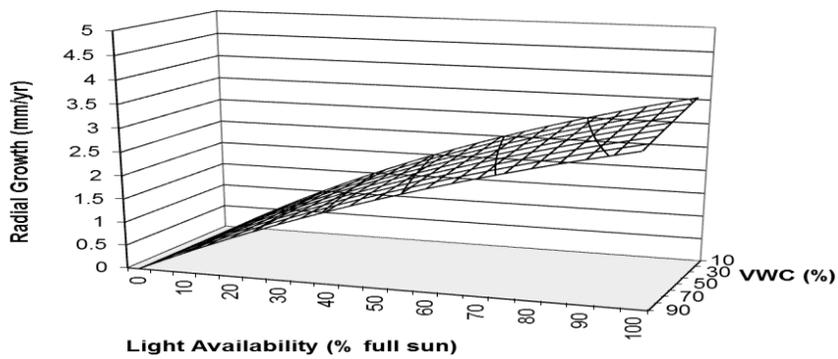


**c**

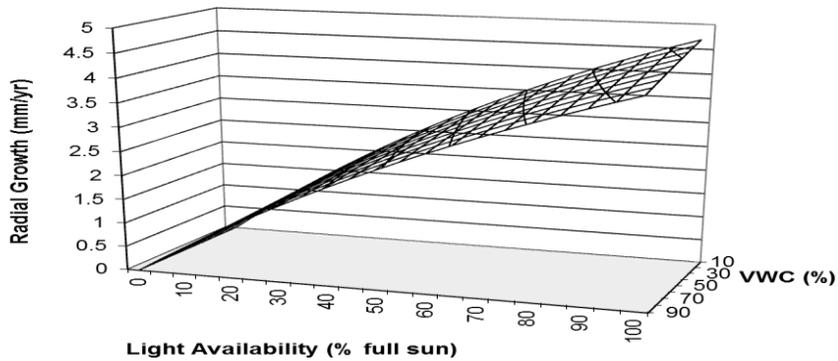
Figure 2.2 Predicted radial growth (RG; mm/yr) as a function of light availability on the three site series, dry, medium and wet using Model 10 ( $RG=(a[\text{site series}] \cdot \text{size}^b) \cdot (1-\exp(-1.0 \cdot c[\text{site series}] \cdot \text{light})))$ ) for: a) a 2 cm root collar diameter; b) a 4 cm root collar diameter; and c) 6 cm root collar diameter tree.



**a**

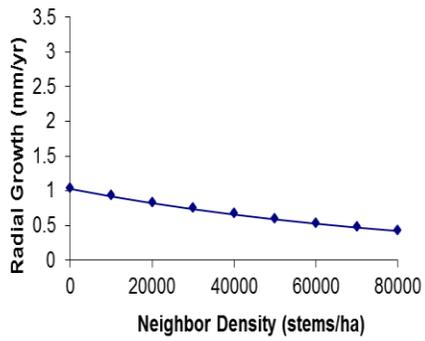


**b**

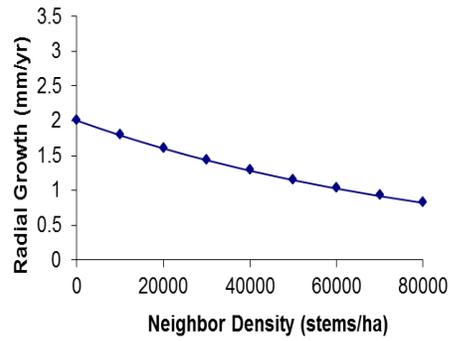


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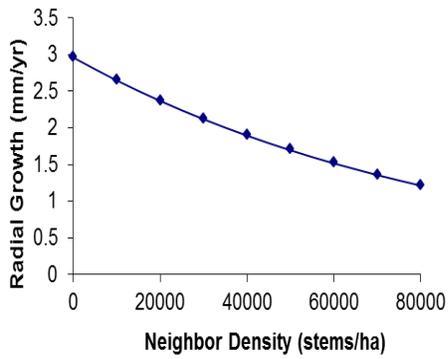
Figure 2.3 Predicted radial growth (RG; mm/yr) as function of light availability and soil water (VWC) using Model 9 ( $RG = (a[\text{site series}] * \text{size}^b) * (1 - \exp(-1.0 * (c + d * \text{moisture}) * \text{light}))$ ) for: a) a 2 cm root collar diameter; b) a 4 cm root collar diameter; and c) 6 cm root collar diameter tree.



**a**



**b**



**c**

Figure 2.4 Predicted radial growth (RG; mm/yr) as function of neighbor density using Model 6 ( $RG=(a[\text{site series}] * \text{size}^b) * (\exp(-i * \text{density}^j))$ ) for: a) a 2 cm root collar diameter; b) a 4 cm root collar diameter; and c) 6 cm root collar diameter tree.

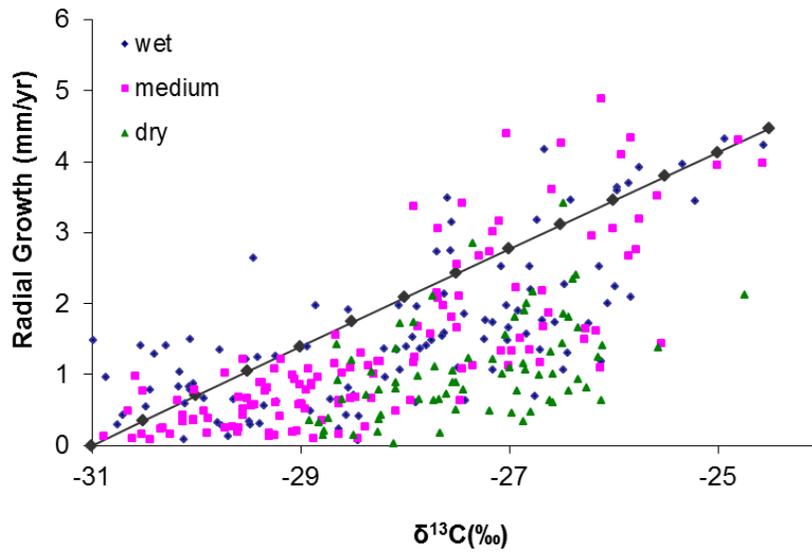
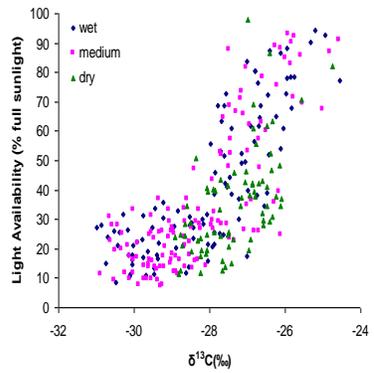
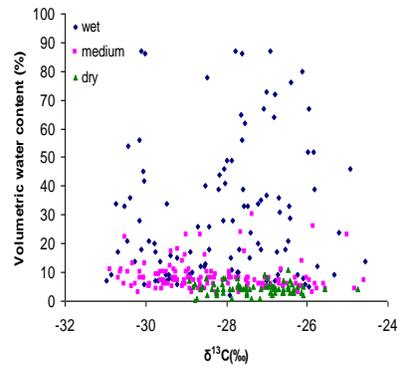


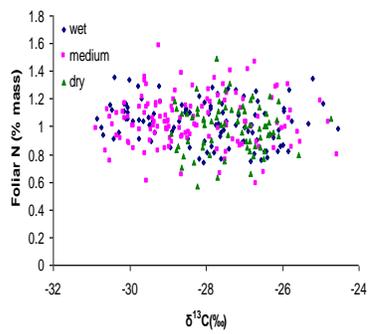
Figure 2.5 Predicted radial growth (RG; mm/yr) as a function of  $\delta^{13}\text{C}$  (‰) overlaid upon observed radial growth data using Model 5  $RG=(a[\text{site series}]\cdot\text{size}^b) * (g*\delta^{13}\text{C}^h)$  for a 4 cm root collar diameter tree.



**a**

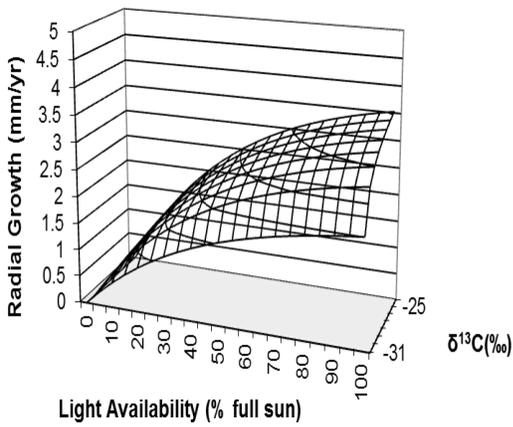


**b**

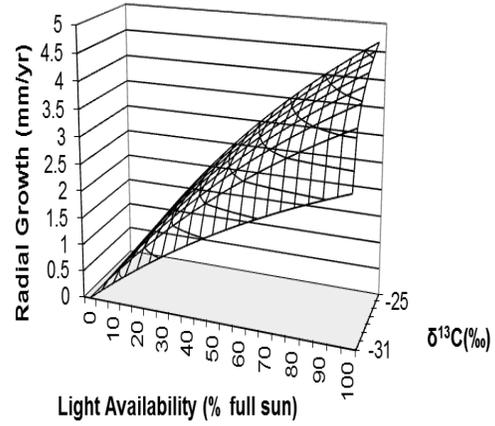


**c**

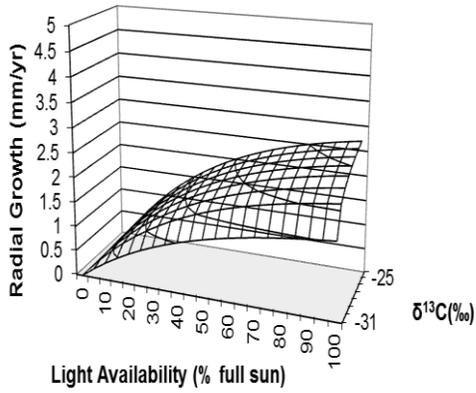
Figure 2.6 Observed: a) light availability x  $\delta^{13}\text{C}$  (‰); b) foliar nitrogen (%mass) x  $\delta^{13}\text{C}$  (‰); and c) volumetric water content (%) x  $\delta^{13}\text{C}$  (‰).



a



b



c

Figure 2.7 Predicted radial growth (RG; mm/yr) as a function of light availability and  $\delta^{13}\text{C}$  (‰) using Model 12  $RG=(a[\text{site series}]*\text{size}^b) * (1-\exp(-1.0*c[\text{site series}]*\text{light})) * (g[\text{site series}]*\delta^{13}\text{C}^h)$  for: a) the wet soil moisture regime; b) the medium soil moisture regime; and c) the dry soil moisture regime. A 4 cm root collar diameter was used for tree size.

## **Chapter 3: Comparing the competitive effects of juvenile and overstory mature trees on juvenile tree growth using a spatially explicit growth model**

### **Introduction**

Individual tree growth models have been used extensively to model adult tree competition and growth, but there are fewer instances where they have been used solely for juveniles such as seedlings and saplings. Individual tree growth models simulate each individual tree as a basic unit with respect to tree growth. They are commonly broken down into two classes, either distance-independent or distance-dependent models. Distance-independent models use non-spatial competition indices and are best suited for even-aged homogenous stands (Lorimer 1983). Distance-dependent models use spatial competition indices that take into account the size, abundance and distance to neighbors (Goldberg and Werner 1987; Wagner and Radosevich 1998; Larocque 2002; Canham et al. 2004). This makes these models better suited to predict tree competition and growth in complex structured stands. The modeling of juvenile tree growth using distance-dependent spatial competition indices appears to be uncommon (Larocque 2002; Boivin et al. 2010). This may be due to the large amount of spatial information required, particularly if very small trees are included as competitors. For example, over 15,000 neighborhood trees were mapped and measured to develop the spatial growth models used in this study. More commonly, juvenile tree growth models have no spatial competition indices and are solely based on light availability (Chen 1997; Wright et al. 1998), light availability plus target tree size (Astrup 2006) or light, soil fertility and ontogeny (Lilles and Astrup 2012).

Distance-dependent individual tree models can be useful for comparing competitive effects among different sized individuals in plant communities. Larger individuals have commonly been found to obtain a disproportionate share of available resources and suppress the

growth of smaller neighbors (Newton and Jolliffe 1998; Schwinning and Weiner 1998; Simard and Sachs 2004). This phenomenon is often referred to as asymmetric competition. In asymmetric competition, the most limiting resource must be pre-emptable, and this is most commonly light (Weiner 1980). Alternatively, symmetric competition occurs when plants compete primarily for below ground resources and their competitive effect is proportional to their size or capacity to take up nutrients or water (Casper and Jackson 1997).

Recently there has been heightened interest in using variable retention silviculture systems rather than conventional clear-cutting in North America because of societal concerns over the environment (Puettmann et al. 2009). In western Canada, these systems are of increasing interest for management of mixed stands that have been affected by the mountain pine beetle (Burton 2010). Variable retention systems allow for the removal of dead lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. Ex Loud) while maintaining a partial canopy of surviving lodgepole pine and other unaffected species. Forest managers have also come to recognize many benefits associated with variable retention systems, including: preserving biological diversity, enhancing regeneration, maintaining visual quality objectives, improving slope stability and reducing carbon losses. To successfully apply silviculture systems that promote regeneration and enhance structural diversity, it is necessary to understand the effects of overstory tree retention on understory juvenile tree growth. The development of a spatially explicit juvenile tree model may thus be useful in predicting adult tree retention effects on juvenile tree growth.

The objectives of this study were to: 1) develop a spatially explicit model capable of predicting juvenile subalpine fir radial growth from target tree size, light availability and a competition index, which includes the size, species and distance to neighboring trees; 2) incorporate the growth model into SORTIE-ND through the development of a new juvenile tree

growth behavior; and 3) run a simulation experiment predicting juvenile tree growth in SORTIE-ND using the new behavior. The goals of the simulation experiment were: a) to compare the competitive effects of juvenile or overstory mature tree neighbors on growth of juvenile subalpine fir; and b) to compare the competitive relationship across a range of neighbor basal area classes. For these two objectives, I hypothesized that: a) adult overstory trees have a greater competitive influence than juvenile trees because of asymmetrical competitive effects; and b) the growth of juvenile trees declines consistently with increasing neighbor basal area, regardless of the identity of neighbors.

## **Methods**

### **Study sites and field sampling**

This study was conducted in the southern interior of British Columbia, Canada, near Kamloops (50°40'N, 120°20'W). All samples were collected within the Thompson Dry Mild variant of the Montane Spruce biogeoclimatic zone (MSdm2). The MSdm2 is characterized by cold winters and moderately short, warm summers (Meidinger and Pojar, 1990). In the MSdm2, forests located on zonal sites (medium soil moisture regime) commonly consist of mixed stands of subalpine fir (*Abies lasiocarpa* [Hook] Nutt.), hybrid white spruce (*Picea glauca* x *Picea engelmannii* [Moench] Voss) and, to a lesser extent, lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. Ex Loud).

Sample sites were selected to provide a range of competitive environments and light conditions. These included mature stands, canopy gaps, regenerating burns or associated mature remnants, and partially cut and clearcut areas. Recently disturbed areas were avoided to ensure measured growth rates were a reflection of the current growing environment. In total, 304

subalpine fir target trees were destructively sampled. The target trees were 1-3m in height (Table 2.1), at least 25m apart (to ensure independence of samples) and were free of defects (forks, crooks, scars, broken leaders, etc.). Each target tree was assessed for total height, root collar diameter (10cm above the ground) and diameter at breast height ((dbh) 130cm above the ground) if the tree was tall enough. To determine target tree radial growth rates, stem disks were collected at 10cm above the ground. In the lab, a Velmex™ micrometer combined with a Nikon™ dissecting scope was used to measure 5 years (1999-2003) of radial growth along the shortest and longest axis found between the pith and outermost growth ring; these values were then averaged per tree. The target tree served as the center of a fixed 3.99m radius plot, where all neighboring trees (>50cm tall) were spatially mapped using an Impulse Laser™ with Mapstar™ attachment. In total over 15,000 neighborhood trees were mapped, assigned an x, y co-ordinate, assessed for species, root collar diameter at 10cm (RCD), dbh and total tree height.

To quantify light availability, hemispherical canopy photos were taken at a height equal to 70 percent of the target tree height. Hemispherical canopy photographs allow characterization of the amount of photosynthetically active radiation at a given location (Canham 1988; Frazer et al. 2000). Photos were taken directly over the target tree stump using a tripod mounted Nikon™ Coolpix 5000 digital camera with a Nikon™ FC-E8 0.21x fish-eye lens. GLI, an index of whole growing season light availability, was then computed from each photograph using the GLA 2.0 software (Frazer et al. 2000). This index integrates the seasonal and diurnal distribution of solar radiation transmitted through the canopy into a single index of available light in units of percent of full sun.

