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Reconstructed height growth trajectories of white spruce (*Picea glauca*) following deciduous release

By

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Dedication

To my parents David Osika and Janet Osika, and my brother Eric Osika

Abstract

My study evaluated the “true” white spruce (*Picea glauca* [Moench] Voss) height growth potential in sites released from deciduous competition. Stem analysis, plus re-measurement data from 60 and 80-year-old trials were used. Interpolated site index (SI, height at breast height age 50) of released spruce was not significantly increased due to late treatment application. However, their height increment 50 years following treatment was elevated by 2.1m. Existing height-age equations for this region showed varying suitability. I fit a new height-age model which allowed for delayed release, this showed a potential 4.1m increase in spruce SI due to release. In a site-specific model, deciduous basal area removal explained significant variation in spruce SI. This model indicated a 7m gain from early release from heavy competition.

These results provide a first long-term estimate of the degree that spruce height growth from mid-age to maturity can be increased by deciduous competition removal.

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Chapter 1. Review of Site Productivity Estimation and General Introduction

The boreal region contains about 90% of Canada's productive forest area (CCFM 2003). Throughout this region, mixed species forests are common on upland sites with deep soils. Pure stands of broadleaf and conifer species may also occupy these sites (Chen and Popadiouk 2002). The western mixedwoods are found in the Boreal Plains ecozone (Ecological Stratification Working Group 1995), extending from south-western Manitoba to north-eastern British Columbia. The characteristic species are trembling aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* [Moench] Voss), black spruce (*Picea mariana* (Mill. BSP.), lodgepole pine ((*Pinus contorta* Dougl. ex. Loud.), jack pine (*Pinus banksiana* Lamb.), balsam poplar (*Populus balsamifera* L.), white birch (*Betula papyrifera* Marsh.), and balsam fir (*Abies balsamea* (L.) Mill.) (Rowe 1959).

In the western boreal, aspen is the dominant broadleaf species, and white spruce is a very commonly-associated conifer (Strong and Leggat 1992). Most stands in this region have originated as a result of disturbances such as fire and wind (or, more recently, harvesting) and exhibit successional patterns which depend on propagule supply, seedbed conditions, ecosite, climate and competition (Lieffers et al. 1996, Weir and Johnson 1998, Peters et al. 2002, Chen and Popadiouk 2002). Normally after a disturbance aspen quickly establish and form an overstorey above the spruce, except in a few gaps, for at least 50-60 years. After this understory phase, white spruce begins to grow through the canopy as aspen decreases in dominance and cover. Eventually, in the absence of fire, wind, harvest or other large scale disturbance, a mixedwood stand may become dominated by white spruce (Chen and Popadiouk 2002).

In addition to disturbance, competition is one of the ecological factors that influence the dynamics of the boreal mixedwood (Chen and Popadiouk 2002). The definition of competition rests on the fact that plants compete for resources (light, water, nutrients, space etc.). As a result, some plants may reduce the availability of these resources to their neighbours. Competition can also be viewed as a situation where the supply of resources is less than the joint requirement of the organisms, and as a result the performance of one or all is impaired (Fitter and Hay 2002). In reality, all species have some potential competitors when they are exploiting a resource because all plants require the same fundamental resources (Fitter and Hay 1981). In plant communities, two types of competition occur, inter-specific competition and intra-specific competition. In the former, individuals of different species compete for the same resources while in the latter plants of the same species compete for the same resources (Smith et al. 1997). Survival will therefore depend on either partitioning of the resources in some way so as to avoid competition, (Fitter and Hay 2002) or development of tolerance to resource limitation. For instance, the shade tolerance of spruce allows it to persist beneath broadleaf species until late in natural stand development (Lieffers et al. 1996).

Generally, reductions in light and other resources by the aspen lead to reductions in diameter and height growth of white spruce (Filipescu and Comeau 2007). Comeau et al. (1993) found that the amount of solar radiation that reaches spruce seedlings is related to the amount of cover and the developmental stages of the competing vegetation. As the competing vegetation increases, light transmittance to the spruce understorey decreases, resulting in a reduction in growth (Wright et al. 1998, Groot 1999, Lieffers and Stadt 1994). Thus, the growth of spruce seedlings is reduced when neighboring vegetation reaches sufficient density and height to reduce light reaching the seedlings. Several observational studies indicate that diameter growth continues to increase with light levels up to full-sky exposure (Wright et al. 1998). However, Lieffers and Stadt (1994) found that about 40% of full sunlight is needed to achieve maximum height growth of seedlings. Very likely, increases in light levels increase the rate of photosynthesis of white spruce which consequently increases growth (Grossnickle 2000).

Additional limitations to spruce growth under an aspen canopy may be inadequate soil moisture and nutrient levels (Groot 1999), though light and moisture may be correlated. Other studies report top damage to spruce from whipping by adjacent aspen trees (e.g. Lees 1966, Steneker 1967). The relationship between aspen competition and spruce growth is complex. It varies with age and is site specific, particularly in stands that are less than 20 years of age (Filipescu and Comeau 2007).

Several studies of a long-term control – release trial have shown increases in spruce growth after the removal of aspen overstorey. For instance, Steneker (1967) stated that the height increment of spruce in physical contact with the aspen crowns can be doubled by release. Yang (1989) reported that such a release treatment increased the spruce height growth in all classes by an average of 42% after 30 years. Generally, white spruce responds to release at all ages, with 30-60 year old trees having the greatest ability to increase growth for a given degree of release (Steneker 1967, Yang 1989, Delong 1997).

The increasing demand for aspen in recent years due to new pulp and oriented-strand board industries makes it desirable to manage these forests for both conifer and broadleaf species and also makes release cutting valuable. Mixed species forests are now being recognized as beneficial for biodiversity and landscape integrity (CCFM 2003). Previous research has illustrated that mixtures of conifers and broadleaf species can be more productive than pure stands (Man and Lieffers 1999: Comeau et al. 2005) and that reasonably good conifer growth can be maintained in intimate mixtures if steps are taken to limit broadleaf competition (Simard and Hannam 2000).

Site Index (SI)

Under current guidelines for sustainable forest management (e.g. ASRD 2006) we need to be able to reliably predict the long term growth and yield of these forests. A large step in this direction could be made by improving our ability to predict tree height growth and site index for mixedwood and pure species stands in order to be able to quantify changes in productivity following release cutting.

Site quality is often expressed by an index related to the productivity of the land (Clutter et al. 1983, Vanclay, 1994). Assessment of site quality can be made by a number of methods. Wood production may be the best indicator of site productivity for forest management purposes. For example, regulations in Alberta use maximum mean annual increment (MAI) (=volume/age) as a productivity measure for regenerated cutblocks (ASRD 2006). However, volume production is difficult to measure and is affected by stand density and stand treatment (Vanclay 1994). A more convenient way which is easier to measure and unaffected by stand density is the use of site index.

Site index is a measure of stand height at a reference age and is based on the relationship between tree height and age (Husch et al. 2003). This measure provides a useful estimate of site productivity in fully stocked, even-aged stands because height growth is closely correlated to the ultimate measure – volume. Height of the upper canopy is a measurable quantity in stereo aerial forest inventories, and is usually the best predictor of stand volume. In ground surveys, height and age can be determined quickly and easily, and height growth of dominant and co-dominant trees usually is not greatly influenced by stand density and stand treatment (Lanner 1985, Husch et al. 2003). Davis et al. (2001) suggest that this measure appears to be the most practical, consistent and useful indicator of site quality. However, in uneven-aged stands, height in relation to age cannot be used to express site quality (Husch et al. 2003). It can also be difficult to determine site index in very young or very old stands (BC Ministry of Forest and Range 2008).

The age at breast height (1.3m) is generally used as the reference age in most site index work. Husch (1956) listed several advantages of using age at breast height rather than total age: it measures tree age after the initial period of establishment and adjustment has passed, thereby eliminating sources of variation such as herbaceous competition and early erratic growth that occurs before a tree reaches breast height**.** The use of breast height age eliminates the necessity of adding arbitrary corrections to convert age at the increment-boring level to total age. According to Peters et al. (2002), aging of white spruce in mixedwood stands using ring count even at the ground level is not valid, since rings developed during the early years are covered by leaf litter accumulation. These authors found a surprising number of spruce had horizontal stems with several years of rings hidden below the litter layer, caused by aspen snags falling on the regenerating spruce. Suppression of white spruce by the overstorey canopy in mixedwood sites may cause several missing rings in white spruce. Peters et al. (2002) determined that natural origin white spruce take 34 years from germination to reach breast height. Breast height age utilizes a standard and conventional point for age determination. However, for poor sites and slow-growing species, the time to reach breast height may be considerable.

Monserud (1984) suggested that trees selected for site index determination should be the best growing (i.e., most vigorous), dominants, as indicated by increment cores and examination of the crown, with no evidence of early suppression or irregular growth in order to reflect the productivity of the site. However, this can be difficult to determine retrospectively (Nigh 2004). Using Huang's (1997) protocol, the number of site trees required per plot should correspond to the 100 largest diameter (at a breast height of 1.3 m above ground) trees per hectare per species to remove the subjectiveness in determining which is dominant.

Height and age data used for the development of site index curves are generally obtained from three sources: 1) measurement of stand height and age on temporary plots, 2) measurement of height and age over time on Permanent Sample Plots (PSP) and 3) reconstruction of height/age development pattern for individual trees through stem analysis techniques (Clutter et al. 1983). My work will primarily use stem analysis.

Stem Analysis

Stem analysis is a technique that examines the growth rings of sections from a tree trunk. This allows the past growth history of a tree stem to be reconstructed. Stem analysis can be performed on standing or felled trees. On felled trees, the analysis is based on complete stem sectioning (Figure 1.1). For instance, cross sectional discs are cut and removed at the ground level, breast height (1.3m) and at intervals up the tree trunk.

The year of formation of each ring on the disc is obtained by counting towards the pith from the cambium at the junction of the bark and wood (the most recent ring being outermost), for each disc or section, height and age pairs are then recorded for building height vs. age (and site index) models (Philip 1994). According to Carmean (1972), the sectioning will frequently miss the terminal bud itself. To compensate for this, the age of each section is raised by one half year, since on average the section will pass half-way through the annual height increment.

In addition to cross-sectioning, longitudinal sectioning can also be used in stem analysis. With this technique, the site tree is split open longitudinally from the base of the tree to reveal the pith and the pith nodes along the stem. Annual height growth can then be measured exactly at the pith nodes, removing the need for Carmean's correction (Nigh 2004). Longitudinal sectioning is difficult to do since the pith is hard to follow precisely with a power saw.

The stem analysis approach is preferred over other techniques since it provides more information on the height growth characteristics of each of the sample tree, this approach also allows for the estimation of polymorphic height growth patterns (Monserud 1984).

A source of error in stem analysis based curves is due to dominance switching (Magnussen and Penner 1996, Raulier et al. 2003, Feng et al. 2006). Trees may not retain their relative position in the hierarchy of heights throughout the life of the stand. Raulier et al. (2003) found that one out of every five trees is replaced every 10 years in the tree group that was used to estimate dominant height. Feng et al. (2006) found that the height of dominant trees selected at maturity was 14% lower than the actual height of the dominant trees in the stand. These suggest that dominant trees selected for stem analysis may not have been dominant at the early stages of stand development and may even not continue to be dominant. Since dominance may change over time, height - age curves fitted to stem analysis may be biased, i.e., height vs. age curves built from stem analysis data may over-predict the dominant height growth of PSPs. Periodic remeasurement of PSPs can give the exact pattern of change of the stand’s dominant height by taking into consideration the dynamics of tree replacement within the stands dominant stratum. However a disadvantage of using PSP data is that most PSPs in Canada were recently established, therefore data may be inadequate for height - age curve modeling. Obtaining stand growth data in this way is also very time consuming and costly. Furthermore, assessment of relative effects, such as the effect of overtopping hardwoods on spruce height growth, may be less affected by dominance switching, since dominance switching occurs in both pure and mixed stands, these effects likely cancel each other out.

Height vs. Age (Site Index) Equations

For most height based methods of site productivity evaluation, height vs. age and site index equations or curves are developed to allow site classification at any age from a sample of heights and ages taken from top trees. Knowing the height of the top trees and their age, one could locate the position of these coordinates on the site index chart for the given species or stand (e.g. Huang 1997) The closest curves read on the chart would be the site index for the stand (Husch et al. 2003). Alternately, the site index value can be obtained from on a table, or the mathematical height vs. age and site index equation re-arranged to solve for site index. The intent is that this gives an estimate of the height growth trajectory that the stand generally would follow during the rest of its life.

Based on the mathematical form of the height and age curves, these equations are classified into anamorphic, polymorphic-disjoint and polymorphic-nondisjoint curve families. The anamorphic curve family assumes that the height of one curve at any age is constantly proportional to the height of the other curve at the same age. In the polymorphic-disjoint curve family there is no constant proportionality relationship and the curves do not cross within the age range of interest. The curves in the polymorphic-nondisjoint curve family also have no constant proportionality relationship, however some of the curves intersect within the age range of interest (Clutter et al. 1983), which may mean that samples at more than one age are necessary to identify the site index, an undesirable trait.

Height - age curves can be fitted using simple non-linear regression techniques performed on height vs. age values (Cieszewski et al. 1993). Most of the techniques used to develop height - age curves have been grouped into three general methods. These are the guide curve method, the parameter prediction method and the difference equation method (Clutter et al. 1983). The guide curve method is used to develop anamorphic site index equations. Generally, in the guide curve method, the height and age data are derived from the measurement of temporary plots, however data from remeasured plots or stem analysis could also be used (Raulier et al. 2003). To give unbiased height - age equations, the full range of site indices must be well chosen in all age classes.

The parameter prediction method is used mostly to fit polymorphic-disjoint height – age equations. The procedure normally requires data from remeasurement or stem analysis. This method involves the following steps: 1) Fit a curve (linear or non-linear height/age function) to each tree or plot. 2) Use each fitted curve to determine a site index value for each tree or plot and, 3) Relate the parameters of the fitted curves to the site index through linear or nonlinear regression procedures (Clutter et al. 1983). The parameter prediction method has a high potential to model a complicated height growth trajectory, but cannot be used directly with data from short observation periods on permanent plots (Elfving and Kiviste 1997).

The difference equation method of fitting height - age equations also requires tree remeasurement or stem analysis data. This method works for anamorphic or polymorphic curve families. The method involves development of the difference form of the height/age equation being fitted. Height at remeasurement (H_2) is expressed as a function of remeasured age (A_2), initial age measurement (A_1) and initial height measurement (H_1) (Clutter et al. 1983). The expression is obtained through the substitution of one parameter in the growth function. When the asymptote parameter is substituted, this produces anamorphic curves and when any other parameter is substituted this produces polymorphic curves with common asymptote. For example, the modified logistic function (Meng and Huang 2009) as a height – age model assumes the existence of a family of curves defined as (Equation 1.1):

$$Ht = \frac{b_1}{1+e^{[b_2+b_3 \ln{(A+1)}]}} \tag{1.1}$$

Where b_1 is unique for each individual height – age curve, with initial measurement data (A_1, H_1) and re-measurement data (A_2, H_2) for a tree or plot. These two points are hypothesized to lie on the same curve and so have the same value for b_1. Since the initial measurement point lies on the curve,

$$Ht_1 = \frac{b_1}{1+e^{[b_2+b_3 \ln(A_1+1)]}} \tag{1.2}$$

Rearranging,

$$b_1 = Ht_1\left[1 + e^{[b_2+b_3 \ln(A_1+1)]}\right] \tag{1.3}$$

The second measurement point lies on the same curve,

$$Ht_2 = \frac{b_1}{1+e^{[b_2+b_3 \ln(A_2+1)]}} \tag{1.4}$$

so

$$b_1 = Ht_2\left[1 + e^{[b_2+b_3 \ln(A_2+1)]}\right] \tag{1.5}$$

Since the right hand side of the equations 1.3 and 1.5 are both equal to b_1 they can then be equated to give

$$Ht_2\left[1 + e^{[b_2+b_3 \ln(A_2+1)]}\right] = Ht_1\left[1 + e^{[b_2+b_3 \ln(A_1+1)]}\right] \tag{1.6}$$

Which, rearranged gives the differenced form of the height – age equation (Equation 1.7)

$$Ht_2 = Ht_1\left[\frac{1+e^{[b_2+b_3 \ln(A_1+1)]}}{1+e^{[b_2+b_3 \ln(A_2+1)]}}\right] \tag{1.7}$$

Also, substituting the index age (50) for A_2 and site index (SI) for H_2, we can use the difference equation to make SI an explicit predictor in the height –age equation (Equation 1.8),

$$Ht_1 = SI\left[\frac{1+e^{[b_2+b_3 \ln(50+1)]}}{1+e^{[b_2+b_3 \ln(A_1+1)]}}\right] \tag{1.8}$$

This demonstrates differencing for a total age – based model. If the age is expressed as breast height age (BHage: ring count at 1.3m), as I did in this thesis, 1.3m is subtracted from the height and site index, then 1.3m added to each side of the equation so that height only is on the left hand side as shown below.

$$Ht_1 = 1.3 + (SI - 1.3) \times \left[\frac{1+e^{[b_2+b_3 \ln(50+1)]}}{1+e^{[b_2+b_3 \ln(A_1+1)]}}\right] \quad (1.9)$$

The difference equation method can be used effectively with data obtained from short observation periods. This method also produces base-age invariant results (Elfving and Kiviste 1997). However with complex height age models, formulating the difference equation is difficult.

Many equations are fit using parameter prediction as it is flexible and straightforward. A differenced form of the model is then built so that site index can be entered directly into the model (i.e. height at reference age, Equation 1.8).

Site Index-Ecological Site Classification (SIBEC)

SIBEC is a comprehensive tool that is used in B.C. to correlate site index with site series within biogeoclimatic ecosystem classification (BEC) units. The technique combines geology, vegetation and climate to classify any site into an ecosystem then assigns a typical site index value for common species in this ecosystem (BC Ministry of Forest and Range 2008). Since both tree growth and plant community characteristics are influenced by various site factors such as climate (light, temperature and precipitation) and soil (moisture, nutrients, and aeration), ecological site classification may be useful in estimating potential productivity. For instance, Wang and Klinka (1996) used soil factors and climate as ecological measures of site quality and found that soil moisture, aeration and nutrient regime have equal importance in affecting white spruce growth, although the role of each as a growth-limiting factor may vary from site to site. According to Mah and Nigh (2003), the SIBEC model is best used for stands where conventional methods (site index curves and growth intercept models) cannot be applied reliably, for instance, in old-growth or very young stands, or in cases where a tree species has not remained dominant in the stand throughout its life (as in boreal mixedwood stands).

A similar system exists in Alberta and Saskatchewan. The ecosite guides (Beckingham et al. 1996a, b, c), give an estimate of site index of common species found in each ecosite. A problem is that ecosites in Alberta often encompass a wide range of edatopes, or nutrient-moisture classes and consequently it may be desirable to develop typical site index values by edatopes.

Also in Alberta, Monserud et al. (2006) related climatic parameters to site productivity for lodgepole pine, and found that the strongest predictors of site index are all measures of heat: the Julian date when GDD5 reaches 100, growing degree days>5^{0}C, and July mean temperature. In his study, measures of precipitation or winter temperatures were essentially uncorrelated with site index.

Ung et al. (2001) linked site index to biophysical parameters. This biophysical or ecosite approach is desirable for dealing with climate change if we could map how these factors change on the landscape. However, the accuracy of biophysical methods of estimating productivity appears to be low, when site index is used as the independent variable in these studies. However, it might be argued that site index may be just as variable and may not be a perfect measure of site productivity.

Height vs. Age (Site index) Conversion Equations

Height - age conversion equations are used for estimating the site index of one species from the site index of another species. According to Clutter et al. (1983), the use of this method depends on the knowledge of the relationship between certain growth patterns of the species of interest and growth patterns of the species available for measurement. This technique is applicable when the species of interest is not present on the land area under study or when good site trees are not available for a species (Nigh 2002). This may be the case in spruce/ aspen stands where spruce grows in the understorey of aspen and are suppressed early in its life (Lieffers et al. 1996). In such a situation, measurement made on aspen can be used to estimate the site index for spruce. Unfortunately, this technique has been developed in mixedwoods using the suppressed spruce site index values from mixedwood stands. The height - age conversion equations (1.10 or 1.11) below can be used to predict the site index of white spruce from aspen and vice versa, in mixed white spruce and aspen stands (Nigh 2002)

$$SI_{SW} = 3.804 + 0.7978 \times SI_{AW}. \quad (1.10)$$

$$SI_{AW} = -4.768 + 1.253 \times SI_{SW} \quad (1.11)$$

Where SI_{Sw} = White spruce site index
SI_{Aw}= Aspen site index

Hostin and Titus (1996) performed a similarly study in Alberta. They found spruce predictions from aspen site index alone were not very precise (RMSE = 2.3m, R^2 = 0.09). However the inclusion of various stand and site attributes improved the model.

The Growth Intercept (GI)

This technique estimates site index from the average annual height growth of young site trees, which is determined from the length of a specified number of successive annual internodes, beginning at some well-defined point on the stem, normally the first node above breast height (Nigh 2004).

