# White spruce advanced regeneration response to Strip Cut Understory Protection harvesting

by

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# Abstract

Understory protection harvesting in boreal mixedwoods, which removes mature trembling aspen (*Populus tremuloides* Michx.) while leaving advance regeneration of white spruce (*Picea glauca* (Moench) Voss), is being used in many parts of northern Alberta, Canada. The harvesting system is a step forward in sustainable forest management by maintaining biodiversity within a stand, producing valuable timber, and following natural succession of a boreal mixedwood stand. From a management perspective there is a need for accurate yield estimations for understory protection harvesting sites. In this thesis I focus on the growth of white spruce advanced regeneration following removal of overstory aspen. Data were collected from five understory protection harvesting sites in northern Alberta and dendroecological techniques were used to determine diameter and height growth responses. Mixed effect- and generalized least square models were built to evaluate spruce growth response following understory protection harvesting and to examine the influence of neighboring spruce and aspen and climate on spruce growth. White spruce grew vigorously following removal of overstory aspen. I found a distinct immediate increase in diameter growth in the year following understory protection harvesting and in the following years, while height growth increases showed a delay of 3 to 5 years after release. Moreover intraspecific competition had a strong negative effect on the growth response of released spruce trees, whereas deciduous competition, mainly from aspen trees had less influence. Climate variables showed a weak influence on spruce growth following harvesting. Results from my research demonstrate the importance of including intraspecific competition in growth models. The incorporation of these results into stand growth models, specifically the Mixedwood Growth Model (MGM), will improve yield estimations for released white spruce.

# Preface

This thesis is an original work by Valerie Sharone Krebs. No part of this thesis has been previously published.

# Acknowledgements

Sincere gratitude goes to my supervisor Phil Comeau, who supported me with his expertise, advice and trust throughout my master program. His passion for the boreal forest brought me to Canada, and I am very thankful that he accepted me as a student in his lab, without having a background in forestry. His encouragement and support of presenting my research to the public enabled me to give talks about my study at the NAFEW 2015 Conference in Veracruz, Mexico and at the IUFRO Meeting 2015 in Edmonton, Alberta. Thank you Phil!

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# Chapter 1

# Introduction

## 1.1 Boreal mixedwood forests in north western Canada

In the southern parts of the Canadian boreal forest mixedwood stands are common. In mixedwood stands we find a mixture of coniferous and deciduous tree species growing together and forming structurally complex and highly productive forests. MacDonald (1995) defines a mixedwood stand as a tree community in which no species exceeds a basal area of 80%. In Alberta and north western Canada, mixedwood stands are most often a mixture of white spruce (*Picea glauca* (Moench) Voss) and trembling aspen (*Populus tremuloides* Michx.) trees. There are also mixtures found with black spruce (*Picea marina* (Mill.) Britton, Sterns & Poggenburg), balsam fir (*Abies balsamea* (L.) Mill.), white birch (*Betula papyrifera* Marshall) and balsam poplar (*Populus balsamifera* L.). In this thesis I will focus on the trembling aspen, white spruce dominated boreal mixedwoods.

Boreal mixedwood forests are known for their high biodiversity compared to single species stands. Structural and ecological diversity due to the mix of different tree species within one stand provide a diverse environment with versatile niches which are occupied by a high variety of species (Macdonald et al. 2010; Cavard et al. 2011).

The "classical" natural dynamics of these stands, following a stand destroying disturbance (e.g. fire, clearcut), consist of four stages. The first stage is "stand initiation" where shade intolerant pioneer trees, mainly trembling aspen, start growing and are the dominant species at the site, while shade tolerant white spruce grows in the understory of aspen. During the subsequent "stem exclusion" and "canopy transition" stages the spruce trees start to take over the canopy and form the main species in the forest. In the last stage "gap dynamics", new trees, aspen as well as spruce start growing in gaps formed by dying trees (Chen and Popadiouk, 2002).

Besides this "classical" model of mixedwood dynamics there are many variations depending on site factors, the stand-initiating disturbance, regeneration processes of individual species, and forest composition in the surrounding landscape. These make the boreal mixedwoods even more complex and difficult to manage in a sustainable way (Macdonald et al. 2010; Bergeron et al. 2014).

There are multiple ecological and economic reasons why mixedwoods should be managed as a mixture of species and according to their natural regeneration cycle. From an ecological point of view the mixed stands can be more resilient to environmental stresses like windthrow and insect attacks, for example from white pine weevil (Taylor et al. 1996; Knoke at al. 2007; Smith et al. 2016). In addition they provide a higher diversity within the stand. Economically higher yields can be derived from mixedwood sites compared to single species stands (Armstrong, 2014; Kabzems et al. 2016). Until the 1990's mixedwoods were mainly used to grow softwood species (spruce) and the hardwood (aspen) was not of high economic value, but during the last 30 years the use of aspen has increased continuously (Armstrong, 2014). In a mixedwood stand the space and light resources can be fully utilized by growing shade tolerant species in the understory and shade intolerant species in the overstory. A single species stand has most often just one canopy with either shade tolerant or intolerant species. Growing spruce trees under an aspen canopy can lead to higher wood quality as trees grow slower and moreover aspen trees can facilitate the growth of white spruce, providing shelter from extreme winds and extreme temperatures (Man and Lieffers, 1999).

## 1.2. Tree growth and silvicultural practices in the boreal mixedwoods

Tree growth is determined by multiple factors such as genetics and age of a tree as well as external factors such as climate, soil, (Vaganov et al. 2006) and competition (Coomes and Allen, 2007).

White spruce is adapted to a wide range of external factors and therefore is one of the most abundant tree species within the boreal forests in Canada. It is found from east to western Canada at elevations up to 1520 m above sea level. The wide distribution indicates its ability to grow in a variety of climatic and soil conditions. White spruce is found in northern areas with a January temperatures as low as -54 °C, to extreme warm temperatures of 43 °C, reported in Manitoba. Mean annual precipitation levels vary between a low of 250 mm and a high of 1270 mm in Yukon and Nova Scotia respectively (Burnes and Honkala, 1990).

The growth of white spruce is influenced by climate, and climate change is expected to influence both growth and the distribution of white spruce in the future. Climate change is expected to result in warmer and drier conditions in Alberta resulting in reduced growth of white spruce in parts of central Alberta (Barber, et al. 2000).

White spruce grows in a wide range of soils, including acid and alkaline, wet and dry, and soils with different fertility levels (Burnes and Honkala, 1990).

In mixedwoods white spruce and trembling aspen often grow intermixed with balsam poplar, paper birch and balsam fir. Due to its shade tolerance, spruce can grow and establish under the canopy of broadleaf species as long as light levels don't go below 8% to 10%. With increasing light levels the growth of white spruce will respond positively (Wright et al. 1998). Therefore, white spruce increment can be enhanced by reducing competition.

Competition is here defined as the negative effects that one tree has on another tree by consuming, or controlling access to resources which are limited in availability, such as light, nutrients and space (Keddy, 2001). The management of competition either from herbaceous or woody competitors is a major aspect of silvicultural management to increase survival and growth of white spruce as several studies show.

Youngblood et al. (2011) analyzed the growth and survival of white spruce seedlings in Alsaka using silvicultural practices compared to untreated stands. They found that scarification before plantation of spruce would increase volume of white spruce up to 86% 11 years after planting. The growth increased even more, up to 195%, when using herbicide treatment on the site before planting.

The process where understory trees are freed from overstory competition is called release and is commonly used in forest management on stands with advanced regeneration (Smith, 1986). The purpose of release is to provide understory trees with more light and space so that they can start to increase growth and form the main canopy. Multiple studies focus on the release response of trees, and show an increased increment of growth after release over a range of sizes and species (Lees, 1966; Yang, 1991; Claveau et al. 2006). A study done by Crossley (1976) shows the increased growth of advanced white spruce, black spruce and alpine fir (*Abies lasiocarpa*, (Hooker) Nuttall), after release. He reports a distinct increment of all three species in diameter and irregular increment in height. Overall growth increments exceed the growth of free grown trees, with no repression over a observed time period of 10 years after release. The exposure of released trees to less competition can physically shock advanced regenerating trees and inhibit their growth in the first years after harvesting (Ferguson and Adams, 1980). However the performance, adjustment time and survival of released trees is highly dependent on the species, their shade tolerance and light conditions before removal (Ruel et al. 2000). Evaluating different morphological factors influencing or indicating growth response of advanced regeneration after release, diameter growth generally responds stronger to the changes induced by the overstory harvesting than height growth. The vigorous growth of a tree before harvesting is positively related to growth response. Growth of the apical leader for advanced regeneration as response to overstory removal seems to be a good stress indicator for moderate- to shade tolerant species after the release cut, since higher light availability has shown a stronger growth of the apical leader compared to the growth of lateral branches and therefore indicating a lower stress level. Damage of advanced regeneration during the overstory removal can reduce the growth of advanced regenerated trees, especially when the bole is injured (Ruel et al. 2000).

Sustainable use of resources and maintenance of biodiversity plays a major role in resource management. Hence the demand for forest management which follows and utilizes the natural dynamics of ecosystems has risen during the last decade and is increasingly becoming part of forestry regulations (Brais et al. 2013).

Silviculture, defined as the tending of a stand so that it's utility for any desired purpose is enhanced and maintained (Smith, 1986) was in the past primarily used within the context of achieving good tree growth. To convert multicohort, multispecies stands to single species stands was believed as the best way growing stands for timber supply (Thorpe and Thomas, 2007). Reliance on even-aged harvesting systems, such as clear cuttings, and the planting of single species stands, has changed the forest landscape away from a landscape with diverse composition towards a forest landscape with a higher percentage of young, even-aged, single species stands.

Nowadays the term silviculture refers to a range of practices which improve stand properties, including ecosystem based management of a stand, where ecological process play an important role and natural dynamics of a stand are used to benefit the growth of trees (Lieffers et al. 2003).

Forest ecosystem management, defined as a management approach "that aims to maintain healthy and resilient forest ecosystems by focusing on a reduction of differences between natural and managed landscapes to ensure long-term maintenance of ecosystem functions and thereby retain the social and economic benefits they provide society" (Gauthier et al. 2009), is gaining in importance in management decision making (Perera et al. 2004)

Partial harvesting is a way of enhancing multi-aged stands and natural regeneration cycles. It can provide diverse and natural forest structures within the forest landscapes and promote continuous timber production (Bergeron and Harvey, 1997; Thorpe and Thomas, 2007). Since aspen trees reach their maximum growth much earlier than white spruce trees, a complete harvesting of both species at the same time in a mixedwood stand would lead to a reduction in yield. At the time when aspen is ready for harvest, spruce trees will still be small and growing in the understory. On the other hand when spruce trees reach merchantability, aspen trees will be slowly decaying (Smith et al. 2016). Therefore partial harvesting can maximize the timber coming from a mixedwood stand by utilizing each species at appropriate times.

Nowadays multiple partial harvesting techniques such as group shelterwood harvesting and strip selection harvesting are used. Usually partial harvesting includes the release of advanced regenerating trees. In Alberta it is required by law to use understory protection harvesting systems if advanced regeneration exists, which is often the case in northern mixedwoods of the province.

## 1.3 Understory Protection Harvesting

Brace and Bella (1988) developed the strip cut understory protection harvesting method for aspen dominated mixedwood stands with a conifer understory (Fig.1.1). It presents an alternative to monoculture stands and clear cuts and uses the softwood- as well as the hardwood-species economically. This harvesting system is based on two harvest entries in a mixedwood stand. The first harvest takes place after the aspen in the overstory is merchantable, which is about 60 years after the stand started to develop. Harvesting machines travel largely along "extraction trails" and harvest all hardwood and merchantable coniferous trees. In the "retention strips", the understory softwood trees are left standing where all merchantable aspen are harvested. In the "windbuffer zones" some hardwood species will be left to protect the released conifers from strong winds. Following overstory removal softwood in the understory increases its growth, especially in diameter, due to better light conditions (Man and Greenway, 2004; Prévost and

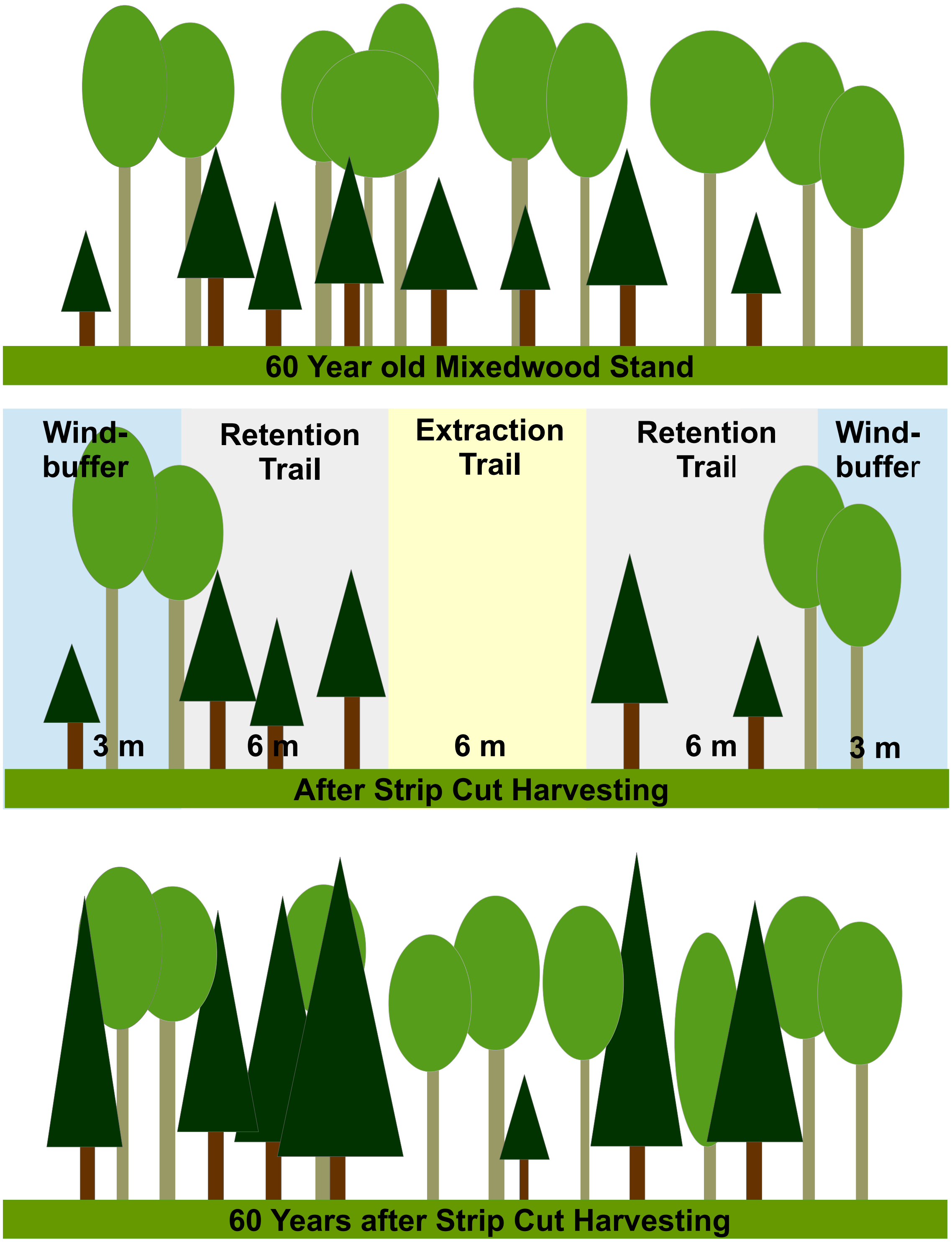

**Figure 1.1** Chart of strip cut understory protection harvesting in a mixedwood stand with trembling aspen (light green) in the overstory and white spruce (dark green) in the understory. Sizes of trails are indicated.

DeBlois, 2014). As soon as the softwood species are merchantable a second harvest takes place and all remaining trees can be harvested in one clearcut. Natural regeneration should now take place on the site. Many SCUP sites are established all over Alberta. An early study, the Hotchkiss River project, was established in 1992 in Alberta, to test windfirmness and growth response of spruce trees following multiple variations of the understory protection harvesting system (MacIsaac, et al. 1999). Eleven different variations of the SCUP harvesting were used, including two-pass harvesting, where machinery enters the stand twice instead of once for aspen harvest to ensure advanced white spruce protection from wind throw. Leaving a windbuffer zone in the one-pass harvesting system, as described before, has been shown to be superior to two-pass harvesting and is therefore now favored by forest companies using understory protection harvesting (Keddy and Sidders, 2007; MacIsaac and Krygier, 2004).

Understory protection harvesting maximizes the yield of mixedwood forests (Man and Lieffers, 1999; Grover, et al. 2014). This harvesting system is a step forward in forestry to maintain biodiversity and natural forest structure and regeneration and it is very cost effective (MacIsaac and Sauder, 2001; Comeau et al. 2005).

## 1.4 The Mixedwood Growth Model

Since SCUP harvesting is getting more and more popular, there is growing interest in estimating timber production from those sites. Yields need to be quantified to answer questions of feasibility, economic efficiency and sustainability of SCUP harvesting sites (Thorpe and Thomas, 2007). Due to a lack of long term studies and long term data, models are needed to forecast yield outcomes from SCUP stands (Bokalo, et al. 2013). Predicting the productivity of stands has a long history, starting with yield tables for single species stands more than 250 years ago. Today computer models are used to predict yields of more complex stands including mixedwood forests (Pretsch, 2009).

In Alberta the Mixed Wood Growth Model (MGM) is available for simulating yields from understory protection harvesting. It is a deterministic, distance-independent, individual tree based model which was originally implemented by Dr. W.S. (Bill) Adams and Dr. S.J. Titus and is currently being developed by Dr. P.G. Comeau and Dr. M. Bokalo (Bokalo and Comeau, 2013).

The model calculates annual height and diameter growth as well as mortality of individual trees primarily based on climate (natural subregion), site (site index), tree size and competitive status as well as overtopping competition.

MGM relies on site index which is based on a height-breast height age curve to define the maximum height increment of trees (100 trees/ha with the largest DBH) on a specific site. This leads to incorrect estimations when looking at trees growing in the understory over a longer time period. As discussed before, white spruce is a shade tolerant species and it can grow very slowly under an aspen canopy, so trees might be old but not very tall. Therefore, the site index-based height-breast height age curve is not directly applicable. Trees tend to be smaller on the site than the height age curve predicts at a certain age. To solve this problem for white spruce (and other shade tolerant species) MGM uses an age at breast height curve instead of a size age curve to predict maximal growth. Breast height age is estimated and used on the height curves. The prediction of diameter is based on the height diameter relationship. For both height and diameter estimates a reduction factor is used to account for competition effects.

The release of white spruce through SCUP harvesting improves tree growth significantly in the first years after the harvest (Grover et al. 2014).

Currently MGM is not able to predict growth of understory spruce from SCUP sites accurately, since it does not account for effects of intra- and interspecific competition after SCUP harvesting. This leads to overestimation of growth response for small spruce trees (<4 cm DBH) after SCUP. On the other hand the model underestimates the release of taller white spruce (> 4 cm DBH), which can be explained by a lack of data coming from sites where large trees are released.

## 1.5 Research objectives

The objective of this study was to develop refined models for estimating the growth response of white spruce release at SCUP sites, including intra- and interspecific competition as well as climate variables. Resulting relationships will be incorporated into MGM and allow more accurate yield estimations from SCUP sites in the future.

To achieve this, I focused on three main objectives, with objective two having multiple secondary objectives:

1. Observe the response of white spruce to SCUP harvesting.
2. Explore the release of white spruce for height and basal area depending on competitive effects.
   2.2 Determine radius of competition impacts.
   2.3 Explore the utility of light measurements for characterizing competition.
   2.4 Compare the influence of different competition indices and determine the influence of coniferous and deciduous competition.
3. Examine the effects of climate on post release growth of white spruce.

# Chapter 2
# Methods

## 2.1 Site description

Data were collected from five study sites in the Central Mixedwoods Natural Subregion of Alberta (Fig. 2.1, Table 2.1) during the summer of 2014 and 2015. Selected stands had trembling aspen growing in the overstory and advanced white spruce regeneration in the understory.

**Table 2.1** Summary of timing of SCUP, time of data collection, geographical position and climate variables (mean annual temperature (MAT), mean annual precipitation (MAP)) for all five study sites: Calling Lake 1 and 2 (CL1 and CL2), Emend (E), Grande Prairie (GP), Slave Lake (SL).

| Site | Plots | Year Harvested | Year data collected | Latitude (°) | Longitude (°) | MAT* (°C) | MAP* (mm/yr) |
|---|---|---|---|---|---|---|---|
| CL1 | 45 | 1998 | 2014 | 55.35 | 113.31 | 1.1 | 486 |
| CL2 | 45 | 2004 | 2015 | 55.34 | 113.39 | 1.1 | 487 |
| E | 45 | 1998 | 2014 | 56.83 | 118.34 | 0.7 | 434 |
| GP | 45 | 2005 | 2014 | 54.85 | 118.88 | 2.4 | 541 |
| SL | 45 | 2004 | 2014 | 55.13 | 114.1 | 1.7 | 496 |

*data extracted from "1981-2010 NA Climate Normals" for each site, available at http://ualberta.ca/~ahamann/data/climatena.html, accessed on May 6th, 2016.