## Analysis

### Model selection

I developed and tested two spatially explicit growth models that are based on work conducted by Canham et al. (2004) (Table 3.1). Model 1 utilizes tree size and the crowding effect of neighbors to predict juvenile radial growth:

$$[\text{Model 1}] \quad \text{Radial Growth} = \text{Size Effect} * \text{Crowding Effect}$$

The size effect is calculated using a basic power function:

$$\text{Size Effect} = a * \text{size}^b$$

where *size* is the target tree root collar diameter at 10cm. The crowding effect is derived from a negative exponential function of a neighborhood competition index (NCI) developed by Canham et al. (2004):

$$\text{Crowding Effect} = \exp(-C * \text{NCI}^D)$$

where C is the crowding effect slope and D is the crowding effect steepness. The NCI is a distance-dependent index that includes neighbor distance from the target tree, size and species:

$$\text{NCI} = \sum_{i=1}^s \sum_{j=1}^n \lambda_i \frac{(\text{RCD}_{ij})^{\alpha_1}}{(\text{distance}_{ij})^{\beta_1}}$$

In the NCI,  $\lambda_i$  refers to a species-specific modifier; *s* is the number of species; *n* is the number of neighbors;  $\alpha_1$  and  $\beta_1$  are parameters to be estimated; RCD is the neighbor root collar diameter (cm); and distance refers to distance to the neighbor (m). In Model 2, light was added as a third predictor variable:

$$[\text{Model 2}] \quad \text{Radial Growth} = \text{Size Effect} * \text{Crowding Effect} * \text{Light Effect}$$

The light effect was calculated using an exponential function of the form:

$$\text{Light Effect} = 1 - \exp(-e * \text{light}^f)$$

where  $e$  and  $f$  are parameters to be estimated and *light* is the percentage of full sun available to the target tree.

The analyses were conducted using the R language and environment (R Development Core Team, 2006) using a package developed by Canham (2002). Maximum likelihood estimates of model parameters were obtained using simulated annealing (a global optimization algorithm) (Goffe et al. 1994). Akaike's Information Criteria ( $AIC_c$ ) appropriate for small sample sizes (Hurvich and Tsai 1989; Burnham and Anderson 2002) was used to distinguish different functional forms of the model. Using these criteria, models with minimum AIC have the greatest empirical support; models that are within 2 AIC units have similar levels of support (Burnham and Anderson 2002). Also, for all models, the error term was assumed to follow a normal distribution. However, since error variances were not equal, a variance function where the error variance was a power of the predicted radial growth was included for all models.

### ***SORTIE-ND growth simulation experiment***

To compare the competitive effects of overstory mature trees versus juvenile trees on juvenile subalpine fir growth, I ran a growth simulation experiment using SORTIE-ND. To run the simulations, a new juvenile growth behaviour "Juvenile NCI Growth" was developed for SORTIE-ND using Model 1 from Table 3.1 (see Appendix A). The "Juvenile NCI Growth" behaviour was written using the C++ programming language and is specifically designed to run with SORTIE-ND. The first step in the simulation experiment involved creating the mature tree stratum, which consisted of three replicate tree maps of randomly distributed overstory mature trees at treatment densities of 400, 1200 and 2500 stems/ha (Figure 3.1). These densities were chosen because they capture the range of mature densities commonly observed in natural and managed stands in these forests. The tree maps were 100 x 100m and run for 80 time steps (80

years). A species mixture of 60% subalpine fir, 20% hybrid spruce, and 20% lodgepole pine was chosen for all maps. Due to the differences in tree map density, SORTIE-ND grew the tree maps at different rates. To ensure all trees were a similar size in each treatment, I took a random sample of trees from the 2500 stems/ha tree maps and used them to populate the 400 and 1200 stems/ha maps. This was done for all three replications. The average tree height in the mature tree stratum was 12.5 m (Figure 3.1).

Three densities of the juvenile tree stratum were identified based on equivalence to the sapwood cross-sectional area of the three mature tree basal areas. Sapwood cross-sectional area correlates strongly with Leaf Area Index, which is directly related to transpiration rates and net primary production (NPP) (Marshall and Waring 1986). The juvenile and mature tree treatment basal area per ha values were thus selected to ensure that the cumulative potential transpiration rates were similar for juvenile and mature trees. The total plot basal area per ha of the three mature treatment densities, 400, 1200 and 2500 stems/ha, were 7, 20 and 40m<sup>2</sup>/ha, respectively. These basal area values were divided by the tree basal area of a representative juvenile tree of 3.5cm RCD (based on the average of sampled trees), resulting in three juvenile tree map densities of 6700, 21000, and 42000 stems/ha (Figure 3.2). The juvenile tree maps of these densities were created using SORTIE-ND and run for approximately 13 time steps to achieve total plot basal areas that matched those of the mature maps. Again, the tree maps were 100 x100m and consisted of a randomly distributed species mixture of 60% subalpine fir, 20% hybrid spruce, and 20% lodgepole pine. As with the mature trees, I ensured that all of the trees in the three juvenile maps were the same size by taking a random sample of juvenile trees from the highest density maps (42,000 stems/ha) to populate the 6700 and 21000 stems/ha tree maps. The average tree height in the juvenile tree stratum was 2.9 m (Figure 3.2).

Once the 18 tree maps were created, six densities multiplied by three replications, I inserted 81 juvenile target trees into each simulated stand using a 10m x 10m grid. The same juvenile target trees were inserted into each of the 18 tree maps. The target tree sizes were representative of the juvenile trees used to develop the growth behavior (Table 2.1). The tree maps were then imported into SORTIE-ND and run for three consecutive time steps using the “Juvenile NCI Growth” behavior shown in Appendix A. The resulting maps were exported and the growth responses of the 81 target juvenile trees were extracted based on their spatial coordinates. The annual growth rate for the three time steps was then averaged for each simulated plot.

Using these steps, I simulated a completely randomized design with two factors: tree stratum (overstory mature neighbors versus juvenile neighbors) and basal area classes (7, 20 and 40 m<sup>2</sup>/ha). To test for differences among treatments, a two-way analysis of variance (ANOVA) was conducted (SAS Inc. 1988). Using plot-level summaries, tests for normality and equal variances showed no transformations were necessary. Differences between treatments were considered significant at  $\alpha = 0.05$ .

## **Results**

### ***Model selection***

Of the two spatially explicit growth models developed, Model 2 had a lower AIC<sub>c</sub> (442.3) and a higher Pseudo-R<sup>2</sup> (0.74) (Table 3.1). Model 1, which included only size and crowding effects, still performed quite well with an AIC<sub>c</sub> of 543.3 and accounted for 62% of the variation. Since this model performed surprisingly well and did not require light as an input variable, it was the basis for developing the spatial juvenile growth behavior for SORTIE-ND. The benefits of

using Model 1 were that this model: 1) avoids use of SORTIE-ND's light model, which can be computationally taxing and unreliable for young trees growing in dense stands; and 2) is a useful tool for evaluating whether juvenile or mature trees have a greater competitive influence on juvenile subalpine fir growth.

### ***SORTIE-ND growth simulation***

The results from the two-way ANOVA showed a significant interaction between the tree strata and basal area classes (Table 3.2). The interaction arose from a convergence of growth rates at the highest basal area class (40 m<sup>2</sup>/ha) (Figure 3.3). At the lowest (7 m<sup>2</sup>/ha) and intermediate (20 m<sup>2</sup>/ha) basal area classes juvenile growth rates were greater when neighbors were mature overstory trees rather than juvenile trees, but this difference between strata disappeared at 40 m<sup>2</sup>/ha (Figure 3.3). The mean target tree radial growth in the 7 m<sup>2</sup>/ha mature stratum was 0.52 cm/year compared to 0.50 cm/year in the juvenile stratum (Figure 3.3). Faster juvenile radial growth also occurred in the mature (0.36 cm/year) than juvenile (0.32 cm/year) stratum in the 20 m<sup>2</sup>/ha density class.

## **Discussion**

In this research, I developed a new juvenile tree radial growth model for subalpine fir and implemented this as a new growth behaviour (Juvenile NCI Growth) in SORTIE-ND. The model predicts juvenile tree growth as a function of target tree size and neighbor crowding. The *Juvenile NCI Growth* behaviour is unique because the majority of existing SORTIE-ND juvenile growth behaviours predict growth as a function of target tree size and light availability. I used the new behaviour in a simulation experiment to compare whether juvenile or mature neighbors have a greater competitive influence on juvenile subalpine fir growth and to determine whether the competitive relationship was consistent across a range of neighbor density classes.

I found that juvenile radial growth was fastest under the canopy of mature trees; however, this was only true for the 7 m<sup>2</sup>/ha and 20 m<sup>2</sup>/ha basal area classes. I thus rejected my first hypothesis based in size asymmetric competition theory, where larger individuals are considered to have a disproportionately greater competitive effect than smaller individuals at suppressing neighbor growth because of their ability to pre-empt light (Newton and Jolliffe 1998; Schwinning and Weiner 1998; Simard and Sachs 2004). Instead, my results indicate that symmetric competition processes dominated, where resource availability to target plants is proportional to competitor size, as is commonly the case where soil water or soil nutrients are more limiting (Schwinning and Weiner 1998).

Given symmetrical competition, the difference in competitive effects between the two strata on juvenile radial growth is likely attributed to niche differences in below ground resource access. Juvenile target trees growing under the mature tree stratum may be accessing more shallow parts of the soil resource profile than mature trees, thereby giving them an advantage over juvenile target trees growing with similar sized neighbors competing for the same niche space. The idea of niche differences in resource access has been recognized for some time. Gause (1932) developed the competitive exclusion principle, which states “two species competing for the same resources cannot coexist if other ecological factors are constant, when one species has even the slightest advantage over another, then the one with the advantage will dominate in the long term”. This is consistent with biodiversity theory, which suggests that species must use resources in different ways to coexist, allowing diverse stands to capture limited resources more efficiently for greater stand biomass production (Tilman et al. 1987; Reese et al. 2001; Cardinale et al. 2006). Similar to species, niche differentiation can also occur among different sized individuals within a stand (Hara et al. 1993). Another possible

explanation for faster juvenile tree growth in the understory of mature trees may be a decrease in understory evaporative demand. Kaufmann (1982) found that the stomatal conductance of subalpine fir growing in the understory increased with increasing relative humidity that often characterizes forest understory conditions. It is reasonable to assume the understory juveniles are able to keep their stomates open for longer periods due to the lower vapour water deficits and lower evaporative demand in the understory.

Target juvenile growth decreased predictably with increasing neighbor density, but stratum interacted significantly with density. Target tree growth was slower in the neighborhood of similar sized juveniles than mature overstory trees at the lower 7 and 20 m<sup>2</sup>/ha neighbor densities, but this difference disappeared at the highest neighbor density. At the lowest density classes, the simulated forests were patchy with open gaps in both the juvenile and mature tree strata, which was a consequence of creating the maps using a random planting function in SORTIE-ND (Figures 3.1 and 3.2). However, as the density increased, the gaps were fewer and resources thus scarcer, until competition became equally intense regardless of neighbor identity. It is likely that at the highest stocking level, both the juvenile and mature stands were approaching site occupancy, where there were few forest gaps and resource niches left to exploit.

## **Conclusions**

At the two lowest density classes of 7 and 20 m<sup>2</sup>/ha, juvenile radial growth was faster under the canopy of mature trees than in the neighborhood of similar sized juvenile trees. These results indicate that symmetric competition processes dominated, where resource availability to target plants is proportional to competitor size, as is commonly the case where soil water or soil nutrients are more limiting. At these densities, it is likely that the different competitive effect of

the two strata on juvenile radial growth was due to niche differences in below ground resource access. There were no discernible differences in juvenile radial growth under the two strata for the highest density class (40 m<sup>2</sup>/ha). At this level of stocking, it appears the juvenile and mature stands were approaching site occupancy, where there were fewer forest gaps and lower soil resource availability.

The spatially explicit juvenile tree growth model developed as a result of this research can be used as a stand-alone model or in conjunction with SORTIE-ND. The “Juvenile NCI Growth” behaviour developed for SORTIE-ND may be particularly useful for predicting juvenile tree growth in dense multi-structured stands. The existing juvenile tree growth behaviours in SORTIE-ND use available light and target tree size to predict tree growth. However, the light model in SORTIE-ND calculates available light at the mid or top of the crown meaning the competitive influence of neighbors that are of equal height or shorter may be underestimated. For this reason, the “Juvenile NCI Growth” behaviour may be a better choice for conducting juvenile tree growth simulations in stands with high levels of understory regeneration.

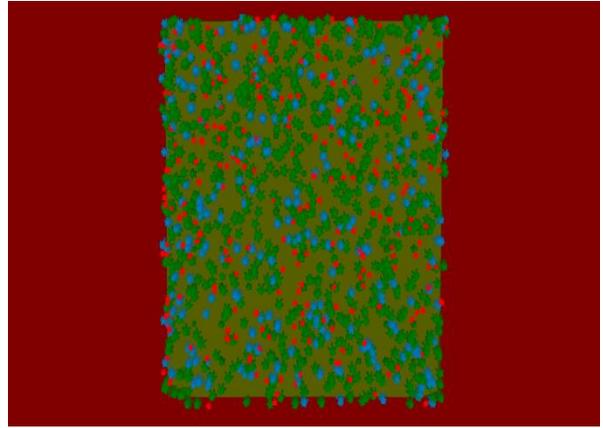
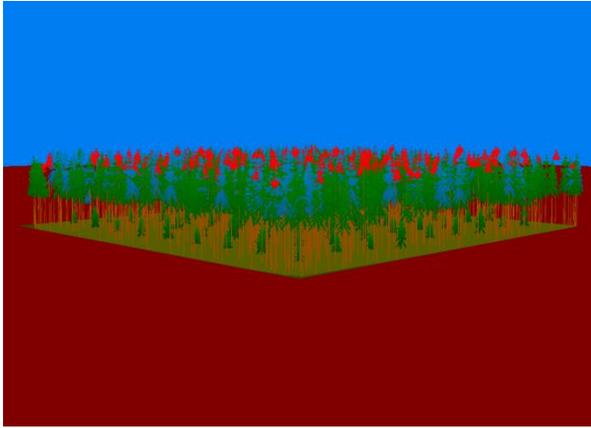
This behaviour may be particularly useful in the development of prescriptions for variable retention silviculture systems. As a result of the mountain pine beetle epidemic in BC, there are many stands where the over story lodgepole pine has been killed leaving behind a partial canopy of non-pine species and a well-developed, sometimes dense, understory of shade-tolerant species such as subalpine fir and hybrid white spruce. Through the use of SORTIE-ND and the “Juvenile NCI Growth” behaviour it would be possible to conduct a number of simulations to test if these stands would benefit from some level of partial harvesting, understory thinning, or be left alone.

Table 3.1 Candidate spatial growth models where Rank = 1 is a more precise model. Variable description: 1) RG (radial growth mm/yr); 2) size (target tree root collar diameter at 10cm above the ground); 3) neighborhood competition index (NCI); and 4) light (% full sun).

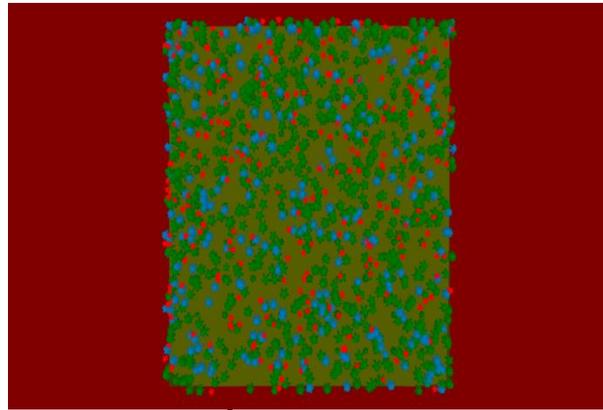
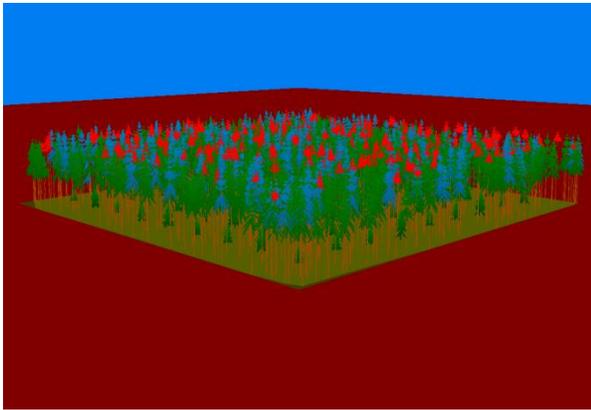
No.	Model	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	Pseudo-R <sup>2</sup>	Rank
1	$RG = a * size^b * \exp(-C * NCI^D)$	543.3	101.0	0.62	2
2	$RG = a * size^b * \exp(-C * NCI^D) * 1 - \exp(-e * light^f)$	442.3	0.0	0.74	1

Table 3.2 Results for analysis of variance for juvenile radial growth for two factors: 1) tree strata (Mature, Juvenile); and 2) basal area classes (7, 20, 40 m<sup>2</sup>/ha).