It is generally believed (BC Ministry of Forest and Range 2008) that for young stands (5-50), growth intercept values provide just as much information on site quality as site index values, but site index values are useful for growth models while, growth intercepts are not. This method may yield high estimates of site index in managed stands (Nigh 2004) since the early height growth of trees above breast height in managed stands may be better and result in high site index estimates.

Site Form (Height-Diameter Relationship)

In uneven-aged stands where site index cannot be used to determine site productivity, the height at a nominated index diameter can be used as a measure of site productivity; this is called the site form (Vanclay 1994). Stout and Shunway (1982) found that the height and diameter relation provided an appropriate site measure. Huang and Titus (1993) used the relationship between tree height and diameter at breast height of dominant and co-dominant trees to measure site productivity for white spruce in mixed species stands and concluded that the measure has many logical properties similar to those of conventional site index, producing curves that are polymorphic and reference diameter invariant. They suggest that the height at a nominated diameter can be used as a simple and quick measure of quantifying site productivity for both uneven aged and mixed species stands. However, site productivity curves developed using this method will be affected by many other factors, since stem diameter is strongly influenced by stand density and wind sway (Lanner 1985, Meng et al. 2008).

Site Index in Mixedwoods

A major limitation to most mixedwood permanent sample plot (PSP) and retrospective sampling programs is that the "true" site index for white spruce cannot be estimated. Spruce is usually shaded by taller species and does not meet the ‘‘top’’tree criteria used to assess site index. Huang (1997) and Cieszewski et al. (1993) developed height - age curves for white spruce using stem analysis data from trees regarded as true top height trees (i.e. the thickest or largest 100 trees per hectare with no overtopping, competitors or damage). However it is difficult to determine if these trees were consistently dominant and free of inter-specific competition during their development. Studies have shown that white spruce is nearly always overtopped by aspen until late in natural stand development (Lieffers et al. 1996). According to Groot (1999) the aspen overstorey reduces the amount of light reaching the understorey spruce to a level below that needed for optimum growth (Lieffers and Stadt 1994). It is possible that a mature white spruce tree currently free of competition might have been overtopped by aspen during the early stages of its development. Selecting a white spruce tree which has always been competition free is therefore difficult. The current practice is to ignore inter-specific competition in the determination of site index for white spruce. Such site index estimates are better regarded as the "apparent site index" estimate and may not be suitable for applications in which the true site index estimates are required. Even "apparent" site index may have limited use due to uncertainty regarding intensities and effects of competition on spruce height development.

In two studies, one initiated in 1936, another in 1951 to 1954, the Canadian Forest Service conducted an aspen removal treatment in the mixedwood region of central Saskatchewan and western Manitoba (Yang 1989). These stands had aspen stump ages ranging from 25 to 60 years with white spruce irregularly dispersed among the aspen. At each of the sites, except the 1936 one, control and full aspen removal treatment were conducted in 0.1 ha plots. One site had an additional partial release treatment, and the 1936 site had a mixedwood control, a light and a heavy partial aspen removal. These stands were re-measured approximately 5, 10, 35 and 50 years later. The stands had 25-60 years of early growth as a mixedwood and now have a similar or longer period where mixedwood and spruce stand development can be compared.

These measurements provide an opportunity and data for quantifying potential gains in site index for released white spruce stands compared to white spruce in mixedwood stands. These stands and re-measurements formed the basis for my thesis.

Conventional forest growth modeling techniques are generally designed to predict the growth and yield of single species. Mixed species forests have been simulated as separate, single species stands, without considering species interactions (e.g. BC Ministry of Forests and Range 2002), though this is not what actually happens in these forests. My study develops some simple techniques to deal with species interactions in mixtures, specifically the effect of broadleaf species on white spruce height growth and site index.

Thesis Overview

This study seeks to evaluate the effect of aspen competition on very long-term (>50 years) white spruce height growth trajectories.

The growth rate of trees above breast height (1.3 m) is a good reflection of the potential productivity of the site. Davis et al. (2001) stated that site index appears to be the most practical, consistent and useful measure of site productivity. It therefore seems appropriate to employ site index to determine any potential gains in spruce retention stands versus mixed species stands.

This thesis has been divided into the four chapters. The current chapter gives a background to the study. Chapter two examines the effect of hardwood removal on white spruce height growth and site index: 1) the height growth trajectory of the top spruce in released stands will be steeper and smoother than that in mixedwood stands, 2) on the same site, the site index of the released stands will be greater than the site index of mixedwood. However since the treatment was applied later than is the practice now, potential site index gain due to early release (stand age <10 years) might be better estimated by the height increase due to release 50 years after treatment, 3) also there is a different shape to the height vs. age curve as a result of the release treatment, more specifically that the existing height vs. age curves developed for white spruce in Alberta and Saskatchewan (Cieszewski et al. 1993, Huang 1997, Huang et al. 2009) will not fit my data, particularly for the release trees. If this is true then an alternate site index curve will be fit. 4) To examine the effects of dominance switching, I examined the "dominant" (actually the thickest or largest 100 spruce per hectare) tree height growth trajectories of white spruce in the sporadic remeasurements of the permanent sample plots vs. the height growth trajectories through stem analysis.
Chapter three quantifies the effect of the amount of broadleaf competition on the degree of release of the dominant white spruce. Deciduous basal area was

evaluated as a readily determined index of deciduous competition. It was based on the assumption that amount of deciduous competition (basal area) can account for differences in height increment between release and control spruce. See APPENDIX 6 for flow charts of my research steps in Chapters 2 and 3.

Chapter four provides a synthesis of my results and suggestions for future research.

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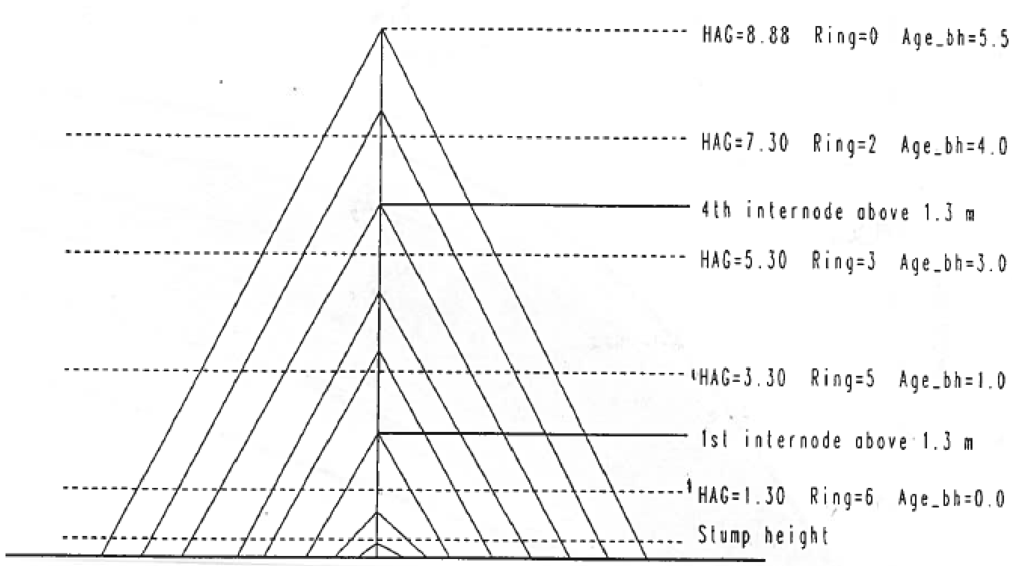

Figure 1-1: An illustration of stem analysis. Dashed lines represent potential sectioning points; diagonal lines represent tree growth rings (Huang 1997).

Chapter 2. Effect of Hardwood Removal on White Spruce Height Growth and Site Index

Introduction

Upland forests in the western boreal region are commonly a mixture of trembling aspen (*Populus tremuloides* Michx) and white spruce (*Picea glauca* [Moench] Voss) although black spruce (*Picea mariana* (Mill. BSP.), lodgepole pine ((*Pinus contorta* Dougl. ex. Loud.), jack pine (*Pinus banksiana* Lamb.), balsam poplar (*Populus balsamifera* L.), white birch (*Betula papyrifera* Marsh.), and balsam fir (*Abies balsamea* (L.) Mill.) also occur (Strong and Leggat 1992). Following disturbances such as fire, wind or harvest, fast-growing aspen dominate the canopy until later in natural stand development (Lieffers et al. 1996). Generally white spruce is overtopped by aspen for the first 90 years and competition for light and other resources such as physical space between these species may occur. In a study by Filipescu and Comeau (2007), reductions in light and other resources by aspen led to reductions in the height and diameter growth of white spruce. Top damage (physical abrasion) to spruce from whipping by adjacent aspen trees has also been reported (Lees 1966, Steneker 1967).

Studies have shown that white spruce growth eventually increases after the removal of aspen overstorey. Juvenile stands (<15-20 years) show little growth release (Bokalo et al. 2007, Lieffers et al. 2007). In a longer-term study, spanning 30 years in mid-aged stands, Yang (1989) reported that such a release treatment increased white spruce height growth in all classes by an average of 42%. An earlier report on the same study, noted that physical contact of the spruce with the aspen crowns may be responsible, spruce growth might be doubled by release from contact (Steneker 1967).

Forest growth models typically use height growth vs. age (site index) of dominant trees as a productivity measure (Cieszewski et al. 1993, Huang 1997, Bokalo et al. 2007, Huang et al. 2009). Potential wood volume production, such as maximum mean annual increment, may be the desired indicator of site productivity (ASRD 2006), but it is difficult to measure and is easily affected by stand density and stand treatment (Vanclay 1994). A more convenient and reliable way to estimate site productivity is with the use of site index (Davis and Johnson 2001). Husch et al. (2003) and Lanner (1985) stated that this measure provides a good estimate of site productivity in fully stocked, even-aged stands because height growth is closely correlated to the ultimate measure – volume. Height and age can be determined quickly and easily, and height growth of dominant and co-dominant trees usually is not greatly influenced by stand density and stand treatment. Since it can be estimated from stereo photos, height of the canopy is also a useful variable in forest inventories.

Height-age curves developed for white spruce (Cieszewski et al. 1993, Huang 1997, Huang et al. 2009) have largely ignored the effects of inter-specific competition that occurs between spruce and overtopping aspen. However it is difficult to determine if these trees were consistently dominant and free of inter-specific competition during their development. It is possible that a mature white spruce tree currently free of competition might have been overtopped by aspen during the early stages of its development (Nigh 2004). Current spruce site index estimates are better regarded as the “apparent” site index and not the potential in pure stands.

This problem is important in managed forests, as industry is taking considerable effort to grow pure spruce stands on former mixedwood sites. The benefits of such efforts are not yet clear (Pitt et al. 2004, Lieffers et al. 2008). To help resolve the effects of hardwood competition on white spruce site index I examined long-term height growth vs. age data for white spruce released from aspen canopy in the historic Canadian Forestry Service MS8 & MS153 trials.

These studies were conducted by the Canadian Forest Service in 1936 (MS-8) and 1951 to 1954 (MS-153) in the mixedwood region of Saskatchewan and western Manitoba (Yang 1989). At each of the sites, except the MS-8 study at Duck Mountain, control and full aspen removal treatments were conducted in 0.1 ha plots. One site (Reserve) had an additional partial (50% broadleaf) release treatment, and the Duck Mountain site had control, light (44% hardwood basal area removal) and heavy (60% hardwood basal area removal) treatments. Permanent sample plots 0.04 ha in size (0.1 ha in Duck Mountain), were established at the time of treatment and re-measured approximately 5, 10, 35 and 50 years later. The stands had 20-60 years of early growth as a mixedwood (pre-treatment) followed by a similar or longer period where mixedwood and pure spruce development can be compared. From these re-measurements and the stem analysis work outlined here, I can quantify potential gains in site index for released white spruce stands compared to white spruce in mixedwoods.

Methods

The Study Areas

For this study I used experimental sites established by the Canadian Forest Service as studies MS-8 and MS-153. MS-8 was established in 1936 in a 50-year stand in the Duck Mountain (DM) Forest Reserve in Manitoba while MS-153 was established in 1951-54 in 20 to 60 year old stands at Big River (BR), Big River Nursery (BRN), Montreal Lake (ML), Candle Lake (CL) (2 blocks), Bertwell (BE) and Reserve (RE) in Saskatchewan and at Riding Mountain (RM) (2 blocks) in western Manitoba (Figure 2.1) (Yang 1989). For this study, Big River Nursery, Montreal Lake and Bertwell were excluded. These stands were lost due to fire and human disturbances such as logging, construction of roads and pipelines. No trees were felled for stem analysis at the light release plot at Duck Mountain due to a lack of time; however the permanent sample plots were re-measured.

The MS-8 stand at Duck Mountain is situated on a southwest slope which is typical of the rolling uplands in the B.18a Mixedwood forest section (Rowe 1972). Clay-loam till forms the parent material of the soils here and sites vary from moderately fresh to moist. The stand was composed mainly of white spruce and aspen which formed about 80% of the pretreatment stand and originated from a fire in the late 1880s. Jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea mariana* (Mill.) BSP.), and a few balsam popular (*Populus balsamifera* L.) and white birch (*Betula papyrifera* Marsh.) were also present (Yang 1989).

MS-153 consists of stands which differ widely in density and basal area (Table 2.2) but the ecosite classifications were similar (Table 2.3). The topography is flat to rolling and the soils are well drained varying from silty clay loams to clay loams. As Table 2.3 indicates, Riding Mountain and Duck Mountain are cooler than the other locations and have a lower heat sum. All stands originated from fire and were typical of mixedwood conditions. The stand at Duck Mountain was the oldest, followed by Reserve. Riding Mountain was the youngest stand. Generally the hardwood overstorey had a stump age 20-30 years older than the spruce understorey (Table 2.1), though this may be partly due to missing below-ground rings (Peters et al. 2002). White spruce were irregularly distributed and the neighborhood growing conditions of the individual spruce varied from completely suppressed to relatively free-growing (Steneker 1967).

Treatments

The following treatments were carried out in MS-8 (1936) and MS-153 (1951-1954) study.

Two 0.10 ha plots plus some unspecified buffer area were subject to light and heavy release cutting at the Duck Mountain stand (MS-8). Trees competing with or overtopping white spruce were removed. Most of the trees removed were aspen and jack pine with a small number of white and black spruce in the lower diameter class also removed. Pre- release basal areas were 39.3 m^2ha^{-1} (control), 40.9 m^2ha^{-1} (light release stand) and 42.0 m^2ha^{-1} (heavy release stand). The light release removed 44% of the basal area and the heavy cutting removed 60% of the total basal area. White spruce age was 50 at stump height at the time of treatment (Yang 1989). The permanent sample plots in MS-8 were 0.10 ha (21m × 45m).

For stands in MS-153, square 0.04 ha (20m × 20m) permanent sample plots were installed within the selected stands. All trees other than white spruce were removed on the treated plots including a 9m surrounding buffer. Reserve had an additional partial release treatment, where 50% of the aspen were removed by systematically cutting every other stem.

Permanent Sample Plot Measurement

White spruce trees in permanent sample plots (PSPs) at all locations were tagged and mapped at establishment. Ring counts of increment cores taken at stump height (0.3m) were used to establish the age of the aspen and spruce in all stands except Duck Mountain where only white spruce age was determined. Trees were measured for diameter at breast height at the time of establishment and then re-measured approximately 5, 10, 35, 50 and 60 years later. A subsample of trees had their heights measured. In addition, a damage assessment (e.g., broken tops, dead, disease, stem lean, etc.) was conducted at establishment and subsequent re-measurement.

Tree Selection (2010)

In this study, two dominant (thickest DBH) white spruce trees were selected within a 200 m^2 area (a 9 × 22.2 m rectangle) in the buffer surrounding each plot. Trees were usually chosen at the north of the 0.04 ha PSP within each control and aspen removal treatment unit, as shade from uncut edges is minimized at the north edge of the treated area. The selected trees were intended to represent the best "site" spruce trees, sampled at a rate of 100/ha, for typical site productivity assessment (Huang 1997). This gives some assurance that the height growth of the selected trees above breast height is an indication of the potential productivity of the site (Nigh 2004).

Variables Measured

The selected trees were measured for diameter at breast height (DBH) and total height. DBH was measured at 1.3m above ground using a diameter tape. To determine breast height, leaf litter accumulations and woody debris on the forest floor were removed down to the mineral soil since white spruce in mixedwood site may have some of its early first height growth buried by these layers (Peters et al. 2002). DBH was measured prior to felling. Total height (m) of all felled trees was obtained using a tape measure along the bole from the breast height mark to the uppermost terminal bud or bud scar (plus the 1.3m to breast height). Height growth during 2010 was ignored since, for most sites, it was incomplete at the time of sampling. Total height was measured after delimbing and prior to sectioning.

Stem Analysis

A total of 36 trees were felled; half in mixedwood control areas and half in aspen removal (release) areas: 8 trees in Riding Mountain block 1 and 2, 4 in Big River, 12 trees in the Candle Lake installations 1 and 2, 8 in Reserve and 4 in Duck Mountain. These trees were felled away from the plots to minimize plot damage. Felled trees were then serially sectioned, that is, removing a 10cm disk at 0.3 m, 1.3 m (above ground) and every meter up the stem to the tip.

Laboratory Analysis

In the laboratory the stem disks, 749 in total, were placed in a 70ºC fan-circulated oven and dried to a stable weight (approximately one week). The sections were then sanded progressively to 220-grit with a table and an orbital sander. Rings were counted manually along two radii, at least 45 degrees apart and avoiding knots, of each section to ensure accurate ageing. When necessary, a microscope was used to distinguish fine rings.

Breast Height Age

Breast height age (BHage) (from ring count of each disk) was determined for each height or disk with age at 1.3m being considered as BHage zero. Height and age data pairs obtained from stem analysis may be biased if, for example, the height of the disk is taken as the tree height for the corresponding tree age (Carmean 1972). Since on average, the section will pass half-way through the annual height increment, the age of each section was raised by one half year (Huang 1997). Height and breast height age data pairs were then plotted to demonstrate the height growth pattern of each spruce in both mixedwood and hardwood removal stands. Since there was wide variation in age at 1.3m within sites, height was also plotted against calendar year to assist with interpretation of these results.

Site Index

Height vs. BHage is typically used for building site curves. For this study site index was defined as the average height at BHage 50 of the two thickest diameter trees per 200 m^2 plot. Since few trees had sections precisely at the height at which the tree reached BHage 50, site indices were determined by linear interpolation. The average increase in site index at each location and the overall percentage increase in site index was determined and compared using a mixed model (SAS PROC MIXED, Sas Institute 2009).

Height Difference 50 Years After Treatment

Since the release treatments occurred later (25-60 years) in stand development, the early height growth of the spruce may have been suppressed and the potential release in site index underestimated . Therefore, similar to determining site index as the height at BHage 50 years, height growth differences 50 years after treatment were determined for each tree in each plot, block and location. This value was determined by subtracting the linearly interpolated height at the treatment year from the interpolated height 50 years after the treatment year. The average height growth difference for each plot and location was calculated and the overall relative release was also determined and compared using a mixed model.

Existing Height-Age Curves

I found three existing height-age curves for spruce in this region: 1) the Saskatchewan white spruce height - age equation developed by Cieszewski et al. (1993), 2) the Alberta height - age equation for white spruce in the central mixedwood region (Huang 1997), and 3) the recent 2009 GYPSY white spruce height - age model (Huang et al. 2009). Due to difficulty in fitting some of these equations as a non-linear mixed model (see autocorrelation analysis below), a simpler logistic function, used for lodgepole pine by Meng and Huang (2009), was also fit to my stem analysis data. All of these functions are expressed in the general form:

$$H_{ij} = 1.3 + f\,(A_{ij}) + e_{ij} \tag{2.1}$$

Where H is the height (m) of the disk j of tree i with breast height age A_{ij} (years), and e_{ij} is the residual error associated with tree i, disk j.

These height - age curves were compared using the average bias ($B = \Sigma_{ij}^{ni,\ nij}\ e_{ij}/N$, where ni is the number of trees, nij is the number of disks in tree i, and N is the total number of disks collected in all trees), the standard error of the bias (bias SE $= \{\Sigma_{ij}^{ni,\ nij}\ (e_{ij} - B)^2/[N(N-1)]\}^{1/2}$), and the coefficient of determination which was calculated as a goodness of fit index by squaring the Pearson correlation coefficient between predicted and observed data. Height – age curves are designed to yield the correct tree site index value at the reference age, so bias below and bias above BHage 50 were also determined to indicate how well the model fit at younger and older ages. For the existing height and age equations, published parameters were used. I fit my own parameters to the Meng and Huang (2009) equation (Equation 2.2) by allowing the asymptote parameter b_1 to vary by tree as a mixed effect, using the SAS NLINMIX macro (Littel et al. 2006). This accounted for differences in site index, as b_1 is the parameter typically differenced out in this equation (Clutter et al. 1983) and replaced with the site index value

(Equation 2.4). I also investigated fitting the Meng and Huang (2009) equation using the difference equation approach (i.e. all possible pairs of heights and ages), but obtained similar results.

$$Ht = \frac{b_1}{1+e^{[b_2+b_3 ln\,(A+1)]}} \qquad (2.2)$$

Autocorrelation

Since the stem analysis data used in this study were repeated measurements within each tree, it was necessary to account for autocorrelation in the analysis for the final equation chosen. Autocorrelation adjusts the variance structure so that any statistical inference (e.g. significance of the parameters, including treatment ones) is done properly I used a non-linear mixed model for this purpose. For a given tree, sections that are close to each other are more closely correlated in their height than sections that are further apart. And, the height – age correspondence of sections from a particular tree are more correlated than this pattern among different trees since some trees and some sites have faster growth than others. To capture this pattern of correlation between any two sections (i and j) within a tree, I used the model:

$$\rho_{\text{secij}} = \rho^{|\text{sec i} - \text{sec j}|} \qquad (2.3)$$

Where ρ is an autoregressive parameter assumed to satisfy $|\rho| < 1$ and i and j are section numbers (sequentially increasing from the base of the tree). I used section numbers instead of section ages as Meng and Huang (2009) did, since I had difficulty converging the model using age differences. Using this power function of section numbers estimated the pattern of the variance structure, which is the goal of modeling the variance. The NLINMIX macro (Littel et al. 2006) in SAS was used to fit the height age equation. Since this macro is difficult to implement, an example of the code used is given in APPENDIX 2.