All of the sites were treated with strip cut understory protection (SCUP) harvesting ranging from 16 to 9 years in the past. Strips were generally NE to SW oriented. Post-treatment stands were dominated by white spruce in the overstory within retention areas, trembling aspen dominated in extraction trails as well as in the buffer strips. Three of the sites (CL1, CL2, SL) are part of a strip cut understory protection study established by the “Mixedwood Management Association” (MWMA), one site is part of the research project “Ecosystem Management Emulating Natural Disturbance” (EMEND) (“E”), and the fifth site (GP) is managed as an adaptive mixedwood site by the Canadian Forest Service (CFS). The sites did not have the exact same dimensions concerning the sizes of the different strips (Table 2.2), but the layout matched the general SCUP design between the sites (Fig.1.1).

**Table 2.2** Size of understory protection harvesting trails for each study site.

| Site | Extraction Trail (m) | Retention Trail (m) | Windbuffer (m) |
|---|---|---|---|
| CL1 | 6[1] | 6[1] | 3[1] |
| CL2 | 6[1] | 6[1] | 3[1] |
| E | 5[2] | 15[2] | |
| GP | 5[3] | 6.5[3] | 5[3] |
| SL | 6[1] | 6[1] | 3[1] |

[1] measurements retrieved from Grover et al. 2014.
[2] measurements retrieved http://www.emendproject.org/pages/read/treatments#harvest, accessed, June 9th 2016.
[3] measurements retrieved from Keddy and Sidders, 2007.

## 2.2 Data collection

At each of the five study sites 45 plots were established within the retention areas, with a white spruce tree in the center. Geographical location of each of the 225 plots was recorded using a Trimble GeoExplorer 6000 series GeoXT handheld device. Moisture regimes were determined for individual plots following "Field Guide to Ecosites of Northern Alberta" (Beckingham and Archibald, 1996). All of the plots were classified as sub-mesic to mesic, which is common for productive upland boreal mixedwoods (Solarik et al. 2012; Armstrong, 2014).

**Table 2.3** Summary of minimum and maximum DBH and height measurements for sampled white spruce at each study site.

| Site | DBH (cm) | | height (m) | |
|---|---|---|---|---|
| | Min | Max | Min | Max |
| CL1 | 2.2 | 11.3 | 2.4 | 9.8 |
| CL2 | 2.4 | 12.2 | 2.4 | 11.1 |
| E | 1.2 | 11.2 | 2.0 | 10.0 |
| GP | 1.9 | 11.3 | 2.4 | 12.2 |
| SL | 2.0 | 12.1 | 2.3 | 10.3 |

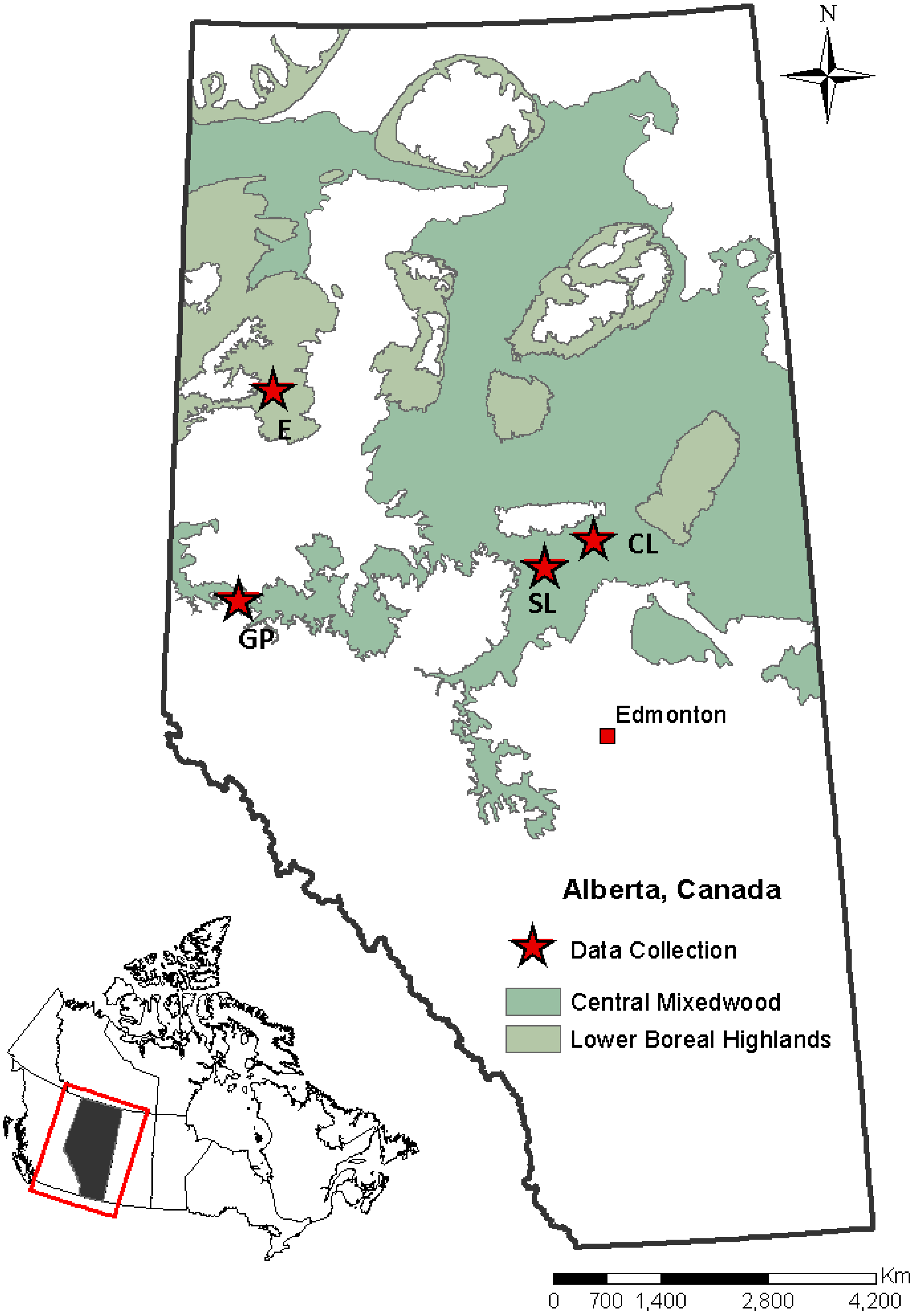

**Figure 2.1** Five study sites within the Boreal Mixedwood Region Alberta, Canada. CL contains two study sites

Each plot had a white spruce tree in the center. Center trees were chosen to cover the range of height and coniferous competition present at each study area. Competition density classes cover low (< 600 trees/ha), moderate (600 to 1000 trees/ha) and high density (> 1000 trees/ha) of coniferous trees surrounding the subject tree. Height of the subject tree was divided into three classes as follows: small (2 to 4.99 m), medium (5 to 6.99m) and tall (7 to ~ 12 m). For each combination of the density and height classes five trees were selected within each stand.

The chosen center white spruce trees were all alive, healthy and did not show any signs of diseases. Height (m) and diameter at breast height (DBH) (cm) of each tree was measured in the field using a height pole and diameter tape respectively. Table 2.3 shows the range of spruce sizes within the collected data set.

The center spruce trees were cut at 30 cm height to provide stem disks for measurements of radial growth over time. Disks were taken at 30 cm and 130 cm height. Height increments over each of the past 15 years were determined by measuring height of each branch whorl (Fabbio et al. 1994; Prévost and DeBlois, 2014).

Competition was measured by recording species, height and DBH of every coniferous and deciduous tree within a 5.64 m and a 3.99 m radius respectively around the center white spruce trees. The distance between the center spruce trees and the competition trees was recorded. When the distance between the center tree to the neighbor tree was smaller than the height of that neighbor tree, then this particular tree was included in the data collection even if it was outside of the measurement radius (Fig. 2.2). Altogether eight species were identified. See table 2.4 for minimum and maximum DBH and height measurements per site for each species.

In early morning, during midsummer (June-August) when the sun angle was still low light levels for each plot were measured 1.00 m above the root collar of the felled center tree by taking hemispherical photographs using a Nikon D90 camera fitted with an 8.5 mm Sigma Fisheye Lens.

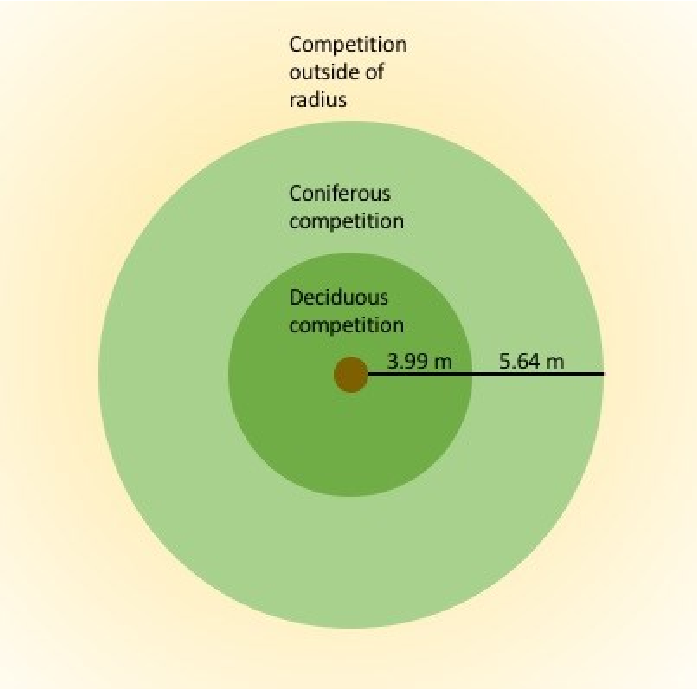

**Figure 2.2** Plot design for competition measurements. Brown dot indicates sample tree in the center of the plot

**Table 2.4** Summary of min, max and mean DBH and height of competition neighbor trees of each recorded species (*Populus tremuloides* (Aw); *Betula papyrifera* (Bw); *Abies balsamea* (Fb); *Populus balsamifera* (Pb); *Picea marina* (Sb); *Picea glauca* (Sw)) once including measured large trees outside of species specific radius and once including only trees within the 3.99 m and 5.64 m radius for deciduous and coniferous trees respectively.

| Species | Whole plot | | | | | | Within species specific radius | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | DBH (cm) | | | height (m) | | | DBH (cm) | | | height (m) | | |
| | Min | Max | Mean | Min | Max | Mean | Min | Max | Mean | Min | Max | Mean |
| Alder | 1.0 | 7.8 | 3.1 | 2.4 | 9.9 | 4.5 | 1.0 | 7.8 | 3.1 | 2.4 | 9.9 | 4.5 |
| Aw | 0.2 | 57.9 | 3.4 | 2.0 | 37.3 | 9.7 | 0.2 | 47.1 | 2.5 | 2.0 | 31.1 | 6.3 |
| Bw | 0.6 | 49.5 | 3.9 | 2.0 | 24.9 | 5.7 | 0.6 | 32.9 | 3.1 | 2.0 | 22.0 | 4.9 |
| Fb | 1.1 | 21.7 | 8.1 | 2.1 | 14.9 | 7.3 | 1.1 | 21.7 | 7.3 | 2.1 | 14.9 | 6.7 |
| Pb | 0.5 | 38.0 | 3.3 | 2.0 | 23.9 | 6.1 | 0.5 | 30.0 | 2.9 | 2.0 | 21.9 | 5.4 |
| Salix | 0.7 | 10.5 | 2.8 | 2.0 | 9.3 | 4.5 | 0.7 | 10.5 | 2.8 | 2.0 | 9.3 | 4.5 |
| Sb | 1.7 | 1.7 | 1.7 | 10.8 | 10.8 | 10.8 | 1.7 | 1.7 | 1.7 | 10.8 | 10.8 | 10.8 |
| Sw | 0.2 | 69.8 | 9.7 | 1.8 | 39.6 | 10.9 | 0.2 | 69.8 | 9.6 | 1.8 | 39.6 | 10.3 |

Additional data (DBH and height measurements taken in 2005 and 2013) for spruce growing in areas that had not been harvested was provided from the CFS for the GP "adaptive mixedwood" site.

Climate data were generated with the ClimateNA v5.21 softwarepackage, available at http://tinyurl.com/ClimateNA, based on methodology described by Hamann et al. (2013). Mean annual temperature (MAT) in °C, mean coldest month temperature (MCMT) in °C, growing degree days above 5 °C (DD5), mean annual precipitation (MAP) in mm, summer heat-moisture index (SHM (Mean warmest month temperature/ (mean summer precipitation/1000))) and annual heat-moisture index (AHM ((MAT+10)/(MAP/1000)) were calculated for the years 1990 to 2013 for each of the study sites separately.

## 2.3 Data processing

### *2.3.1 Basal area increment*

**Figure 2.3** Sample disc after sanding, from site SL, SCUP harvesting happened in 2004, increased ring width is visible in 2005.

In total 450 discs were air dried and sanded with progressively finer grit sand paper (grit 80, 120 and 220) (Fig. 2.3). Ring width (mm) was measured along each of 4 radii for each disc using the "WinDendro" computer program (Regent Instruments Canada Inc, 2009). Mean ring width, or radius, for each year was calculated by taking the mean of the 4 measured radii from each disc. The basal area (BA) (cm) and basal area increment (BAI) ($cm^2$) were calculated for each year using the equations

$$BA_t = \pi * r^2 \text{ (Equation 2.1)},$$

$$BAI = BA_{t2} - BA_{t1} \text{ (Equation 2.2)}$$

were "r" is the stem radius (cm) at the end of each year, "t" is representing the year. $BA_{t2}$ represents BA ($cm^2$) at the end of the year for which the BAI is calculated and $BA_{t1}$ equals the BA the previous year. Using BAI instead of ring width is a common way of showing tree wood production within one year (Visser, 1995; Rubino and McCarthy 2000). For the final analysis

BA as well as BAI at 30 cm above root collar were used instead of BA and BAI at breast height, since they would contain more rings.

Periodic annual BAI ($cm^2/yr$) was calculated for 3 year periods using following equation:

$$PAI_{BA} = \frac{BA_{t3} - BA_{t1}}{t3 - t1} \text{ (Equation 2.3)}$$

were PAI stands for periodic annual increment and t3 is the last year of the 3 year period and t1 the first. PAI was calculated starting two years before SCUP to nine years after SCUP, resulting in four time periods: P0, P1, P2, and P3. P0 represents the two years before SCUP plus the increment in the year of SCUP (the control period), P1 represents increment in the first 3 years after SCUP, P2 the increment in years four to six after SCUP and P3 years seven to nine.

Initial BA was determined as the BA at 30 cm above root collar at one year before SCUP for the analysis of spruce release response and as the BA at 30 cm above root collar at year 7 (the first year of period 3) for analysis of effects of competition on spruce growth.

### *2.3.2 Height increment*

Height increment (m/yr) was calculated as follows from the collected field measurements:

$$Ht_{inc} = Ht_{t2} - Ht_{t1} \text{ (Equation 2.4)}$$

were $Ht_{t2}$ represents the height of the tree for the year in which height increment was calculated and $Ht_{t1}$ is the year before.

Periodic height increment ($PAI_{Ht}$) (m/yr) was calculated for periods of three years the same way as for $PAI_{BA}$:

$$PAI_{Ht} = \frac{Ht_{t3} - Ht_{t1}}{t3 - t1} \text{ (Equation 2.5)}$$

Initial height was determined as the height one year before SCUP for spruce release response and as the initial height at year 7 (the first year of period 3) for analysis of effects of competition on spruce growth.

### *2.3.3 Control data GP*

To evaluate differences between released and non-released spruce BAI ($cm^2/yr$) and height increment (m/y) were calculated between 2005 and 2013 for spruce in the control plot at the GP site for comparison with growth in the plot that received understory protection harvesting. BA and height in 2005 were used as initial size measurements.

### *2.3.4 Competition indices*

Six different competition indices (CI) were calculated (Table 2.5) for coniferous and deciduous trees separately. $CI1_{total}$ is the sum of BA ($m^2$) of all competing trees and $CI1_{larger}$ is the sum of BA ($m^2$) of all competing trees with a larger BA ($m^2$) than the subject (center) tree. CI2 is a distance independent index which reflects the sum of ratios between the DBH (cm) of all competing trees and the DBH (cm) of the subject tree. Hegyi's index is the ratio between the DBH (cm) of competing trees and the DBH (cm) of the subject tree weighted by their distances (m) (Hegyi, 1970). CI4 is a DBH (cm) distance (m) ratio (Cortini and Comeau, 2008) which excludes the DBH (cm) of the subject tree. Index CI5 is representing total light (% of full sun light) levels at each subject tree.

Each competition index was calculated for both coniferous and deciduous trees separately and included surrounding trees taller than the subject tree outside as well as inside the 5.64 m (coniferous) and 3.99 m (deciduous) radius.

**Table 2.5** Competition indices and formulas used for their calculation.

| Competition Index | Formula | Values |
|---|---|---|
| CI1: BA total | $CI1_{total} = \sum_{i=1}^{n} BA_i$ | $BA_i$=competitor ba |
| CI1: BA larger | $CI1_{larger} = \sum_{i=1}^{n} BA_{i\,(larger\ t)}$ | $BA_i$ =competitor ba larger |
| CI2: Distance independent | $CI2 = \sum_{i=1}^{n} \frac{DBH_i}{DBH_t}$ | $DBH_i$=DBH neighbor, $DBH_t$= DBH center tree |
| CI3: Hegyi's | $CI3 = \sum_{i=1}^{n} \frac{DBH_i}{(DBH_t)(Distance_{ti})}$ | $DBH_i$=DBH neighbor, $DBH_t$= DBH center tree; $Distance_{ti}$= distance neighbor main tree |
| CI4: Diameter distance ratio | $CI4 = \sum_{i=1}^{n} \frac{\mathrm{DBH}_i}{Distance_{ti}}$ | $DBH_i$=DBH neighbor, $Distance_{ti}$= distance neighbor main tree |
| CI5: Light levels | $\mathrm{CI5} = \mathrm{Total\ light}$ | % |

### *2.3.5 Light level*

Hemispherical photos were analyzed using the software "SLIM" (Spot Light Interception Model) which calculates the fractional transmittance from the pictures (Comeau et al. 2003 a). The program calculates total, diffuse and direct PPFD (photosynthetic photon flux density) for each subject tree, which is a measure of the amount of light falling on a given surface during the growing season. Total PPFD (%) was used for analysis.

## 2.4 Statistical analysis

Statistical analyses were conducted using the *R* computer program (R Core Team, 2015) and the *nlme* packages from Pinheiro et al. (2015) for creating mixed effects models. To calculate coefficient of determination ($R^2$) the package *MuMIn* from Bartón, (2015) was used which calculates $R^2$ for mixed effects models as suggested in Nakagawa and Schielzeth (2013).

A significance level of $\alpha = 0.05$ was used.

### *2.4.1 Spruce response to SCUP*

Comparisons of PAI were done before and after SCUP. Mixed effects models were used to account for the non-independence of the data, since trees were nested in sites and each trees repeated measurements were taken to examine growth over time.

Diagnostic plots of the normalized residuals were used to assess model fit, (Pinheiro and Bates, 2000, pp. 239 ff.).

Only trees containing measurements in all time periods were used in this analysis. PAI for height and BA were treated as continuous variables while period, site and tree id were treated as categorical variables.

Mixed effects models were built and correlation structures were introduced to account for the repeated measurements of the individual spruce trees (Pinheiro and Bates, 2000, pp.226 ff.). Variance structures were applied to model heterogeneity of variance between sites (Zuur et al. 2009, pp.71ff.). The best models were chosen by comparing AIC (Akaike information criterion) values of the different models, which measures the goodness of the model fit; the lower the AIC values the better the model fits (Zuur et al. 2009).

Following model selection, mean PAI before SCUP (P0) was compared to the three following periods by comparing least-squares means (LS means) of the best model using Tukeys HSD (Honest Significant Difference) test in the *lsmeans* package in *R* (Lenth, 2016).

Furthermore nonlinear mixed effects models were built to examine the growth response of BAI and height increment for each year after SCUP with the random effect of site. BA and height for each year were analyzed for all sites 1 to 9 years after SCUP. Additionally BA response was investigated 1 to 16 years after SCUP for sites CL1 and E due to more available data since sites were harvested in 1998. Only trees with measurements over the full observed time periods were used in this analysis. Both increment and years after SCUP were treated as continuous variables. Three different curves were fit to examine growth in relation to time since release: a power function (Equation 2.6), an exponential function (Equation 2.7) and a polynomial function (Equation 2.8).

$$BAI/Height\ increment_{tij} = a * Year\ since\ SCUP\ {}_{ij}{}^{b} + \varepsilon_{tij} \text{ (Equation 2.6),}$$

$$BAI/Height\ increment_{tij} = a * e^{\frac{b}{Year\ since\ SCUP\ ij}} + \varepsilon_{tij} \text{ (Equation 2.7),}$$

$$BAI/Height\ increment_{tij} = \frac{Year\ since\ SCUP_{ij}}{a+b*Year\ since\ SCUP_{ij}} + \varepsilon_{tij} \text{ (Equation 2.8),}$$

where *t* indicates the year since SCUP, *i* the tree and *j* the site. Parameters *a* and *b* were estimated, and $\varepsilon_{tij}$ is the residual standard error. First the three curves were fit into a null model in which random effects on parameters *a* and *b* were tested without including a variance and correlation structure, as suggested in Fang and Bailey (2001). Variance structures were included in the best models to improve model fit and correlation structures had to be included to account for the non- independence of the yearly measurements within each tree (Pinheiro and Bates, 206ff). AIC values were used to determine the best model by comparing the three different equations (Equation 2.6-2.8).