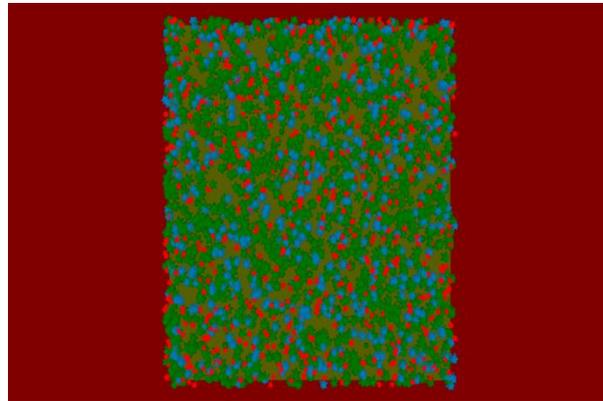
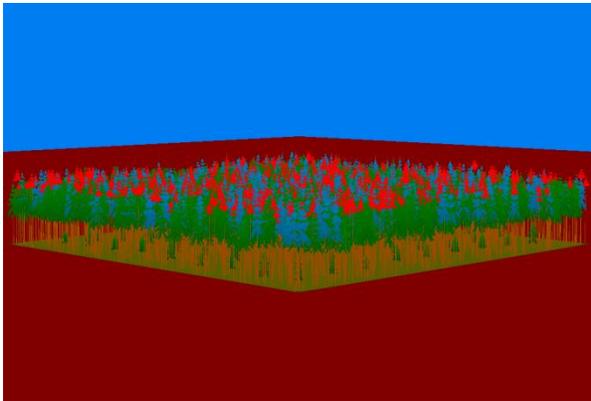
<b>Effect</b>	<b>F-value</b>	<b>P&gt;F</b>
Stratum	39.34	<0.0001
Basal Area Class	3334.15	<0.0001
Stratum*Basal Area Class	8.77	0.0002



a) 400 stems/ha mature tree stratum, total plot basal area =  $6.5\text{m}^2/\text{ha}$ , average neighbor height = 12.5m

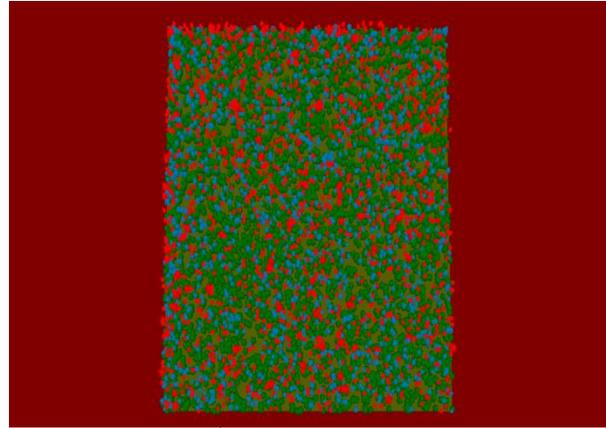
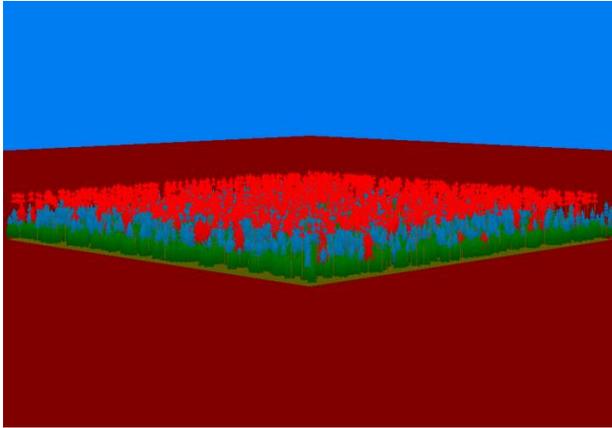


b) 1200 stems/ha mature tree stratum, total plot basal area =  $19.5\text{m}^2/\text{ha}$ , average neighbor height = 12.5m

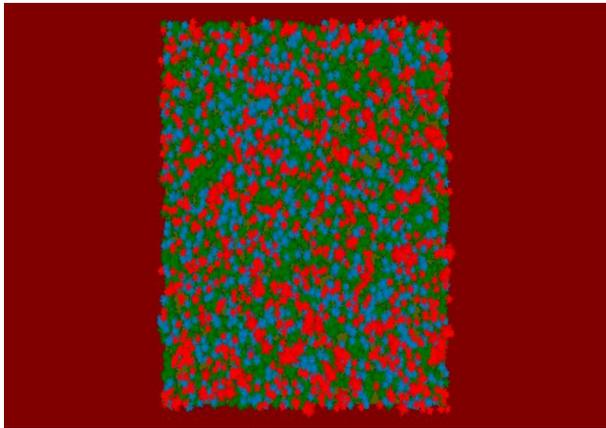
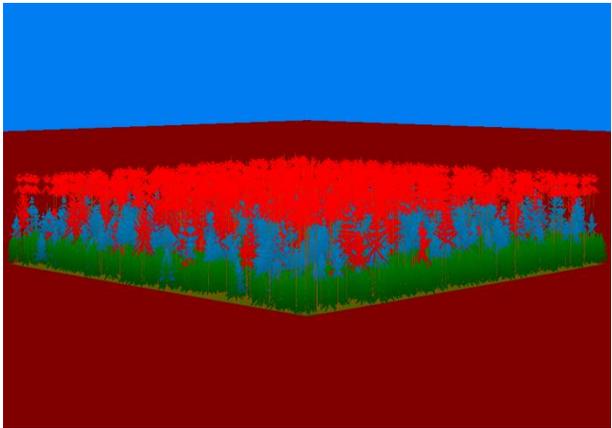


c) 2500 stems/ha mature tree stratum, total plot basal area =  $40.2\text{m}^2/\text{ha}$ , average neighbor height = 12.5m

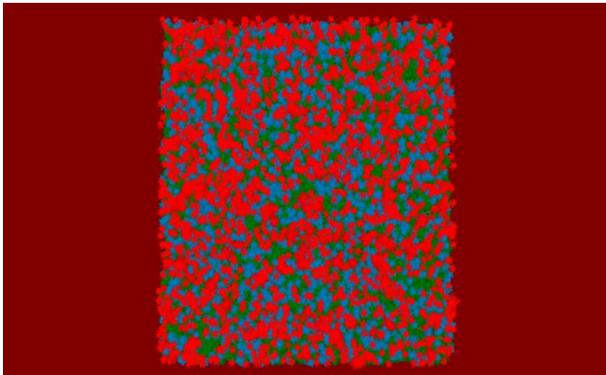
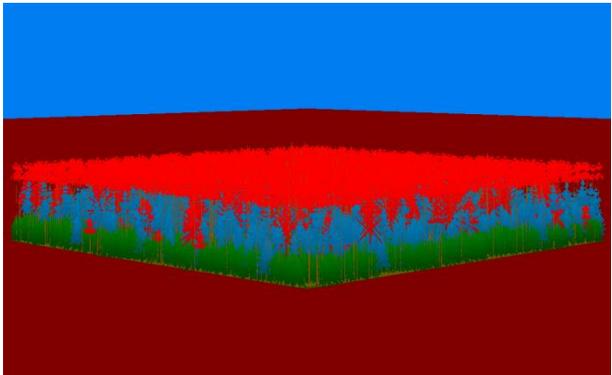
Figure 3.1 Plot visualizations of the mature tree stratum (replication #1). Green = subalpine fir, Red = lodgepole pine, Blue = hybrid spruce.



a) 6700 stems/ha juvenile tree stratum, total plot basal area =  $6.5\text{m}^2/\text{ha}$ , average neighbor height = 2.9m



b) 21000 stems/ha juvenile tree stratum, total plot basal area =  $20.6\text{m}^2/\text{ha}$ , average neighbor height = 2.9m



c) 42000 stems/ha juvenile tree stratum, total plot basal area =  $41.0\text{m}^2/\text{ha}$ , average neighbor height = 2.9m

Figure 3.2 Plot visualizations of the juvenile tree stratum (replication #1). Green = subalpine fir, Red = lodgepole pine, Blue = hybrid spruce.

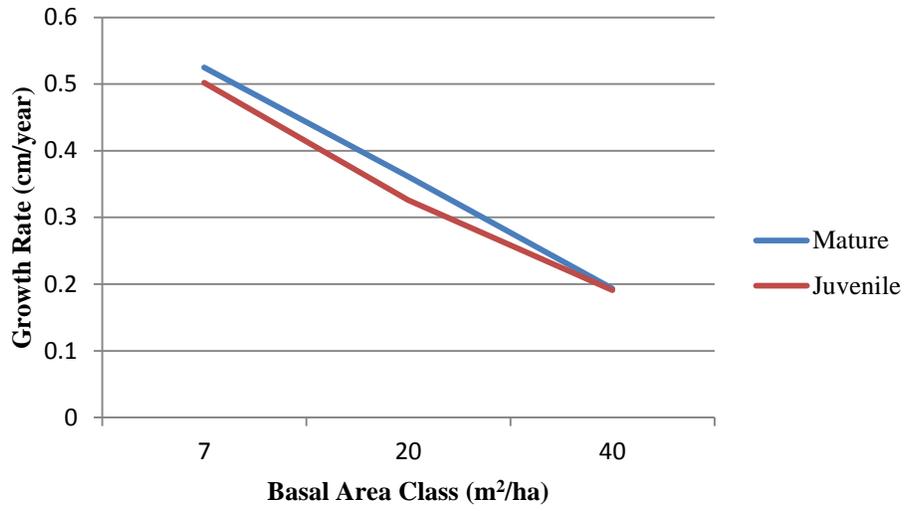


Figure 3.3 Mean target tree radial growth (cm/year) for the two strata (Mature and Juvenile) and three basal area classes (7, 20, and 40 m<sup>2</sup>/ha).

## **Chapter 4: Using SORTIE-ND to explore the influence of site quality on stand growth and development**

### **Introduction**

SORTIE-ND is a spatially explicit individual tree growth model, originally developed as a small scale disturbance model in the early 1990's (Pacala et al. 1993; Pacala et al. 1996). More recently, the model has been modified and re-parameterized to forecast growth of mixed species stands in the northern interior of British Columbia (BC), Canada (Kobe and Coates 1997; Wright et al. 1998, 2000; Canham et al. 1999; LePage et al. 2000; Astrup 2006; Coates et al. 2009; Thorpe et al. 2010). To conduct a simulation in SORTIE-ND, the user must select from a number of pre-programmed models called "behaviors" that will affect a tree throughout the simulation period. There are a range of behaviors that roughly correspond to biological processes including: disturbance, substrate for germination, seedling establishment, planting, growth, and mortality. To use a behavior, the user usually has to provide estimates of all model coefficients for the behavior; estimates are usually derived from field-based observational studies and experiments. The user also has to specify which behaviors apply to each life cycle stage, particularly: seed, seedling, sapling, adult, snag and woody debris. In SORTIE-ND, seedlings are specifically trees less than 1.3m in height, whereas saplings are taller than seedlings, but are usually limited to a maximum of 4-5 cm diameter at breast height (dbh; 1.3 m above ground). Collectively, these two life stages are often referred to as "juveniles". Adults are larger than saplings and were considered to be trees > 5 cm dbh in this study. In SORTIE-ND, all of the behaviors, the order of execution, coefficients for all models, and the life cycle stages that behaviors pertain to are part of a file called a "parameter file". In BC, parameter files have been created and tested for "medium" site productivities in the Interior Cedar-Hemlock (ICH) and Sub-boreal Spruce (SBS) ecological zones (Canham et al. 2004; Coates et al. 2009; Thorpe et al.

2010). This narrow range of site productivity and ecological zones covered limits the use of SORTIE-ND for stand growth predictions.

Site quality is an important determinant of tree growth (Oliver and Larson 1997). In chapter 2, I confirmed the importance of site quality on juvenile subalpine fir growth (*Abies lasiocarpa* [Hook] Nutt.). In particular, I used site series, which classifies site quality based on soil moisture and nutrient availability (Meidinger and Pojar 1991), topographical and soil morphological properties, and the presence or absence of key indicator species. However, in my study area, soil moisture regime is strongly positively correlated with soil nutrient regime, and hence it is sufficient to represent site series by soil moisture regime alone (Lloyd et al. 1990). I found that juvenile subalpine fir radial growth was fastest on medium sites (i.e., sites with a medium soil moisture regime), followed by wet and dry sites. Site quality also affects adult tree growth, as demonstrated by the practice of using site index trees to infer a site's productivity (Mah and Nigh 2003; Nigh 2010). Site index is defined as the average height of free grown trees at a reference age. Since site quality is an important predictor of tree growth, SORTIE-ND should improve with its inclusion in growth predictions.

The objective of this study was to examine how the inclusion of site quality would affect growth predictions. To do this, the "Logistic growth with size dependent asymptote" juvenile tree growth behavior in SORTIE-ND was parameterized for three site series using juvenile tree data collected from dry, medium and wet site series. Since I had confirmed that radial growth of juvenile trees of subalpine fir was fastest on the medium site series in Chapter 2, I hypothesized that this faster growth would result in a higher total basal area per ha than the other two site series at the end of a 100-year forecast period.

## Methods

### Study sites and field sampling

This study was conducted in the southern interior of BC, Canada, near Kamloops (50°40'N, 120°20'W). All tree samples and field measurements were collected within the Thompson Dry Mild variant of the Montane Spruce biogeoclimatic zone (MSdm2). The MSdm2 is characterized by cold winters and moderately short, warm summers (Meidinger and Pojar, 1990). In the MSdm2, forests located on zonal sites (medium soil moisture regime) commonly consist of mixed stands of subalpine fir, hybrid white spruce (*Picea glauca* x *Picea engelmannii* [Moench] Voss) and, to a lesser extent, lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. Ex Loud).

Sample sites were selected to provide a range of light and site quality conditions. To capture a range of light conditions, I sampled mature stands, canopy gaps, regenerating burns or associated mature remnants, and partially cut and clearcut areas. Recently disturbed areas were avoided to ensure measured growth rates were a reflection of site quality, not disturbance. I sampled three site series that represent dry (03), medium (01,04), and wet soil moisture regimes (05) as defined by Lloyd et al. (1990). Site series is an index of site quality based on soil moisture and nutrient availability (Meidinger and Pojar, 1991), and is based on topographical and soil morphological properties as well as the presence or absence of key indicator species.

In total, 304 juvenile subalpine fir target trees were destructively sampled. The target trees were 1-3m in height (Table 1.1), at least 25m apart (to ensure independence of samples) and were free of defects (forks, crooks, scars, broken leaders, etc.). Each target tree was assessed for total height and root collar diameter (RCD; 10cm above the ground), as well as diameter at breast height (dbh; 130cm above the ground) for trees above 1.3 m tall. To determine target tree radial growth rates, stem disks were collected at 10cm above the ground. In the lab, a

Velmex™ micrometer combined with a Nikon™ dissecting scope was used to measure 5 years (1999-2003) of radial growth along the shortest and longest axis found between the pith and outermost growth ring; these values were then averaged per tree. To quantify light availability, hemispherical canopy photos were taken at a height equal to 70 percent of the target tree height. Hemispherical canopy photographs allow characterization of the amount of photosynthetically active radiation at a given location (Canham 1988; Frazer et al. 2000). Photos were taken directly over the target tree stump using a tripod mounted Nikon™ Coolpix 5000 digital camera with a Nikon™ FC-E8 0.21x fish-eye lens. GLI, an index of whole growing season light availability, was then computed from each photograph using the GLA 2.0 software (Frazer et al. 2000). This index integrates the seasonal and diurnal distribution of solar radiation transmitted through the canopy into a single index of available light in units of percent of full sun.

## **Analysis**

### ***Model parameterization***

I obtained estimated parameters for the “Logistic growth with size dependent asymptote” juvenile tree growth behavior in SORTIE-ND for each of the three site series. Parameter estimates were obtained from juvenile tree growth data collected on dry, medium and wet sites. This behavior was chosen because it was the only non-spatial size-dependent juvenile growth behavior available in SORTIE-ND and because size was demonstrated to be an important predictor of juvenile tree growth in chapter 2. Further, Astrup (2006) found this model to be a good predictor of diameter growth of juvenile hybrid white spruce that were similar in size and shade tolerance to the subalpine fir trees in this study. The “Logistic growth with size dependent asymptote” behavior is a logistic function where the asymptote increases linearly with the size of

the tree. The behavior utilizes tree size and light availability as predictor variables and it calculates annual radial growth (RG; mm) using:

$$[\text{Model 1}] \quad \text{RG} = \frac{a+(b*size)}{1+e^{(c-(d*light))}}$$

where *size* is the RCD; *light* is the percentage of full sun available to the target tree; and *a* through *d* are parameters to be estimated.

