Incorporating genetic gain into growth and yield projections for Alberta’s white spruce and lodgepole pine tree improvement programs

by

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Abstract

Forest Management in Alberta, Canada, has been facing challenges from a shrinking forest land-base over the past few decades. Tree improvement is recognized as one of the most efficient approaches in addressing this issue. However, there are still some knowledge gaps limiting the application and benefit assessment of tree improvement programs. Given that white spruce (*Picea glauca* (Moench) Voss) and lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.) are the two most important commercial tree species in Alberta, these species are the focus of this thesis.

In this thesis, five chapters are included, with three data chapters (Chapters 2-4) focusing on estimating: 1) genetic gain at rotation age and corresponding growth and yield from improved white spruce and lodgepole pine seedlots; 2) climate change effects on improved white spruce and lodgepole pine performances; and 3) early growth of improved white spruce in mixedwood stands in northeastern Alberta.

In Chapter 2, taking advantage of the latest height measurements from progeny trials in the province of Alberta, I adjusted and compared two available age-age correlation equations developed previously by Lambeth (1980) and Rweyongeza (2016). The results indicated that the adjusted Lambeth equations, with re-estimated parameters, were the most accurate for both species and should be incorporated into Alberta's growth and yield models. The phenotypic age-age correlation showed no significant deviation from the genetic age-age correlation for either species. The stand volume generated from the growth and yield projection system (GYPSY) model using the newly adjusted Lambeth equations showed that white spruce had a higher age-age correlation when given the same selection and rotation ages, and therefore, a higher percentage improvement in volume per hectare compared to lodgepole pine regardless of rotation age.

In Chapter 3, the most recent height measurements from progeny and provenance trials, and three Representative Concentration Pathways (RCPs) were selected to incorporate climate change into growth and yield predictions for both species. An adjusted Pooled Transfer Function (PTF) was developed, which relates standardized population height with population climate transfer distance and population climate and was merged with GYPSY using the newly adjusted Lambeth equations to predict the effects of climate change on the growth and yield of unimproved and improved stands in Alberta. The simulation results indicated that height growth was strongly influenced by the mean coldest month temperature (MCMT, averaged over the daily mean temperature) for white spruce and mean annual precipitation (MAP) for lodgepole pine. By 2090, climate change-related growth expansions for white spruce stands are expected to be greater in areas with low provenance MCMT than in areas with high provenance MCMT for both improved and unimproved seedlots, regardless of the RCPs. Unimproved and improved lodgepole pine stands, however, are expected to show decreased height growth in most regions in Alberta. For both species under all three RCPs, improved seedlots will be outgrown by unimproved seedlots in locations where climate change favours height growth, while improved seedlots will retain their growth advantage over unimproved seedlots in locations where climate change shows an overall negative effect on height growth.

In Chapter 4, data collected from four Forest Management Units (FMUs) in northeastern Alberta were used. The results indicated that, in the mixed white spruce and trembling aspen (*Populus tremuloides* Michx.) stands, the improved white spruce seedlot, which originated from a tree improvement program with an approved height gain of 1.9% at a 100-year rotation, did not show any advantage in height or diameter at an early stage. A distance-independent competition index based on Lorimer's index, that included size ratio between competitor aspen and subject spruce, accounted for most of the variation in averaged diameter and height increments from 2016-2018 (age of trees 8-10 years), when a power function was used in the competition analysis (competition index was the explanatory variable, and averaged diameter and height increments were the response variable). The competition effects on height and diameter growth differed significantly. For both unimproved and improved seedlots across ecosites, height growth was less sensitive to the competition effects than diameter growth.

These results in this thesis fill some of the current knowledge gaps, through providing accurate age-age correlation equations and an adjusted PTF to estimate growth and yield of improved forest stands under climate change.

Preface

The data used in Chapters 2 and 3 are from all white spruce and lodgepole pine tree improvement programs in Alberta, which were made available by Alberta Agriculture and Forestry (AAF) and the forest industry. The data for white spruce and trembling aspen mixedwood stands used in Chapter 4 were collected from four Forest Management Units (FMUs) managed by Alberta-Pacific Forest Industries Inc. (Al-Pac). The data analyses from Chapters 2 to 4 are original work by Dawei Luo, with the assistance of Drs. Barb R. Thomas, Phil G. Comeau, Yuqing Yang, Greg A. O'Neill and Esteban Galeano Gomez.

Chapter 2 has been published as Luo, D. and Thomas, B.R. (2021), "An analysis of age-age correlations in white spruce and lodgepole pine and how it applies to the growth and yield projection system (GYPSY) in Alberta", *Forest Ecology and Management*, vol. 482, 1-16. I was responsible for data analysis and manuscript composition. Barb R. Thomas was the supervisory author and was involved with concept formation and manuscript composition. Chapters 3 and 4 are currently being submitted to peer reviewed journals. In Chapters 3 and 4, I was responsible for data analysis and manuscript composition. Greg A. O'Neill, Yuqing Yang, Esteban Galeano Gomez and Barb R. Thomas are the co-authors in Chapter 3, and assisted me with manuscript editing and data analysis. Phil G. Comeau and Barb R. Thomas are co-authors in Chapter 4 and assisted with the sampling design for data measurement on existing stands, data analysis and manuscript editing.