To compare the control data with the SCUP data at site GP for the years 2005 and 2013, initial size, BAI and height increment were treated as continuous variables, and treatment (SCUP or control) was treated as a categorical variable. Analysis of covariance (ANCOVA) was conducted to test the null hypothesis that there is no significant difference in growth of spruce between the control and SCUP sites, where initial size was used as a covariate. Homogenous slopes between covariate and treatment were tested as well as independence of covariate and treatment, which are required before running an ANCOVA. Diagnostic plots of residuals, histograms of residuals and fitted versus standardized values were used to assess model fit. Performing Tukey HSD test on LS means allowed a comparison between the control and SCUP treatment after ANCOVA (Logan, 2010).

### *2.4.2 Effects of competition on spruce growth after understory protection harvesting*

For this analysis only the height and BA increment data from the last growing period (P3) was chosen as a response variable since the competition data were collected in 2014 or 2015 and not repeated over time.

#### *2.4.2.1 Difference between coniferous and deciduous competition indices including only trees within radius versus all trees within a plot*

To determine whether competing trees outside of the radius borders (5.64 m for coniferous and 3.99 m for deciduous competition) had an impact on the defined competition indices and the significance of each species on the effect of competition, mixed models were built with $PAI_{Ht}$ and $PAI_{BA}$ in period 3 (after SCUP) as dependent variables, and competition indices as independent variables; site was used as a random variable. For each height and BA, four models were built using the competition indices $CI1_{larger}$, CI2, CI3 and CI4 (Table 2.5). Both coniferous and deciduous competition were separately included in each model. Each model was run twice, once incorporating all trees within the plot in the competition index and once just using the trees within the species specific search radius. Comparisons of resulting $R^2$ values between the two matching models was conducted.

#### *2.4.2.2 Light measurements and their ability to characterize competition*

The competition indices, $CI1_{total}$, $CI1_{larger}$, CI2, CI3, CI4, were tested for their ability to predict measured total light levels in each plot. Since size, in this case DBH, of the trees is not relevant for light analysis it was set to 1.0 in the competition indices CI2 and CI3. Due to the transformation CI3 resulted in the same competition index as CI4 and was therefore not used in this analysis. Linear mixed models were built using site as a random factor (Equation 2.9):

$$Total\ light_{ij} = \beta_0 + \beta_1 CI\ conif_{ij} + \beta_2\ CIdecid_{ij} + \varepsilon_{ij}\ \text{(Equation 2.9)},$$

where *Total light*$_{ij}$ is the $i^{th}$ light observation within site $j$. $\beta_0$ is the intercept within each site, $\beta_1$ and $\beta_2$ are the coefficients for $CI_{conif}$ and $CI_{decid}$ of each observation within each of the five sites and $\varepsilon_{ij}$ is the residual standard error.

Additional a *ln* transformation was applied on total light levels since previous research showed an exponential relationship between light and competition and were compared to the models with non transformed total light levels (Comeau et al. 2003 b; Filipescu and Comeau, 2007 a).

Overall model fits were compared using $R^2$ values.

#### *2.4.2.3 Comparison of competition indices*

Sixteen competition models for height and BA were tested against each other using the six different indices (Table 2.5) utilizing coniferous and deciduous competition combined and separately to determine the best fitting CI. Linear mixed effects models (Equation 2.10) were fit using maximum likelihood (ML) approach, which allows a comparison between models with different explanatory variables (Pinheiro and Bates, 2000, p. 87, Zuur et al. 2009, p.122). The following linear model was used

$$PAI_{ij} = \beta_0 + \beta_1\ CIconif_{ij} + \beta_2\ CIdecid_{ij} + \varepsilon_{ij}\ \text{(Equation 2.10)},$$

where $PAI_{ij}$ is the $i^{th}$ $PAI_{Ht/BA}$ observation within site $j$. $\beta_0$ is the intercept within each site, $\beta_1$ and $\beta_2$ are the coefficients for $CI_{conif}$ and $CI_{decid}$ of each observation within each of the five sites and $\varepsilon_{ij}$ is the residual standard error.

The model with the lowest AIC value was considered as the best fitting model. The best fitting model was then refit using restricted maximum likelihood (REML) for coefficient estimation and $R^2$ calculations.

The linear mixed effects models described above were used to capture the impact of each competition index.

Additional models were built to evaluate effects of competition and initial size on spruce growth. Since the relationship between size and growth, and competition and growth is not linear a combination of exponential competition and the power of initial size as used in Comeau et al. (2003b) and Cortini and Comeau (2008) (Equation 2.11) was used in the models.

$$PAI_{ij} = a + b_1 * e^{(b_2 * CIcon_{ij} + b_3 * CIdecid_{ij})} * in.Ba_{ij}^{c} + \varepsilon_{ij} \text{ (Equation 2.11),}$$

where $\mathrm{PAI}_{ij}$ is the $i^{th}$ $PAI_{Ht/BA}$ observation within site $j$ in period 3. $CI_{con}$ and $CI_{decid}$ are the competition indices for coniferous and deciduous species for each tree within site, and *in. Ba* is the BA in the year before SCUP harvesting and $\varepsilon_{ij}$ is the residual standard error. $a$, $b_1$, $b_2$, $b_3$, and $c$ are parameters to be estimated. To avoid collinearity between initial size and size dependent competition indices, only size independent indices were used: $\mathrm{CI1}_{\mathrm{total}}$, $\mathrm{CI1}_{\mathrm{larger}}$, CI4 and CI5 (Filipescu and Comeau 2007 b*).* CI2 was transformed as the sum of $\mathrm{DBH}_{\mathrm{larger}}$ and also tested in the models. Mixed effects models were built, parameters *a, b1, b2, b3* and *c* were estimated and tested as random effects as suggested by Fang and Bailey (2001) using REML. For the three competition indices separately the parameters were tested as random effects and variance structures for the individual study sites on initial BA were included. The best model was chosen based on the lowest AIC values. Due to the complexity of the models not all combinations of random effects and competition indices converged. Subsequently the best models for each competition index were fit again using ML, which then allowed for a comparison of AIC values between the different competition indices (Pinheiro and Bates, 2000, p. 87, Zuur et al. 2009, p.122). To choose the best fitting models AIC values of the models were compared. The models were then refit using REML for parameter estimation. Diagnostic plots of standardized residuals versus fitted values and normality of random effects were conducted to test model fit (Pinheiro and Bates, 2000, pp.174 ff.).

### *2.4.3 White spruce growth response to climate after SCUP*

For each site separately, generalized least squares models (GLS) were built to detect the influence of the 6 different climate variables on the BA growth of the spruce trees after SCUP. The GLS method allows the use of correlation structures which were applied on the individual tree to account for the repeated measurements taken within each of the trees over the years (Zuur et al. 2000, p. 71). BAI after SCUP was used as a response variable and log transformed. Climate variables, MAT, MAP, DD5, SHM and AHM were used as explanatory variables. Besides the effects of climate variables corresponding to each year, the effects of the climate variables from the previous year were also included in the analysis.

The following null model was created which included initial size of the tree before SCUP and the best fitting competition index as explanatory variables, because those factors capture a major amount of variability in the growth of trees:

$$BAI_{ti} = \beta_0 + \beta_1\ int.BA_i + \beta_2\ CI_i + \varepsilon_{ti} \text{ (Equation 2.12),}$$

where $BAI_{ti}$ is the BAI for the $t^{\text{th}}$ year within the $i^{\text{th}}$ tree. $\beta_0$ is the intercept within each site, $\beta_1$ and $\beta_2$ are the coefficients for *initial BA* and *CI* of each yearly observation within each of the 45 trees per site. $\varepsilon_{ii}$ is the residual standard error. Climate variables were divided in temperature dependent variables (MAT, MCMT, DD5) and precipitation dependent variables (MAP, SHM, AHM). Each climate factor was added to the null model, first one by one and then combined (Equation 2.13).

$$BAI_{ti} = \beta_0 + \beta_1\ int.BA_i + \beta_2\ CI_i + \beta_3\ Temperature_t + \beta_4\ Moisture_t + \varepsilon_{ti} \text{ (Equation 2.13)}$$

This was done for temperature and precipitation variables separately. AIC values were used to determine the best fitting temperature and precipitation factors. Finally, the best temperature and precipitation variables were included in the basic null model for each site separately.

# Chapter 3

# Results

## 3.1 Spruce response to SCUP

Both diameter and height increment increased after understory protection harvesting. For all sites except site CL, the BA response was immediate and very steep. Height, in contrast, responded more gradually and with a delay of a few years (Fig 3.1).

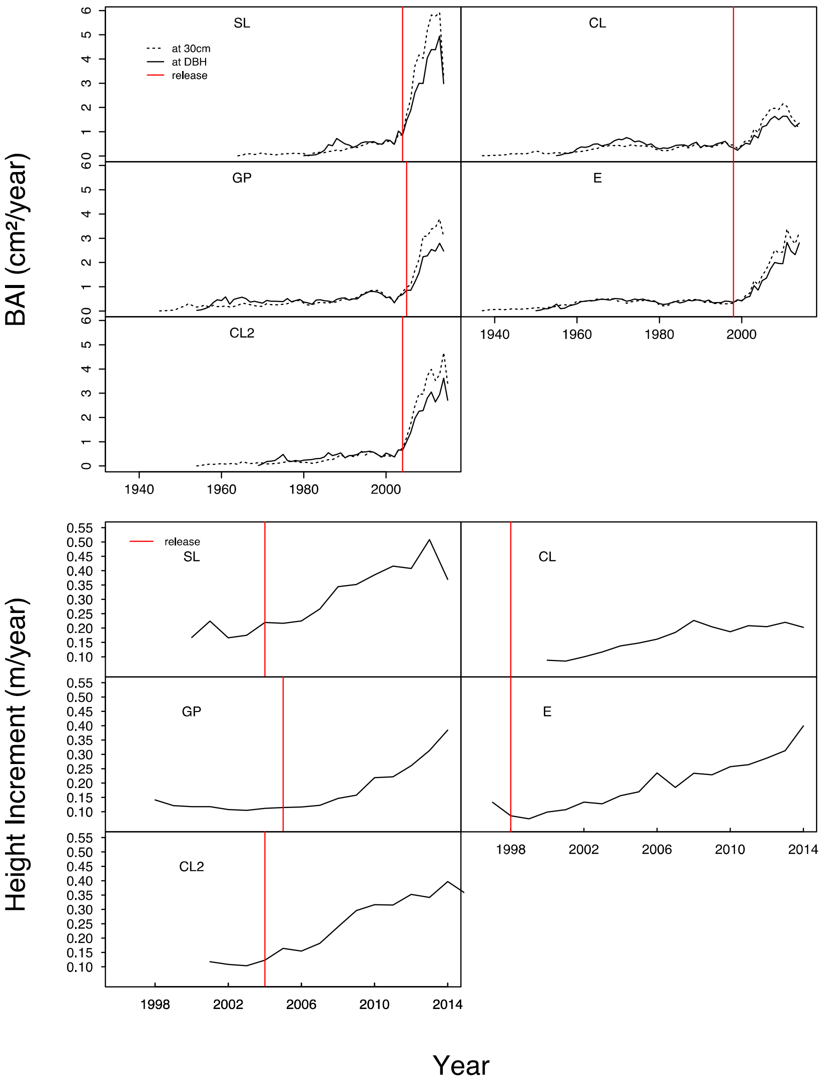

**Figure 3.1** Mean BA and height increment over years for each study site. The red line represents the year of SCUP (release).

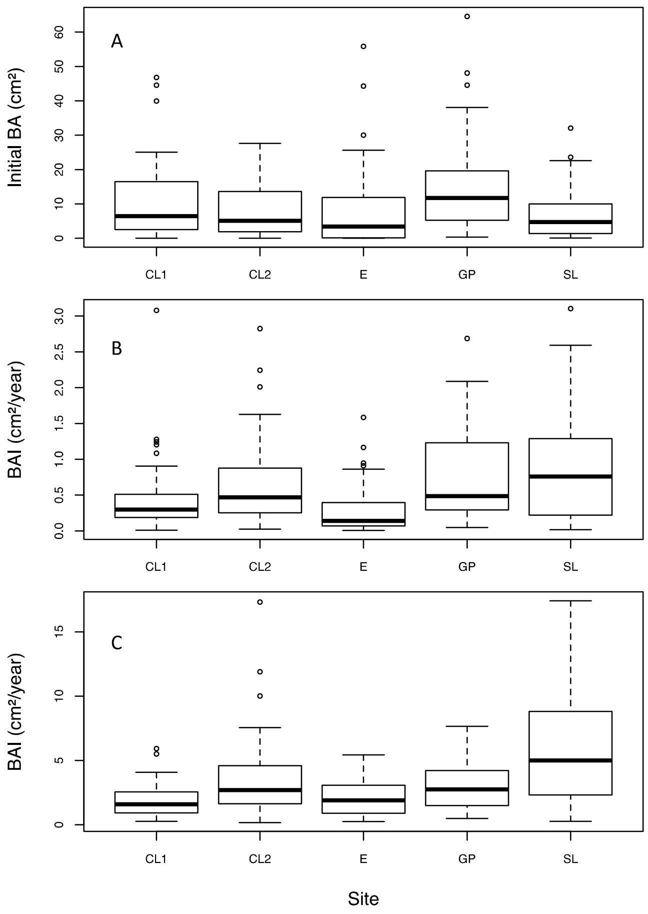

**Figure 3.2** Boxplots of initial BA (A), BAI 1 year before SCUP (B) and nine years after SCUP (C) for each of the five study sites.

The range of initial size of sampled trees was between just over 0 to ~ 60 cm$^2$ before harvesting at all 5 study sites (Fig. 3.2). BAI one year before and 9 years after SCUP differed between the sites with sites CL1 and E having the lowest increment and the smallest increment range, site SL had the highest increment and the biggest range (Fig 3.2).

The inclusion of a random effect on site improved model fit significantly (Table 3.1).

Comparing AIC values of 8 models (Table 3.1) resulted in selection of model M5 as the most parsimonious model for BA and height response. Using tree ID within site as a random factor allowed the intercept of the model to vary from ID to ID. The correlation structure was used for modeling the dependence between the measurements for each tree within each site (Pinheiro and Bates 2000). The auto-regressive correlation structure (corAr1) denoted equal variances between repeated measurements and decreasing covariance with increasing separation between time periods. Using the varIdent structure on site allowed a different variance structure for each site (Zuur et al. 2009, pp. 75ff.). The final model had a good fit which is shown by the even distribution of the residuals around 0 in figure 3.3.

**Table 3.1** Six competing mixed effects models for periodic height and BA response after SCUP. AIC values indicate model fit.

| Model | Res-ponse | Fixed effect | Random effect | Correlation structure | Variance structure | AIC |
|---|---|---|---|---|---|---|
| M0 | BA | Period | | | | 3169.18 |
| M1 | BA | Period | Site/ID | - | - | 2697.58 |
| M2 | BA | Period | Site/ID | CorCompSym (site/ID) | - | 2699.58 |
| M3 | BA | Period | Site/ID | CorAr1 (site/ID) | - | 2410.17 |
| M4 | BA | Period | Site/ID | CorSym (site/ID | - | 2291.00 |
| M5 | BA | Period | Site/ID | CorAr1 (site/ID) | varIdent(site) | **2058.45** |
| M6 | BA | Period | Site/ID | - | varIdent(site) | 2386.63 |
| M0 | height | Period | | | | -984.94 |
| M1 | height | Period | Site/ID | - | - | -1102.01 |
| M2 | height | Period | Site/ID | CorCompSym (site/ID) | - | -1100.01 |
| M3 | height | Period | Site/ID | CorAr1 (site/ID) | - | -1114.64 |
| M4 | height | Period | Site/ID | CorSym (site/ID | - | -1129.61 |
| M5 | height | Period | Site/ID | CorAr1 (site/ID) | varIdent(site) | **-1145.05** |
| M6 | height | Period | Site/ID | - | varIdent(site) | -1128.55 |

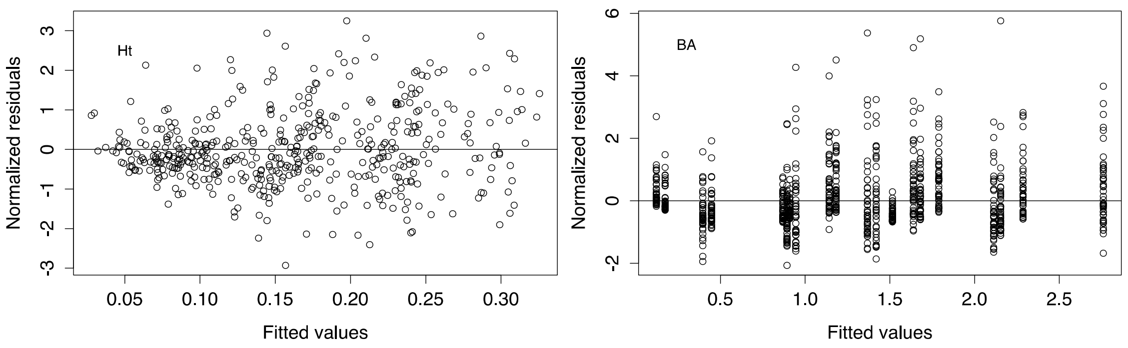

**Figure 3.3** Normalized residuals for the two best fitting periodic height- and BA increment models.

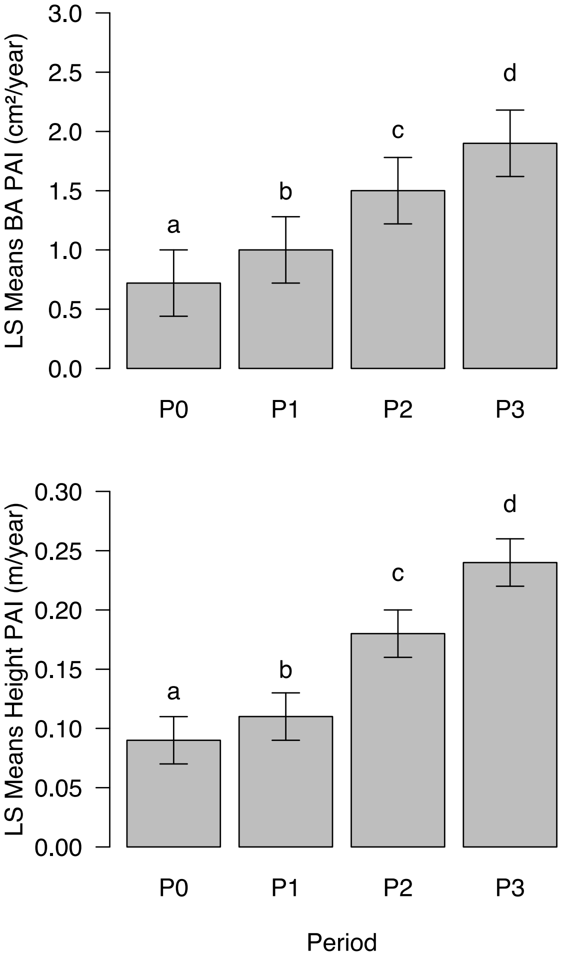

**Figure 3.4** Barplot of LS means of best model (M5) for BA- and mean height PAI over 4 periods: P0=before SCUP (3yr), P1 (1-3 yr), P2 (4-6 yr), P3 (7-9 yr)=after SCUP. Standard errors are shown and each different letter indicates a significant ($p \leq 0.05$) difference between the periods.

LS means comparisons of the mean PAI using M5 detected significantly higher increment for each time period after SCUP (P1-P3) compared to the time period before SCUP (P0) for height and BA (Fig. 3.4).

BA responded immediately after harvesting of the overstory with an increased increment in P1 compared to P0. Height increment increased as well in P1 compared to P0, but increment in P2 was substantially larger, suggesting a slight lag in height growth response. Comparing P3 to P0 using LS means the mean PAI increased about 2.7 times and 2.8 times for BA and height respectively. There was a noticeable difference between sites (Fig. 3.5) where mean height and

BA increment over all periods were highest at site SL, (0.22 m and 2.39 cm$^2$ respectively), and lowest at site E (mean PAI$_{Ht}$, 0.08 m) and site CL1 (mean PAI$_{BA}$, 0.64 cm$^2$).

Looking at the yearly growth of released spruce the inclusion of a variance function, class varIdent, on site resulted in superior fit for all models compared to a model without a variance function. Furthermore the inclusion of a correlation structure improved model fit as shown by lower AIC values. Using an auto-regressive (AR1) correlation structure resulted in the best model fit for all models.