Parameter estimates for the model were obtained using the field data and the (nls) function in the R language and environment (R Development Core Team, 2006, Version 2.8.1). The default algorithm, the Gauss-Newton algorithm, was used to obtain the final parameter estimates. Initial starting values were chosen based upon work conducted by Astrup (2006), although additional values were tested to ensure a global optimum was obtained. The accuracy of the fitted model was evaluated using root mean squared error (RMSE):

$$RMSE = \sqrt{\sum_{i=1}^n \left[ \frac{(Y_i - \hat{Y}_i)^2}{n} \right]}$$

and Pseudo-R<sup>2</sup>:

$$Pseudo - R^2 = 1 - \frac{\sum_{i=1}^n (Y_i - \hat{Y}_i)^2}{\sum_{i=1}^n (Y_i - \bar{Y})^2}$$

where  $Y_i$  is the actual value for measurements 1 to  $n$ ;  $\bar{Y}$  is the sample mean;  $\hat{Y}_i$  is the predicted value from the fitted equation; and  $n$  is the number of trees. The parameter estimates from this

analysis were entered into the three SORTIE-ND parameter files representing dry, medium and wet site series. Then, this model was used to predict the annual radial growth of juvenile trees up to 5cm dbh within SORTIE-ND. For trees larger than 5cm dbh, the adult “NCI growth behavior” was used to predict annual radial growth. Parameter estimates for the adult “NCI growth behavior” were based on prior estimates for medium sites in the SBS zone (Thorpe et al. 2010), since no parameter estimates were available for the MS zone.

### ***SORTIE-ND growth simulation***

Once the parameter files were available, simulations using SORTIE-ND were run to forecast the growth and development of a stand over 100 years. The same tree map was used for the starting conditions in each simulation. The tree map was created in SORTIE-ND and consisted of a pure subalpine fir stand planted at 1200 stems/ha using the random planting function. This density was chosen because it represents an average density for a managed regenerating forest in British Columbia (Weaver 2012). The tree map was imported into each simulation at time step 0 and run for 100 time steps or 100 years. The same mortality behaviors were utilised in all three of the simulations.

## **Results**

The parameter estimates and associated standard errors for Model 1 are given in Table 4.1. Residual plots indicated no lack of fit nor unequal variances for any of the three site series (Figure 4.1). Estimates of the RMSEs were relatively low at 0.508, 0.481 and 0.544 mm/yr for the dry, medium and wet sites, respectively, indicating a more precise model for medium sites (Table 4.2).

The SORTIE-ND simulation indicated how site series affected the growth and development of the simulated stand. The total stand basal area increased fastest on the medium sites throughout the 100 year simulation (Figure 4.2). Over the simulation period, the medium site achieved a total basal area of 48.1 m<sup>2</sup>/ha, followed by the wet site (47.6 m<sup>2</sup>/ha) and the dry site (47.1 m<sup>2</sup>/ha). Juvenile trees (<5cm dbh) also reached adult size (>5cm dbh) on the medium sites much faster than other two site series (Figure 4.2). This transition started to occur at 12 years on the medium site (i.e. time step 12), but was much longer at 21 years and 25 years on the wet and dry sites, respectively. During the 100 year simulation, adult mean dbh was consistently larger on the medium site followed by the wet and dry site, reflecting earlier juvenile growth differences (Figure 4.3). Adult tree density was initially similar on all the site series; however, at approximately 75 years into the simulation, the medium site started to self-thin at a higher rate than in wet or dry sites (Figure 4.4). As a result, there were more stems/ha on the dry site (1032 stems/ha) than there were on the wet (1012 stems/ha) and medium site (965 stems/ha) at 100 years. This resulted in similar basal areas for all three sites at 100 years (Figure 4.2).

## **Discussion**

In this study, site series was incorporated into the juvenile growth model for subalpine fir resulting in changes in the juvenile and adult growth over a 100-year forecast period using SORTIE-ND. At the beginning of the simulation period, juvenile trees (trees < 5cm dbh) reached adult tree size (trees > 5cm dbh) fastest on the medium site followed by the wet and dry sites, as expected based on the results presented in Chapter 2. It is possible that some of the wet sites sampled in this study experienced short term seasonal flooding, which would decrease photosynthetic rates and growth (Zaerr 1983; Kozlowski 1984). Kayahara et al. (1996) found

that mature lodgepole pine and hybrid white spruce grew fastest on sites with no water deficit or surplus during the growing season, and slowest on very dry or wet sites. Total stand basal area also initially increased the fastest on the medium sites; however, by the end of the simulation period, total stand basal area was similar on all three sites. This unexpected result was likely due to greater density-dependent mortality on the medium than dry or wet sites because it had the lowest stand density at 100 years.

## **Conclusions**

The results from this study suggest that incorporating site quality into SORTIE-ND would be beneficial. It would prevent over-estimation of yield on wet or dry sites, thus allowing the model to be applied more accurately over a broader range of ecological conditions. Efforts to collect parameter data, particularly adult tree data, for SORTIE-ND in British Columbia have largely focused on medium sites in the Interior Cedar-Hemlock and Sub-boreal Spruce ecological zones (Canham et al. 2004; Coates et al. 2009; Thorpe et al. 2010). This is likely due to the large expenditure required to collect spatial adult tree parameter data. One possible mechanism for incorporating site quality into SORTIE-ND would be to develop separate parameter files for different site series within an ecological zone as was done in this study for juvenile subalpine fir trees or to incorporate site series into the models as was done in chapter 2. Based on current sampling techniques, it may be cost prohibitive to collect adult tree parameter data for a wider range of ecological conditions; however, there are a number of recent technological advances that may make this easier and more economical in the future. For example, ground based scanning LiDAR (Light Detection and Ranging) technology has been shown to be reasonably precise for measuring a range of stand attributes, including stem

location, tree height, tree diameter, and crown attributes (Hopkinson et al. 2004; Yao et al. 2011). Also, the recent use of Unmanned Aerial Vehicles (UAVs) in conjunction with airborne LiDAR technology offer promise for those wanting to collect high resolution data at much lower cost than fixed wing manned aircraft (Wallace et al. 2012).

Table 4.1 “Logistic growth with size dependent asymptote” (Model 1) parameter estimates and associated approximate standard errors (~SE). Site series (dry, medium and wet soil moisture regimes).

Parameter	Dry		Medium		Wet	
	Estimate	~SE	Estimate	~SE	Estimate	~SE
a	0.7211	0.3931	1.3364	0.4698	0.4838	0.3766
b	0.3035	0.1068	0.6378	0.1169	0.6287	0.0846
c	2.5022	0.6867	2.5506	0.2284	1.8370	0.3492
d	0.0897	0.0285	0.0607	0.0087	0.0603	0.0156

Table 4.2 Pseudo-R<sup>2</sup> and root mean squared error (RMSE) for annual radial growth models. Site series (dry, medium and wet soil moisture regimes).

Site Series	Pseudo-R <sup>2</sup>	RMSE (mm/yr)
Dry	0.474	0.508
Medium	0.871	0.481
Wet	0.760	0.544

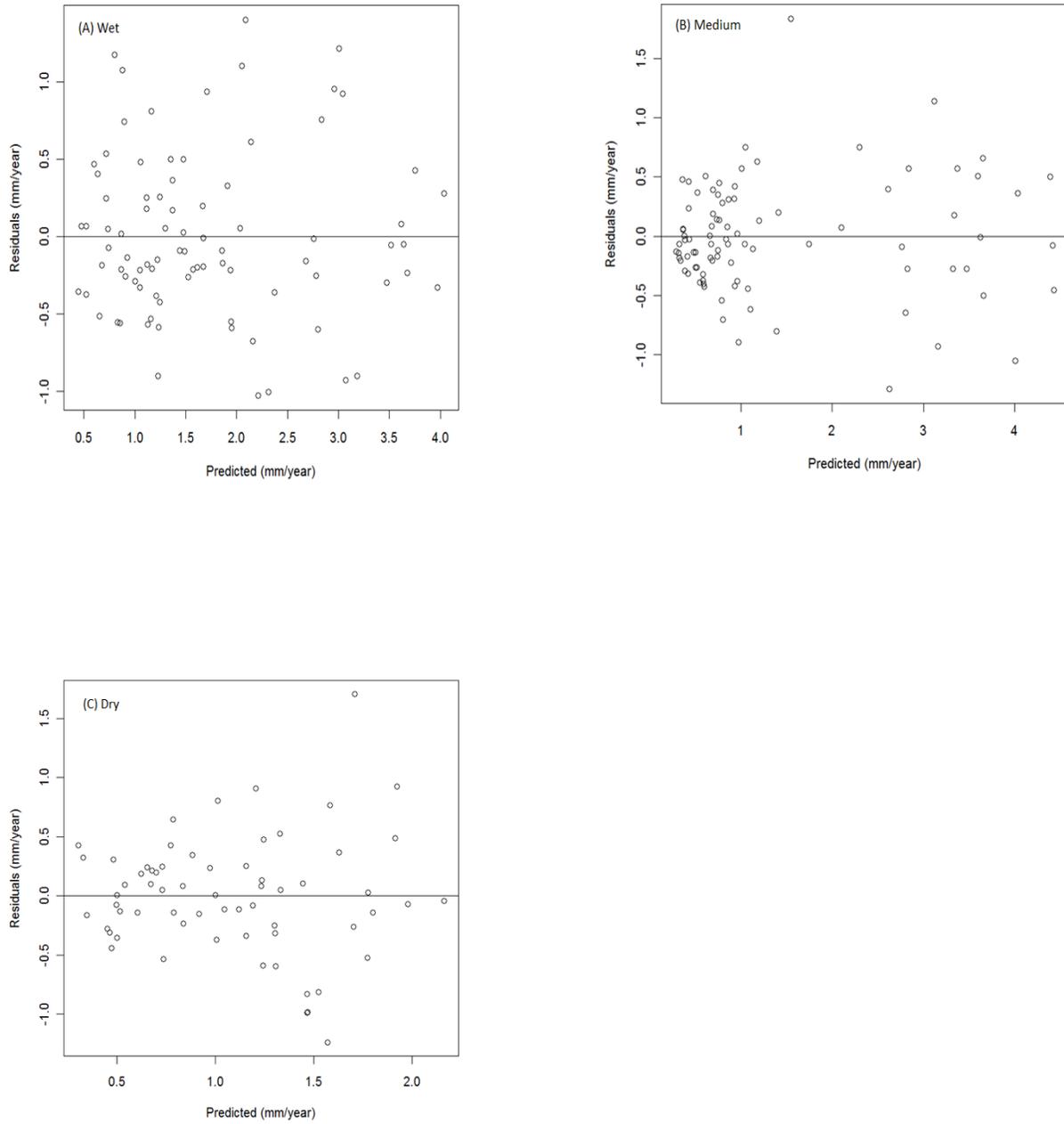


Figure 4.1 Juvenile radial growth residual plots for: a) dry; b) medium; and c) wet site series.

Residuals were calculated as predicted value – observed value.

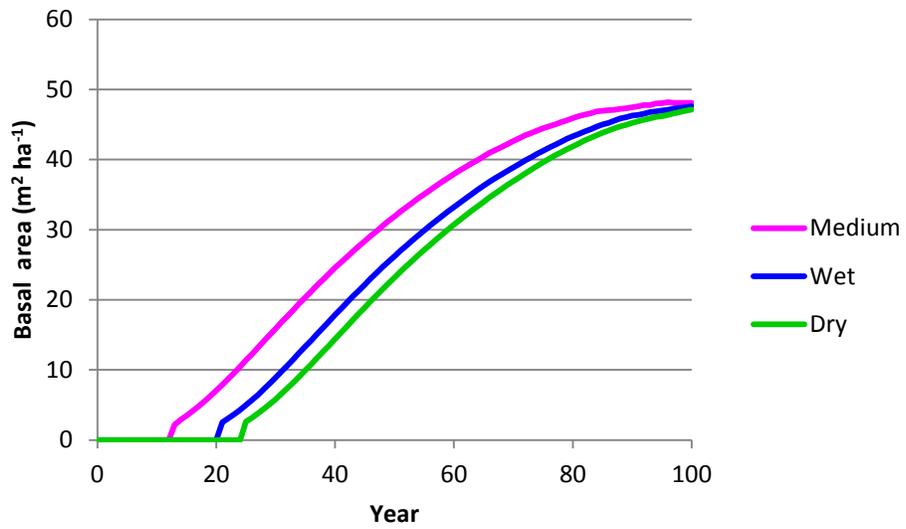


Figure 4.2 SORTIE-ND predicted adult (trees > 5cm dbh) basal area (m<sup>2</sup>/ha) over 100 years for dry, medium and wet site series.

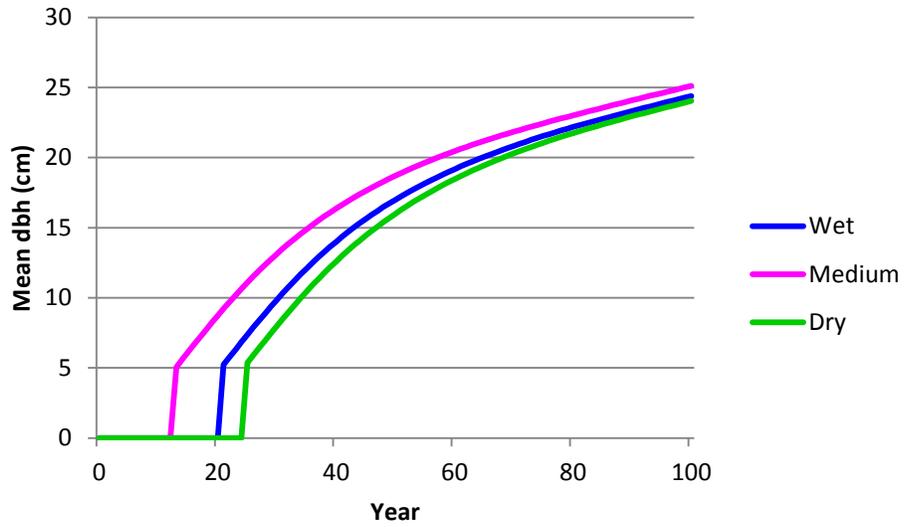


Figure 4.3 SORTIE-ND predicted adult (trees > 5cm dbh) mean stem diameter over 100 years for dry, medium and wet site series.

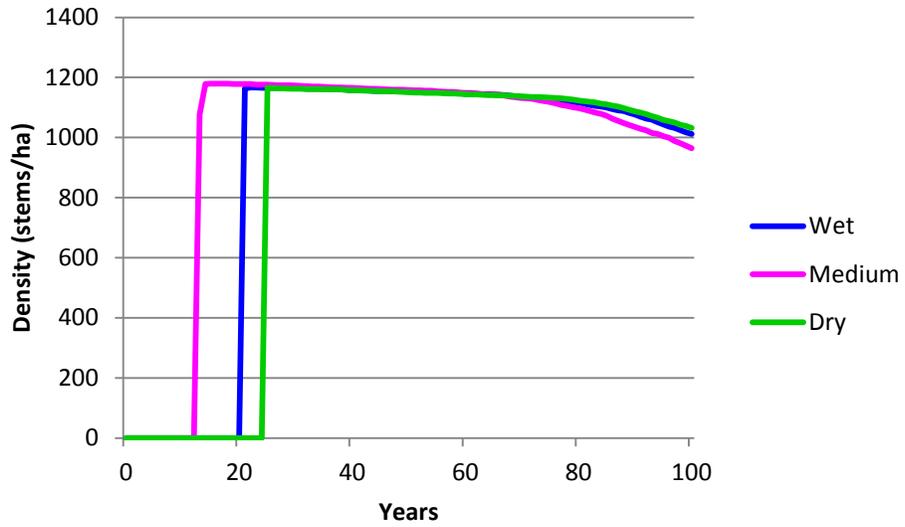


Figure 4.4 SORTIE-ND predicted adult (trees > 5cm dbh) density (stems/ha) over 100 years for dry, medium and wet site series.