Treatment Response in the Height – age Equations

The equation considered in this study to model the treatment response was the differenced form of the modified logistic function presented by Meng and Huang 2009 which is expressed as:

$$Ht = 1.3 + (SI - 1.3) \times \left[\frac{1+exp[\, b_2+b_3\, ln(50+1)]}{1+exp[b_2+b_3\, ln(A+1)]}\right] \tag{2.4}$$

Where *Ht* and *A* are respectively the height and breast height age of the top trees, *SI* is the site index, and b_2 and b_3 are the shape parameters.

For modeling the height vs. age trajectory of the top spruce from BHage 1 to maturity under various SI values, Equation 2.4 would be sufficient. However, the treatment was applied later in this study, so the spruce grew under two different height – age regimes, the pre-treatment mixedwood regime (lower SI), and the post-treatment released regime (potentially higher SI). However, switching to a second SI value at the time of treatment would cause a sudden jump in the height – age curve, representing the change to the height at this age that a higher SI would suggest. Since a tree released later in stand development cannot regain the growth it would have had under a higher SI from BHage 1, and since the height growth rate after release should be higher, I developed a height –age curve which allows a switch to a higher SI but subtracts the height difference which cannot be regained. The treatment equation was derived from Equation 2.4 above, by taking the difference between the old and new SI curves at the time treatment is done, then subtracting this from the treated tree curve as shown below:

$$Ht = 1.3 + (SI - 1.3 + tmt * t_1)\left(\frac{b_4}{b_5}\right) - \left[1.3 + (SI - 1.3 + tmt * t_1)\left(\frac{b_4}{b_6}\right) - \left\{1.3 + (SI - 1.3\left(\frac{b_7}{b_8}\right)\right\}\right]$$

$$b_4 = 1 + \exp[\,(b_2 + \ tmt * t_2) + (b_3 + \ tmt * t_3)\ln(50 + 1)]$$

$$b_5 = 1 + \exp[\,(b_2 + \ tmt * t_2) + (b_3 + \ tmt * t_3)\ln(A + 1)]$$

$$b_6 = 1 + \exp[\,(b_2 + \ tmt * t_2) + (b_3 + \ tmt * t_3)\ln(B + 1)]$$

$$b_7 = 1 + exp[b_2 + b_3 ln(50 + 1)]$$

$$b_8 = 1 + exp[b_2 + b_3 ln(B + 1)]$$

(2.5)

Where SI is the site index of the control trees (averaged for each location), A is the breast height age, B is the age at breast height at which each treated tree was released, b_2, and b_3 are shape parameters, and t_1, t_2 and t_3 are treatment parameters which modify SI, b_2, and b_3 respectively. The variable *tmt* indicates a release treatment: if $A>B$ and the treatment was not control, $tmt = 1$, otherwise $tmt = 0$. Simplifying the above equation yields:

$$Ht = 1.3 + (SI - 1.3 + tmt * t_1) * b_4\left(\frac{1}{b_5} - \frac{1}{b_6}\right) + (SI - 1.3)\left(\frac{b_7}{b_8}\right)$$

(2.6)

Where all variables and parameters are as defined above.

In competition studies, the competition-free height is usually used as the maximum value, then competition reduces the response (here it is height). Ideally I would use the released plot SI value as a maximum, since released SI is closer to the “true” unsuppressed spruce site index, but in this case the treatment was applied late so the true SI is not known. Also, mixedwood site index values are currently the ones which are used throughout the region. Therefore, the treatment response in terms of SI increase (parameter t_1) is expected to be positive when trees are released.

A null model (Equation 2.4) with control site index and the shape parameters (b_2, b_3) only was fit first using the NLINMIX macro with autocorrelation modeled as noted above. Since I expected the slope of the height – age curve to increase due to release, the first place I looked was for an increase in SI (which strongly controls the overall slope of Equation 2.4) via a positive parameter t_1. Secondly, I looked for a change in the shape of the height – age curve (parameters b_2 and b_3), via adjustments to t_2 and t_3). I tested combinations of the treatment parameters (t_1 only, t_1 *and* t_2, t_1 *and* t_3, t_1, t_2 and t_3) for significance by examining their t-statistic with the level of significance defined at 0.05. Treatment models were compared among themselves and with the null model (no treatment effect).

Permanent Sample Plot (PSP) Top Height

An assessment of the "top" height (the four thickest or largest dbh white spruce trees per plot of 400 m^2) for each of the re-measurement times: 1951-1954, 1956-1959, 1961-1964, 1985, 2001 and 2010 was done. Damage was considered in this analysis, that is, all trees with broken tops, forks, multiple leaders, crooks, overtopped, unhealthy, leaning etc were excluded. The mean top height was determined for each plot and compared to stem analysis data. This could only be done for only four locations: Riding Mountain, Big River, Candle Lake and Reserve, due to sparse historical data at Duck Mountain.

Results

Changes in Height Growth Trajectories and Site Index in Control vs. Release Stands

Following hardwood removal in 1936 at Duck Mountain, and 1951-1954 for the other sites, the height vs. age trajectory of the released spruce did appear steeper and smoother than that of the control trees (Figs. 2.2 - 2.6). Candle Lake Block 1 was the only exception, as there was very little difference between control and release trajectory here.

There was wide variation in the calendar year when spruce reached breast height, and these initial differences persisted for several decades (Figs. 2.2-2.6). However, the height increments (slope of the height vs. age relationship) were generally similar for all trees prior to treatment. Following treatment, the control trees either grew very little (Riding Mountain (RM) Block 2, Candle Lake (CL) Block 2) then increased in later years, or showed the opposite pattern of initially strong growth and later suppression (RM Block 1, Big River (BR), Duck Mountain (DM), Reserve (RE)). For released trees the general trend was for increased growth.

In some sites, release occurred only a few years before the reference breast height age (BHage) of 50, so the overall increase in site index in the released stands was a relatively low 6%, and varied considerably with location from -19% to 45% (Fig. 2.7, Table 2.4). The mixed model analysis of SI values indicated firstly that we could consider the two blocks within the RM and CL locations as separate "locations" since a likelihood ratio test (LRT) indicated no significant change in model fit by nesting the blocks within locations vs. considering them as distinct locations. Secondly, the test of significance ($p < 0.05$) on the SI of the control and release trees showed that treatment did not significantly explain the overall differences in SI (p= 0.181) (Table 2.5).

The difference in height growth 50 years after treatment was therefore examined. Height growth in the 50 years following treatment showed an average 22% or 2.1m increase over control (Fig. 2.8, Table 2.6). RM recorded the highest relative height growth release (50%), followed by DM (41%), RE (15%), CL (4%) and BR (-0.02%) (Table 2.6). The overall relative height growth release was 22%. LRT analysis again supported the inclusion of the RM and CL blocks as separate sites rather than nested blocks. Tests of the treatment effect showed that the height growth was significantly higher for released spruce (p=0.016, Table 2.7).

Existing Height – Age Equations Fit

Three existing equations for white spruce from the western mixedwood boreal were evaluated, using the site index values averaged among the trees within each treatment group (control, release). The four parameter equation developed by Huang (1997), using white spruce stem analysis data collected in the central mixedwood region of Alberta, fitted my stem analysis data best (Table 2.8). R^2 was high, at 0.969, the bias standard error was the lowest (1.144m), this equation had the least overall mean bias of 0.029, and biases below and above breast height age 50 were also the lowest. The unpublished two parameter model by Cieszewski et al. (1993), developed from Saskatchewan data, had the second-lowest mean bias. However it considerably overestimated height for young trees (<BHage 50), and underestimated height for older trees (≥BHage 50). The four parameter GYPSY 2009 model (Huang et al. 2009), developed using data from permanent sample plots in Alberta, had the highest bias standard error (1.46) and highest overall mean bias.

I had considerable difficulty refitting the apparently best four-parameter Huang (1997) equation as a nonlinear mixed model, to allow proper accounting for the autocorrelation in my stem analysis data. I therefore tried the simpler logistic-type function used by Meng and Huang (2009) for lodgepole pine. I fit this to my stem analysis data using a nonlinear mixed model (see Methods) and found the second-lowest bias in young and old trees and the third-lowest bias standard error. R^2 was lowest for this model however.

Treatment Height - Age Curve vs. Control Height Age Curve

For modeling the height response of trees, I selected the Meng and Huang (2009) height – age function due to its simplicity (two parameters plus site index in the differenced form (Equation 2.4) and reasonable fit (Table 2.8). This equation could also be readily fit using the SAS NLINMIX macro (Littel et al. 2006) to account for autocorrelation within trees.

To add in treatment effects, I tested increasingly complex models (Equation 2.4 and 2.6). In all, I used the control tree site index from the location (or block), and, except for the null model, an indicator variable (*tmt*), which was set to one after a tree was released, zero otherwise. The simplest model was a null model with no treatment effect. This model had the poorest fit (R^2 =0.883, residual standard error (RSE) =2.275). The next model allowed the release treatment to alter the site index value additively with parameter t_1, which showed a significant 4.1m upward shift in site index for released trees. R^2 was 0.918 and RSE 2.01 for this model. The next two models also allowed treatment to alter the shape of the height vs. age curve (controlled by parameters b_2 and b_3, and the treatment shifts by parameters t_2 and t_3). Neither of these additional treatment effects on curve shape were significant (P=0.7601, P=0.9402 respectively). The best and simplest model appears to be a simple additive effect of release on the site index value of white spruce (Equation 2.7, Figure 2.9). Further fit statistics are given in Table 2.9.

Figure 2.10 shows that the residuals (actual height minus predicted height) are equally spread above and below the range of the predictors (breast height age, treatment) or predicted height. The apparent bias with respect to mixedwood (control) site index can be explained by location differences. I expanded these plots to show that there is no bias for control trees or released trees before treatment (*tmt*=0, Fig 2.10e). For released trees (*tmt*=1), the overall result is unbiased, but the location with the lowest control site index (Riding Mountain) underestimates the release, while one of the locations with the higher control site index (Reserve) overestimates the release. These location differences are to be expected, since in this analysis, locations and blocks act as replicates. In Chapter 3 of my thesis I try to further account for this variation.

PSP Height Growth Trajectories vs. Stem Analysis Height Growth Trajectories

Figure 2.11-2.14 shows the height growth trajectories of the "top" white spruce based on PSP measurement in 1951-54, 1956-59, 1961-64, 1985, 2001 and 2010, as well as the "top" two trees sampled for stem analysis in 2010. In most of the plots, the mean top height assessed by selecting the thickest trees at each remeasurement within the PSP data, was above the mean height of the top trees sampled in 2010 for stem analysis. This appears to be more pronounced in the control than in the released stands, especially in the early years (Figure 2.11-2.14). In Candle Lake block 2 there were two full release plots and Reserve had two partial release plots in addition to the full release. In one of those partial release plots at Reserve, the height trajectories of the white spruce based on periodic measurement of the PSP showed declines after the 1980s (Figure 2.13).

Discussion

Changes in Height Growth Trajectories and Site Index in Control vs. Release Stands

This study showed that removing the broadleaf species in mixedwood stands generally led to more rapid height growth of "top" white spruce, selected as the thickest or largest 100/ha. In 13 out of the 16 released trees sampled, or in four of the five locations, the released "top" spruce were taller than their counterparts in the mixedwood controls in the 2010 sampling year. Site index, determined by interpolating the height of the stem section with age above and below BH age 50, was not significantly higher for the released trees over all the locations and blocks, but the release was applied so close to the site index reference age (breast height age 50) in most locations, that few trees had much time to respond to the treatment. Riding Mountain was a notable exception, with early release and an apparently large SI release.

Since the current silvicultural practice is to release spruce much earlier (typically <15 years stand age), examining the height growth 50 years following treatment may be a better assessment of the possible change in site index due to release treatment. This measure also adjusts for the initial size of the spruce at the time of release. I found a 22% increase in height growth 50 years post-treatment. Variations across locations also dominated the response, with significant increases at the three eastern sites (Reserve, Duck Mountain, and Riding Mountain) and no increase in the other two. This 22% increase in height growth is a smaller value than earlier reports of height release from this study (Steneker 1967, Yang 1989), possibly because my trees are a new sample from just outside the permanent sample plot these other studies used or possibly because the deciduous competition is now declining in some of these locations (Table 2.2). There may not be as much difference in competition between the control and release plots as earlier. My results support the general conclusion of height suppression due to broadleaf competition, but clearly point to site-dependent variation, much as Filipescu and Comeau (2007) noted for the same region.

These height responses are snapshots during much longer height trajectories 56 – 74 years following treatment. Heights vs. age curves provide a better basis for comparing the overall response to treatment, and are an important component of many forest growth models.

Do Existing Height and Age Equations Fit Released Spruce?

We evaluated existing height vs. age curves for the data, particularly to evaluate if these models, which were developed for mixedwood spruce would fit the released tree responses. All four models tested had generally reasonable fits, with R^2>0.95 and standard error <1.5m (Table 2.8). The four parameter equation developed by Huang (1997), which fitted best to my data, had been developed from stem analysis data collected in the Central Mixedwood natural subregion of Alberta. The superior fit was likely due to the high number of parameters, similar stem analysis sampling technique and similar ecological region. This reasonable fit of a commonly-used model is reassuring, and suggests it may be suitable for modeling the height vs. age trajectories and estimating site index from height – age samples for both mixedwood and pure white spruce. The Huang et al. (2009) GYPSY white spruce model did not fit as well, probably due to the fact that this model was fitted to permanent sample plot data, rather than stem analysis. The equation developed by Cieszewski et al. (1993) had a low overall bias, but underestimated young tree growth, and overestimated the height of older trees. However, the two parameter Meng and Huang (2009) model was one of the few which converged for estimating the autocorrelation structure of my data, and had nearly as good a fit as the best model (Huang 1997).

Modeling the Treatment Response in a Height-Age Equation

Since release was not applied early in stand development, I developed a treatment response model which allowed for similar height – age trajectories until treatment, then estimated any change in the site index value and curve shape in response to treatment. By subtracting the difference in the released and control tree height vs. age curve at the time of release, this model allowed an altered (steeper) height growth rate due to release, while recognizing that the released trees could not regain the height they may have had if they had been released before breast height age 0. Most of the response could be accounted for by a 4.1 m uplift in the site index value (t_1 estimate, Equation 2.7, Table 2.9, Figure 2.9). This does not mean the released trees actually reached a height 4.1 m taller than controls at BH age 50, but that their growth subsequent to release matched the slope of trees with a site index 4.1 m greater.

The model could not be improved further by the addition of t_2 and t_3 parameters (Equations 2.8 and 2.9, Table 2.9), suggesting there was no change in the general shape of the height vs. age curve after release. Since the juvenile trajectory after release is altered entirely by the site index shift, these results support the use of height – age estimates in juvenile "performance" surveys to estimate future site index for pure as well as mixedwood spruce. There is still the caveat that much earlier release may result in a different shape of the height vs. age curve. However, a juvenile dataset of up to 9 years stand age showed no height difference between pure spruce released 4 years previous and spruce growing in a mixedwood (Bokalo et al. 2007). Only the height/DBH ratio was affected by release in this study, suggesting that release effects on height may be evident somewhat later, e.g. by the age the plots in my study were treated (25-60 years stand age).

A location effect remains in these height –age equations, as is shown by the residual plots (Figure 2.10c, e). Riding Mountain (control site index 10.3m) had the highest release, and was therefore underestimated by the overall release model. Likewise Reserve and Duck Mountain showed negative release, and had negative residuals (Fig. 2.10). In Chapter 3, I examine location-specific attributes which may improve this model.

Released spruce showed steeper and visually smoother height growth patterns than the control. This may be due to the increased availability of resources (physical space, light, water, nutrients). Control trees show quite variable height growth among the locations, probably due to mechanical injury from whipping caused by adjacent aspen trees (Lees 1966). The abrupt change and near-cessation of growth supports the hypothesis of the spruce tops reaching the lower aspen branches, and being physically prevented by whipping damage from growing taller. The later restarting of height growth for many control spruce may be the time when the broadleaf tree causing the damage died or lost the offending branch. Low light transmittance, water or nutrient competition could also be responsible for reduced height growth in the control mixedwoods (Filipescu and Comeau 2007), though this would be less likely to create the abrupt changes in height growth seen in my stands. The similar growth pattern between the release trees and the control trees at Candle Lake Block 1 might be due to low broadleaf competition levels in the whole stand (Table 2.2).

PSP Height Growth Trajectories vs. Stem Analysis Height Growth Trajectories

Remeasurements were limited, but the top trees in the Permanent Sample plots were generally taller than the top trees I selected in 2010 for stem analysis at the time of establishment or the early years of stand development. This suggests that the trees selected for stem analysis were not necessarily dominant at the younger stage and concurs with the dominance switching issue noted by Dahms (1963), Magnussen and Penner (1996), Raulier et al. (2003) and Feng et al. (2006). Interestingly, I observed recent evidence of leader damage (broom-like whorls where a lateral branch took over as leader) in top trees selected in the released spruce stands. This damage may be caused by wet snow, ice-storms or intense winds as well as abrasion and supports the dominance switching argument. Site index curves developed using the stem analysis technique will therefore tend to underestimate dominant height for the ages younger than the age at the time of selection. I acknowledge this source of error for my height – age equations, but note that both the control and released trees could be subject to intra-specific dominance switching, so the direction and approximate magnitude of the release effect should still be valid. It was not possible to fit meaningful height – age curves to the permanent sample plot data from these locations, since there were so few re-measurements, and height was not consistently sampled in the older measurements.

Results from my study show that there is an increase in spruce site index after release from deciduous competition. Actual site index increased by 6% across the locations and interpolating height difference 50 years after treatment due to late release showed a 22% increase in white spruce height growth. Overall my model indicated that white spruce after release grew in height at a rate similar to a height-age curve with a site index of 4.1m greater than the site index of mixedwood spruce.

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Table 2-1: White spruce and trembling aspen ages when treated for each study site. [a] age at stump height (0.3m) , b aspen age not determined (data from Yang 1989).

Study Area	Date of Establishment	Age at stump height (0.3m) (Years)	
		Spruce	Aspen
Candle Lake 1	1953	15-40	45-60
Candle Lake 2	1953	15-50	50-60
Big River	1953	35-50	55-60
Riding Mountain	1954	20-35	25-40
Reserve	1951	25-60	50-60
Duck Mountain	1936	50	b

Table 2-2: Site information for all study areas. Tmt=treatment, DecBA=deciduous basal area, DecN=deciduous density, ConBA=conifer basal area, ConN=conifer density. Conifer basal area and density are almost entirely white spruce. SK = Saskatchewan, MB = Manitoba, C=control plot, R=full release plot, LR=light release plot, HR=heavy release plot, PR=partial release plot.

Location	Tmt year	Plot no.	Tmt	At the time of establishment				2010 measurement			
				DecBA (m^2/ha)	DecN (stems/ha)	ConBA (m^2/ha)	ConN (stems/ha)	DecBA (m^2/ha)	DecN (stems/ha)	ConBA (m^2/ha)	ConN (stems/ha)
BR, SK	1953	11	C	20.6	1325	7.4	1600	8.2	475	28.9	1325
		12	R	0.0	0	9.3	2025	0.0	0	52.8	1650
CL, SK	1953	2	R	0.0	0	0.4	150	1.8	500	19.6	1900
		3	C	20.0	1775	0.7	425	7.7	1200	25.0	725
		4	R	0.0	0	0.3	200	0.4	75	18.2	425
		5	C	23.0	1150	4.3	1725	5.4	825	25.4	1500
		6	R	12.9	750	7.7	2675	0.0	0	36.5	675
		7	C	21.4	1150	4.1	1725	5.1	925	31.2	2025
		8	R	16.3	1025	3.6	1150	0.0	0	30.3	525
DM, MB	1936	3	LR	11.3	1665	7.1	1658	14.4	250	18.5	610
		4	C	27.8	3741	6.2	1202	33.6	900	20.1	1270
		5	HR	8.0	645	5.5	1150	11.4	720	20.8	290
RE, SK	1953	1	PR	10.1	518	4.1	525	21.7	725	17.1	350
		4	C	24.6	925	2.3	175	25.6	2350	9.0	225
		5	R	0.0	0	6.5	250	2.8	1150	23.9	150
		6	PR	10.5	600	5.8	275	15.3	1275	2.2	125
R M, MB	1954	19	C	28.8	4700	1.7	2100	30.9	675	3.1	175
		20	R	0.0	0	2.7	3000	1.0	75	35.4	1075
		21	C	24.3	3650	4.2	5875	24.3	650	10.1	1050
		22	R	0.0	0	1.8	2350	0.0	0	39.6	1300

Table 2-3: Study location information. Ecosites were classified according to Beckingham et al. (1996), 1961-1990 climate normal information was obtained using Wang and Haman's (2005) Climate Prairie Provinces interpolation software using each location's latitude, longitude and elevation, except for *Riding Mountain mean annual temperature (MAT) and precipitation (MAP) data, which were obtained directly from Environment Canada's Wasagaming station (Environment Canada 2011). The apparent site index (SI) of the control spruce trees was determined from fitting equation 2.4 (Methods) and averaging the site index values by location.