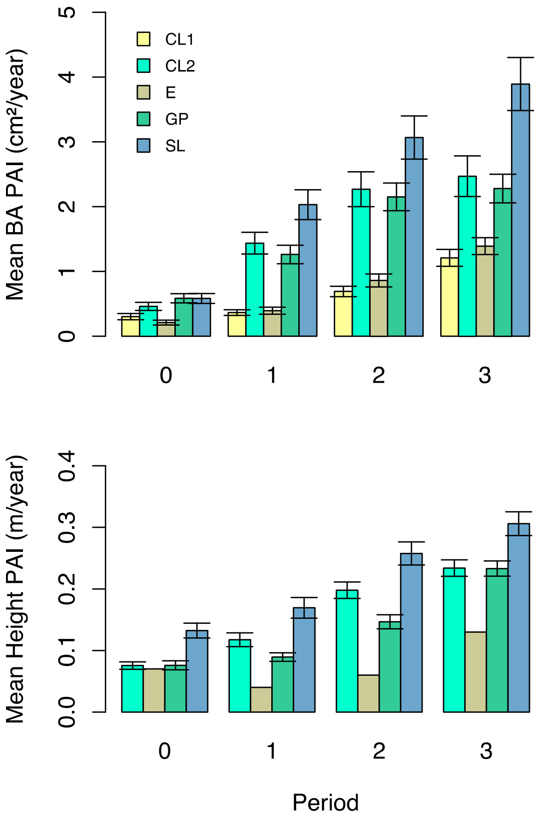

**Figure 3.5** Barplot of means for PAI$_{Ht/BA}$ at all 5 study sites over 4 periods: P0=before SCUP, P1, P2, P3= after SCUP**.** Standard deviations are shown.

Table 3.2 shows the AIC values for the best model of the yearly growth response for each of the observed curves (power, exponential, polynomial). BAI and height increment models including all study sites were analyzed over a 9 year period (models A and model C) and BAI for CL1 and E (models B) was analyzed over a 16 year period. For BAI the polynomial curve fit the data the best. When all sites were included the best model had a random factor on parameters *a* and *b*. For sites CL1 and E the best model had a random effect only on parameter *b* (Table 3.3).

**Table 3.2** Three competing mixed effects models for yearly height and BA increment after SCUP. AIC values indicate model fit.

| Model | Response | Function | Fixed effect | Random effect | Correlation structure | Variance structure | AIC |
|---|---|---|---|---|---|---|---|
| A1* | BAI | Power | a+ b | a | CorAr1(Site/ID) | varIdent(site) | 4661.45 |
| A2* | BAI | Exponential | a+ b | a | CorAr1(Site/ID) | varIdent(site) | 4693.88 |
| A3* | BAI | Polynomial | a+ b | ab | CorAr1(Site/ID) | varIdent(site) | **4608.20** |
| B1* | BAI | Power | a+ b | b | CorAr1(Site/ID) | varIdent(site) | 2383.73 |
| B2* | BAI | Exponential | a+ b | ab | CorAr1(Site/ID) | varIdent(site) | 2376.57 |
| B3* | BAI | Polynomial | a+ b | b | CorAr1(Site/ID) | varIdent(site) | **2372.72** |
| C1* | Ht inc. | Power | a+ b | a | CorAr1(Site/ID) | varIdent(site) | **-2132.75** |
| C2* | Ht inc. | Exponential | a+ b | a | CorAr1(Site/ID) | varIdent(site) | -2052.03 |
| C3* | Ht inc. | Polynomial | a+ b | a | CorAr1(Site/ID) | varIdent(site) | -2108.48 |

* A is representing the BAI data for all sites over 1-9 years after SCUP
B is representing the BAI data for sites CL1 and E 1-16 years after SCUP
C is representing the Ht increment data for all sites over 1-9 years after SCUP

Parameter *b* was not significant in models A3 and B3 for BAI, shown by the inclusion of 0 in its 95% confidence interval (Table 3.3). Parameter *a* was significant. Random effects for a and b were significant in model A3, and the random effect in b was significant in model B3.

BAI increment increases strongly in the first 1 to 5 years after SCUP and then starts slowly to flatten off at sites CL2, GP and SL (Fig. 3.6). BAI at site CL1 starts to flatten off about 7 years after SCUP, whereas the growth at site E is increasing continuously and not starting to flatten off when reaching the maximum of the observed years after SCUP (Fig. 3.6; Fig 3.7). The inclusion of random effects in model A3 and B3 was necessary as shown by the deviation between the fixed and random effects curves. Concerning model A3 the fixed effects curve underestimates the growth response at sites CL2, GP and SL, whereas the fixed effects overestimates the growth at sites CL1 and E. When we look at the 16 year time interval we see that the fixed effects curve underestimates the growth on site E and overestimates the growth response to SCUP at site CL1 (Fig 3.6).

The model of height growth increment as a response to SCUP had the best model fit using the power function and a random effect on *a* (Table 3.2). All estimated parameters, fixed and random, were significant in the model (Table 3.3). Figure 3.8 illustrates a constant increment in height over the observed 9 years after SCUP. Over this period height increment continuous to increase but at a deceased rate. At sites CL2, and SL the fixed effects curve underestimates height increment, whereas at sites E and GP the fixed effects curve overestimates height response after SCUP.

Fit of normalized residuals shows an even distribution around 0 for all three models which verifies good model fit (Fig. 3.9).

**Table 3.3** Estimates for fixed and random effects and their 95% confident intervals in equation 2.6 – 2.8 for best fitting non linear models. Response variables are BAI and height increment over 9- (Model A3 and C1) and 16 years (Model B3).

| | Parameters | | Random effects | |
|---|---|---|---|---|
| | a | b | a | b |
| Model A3 BA | | | | |
| Estimated parameter | 3.035 | 0.005 | 2.936 | 0.207 |
| (95% Confident interval) | (0.39 - 5.68) | (-0.19 - 0.20) | (1.48 - 5.83) | (0.1 - 0.44) |
| Model B3 BA | | | | |
| Estimated parameter | 3.669 | 0.254 | | 0.200 |
| (95% Confident interval) | (2.33 - 5.00) | (-0.04 - 0.55) | | (0.07 - 0.93) |
| Model C1 Ht | | | | |
| Estimated parameter | 0.104 | 0.553 | 0.031 | |
| (95% Confident interval) | (0.07 - 0.14) | (0.47 - 0.63) | (0.02 - 0.07) | |

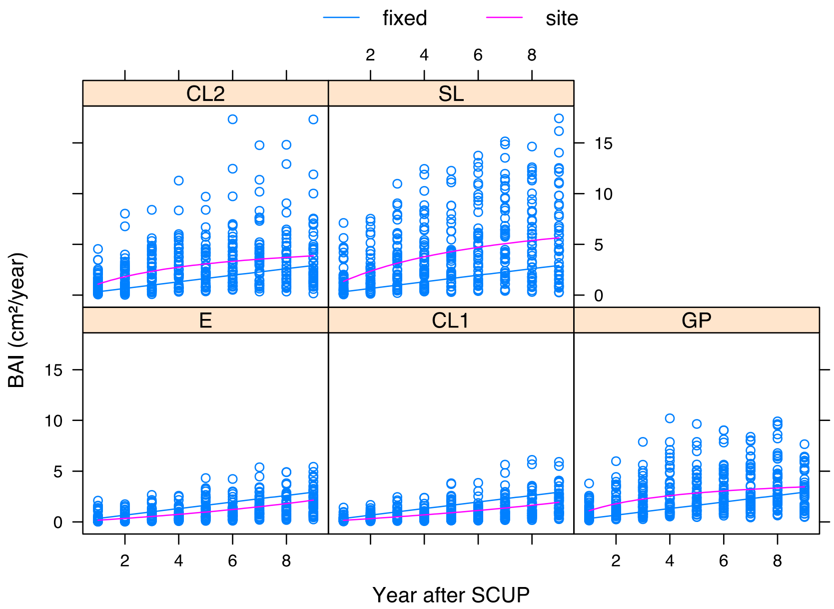

**Figure 3.6** Fixed effects (population level) in blue and site effects (stand level) in pink for BAI as response to years after SCUP for a 9 year period in model A3 (Table 3.2). Each of the five sites is indicated in the box above.

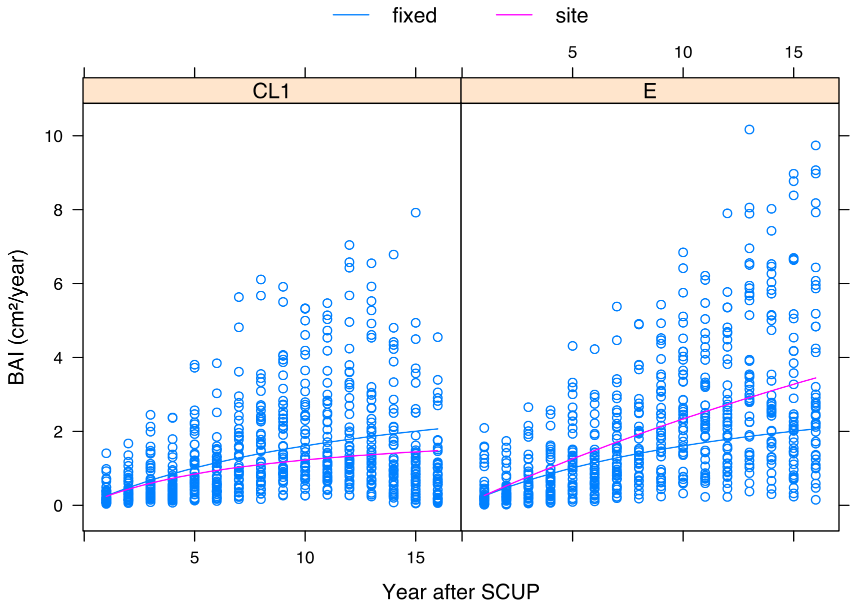

**Figure 3.7** Fixed effects (population level) in blue and site effects (stand level) in pink for BAI as response years after SCUP for a 16 year period in model A3 (Table 3.2). Site are indicated in the box above the diagram.

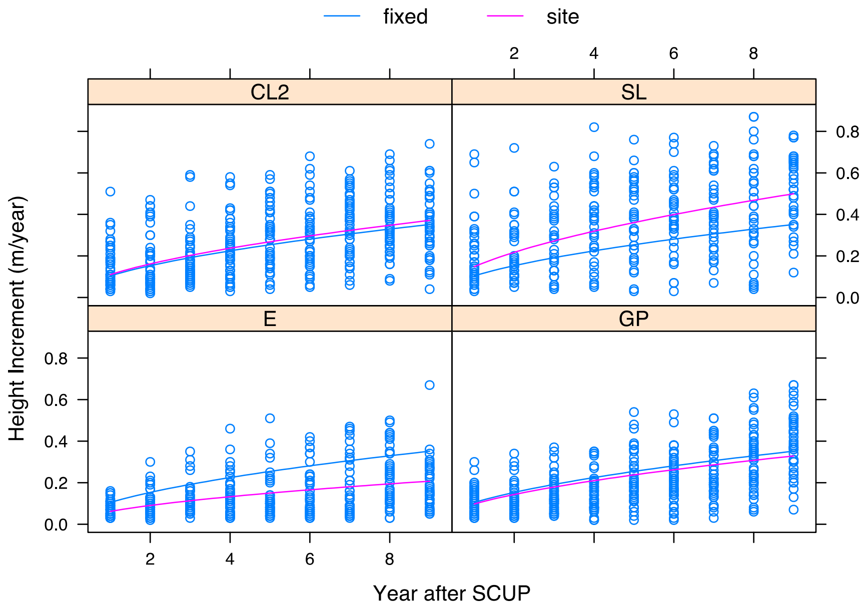

**Figure 3.8** Fixed effects (population level) in blue and site effects (stand level) in pink for height increment as response to years after SCUP for a 9 year period in model A3 (Table 3.2). Each of the five sites is indicated in the box above the diagram.

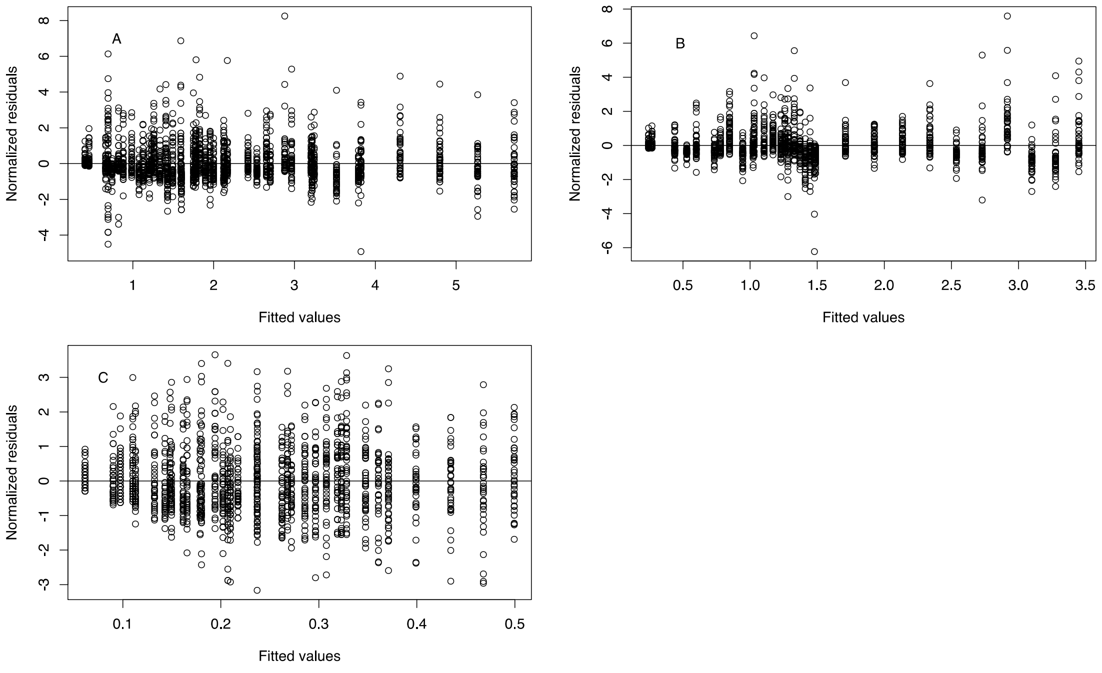

**Figure 3.9** Normalized residuals for the tree best yearly BAI, A, B, and height increment, C, models.

Comparison of GP control to SCUP illustrates the significant impact of understory protection harvesting treatment on growth of white spruce. Performing an HSD test on the LS means after ANCOVA revealed a significant 2.2 times and 1.3 times higher increment in BA and height respectively, following understory protection harvesting compared to the control block during the eight-year time interval between 2005 and 2013 (Fig. 3.10), SCUP harvesting was applied in 2005. Unfortunately, this was the only location where an untreated control block, with a range of tree sizes matching the treated block, was available. The three MWMA sites do not include unharvested control blocks. While the EMEND site has an unharvested control, examination of data from the appropriate block indicated that spruce were all substantially larger than those in the treated blocks, precluding use of these data for growth comparisons.

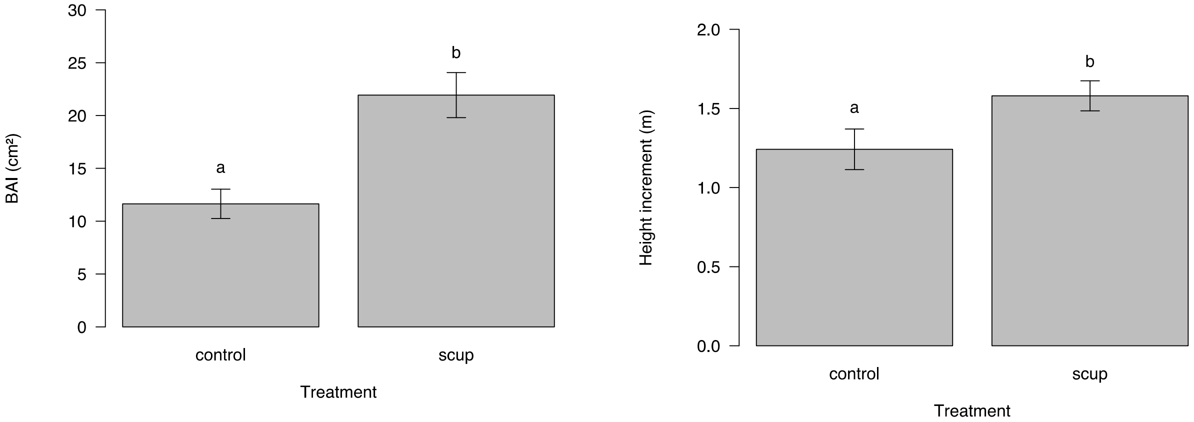

**Figure 3.10** Bargraph of mean BA- and mean height PAI between 2005 and 2013 at site GP on control and SCUP plots. Standard errors are shown and each different letter indicates a significant ($p \leq 0.05$) difference between control and SCUP

## 3.2 Effects of competition on spruce growth after understory protection harvesting

### *3.2.1 Difference between coniferous and deciduous competition indices including only trees within radius versus all trees within a plot*

Comparisons of competition indices calculated using all trees versus using only trees within the species specific radii showed differences in significance levels only in M1 for BAI for deciduous trees (Table 3.4). The seven other models were not sensitive to which trees were included in the calculation of competition indices.

Resulting $R^2$ values from the different models indicate that using all trees within the plots for competition indices adds up to 2% explained variance to the model (Table 3.4) compared to using only the trees within the search radius.

Coniferous competition was significant in all, where deciduous competition was not significant in models M1 and M4 for height and M4 for BA. Those models used competition indices (CI1 and CI4) which are independent of the size of the main sample tree.

**Table 3.4** $R^2$ and p-values for 8 competing models including all trees within plot or only trees within species specific radius (5.64 m coniferous, 3.99 m deciduous). $R^2$ was calculated for $PAI_{Ht/BA}$ separately for each index at period 3 after SCUP. P-values shows significance (<0.05) of coniferous or deciduous trees in the model.

| | | | | $R^2$ | | P value | | | |
|---|---|---|---|---|---|---|---|---|---|
| Model | Response | Fixed effect | Random effects | Plot | Radius | Plot | | Radius | |
| | | | | | | decid | con | decid | con |
| M1 | $PAI_{BA}$ | CI1$_{larger}$decid +CI1$_{larger}$ con | Site | 0.23 | 0.22 | **0.17** | <0.05 | <0.05 | <0.05 |
| M2 | $PAI_{BA}$ | CI2 decid +CI2 con | Site | 0.43 | 0.41 | <0.05 | <0.05 | <0.05 | <0.05 |
| M3 | $PAI_{BA}$ | CI3 decid +CI3 con | Site | 0.42 | 0.40 | <0.05 | <0.05 | <0.05 | <0.05 |
| M4 | $PAI_{BA}$ | CI4 decid +CI4 con | Site | 0.24 | 0.24 | **0.96** | <0.05 | **0.96** | <0.05 |
| M1 | $PAI_{Ht}$ | CI1$_{larger}$decid +CI1$_{larger}$ con | Site | 0.39 | 0.37 | **0.22** | <0.05 | **0.27** | <0.05 |
| M2 | $PAI_{Ht}$t | CI2 decid +CI2 con | Site | 0.44 | 0.42 | <0.05 | <0.05 | <0.05 | <0.05 |
| M3 | $PAI_{Ht}$ | CI3 decid +CI3 con | Site | 0.45 | 0.44 | <0.05 | <0.05 | <0.05 | <0.05 |
| M4 | $PAI_{Ht}$ | CI4 decid +CI4 con | Site | 0.40 | 0.40 | **0.41** | <0.05 | **0.32** | <0.05 |

Coniferous and deciduous competition are entered separately in the model
Con: coniferous
Decid: deciduous

### *3.2.2 Light measurements and their ability to characterize competition*

The linear mixed model performed better in modeling total light levels than a simple linear model. Total light levels were best predicted using CI2 transformed (sum of DBH) and CI4 which is the distance dependent index (Table 3.5). Both indices explained about 35% of variance in the data. There was not a wide difference between indices in their ability to predict total light levels (Table 3.5). The worst model fit was achieved by using sum of $\mathrm{CI1}_{\mathrm{larger}}$ as a predictor variable which explained about 31% variance in the data. Furthermore the comparisons of $R^2$ values showed that the logarithmic transformation of total light did not result in a better model fit than the non-transformed data (not shown).