## **Chapter 5: Summary and conclusions**

A major goal of forest ecology research has been to determine the effect of multiple resources on juvenile tree growth (Canham et al. 1996; Finzi and Canham 2000; Jose et al. 2003; Bigelow 2009; Lilles and Astrup 2012). Light, water and nutrients each play an important role in the growth of juvenile trees. With a better understanding of the relative importance of these resources, we can gain a better understanding of the growth and development of forest ecosystems. An important part of predicting the growth and development of juvenile trees involves determining the competitive effect of neighbors. Although it is generally understood that the density of neighbors has an influence on tree growth (Harper 1977; Lavigne 1988), we have a poor understanding of neighbor effects across resource gradients. With improved insight into the relative importance of light, water and nutrient availability across resource gradients, and the effect of competitors on this availability, we can develop and improve growth models that aid in sustainable management of forest resources.

### **General dissertation objectives**

The general dissertation objectives were as follows:

- 1) The objective of Chapter 2 was to determine the effects of multiple resources (light, water, nutrients) on the growth of juvenile subalpine fir across gradients of canopy retention and site quality, and to determine whether the density-growth relationship varied across a range of site qualities.
- 2) The objective of Chapter 3 was to use relationships derived in Chapter 2 to develop a spatially explicit juvenile growth model for subalpine fir. Then, by implementing this model in the

existing stand development model SORTIE-ND, simulation experiments could be used to test if juvenile or mature trees have a greater competitive influence on juvenile subalpine fir growing across a range of basal area classes.

3) In Chapter 4, the objective was to test the influence of site represented by site series on juvenile subalpine fir growth. To achieve this objective, a juvenile growth model that included site series to predict radial growth was implemented in SORTIE-ND.

## **Important findings**

### **Findings in relation to Objective #1**

*Light had the largest influence on juvenile subalpine fir growth.*

In Chapter 2, I found that site quality had no influence on radial growth below 30% light availability. Above 30%, however, radial growth was fastest on medium sites and slowest on dry sites. There was no clear light saturation point on any site quality.

*Delta-<sup>13</sup>C was also important in predicting radial growth and it provided insight into the relative importance of light, water and nutrients in regulating subalpine fir growth.*

I found a strong relationship between light and  $\delta^{13}\text{C}$ , which further supports the overall importance of light as a growth regulating factor for juvenile subalpine fir. Delta-<sup>13</sup>C values for juvenile subalpine fir ranged from -30.98‰ to -24.56‰, with the lowest  $\delta^{13}\text{C}$  values (< -28.9‰) on wet and medium site series at light levels below 37%. These low  $\delta^{13}\text{C}$  values may be attributed to lower evapo-transpirational demands in the low light and high soil moisture environment of these site series. Higher  $\delta^{13}\text{C}$  values were associated with faster growth rates regardless of light availability and were most likely caused by higher photosynthetic capacity.

***Tree size was the third most important predictor variable for juvenile tree growth.***

Tree size was the third most important predictor of radial growth, accounting for 28-30% of the variation in subalpine fir radial growth

***Soil water was a poor predictor of juvenile tree growth.***

The effect of soil water availability (as measured by volumetric water content) on juvenile tree radial growth was weak. A model that included soil water availability as a predictor suggested that radial growth was fastest on sites with lower volumetric soil moisture content. However, this model performed only marginally better than a simpler light-growth model. Rather than providing evidence that water was not limiting, these results may simply indicate that saplings experienced more variation in light than in water availability.

***Measurement of foliar N did not improve growth predictions.***

Despite the known importance of N limitations in many BC forest ecosystems, natural variation in foliar N availability did not play a role in predicting juvenile subalpine fir radial growth. It is possible that the natural range of variation in N availability was smaller than the potential range of subalpine fir growth response to other limitations.

***Simple, non-spatial quantification of neighbor density only slightly improved model predictions.***

Models that included neighbor density, expressed as the number of stems/ha within a 3.99 m radius of the target tree, only resulted in small gains in subalpine fir radial growth predictability.

A simple density-growth model did perform slightly better than the size-growth model, showing a decrease in radial growth at higher neighbor densities.

### **Findings in relation to Objective #2**

In Chapter 3, I developed a new spatially explicit juvenile tree growth behavior (Juvenile NCI growth) that predicts juvenile subalpine fir growth from target tree size and a competition index, which includes size, species and distance to neighboring trees. The new growth behavior was used in a SORTIE-ND simulation to: 1) compare the competitive effects of juvenile and overstory mature tree neighbors on the growth of juvenile subalpine fir; and 2) compare the competitive relationship across a range of neighbor basal area classes. The simulations showed that juvenile radial growth was faster under the canopy of mature trees than in the neighborhood of similar sized juveniles at the two lowest density classes, 7 and 20 m<sup>2</sup>/ha. These findings indicate that symmetric competition processes dominated, where resource availability to target plants is proportional to competitor size. At the highest density class, I did not find any differences in juvenile radial growth between the two tree strata. At this level of stocking, it appears that juvenile and mature stands were approaching site occupancy, resulting in fewer forest gaps and lower soil resource availability. As expected, the growth of juvenile trees declined with increasing neighbor basal area regardless of the identity of neighbors.

### **Findings in relation to Objective #3**

In Chapter 4, I parameterized three separate parameter files using the “Logistic growth with size dependent asymptote” juvenile tree growth behavior in SORTIE-ND with juvenile tree data collected from dry, medium and wet site series. Simulations in SORTIE-ND were then used to examine the influence of site series on the growth and development a 100 year-old subalpine fir

stand. Findings from the study showed that site series did have an influence on the growth and development of the stand. At the beginning of the simulation period, juvenile trees (trees < 5cm dbh) reached adult tree sizes (trees > 5cm dbh) quicker on the medium sites than on the wet or dry sites. The basal area per ha also initially increased faster on the medium sites; however, by the end of the simulation period, the stand basal areas per ha were similar on all three sites. This unexpected result was likely due to greater density-dependent mortality on the medium than dry or wet site series as evidenced by the lowest stand density at 100 years. The results from this study suggest that incorporating site quality is important for juvenile tree growth. In terms of model improvements, adding site series into SORTIE-ND could prevent over-estimation of yields on wet or dry MSdm<sup>2</sup> sites, thus allowing the model to be applied more accurately over a broader range of ecological conditions. This may also be true for ecological zones other than the Montane Spruce zone. For example, SORTIE-ND currently only includes parameters for the medium sites of the Interior Cedar-Hemlock and Sub-boreal Spruce ecological zones (Canham et al. 2004; Coates et al. 2009; Thorpe et al. 2010).

### **Relating the dissertation chapters to each other and their overall contribution to the field of study**

The amount of field data collected in this research was extensive, making it one of the most in-depth studies investigating the role of multiple resources (light, water, nutrients) on juvenile tree growth of any tree species (Canham et al. 1996; Finzi and Canham 2000; Jose et al. 2003; Bigelow 2009; Lilles and Astrup 2012). In total, 304 juvenile subalpine fir trees were sampled across gradients of canopy retention and site quality. To assess the role of competition and to determine whether the density-growth relationship varied across a range of site qualities, over 15,000 neighbor trees were stem mapped and measured. Further, several growth factors were

examined with regards to their impacts on juvenile tree growth. In chapter 2, the effects of light, moisture, nutrients and neighbor density on juvenile tree growth were examined. This led to the major conclusions that: 1) light availability had the largest influence on juvenile tree growth; 2) Delta-13C was the second most important growth predictor; 3) tree size also improved growth predictions; 4) soil moisture was a weak growth predictor; 5) foliar N levels did not improve growth predictions; and 6) density, as expressed as stems/ha, improved growth predictions negligibly. The results from Chapter 2 helped to determine the important predictor variables (light and tree size) that were used in investigating the importance of competition, particularly spatially explicit competition on the development of juvenile trees (Chapter 3). The chosen spatial model utilized tree size and the crowding effect of neighbors to predict juvenile radial growth. This model was then incorporated into SORTIE-ND as a new juvenile growth behavior, “Juvenile NCI Growth”, and used to test whether juvenile or mature trees have a greater competitive influence on juvenile subalpine fir growth under three basal area classes. Here, I found that juvenile radial growth was faster under the canopy of mature trees than in the neighborhood of similar sized juveniles at the two lowest density classes, 7 and 20 m<sup>2</sup>/ha. This indicated that symmetric competition processes dominated. I also found that at the highest density class, there were no differences in juvenile radial growth between the two neighbor strata. Chapter 4 was designed to test the influence of site series on growth predictions using SORTIE-ND. Three separate parameter files were developed using the “Logistic growth with size dependent asymptote” juvenile tree growth behavior in SORTIE-ND. This behavior was chosen because it was the only non-spatial size-dependent juvenile growth behavior available in SORTIE-ND and because size was demonstrated to be an important predictor of juvenile tree growth in chapter 2. The three parameter files were parameterized using juvenile tree data

collected from dry, medium and wet site series. Simulations using SORTIE-ND were then run to test the influence of site series on the growth and development a 100 year old subalpine fir stand. I found that site series did have an influence on the growth and development of the stand, which suggests that incorporating site quality into SORTIE-ND would improve longer term growth and yield predictions.

### **Future research directions**

To gain additional insight into stand development in the Montane Spruce ecological zone (Meidinger and Pojar, 1990), it would be beneficial to conduct similar research for other species, in particular lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. Ex Loud) and hybrid white spruce (*Picea glauca* x *Picea engelmannii* [Moench] Voss), common species in this ecological zone. Understanding how juveniles of all three species compete and respond to light, water and nutrient availability would be helpful in understanding responses to silvicultural treatments and improve predictions of species composition and growth trajectories. Continued development of SORTIE-ND by incorporating site quality into growth predictions for other ecological zones would also be beneficial. As noted earlier, SORTIE-ND is currently parameterized for the “medium” site series of Interior Cedar-Hemlock and Sub-boreal Spruce ecological zones (Canham et al. 2004; Coates et al. 2009; Thorpe et al. 2010). This narrow range of site conditions limits the ability of SORTIE-ND to provide stand growth predictions across the range of site qualities characteristic of these two ecological zones. In the near future, it is likely that remote sensing techniques such as ground-based scanning LiDAR (Light Detection and Ranging) technology (Hopkinson et al. 2004; Yao et al. 2011) or perhaps even unmanned Aerial Vehicles (UAVs) in conjunction with airborne LiDAR technology (Wallace et al. 2012) will

make the collection of parameter data more affordable. This will facilitate examination of relationships and development of forecast models as in this dissertation.

## References

- Agriculture Canada Expert Committee on Soil Survey, 1987. The Canadian system of soil classification. Agric. Can., Ottawa, Ont., Agric. Can. Pub. No. 1646.
- Aston, A.R., 1979. Rainfall interception by eight small trees. *Journal of Hydrology* 42: 383-396.
- Astrup R. 2006. Modeling growth of understory aspen and spruce in western boreal Canada. [PhD. Thesis]: University of British Columbia. 159 pp.
- Aussenac, G., and Granier, A. (1988). Effects of thinning on water stress and growth in Douglas-fir. *Canadian Journal of Forest Research* 18: 100-105.
- Baldwin, V.C. Jr., Peterson, K.D., Clark, A. III, Ferguson, R.B., Strub, M., and Bower, D.R. 2000. The effects of spacing and thinning on stand and tree characteristics of 38-year-old Loblolly Pine. *Forest Ecology and Management* 137: 91-102.
- Ballard, T.M., and Carter, R.E., 1985. Evaluating forest stand nutrient status. B.C. Ministry of Forests, Victoria. B.C., Land Management Report No. 20.
- Berry, S. C., Varney, G.T., and L. B. Flanagan, L.B. 1997. Leaf  $\delta^{13}\text{C}$  in *Pinus resinosa* trees and understory plants: Variation associated with light and  $\text{CO}_2$  gradients. *Oecologia* 109: 499-506.
- Bigelow, S.W, North, M.P. and Horwath, W.R. 2009. Resource-dependent growth models for Sierran mixed-conifer saplings. *The Open Forest Science Journal* 2: 31-40.
- Boivin, F., Paquette, A., Papaik, M.J., Thiffault, N., and Messier, C. 2010. Do position and species identity of neighbours matter in 8–15-year-old post-harvest mesic stands in the boreal mixedwood *Forest Ecology and Management* 260: 1124-1131.

- Brais, S., Camiré, C., Bergeron, Y., and Paré, D. 1995. Changes in nutrient availability and forest floor characteristics in relation to stand age and forest composition in the southern part of the boreal forest of northwestern Québec. *Forest Ecology and Management* 76: 181–189.
- Brockley, R.P. 2001. Foliar sampling guidelines and nutrient interpretative criteria for lodgepole pine. B.C. Ministry of Forests, Victoria, B.C. Extension Note 52.
- Burnham, K.P. and Anderson, D.R. 2002. Model selection and multimodel inference, a practical information-theoretic approach. Second edition. Springer-Verlag New York, Inc. 488 p.
- Burns, R.M. and Honkala, B.H. 1990. *Silvics of North America, Vol. 1, Conifers*. Washington DC: U.S.D.A. Forest Service Agriculture Handbook 654.  
[http://www.na.fs.fed.us/spfo/pubs/silvics\\_manual/table\\_of\\_contents.htm](http://www.na.fs.fed.us/spfo/pubs/silvics_manual/table_of_contents.htm), accessed 15-Nov-2007.
- Burton, P.J. 2010. Striving for sustainability and resilience in the face of unprecedented change: the case of the mountain pine beetle outbreak in British Columbia. *Sustainability* 2: 2403-2423.
- Canham, C.D. 1988. An index of understory light levels in and around canopy gaps. *Ecology*, 69: 1634–1638.
- Canham, C.D., Berkowitz, A.R., Kelly, V.R., Lovlett, G.M., Ollinger, S.V., and Schnurr, J. 1996. Biomass allocation and multiple resource limitation in tree seedlings. *Canadian Journal of Forest Research* 26: 1521-1530.
- Canham, C.D., Coates, K.D., Bartemucci, P., and Quaglia, S. 1999. Measurement and Modeling of Spatially-explicit Variation in Light Transmission Through Interior Cedar-Hemlock Forests of British Columbia. *Canadian Journal of Forest Research* 29: 1775-1783.

- Canham, C.D. 2002. SORTIE-ND - Software for spatially-explicit simulation of forest dynamics. <http://www.sortie-nd.org/>, accessed 10-Oct-2006.
- Canham, C.D., LePage, P., and Coates, K.D. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Canadian Journal of Forest Research* 34: 778-787.
- Cardinale, B.J., Duffy, D., Wright, J.E., Downing, J.P., Sankaran, A.L., and Srivastava, M. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443: 989-992.
- Carter, R.E., and Klinka, K. 1992. Variation in shade tolerance of Douglas fir, western hemlock, and western redcedar in coastal British Columbia. *Forest Ecology and Management* 55: 87-105.
- Carter, G.A., and Smith, W.K. 1985. Influence of shoot structure on light interception and photosynthesis in conifers. *Plant Physiology*. 79: 1038-1043.
- Casper, B.B., and Jackson, R.B. 1997. Plant competition underground. *Annual Review of Ecology and Systematics* 28: 545-570.
- Chapin, F.S. III, Bloom, A.J., Field, C.B., and Waring, R.H. 1987. Plant responses to multiple environmental factors. *Bioscience* 37: 49-57.
- Chapin, F.S. III, Matson, P.A., and Mooney, H.A. 2002. *Principles of Terrestrial Ecosystem Ecology*, Springer, New York.
- Chen, J., Franklin, J.F., and Spies, T.A. 1995. Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecological Applications* 5: 74-86.
- Chen, H.Y.H., Klinka, K., and Kayahara, G.J. 1996. Effects of light on growth, crown architecture and specific leaf area for naturally established *Pinus contorta* var. *latifolia* and

- Pseudotsuga menziesii* var. *glauca* saplings. *Canadian Journal of Forest Research* 26: 1149-1157.
- Chen, H.Y.H. 1997. Interspecific responses of planted seedlings to light availability in interior British Columbia: survival, growth, allometric patterns, and specific leaf area. *Canadian Journal of Forest Research* 27: 1383-1393.
- Claveau, Y., Messier, C., Comeau, P.G. and Coates, K.D. 2002. Growth and crown morphological responses of boreal conifer seedlings and saplings with contrasting shade tolerance to a gradient of light and height. *Canadian Journal of Forest Research* 32: 458-468.
- Coates, K.D., and Burton, P. J. 1999. Growth of planted tree seedlings in response to ambient light levels in northwestern interior cedar-hemlock forests of British Columbia. *Canadian Journal of Forest Research* 29: 1374-1382.
- Coates, K.D., Canham, C.D., and LePage, P.T. 2009. Above-versus below-ground competitive effects and responses of a guild of temperate tree species. *Journal of Ecology* 97, 118–130.
- Coomes, D.A., and Grubb, P.J. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecological Monographs* 70:171-207.
- Cui, M., and Smith, W.K. 1991. Photosynthesis, water relations and mortality in *Abies lasiocarpa* seedlings during natural establishment. *Tree Physiology* 8:37-46.
- Drever, C.R., and Lertzman, K.P. 2001. Light-growth responses of coastal Douglas-fir and western redcedar saplings under different regimes of soil moisture and nutrients. *Canadian Journal of Forest Research* 31: 2124-2133.