Location	**Treatment year**	**Ecosite**	**MAP (mm)**	**MAT (^{O}C)**	**Growing degree days(>5^{o}C)**	**Ave. control SI**
Big River, SK	1953	D3.2	433	0.6	1447	15.3
Candle Lake 1&2, SK	1953	D4.2	438	0.6	1451	16.9
Duck Mountain, MB	1936	D3.4	552	0.5	1280	14.1
Reserve, SK	1951	D3.2	472	0.5	1427	16.0
Riding Mountain, MB	1954	D3.2	508*	0*	1248	12.0

Table 2-4: Site index values determined by linear interpolation among stem sections. Values are means of release and control trees at the various locations.

Location	Treatment		% increase in (SI)
	Release	Control	
Riding Mountain	14.96	10.29	45.32
Big River	16.13	15.15	6.40
Candle Lake	17.90	17.38	3.02
Reserve	13.00	15.95	-18.51
Duck Mountain	12.43	13.90	-10.61

Table 2-5: ANOVA for site index (SAS Proc Mixed analysis).

Source	Error DF	Sum of Square	Mean Square	F Value	Pr > F
Treatment	5	11.22	11.22	2.42	0.181
Location	2.196	47.45	11.86	0.94	0.565
Block(Location)	5	27.43	13.71	2.95	0.142

Table 2-6 Height growth difference 50 years after treatment. Values were obtained by subtracting the height 50 years following treatment from height of the tree at treatment. Mean values of release and control trees are reported.

Location	**Height difference 50 yrs. after treatment (m)**		**Relative Release**
	Release	**Control**	
Riding Mountain	14.54	9.68	1.50
Big River	13.48	13.76	0.98
Candle Lake	17.26	16.67	1.04
Reserve	14.82	12.84	1.15
Duck Mountain	12.35	8.74	1.41

Table 2-7 ANOVA for Height growth difference 50 years after treatment (SAS Proc Mixed analysis).

Source	**Error DF**	**Sum of Squares**	**Mean Square**	**F Value**	**Pr > F**
Treatment	6	24.66	24.66	11.08	**0.0158**
Location	2	66.57	16.64	2.56	0.3003
block(Location)	6	13.02	6.51	2.92	0.1298

Table 2-8: Comparison of results from collected data to existing height – age equations using published parameters (except for Meng and Huang 2009 where I fit my own parameters). R^2 was used as a goodness of fit index, by squaring the Pearson correlation coefficient determined between predicted and observed data.

Height – Age Equations	**N**	**Bias Standard Error**	**R^2**	**Average Bias**	**Bias Below BHage 50**	**Bias Above BHage 50**
Cieszewski et al. (1993)	749	1.303	0.961	-0.061	0.783	-0.426
Huang (1997)	749	1.144	0.969	0.029	0.035	0.027
Huang et al. (2009)	749	1.457	0.969	-0.730	-1.032	-0.600
Based on Meng and Huang (2009)	749	1.352	0.957	0.153	-0.099	0.262

Table 2-9: Treatment height - age model vs. null (without treatment effect) height age model. b_2 and b_3 are the shape parameters, t_1, t_2 and t_3 are the release treatment parameters.

Fit Statistics							
Equation	-2 Res Log Likelihood	AIC (smaller is better)	AICC (smaller is better)	BIC (smaller is better)	DF	R^2	RMSE
2.4	1041.3	1045.3	1045.3	1048.2	643	0.883	2.275
2.7	977.1	981.1	981.1	984.0	642	0.918	2.006
2.8	980.2	984.2	984.2	987.1	641	0.918	2.010
2.9	981.8	985.8	985.9	988.8	641	0.918	2.008

Solution for Fixed Effects					
Equation	Effect	Estimate	Standard Error	t Value	Pr > |t|
2.4	b_2	6.5947	0.1600	41.27	<.0001
	b_3	-1.5107	0.0640	-23.77	<.0001
2.7	b_2	6.2991	0.1575	39.98	<.0001
	b_3	-1.5063	0.0572	-26.32	<.0001
	t_1	4.0764	0.5228	7.80	<.0001
2.8	b_2	6.3033	0.1590	39.65	<.0001
	b_3	-1.5120	0.0601	-25.14	<.0001
	t_1	4.0142	0.5605	7.16	<.0001
	t_2	0.0247	0.0810	0.31	0.7601
2.9	b_2	6.2960	0.1601	39.31	<.0001
	b_3	-1.5037	0.0644	-23.34	<.0001
	t_1	4.0935	0.5716	7.16	<.0001
	t_3	-0.0028	0.0373	-0.08	0.9402

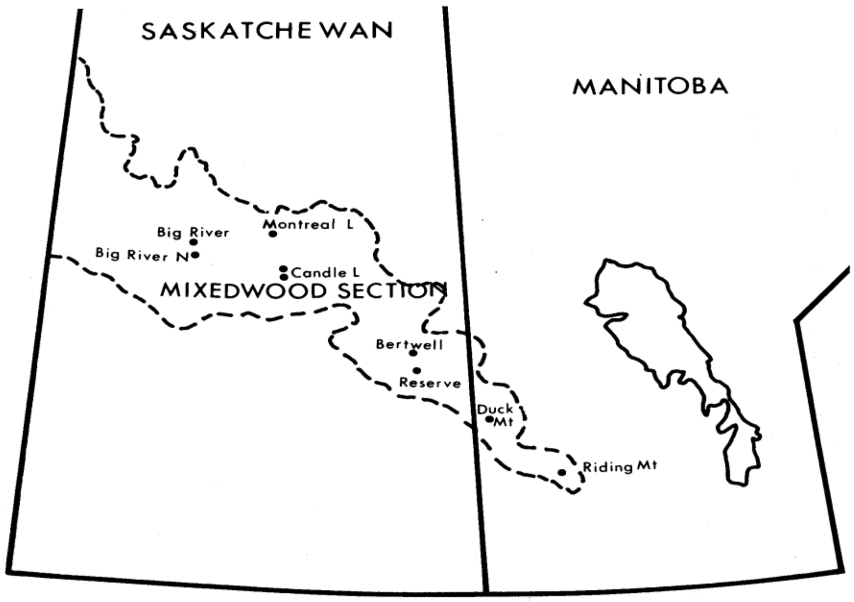
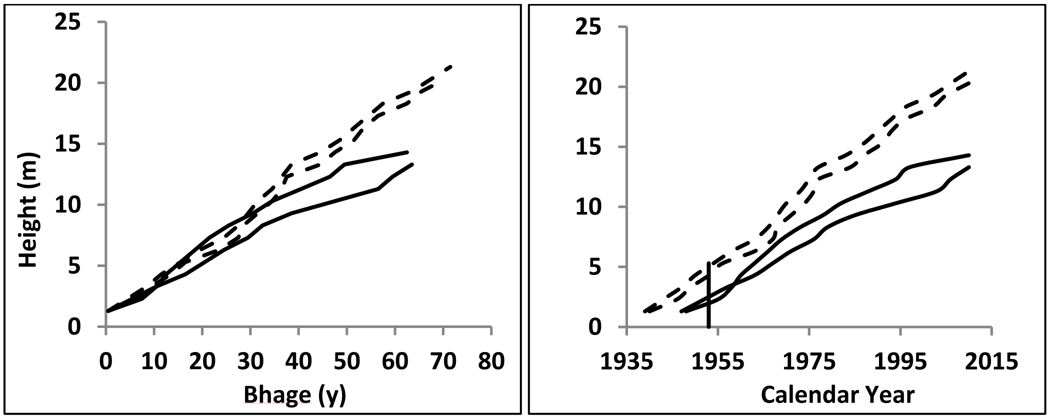


Figure 2-1: Study site locations. The area within the dashed lines indicates the mixedwood section extending from central Saskatchewan to south western Manitoba (Yang 1989).

Block 1



Block 2

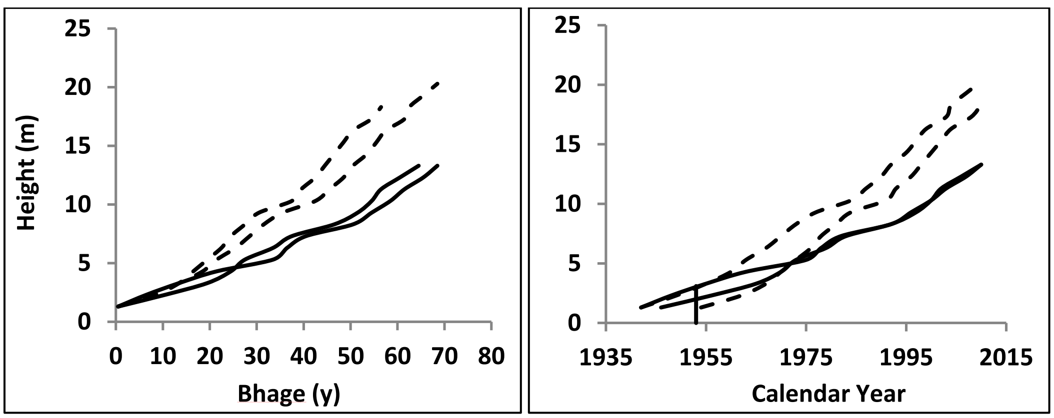


Figure 2-2: Actual height growth trajectories for eight sampled white spruce at Riding Mountain blocks 1 and 2. The solid curves (—) represent control (mixedwood) top trees, and the dotted curves (---) represent full release top trees. The solid vertical line shows the release year (1954).

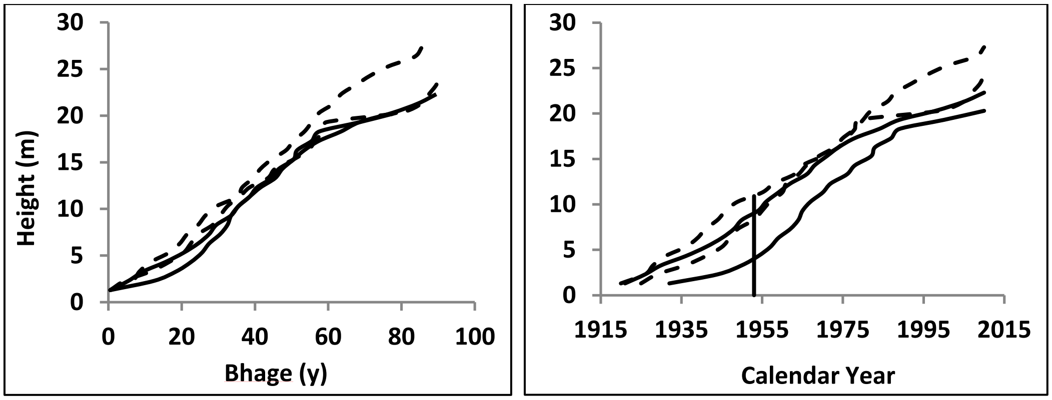


Figure 2-3: Actual height growth trajectories for four sampled white spruce at Big River. The solid curves (—) represent control (mixedwood) top trees, and the dotted curves (---) represent full release top trees. The solid vertical line shows the release year (1953).

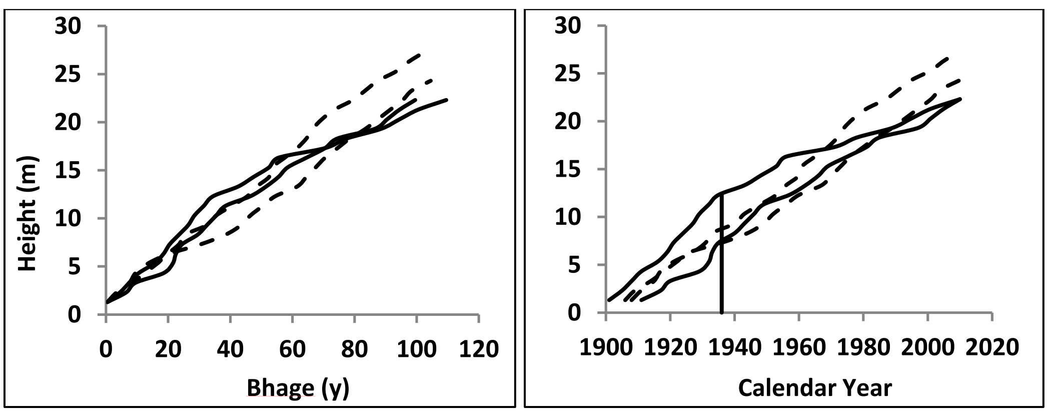
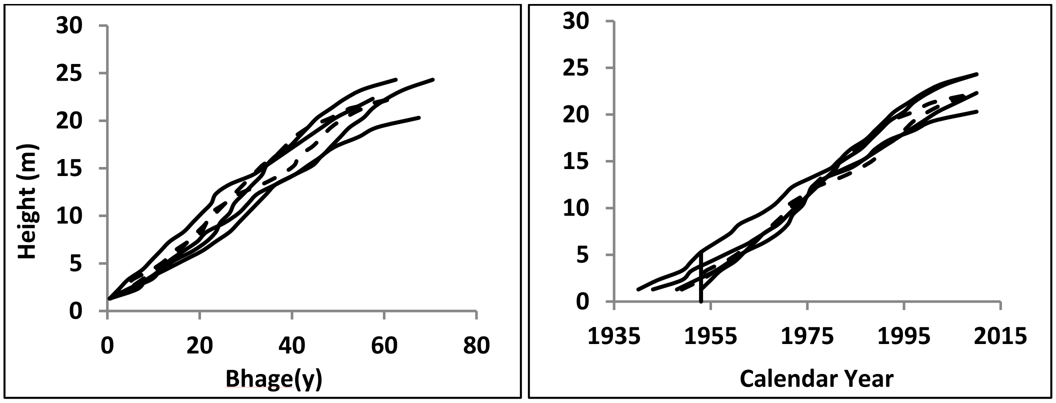


Figure 2-4: Actual height growth trajectories for four sampled white spruce at Duck Mountain. The solid curves (—) represent control (mixedwood) top trees, and the dotted curves (---) represent full release top trees. The solid vertical line shows the release year (1936).

Block 1



Block 2

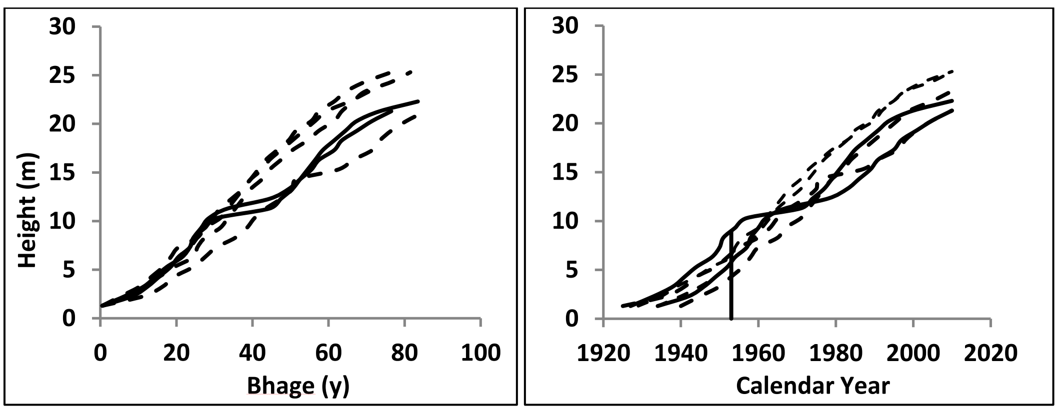


Figure 2-5: Actual height growth trajectories for twelve sampled white spruce at Candle Lake blocks 1 and 2. The solid curves (—) represent control (mixedwood) top trees, the dotted curves (---) represent full release top trees. The solid vertical line shows the release year (1953).

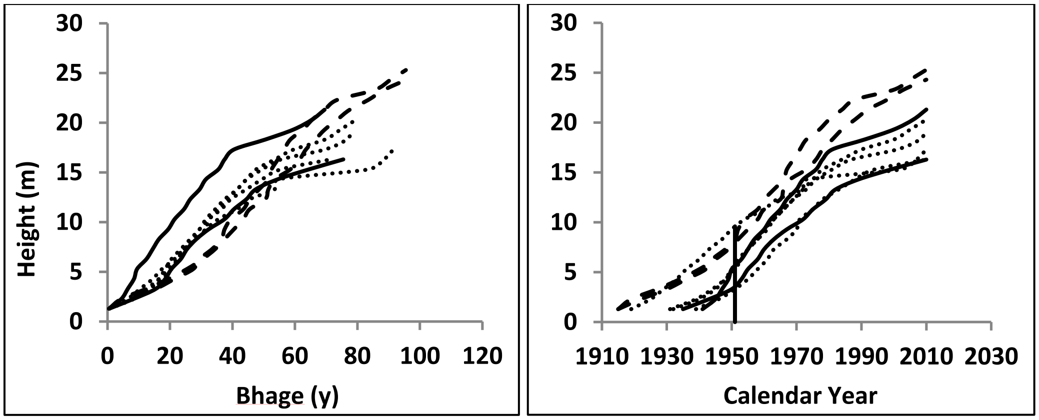


Figure 2-6: Actual height growth trajectories for eight sampled white spruce at Reserve. The solid curves (—) represent control (mixedwood) top trees, the long dotted curves (- - -) represent full release top trees, the short dotted curves (….) represent partial release top trees. The solid vertical line shows the release year (1951).

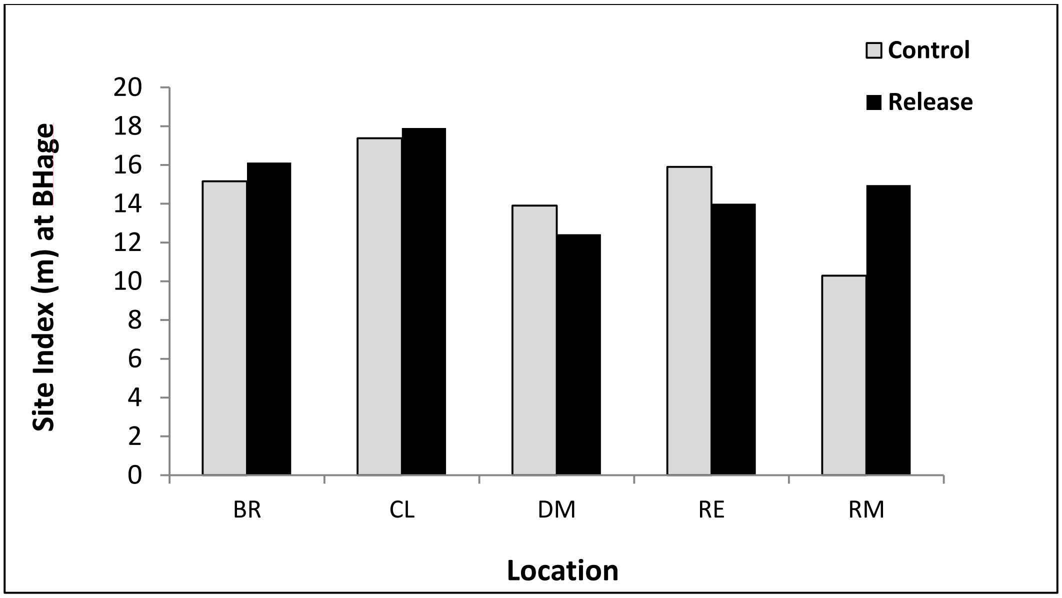


Figure 2-7: Site index of release and control stands for all study sites. Grey bars represent the average control site index and the black bars represent the average site index of the released trees. BHage=Breast Height age (years) at 1.3 m above ground.

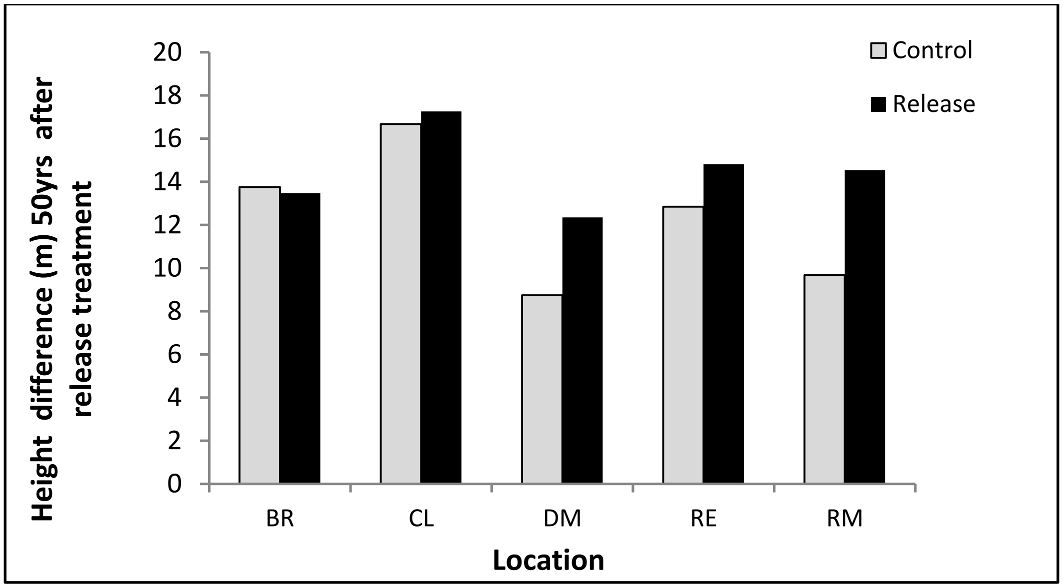


Figure 2-8: Height growth difference 50 years past treatment for all study sites. Grey bars represent the average control height increment and the black bars represent the average height increment of the released trees.