**Table 3.5** Results of model selection for best fitting competition index representing light levels. Fixed and random effects and $R^2$ values are shown for each of the four models.

| Model | Response | Fixed effect | Random effect | $R^2$ |
|---|---|---|---|---|
| M1 | Total light | CI $1_{\mathrm{total}}$ Con + CI $1_{\mathrm{total}}$ Decid | Site | 0.32 |
| M2 | Total light | CI $1_{\mathrm{larger}}$ Con + CI $1_{\mathrm{larger}}$ Decid | Site | 0.31 |
| M3 | Total light | CI 2 Con* + CI 2 Decid* | Site | **0.35** |
| M4 | Total light | CI 4 Con + CI 4 Decid | Site | **0.35** |

* size of main tree was set to 1.0 for calculation of competition index
Coniferous and deciduous competition are entered separately in the model.
Con: coniferous
Decid: deciduous

**Table 3.6** Estimates of parameters for fixed effects and their 95% confident intervals in equation 2.9, residual standard error (SD) for best fitting model M3. Response is total light and explanatory variables are CI2 coniferous and CI2 deciduous.

| | Parameter estimations | | | Residual SD | $R^2$ |
|---|---|---|---|---|---|
| | Intercept | CI 2 con* | CI 2 decid* | | |
| | | | | 10.5 | 0.35 |
| Estimated parameter | 48.26 | -0.07 | -0.02 | | |
| (95% Confident interval) | 41.13-55.39 | (-0.10 - -0.05) | (-0.06 - 0.02) | | |

* size of main tree was set to 1.0 for calculation of competition index
Con: coniferous
Decid: deciduous

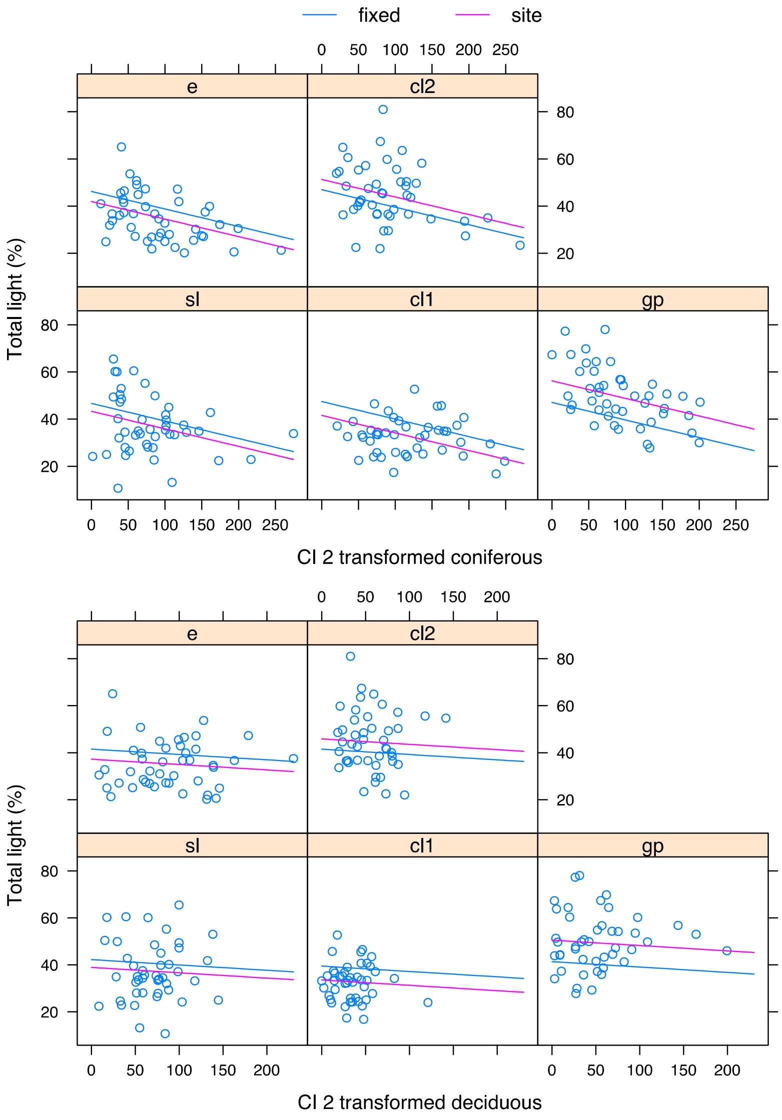

**Figure 3.11** Fixed effects (population level) in blue and site effects (stand level) in pink for total light as response to CI2 transformed coniferous and CI2 transformed deciduous in model M3 (Table 3.5). Each of the five sites is indicated in the box above the diagram.

Model M3 and M4 performed equally well but M3 uses the simpler competition index and therefore was considered the better model. Table 3.6 gives the parameter estimates for M3 and figure 3.11 illustrates the relationship between CI2 transformed and total light levels for each site. Coniferous competition was significant in the model whereas deciduous competition was not.

The larger negative values for the coniferous coefficients indicate a stronger effect of coniferous competition on light levels; it was about 1.85 times the impact of deciduous competition (Table 3.6). Figure 3.11 shows the differences between each site and the importance of including site as a random factor in the model (pink curve), with sites GP and CL2 having the highest total light levels and site CL1 the lowest.

### *3.2.3 Comparison of competition indices*

#### *3.2.3.1 Linear mixed-effects competition models*

The poorest model fits (model with the highest AIC values) were from the linear models using size independent competition indices $CI1_{total}$, $CI1_{larger}$, CI4 and CI5. Furthermore, including only deciduous trees in the competition indices resulted in worse model fit than using just coniferous trees (Table 3.7). The poor model fit of deciduous competition is comparable with the model fit of CI5, the competition index derived from light measurements.

The best fit for $PAI_{Height}$ and $PAI_{BA}$ in period 3 was for linear models M10 (CI3 Hegyi's competition index for both coniferous and deciduous trees) and M7 (CI2 distance independent index for both coniferous and deciduous trees) respectively. In both cases the indices include the size of the subject tree and CI3 is also distance dependent. Both models include coniferous and deciduous competition separately.

Table 3.8 shows the estimated parameters for the two best fitting models as well as standard deviation of the residuals and the coefficients of determination ($R^2$). Coniferous competition coefficients in both models have a larger negative value compared to deciduous competition which reflects a stronger negative relationship. Explained variance in growth due to competition was 49% in the height model, which was higher than in the BA model where it achieved 43%.

Other than the deciduous CI in the height model, all parameters were significant and did not include zero in their 95% confident interval estimates.

**Table 3.7** Results of linear model selection. AIC values, fixed effects and random effects of 16 competing mixed effects models for $PAI_{Ht/BA}$ as response variable in period 3, using the 6 competition indices (Table 2.5) and site as a random factor.

| Model | Response | Fixed effects | Random effects | AIC |
|---|---|---|---|---|
| M1 | $PAI_{BA}$ | CI $1_{total}$ Con+ CI $1_{total}$ Decid | Site | 909.52 |
| M2 | $PAI_{BA}$ | CI $1_{total}$ Con | Site | 908.19 |
| M3 | $PAI_{BA}$ | CI $1_{total}$ Decid | Site | 913.69 |
| M4 | $PAI_{BA}$ | CI $1_{larger}$ Con+ CI $1_{larger}$ Decid | Site | 901.33 |
| M5 | $PAI_{BA}$ | CI $1_{larger}$ Con | Site | 903.92 |
| M6 | $PAI_{BA}$ | CI $1_{larger}$ Decid | Site | 909.19 |
| M7 | $PAI_{BA}$ | CI 2 Con+ CI 2 Decid | Site | **843.81** |
| M8 | $PAI_{BA}$ | CI 2 Con | Site | 857.96 |
| M9 | $PAI_{BA}$ | CI 2 Decid | Site | 882.49 |
| M10 | $PAI_{BA}$ | CI 3 Con+ CI 3 Decid | Site | 855.27 |
| M11 | $PAI_{BA}$ | CI 3 Con | Site | 870.91 |
| M12 | $PAI_{BA}$ | CI 3 Decid | Site | 887.72 |
| M13 | $PAI_{BA}$ | CI 4 Con+ CI 4 Decid | Site | 908.99 |
| M14 | $PAI_{BA}$ | CI 4 Con | Site | 907.41 |
| M15 | $PAI_{BA}$ | CI 4 Decid | Site | 914.33 |
| M16 | $PAI_{BA}$ | CI 5 Light | Site | 904.25 |
| M1 | $PAI_{Ht}$ | CI $1_{total}$ Con+ CI $1_{total}$ Decid | Site | -454.91 |
| M2 | $PAI_{Ht}$ | CI $1_{total}$ Con | Site | -456.79 |
| M3 | $PAI_{Ht}$ | CI $1_{total}$ Decid | Site | -447.24 |
| M4 | $PAI_{Ht}$ | CI $1_{larger}$ Con+ CI $1_{larger}$ Decid | Site | -458.94 |
| M5 | $PAI_{Ht}$ | CI $1_{larger}$ Con | Site | -460.11 |
| M6 | $PAI_{Ht}$ | CI $1_{larger}$ Decid | Site | -448.30 |
| M7 | $PAI_{Ht}$ | CI 2 Con+ CI 2 Decid | Site | -470.61 |
| M8 | $PAI_{Ht}$ | CI 2 Con | Site | -471.70 |
| M9 | $PAI_{Ht}$ | CI 2 Decid | Site | -452.55 |
| M10 | $PAI_{Ht}$ | CI 3 Con+ CI 3 Decid | Site | **-473.34** |
| M11 | $PAI_{Ht}$ | CI 3 Con | Site | -471.71 |
| M12 | $PAI_{Ht}$ | CI 3 Decid | Site | -455.05 |
| M13 | $PAI_{Ht}$ | CI 4 Con+ CI 4 Decid | Site | -453.91 |
| M14 | $PAI_{Ht}$ | CI 4 Con | Site | -455.85 |
| M15 | $PAI_{Ht}$ | CI 4 Decid | Site | -448.09 |
| M16 | $PAI_{Ht}$ | CI 5 Light | Site | -448.47 |

Coniferous and deciduous competition are entered separately in the model.
Con: coniferous
Decid : deciduous

**Table 3.8** Estimates of coefficients for fixed effects and their 95% confident intervals in equation 2.10, residual standard error (SD) and coefficient of determination ($R^2$) for best fitting linear models. Response variables are $PAI_{Ht/BA}$ in period 3. CI used are CI3 for height and CI2 for BA.

| | Parameter estimates | | | Residual SD | $R^2$ |
|---|---|---|---|---|---|
| | Intercept ($\beta_0$) | CI coniferous($\beta_1$) | CI deciduous($\beta_2$) | | |
| **$PAI_{BA}$** | | CI 2 | CI 2 | 1.504 | 0.43 |
| Estimated parameter | 3.625 | -0.056 | -0.046 | | |
| (95% Confident interval) | ( 2.719 - 4.531) | (-0.073 - -0.040) | (-0.069 - -0.024) | | |
| **$PAI_{HT}$** | | CI 3 | CI 3 | 0.799 | 0.49 |
| Estimated parameter | 0.242 | -0.004 | -0.002 | | |
| (95% Confident interval) | (0.176- 0.309) | (-0.006 - - 0.003) | (-0.004 - 5.775e-05) | | |

### *3.2.3.2 Non-linear mixed-effects competition models*

Using a mixed model with random effects for each site resulted in a significantly better model fit than using no mixed model.

Due to complexity of the non-linear mixed-effects model (Equation 2.11), models with more than one random effect did not converge, hence only models with one random effect for each site could be compared with each other for the same competition index.

#### *Basal Area*

A random effect on the power of coefficient *c* resulted in the best fitting model for $PAI_{BA}$ for the five different competition indices (Table 3.9). CI2 transformed (sum of DBH) had the best fit looking at AIC values, followed closely by CI4 and CI1. The inclusion of a power variance function on initial size for each separate site resulted in an improvement of the model fit. Overall CI5, light (%), had the weakest impact on $PAI_{BA}$ during period 3.

Looking at the best fitting model, M3, initial BA and coniferous competition had a significant impact on $PAI_{BA}$. This is shown in Table 3.10 where the coefficient estimates for initial BA (*c*) and coniferous competition (*b2*) don't include zero. For deciduous (*b3*) competition the 95%

**Table 3.9** Results of non-linear model selection. AIC values, fixed effects and random effects of five competing mixed effects models for $PAI_{Ht/BA}$ as response variable in period 3, using 4 competition indices separately calculated for coniferous and deciduous competition (Table 2.5).

| Model | Response | Competition index | Fixed effects | Random effect | AIC |
|---|---|---|---|---|---|
| M1 | $PAI_{BA}$ | CI $1_{total}$ | a,b1, b2,b3,c | c | 491.52 |
| M2 | $PAI_{BA}$ | CI $1_{larger}$ | a,b1, b2,b3,c | c | 490.2 |
| M3 | $PAI_{BA}$ | CI 2 * | a,b1, b2,b3,c | c | **478.76** |
| M4 | $PAI_{BA}$ | CI 4 | a,b1, b2,b3,c | c | 488.9 |
| M5 | $PAI_{BA}$ | CI 5 | a,b1, b2,b3,c | c | 551.6 |
| M1 | $PAI_{Ht}$ | CI $1_{total}$ | a,b1, b2,b3,c | a | -488.27 |
| M2 | $PAI_{Ht}$ | CI $1_{larger}$ | a,b1, b2,b3,c | a | **-491.7** |
| M3 | $PAI_{Ht}$ | CI 2 * | a,b1, b2,b3,c | b1 | -480.0 |
| M4 | $PAI_{Ht}$ | CI 4 | a,b1, b2,b3,c | b2 | -486.0 |
| M5 | $PAI_{Ht}$ | CI 5 | a,b1, b2,b3,c | a | -461.6 |

* size of main tree was set to 1.0 for calculation of competition index

confidence interval includes 0 which means that deciduous competition is not significant in that model.

The strong positive relationship between initial BA and $PAI_{BA}$ for M3 is shown in figure 3.12 for each site separately, the large parameter estimate for *c* in table 3.10 is an indicator of this strong relationship.

The higher negative value estimate for *b2* compared to *b3* indicates a stronger negative impact of coniferous competition than deciduous competition on the $PAI_{BA}$ in period 3 (Table 3.10, Fig. 3.12). The negative impact of competition due to coniferous competition has a very steep curve, whereas the curve of deciduous competition is close to level which indicates a weak impact of deciduous competition on $PAI_{BA}$.

Figure 3.12 shows both the fixed effects and full mixed model (including both fixed and random effects) for each site and their clear deviation from each other, which makes inclusion of site as a random factor necessary. The highest overall $PAI_{BA}$ at period 3 was reached at site SL with a mean of 3.89 $cm^2$, site CL1 had the lowest with a mean of 1.21 $cm^2$. The random effect in M3 explained 6% of the variance in the model.

Figure 3.13 indicates overall good fit of model M3. The residuals are normal and evenly distributed and random effects are within one straight line in the Q-Q plot.

M3 is considered the best fitting model for $\text{PAI}_{\text{BA}}$ in period 3 using the sum of DBH (CI2 transformed) as the competition index and a random effect on initial size.

**Table 3.10** Estimates of parameters for fixed and random effects and their 95% confident intervals for equation $PAI_{ij} = a + b_1 * e^{(b_2 * CIcon_{ij} + b_3 * CIdecid_{ij})} * in.Ba_{ij}^{c} + \varepsilon_{ij}$ for the best BA and height model. Response variables are $\text{PAI}_{\text{BA/Ht}}$ in period 3.

| | Parameters | | | | | Random effects |
|---|---|---|---|---|---|---|
| | a | b1 | b2 | b3 | c | |
| $\text{PAI}_{\text{BA}}$ Competition Index 2 * | | | | | | |
| | | | | | | c |
| Parameter estimate | 0.08 | 0.33 | -0.01 | 0.0003 | 0.75 | 0.05 |
| (95% Confident interval) | ( - 0.02 - 0.17) | (0.23 - 0.44) | ( - 0.008 - - 0.005) | ( - 0.001 - 0.002) | 0.65-0.85 | (0.03 - 0.11) |
| $\text{PAI}_{\text{Ht}}$ Competition Index $1_{\text{larger}}$ | | | | | | |
| | | | | | | a |
| Parameter estimate | 0.15 | 0.03 | -9.36 | 1.55 | 0.49 | 0.04 |
| (95% Confident interval) | (0.09 - 0.20) | ( - 0.01 - 0.06) | ( - 15.80 - - 2.92) | ( - 3.62 - 6.73) | (0.16 - 0.83) | (0.02 - 0.09) |

* size of main tree was set to 1.0 for calculation of competition index

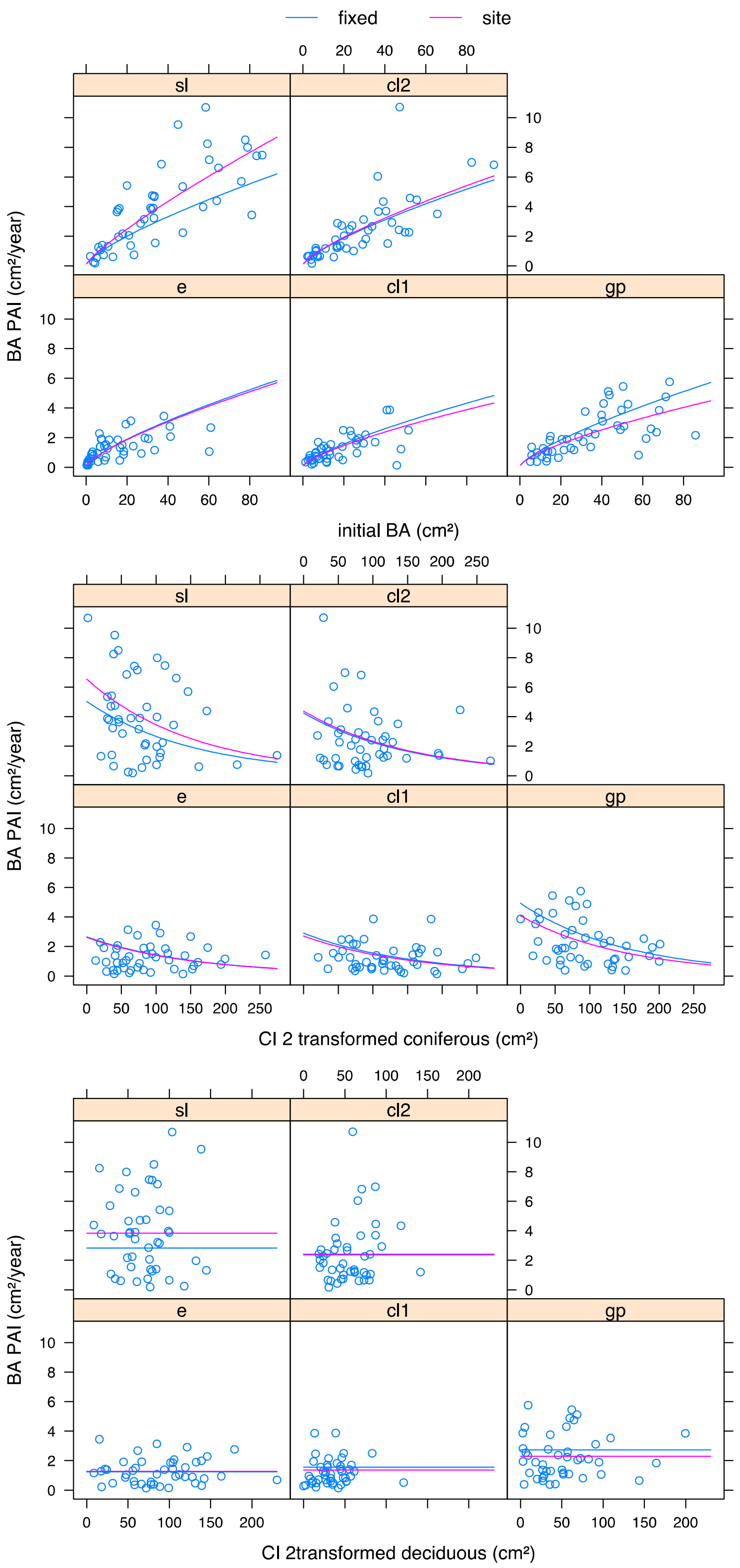

**Figure 3.12** Fixed effects (population level) in blue and site effects (stand level) in pink for PAI$_{BA}$ in in period 3 as response to initial BA, CI2 transformed coniferous competition and CI2 transformed deciduous competition in model M3 (Equation 2.11). Each of the five sites is indicated in the box above the diagram.