- Duchesneau, R., Lesage I., Messier C. and H. Morin. 2001. Effects of light and intraspecific competition on growth and crown morphology of two size classes of understory balsam fir saplings. *Forest Ecology and Management* 140:215–225.
- Dupouey, J.L., Leavitt, S.W., Choisnel E., and Jourdain, S. 1993. Modeling carbon isotope fractionation in tree rings based on effective evapotranspiration and soil water status. *Plant, Cell and Environment* 16: 939-947.
- Fahlvik, N., and Nystroöm, K. 2006. Models for predicting individual tree height increment and tree diameter in young stands in southern Sweden. *Scandinavian Journal of Forest Research*. 21: 16-28.
- Farquhar, G.D., O’Leary, M.H., and Berry, J.A. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology* 9: 121-137.
- Farquhar, G.D., Ehleringer, J.R., and Hubick, K.T. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* 40: 503-537.
- Field, C., and Mooney, H.A. 1986. The photosynthesis-nitrogen relationship in wild plants. In: Givnish TJ, *On the economy of plant form and function*. Cambridge University Press, Cambridge, pp 25-55.
- Filipescu, C. and Comeau, P. 2007. Competitive interactions between aspen and white spruce vary with stand age in boreal mixed woods. *Forest Ecology and Management* 247: 175-184.
- Finzi, A.C., and Canham, C.D. 2000. Sapling growth in response to light and nitrogen availability in a Southern New England forest. *Forest Ecology and Management* 131: 153-165.

- Fløistad I.S., and Patil G.G. 2002. Growth and terminal bud formation in *Picea abies* seedlings grown with alternating diurnal temperature and different light qualities. *Scandinavian Journal of Forest Research* 17: 15-27.
- Frazer, G.W., Canham, C.D., and Lertzman, K.P. 2000. Technological Tools: Gap Light Analyzer, Version 2.0. *Bulletin of the Ecological Society of America* 81: 191-197.
- Gause, G. F. 1932. Experimental studies on the struggle for existence. *Journal of Experimental Biology* 9: 389-402.
- Goffe, W.L., Ferrier, G.D., and Rogers, J. 1994. Global optimization of statistical functions with simulated annealing. *Journal of Econometrics*: 60: 65-99.
- Goldberg, D. E., and Werner, P.A. 1983. Equivalence of competitors in plant communities: a null hypothesis and a field experimental approach. *American Journal of Botany* 70: 1098-1104.
- Grassi, G. and Giannini, R. 2005. Influence of light and competition on crown and shoot morphological parameters of Norway spruce and silver fir saplings. *Annals of Forest Science* 62: 269-274
- Grime, J.P. (1973) Competitive exclusion in herbaceous vegetation. *Nature* 242: 344-347.
- Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111: 1169-1194.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, London, UK.
- Harcombe, P.A. 1987. Tree life tables. *BioScience* 37: 557- 68.
- Harrington, T. B., C. M. Dagley, and M. B. Edwards. 2003. Above- and belowground competition from longleaf pine plantations limits performance of reintroduced herbaceous species. *Forest Science* 49: 681–695.

- Harrington, T.B. 2006. Five year growth responses of Douglas-fir, western hemlock, and western redcedar seedlings to manipulated levels of overstory and understory competition. *Canadian Journal of Forest Research* 26: 2439-2453.
- Haynes, R.J. 1986. The decomposition process: Mineralization, immobilization, humus formation and degradation. Pages 52-126 in R.J Haynes editors. *Mineral Nitrogen in the plant soil system*. Academic Press, Orlando FL.
- Heithecker, T.D., and Halpern, C.B. 2007. Edge-related gradients in microclimate in forest aggregates following structural retention harvests in western Washington. *Forest Ecology and Management* 248: 163–173.
- Hodges, J. D., and Scott, D.R.M. 1968. Photosynthesis in seedlings of six conifer species under natural environmental conditions. *Ecology* 49: 973-981.
- Hurvich, C.M., and Tsai, C.L. 1989. Regression and time series model selection in small samples. *Biometrika* 76: 297-307.
- Ingestad, T., and Agren, G.I. 1991. The influence of plant nutrition on biomass allocation. *Ecological Applications* 1: 168-174.
- Jose, S., Merritt, S., and Ramsey, C.L. 2003. Growth, nutrition, photosynthesis and transpiration responses of longleaf pine seedlings to light, water and nitrogen. *Forest Ecology and Management* 180: 335–344.
- Kaufman, M.R. 1982. Leaf conductance as a function of photosynthetic photon flux density and absolute humidity difference from leaf to air. *Plant Physiology* 69: 1018-22.
- Kayahara, G., Klinka K., and Marshall, P. 1996. The relations of site index to site factors for lodgepole pine, interior spruce, and subalpine fir in central British Columbia, Canada. B.C. Ministry of Forests, Victoria, B.C. Unpublished Report.

- King, D.A. 1997. Branch growth and biomass allocation in *Abies amabilis* saplings in contrasting light environments. *Tree Physiology* 17:251–258.
- Klaassen, W., Bosveld, F.C., de Water, E., 1998. Water storage and evaporation as constituents of rainfall interception. *Journal of Hydrology* 212/213: 35–50.
- Klinka, K., Wang, Q., Kayahara, G.J., Carter, R.E., and Blackwell, B.A. 1992. Light growth response relationships in Pacific silver fir (*Abies amabilis*) and subalpine fir (*Abies lasiocarpa*). *Canadian Journal of Botany* 70: 1919-1930.
- Klinka, K., Worrall, J., Skoda, L., and Varga, P. 2000. The Distribution and Synopsis of the Ecological and Silvical Characteristics of Tree Species of British Columbia's Forests. Canadian Cartographics Ltd., 57B Clipper St., Coquitlam, BC, Canada, 180 pp.
- Kneeshaw, D.D., Williams, H., Nikinmaa, E., and Messier, C. 2002. Patterns of above and below-ground response of understory conifer release 6 years after partial cutting. *Canadian Journal of Forest Research* 32: 255–265.
- Kobe, R.K., and Coates, K.D. 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. *Canadian Journal of Forest Research* 27: 227–236.
- Kobe, R.K. 2006. Sapling growth as a function of light and landscape-level variation in soil water and foliar nitrogen in northern Michigan. *Oecologia*. 147:119-133.
- Kohyama, T. 1980. Growth pattern of *Abies mariesii* saplings under conditions of open-growth and suppression. *Botanical Magazine [Tokyo]* 93: 13-24.
- Kolb, T. E., and K. C. Steiner. 1990. Growth and biomass partitioning of northern red oak and yellow-poplar seedlings: effects of shading and grass root competition. *Forest Science* 36: 34-44.

- Koppenaar, R.S., Hawkins, B.J., and Mitchell, A.K. 1995. Acclimation of natural and planted Amabilis fir to clearcut and stand edge microclimates on a coastal montane reforestation site. Canada – British Columbia Forest Resource Development Agreement. Canada Forest Service and B.C. Ministry of Forests, Victoria, B.C. FRDA Rep. 232.
- Kozlowski, T.T. 1984. Responses of woody plants to flooding. In *Flooding and Plant Growth*. Ed. T.T. Kozlowski. Academic Press, New York, p. 129-163.
- Kozlowski, T.T., Kramer, P.J., and Pallardy, S.G. 1991. *The Physiological Ecology of Woody Plants*. Academic Press, San Diego, USA, pp. 390.
- Kozlowski, T.T. and Pallardy, S.G. 2002. Acclimation and adaptive responses of woody plants to environmental stresses. *The Botanical Review* 68: 270–334.
- Krajina, V.J. 1969. Ecology of forest trees in British Columbia. *Ecology of Western North America* 2(1): 1.146.
- Kramer, P.J. 1969. *Plant and soil water relationships: a modern synthesis*. McGraw-Hill. New York.
- Kramer P.J., and Kozlowski, T.T. 1979. *Physiology of Woody Plants*. Academic Press, New York.
- Kranabetter, J.M., Banner, A., and Shaw, J. 2003. Growth and nutrition of three conifer species across site gradients of north coastal British Columbia. *Canadian Journal of Forest Research* 33: 313-324.
- Kranabetter, M. 2008. Interacting effects of soil nitrogen supply and light availability on understory sapling growth and foliar attributes. [PhD. Thesis]: University of British Columbia. 114 pp.

- Kranabetter, J.M., Simard, S.W., Guy, R. D., and Coates, K.D. 2009. Species patterns in foliar nitrogen concentration, nitrogen content and  $^{13}\text{C}$  abundance for understory saplings across light gradients. *Plant and Soil* 327: 389-401.
- Lanner, R.M. 1985. On the insensitivity of height growth to spacing. *Forest Ecology and Management* 13: 143-148.
- Lavigne, M.B. 1988. Stem growth and respiration of young balsam fir trees in thinned and unthinned stands. *Canadian Journal of Forest Research* 18: 483-489.
- LePage, P.T., Canham, C.D., Coates, K.D., and Bartemucci, P. 2000. Seed abundance versus substrate limitation of seedling recruitment in northern temperate forests of British Columbia. *Canadian Journal of Forest Research* 30: 415-427.
- Lieffers, V.J., and Stadt, K.J. 1994. Growth of understory *Picea glauca*, *Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstory light. *Canadian Journal of Forest Research* 24: 1193-1198.
- Lindh, B.C., Gray, A.N., Spies, T.A., 2003. Responses of herbs and shrubs to reduced root competition under canopies and in gaps: a trenching experiment in old-growth Douglas-fir forests. *Canadian Journal of Forest Research* 33: 2052–2057.
- Lilles, E., and Astrup, R. 2012. Multiple resource limitation and ontogeny combined: a growth rate comparison of three co-occurring conifers. *Canadian Journal of Forest Research* 42: 99-110.
- Livingston, N.J., Whitehead, D., Kelliher, F.M., Wang, Y.P., Grace, J.C., Walcroft, A.S., Byers, J.N., McSeveny, T.M., and Millard, P. 1998. Nitrogen allocation and carbon isotope fractionation in relation to intercepted radiation and position in a young *Pinus radiata* D. Don tree. *Plant Cell Environment* 21: 795–803

- Lloyd, D., Angove, K., Hope, G., and Thompson, C. 1990. A guide to site identification and interpretation for the Kamloops Forest Region. British Columbia Ministry of Forests, Victoria, B.C. Land Management Handbook 23.
- Lusk, C.H., and Reich, P.B. 2000. Relationships of leaf dark respiration with light environment and tissue nitrogen content in juveniles of 11 cold-temperature tree species. *Oecologia* 123: 318-329.
- MacFarlane, D.W., and Kobe, R.K. 2006. Selecting models for capturing tree-size effects on growth–resource relationships. *Canadian Journal of Forest Research* 36: 1695-1704.
- Mah, S., and Nigh, G.D. 2003. SIBEC site index estimates in support of forest management in British Columbia. Technical Report 004. Research Branch, BC Ministry of Forests, Victoria, BC, 20 pp.
- Makinen, H., and Isomaki, A. 2004. Thinning intensity and long-term changes in increment and stem form on Norway spruce trees. *Forest Ecology and Management* 201: 295-309.
- Man, R.Z., and Lieffers, V.J. 1997. Seasonal photosynthetic responses to light and temperature in white spruce seedlings planted under an aspen (*Populus tremuloides*) canopy and in open conditions. *Tree Physiology* 17: 437-444.
- Marshall, J.D., and Waring, R.H. 1986. Comparison of methods of estimating leaf-area index in old-growth Douglas-fir. *Ecology* 67: 975-979.
- Martin, P.H., Canham, C.D., and Kobe, R.K. 2010. Divergence from the growth–survival tradeoff and extreme high growth rates drive patterns of exotic tree invasions in closed-canopy forests. *Journal of Ecology* 98:778–789.

- Meidinger, D., and Pojar, J. 1991. Ecosystems of British Columbia. British Columbia Ministry of Forests, Victoria, B.C. Special Report 6.
- Messier, C. 1996. Managing light and understory vegetation in boreal and temperate broadleaf-conifer forests. In: Comeau, P.G. & Thomas, K.D. (eds.). *Silviculture of temperate and boreal broadleaf conifer mixtures*. Land management hand-book 36, Ministry of forests, Victoria, B.C.
- Messier, C., Parent, S., and Bergeron, Y. 1998. Characterization of understory light environment in closed mixed boreal forests: effects of overstory and understory vegetation. *Journal of Vegetation Science* 9: 511-520.
- Messier, C., Doucet, R., Ruel, J.C., Claveau, Y., Kelly, C., and Lechowicz, M.J. 1999. Functional ecology of advance regeneration in relation to light in boreal forests. *Canadian Journal of Forest Research* 29: 812-823.
- Mitchell, A.K., Arnott, J.T. 1995. Effects of shade on the morphology and physiology of *Amabilis* fir and western hemlock. *New Forests* 10: 79-98.
- Mitchell, K.A., Bolstad, P.V., and Vose, J.M. 1999. Interspecific and environmentally induced variation in foliar dark respiration among eighteen southeastern deciduous species. *Tree Physiology* 19: 861-870.
- Mori, A., and Takeda, H. 2003. Light-related competitive effects of overstory trees on the understory conifer sapling in a subalpine forest. *Journal of Forest Research* 8: 163–168.
- Newton, P.F., and Jolliffe, P.A. 1998. Assessing processes of intraspecific competition within spatially heterogeneous black spruce stands. *Canadian Journal of Forest Research* 28: 259-275.

- Nguyen-Queyrens, A., Ferhi, A., Loustau, D., and Guehl J.M. 1998. Within-ring delta C-13 spatial variability and interannual variations in wood cellulose of two contrasting provenances of *Pinus pinaster*. *Canadian Journal of Forest Research* 28: 766-773.
- Nyland, R.D. 2002. *Silviculture*, McGraw-Hill Series in Forest Resources, 2nd edn. McGraw-Hill, New York.
- Oliver, C. D., and B. C. Larson 1990. *Forest stand dynamics*. McGraw-Hill, New York.
- Pacala, S.W., Canham, C.D., and Silander, J.A. 1993. Forest models defined by field measurements: I. The design of a north-eastern forest simulator. *Canadian Journal of Forest Research* 23:1980-1988.
- Pacala, S.W., Canham, C.D., Silander, J.A., and Kobe, R.K. 1994. Sapling growth as a function of resources in a north temperate forest. *Canadian Journal of Forest Research* 24: 2172-2183.
- Pacala, S.W., Canham, C. D., Saponara, J., Silander, J.A., Kobe, R. K., and Ribbens, E. 1996. Forest models defined by field measurements: II Estimation, error analysis, and dynamics. *Ecological Monographs* 66: 1-43.
- Pearcy, R.W., and Pfitsch, W.A. 1991. Influence of sunflecks on the d13C of *Adenocaulon* bicolor plants occurring in contrasting forest understory micro sites. *Oecologia* 86: 457-462.
- Peterson, J.A., Seiler, J.R., Nowak, J., Ginn, S.E., and Kreh, R.E. 1997. Growth and physiological responses of young loblolly pine stands to thinning. *Forest Science* 43: 529-534.
- Prescott, C.E., Zabek, L.M., Staley, C.L., and Kabzems, R. 2000. Decomposition of broadleaf and needle litter in forests of British Columbia: influences of litter type, forest type and litter mixtures. *Canadian Journal of Forest Research* 30: 1742-1750.

- Puettmann, K.J., Coates, K.D. and Messier, C. 2008. *A Critique of Silviculture: Managing For Complexity*. Island Press, Washington, DC: Island Press. 206 pp.
- R Development Core Team, 2006. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. <http://www.Rproject.org>.
- Radwan, M.A., and Harrington, C.A. 1986. Foliar chemical concentrations, growth, and site productivity relations in western red cedar. *Canadian Journal of Forest Research* 16: 1069-1075.
- Rambo, T., and North, M., 2009. Canopy microclimate response to pattern and density of thinning in a Sierra Nevada forest. *Forest Ecology and Management* 257: 435-442.
- Rees, M., Condit, R., Crawley, M., Pacala, S. and Tilman, D. 2001. Long-term studies of vegetation dynamics. *Science* 293: 650-655.
- Reich, P.B., Kloeppel, B.D., Ellsworth, D.S., and Walters, M.B. 1995. Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous species. *Oecologia* 104: 24-30.
- Robson, T.M., Rodri'guez-Calcerrada, J., Sa'nchez-Go'mez, D., and Aranda, I. 2009. Summer drought impedes beech seedling performance more in a sub-Mediterranean forest understory than in small gaps. *Tree Physiology* 29: 249-259.
- Runion, G.B., Entry, J.A., Prior, S.A., Mitchell, R.J., and Rogers, H.H., 1999. Tissue chemistry and carbon allocation in seedlings of *Pinus palustris* subjected to elevated atmospheric CO<sub>2</sub> and water stress. *Tree Physiology* 19, 329-335.
- Runkle, J.R., and Yetter, T.C. 1987. Treefalls revisited: gap dynamics in the southern Appalachians. *Ecology* 68: 417-424.