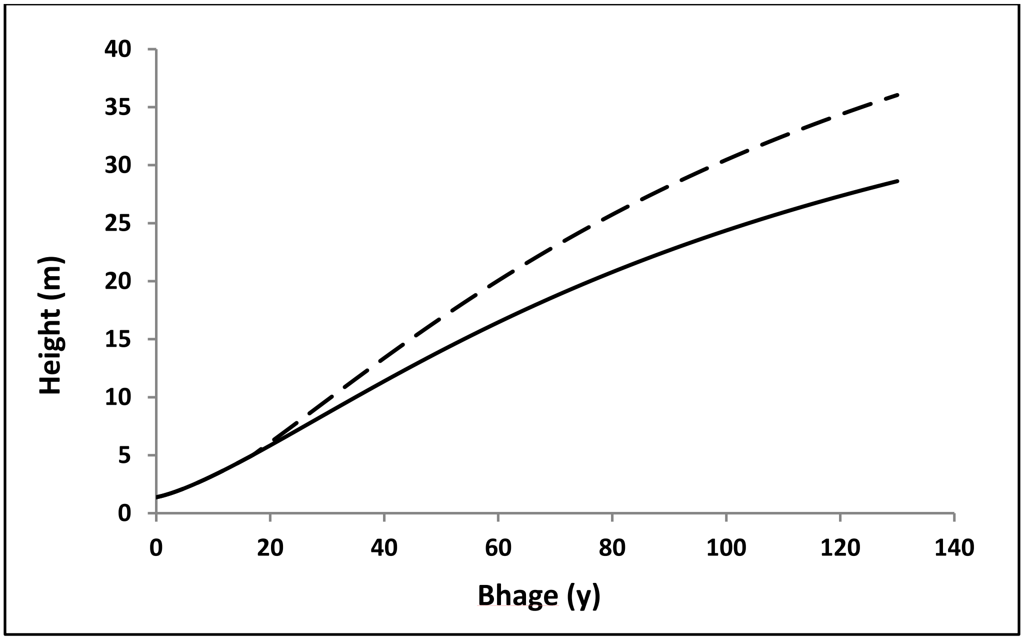


Figure 2-9: Effect of release treatment on the white spruce height – age curve. In this figure, the treatment was imposed (treatment indicator set to 1) when the spruce was at BHage 17. The dashed curve (- - -) represents top spruce height growth under release treatment and the solid curve (—) represents top spruce height growth in the control (mixedwood) stands.

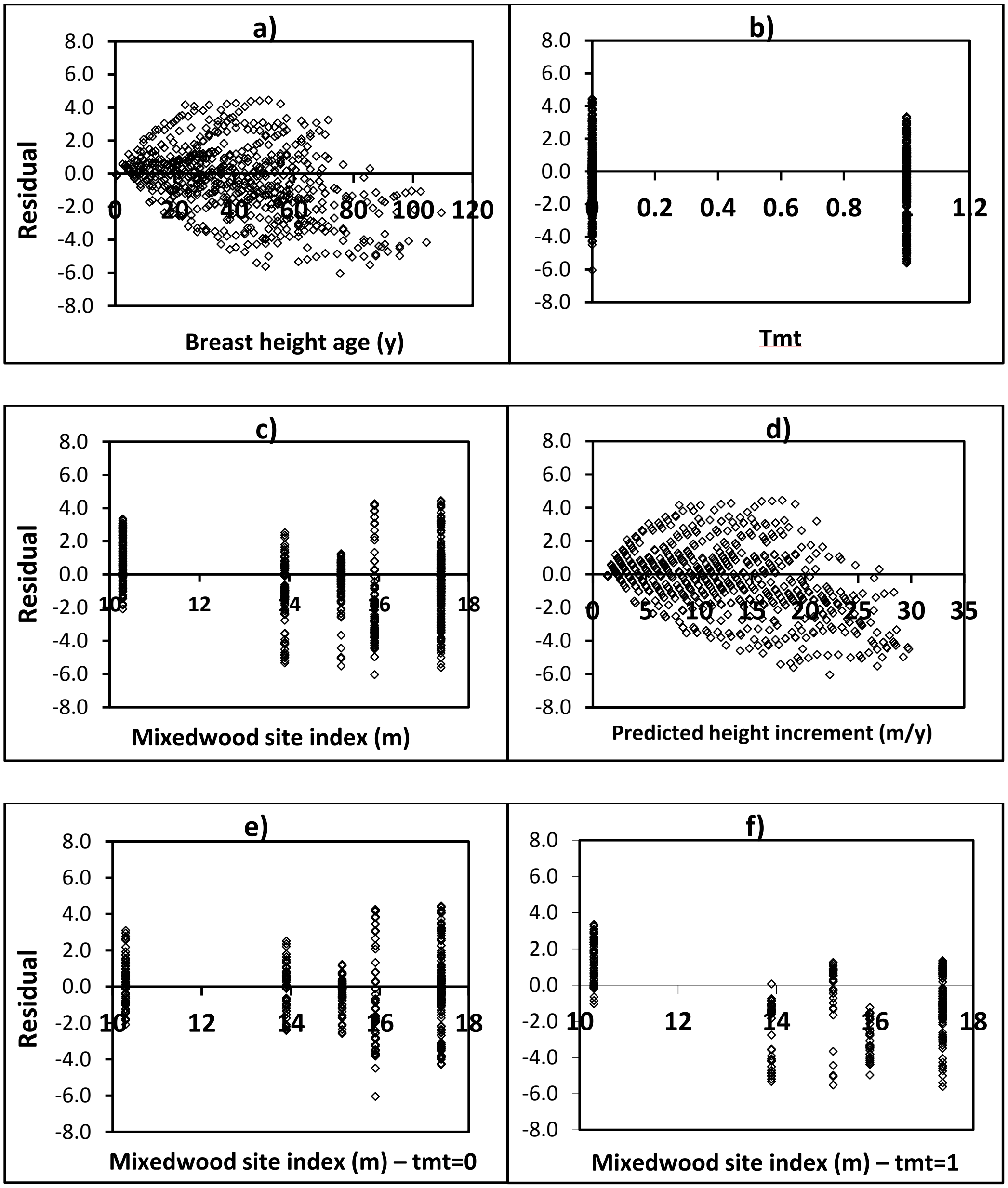
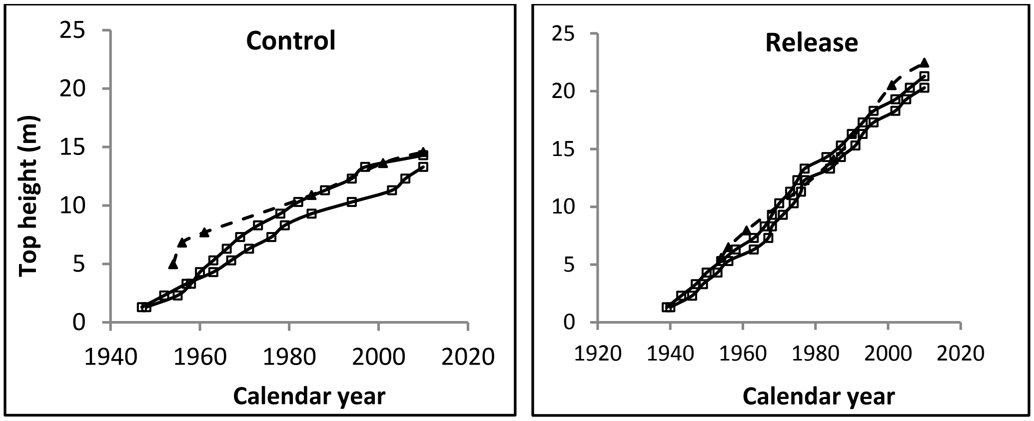


Figure 2-10: Residual plots from the chosen model (equation 2.5) plotted against predicted variables: breast height age (BHage), treatment (*tmt*), control (mixedwood) SI and the predicted height increment, control (mixedwood) SI when *tmt* is set to 0, control (mixedwood) SI when *tmt* is set to 1.

Block 1

a) b)



Block 2

a) b)

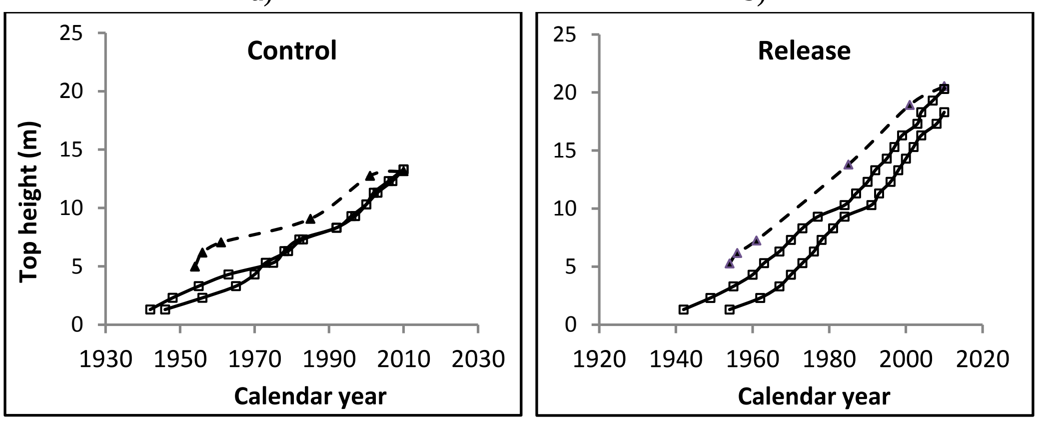


Figure 2-11: Height growth trajectories based on PSP or stem analysis data for Riding Mountain blocks 1 and 2. Graph a) represents top white spruce in control (mixedwood) plots, b) represents top trees in full release plots. The dotted curves with triangles indicate PSP top white spruce and the solid curves with diamonds represent stem analysis top white spruce.

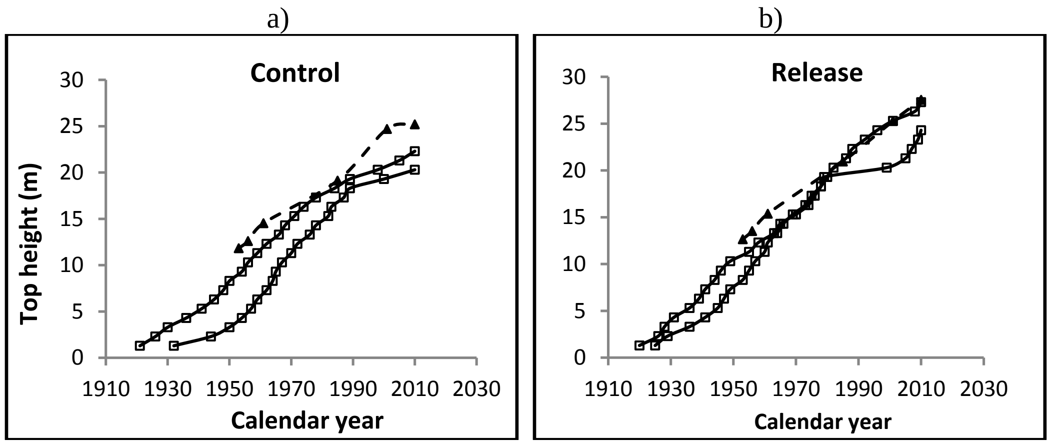


Figure 2-12: Height growth trajectories based on PSP or stem analysis data for Big River. The dotted curves with triangles indicate PSP top white spruce and the solid curves with diamonds represent stem analysis top white spruce.

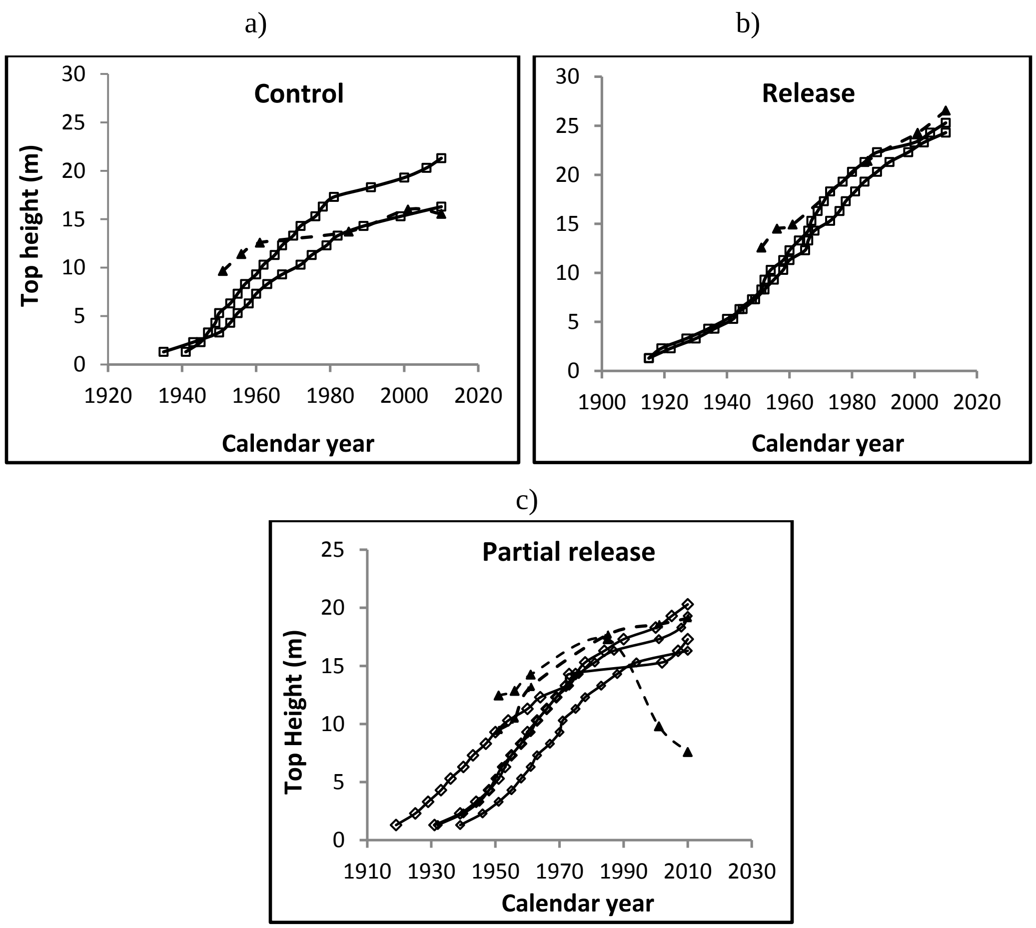
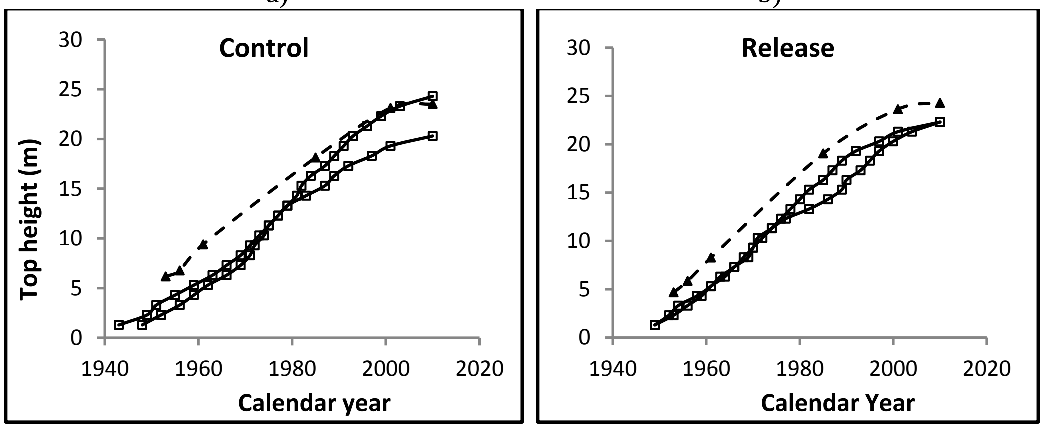


Figure 2-13: Height growth trajectories based on PSP data or stem analysis data for Reserve. The dotted curves with triangles indicate top white spruce selected from each PSP re-measurement and the solid curves with diamonds represent stem analysis top white spruce.

Block 1

a) b)



Block 2

a) b)

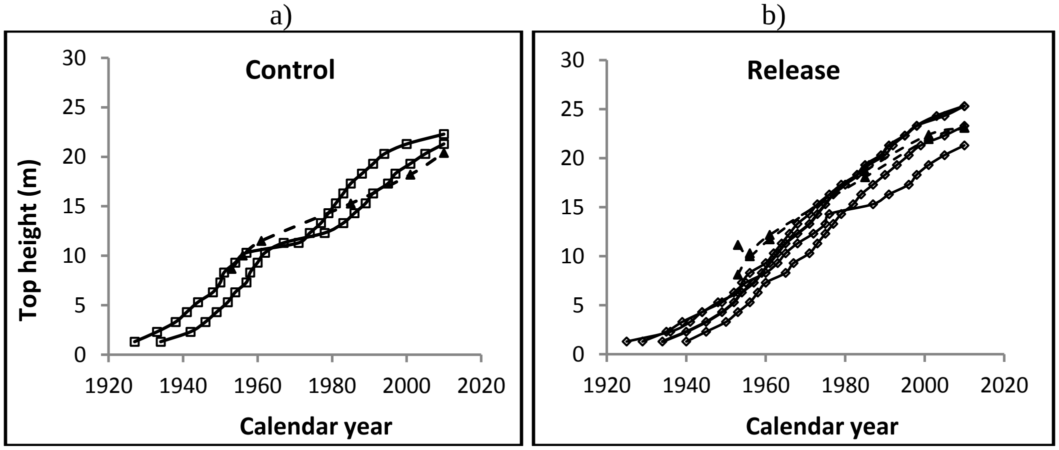


Figure 2-14: Height growth trajectories based on PSP or stem analysis data for Candle Lake blocks 1 and 2. The dotted curves with triangles indicates PSP top white spruce and the solid curves with diamonds represent stem analysis top white spruce.

Chapter 3. Quantifying Local Effects of Deciduous Competition on White Spruce Height – Age Growth Curves

Introduction

Potential site quality and productivity for a given tree species is frequently estimated using site index, the height of the dominant trees in a site at a reference age (Davis et al. 2001). Husch et al. (2003) and Lanner (1985) state that this measure provides a good estimate of site productivity in fully stocked, even-aged stands because height growth is closely correlated to the ultimate measure – volume. Height and age can be determined quickly and easily, and height growth of dominant and co-dominant trees usually is not greatly influenced by stand density and stand treatment (Lanner 1985). Potential wood volume production, such as maximum mean annual increment, may be the desired indicator of site productivity (ASRD 2006), but this is difficult to measure and is easily affected by stand density and stand treatment (Vanclay 1994).

In the western boreal forest, the two primary species, trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* [Moench] Voss) usually occur in mixtures (Strong and Leggat 1992). White spruce is often overtopped by aspen until late in natural stand development (Lieffers et al. 1996). Consequently, competition between these species for light, space and other resources makes it difficult to determine the true potential site productivity of white spruce based on height growth. Research has shown that reductions in light and other resources by aspen lead to reductions in the height growth as well as in the diameter and volume growth of white spruce (Filipescu and Comeau 2007). Height growth is also affected by physical abrasion from whipping by adjacent aspen trees (Lees 1966, Steneker 1967).

Previous studies have shown that white spruce growth generally increases after the removal of aspen overstorey. Yang (1989) reported that such a release treatment increased white spruce height growth in all size classes by an average of 42% after 30 years. In an earlier report on the same study, Steneker (1967) noted that physical contact of the spruce with the aspen crowns may be responsible, with spruce height growth being doubled by release from contact.

Existing height vs. age and site index curves developed for white spruce (Cieszewski et al. 1993, Huang 1997, Huang et al. 2009) largely ignore the effect of inter-specific competition that occurs between spruce and overtopping aspen. Site trees selected for stem analysis in these studies were the thickest 100 trees per hectare with no overtopping, competitors or visible damage at the time of sampling. However it is difficult to determine if these trees were consistently dominant and free of inter-specific competition during their development. Nigh and Love (1999) found that 75% of apparently healthy spruce chosen for longitudinal stem analysis had evidence of previous leader damage. Selecting a white spruce tree which has always been competition free is highly unlikely since white spruce growing in a mixedwood stand is usually overtopped by aspen until late in natural stand development (Lieffers et al. 1996). Current spruce site index estimates are better regarded as the ‘‘apparent’’ site index and not the potential in pure stands. Up to now, managers have been unable to estimate the true potential.