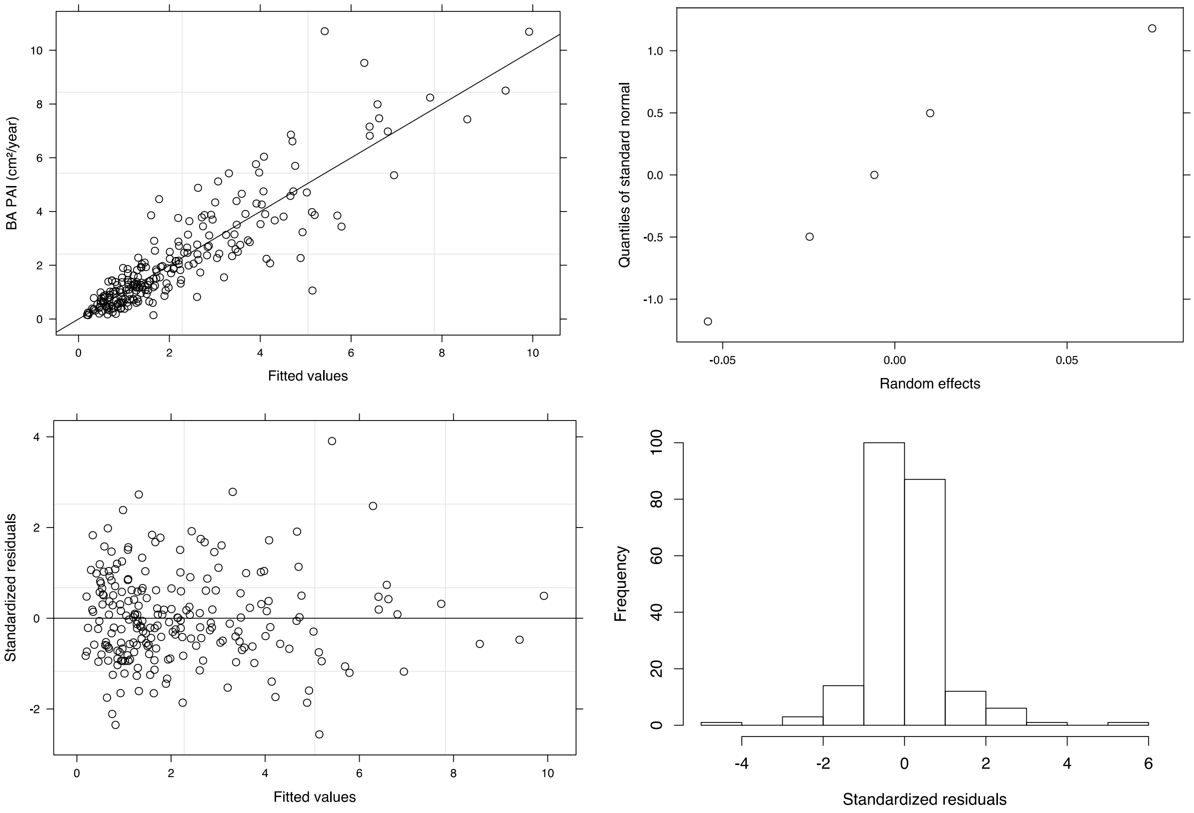

**Figure 3.13** Scatter plots of standardized residuals against fitted $PAI_{BA}$ values, histograms of the standardized residuals and Q-Q plot of random effects for the best fitting $PAI_{BA}$ model in period 3 (M2).

*Height*

The inclusion of a random effect for site resulted in a lower AIC value and a better model fit than a model without this random effect. A random effect on *a*, *b1* and *b2* showed good model fit for the $PAI_{Height}$ model, comparing AIC values (not shown) of models with random effects on either coefficient *a*, *b1*, *b2*, *b3*, *c*. The best model fit, M2, was achieved using *a* as a random factor for each site and the size independent $CI1_{larger}$ (lowest AIC value). The second best model fit was obtained by $CI1_{total}$ and a random effect on *a*. Light as a competition index combined with a random factor on *a* resulted in the worst model fit (Table 3.9). The inclusion of a variance structure did not improve model fit, therefore it was not included in the height model.

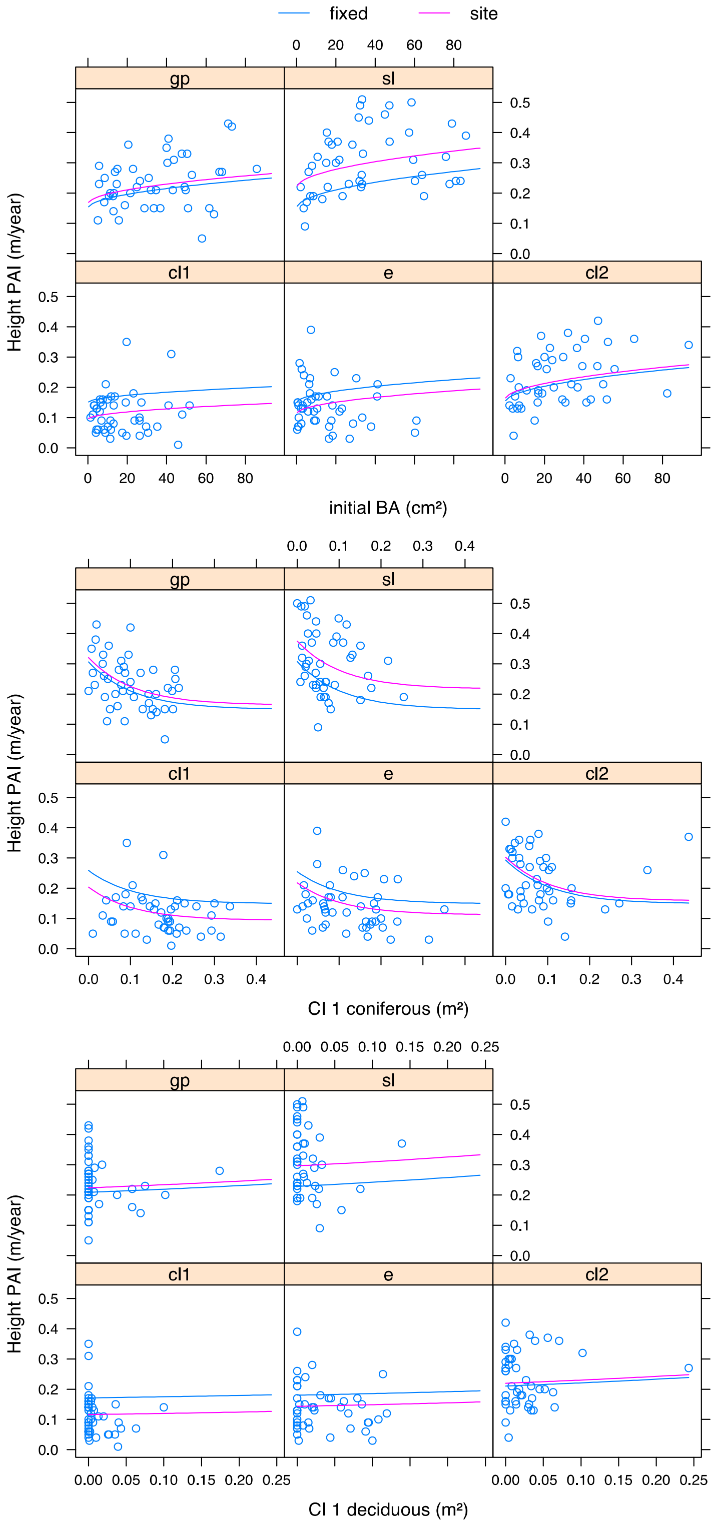

**Figure 3.14** Fixed effects (population level) in blue and site effects (stand level) in pink for $PAI_{Ht}$ in period 3 as response to initial BA, $CI1_{larger}$ coniferous competition and $CI1_{larger}$ deciduous competition in model M2 (Equation 2.11). Each of the five sites is indicated in the box above the diagram.

Examining the significance levels of the competition indices the same findings apply for the height model as observed in the BA model: initial BA and coniferous competition were significant in the model whereas deciduous competition was not (Table 3.10), shown by the inclusion of zero in the parameter estimates.

While initial BA had a significant positive impact on $PAI_{BA}$, for $PAI_{Ht}$ the relationship was not as strong (Table 3.10).

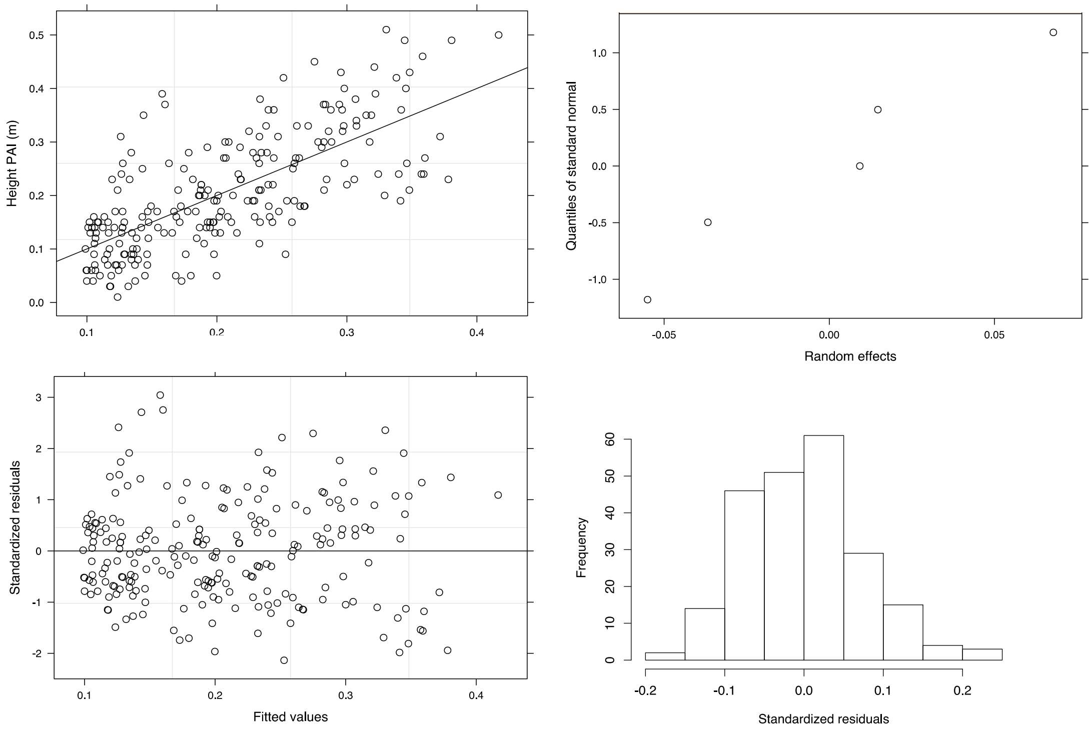

**Figure 3.15** Scatter plots of standardized residuals against fitted $PAI_{Ht}$ values, histograms of the standardized residuals and Q-Q plot of random effects for the final height PAI model in period 3.

The less negative values for *b3* (deciduous) estimates compared with the lower negative values for the coniferous estimates (*b2*) indicate a stronger negative impact of coniferous competition on the height growth of white spruce than deciduous competition. This is also shown in figure 3.14, where $PAI_{Height}$ increases with increasing deciduous competition while for coniferous competition it follows the expected negative trend, decreasing with increasing competition.

Looking at this figure it becomes very clear that the inclusion of a random effect does significantly improve model fit, shown by the deviation between the fixed effects curve and the curve individually for each site. Site SL reached the highest mean $\mathrm{PAI}_{\mathrm{Height}}$ during period 3 with an average of 0.30 m, site CL1 had the lowest with an average of just 0.11 m.

The variance explained by the height model adds up to about 29% by using a random effect on site in the model. The distribution of the residuals and the random effects confirm good overall model fit (Fig. 3.15).

## 3.3 Climate effects on white spruce growth after SCUP harvesting

Each of the six calculated climate variables is shown in figure 3.16 for each of the study sites separately from 1990 to 2013. The yearly trends are very similar between the sites during the 23-year interval; site GP having the highest temperatures and site E the lowest. Highest precipitation values are calculated for site GP and lowest for site E. Moisture indices are overall lowest at site GP and highest at site E. At the other three sites the climate variables fluctuated between those extremes.

The diamond symbols in figure 3.16 indicate the year of harvesting for each of the five study sites. The harvesting did not happen simultaneously at each site, but in different years. Therefore climate data and years after SCUP harvesting do not correspond between sites but differ, while climate data are very similar between sites in corresponding years.

Table 3.11 shows the minimum and maximum values for each site and each climate variable. Both figure 3.16 and table 3.11 display a small variation of the climate variables after SCUP with just a few outstanding peaks and lows.

For the analysis of climate variables $\mathrm{CI1}_{\mathrm{larger}}$ for coniferous trees was used in the null model representing competition (Equation 2.12). Adding the twelve different climate variables into the model resulted in different significant and best fitting climate variables for each site (Table 3.12).

The three best temperature related variables were $\mathrm{MCMT}_{\mathrm{previous}}$, MCMT, and $\mathrm{DD5}_{\mathrm{previous}}$. $\mathrm{DD5}_{\mathrm{previous}}$ was the best variable at two sites, CL1 and E, $\mathrm{MCMT}_{\mathrm{previous}}$ was significant at sites CL2 and SL and MCMT at site GP. The two best fitting moisture related variables were MAP and SHM, with MAP being the most reoccurring at 4 sites, CL1, CL2, E and GP.

**Table 3.11** Minimum and maximum values and their deviation of each climate variable within each site in the years after SCUP (CL1: 1999-2013; CL2: 2005-2013; E: 1999-2013; GP: 2006-2013; SL: 2005-2013).

| Site | Climate variable | Min | Max | Deviation |
|---|---|---:|---:|---:|
| CL1 | MAT | 0.1 | 2.2 | 2.1 |
| CL2 | MAT | 0.1 | 2.2 | 2.1 |
| E | MAT | -0.2 | 1.8 | 2 |
| GP | MAT | 1.4 | 3.2 | 1.8 |
| SL | MAT | 0.6 | 2.7 | 2.1 |
| CL1 | DD5 | 1039 | 1447 | 408 |
| CL2 | DD5 | 1164 | 1451 | 287 |
| E | DD5 | 1064 | 1377 | 313 |
| GP | DD5 | 1234 | 1435 | 201 |
| SL | DD5 | 1228 | 1521 | 293 |
| CL1 | MCMT | -19.8 | -10.3 | 9.5 |
| CL2 | MCMT | -19.2 | -10.4 | 8.8 |
| E | MCMT | -20 | -12.4 | 7.6 |
| GP | MCMT | -16.5 | -7.1 | 9.4 |
| SL | MCMT | -18.3 | -9.3 | 9 |
| CL1 | MAP | 438 | 542 | 104 |
| CL2 | MAP | 451 | 540 | 89 |
| E | MAP | 367 | 511 | 144 |
| GP | MAP | 455 | 617 | 162 |
| SL | MAP | 442 | 530 | 88 |
| CL1 | SHM | 37.7 | 54 | 16.3 |
| CL2 | SHM | 38 | 54 | 16 |
| E | SHM | 43.6 | 72.2 | 28.6 |
| GP | SHM | 36.7 | 59.4 | 22.7 |
| SL | SHM | 39.2 | 53.9 | 14.7 |
| CL1 | AHM | 20.2 | 26.9 | 6.7 |
| CL2 | AHM | 21.3 | 26.1 | 4.8 |
| E | AHM | 21 | 29.6 | 8.6 |
| GP | AHM | 20 | 28.9 | 8.9 |
| SL | AHM | 22.1 | 27.6 | 5.5 |

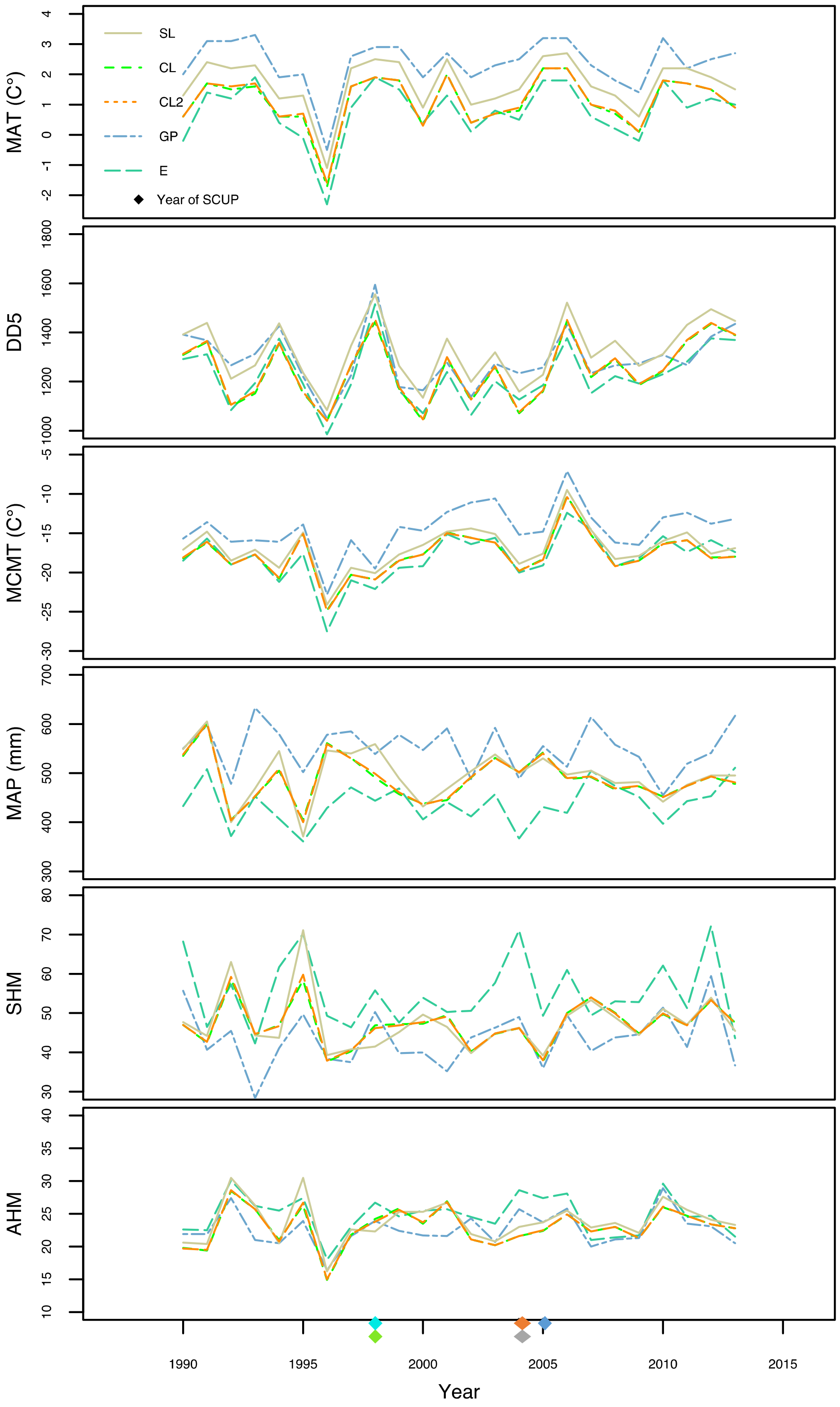

**Figure 3.16** Annual climate variables including mean annual temperature (°C) (MAT), growing degree days (DD5), mean coldest month temperature (°C) (MCMT), mean annual precipitation (mm) (MAP), summer heat moisture index (SHM) and annual heat moisture index (AHM) from 1990 to 2013. Diamond symbols indicate the year of SCUP harvesting. Each site is shown in a different color.

**Table 3.12** Best fitting climate variables for each study site indicated with a "1". Temperature and moisture variables were tested separately.

| Climate variable | Site | | | | | Sum |
|---|---|---|---|---|---|---|
| | CL1 | CL2 | E | GP | SL | |
| MAT | | | | | | 0 |
| MCMT | | | | 1 | | 1 |
| DD5 | | | | | | 0 |
| MAT prev. | | | | | | 0 |
| MCMT prev. | | 1 | | | 1 | 2 |
| DD5 prev. | 1 | | 1 | | | 2 |
| MAP | 1 | 1 | 1 | 1 | | **4** |
| SHM | | | | | 1 | 1 |
| AHM | | | | | | 0 |
| MAP prev. | | | | | | 0 |
| SHM prev. | | | | | | 0 |
| AHM prev. | | | | | | 0 |

The inclusion of both the best fitting temperature and moisture variable into the null model improved model fit for each site, shown by the lower AIC values (Table 3.13). Residual standard error decreased between 0.07 and 0.13 with the inclusion of climate in the null model.

In the final model initial size was significantly positive related to the growth of the white spruce trees at all sites besides site E, where it was positive but not significant. Competition on the other hand was negatively related to growth at sites CL1, CL2, GP and SL, but the relationship was not significant. At site E the relationship was positive but also not significant. All climate variables were significant in the final models, shown by the 95% confidence intervals of the coefficient estimates in table 3.14 which do not include 0.

Figure 3.17 shows the mean BAI increment for each study site and the two best fitting climate variables. Even though all of variables were significant the graphs indicate substantial variability. For instance, at site CL1 there is a constant fluctuation of $DD5_{previous}$ over the observed time period and a general increase of DD5. BAI is also constantly increasing, but there is no direct effect of the fluctuations of the climate variables visible in BAI.

**Table 3.13** Correlation structure and AIC values for each null model (M0) and model with best fitting temperature and moisture climate variables (M1) for each site explaining BAI (log transformed) after SCUP. P values comparing the null model and best model for each site.

| Site | Model | Correlation structure | Variables from the null model | Climate variables | AIC | P-value* |
|---|---|---|---|---|---|---|
| CL1 | M0 | Ar1 (ID) | CI 1, int. BA | | 776.08 | |
| CL1 | M1 | Ar1 (ID) | CI 1, int. BA | DD5prev, MAP | 662.36 | <0.05 |
| CL2 | M0 | Ar1 (ID) | CI 1, int. BA | | 362.56 | |
| CL2 | M1 | Ar1 (ID) | CI 1, int. BA | MCMTprev, MAP | 224.63 | <0.05 |
| E | M0 | Ar1 (ID) | CI 1, int. BA | | 772.20 | |
| E | M1 | Ar1 (ID) | CI 1, int. BA | DD5prev, MAP | 676.01 | <0.05 |
| GP | M0 | Ar2 (ID) | CI 1, int. BA | | 360.98 | |
| GP | M1 | Ar2 (ID) | CI 1, int. BA | MCMT, MAP | 289.87 | <0.05 |
| SL | M0 | Ar1 (ID) | CI 1, int. BA | | 413.38 | |
| SL | M1 | Ar1 (ID) | CI 1, int. BA | MCMTprev, SHM | 334.63 | <0.05 |

* P-value comparing fit of M0 with fit of M1 for each site

For site CL1 the inclusion of $DD5_{previous}$ and MAP to the null-model resulted in the best model with the lowest AIC value and a residual standard error of 1.09. $DD5_{previous}$ was negative and MAP slightly positive related to BAI increment. (Table 3.14, Fig. 3.17).