- Sack, L., and Grubb, P.J. 2002. The combined impacts of deep shade and drought on the growth and biomass allocation of shade tolerant woody seedlings. *Oecologia* 131: 175-185.
- Simard, S.W., and Sachs, D.L. 2004. Assessment of interspecific competition using relative height and distance indices in an age sequence of seral interior cedar-hemlock forests in BC. *Canadian Journal of Forest Research* 34: 1228-1240.
- Sjolte-Jorgensen, J. 1967. The influence of spacing in the growth and development of coniferous plantations. *International Review of Forestry Research* 2: 43-94.
- Sparks, J.P., and Ehleringer, J.R. 1997. Leaf carbon isotope discrimination and nitrogen content for riparian trees along elevational transects. *Oecologia* 109: 362-367.
- Sprengel, C. 1828. Von den Substanzen der Ackerkrume und des Untergrundes. *Journal fur Technische und Okonomische Chemie* 2: 423-474; 3: 42-99, 313-352, and 397-421.
- Smith, D.W. 1986. *The Practice of Silviculture*, John Willy and Sons, New York, 527 pp.
- Schwinning, S., and Weiner, J. 1998. Mechanisms determining the degree of size-asymmetry in competition among plants. *Oecologia* 113: 447-455.
- Takahashi, K. 1996. Plastic response of crown architecture to crowding in understory trees of two co-dominating conifers. *Annals of Botany* 77: 159-164.
- Thibodeau, L., Raymond, P., Camiré, C., and Munson, A.D. 2000. Impact of pre-commercial thinning in balsam fir stands on soil nitrogen dynamics, microbial biomass, decomposition, and foliar nutrition. *Canadian Journal of Forest Research* 30: 229-238.
- Thorpe, H.C., Astrup, R., Trowbridge, A., Coates, K.D. 2010. Competition and tree crowns: a neighborhood analysis of three boreal tree species. *Forest Ecology and Management* 259: 1586-1596.

- Tilman, D. (1987) On the meaning of competition and the mechanisms of competitive superiority. *Functional Ecology* 1: 304-315.
- Tilman, D., Lehman, C. and Thompson, K. 1997. Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Natl. Acad. Sci. USA* 94: 1857–1861.
- Van Veen, J.A., and Kuikman, P.J. 1990. Soil structural aspects of decomposition of organic matter by microorganisms. *Biogeo- chemistry* 11: 213-223.
- Wallace, L., Lucieer, A., Watson, C., and Turner, D. 2012. Development of a UAV-LiDAR System with Application to Forest Inventory. *Remote Sensing* 4(6): 1519-1543.
- Walters, M.B., Lajzerowicz C.C., and Coates K.D. 2006. Soil resources and the growth and nutrition of tree seedlings near harvest gap forest edges in interior cedar-hemlock forests of British Columbia. *Canadian Journal of Forest Research* 36: 62-76.
- Wagner, R.G., and Radosevich, S.R. 1998. Neighborhood approach for quantifying interspecific competition in coastal Oregon forests. *Ecological Applications* 8: 779–794.
- Wang, G.G., and Klinka, K. 1997. White spruce foliar nutrient concentrations in relation to tree growth and soil nutrient amounts. *Forest Ecology and Management* 98: 89–99.
- Warren, C.R., McGrath, F.F., and Adams, M.A. 2001. Water availability and carbon isotope discrimination in conifers. *Oecologia* 127:476-486.
- Weaver, D. 2012. *Silviculture Survey Procedures Manual -Regen Delay, Stocking and Free Growing Surveys - plus Alternative Survey Methodologies*. BC Ministry of Forests, Lands and Natural Resources Operations, Resource Practices Branch, 293 pp.
- Weiner, J. 1990. Asymmetric competition in plant populations. *Trends in Ecology and Evolution* 5: 360-64.
- Williams, H., Messier, C. and Kneeshaw, D.D. 1999. Effects of light availability and

- sapling size on the growth and crown morphology of understory Douglas-fir and lodgepole pine. *Canadian Journal of Forest Research* 29: 222-231.
- Wilson, J.B. 1988. A review of evidence on the control of shoot:root ratio, in relation to models. *Annals of Botany* 61: 433-449.
- Wright, E.F., Coates, K.D., Canham, C.D., and Bartemucci, P. 1998. Species variability in growth response to light across climatic regions in northwestern British Columbia. *Canadian Journal of Forest Research* 28: 871-886.
- Wright, E.F., Canham, C.D., and Coates, K.D. 2000. Effects of suppression and release on sapling growth for 11 tree species of northern, interior British Columbia. *Canadian Journal of Forest Research* 30: 1571-1580.
- Yao, T., Yang, X. Y., Zhao, F., Wang, Z. S., Zhang, Q. L., Jupp, D. L. B., Culvenor, D. S., Newnham, G. J., Ni-Meister, W., Schaaf, C. B., Woodcock, C. E., and Strahler, A. H. (2011). Measuring forest structure and biomass in New England forest stands using Echidna ground-based lidar. *Remote Sensing of Environment* 115: 2965–2974.
- Zaerr, J.B. 1983. Short-term flooding and net photosynthesis in seedlings of three conifers. *Forest Science* 29: 71-78
- Zahner, R., 1968. Water deficits and growth of trees. In : Kozlowski, T.T. (Ed.), *Water Deficits and plant growth*, Vol. 2. Academic Press, London, pp. 191-254.

# Appendices

## Appendix A: Juvenile NCI Growth behavior. C++ Code.

```
//-----  
#include "NCIJuvenileGrowth.h"  
#include "TreePopulation.h"  
#include "Allometry.h"  
#include "SimManager.h"  
#include "ParsingFunctions.h"  
#include "Plot.h"  
#include "GrowthOrg.h"  
#include <stdio.h>  
  
////////////////////////////////////  
/  
// Constructor  
////////////////////////////////////  
/  
clNCIJuvenileGrowth::clNCIJuvenileGrowth(clSimManager * p_oSimManager) :  
    clWorkerBase(p_oSimManager), clBehaviorBase(p_oSimManager),  
    clGrowthBase(p_oSimManager) {  
    try  
    {  
        //Set namestring  
        strcpy( m_cNameString, "ncijuvenilegrowthshell" );  
  
        //Null out our pointers  
        mp_iGrowthCodes = NULL;  
        mp_fAlpha = NULL;  
        mp_fBeta = NULL;  
        mp_fMaxGrowth = NULL;  
        mp_fLambda = NULL;  
        mp_fMaxCrowdingRadius = NULL;  
        mp_iIndexes = NULL;  
        mp_fCrowdingSlope = NULL;  
        mp_fCrowdingSteepness = NULL;  
        mp_fSizeEffectB = NULL;  
        mp_fSizeEffectA = NULL;  
  
        //Version 2  
        m_fVersionNumber = 1.0;  
        m_fMinimumVersionNumber = 1.0;  
    }  
    catch ( modelErr & err )  
    {  
        throw( err );  
    }  
    catch ( modelMsg & msg )  
    {  
        throw( msg );  
    } //non-fatal error  
    catch ( ... )  
    {  
        modelErr stcErr;  
        stcErr.iErrorCode = UNKNOWN;  
    }  
}
```



```

}

mp_fMinimumNeighborDiam10 = new float[iNumTotalSpecies];
mp_fAlpha = new float[m_iNumBehaviorSpecies];
mp_fBeta = new float[m_iNumBehaviorSpecies];
mp_fCrowdingSlope = new float[m_iNumBehaviorSpecies];
mp_fCrowdingSteepness = new float[m_iNumBehaviorSpecies];
mp_fSizeEffectA = new float[m_iNumBehaviorSpecies];
mp_fMaxGrowth = new float[m_iNumBehaviorSpecies];
mp_fSizeEffectB = new float[m_iNumBehaviorSpecies];
mp_fMaxCrowdingRadius = new float[m_iNumBehaviorSpecies];
mp_fLambda = new float * [m_iNumBehaviorSpecies];
for ( i = 0; i < m_iNumBehaviorSpecies; i++ )
{
    mp_fLambda[i] = new float[iNumTotalSpecies];
    for ( j = 0; j < iNumTotalSpecies; j++ )
        mp_fLambda[i] [j] = 0;
}

//Make the list of indexes
mp_iIndexes = new short int[iNumTotalSpecies];
for ( i = 0; i < iNumTotalSpecies; i++ ) mp_iIndexes[i] = -1;
for ( i = 0; i < m_iNumBehaviorSpecies; i++ )
    mp_iIndexes[mp_iWhatSpecies[i]] = i;

//Set up our floatVal array that will extract values only for the species
//assigned to this behavior
p_fTempValues = new floatVal[m_iNumBehaviorSpecies];
for ( i = 0; i < m_iNumBehaviorSpecies; i++ )
    p_fTempValues[i].code = mp_iWhatSpecies[i];

//Fill the variables

//*****
// General parameters
//*****
//Maximum potential growth
FillSpeciesSpecificValue( p_oElement, "gr_juvNCIMaxPotentialGrowth",
    "gr_jnmpgVal", p_fTempValues, m_iNumBehaviorSpecies, p_oPop, true );
//Transfer to the appropriate array buckets
for ( i = 0; i < m_iNumBehaviorSpecies; i++ )
    mp_fMaxGrowth[i] = p_fTempValues[i].val;

//*****
// Crowding effect parameters
//*****
//Max crowding radius
FillSpeciesSpecificValue( p_oElement, "gr_juvNCIMaxCrowdingRadius",
    "gr_jnmcrVal", p_fTempValues, m_iNumBehaviorSpecies, p_oPop, true );
//Transfer to the appropriate array buckets
for ( i = 0; i < m_iNumBehaviorSpecies; i++ )
    mp_fMaxCrowdingRadius[i] = p_fTempValues[i].val;

//Neighbor dbh effect (alpha)
FillSpeciesSpecificValue( p_oElement, "gr_juvNCIAlpha", "gr_jnaVal",
    p_fTempValues, m_iNumBehaviorSpecies, p_oPop, true );
//Transfer to the appropriate array buckets

```

```

for ( i = 0; i < m_iNumBehaviorSpecies; i++ )
    mp_fAlpha[i] = p_fTempValues[i].val;

//Neighbor distance effect (beta)
FillSpeciesSpecificValue( p_oElement, "gr_juvNCIBeta", "gr_jnbVal",
    p_fTempValues, m_iNumBehaviorSpecies, p_oPop, true );
//Transfer to the appropriate array buckets
for ( i = 0; i < m_iNumBehaviorSpecies; i++ )
    mp_fBeta[i] = p_fTempValues[i].val;

//Lambda
for ( i = 0; i < iNumTotalSpecies; i++ )
{
    sprintf( cName, "%s%s%s", "gr_juvNCI",
        p_oPop->TranslateSpeciesCodeToName( i ), "NeighborLambda" );
    FillSpeciesSpecificValue( p_oElement, cName, "gr_jnlVal",
p_fTempValues,
        m_iNumBehaviorSpecies, p_oPop, true );
    for ( j = 0; j < m_iNumBehaviorSpecies; j++ )
        mp_fLambda[j][i] = p_fTempValues[j].val;
}

//Minimum neighbor Diam10
FillSpeciesSpecificValue( p_oElement, "gr_juvNCIMinNeighborDiam10",
    "gr_jnmndVal", mp_fMinimumNeighborDiam10, p_oPop, true );

//Crowding Slope (C)
FillSpeciesSpecificValue( p_oElement, "gr_juvNCICrowdingSlope",
    "gr_jncslVal", p_fTempValues, m_iNumBehaviorSpecies, p_oPop, true );
//Transfer to the appropriate array buckets
for ( i = 0; i < m_iNumBehaviorSpecies; i++ )
    mp_fCrowdingSlope[i] = p_fTempValues[i].val;

//Crowding Steepness (D)
FillSpeciesSpecificValue( p_oElement, "gr_juvNCICrowdingSteepness",
    "gr_jncstVal", p_fTempValues, m_iNumBehaviorSpecies, p_oPop, true );
//Transfer to the appropriate array buckets
for ( i = 0; i < m_iNumBehaviorSpecies; i++ )
    mp_fCrowdingSteepness[i] = p_fTempValues[i].val;

//NCI dbh divisor
FillSingleValue( p_oElement, "gr_juvNCIDiam10Divisor", &
m_fDiam10Divisor, true );

//Whether to include snags
FillSingleValue( p_oElement, "gr_juvNCIIncludeSnagsInNCI", &
m_bIncludeSnags, true );

//*****
// Size effect parameters
//*****
//Size effect a
FillSpeciesSpecificValue( p_oElement, "gr_juvNCISizeEffectA",
"gr_jnseaVal",
    p_fTempValues, m_iNumBehaviorSpecies, p_oPop, true );
//Transfer to the appropriate array buckets
for ( i = 0; i < m_iNumBehaviorSpecies; i++ )

```





```

for (i = 0; i < m_iNumSpeciesTypeCombos; i++) {

    //Get the code from growth org
    mp_iGrowthCodes[mp_iIndexes[mp_whatSpeciesTypeCombos[i].iSpecies]]
    [mp_whatSpeciesTypeCombos[i].iType - clTreePopulation::seedling]
        = mp_oGrowthOrg->GetGrowthCode(mp_whatSpeciesTypeCombos[i].iSpecies,
            mp_whatSpeciesTypeCombos[i].iType);
}
}

////////////////////////////////////
// DoShellSetup()
////////////////////////////////////
void clNCIJuvenileGrowth::DoShellSetup(xercesc::DOMDocument * p_oDoc) {
    AssembleUniqueTypes();
    ReadParameterFile( p_oDoc );
    ValidateData();
    GetTreeMemberCodes();
}

////////////////////////////////////
// AssembleUniqueTypes
////////////////////////////////////
void clNCIJuvenileGrowth::AssembleUniqueTypes() {
    short int * p_iTypesList, //for assembling the list of unique types
        i, j; //loop counters
    bool bFound; //flag used in assembling list of unique types

    //Declare the temp. types array to be as big as the combo list to make
    //sure we have space for everything, and initialize values to -1
    p_iTypesList = new short int[m_iNumSpeciesTypeCombos];
    for (i = 0; i < m_iNumSpeciesTypeCombos; i++)
        p_iTypesList[i] = -1;

    m_iNumBehaviorTypes = 0;
    //Go through each combo, and for the type for that combo, if it's not
    //already on the temp list, add it
    m_iNumBehaviorTypes = 0;
    for (i = 0; i < m_iNumSpeciesTypeCombos; i++) {
        bFound = false;
        //Test to see if this type is already on the list
        for (j = 0; j < m_iNumBehaviorTypes; j++) {
            if (mp_whatSpeciesTypeCombos[i].iType == p_iTypesList[j]) {
                bFound = true;
                break;
            }
        }
        if ( !bFound) {
            //Add the type to the list and increment the number of found species
            //by one
            p_iTypesList[m_iNumBehaviorTypes] = mp_whatSpeciesTypeCombos[i].iType;
            m_iNumBehaviorTypes++;
        }
    } //end of for (i = 0; i < m_iNumSpeciesTypeCombos; i++)

    mp_iWhatBehaviorTypes = new short int[m_iNumBehaviorTypes];
}

```



```

        sprintf( cQueryPiece, "%d%s", mp_iWhatBehaviorTypes[i], "," );
        strcat( cQuery, cQueryPiece );
    }
    sprintf( cQueryPiece, "%d", mp_iWhatBehaviorTypes[m_iNumBehaviorTypes -
1] );
    strcat( cQuery, cQueryPiece );

    p_oNCITrees = p_oPop->Find( cQuery );

    //*****
    // Loop through and to calculate growth for each tree
    //*****
    p_oTree = p_oNCITrees->NextTree();
    while ( p_oTree )
    {
        iSpecies = p_oTree->GetSpecies();
        iType = p_oTree->GetType();

        if ( -1 == mp_iGrowthCodes[mp_iIndexes[iSpecies]] [iType -
clTreePopulation::seedling] )
            goto nextTree;

        //Make sure tree's not dead
        iDeadCode = p_oPop->GetIntDataCode( "dead", p_oTree->GetSpecies(),
p_oTree->GetType() );
        if ( -1 != iDeadCode ) {
            p_oTree->GetValue( iDeadCode, & iIsDead );
            if ( notdead != iIsDead ) goto nextTree;
        }

        p_oTree->GetValue( p_oPop->GetDiam10Code( iSpecies, iType ), & fDiam10
);

        //First calculate the pieces that have no diameter component and thus
        //will not change in our loop

        //Get NCI
        fNCI = CalculateNCI( p_oTree, p_oPop, p_oAllom, p_oPlot );
        if ( fNCI > 0 )
            fCrowdingEffect = exp( -mp_fCrowdingSlope[mp_iIndexes[iSpecies]] *
                pow( fNCI, mp_fCrowdingSteepness[mp_iIndexes[iSpecies]] ) );
        else fCrowdingEffect = 1;
        //Make sure it's between 0 and 1
        if ( fCrowdingEffect < 0 ) fCrowdingEffect = 0;
        if ( fCrowdingEffect > 1 ) fCrowdingEffect = 1;

        //To correctly compound growth over the number of years per timestep,
        //we have to loop over the number of years, re-calculating the parts
        //with diam10 and incrementing the diam10 each time
        fAmountDiamIncrease = 0;
        for ( i = 0; i < fNumberYearsPerTimestep; i++ )
        {
            //Get the tree's size effect
            fSizeEffect = mp_fSizeEffectA[mp_iIndexes[iSpecies]] *
                pow(fDiam10, mp_fSizeEffectB[mp_iIndexes[iSpecies]]);