In the 1930’s and 1950’s the Canadian Forest Service established two studies (MS-8 and MS-153) in the mixedwood region of Saskatchewan and western Manitoba (Yang 1989). In these studies, paired control and aspen removal treatment were conducted in ~0.1 ha plots of 15-60 year-old stands. All sites but Duck Mountain had full aspen removal treatments, two sites (Duck Mountain, Reserve) had partial release treatments. Permanent sample plots were established at the time of treatment and re-measured approximately 5, 10, 35, 50 and 60 years later. These measurements included measurements of all trees taller than 1.3m, though only the white spruce trees were permanently tagged. I conducted stem analysis on site trees in the buffer regions of these sites in the summer of 2010, and developed the treatment-sensitive height vs. age curves described in chapter 2 of this thesis. However, in addition to site index and treatment, there was site-to-site variation unaccounted for. In this chapter, I explore the hypotheses that some of this variation might be explained by the amount of deciduous competition.

Methods

The Study Areas

The Canadian Forest Service established a series of experimental aspen removal (spruce release) sites in the provinces of Saskatchewan and Manitoba. The MS-8 study was established in 1936 in a 50-year stand in the Duck Mountain (DM) Forest Reserve in Manitoba, and the MS-153 study was established from 1951-54 in 20 to 60 year old stands at Big River (BR), Big River Nursery (BRN), Montreal Lake (ML), Candle Lake (CL) (2 blocks), Bertwell (BE) and Reserve (RE) in Saskatchewan and at Riding Mountain (RM) (2 blocks) in western Manitoba (Figure 3.1) (Yang 1989). For this study, Big River Nursery, Montreal Lake and Bertwell were excluded. These were lost due to fire and human disturbances such as logging, construction of roads and pipelines. Two plots from the original experiment at Big River, two plots at Candle Lake and two plots at Reserve were also lost to similar disturbances.

The MS-8 stand at Duck Mountain is situated on a southwest slope which is typical of the rolling uplands in the B.18a Mixedwood forest section (Rowe 1972). Clay-loam till forms the parent material of the soils. The stand was composed mainly of white spruce and aspen which formed about 80% of the pretreatment stand and originated from a fire in the late 1880s. Jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea mariana* (Mill.) BSP.), and a few balsam popular (*Populus balsamifera* L.) and white birch (*Betula papyrifera* Marsh.) were also present (Yang 1989).

The MS-153 study consists of stands which differed widely in stocking (Table 3.1) but the ecosite classifications were similar (Table 3.2). Their topography is flat to rolling and the soils are well drained varying from silty clay loams to clay loams. Riding Mountain and Duck Mountain are cooler than the locations and have a lower heat sum (Table 3.2). All stands originated from fire and were typical of mixedwood conditions. White spruce were irregularly distributed and the neighborhood growing conditions of the individual spruce varied from completely suppressed to relatively free-growing (Steneker 1967).

Treatments

Two 0.10-ha (~21 × 46 m) plots plus an unspecified surrounding buffer were subject to light and heavy release cutting at the Duck Mountain stand (MS-8). In this location, the heavy release cutting removed 60% of the deciduous basal area while the light release cutting removed 44%. Trees competing with or overtopping white spruce were removed. Most of the trees removed were aspen and jack pine with a few small diameter white and black spruce. Pre-release deciduous basal areas were $39.3m^2ha^{-1}$ (control), $40.9m^2ha^{-1}$ (light release) and $42.0m^2ha^{-1}$ (heavy release stands). An additional plot was left as an uncut mixedwood control. White spruce age was 50 at stump height at the time of treatment (Yang 1989).

For stands in the MS-153 study, square 0.04-ha (20m × 20m) permanent sample plots were installed within the selected stands. All trees other than white spruce were removed on the treated plots including a 9m surrounding buffer. The Reserve stand had an additional partial release treatment, where 50% of the aspen were removed by systematically cutting every other stem.

Permanent Sample Plot Measurements

White spruce trees within the permanent sample plots in all locations were tagged and mapped at establishment (other species were not tagged). A number of stump height (0.3m) ring counts were made to establish the age of the aspen and spruce in all stands except Duck Mountain where only white spruce age was determined. Plot trees (all species >1.3m tall) were measured for diameter at breast height at the time of establishment and then re-measured after approximately 5, 10, 35, 50 and 60 years (MS-153), or 50, 65, and 74 years (MS-8). Deciduous trees were mapped in 2001-2002, though not tagged. Heights of a sample of trees of the major species (aspen, white spruce) were measured in most re-measurement years. All but the last measurements were taken by Canadian Forest Service personnel. I sampled these stands with a group of University of Alberta colleagues in 2010, and measured height, DBH, and height to crown base of all species, and added tags to species other than white spruce, linking them to the tree codes on the 2001-2 maps. A damage assessment (broken tops, dead, disease, stem lean, etc.) was conducted at all measurements.

Tree Selection (2010)

For my study, two "top" (dominant) white spruce trees were selected for stem analysis within a 9 × 22.2 m (200 m^2) area in the buffer surrounding each plot. These sample trees were usually chosen to the north of the 0.04ha PSP, within each ~0.1 ha control and aspen removal treatment unit, as shade from uncut edges is minimized at the north edge of the treated area. The selected trees were intended to represent the best "site" spruce trees, sampled at a rate of 100/ha, for typical site productivity assessment (Huang 1997). Trees selected were those with the thickest or largest diameter. This sample of the thickest trees increases the likelihood that the height growth of the selected trees above breast height is an indication of the potential productivity of the site (Nigh 2004).

These stem analysis trees were marked and measured for diameter at breast height (DBH, at 1.3m), and total height. DBH was measured using a diameter tape at 1.3m above ground. For establishing the breast height reference point, leaf litter accumulation and woody debris was removed since white spruce may have some of its earliest height growth buried as these layers accumulate during stand development after fire (Peters et al. 2002).

Selected trees were felled away from the permanent sample plot whenever possible, and delimbed. Total height was measured from the breast height mark (including the 1.3m below) when trees were on the ground.

Stem Analysis

A total of 36 trees were felled in both mixedwood (control) and aspen removal (release) plots: 8 trees in Riding Mountain blocks 1 &2, 4 in Big River, 12 trees in the Candle Lake blocks, 8 in Reserve and 4 in Duck Mountain. Only the control and heavy release treatment at Duck Mountain (MS-8) were sampled due to time constraints. Felled trees were serially sectioned, removing a ~10cm disk at 0.3 m above ground, 1.3 m, and every meter up the stem to the top.

In the laboratory, the disks, 749 in total, were placed in a 70ºC fan-circulated oven and dried to a stable weight for approximately one week. The sections were then sanded progressively to 220-grit with a table and an orbital sander. Rings were counted manually along two radii of each section to ensure accurate ageing. When necessary, a microscope was used to distinguish fine rings.

Breast Height Age

Breast height age (BHage) was determined by subtracting the ring count for the disk taken at each height from the ring count for the breast height (1.3m height) disk. Height and age data pairs obtained from stem analysis may be biased if for example, the height of the disk is taken as the tree height for the corresponding ring count (Carmean 1972). Since on average, the section will pass half-way through the annual height increment, the age of each section was raised by one half year (Huang 1997). Height and breast height age data pairs were then plotted to demonstrate the actual height growth pattern of each spruce in both mixedwood and hardwood removal stands.

Height vs. Age Curve Fitting

Height vs. breast height age is typically used for building site curves. For this study, site index was defined as the average height at BHage 50 of the two thickest diameter trees per 200m^2 plot. In Chapter 2 of this thesis, I found Equations 3.1 and 3.2 below suitable for modeling the height growth trajectory of these trees.

$$Ht = \frac{b_1}{1+e^{[b_2+b_3 \ln(A+1)]}} \qquad (3.1)$$

SI is substituted for parameter b_1 in the orginal equation (Equation 3.1) by differencing it in terms of b_1 (Clutter et al. 1983), then choosing one height – age pair to be (H=SI, Bhage=50) (Equation 3.2).

$$Ht = 1.3 + (SI - 1.3) \times \left[\frac{1+exp[\, b_2+b_3\, ln(50+1)]}{1+exp[b_2+b_3\, ln(A+1)]}\right] \qquad (3.2)$$

In this chapter, I expanded my analysis to account for measurable site differences in the height growth response. I fit Equation 3.1 to height-age data from each tree, then estimated the site index of each tree by setting BHage to 50. The average of the control tree site index values was then taken as the “realized” site index value for mixedwood spruce at each location.

In these stands, deciduous competition varied with time. In particular, there was an abrupt shift in competition when the release (deciduous harvest) treatments were applied. To allow for this, the derivative of the height – age equation (see equation 3.4 below) was used because the height increment at a particular year is influenced by the current level of competition at that same year (or perhaps several previous years) and not the competition of the past or the future.

Autocorrelation Technique

Since the stem analysis data used in this study was used to generate repeated measures of height increment and age on each tree, there was the need to account for autocorrelation in the analysis. Autocorrelation adjusts the variance structure so that any statistical inference (e.g. significance of the parameters, including treatment ones) is done properly. For this reason, the SAS non linear mixed macro (%NLINMIX, Littel et al. 2006) was used. For a given tree, sections that are close to each other are more closely correlated in their height than sections that are further apart. And, the height increment – age correspondence of sections from a particular tree are more correlated than this pattern among different trees since some trees and some sites have faster growth than others. To capture this pattern of correlation between any two sections (i and j) within a tree, I used the model:

$$\rho_{secij} = \rho_{basic}^{|sec\ i - sec\ j|} \quad (3.3)$$

Where ρ is an autoregressive parameter assumed to satisfy $|\rho| < 1$ and i and j are section numbers (sequentially increasing from the base of the tree). I used section numbers instead of section ages as Meng and Huang (2009) did, since I had difficulty converging the model using age differences. Using this power function of section numbers estimated the pattern of the variance structure, which is the goal of modeling the variance. This yielded a lower likelihood statistic than was obtained based on the assumption of simple autocorrelation within trees (compound symmetry). An example of SAS code used to model height vs. age and height increment vs. age (plus competition factors) is shown in APPENDIX 5.

Site Differences

Site differences in the degree of release response may be due to several factors. Three were relatively simple to measure: ecosite, climate and deciduous competition. I conducted ecosite classification (Beckingham et al. 1996) and found that the locations were all BMd ecosites, with only minor differences in the plant community type (3.2 and 4.2). I did not investigate this factor further. I obtained climate data using the climate Prairie Provinces interpolation software (Wang et al. 2006), which interpolates among climate stations to estimate local climate parameters. I used 1961-1990 normals for mean annual temperature (MAT), precipitation (MAP), and growing degree days >5 C (Table 3. 2). The software yielded an anomalous MAT for Riding Mountain, perhaps due to its position at the edge of the Manitoba escarpment. The Wasagaming weather station is also above the escarpment, within 10 km of the site and within 40m elevation, so MAT and MAP were obtained directly from this station (Environment Canada 2011). The correlation of these variables plus the correlation of the difference in deciduous competition (basal area) between control and released plots, with a standardized measure of height increment for the 50 years following release treatment (Figure 3.2) was examined to identify likely predictors for location differences in the release response (Table 3.3).

Deciduous Competition Assessment

The effect of deciduous competition on white spruce top height growth was investigated by considering the deciduous basal area in the site index equation. This competition measure was chosen because of its high correlation with height increment (Table 3.3), its ease of measurement and since it considers both the size and density of trees. Stadt et al. (2007) and Filipescu and Comeau (2007b) found basal area as good a predictor of DBH growth of mature trees in this forest region as many other more complex indices.

Competition factors were introduced into the height increment vs. age equation to modify each of the three typical curve parameters (SI, b_2, b_3). The corresponding modifiers were the parameters c_1, c_2, *and* c_3.

For height increment vs. age, the derivative of equation 3.2 was used. This equation was in the form:

$$HI = -\frac{b_3\,\{51^{b_3}\exp(2b_2)+\exp(b_2)\}(c_1\Delta DecBA + SI - 1.3)(A+1)^{b_3-1}}{(A+1)^{2b_3}exp(2b_2)+2(A+1)^{b_3+1}exp(b_2)+1}$$

$$b_2 = b_2{}' + c_2\Delta DecBA$$

$$b_3 = b_3{}' + c_3\Delta DecBA$$

(3.4)

Where A is the breast height age, SI is the control (mixedwood) site index, b_2 and b_3 are general shape parameters, b_2' and b_3' are the control curve shape parameters, c_1, c_2 and c_3 are competition parameters and *ΔDecBA* is the difference between control and release deciduous basal area. Note *ΔDecBA* often was equal to control deciduous BA for full release (since typical release plot deciduous BA=0), but is lower for partial release plots (where deciduous BA>0). In this equation *HI* represents height increment for each year.

Deciduous Basal Area

In my data, there is a stem-analysis-based record of white spruce height growth extending back many years before the release treatments were applied and the first measurements of deciduous competition were taken. In order to couple the deciduous competition with the height growth of the spruce, for investigating the potential effects of earlier release than was conducted in MS-8 and MS-153, it was necessary to estimate the amount of deciduous competition from the establishment of the stand to the present. Huang et al. (2009) developed a deciduous basal area increment equation (Equation 3.5, APPENDIX 4) for Alberta, which was applied here. I used the equations given in Huang et al. (2009) to calculate BAINC (basal area increment), and accumulated the total deciduous

BA from stand initiation to 130 years (age of the oldest stand). This equation could then be used to model the dynamics of deciduous BA in the stand.

Statistical Analysis

The SAS %NLINMIX macro (Littel et al. 2006) was used to fit the spruce height increment vs. age and deciduous competition models. All models were compared using the root mean square error (RMSE), the coefficient of determination (R^2 = regression sum-of-squares / total corrected sum-of-squares). The competition parameters (c_1, c_2, c_3) were tested for significance by examining their P values against the level of significance defined at 0.05.

Results

Height Increment 50 Years Past Treatment

The height increment 50 years after treatment was examined for both the control and release plots at each location (Figure 3.2). Riding Mountain had the highest relative height growth release (50%), followed by Duck Mountain (41%). At Reserve the difference in height growth between the control and full release plots was 15%, Candle Lake recorded 4% and Big River was -0.02%. The overall relative height growth release was 2.1 m or 22%. In chapter two of this thesis I found the 22% increase in growth to be a significant uplift (p=0.016). This height increment provided a useful, simple measure to start investigating reasons for location differences.

Correlation Analysis

Table 3.4 shows that competition model 3.4a, a model which included only c_1, a parameter affecting the SI value, was the best fit based on the R^2, RMSE and the *P* values of the competition parameters (c_1, c_2 and c_3) of each of the models. The best model gave an R^2 of 0.120 and RMSE of 0.174 (Table 3.4). Parameter c_1 characterizes the overall effects of competition on site index which was an increase of 0.28 times the difference in control vs. removal deciduous BA (Table 3.4). A model with parameters c_2 and c_3 or both (model 3.4b, 3.4c 3.4d, Table 3.4) did not have a significant t statistic for these, indicating that they did not contribute much to the model and therefore could be removed.

Changes in Mixedwood Deciduous Competition with Time

Figure 3.3 shows that deciduous basal area in the control plots varied, and was generally declining with time. At Reserve, Riding Mountain and Duck Mountain locations, deciduous basal area increased from the time of stand establishment to a peak at stand ages 94, 87 and 119 years (calendar year: 1985, 2001 and 2001 respectively) before it declined. However Reserve recovered at 112 years stand age. At Big River and Candle Lake, basal area in deciduous control plots declined to low values following establishment of the plots. Unfortunately there is little data from the early re-measurements to allow us to assess the rate of this decline in the deciduous component. For the present study, I assumed a linear decline and I linearly interpolated any recovery in deciduous basal area in the released plots between measurements. I combined these deciduous BA estimates with the measured height increments to build a competition model (Equation 3.4).

Competition Model

Table 3.4 shows that competition model 3.4a, a model which included only c_1, a parameter affecting the SI value, was the best fit based on the R^2, RMSE and the P values of the competition parameters (c_1 c_2 and c_3) of each of the models. The best model gave an R^2 of 0.120 and RMSE of 0.174 (Table 3.4). Parameter c_1 characterizes the overall effects of competition on site index which was an increase of 0.28 times the difference in control vs. removal deciduous BA (Table 3.4). Parameters c_2 and c_3 or both (model 3.4b, 3.4c 3.4d, Table 3.4) did not have a significant t statistic, indicating that they did not contribute much to the model and therefore could be removed.

Figure 3.4 shows results from the competition-sensitive height growth model (equation 3.4a) for each site. At Riding Mountain where the average white spruce BHage was 16 years at treatment, a 30 m^2/ha deciduous BA removal caused a high release effect (6m increase in SI) as shown in figure 3.4 while a low release response is obtained at Big River and Candle Lake where deciduous BA were declining at treatment. The two partial release plots at Duck Mountain and

Reserve recorded negative release response for some trees compared to the control.

To extend my results, I illustrated how the competition-sensitive height growth model (equation 3.4a) behaved when a typical deciduous overstory, with basal area trajectory given by the aspen basal area increment equation of Huang et al. (2009), was removed before the spruce reached BHage 0 (Figure 3.5). This early removal showed a potential 7m gain in white spruce site index, over a typical mixedwood spruce site index of 14 m.

My competition model showed some outlying residuals above the zero line (Figure 3.6, by convention, positive residuals indicate underestimation) along the whole range of the variables (predicted height increment, breast height age, difference in deciduous basal area, and mixedwood site index) for model 3.4a. I looked for site-specific patterns in these residuals but found no clear pattern. The only obvious pattern appears to be some poor fit at young spruce ages.

Discussion

Results from this study indicate that differences in the amount of deciduous competition can account for variation in release of the top white spruce in western boreal mixedwood stands. The 50-year height increment following treatment was strongly correlated (*r*=0.80) with the amount of deciduous basal area removed. For the Riding Mountain stand, a 30 m^2/ha deciduous removal when the spruce were at a breast height age of 16, caused an increase in spruce site index of about 6m. Conversely, removal of the already declining deciduous competition at Big River and Candle Lake resulted in very little growth increase over the untreated control, soon after treatment; there was little competition to be released from. Since additional changes to the height vs. age curve shape related to deciduous basal area were not significant, it appears that the competition effect can be treated solely as an adjustment to the spruce site index value.

Competition Model

In this study, basal area worked well as an index of deciduous competition. The coefficient of determination for the best model (R^2) was not very high because height increment rather than height attained was used. Most other work has used height vs. age, but the high R^2 values obtained in this way are somewhat misleading. Height of a tree at a given time will nearly always be well-correlated with height a few years later, resulting in inflation of R^2 values. In this study, it was important to model the height growth response due to the abrupt removal of the deciduous competition and allow subsequent height growth to respond to this removal. This also allowed this model to respond to more gradual changes in the amount of deciduous competition over time (Huang et al. 2009).

The response to deciduous competition was not completely smooth and site variations remain. The Reserve site, for example, behaves oddly. This is consistent with other studies that indicate that competition effects vary between locations (Filipescu and Comeau 2007) and with the fact that competition levels also vary between stands. At Reserve, I found few white spruce in the buffer regions, so there were limited options for selecting the best trees.

If physical abrasion (leader whipping) is an important mechanism of spruce suppression by deciduous species, as suggested by Steneker (1967), it is not surprising that the response is noisy. A detailed spatial model might be able to estimate abrasion more readily, but would have to account for complex factors such as the tendency of deciduous stems to lean away from clusters. I saw many episodes of previous and current leader damage on my spruce, but observed as much damage in the release as well as the control plots. This damage may be caused by wet snow, ice-storms or intense winds as well as abrasion. All these factors may lead to the dominance switching among the leading trees I noted in Chapter 2, and by numerous other studies (Dahms 1963, Magnussen and Penner 1996, Raulier et al. 2003, Feng et al., 2006). For a general, non-spatial model, the spruce response to deciduous basal area observed here is reasonably strong. If these five locations are typical of the region, the overall average site index release due to deciduous removal is 4.1m as shown in Chapter 2.

My study also suggests that releasing white spruce from deciduous competition could result in a higher release effect if done earlier. For example, there was a stronger response at Riding Mountain, which was released at breast-height age 16, compared to the smaller response following release at BHage 36 at Duck Mountain (Figure 3.4), even though both stands had similar levels of deciduous basal area (Fig 3.3). When I used a typical deciduous basal area vs. age trajectory (Huang et al. 2009, APPENDIX 4) and computationally "released" the spruce before they reached breast height, the response is even more marked, showing a potential site index rise of 7m over a typical mixedwood spruce value of 14m, representing an increase of 50%. These results are consistent with findings of Wagner and Robinson (2006), Maguire et al (2009) that have shown that competition reduction treatments applied earlier in the life of trees generally result in trees of larger sizes.