Adding $MCMT_{previous}$ and MAP to the null-model for site CL2 resulted in the best model with a positive relationship between $MCMT_{previous}$ and growth, and a negative relationship between growth and MAP. Overall the model had a residual standard error of 0.84 (Table 3.14, Fig. 3.17).

$DD5_{previous}$ and MAP added to the null-model resulted in residual standard error of 1.55 for site E, whereas $DD5_{previous}$ was negative and MAP positive related to BAI of white spruce (Table 3.14, Fig. 3.17).

MCMT as a temperature measure and MAP were the best fitting climate variables at site GP. MCMT was negative and MAP was positive linked with the white spruce growth and the whole model had a residual standard error of 0.80 at site GP (Table 3.14, Fig. 3.17).

$MCMT_{previous}$ and SHM were both positive related to the growth of the sampled trees at site SL. (Table 3.14, Fig. 3.17). Residual standard error was 1.03. Normalized residual plots confirm a good fit of all five model (Fig. 3.13).

**Table 3.14** Estimates of parameters for variables and their 95 % confident intervals for climate models ($BAI_{ti} = \beta_0 + \beta_1\ int.BA_i + \beta_2\ CI_i + \beta_3\ Temperature_t + \beta_4\ Moisture_t + \varepsilon_{ti}$).

| Site | Estimates | Parameter | | | | | Residual SD |
|---|---|---|---|---|---|---|---|
| | | Intercept ($\beta_0$) | Int. BA ($\beta_1$) | CI ($\beta_2$) | Temperature Variable ($\beta_3$) | Moisture Variable ($\beta_4$) | |
| CL1 | Parameter | -0.4157 | 0.0243 | -2.3553 | -0.0009 | 0.0025 | 1.09 |
| | (95% Confident interval) | (-1.24 - 0.41) | (-0.003 - 0.051) | (-6.19 - 1.48) | (-0.001 - -0.0007) | (0.001 - 0.003) | |
| CL2 | Parameter | 4.2551 | 0.0663 | -1.6590 | 0.0336 | -0.0071 | 0.84 |
| | (95% Confident interval) | (3.50 - 5.01) | (0.04 - 0.09) | (-4.14 - 0.82) | (0.03 - 0.04) | (-0.008 - -0.006) | |
| E | Parameter | -0.8719 | 0.0285 | 1.4487 | -0.0008 | 0.0023 | 1.55 |
| | (95% Confident interval) | (-1.71 - -0.04) | (-0.009 - 0.07) | (-4.05 - 6.95) | (-0.001 - -0.0006) | (0.002 - 0.003) | |
| GP | Parameter | 0.6851 | 0.0230 | -2.7953 | -0.0412 | 0.0012 | 0.80 |
| | (95% Confident interval) | (-1.154 - -0.22) | (0.009 - 0.04 | (-5.83 - 0.24) | (-0.06 - -0.03) | (0.0006 - 0.0.002) | |
| SL | Parameter | 0.1693 | 0.0863 | -3.4353 | 0.0235 | 0.0147 | 1.03 |
| | (95% Confident interval) | (-0.48 - 0.81) | (0.0.05 - 0.13) | (-8.36 - 1.49) | (0.01 - 0.03) | (0.008 - 0.02) | |

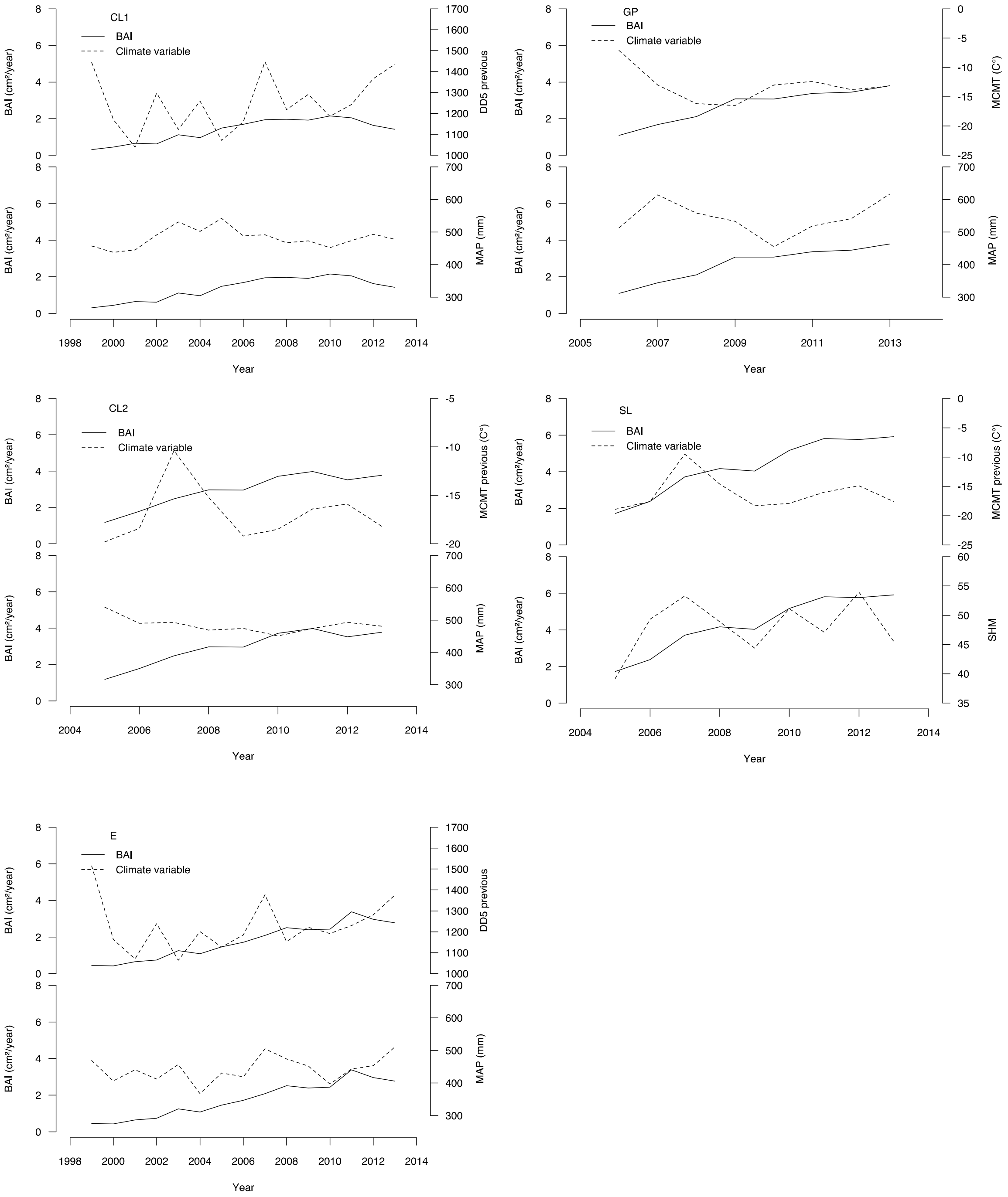

**Figure 3.17** Mean BAI and two best fitting climate variables over time for each site separately after SCUP harvesting.

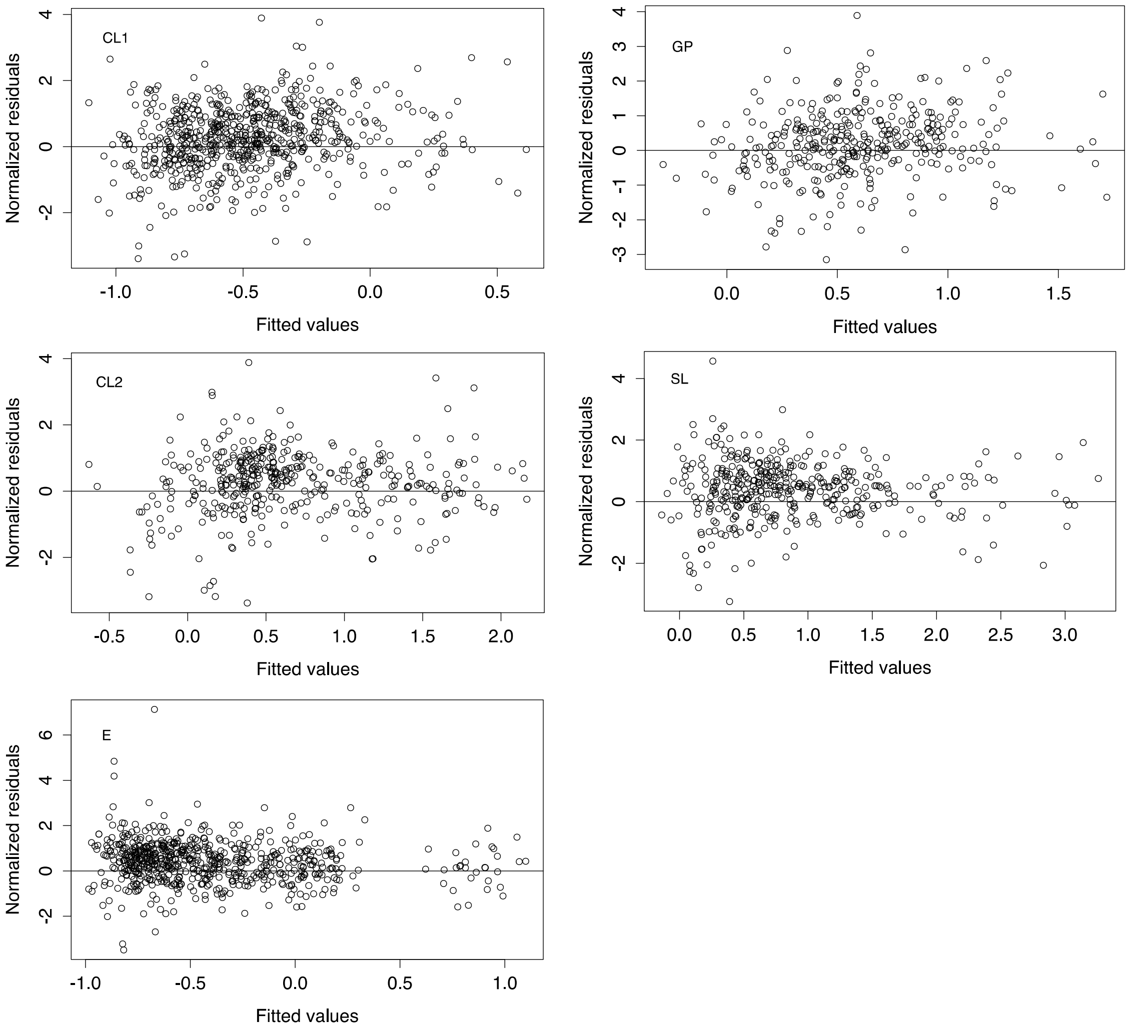

**Figure 3.18** Normalized residuals against fitted values for the final climate models for each site separately.

# Chapter 4

# Discussion

## 4.1. Spruce response to SCUP

As reported by former studies of spruce release (Lees, 1966; Yang, 1991) and understory protection experiments (Man and Greenway, 2004; MacIsaac and Krygier, 2009; Grover et al. 2014) my study shows a significant increase in height and diameter growth of white spruce after understory protection harvesting (Fig 3.1). This increment can be due to many factors such as increased light levels, increased space, as well as increased moisture and nutrient availability (Man and Greenway, 2004). Nevertheless, the response of spruce depends on several factors including site quality, vigor, size of released spruce and the release intensity (Welham et al. 2002).

Vigor and size before release do influence the growth response of the trees. Man and Greenway (2004) show in their meta-analysis that the height response increases over 100% in the first year after harvesting if trees are between 5 to 7 m in height at time of harvesting. When they are taller than 7 m in height before harvesting their increment drops. Trees with 20 m height before release would increase about 80% in the first year after release. Pothier et al. (1995) confirms this finding, stating that there is a better height growth rate of small trees, particularly in the first 30 years after SCUP. In this study trees were still relatively small in height, between 0.4 and 11.4 m at the time of field measurements and a mean of 3.3 m at the year before release, which explains the strong height growth response.

The effects of site quality are indicated in our study by noticeable differences between the five sites. Site CL1 has the lowest increment before SCUP and even though the increment of trees at site CL1 is increasing after SCUP they still have the lowest increment compared to the other sites 9 years after release. On the other hand site SL had the overall highest increment in BA per year, both before and after SCUP (Fig. 3.2). Yang (1991) confirmed those differences between sites, but still he concluded that spruce release will lead to increased growth response even on poor sites. Over a 35 year time period he detected an 82% increase in volume on released spruce compared to the untreated control.

BAI was increased immediately after SCUP while height increment responded with a delay of about three to five years after SCUP (Fig. 3.1, 3.4). This trend is also found in the meta-analysis of Man and Greenway (2004) in which they compared the release response of white spruce across multiple studies. A delay in growth response can be related to the allocation of growth from the trunk into the roots as reported from Urban et al. (1994) and Claveau et al. (2006). By investing first in roots and diameter instead of height the tree will be more resilient to windthrow (Liu et al. 2003; MacIsaac and Krygier, 2009). Kneeshaw at al. (2002) confirmed the delayed height increment in their study of lodgepole pine (*Pinus contorta* Dougl. ex Loud.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) response to release. They found immediate increment of roots the year following harvest, but a delay of height growth increment for 2 years after release. Instead of relating those growth patterns to windfirmness, they argue that the immediate growth of roots will allow more water uptake for the tree which in turn leads to a higher photosynthetic activity. Once the tree has grown enough fine roots to meet nutrient and water demand, its height growth will increase. A second reason for the delay in height growth could be related to the conditions prior to the harvesting. Height growth response to release of advanced grand fir showed a delay in the study of Ferguson and Adams (1980). They partly explained the reduced growth response to the fact that height growth is influenced by the previous year conditions which controls the number of cells initiated in the bud.

Most of the studies done on white spruce release detect a stronger response of BAI than height increment (Yang 1991; Welham et al. 2002; Man and Greenway 2004; Grover et al. 2014). In my study the periodical model showed a stronger height- than BA increment for spruce release, nine years after SCUP. The yearly growth analysis shows BA increment plateauing at about 5 years after SCUP at 3 of our study sites, whereas the curve of height increment is continuously increasing (Fig. 3.8). This pattern was also found in Kneewshaw et al. (2002). Man and Greeenway (2004) state in their paper that there could be a shift in growth from an increased diameter increment to a stronger increment in height once the trees added enough growth to the diameter to be stable enough to resist windthrow. Since observed trees in this study were relatively small in height they were not as prone to windthrow. Therefore, the trees did not take many years to reach the diameter at which they were stable against windthrow, instead they could accelerate height increment fairly soon after SCUP.

The results from the GP SCUP and control site match most other white spruce release studies, where a control was present (Lees, 1966; Steneker 1967). Over a time period of eight years the height increment increased by about 36% and BA increment more than doubled at the SCUP plots compared to the control. In his ten-year study, Steneker (1967) reported similar values where white spruce was released from aspen competition. Man and Greenway (2004) report in general lower increases for spruce growth increment but a higher increment in BA than in height.

On the control site trees were in low light conditions. Lieffers and Stadt (1994) show an increased height diameter ratio with decreasing light levels. White spruce in the control plot increases in height growth to reach higher light levels, whereas trees at the SCUP site first invest in their BAI to become windfirm. This explains the higher increment in BAI compared to the height increment on the SCUP versus control site.

## 4.2 Effects of competition on growth of white spruce

### *4.2.1 Difference between coniferous and deciduous competition indices, including only trees within radius versus all trees within a plot*

This study shows that a search radius of 5.64 m and 3.99 m for coniferous and deciduous trees respectively is sufficient to capture the influence of competing trees on subject trees at our study sites. This search radius is approximately twice the size of the overall mean crown of the overstory in the observed stands. Lorimer (1983) shows in his study that the variance in tree growth explained by competition increases sharply until the search radius of competition exceeds a size of about 2 to 3 times the mean crown size of overstory trees in the stand, after that point it starts to level off. Stadt and Lieffers (2000) report a crown radius between 1.2 to 2.2 m for overstory white spruce trees with a height between 20.1 to 28.9, and trees with a mean of 9.4 m in height have a corresponding mean crown size of 1.7 m radius for understory trees. We did not measure crown size but coniferous trees sampled in this study were generally under 10 m in height (Table 2.3). Therefore we can assume that a search radius of 5.64 m for coniferous trees was at least 2 to 3 times the mean crown radius in our stands and hence sufficient for measuring coniferous competition.

For deciduous trees, mainly aspen, poplar and deciduous shrubs, the 3.99 m search radius for competition fit well, since the regenerated deciduous trees after SCUP, around the spruce trees, were still small in size (Table 2.4) (Cortini and Comeau 2008; Harper et al. 2009). Recorded larger trees were mainly outside of the 5.64 m search radius and within the windbuffer zones of the SCUP harvesting plots, and did not appear to have major competitive impacts. Smith et al. (2016) did a study on spruce response following partial cuttings of different aspen densities. Testing multiple radii for competition measurements between 10 m and 5 m around the sample trees they found that the 5 m radius was best for representing competition impacts on radial growth.

However, some studies suggest larger search radii to maximize variance explained by competition (Simard and Sachs, 2004; Contreras et al. 2011). Findings of Simard and Sachs show that the preferred search radius for competition trees increases with increasing age of a stand.

The inclusion of trees outside of the radius did in fact improve the models, but explained variance increased by only about 2%. Considering the additional time and work during field measurements this 2% gain is negligible.

As Biging and Dobbertin (1995) phrase it: “It is difficult, if not impossible, to define an exact zone of influence for use in a competition index for individual trees that includes all competitors and sources of competition for scarce resources”. Since this analysis shows a good representation of the competition within species specific radii without the inclusion of taller surrounding trees, for further analysis, only the trees within this radius were included in my models.

### *4.2.2 Light measurements and their ability to characterize competition*

Light availability is known to decrease with increasing overstory competition. Previous studies have shown the best fit of light and competition was achieved by using an exponential function (Comeau et al. 2003 b), but surprisingly in this study there was no improvement of the model when using the *ln* transformation.

The distance independent index CI2 worked as well as the distance dependent competition index CI4 for predicting light levels using a linear relationship. This contradicts some previous studies which showed BA within the plot represented light levels best and the inclusion of proximity (distance between subject tree and competitor) did downgrade the model fit (MacDonald et al. 1990; Comeau et al. 2003 b). Those results come from studies where light levels were measured in more or less uniform stands of the same species and same age. Stands in my study were more complex, representing mixedwoods with aspen and spruce trees and an applied harvesting which created greater complexity in the stands and a variation in light levels (Harper et al. 2009). Beaudet et al. (2011) showed that light levels do increase in a stand following partial harvesting, but point out that there is a spatial factor influencing light levels. Stadt et al. (1997) emphasized that the spatial pattern might not be significant in stands with closed canopy and uniform structure, but may be important in complex stands with a heterogenous canopy, as found in these mixedwoods following understory protection harvesting. The inclusion of spatial patterns will account for those differences and can result in a better model fit (Stadt et al. 1997).The fact that the stands in my study are intermediate in complexity explains the equal fit of distance independent and distance dependent indices.

### *4.2.3 Comparison of competition indices*

The investigation of effects of competition on white spruce growth in the boreal mixedwoods and plantations is the subject of many published papers: Yang, 1991; Biging and Dobbertin, 1995; Huang et al. 2013; Neufeld et al. 2014, and many more. In those papers several different competition measurements have been used: distance-independent measures, measures of spatial pattern, measures of BA, height and crown size of trees, as well as light levels as a measure of competition. The competition indices used in this study covered a range of distance-dependent (CI3, CI4), independent (CI1, CI2, CI5), and size dependent (CI2, CI3) competition measures. BA, DBH and light levels were used as a measure of competition (Table 2.5). I chose those measurements because they are easy to collect and they showed good fit in previous research.

#### *4.2.3.1 Linear mixed-effects competition models*

The linear mixed-effects models were built to investigate the overall fit of the different competition indices. The poorest fit was seen with indices which were not using size of the subject tree. Lorimer (1983) suggests the inclusion of subject tree size in the competition index to improve predictability of competition impact on the tree. He argues, “initial diameter is in itself a kind of competition index”. He is referring to characteristics of an even aged stand where small trees tend to grow slow due to competition of surrounding trees within the stand. Large trees in contrast are exposed to very little competition in those stands. These features of the stand indicate high competition on small trees and low competition for taller trees. Therefore initial diameter or size could be used as competition index by itself in even aged stands (Alemdag, 1978). But if a stand is managed, this pattern can certainly change and another index for competition is needed (Lorimer 1983). Nevertheless, this shows how important the inclusion of initial size is in estimating the growth of trees. Including initial size in the model accounts for the trees past growing history (Hatch et al. 1975).