```

```

        //Make sure it's bounded between 0 and 1
        if ( fSizeEffect < 0 ) fSizeEffect = 0;
        if ( fSizeEffect > 1 ) fSizeEffect = 1;

        //Calculate actual growth in cm/yr
        fTempDiamIncrease = mp_fMaxGrowth[mp_iIndexes[iSpecies]] *
            fSizeEffect * fCrowdingEffect;

        //Add it to the running total of diameter increase
        fAmountDiamIncrease += fTempDiamIncrease;

        //Increase the diameter for the next loop
        fDiam10 += fTempDiamIncrease;

    }

    //Assign the growth back to "Growth" and hold it
    p_oTree->SetValue( mp_iGrowthCodes[mp_iIndexes[iSpecies]]
        [iType - clTreePopulation::seedling],
fAmountDiamIncrease );

    nextTree:
    p_oTree = p_oNCITrees->NextTree();
}
}
catch ( modelErr & err )
{
    throw( err );
}
catch ( modelMsg & msg )
{
    throw( msg );
} //non-fatal error
catch ( ... )
{
    modelErr stcErr;
    stcErr.iErrorCode = UNKNOWN;
    strcpy( stcErr.cFunction, "clNCIJuvenileGrowth::PreCalcGrowth" );
    throw( stcErr );
}
}

////////////////////////////////////
// CalculateNCI
////////////////////////////////////
float clNCIJuvenileGrowth::CalculateNCI( clTree * p_oTree, clTreePopulation *
p_oPop, clAllometry *p_oAllom, clPlot * p_oPlot )
{
    try
    {
        clTreeSearch * p_oAllNeighbors; //neighborhood trees within crowding
radius
        clTree * p_oNeighbor; //competing neighbor
        char cQuery[75]; //format search strings into this
        float fNCI = 0, //nci - the end result of all this math
            fDistance, //distance between target and neighbor
            fDiam10, //neighbor's dbh

```

```

    fTemp,
    fNeighX, fNeighY, //holders for the neighbor tree's X and Y
    fTargetX, fTargetY; //holders for the target tree's X and Y location
int iIsDead; //whether a neighbor is dead
short int iNeighSpecies, iNeighType, //species and type for neighbor
    iTargetSpecies, //target tree's species
    iDeadCode; //neighbor's dead code

iTargetSpecies = p_oTree->GetSpecies();

//Format the query to get all competing neighbors
p_oTree->GetValue( p_oPop->GetXCode( iTargetSpecies, p_oTree->GetType()
), & fTargetX );
p_oTree->GetValue( p_oPop->GetYCode( iTargetSpecies, p_oTree->GetType()
), & fTargetY );

//Get all trees within the max crowding radius - seedlings don't compete
sprintf( cQuery, "%s%f%s%f%s%f%s", "distance=",
mp_fMaxCrowdingRadius[mp_iIndexes[iTargetSpecies]], "FROM x=", fTargetX,
    "y=", fTargetY, ">::height=0");
p_oAllNeighbors = p_oPop->Find( cQuery );

//Loop through and assess the competitive effects of each
p_oNeighbor = p_oAllNeighbors->NextTree();

while ( p_oNeighbor ) {
    if ( p_oNeighbor == p_oTree ) goto nextTree;

    iNeighSpecies = p_oNeighbor->GetSpecies();
    iNeighType = p_oNeighbor->GetType();

    if (clTreePopulation::snag == iNeighType && !m_bIncludeSnags) goto
nextTree;

    //Make sure the neighbor's not dead
    iDeadCode = p_oPop->GetIntDataCode( "dead", p_oNeighbor->GetSpecies(),
p_oNeighbor->GetType() );
    if ( -1 != iDeadCode ) {
        p_oNeighbor->GetValue( iDeadCode, & iIsDead );
        if (iIsDead != notdead && iIsDead != natural) goto nextTree;
    }

    //Get diam10 - if it's an adult, use the sapling allometry from dbh
    if (clTreePopulation::seedling == iNeighType ||
        clTreePopulation::sapling == iNeighType) {
        //Get the neighbor's diam10
        p_oNeighbor->GetValue( p_oPop->GetDiam10Code( iNeighSpecies,
iNeighType ), & fDiam10 );
    } else {
        p_oNeighbor->GetValue( p_oPop->GetDbhCode( iNeighSpecies, iNeighType
), & fTemp );
        fDiam10 = p_oAllom->ConvertDbhToDiam10(fTemp, iNeighSpecies);
    }

    if ( fDiam10 < mp_fMinimumNeighborDiam10[iNeighSpecies] ) goto
nextTree;

```

```

        //Get the neighbor's X and Y values
        p_oNeighbor->GetValue( p_oPop->GetXCode( iNeighSpecies, iNeighType ), &
fNeighX );
        p_oNeighbor->GetValue( p_oPop->GetYCode( iNeighSpecies, iNeighType ), &
fNeighY );

        //Get the distance between the two trees
        fDistance = p_oPlot->GetDistance( fTargetX, fTargetY, fNeighX, fNeighY
);

        //Only goto nextTree if distance is not 0 - it will be a fluke
condition to
        //allow a tree that is literally standing on top of another one not to
//affect it competitively, but there it is
if ( fDistance < VERY_SMALL_VALUE) goto nextTree;

        //Add competitive effect to NCI
        fNCI += mp_fLambda[mp_iIndexes[iTargetSpecies]] [iNeighSpecies]
                * ( pow( ( fDiam10 / m_fDiam10Divisor ),
mp_fAlpha[mp_iIndexes[iTargetSpecies]] )
                / pow( fDistance, mp_fBeta[mp_iIndexes[iTargetSpecies]] ) );

        nextTree:
        p_oNeighbor = p_oAllNeighbors->NextTree();
    }

    return fNCI;
}
catch ( modelErr & err )
{
    throw( err );
}
catch ( modelMsg & msg )
{
    throw( msg );
} //non-fatal error
catch ( ... )
{
    modelErr stcErr;
    stcErr.iErrorCode = UNKNOWN;
    strcpy( stcErr.cFunction, "clNCIJuvenileGrowth::CalculateNCI" );
    throw( stcErr );
}
}

////////////////////////////////////
/
// SetNameData()
////////////////////////////////////
/
void clNCIJuvenileGrowth::SetNameData(char * cNameString) {

    //Check the string passed and set the flags accordingly
    if ( strcmp( "NCI Juvenile Growth", cNameString ) == 0 )
    {
        m_iGrowthMethod = diameter_auto;
    }
}

```

```

}
else if ( strcmp( "NCI Juvenile Growth diam only", cNameString ) == 0 )
{
    m_iGrowthMethod = diameter_only;
}
else
{
    modelErr stcErr;
    stcErr.iErrorCode = BAD_DATA;
    sprintf( stcErr.cMoreInfo, "%s%s%s", "Unrecognized behavior name \\"",
cNameString, "\".\" );
    strcpy( stcErr.cFunction, "clNciGrowth::SetNameData" );
    throw( stcErr );
}
}

```

## Appendix B: Juvenile NCI Growth behavior. C++ Shell.

```
//-----  
#ifndef NCIJuvenileGrowthH  
#define NCIJuvenileGrowthH  
//-----  
#include "GrowthBase.h"  
#include "NCIBase.h"  
  
class clSimManager;  
class clTree;  
class clTreePopulation;  
class clAllometry;  
class xercesc::DOMDocument;  
  
/**  
 * NCI juvenile growth - Version 1  
 *  
 * This is a growth shell object which applies a variant on the NCI  
 (neighborhood  
 * competition index) function designed for juvenile trees.  
 *  
 * Growth per year is Growth = Max Growth * Size Effect * Crowding Effect.  
 * The amount of growth is in cm/year. For multi-year timesteps, the behavior  
 * will calculate total growth with a loop. Each loop iteration will increment  
 * dbh for one year. For each year, the Size Effect (SE) value is  
 recalculated  
 * with the previous year's new dbh value. All values for each year of growth  
 * are summed to get the growth for the timestep.  
 *  
 * Size Effect = a * d10 ^ b, where d10 is diameter at 10 cm height. Crowding  
 * Effect = exp(-C * NCI ^ D). NCI is calculated with d10, not dbh, even for  
 * adults; the d10 - dbh conversion equation will be used with the sapling  
 * parameters.  
 *  
 * This can only be applied to seedlings and saplings. An error will be  
 thrown  
 * otherwise.  
 *  
 * The parameter file call string for this to be diameter-incrementing with  
 * auto-height updating is "NCI Juvenile Growth"; for diameter-only  
 incrementing,  
 * use "NCI Juvenile Growth diam only". The namestring for this behavior is  
 * "ncijuvenilegrowthshell".  
 *  
 * Copyright 2010 Charles D. Canham.  
 * @author Lora E. Murphy  
 *  
 * <br>Edit history:  
 * <br>-----  
 * <br>March 23, 2010 - Created (LEM)  
 */  
class clNCIJuvenileGrowth : virtual public clGrowthBase {  
 //note: need the virtual keyword to avoid base class ambiguity.
```

```

public:

/**
 * Constructor.
 * @param p_oSimManager Sim Manager object.
 */
    clNCIJuvenileGrowth(clSimManager *p_oSimManager);

/**
 * Destructor.
 */
~clNCIJuvenileGrowth();

/**
 * Returns the value in the tree's float data member that holds the value
 * that was calculated by PreGrowthCalcs().
 *
 * @param p_oTree Tree to which to apply growth.
 * @param p_oPop Tree population object.
 * @param fHeightGrowth Amount of height growth, in m (ignored).
 * @return Amount of diameter growth, in cm.
 */
float CalcDiameterGrowthValue(clTree *p_oTree, clTreePopulation *p_oPop,
float fHeightGrowth);

/**
 * Calculates growth for all NCI trees. The values are stashed in the
 * "Growth" tree float data member for later application.
 *
 * Steps:
 * <ol>
 * <li>Get all trees for this behavior.</li>
 * <li>For each tree, calculate NCI<sub>i</sub> by calling the function in
the
 * function pointer NCI. Stash the value in "Growth" for each tree.</li>
 * <li>Go through all the NCI trees again. Calculate the amount of growth
for
 * each using the equations above. Use the function pointers to make sure
 * that the proper function forms are used. Stash the end result in
 * "Growth".</li>
 * </ol>
 * This must be called first of any growth stuff, since it uses other trees'
 * dbhs to calculate NCI, and these must be before growth has been applied.
 *
 * Growth per timestep is calculated by looping over the number of years
 * per timestep and incrementing the dbh.
 *
 * @param p_oPop Tree population object.
 */
void PreGrowthCalcs( clTreePopulation *p_oPop );

/**
 * Does setup.
 * <ol>
 * <li>AssembleUniqueTypes() is called to create a list of unique behavior
 * types.</li>
 * <li>ReadParameterFile() is called to read the parameter file's data.</li>

```

```

* <li>ValidateData() is called to validate the data.</li>
* <li>GetTreeMemberCodes() is called to get tree data return codes.</li>
* <li>SetFunctionPointers() is called to set up our function pointers.</li>
* </ol>
*
* @param p_oDoc DOM tree of parsed input tree.
*/
void DoShellSetup(xercesc::DOMDocument *p_oDoc);

/**
* Captures the namestring passed to this behavior. This is overridden from
* clBehaviorBase so we can capture the namestring passed. Since this class
* can create multiple kinds of behaviors that function differently, this
will
* capture what kind of behavior this is supposed to be.
*
* @param cNameString Behavior's namestring.
*/
void SetNameData(char *cNameString);

protected:

short int **mp_iGrowthCodes; /**<Holds return data codes for the "Growth"
tree data member. Array size is number of species to which this behavior
applies by 2 (seedlings and saplings).*/
short int *mp_iWhatBehaviorTypes; /**<List of types managed by this
behavior.*/
short int m_iNumBehaviorTypes; /**<Number of types managed by this
behavior.*/

/**Lambda for NCI. Array is sized number of behavior species by number of
total
* species. This array is accessed by using the species number as an array
* index.*/
float **mp_fLambda;

/**Neighbor diam10 effect. @htmlonly &alpha; @endhtmlonly variable in
Crowding
* Effect equation. Array is sized number of species to which this behavior
* applies. This array is accessed by using the index returned for
* mp_iIndexes[species number].*/
float *mp_fAlpha;

/**Neighbor distance effect. @htmlonly &beta; @endhtmlonly variable in
* Crowding Effect equation. Array is sized number of species to which
* this behavior applies. This array is accessed by using the index
returned
* for mp_iIndexes[species number].*/
float *mp_fBeta;

/**Crowding effect slope. C in Crowding Effect equation. Array is sized
* number of species to which this behavior applies. This array is
accessed
* by using the index returned for mp_iIndexes[species number].*/
float *mp_fCrowdingSlope;

/**Crowding effect steepness. D in Crowding Effect equation. Array is sized

```

```

    * number of species to which this behavior applies. This array is
    accessed
    * by using the index returned for mp_iIndexes[species number].*/
    float *mp_fCrowdingSteepness;

    /**The minimum Diam10, in cm, of neighbors to be included in NCI
    calculations.
    * Array is sized total number of species.*/
    float *mp_fMinimumNeighborDiam10;

    /**Size effect "a" parameter. Array is sized number of species to which
    this
    * behavior applies. This array is accessed by using the index returned
    for
    * mp_iIndexes[species number].*/
    float *mp_fSizeEffectA;

    /**Size effect "b" parameter. Array is sized number of species to which
    this
    * behavior applies. This array is accessed by using the index returned
    for
    * mp_iIndexes[species number].*/
    float *mp_fSizeEffectB;

    /**Maximum growth, cm/yr. Array is sized number of species to which this
    * behavior applies. This array is accessed by using the index returned
    for
    * mp_iIndexes[species number].*/
    float *mp_fMaxGrowth;

    /**Maximum search radius, in meters, in which to look for crowding
    * neighbors. For calculating the Crowding Effect. Array is sized
    * number of species to which this behavior applies. This array is accessed
    * by using the index returned for mp_iIndexes[species number].
    */
    float *mp_fMaxCrowdingRadius;

    /**The value to divide diam10 by in NCI.  $q$  in the NCI equation
    above.
    * May be set to 1.*/
    float m_fDiam10Divisor;

    /**Speeds access to the arrays. Array size is is number of
    * species.*/
    short int *mp_iIndexes;

    /**Whether or not to include snags in NCI*/
    bool m_bIncludeSnags;

    /**
    * Calculates the NCI value for a tree.
    * @htmlonly
    <center>NCIi =  $\sigma$ ;
    &lambda;k ( (D10k/q) $\alpha$ /distance $\beta$ );</sup></center>
    @endhtmlonly
    * @param p_oTree Tree for which to calculate NCI.

```

```

* @param p_oPop Tree population object.
* @param p_oPlot Plot object.
* @return NCI value.
*/
float CalculateNCI( clTree * p_oTree, clTreePopulation * p_oPop, clAllometry
*p_oAllom, clPlot * p_oPlot);

/**
* Makes sure all input data is valid. The following must all be true:
* <ul>
* <li>Max radius of neighbor effects must be >= 0</li>
* <li>Max growth for each species must be > 0</li>
* <li>dbh divisor must be > 0</li>
* </ul>
* @throws modelErr if any of the above conditions are not met.
*/
void ValidateData();

/**
* Gets the return codes for needed tree data members.
* @throws modelErr if a code comes back -1 for any species/type combo to
* which this behavior is applied.
*/
void GetTreeMemberCodes();

/**
* Reads data from the parameter file.
* @param p_oDoc DOM tree of parsed input tree.
* @throws modelErr if this behavior has been applied to any types except
* sapling and seedling.
*/
void ReadParameterFile( xercesc::DOMDocument *p_oDoc );

/**
* Assembles a unique list of types applied to this behavior and places it
in
* mp_iWhatBehaviorTypes.
*/
void AssembleUniqueTypes();
};
//-----
#endif

```