Changes in Mixedwood Deciduous Competition with Time

The decline in deciduous BA differed among the sites. This dieback is due to mortality exceeding the trees' growth rate. Trees die as a result of some environmental, pathological and or entomological factors which may impact on stands at any point in their development. This may happen in old stands which are declining in vigor and characterized by slower growth. Frey et al. (2004) noted that the primary factors inciting deciduous mortality in mature stands are drought, defoliation, extreme weather events (e.g. late winter thaw-freeze which may cause bud and roots damage, rapid but brief warm winter chinook winds which lead to desiccation, severe spring frost damage to foliage) and wildlife stem damage. Defoliation and drought are the most important agents as they severely impact the carbon production and carbon reserves which are necessary for repairs of damaged tissue and defense. Peterson and Peterson (1992) stated that although aspen can tolerate long periods of flooding, the productivity of aspen decreases as soil internal drainage changes to imperfectly drained and spruce becomes a more prominent component than aspen. Kabzems and Garcia (2004) found that aspen growing in regions with cooler summers and winters tend to be longer-lived. According to Chen and Papadiuk (2002) aspen usually lives for less than 125 years in boreal mixedwood stands apart from the occurrence of insects and diseases. However as stands age, the competition status of aspen is reduced in relation to understory spruce (Lieffers et al. 2002). In my study, the deciduous basal area declined earlier at Big River and Candle Lake, possibly because these sites are drier and warmer than the others (Table 3.2).

Model fitting indicates some outliers in the data. Riding Mountain, which had the highest release, was underestimated by the overall model. For Reserve and Duck

Mountain, where the difference between site index in release and control was negative, I observed negative residuals.

These results point to early release from a typical deciduous BA of 30 m^2/ha, offering a possible 7m uplift in site index. Boateng et al (2009) show that vegetation control (willow, alder and some aspen) can increase both height at age 19 and estimated site index in a spruce plantation. Their results showed a similar 6m increase in spruce site index due to vegetation control. Once early release trials, such as that of Boateng et al. (2009) or the Western Boreal Growth and Yield Association's long-term study (Bokalo et al. 2007), reach an age where their site index can be reliably estimated, the uplift indicated here can be verified. However, equation 3.4a may be the best estimate we have of the effect of deciduous competition on spruce height-age growth until this time.

The growth intercept approach used in predicting the site index of juvenile stands (Nigh and Martin 2001) could work but only if release happens immediately. If release happens later, the growth intercept technique would have to be calibrated for much taller trees, a difficult process. By building a competition-sensitive site index curve for white spruce, my model circumvents the need for growth intercept calibration.

When true, competition-free site index values for white spruce have been obtained, from long-term studies of early-released pure spruce stands (e.g. Bokalo et al. 2007), equation 3.4a could be simplified. Instead of the difference in deciduous basal area between release and control plots, the deciduous basal area alone could be used. The competition coefficient (c_1) should retain a similar value as it has in this study, only it would become negative, as the deciduous BA would reduce spruce height growth from that predicted under the true SI value. In this case, since the apparent mixedwood SI value is used, the degree of deciduous BA removal would increase height growth.

My height growth model responded only to deciduous tree competition, but only accounted for 12% of the variation in height increment. Addtional variation in height increment may be explained by understorey competitors such as *Calamagrostis canadensis* (blue joint grass) which frequently competes with the spruce for resources such as soil water and nutrients (Comeau et al. 2004). *Calamagrostis* competition is typically more severe when deciduous trees are removed (Lieffers and Stadt 1994), though in my study, the spruce were well-established at the time of release, and may have provided enough shade to suppress this grass.

It should be noted however that juvenile white spruce planted or growing under the deciduous canopy may have some advantages. Overwinter injury to very young spruce is reduced since the deciduous trees capture and maintain snow cover over the seedlings. There is less summer frost damage due to alteration of the radiation exchange surface to the forest canopy from the ground level, and a reduction in the vapor pressure deficit due to reduced daytime understory temperatures (Man and Lieffers 1999). Terminal weevil and spruce budworm damage to white spruce is also reduced by overhead shading (Taylor et al. 1996, MacLean 1996). The effects of deciduous trees must be considered in this broader context.

However, the results of this very long-term controlled experimental study are compelling, and point to an overall pattern of greater height growth under decreasing levels of deciduous tree competition. A 30 m^2/ha deciduous basal area removal could cause an increase in site index of about 6m when released at Bhage 16. Even earlier release from a typical deciduous tree canopy may increase site index by as much as 50%, or 7 m.

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Table 3-1: Site information for all study areas. Tmt=treatment, DecBA=deciduous basal area, DecN=deciduous density, ConBA= conifer basal area, ConN=conifer density. Conifer basal area and density are almost entirely white spruce. SK = Saskatchewan, MB = Manitoba, C=control plot, R=full release plot, LR=light release plot, HR=heavy release plot, PR=partial release plot.

Location	**Tmt year**	**Plot no.**	**Tmt**	**At the time of establishment**				**2010 measurement**			
				DecBA (m^2/ha)	**DecN (stems/ha)**	**ConBA (m^2/ha)**	**ConN (stems/ha)**	**DecBA (m^2/ha)**	**DecN (stems/ha)**	**ConBA (m^2/ha)**	**ConN (stems/ha)**
BR, SK	1953	11	C	20.6	1325	7.4	1600	8.2	475	28.9	1325
		12	R	0.0	0	9.3	2025	0.0	0	52.8	1650
CL, SK	1953	2	R	0.0	0	0.4	150	1.8	500	19.6	1900
		3	C	20.0	1775	0.7	425	7.7	1200	25.0	725
		4	R	0.0	0	0.3	200	0.4	75	18.2	425
		5	C	23.0	1150	4.3	1725	5.4	825	25.4	1500
		6	R	12.9	750	7.7	2675	0.0	0	36.5	675
		7	C	21.4	1150	4.1	1725	5.1	925	31.2	2025
		8	R	16.3	1025	3.6	1150	0.0	0	30.3	525
DM, MB	1936	3	LR	11.3	1665	7.1	1658	14.4	250	18.5	610
		4	C	27.8	3741	6.2	1202	33.6	900	20.1	1270
		5	HR	8.0	645	5.5	1150	11.4	720	20.8	290
RE, SK	1953	1	PR	10.1	518	4.1	525	21.7	725	17.1	350
		4	C	24.6	925	2.3	175	25.6	2350	9.0	225
		5	R	0.0	0	6.5	250	2.8	1150	23.9	150
		6	PR	10.5	600	5.8	275	15.3	1275	2.2	125
R M, MB	1954	19	C	28.8	4700	1.7	2100	30.9	675	3.1	175
		20	R	0.0	0	2.7	3000	1.0	75	35.4	1075
		21	C	24.3	3650	4.2	5875	24.3	650	10.1	1050
		22	R	0.0	0	1.8	2350	0.0	0	39.6	1300

Table 3-2: Ecosite and climate information for the five study sties. Ecosites were classified according to Beckingham et al. (1996), 1961-1990 climate normal information was obtained using Wang and Haman's (2005) Climate Prairie Provinces interpolation software using each location's latitude, longitude and elevation, except for *Riding Mountain mean annual temperature (MAT) and precipitation (MAP) data, which were obtained directly from Environment Canada's Wasagaming station (Environment Canada 2011). The apparent site index (SI) of the control spruce trees was determined from fitting equation 3.2 (see Methods).

Location	**Treatment year**	**Ecosite**	**MAP (mm)**	**MAT (^{O}C)**	**Growing degree days(>5^{o}C)**	**Ave. control SI**
Big River, SK	1953	D3.2	433	0.6	1447	15.3
Candle Lake 1&2, SK	1953	D4.2	438	0.6	1451	16.9
Duck Mountain, MB	1936	D3.4	552	0.5	1280	14.1
Reserve, SK	1951	D3.2	472	0.5	1427	16.0
Riding Mountain, MB	1954	D3.2	508*	0*	1248	12.0

Table 3-3: Ranges in selected climatic and stand variables and correlation with Htdiff for the 5 study sites. Htdiff =Height increment 50 yrs after release, Annual Precip.(mm)= Annual mean precipitation, Annual Temp(^{O}C)=Annual mean temperature, GDD (>5^{O}C) = Growing degree days above 5C, ∆DecBA (m^2/ha)=difference in deciduous basal area between the control and release stands at treatment.

Variable	**N**	**Mean**	**Minimum**	**Maximum**
Htdiff	10	0.82	-3.82	5.62
Annual Precip.(mm)	10	473.10	433.00	552.00
Annual Temp(^{O}C)	10	0.44	0.00	0.60
GDD (>5^{O}C)	10	1386	1248	1451
∆DecBA	10	16.28	-0.11	26.59

	Annual Precip.(mm)	**Annual Temp(^{O}C)**	**GDD (>5^{O}C)**	**∆DecBA (m^2/ha)**
Htdiff (m)	0.598 0.068	-0.571 0.085	-0.623 0.054	0.778 **0.008**

Table 3-4: Comparison of competition models. DecBA= deciduous basal area, b_1',b_2' and b_3' = control curve shape parameters, c_1, c_2 and c_3= competition parameter.

Fit Statistics							
Equation	-2 Res Log Likelihood	AIC (smaller is better)	AICC (smaller is better)	BIC (smaller is better)	DF	R^2	RMSE
3.4a	-462.8	-458.8	-458.8	-455.6	674	0.120	0.174
3.4b	-456.0	-452.0	-452.0	-448.9	673	0.121	0.174
3.4c	-453.8	-449.8	-449.8	-446.7	673	0.120	0.174
3.4d	-448.5	-444.5	-444.4	-441.3	672	0.121	0.174

Solution for Fixed Effects						
Equation	Competition Variable	Effect	Estimate	Standard Error	t Value	Pr > |t|
3.4a	DecBA	b_2'	6.4600	0.1496	43.20	<.0001
		b_3'	-1.4115	0.06394	-22.08	<.0001
		c_1	**0.2795**	0.03057	9.14	<.0001
3.4b	DecBA	b_2'	6.4225	0.1635	39.27	<.0001
		b_3'	-1.4315	0.06722	-21.30	<.0001
		c_1	0.2647	0.03483	7.60	0.3981
		c_2	0.008208	0.009708	0.85	0.0737
3.4c	DecBA	b_2'	6.4620	0.1535	42.09	<.0001
		b_3'	-1.4327	0.07472	-19.18	<.0001
		c_1	0.2769	0.03112	8.90	<.0001
		c_3	0.001700	0.004182	0.41	0.6844
3.4d	DecBA	b_2'	6.3648	0.1673	38.04	<.0001
		b_3'	-1.3900	0.07533	-18.45	<.0001
		c_1	0.2505	0.03655	6.85	<.0001
		c_2	0.02482	0.02069	1.20	0.2307
		c_3	-0.00767	0.007739	-0.99	0.3218

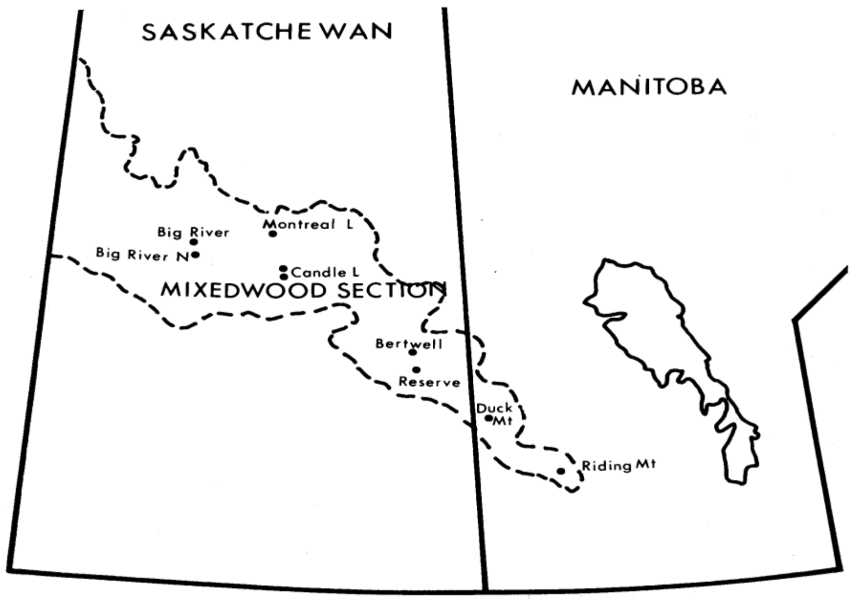

Figure 3-1 Study site locations. The dashed area indicates the mixedwood section extending from central Saskatchewan to south western Manitoba (Yang 1989).

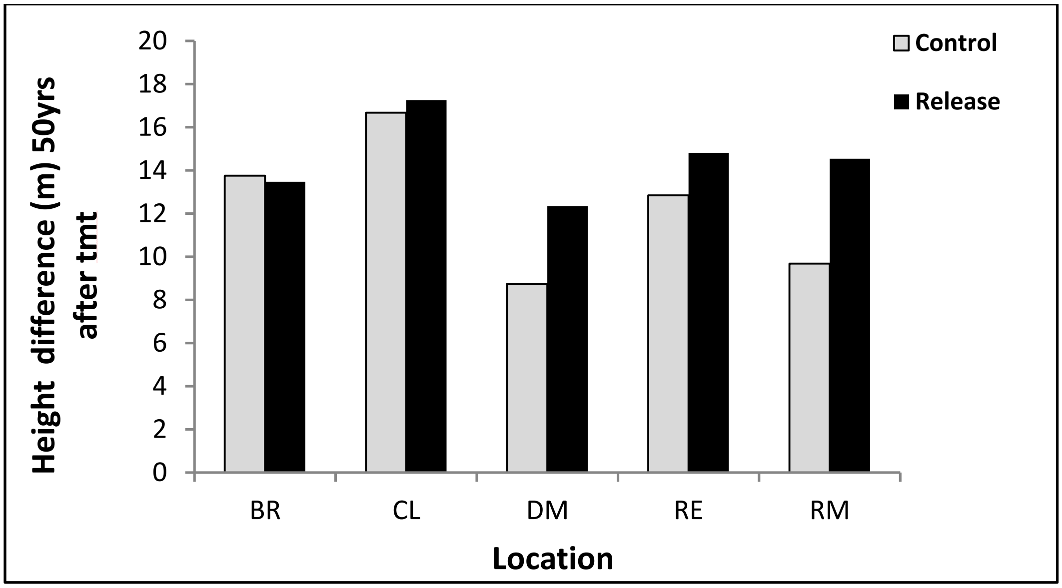

Figure 3-2: Height growth difference 50 years past treatment for all study sites Grey bars represent the average control height increment and the black bars represent the average height increment of the released trees. “Tmt” is the aspen removal treatment.

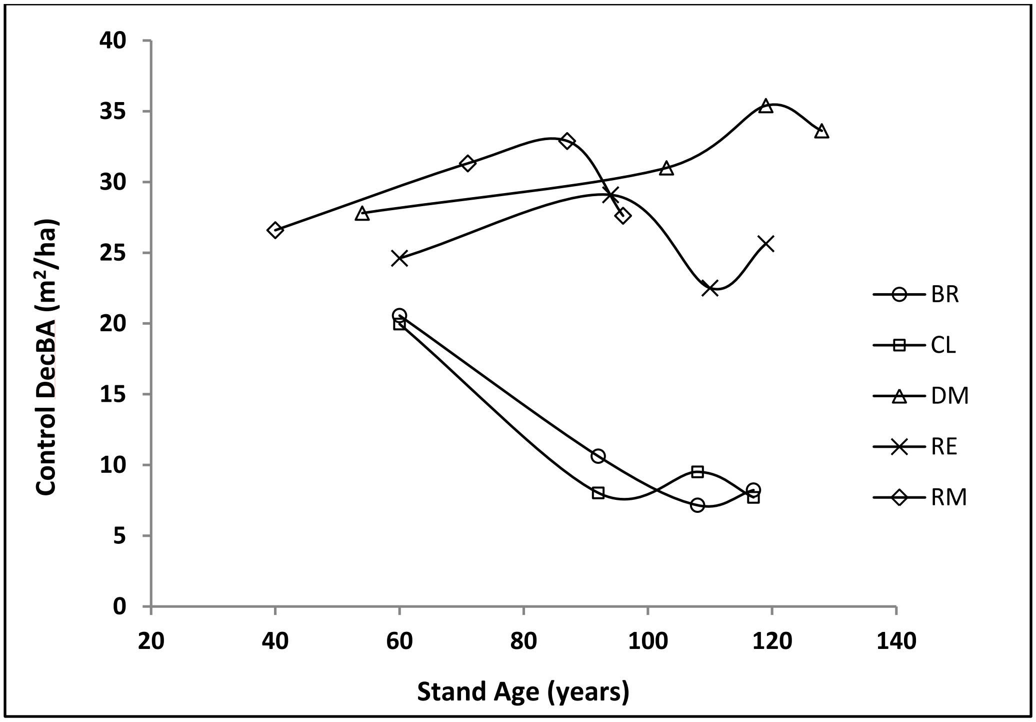

Figure 3-3: Control deciduous basal area (DecBA) plotted against stand age. The curves with diamond symbols indicates control DecBA trajectory in RM, the curve with triangles indicates control DecBA trajectory in DM, the curve with stars indicates control DecBA trajectory in RE, the curve with circles indicates control DecBA trajectory in BR and the curve with squares indicates control DecBA trajectory in CL.

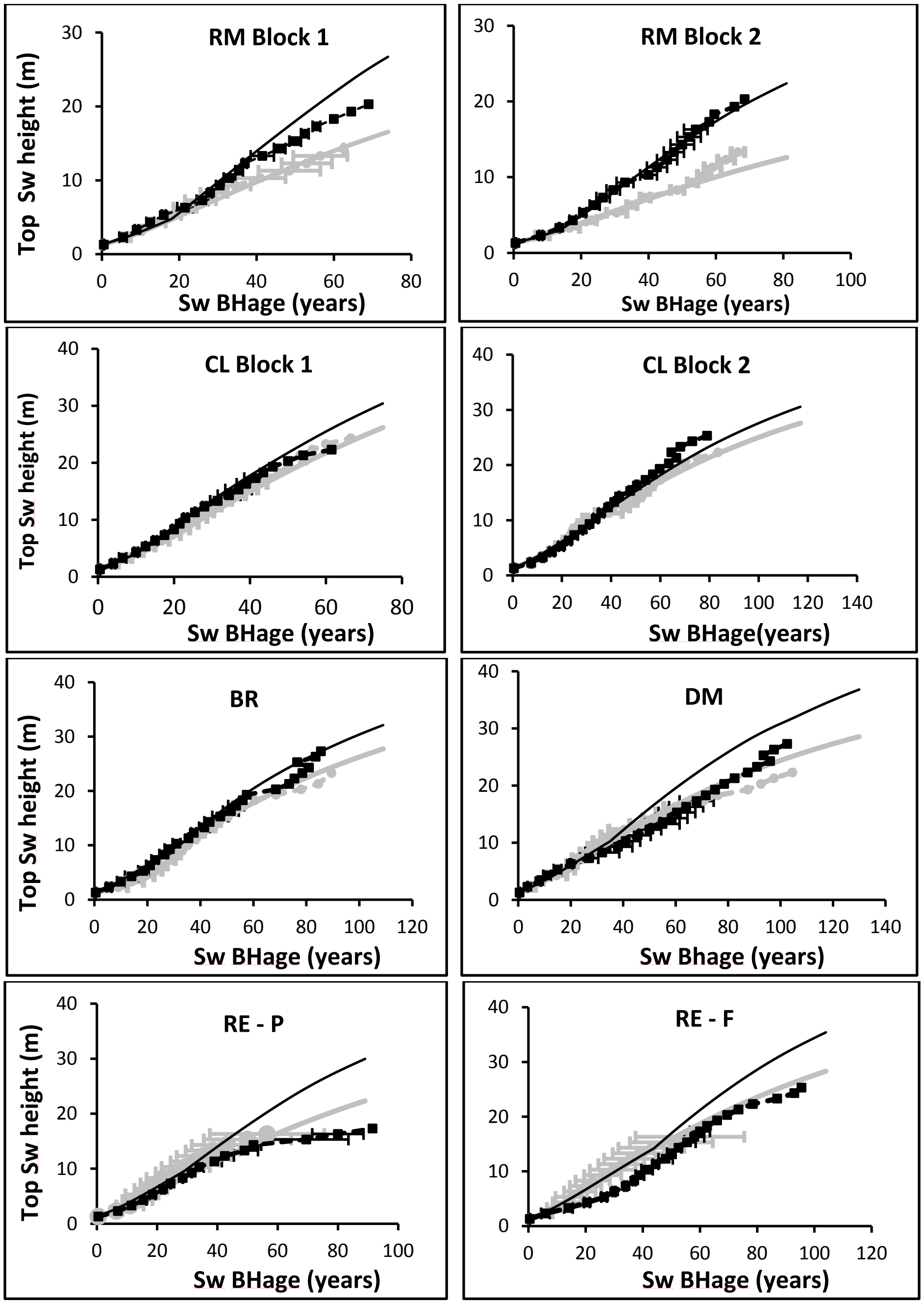

Figure 3-4: "Top" white spruce height vs. breast height age (Bhage) for each location with their respective deciduous basal area removals. The solid black line (—) represents the modeled release trees, the solid grey lines (—) represents the modeled control trees. Black dotted lines (---) with bars (standard errors) represent the mean and SE of the actual released trees' trajectory, and the grey dotted lines (---) and bars indicate the mean and SE of the actual control trees' trajectory. RE – P = Reserve partial release plot, RE - F. = Reserve full release plot.