As several studies report (Biging and Dobbertin, 1995; Comeau et al. 2003; Stadt et al. 2007) initial size of the subject tree is crucial in determining competition impact on spruce growth due to the growth pattern of trees. Younger trees increase their diameter and height growth due to enhanced photosynthetic activity by producing new leaves. The increment of crown size and leaf area is closely related to the increment of DBH. Growth of older trees decreases with increasing diameter and height, resulting in a non linear relationship between initial size and tree growth (Stadt et al. 2007)

MacDonald et al. (1990) found that measurements of light were more effective in predicting competition than field measurements of the height or BA of competitor trees. Those findings are supported by several studies with good model fit of light measurements correlated with tree growth (Comeau and Heineman, 2003; Comeau et al. 2003b; Filipescu and Comeau 2007 a; Cortini and Comeau, 2008). In this study however, CI5, the competition index derived from light measurements was poorly correlated with the growth of white spruce and did not result in a good model fit. I used a static height for each of the light measurements (1.00 m above root collar) independent of the size of the measured tree. Research indicates that growth models are better correlated with competition indices when light measurements are taken from the top or mid-crown of a tree compared to competition indices with light levels taken from the bottom of the tree (Harper et al. 2009). By using a relative height to crown ratio for the light measurements, light levels can be measured at the height of the tree where most needles and leaves are, and therefore where most photosynthesis happens. Using a static height of 1.00 m above the tree did not represent the area of highest photosynthetic activity and can explain the weak fit of index CI5 in this study. Moreover, light measurements do not account for competition for water, nutrients, the effects of low growing vegetation or soil and microsites differences, which also influence the growth of the trees (Filipescu and Comeau, 2007 b; Stadt et al. 2007).

The best fitted competition indices were CI2 and CI3 for $PAI_{BA}$ and $PAI_{Height}$ respectively. Both indices include the size of the subject trees, whereas CI3 also accounts for proximity measures between subject and competition tree. CI3, the Hegyis index, gives greater weight to trees which are closer to the main trees and therefore are expected to repress the main tree more than trees further away (Lorimer, 1983). Distance dependent and independent indices were compared in many studies with different outcomes. Contreras et al. (2011), for example, found better performance with distance dependent indices when modeling tree growth of different conifer species in Montana. In contrast, Filipescu and Comeau (2007 b) analyzed competition of aspen affecting white spruce growth concluding that distance independent indices are slightly better in predicting growth. It seems difficult to prioritize distance-dependent over independent indices. The findings are inconsistent and seem to depend on stand age and complexity, tree size, and tree status. The sum of $BA_{larger}$, CI1, also had good performance, and is the most simple index. CI4 and CI5 performed the worst.

Overall coniferous competition performed better than deciduous competition when entered alone in the model. This was to be expected and is in agreement with prior studies (Stadt et al. 2007; Huang et al. 2013) since the coniferous trees were taller and denser at most sites compared to deciduous trees which were relatively small within our search radius. Most deciduous trees on my study sites regenerated just after SCUP, whereas the competing coniferous trees were older and longer on the site. Stadt et al. (2007) showed that there is a significantly better model fit when competition on white spruce is separately calculated for spruce and aspen trees and afterwards combined in the model. He also found that coniferous competition had a greater effect of spruce growth than deciduous competition.

The strong relationship between conifer competition and spruce growth can be explained by the low transmittance of light through coniferous tree canopies (Stadt et al. 2000). In their paper, Stadt et al. (2000), evaluated a light transmission model for different coniferous and deciduous species. They found that light was transmitted least through coniferous species in the overstory followed by coniferous species in the understory and best transmitted through deciduous species while they have their leaves on. The continuous shading of coniferous species compared to the seasonal shading of broad leaved species is also major reason for the stronger effect of intraspecific competition versus deciduous competition (Constabel and Lieffers, 1996).

Hawkins et al. (2013) did a study in British Columbia, Canada, to examine thresholds of birch competition on white spruce. White spruce trees had a DBH mean between 2.72 cm and 9.04 cm and birch trees had a mean DBH between 2.98 cm and 4.40 cm at the different study sites. 4,000 stems per $ha^{-1}$ was identified as an important threshold, everything over would have a significant impact on the growth of spruce trees. The fact that aspen density in my study were generally below 4,000 stems per $ha^{-1}$ may be another reason why there was a very weak relationship between deciduous competition and spruce growth.

In addition deciduous species could have a positive effect on the growth of white spruce. In fall when deciduous trees shed their leaves they could serve as nutrient source in mixed forests and thereby effect spruce growth positively instead of negatively. Studies done in black spruce, aspen mixtures in Quebec, Canada, showed a positive link between nutrient availability in mixtures and a positive effect of aspen on black spruce growth compared to pure black spruce stands (Légaré et al. 2005; Laganière et al. 2010). These effects have not been confirmed in mixedwood stands in northwestern Canada (Stadt et al. 2007; Neufeld et al. 2014).

Combining deciduous and coniferous competition in one model did improve each of the BAI models but not all height models. For height, coniferous competition alone seemed to have a better model fit for some of the competition indices. This is likely resulting from the fact that height growth is responding asymptotically to increasing light levels. Increasing light levels above 40% does not increase height growth while diameter growth, which is more sensitive to competition, responds in a continuous fashion to changes in competition (Wright et al. 1998).

#### *4.2.3.2 Non-linear mixed-effects competition models*

The function utilizing a combination of exponential competition and the power of initial size fitted the data very well. Comeau at al. (2003 b) and Cortini and Comeau (2008) showed a very good fit of this function, looking at the growth of white spruce exposed to either competition due to paper birch or various shrub species. Since initial size is included in the function, only competition indices which did not already include initial tree size were tested in these models (CI1, CI4, CI5). The reason for this was a concern raised due to the inflation of coefficients of determination when size is included twice in the model (Filipescu and Comeau, 2007 b). In this way collinearity between competition index and initial size was avoided.

The good fit of the data in the non-linear model is reasonable since tree growth is not linearly correlated with either initial size, or competition as the figures 3.12 and 3.14 indicate. The trees increase in $PAI_{BA/Height}$ very strongly if initial BA is small, but with increasing BA $PAI_{BA/Height}$ starts to level off, and will finally decrease (Bowman et al. 2013). The decrease is not shown in our graphs since initial tree size was still small (< 80 $cm^2$). $PAI_{BA/Height}$ is exponentially decreasing with increasing competition. Similar trends were found by Filipescu and Comeau (2007 a) as well as Comeau et al. (2003 b) and support the findings in this study. Deciduous competition influences the growth in a minor way compared to coniferous competition which is about 4 times stronger for $PAI_{BA}$ and 6 times for $PAI_{Height}$. Those findings agree with results from analysis of competition using the linear model and conform with previous studies where deciduous competition had a lower impact on spruce growth compared to intraspecific competition (Stadt et al. 2007; Huang et al. 2013).

The testing of the five different competition indices revealed, as discussed for the linear model, the worst fit for the light derived competition index CI5. The other competition indices fit the data similarly well, especially for the BA model. However, the $CI1_{larger}$ for height and CI2 transformed were considered the best fitting index, and represents the simplest index tested within this study.

Simple competition measures like BA and DBH have been proven to be a good proxy for competition in combination with size measures of the subject tree (Biging and Dobbertin, 1995; Filipescu and Comeau, 2007 b). Lorimer (1983) found the highest correlations between competition and tree growth when the competition included trees with DBH larger than the subject tree. To explain those findings Weiner (1986) demonstrated an asymmetric relationship between light competition due to large plants compared to light competition resulting from small plants. Newton and Jolliffe (1989) describe this as a “preemption” process in which “large-sized competitors passively prevent solar resources from reaching smaller-sized competitors” resulting in a proportional larger influence of tall trees on the subject tree than small trees.

Our research confirms this finding by the better fit of $BA_{larger}$ than $BA_{total}$ as a competition index in the model. Simard and Sachs (2004) show the preemption process affecting younger stands.

On the other hand, in older stands shorter trees may become more relevant in the competition process. The closed canopy in older stands explains those findings where competition for light becomes less relevant but soil, nutrient and water resources become the focus of competition. Since our stand was exposed to the SCUP harvesting it is representing a stand with an open canopy, so that larger trees still have a stronger competition influence on the spruce trees than small trees.

## 4.3 Climate effects on spruce growth after SCUP harvesting

Improvement in growth response by inclusion of climate variables in growth models has been shown in several studies, and conforms with the results in this study (Snowdon, 2001; Cortini, et al. 2012). By adding climate variables to the model we account for more variation on each sampled site, since effects of site can be explained partially by climate. Cortini et al. (2011) found that climate variables explain between 18% to 37% of variation within their white spruce growth data.

My analysis resulted in different best fitting climate variables for each site. Multiple reasons can explain those findings. First of all, even though sites had similar climatic trends over time there were differences in all the measured variables between the five study sites (Fig. 3.16). Secondly, given the differences in climate between the sites, different climate factors may be limiting. Additionally, the measurements of BAI after SCUP cover different years and therefore also include different ranges of climatic variables (Table 3.11). For instance, sites CL1 and E received SCUP harvesting in 1998; they are representing the two sites which were harvested the earliest and monitored over the longest time period (16 years) in this study. Chronologically harvesting happened at sites SL and CL2 in 2004 and in 2005 at site GP. There was a drop in DD5 in the years 2000 and 2002. Growth measurements were observed for those years only at sites CL1 and E, which are also the two only sites incorporating $DD5_{previous}$ in the best fitting climate models. This could show that the two years of low DD5 values have had a very strong impact on the growth of white spruce in the following year and therefore $DD5_{previous}$ was considered as the best fitting temperature variable only for sites CL1 and E.

Furthermore climate effects can be spatially dependent due to differences in site characteristics such as topography, effects of competition in the overstory and low growing vegetation

(Filipescu and Comeau, 2007 a; Jiang et al. 2016). These factors can contribute to different fits of climatic variables for each of the study sites.

Looking at each of the climate models, MAP was used most often, and was significantly related with BAI at four of the five sites. At site CL2 it was negatively related with the BAI which is not consistent with other literature, where the increase in precipitation favors tree growth and low precipitation can often be a limiting factor (Galván et al. 2014; Grey et al. 2016). If we look at figure 3.17 we see the positive increment of BA at site CL2 and the negative trend of precipitation. Even so precipitation was negatively related to BAI in our model; but this does not mean that the lower precipitation caused the increasing increment. The effects of SCUP harvesting could be so strong that the precipitation does not influence the actual increment of our sampled trees as long as it is not reaching limiting thresholds of precipitation for white spruce growth.

Increasing temperatures and prolonged growing periods due to climate warming in the last decades and future years are believed to support increases in growth of boreal tree species (Eggers et al. 2008). This is contradictory to our findings where $DD5_{previous}$, the growing degree days in the previous year, were negatively correlated with the increment in spruce growth. But the warmer temperatures and earlier springs can also lead to drought stress in trees and promote competition between trees which results in a decreased growth response or even higher mortality rates of trees (Peng et al. 2011; Stinziano and Way, 2014). Peng et al. (2011) found increased mortality rates of white spruce within the boreal mixedwoods in Canada between the 1970's and 2008 which he relates to drought stress caused by climate warming.

In the present study $MCMT_{previous}$ and MCMT were positively and negatively correlated at sites SL and GP respectively. Comparing those two sites and their MCMT's in the observed time period we can see that there was overall a lower MCMT at site SL than at site GP. The coldest MCMT at site GP was -16.5 °C and the warmest -7.1 °C whereas at site SL they were -18.3 °C and -9.3 °C respectively (Table 3.11). Those values are within reported temperature ranges for the observed regions, which are -19.3 °C to -15.7 °C (Grey et al. 2016), but the colder winter climate at site SL is closer to observed lowest temperatures in that region and therefore the climate may have a stronger effect at this site than at site GP as stated by Griesbauer and Green

(2012). Therefore increasing MCMT at site SL will positively effect BAI whereas at site GP the increase in MCMT will have little influence on growth response of spruce.

Even though climate is having significant impacts on tree growth, all climate models in this study should be observed with caution, since harvesting of aspen as well as competition are playing a major role in determining spruce growth (Cortini et al. 2011). This is reflected in this thesis by the inconsistent coefficient estimates of the same climate parameters.

The continuous increases in BA increment after SCUP at the sites was discussed earlier, only focusing on the competition effects and not the climate effects in period 3 after harvesting. Even though all of the climate variables included in the model are significant, the correlation between them and BAI was not always visible (Fig. 3.17) and even sometimes contradicted our expectations. This may be due to the fact that the trees are in a phase of high growth increment after the SCUP harvesting and as long as climate variables are not reaching limiting conditions the spruce trees will perform better than usual, and are less responsive to changes in climate. White spruce is known for its ability to grow well even under extreme climate conditions (Burns and Honkala, 1990). Griesbauer and Green (2012) reported that trees are more likely to be influenced by stand level characteristics, such as competition, if growing in the midrange of their climate thresholds. If they are growing in a climate which is at the edge of their climate thresholds climate is expected to have a strong influence on tree growth. Since our climate variables only had minor effects on residual standard error we can conclude that climate does not explain much of the variation in our data, but that most variation accounted for in the BAI response is due to the SCUP harvesting and competition. The influence climate variables have on BAI seems to be reduced in the first few years after SCUP compared to an untreated stand. Over a longer time period we expect the positive SCUP effects to decline and the influence of climate variation to become stronger.

## 4.4 Application of results and incorporation of models into MGM

Yield predictions from natural or managed forest stands are difficult. Forests are complex systems and it takes many years until a stand reaches maturity. Until a stand is merchantable multiple factors influence the growth of its trees. If those factors change, naturally or through management application, the growth of the trees is likely to respond either positively or negatively. Therefore, the prediction of stand growth is not simple and models need to be calibrated with a variety of data sets which represent the growth response due to natural and management induced changes (Battaglia and Sands, 1998).

As an individual tree based model MGM uses data collected from single trees. It tries to predict the yield of a stand depending on the size of the trees, site effects and competition measures. Grover et al. (2014) express the need for data inclusion from SCUP sites into MGM to improve model performance for those sites. This study detected and quantified the growth response of white spruce after SCUP harvesting. The incorporation of my findings into MGM will allow more precise estimation of yield of SCUP stands in northern Alberta, Canada.

MGM utilizes size in the model for yield predictions, and models in this study confirm the importance of the inclusion of size in predicting release response, for either height or BA estimations of white spruce after SCUP.

Currently, growth functions used in MGM do not consider effects of intraspecific competition on growth of small spruce after release, which leads to the overestimation of growth response of small trees. This study detected and quantified the competition effects suppressing white spruce growth after SCUP harvesting. Those effects need to be incorporated into the MGM to allow for a more precise estimation of yield of SCUP stands in northern Alberta, Canada.

MGM accounts already for species specific competition and its impact on the growth of white spruce when growing on a non managed site. The competition models in this study confirm the importance of distinguishing competition caused by different species. Coniferous species have a stronger influence on spruce growth than deciduous trees.

Furthermore MGM is a distance independent model which does not account for any spatial relationships between trees in a stand. Distance independent competition indices $CI2_{transformed}$ and $CI1_{larger}$ for BA and height predictions respectively performed best in this study and are therefore easy to incorporate in the model.

Increment of white spruce after SCUP is dominated by competition and size effects whereas the influence of climate variables is not very strong after SCUP harvesting. Therefore, I suggest to continue using Natural Subregions in the model as a variable accounting for climate effects.

Results from my research will contribute greatly to the improvement of MGM in predicting growth of released white spruce after SCUP harvesting. By accounting for competition, the growth of small trees will no longer be overestimated and estimations will be much more realistic. However there are still a few questions which need to be addressed. For example, this study did not include very large trees, > 12m height at the time of measurements; how will they respond to the release, receiving no or just a little competition from overtopping trees?

Further studies are needed to quantify the duration of release response and the dynamics of competition on release.

To answer those questions permanent sample plots (PSP's) need to be established and monitored on SCUP sites. Data from permanent sample plots would also offer valuable information on when and to what extent climate effects influence the growth of spruce significantly.

Site index is used in MGM to determine site productivity. Since white spruce trees at SCUP sites were suppressed in the first few years of their growth, they are smaller in height than trees growing on the same site without any shade. Hence the use of the site index derived from total height and age carries this suppression of growth in itself and therefore is inappropriate for MGM use. Grover et al. (2014) suggest the use of a site index coming from open grown white spruce trees with approximately the same size and age of the white spruce trees after SCUP harvesting. But due to the lag of increased of spruce growth after release those trees would not reflect the correct site index for spruce on SCUP sites either. Alternative ways to estimate site index using site factors or correlations with other tree species may have to be used to estimate spruce site index.

# Chapter 5 Conclusion

This thesis focuses on the release response of white spruce advanced regeneration following understory protection harvesting and the influence of extrinsic factors in boreal Alberta, Canada. The study confirmed expectations of a positive growth response of advanced white spruce regeneration after SCUP harvesting. BA responded immediately to the harvesting of aspen, whereas height responded 3-5 years after release, but with an overall higher increase in growth than BA. Overall the growth increment 9 years after SCUP was about three times higher for both height and BA compared to the white spruce growth before SCUP.

As predicted, growth increment decreased with increasing competition from neighboring spruce trees. Competition from deciduous species showed a weak relationship with growth of the spruce trees. The better performance of distance independent competition indices indicates that the arrangement of competitors does not play a major role on SCUP sites.

My findings show that the inclusion of climate variables in early growth response models for white spruce can be neglected, since intraspecific competition is the major driving factor for increased growth response. As long as climate variables are not going above or below threshold values, the growth increment is not likely to be significantly constrained by climate.

Long term studies are needed to monitor white spruce release response on SCUP sites. Long term studies will show if increased growth of released spruce will continue over decades. In this thesis it was only possible to show the growth increment in the first years after SCUP. Including control plots of mixedwood sites without SCUP harvesting and white spruce plantation sites, where white spruce trees are not exposed to overtopping competition would allow direct growth comparison between the different management approaches. Yield implications and comparisons could be derived from the SCUP managed mixedwood stands, unmanaged mixedwood stands and managed pure whites spruce stands. The inclusion of those control sites could help in mixedwood management decision making and improve the amount and quality of timber supply.

Including findings and results from my study in MGM will improve accuracy of the model for white spruce growth predictions from SCUP sites. Growth of small white spruce trees will no longer be overestimated when intraspecific competition is included in the MGM. For long term growth response further research is needed.

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# Appendices

## A.1 R code for modeling release response of BA and height after SCUP

*Eqs. 2.8 and model A3 (p. 20 and 29)*

```
bai =nlme(bai~(year_rel/(a+(b*year_rel))),
        data= sites_ba,
        start=c(a=0.5,b=0.1),
        control=ctrl,
        random=a+b~1,
        fixed=a+b~1,
        weights=varIdent(form=~1|site),
        corr=corAR1(form=~1|site/tree_id))
```

*Eqs. 2.6 and model C1 (p. 20 and 29)*

```
ht =nlme(hti~a*year_rel^b,
        data= sites_ht,
        start=c(a=1.3,b=3),
        control=ctrl,
        random=a~1,
        fixed=a+b~1,
        weights=varIdent(form=~1|site),
        corr=corAR1(form=~1|site/tree_id))
```

## A.2 R code for modeling light depending on competition indices

*Eqs. 2.9 and model M3 (p. 21 and 35)*

```
light.lme=lme(total_light~dbh_con_5.64+dbh_decid_3.99,
            data=dat,
            random=~1|site)
```

## A.3 R code for modeling BAI and Ht increment in period 3 after SCUP depending on competition (linear)

*Egs. 2.10 and model M7 for BA (p. 22 and 38)*

```
ba.lme=lme(pai_ba~CI2_decid_plot+CI2_con_plot,data=p3,
            random=~1|site)
```

*Egs. 2.10 and model M10 for height (p. 22 and 38)`*

```
ht.lme=lme(pai_ht~CI3_con_plot+CI3_decid_plot,
            data=p3,
            random=~1|site)
```

## A.4 R code for modeling BAI and Ht increment in period 3 after SCUP depending on competition (non-linear)

*Eqs 2.11 and model M3 for BA (p. 23 and 40)*

```
Ba_nlme =nlme(pai_ba~a+b1*exp(b2*dbh_5.64con+b3*dbh_3.99decid)*in.ba^c,
                 data=ba_sites,
                 fixed=a+b1+b2+b3+c~1,
                 start=c(a=-1001,b1=0.004, b2=-0.08,b3=0.01,c=2.2),
                 random=(c~1),
                 weights=varIdent(form=~1|site))
```

*Eqs 2.11 and model M2 for height (p. 23 and 40)*

```
ht_nlme =nlme(pai_ht~a+b1*exp(b2*ba_1_m_5.64con+b3*ba_1_m_3.99decid)*in.ba^c,
                 data=ht_sites,
                 fixed=a+b1+b2+b3+c~1,
                 start=c(a=0.0035,b1=0.926644,b2=-5.48,b3=-0.94,c=0.755),
                 random=a~1)
```

## A.5 R code for modeling BAI after SCUP depending on climate

*Eqs. 2.13 and model M1 for site CL1 (p. 24 and 50)*

```
cl1.gls=gls(log_bai~initial_size+ba_l_m_5.64con+DD5_bef+MAP,
            data=claft,
            corr=corAR1(form=~1|tree_id))
```