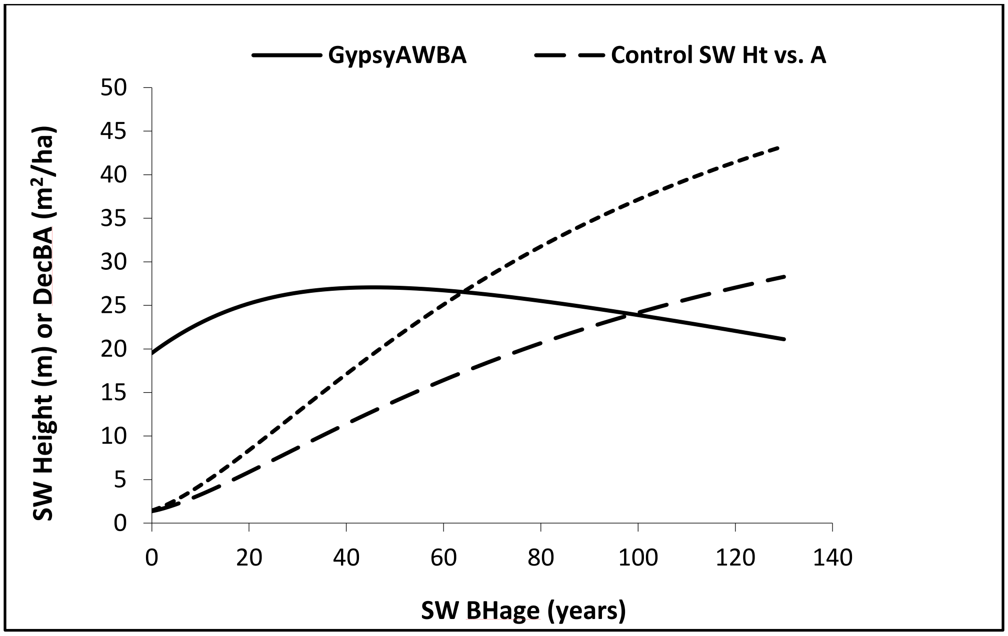

Figure 3-5: White spruce height vs. breast height age (Bhage) and deciduous basal area (DecBA). The solid line (—) represents a typical deciduous stand basal area trajectory (Huang et al. 2009) over time, assuming a stand age of 34 years at the time natural-origin spruce reach breast height. The long dotted line (– – –) represents the control (mixedwood) spruce height vs. age trajectory and the short dotted line (---) represents the height vs. age trajectory of spruce released at Bhage 0.

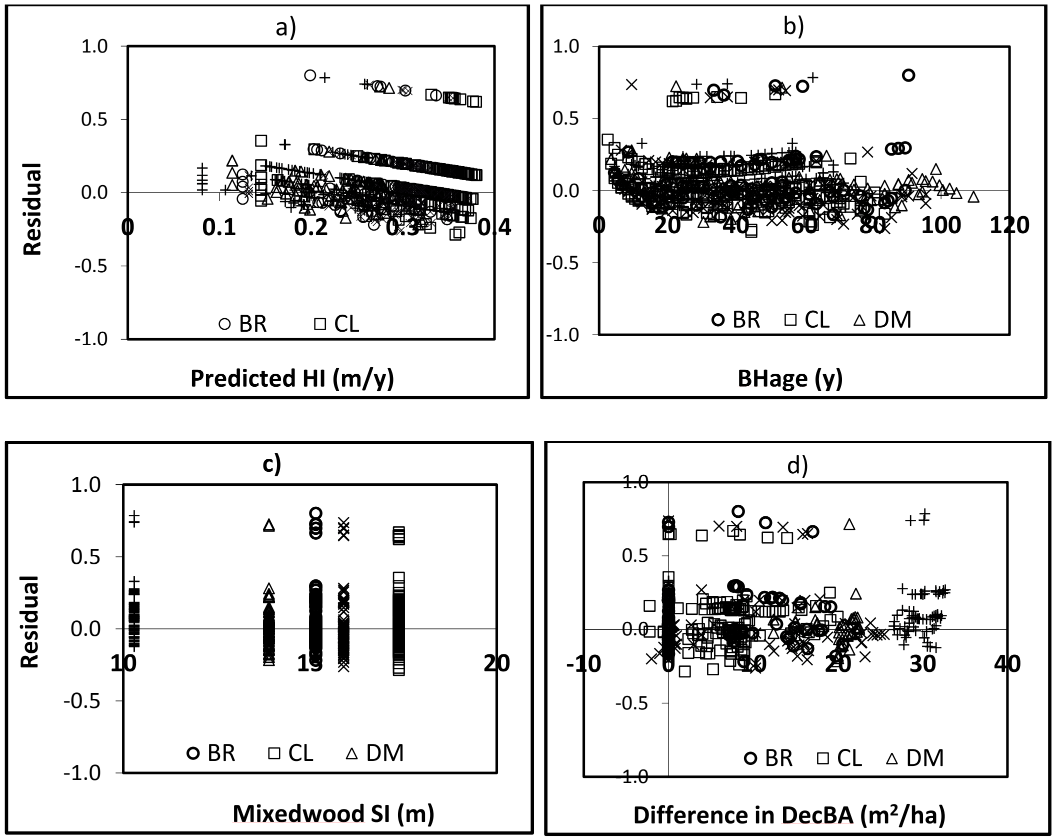

Figure 3-6: Residual plots from the chosen model (equation 3.4a) plotted against predicted variables: predicted height increment (HI), breast height age (BHage), control (mixedwood) SI and difference in deciduous basal area (DecBA).

Chapter 4. Conclusions and Recommendations for Future Research

Potential white spruce productivity in mixed species forests is difficult to determine because white spruce are most often overtopped by fast growing deciduous species like aspen and hence suffer reduced height growth. Previous work on spruce height – age curves (Cieszewski et al. 1993, Huang 1997, Huang et al. 2009) ignored the effects of inter-specific competition in the determination of white spruce site index (the height of the thickest, ("top") trees at breast height age 50). These studies do not address the "true" white spruce site productivity in the boreal mixedwood, i.e. how well spruce would grow without being overtopped early in its development. Therefore the focus of this thesis was to evaluate the effect of deciduous competition on very long-term (>50 years) white spruce height growth trajectories.

Experimental plots established by the Canadian Forest Service (MS-8 and MS-153) in the 1930s and 1950s across central Saskatchewan and south-western Manitoba were used for this study. These stands have both mixedwood (control) and aspen removal treatment plots and were re-measured periodically following treatment. My stem analysis work and the historical measurements provided data for reconstructing site index curves quantifying any potential gains in spruce height growth and site index due to release from deciduous competition.

In chapter two of this thesis, I examined the effect of deciduous removal on white spruce height growth and site index and found that:

1) The top height growth trajectory of spruce in released stands was statistically steeper and visually smoother than that in mixedwood stands. In Riding Mountain, where the highest release response was obtained, the released trees grew much more rapidly than the control. At Big River and in Candle Lake Block 2, and Reserve, released spruce also appeared to have a steeper height – age

trajectory than the controls. In Duck Mountain and Reserve, most of the height gains due to release occurred in later years. Only in Candle Lake Block 1 was there no evidence of release.

2) Site index values for the released stands were greater than the site index of the mixedwood spruce in a few locations only. The highest SI was recorded in Riding Mountain. However the overall effect was not significant as this site index effect varied by location, and was negative in some. Since the treatment was applied late, i.e. a number of white spruce were 30-60 years at the time of release, potential site index gain due to early release may be better estimated by the height increment 50 years after release treatment. I found that this height growth measure increased by 2.1m (22%) after release, and that this was a significant gain. This is a simple, preliminary estimate of how site index might change if a release treatment was done very early in stand development.

3) Existing site index curves developed for white spruce in Alberta and Saskatchewan (Cieszewski et al. 1993, Huang 1997, Huang et al. 2009) fit my data, however, the equations of Cieszewski et al. (1993) and Huang et al. (2009) had some bias problems. The more complex model (four parameter equation) by Huang (1997) gave the best fit to my stem analysis height – age data but this would not allow me to model autocorrelation within trees. Therefore the simple, two parameter equation developed by Meng and Huang (2009) was selected for further analysis in chapters two and three of this thesis. However, the good fit of the Huang (1997) Central Mixedwood subregion equation to both control and released spruce, suggests it is useful for projecting the height – age trajectories of spruce in the western mixedwood region.

4) The treatment response height – age equation showed that most of the release response could be accounted for by a 4.1 m gain in the site index value. The

model could not be improved further by the addition of adjustments to the general shape of the site index equation. My results therefore suggest that there is no different shape to the site index curve due to release treatment. The 4.1m uplift in site index represents a second, more refined estimate of the overall effect of complete deciduous removal in this region. Further, the similar shape of the released and mixedwood spruce height – age curves suggests that it is not necessary to build an alternate curve for different treatments. This supports straightforward "look-ups" of site index from height and age data in juvenile to mature spruce stands, regardless of their treatment.

5) By examining the "top" (thickest or largest diameter 100 spruce per hectare) tree height growth trajectories of white spruce in the re-measurements of the PSPs vs. the height growth trajectories by stem analysis, I found that the stem analysis top trees were below the PSP top trees at the time of release. This provides some evidence that the trees selected for stem analysis were not necessarily dominant at the younger stage and therefore dominance switching does affect the shape of the height – age curves for released and control trees (Dahms 1963, Magnussen and Penner 1996, Raulier et al. 2003, Feng et al., 2006). However, this would affect both situations, so the direction and pattern of my responses should still be valid.

The variations in the response of spruce to release observed among locations in chapter two may be due to several factors. In Chapter three, I examined ecosite differences (Beckingham et al. 1996) but these were similar. I investigated differences due to climatic factors (mean annual precipitation, mean annual temperature and growing degree days>5^{O}C) and the amount of deciduous removal at these sites, and related these to the height increment 50 years after release. I found that the amount of deciduous basal area removal at the time of release was most strongly and significantly correlated to the height increment, while the climatic factors were less correlated to height increment. Hence, I investigated the effect of the amount of deciduous basal area on the degree of release of the dominant white spruce. I modeled height increment rather than height because the amount of deciduous competition at a particular year most likely influences the height growth rate at that year: gradual changes and abrupt releases from deciduous competition could then be modeled. The effect of deciduous removal simply increased spruce site index value by a factor of 0.28 multiplied by the basal area removed (in m^2/ha). These results clearly show that differences in spruce height increment between release and control treatments are linked to deciduous competition, and the response could be as much as 6m where deciduous basal area was high (30 m^2/ha). I also extrapolated that the effect of release from deciduous competition very early in stand development could increase site index up to 7m.

Early release treatment will undoubtedly increase volume production of white spruce in the long term. Yang (1989) reported an increase in spruce total volume of 93% after 30 years of release. Thus, deciduous tree removal offers a substantial benefit to conifer yield. Forest managers should also consider the loss of deciduous yield due to release treatment, as approximately 30 m^2/ha basal area was lost when the deciduous species were removed. The relative value of both species groups needs to be considered in any decision to treat mixedwoods.

Furthermore, in the face of climate change, the risk of growing pure white spruce rather than mixed deciduous – white spruce stands needs to be considered. Deciduous species such as aspen are more drought and fire tolerant than spruce (Peterson and Peterson 1992), so may offer insurance against such climate-warming induced losses.

Contributions

- This is the first long term study of spruce site index gain due to release from hardwood competition and gives the best estimate to date of the effect of deciduous competition on spruce height-age growth.

- The results from my study show that although release treatment can result in a gain in spruce site index, timing is important for realizing this site index gain. Earlier release appears to be better, though other work (Bokalo et al. 2007) indicates that spruce in the first 9 years of stand development did not demonstrate height release from deciduous competition 4 years after deciduous removal. This knowledge is valuable to support decisions made on mixedwoods management and site productivity evaluation in the western boreal.

Recommendations for future research

- Further study to examine or quantify volume and diameter growth in relation to the release of white spruce from deciduous competition is needed.

- This work underscores the value of very long-term forest research. The vision of the Canadian Forest Service in maintaining these plots for over 60 years is exemplary, and is now providing vital information on forest dynamics which would otherwise be difficult to obtain. I hope the obvious value of the CFS MS8 and MS153 studies contributes to continuing, reliable measurements of other long-term permanent sample plot programs maintained by the CFS, the provinces and forest industry. The Western Boreal Growth and Yield Association plots (Bokalo et al. 2007), the Mixedwood Management

Association Dynamics Aspen Density Experiment (MWMA 2007) are notable examples, which will enhance forest management in the next decades.

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Appendices

Appendix 1: Existing height – age equations

- Cieszewski et al. (1993) Equation:

$$Ht = 1.3 + \left[\frac{(SI - 1.3) + C + \sqrt{((SI - 1.3) - C)^2 + 4(SI - 1.3)C}}{2 + \frac{4b_0/B\text{hage}^{b_1}}{(SI - 1.3) - C + \sqrt{((SI - 1.3) - C)^2 + 4(SI - 1.3)C}}} \right], C = \frac{b_0}{50^{b_1}}$$

Parameters b_0=4915.689 b_1=1.379241

- Huang (1997) Equation:

$$Ht = 1.3 + (SI - 1.3) \times \left[\frac{1 + b_0(SI - 1.3) + \exp\left[(b_1 + b_2 \ln(50 + b_3) - \ln(SI - 1.3)\right]}{1 + b_0(SI - 1.3) + \exp\left[(b_1 + b_2 \ln(Bhage + b_3) - \ln(SI - 1.3)\right]} \right]$$

Parameters b_0= 0.044435 b_1=11.381718 b_2=-1.944325 b_3=6.728764 (Central Mixedwood natural subregion).

- The GYPSY Equation, Huang et al. (2009):

$$Ht = 1.3 + SI \times \left[\frac{1 + \exp\left(b_1 + b_2 \sqrt{\ln(1 + 50)} + b_3[\ln(SI)]^2 + b_4 \sqrt{50}\right.}{1 + \exp\left(b_1 + b_2 \sqrt{\ln(1 + Bhage)} + b_3[\ln(SI)]^2 + b_4 \sqrt{50}\right.} \right]$$

Parameters b_1=13.07921 b_2=-6.03800 b_3=-0.25712 b_4=0.178732

- The modified logistic function, Meng and Huang (2009):

$$Ht = 1.3 + (SI - 1.3) \times \left[\frac{1 + \exp[\, b_2 + b_3 \ln(50 + 1)]}{1 + \exp[b_2 + b_3 \ln(Bhage + 1)]}\right]$$

Parameters b_2=6.7307, b_3=-1.6041

Appendix 2: Example SAS code for NLINMIX macro

```
title "nlinmix",
%inc "C:\Program Files\SAS\nlinmix.sas",
%nlinmix(data=diana1,
  model=%str(
    num = (1+exp((b2)+(b3)*(log(1+50)))),
    den = (1+exp((b2)+(b3)*(log(1+A)))),
    denta =(1+exp((b2)+(b3)*(log(1+B)))),
    predv = 1.3+(si-1.3+tmt*t1)*num*(1/den-1/denta)+(si-1.3)*num/denta, ),
  parms=%str(b2=7 b3=-1.4 t1=0),
  stmts=%str(
    class treeid sec,
    model pseudo_y = d_b2 d_b3 d_t1/ noint notest solution cl,
          repeated sec / type=sp(pow) (BHage) sub=treeid r rcorr,
  ),
  expand=zero
)
run,
```

Appendix 3: Competition Models.

$$HI = -\frac{b_3\,\{51^{b_3}\exp(2b_2) + \exp(b_2)\}(c_1\Delta DecBA + SI - 1.3)(A+1)^{b_3-1}}{(A+1)^{2b_3}exp(2b_2) + 2(A+1)^{b_3+1}exp(b_2) + 1}$$

$b_2 = b_2'$

$b_3 = b_3'$ (3.4a)

Where,

HI=Height increment

A = breast height age

SI = control (mixedwood) site index

b_2 and b_3 = general shape parameters

b_2’ and b_3’ = control curve shape parameters

c_1 = competition parameter

ΔDecBA = difference between control and release deciduous basal area

$$HI = -\frac{b_3\,\{51^{b_3}\exp(2b_2) + \exp(b_2)\}(c_1\Delta DecBA + SI - 1.3)(A+1)^{b_3-1}}{(A+1)^{2b_3}exp(2b_2) + 2(A+1)^{b_3+1}exp(b_2) + 1}$$

$\mathrm{b}_2 = \mathrm{b}_2' + \mathrm{c}_2\Delta\mathrm{DecBA}$

$b_3 = b_3'$ (3.4b)

Where

c_2 = competition parameters

All others are as defined before

$$HI = -\frac{b_3 \{51^{b_3} \exp(2b_2) + \exp(b_2)\}(c_1 \Delta DecBA + SI - 1.3)(A+1)^{b_3 - 1}}{(A+1)^{2b_3} exp(2b_2) + 2(A+1)^{b_3+1} exp(b_2) + 1}$$

$$b_2 = b_2'$$

$$b_3 = b_3' + c_3 \Delta DecBA \qquad (3.4c)$$

Where

c_3 = competition parameter

All others are as defined before

$$HI = -\frac{b_3 \{51^{b_3} \exp(2b_2) + \exp(b_2)\}(c_1 \Delta DecBA + SI - 1.3)(A+1)^{b_3 - 1}}{(A+1)^{2b_3} exp(2b_2) + 2(A+1)^{b_3+1} exp(b_2) + 1}$$

$$b_2 = b_2' + c_2 \Delta DecBA$$

$$b_3 = b_3' + c_3 \Delta DecBA \qquad (3.4d)$$

All parameters and symbols are as defined before.

Appendix 4 Gypsy Aspen Basal Area Increment Model (Huang et al. 2009)

$$BAINC = \frac{10^{-4} a_1 Bhage_1^2\, exp\left(-a_2 Bhage_1^{(1/2+a_1)}\right) \times \left[\ln\left(1 + N_0\ \sqrt{1 + Bhage_1}\right)\right]^2 SI_{aw} SC_1^{a_5}}{10(1 + BA_1)^{a_3}\left[1 + \exp\left(1 - \frac{l\,\mathrm{n}(1 + SC_1^2)}{2}\right)\right]} + k$$

$$K = a_4 ln(0.01 + Bhage_1/10)$$

(3.5)

BAINC=basal area increment

N_0=aspen density in the previous year (stems/ha)

SC=species composition: aspen density/total stand density

a_1, a_2, a_3, a_4 and a_5 are parameters with values:

a_1 = 0.751313, a_2 = 0.018847, a_3 = 1.143762, a_4 = -0.03475, and a_5 = 0.835189.

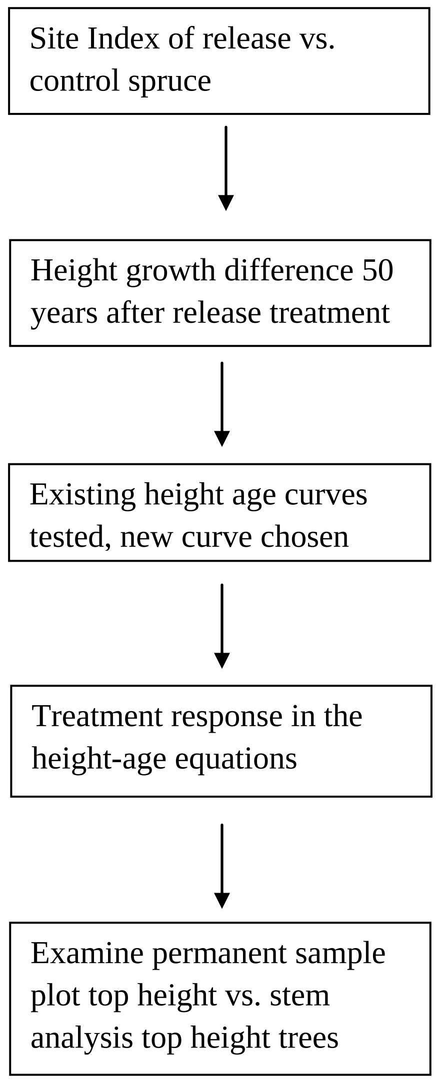
Appendix 5: Example SAS Program for NLINMIX Macro

```
title "nlinmix",

%inc "C:\Program Files\SAS\nlinmix.sas",
%nlinmix(data=diana2,
  model=%str(
  b2=b2',
  b3=b3',
  predv=-((10*exp(2*b2)* b3*3** b3*17** b3+10*exp(b2)* b3)*c1*diffdecba+
        (10*exp(2*b2)* b3*3** b3*17**B3+10*exp(b2)* b3)*si-13*exp(2*b2)*
        b3*3** b3*17** b3-13*exp(b2)* b3)*( bhage +1)** b3/
        ((bhage +1)**(2* b3)*(10*exp(2*b2)* bhage +10*exp(2*b2))+
        (bhage+1)** b3*(20*exp(b2)* bhage +20*exp(b2))+10* bhage +10), ),
  parms=%str(c1=0.1 b2'=6.5 b3'=-1.6),
  stmts=%str(
    class treeid sec,
    model pseudo_y = d_c1 d_b2' d_b3' / noint notest solution cl,
          repeated sec / type=sp(pow) (Bhage) sub=treeid r rcorr,
  ),
  expand=zero
)
run,
```

Appendix 6: Flow diagram of chapters 2 and 3

Chapter 2 flow diagram



Chapter 3 flow diagram