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Table of Contents

List of Tables

List of Figures

Glossary of Terms

AIC	Akaike's Information Criterion
AFGRMs	Alberta Forest Genetic Resource Management and Conservation Standards
AMB	Average model bias
BLUEs	Best Linear Unbiased Estimates
BLUPs	Best Linear Unbiased Predictions
BV	Breeding value
CanSEM2	Canadian Earth System global circulation model
CPP	Controlled Parentage Program
DBH	Diameter at breast height (1.3m)
EF	Efficiency
GW	Genetic worth
GYPSY	Alberta's Growth and Yield Projection System
Htp	Height proportion between specified populations
IGFs	Individual Genecology Functions
Pl	Lodgepole pine
PTF	Adjusted Pooled Transfer Function
RCP	Representative Concentration Pathways
RMB	Relative model bias
RMSE	Root mean square error
RMSEP	Root mean square error of prediction
SI	Site index
Sw	White spruce
URF	Universal Response Function
UTF	Universal Transfer Function

Chapter 1: General Introduction

1.1 Background of forestry in Alberta, Canada

Canada has 347 million ha of forest which account for 9% of the world's forests and covers 38% of Canada's land area. About 270 million ha of Canada's forests are located in the boreal zone (Natural Resources Canada 2019). In Alberta, approximately 60% of the area is forested, with a majority of the forest land in the vast Boreal Forest Natural Region, and an additional strip of forested land running down the eastern slopes of the Rocky Mountain and Foothills Natural Regions (AWA 2021).

Forests play an important role for Canadians with their huge economic and ecological values. In 2019, there were over 200,000 people hired by the forest sector, and over 20 billion dollars contributed to Canada's Gross domestic product (GDP) from Canada's forest sector. In addition, over 70% of Canada's indigenous people live in or near forests (Natural Resources Canada 2019). The forest industry is also one of the pillars of industry in Alberta and directly employs 18,700 Albertans and 25,300 people in supporting occupations and revenues exceeded $6.5 billion dollars in 2020 (GoA 2021).

1.2 Background of tree improvement

1.2.1 History of tree improvement

Plant breeding has a long history and can be traced back to approximately 13,000 years ago in the Near East, and subsequently and independently in many different parts of the world (Balter 2007). Since the beginning of agriculture, humans have noted the importance of selecting plants with desirable characteristics as seed sources for the future. As time progressed, people started incorporating trees into the range of plant breeding, and using trees as timber, firewood and pulp. Records of systematic management of forests have been found in many civilizations since timber and firewood were the basic resources for energy, construction and housing in the preindustrial age (Mirov and Hasbrouck 1976; Rackham 2001; Grove and Rackham 2003; Radkau 2011).

Modern tree breeding was first introduced by Hans Carl von Carlowitz, who wrote the first comprehensive treatise about sustainable yield forestry in 1713 (Carlowitz 2017). In the 19th century, the theories of inheritance and natural selection contributed by Mendel (1865) and Darwin (1859) made it possible to understand the genetics behind the application of plant breeding.

Tree improvement involves the application of principles of forest genetics in developing high yielding, healthy and sustainable plantation forests. Following principles of forest genetics and relevant disciplines, tree improvement changes the genotypes of plants by selecting specific heritable traits that can meet human needs, such as larger volume, faster growth and better disease resistance (White *et al.* 2007). A tree improvement program includes a continuous cycle of population selection, breeding and testing (White *et al.* 2007). Healthy parent trees are first selected in natural stands, and their scions and seeds are collected. Through progeny trials, in which the growth variation attributed to genotypes is tested in specific environments using collected seeds, families with improved traits of interest are selected. Seed orchards are then established with scions from selected families to produce improved seed for reforestation, and selected families are preserved for use in the next breeding cycle (White *et al*. 2007).

Tree improvement programs started in the first half of the 20th century, with scattered efforts in provenance testing and selection. Since the 1950s, large scale tree improvement programs meant to develop field methods including selection, grafting, pollen extraction, controlled pollination and progeny tests have been established in more than 14 countries. Today, tree improvement is a widely used method for getting genetically improved varieties of forest trees (White *et al.* 2007).

1.2.2 Tree improvement development in Canada

In Canada, research in tree improvement was initiated in the 1910s with testing and selecting non-native species, used primarily as shelterbelts in the Prairies (Fowler and Morgenstern 1990). To address the unacceptably high losses caused by fire, insects and fungal diseases, and to increase the harvestable forest wood, since the 1970s, more intensive forest management throughout the entire country has been applied (Fowler and Morgenstern 1990). In the meantime, reforestation by seeding and planting has become a commonly accepted method as a part of forest management. Reforestation also brings with it the recognition and importance that superior seedlings can be achieved via genetic methods (Fowler and Morgenstern 1990).

1.2.3 Tree improvement development in Alberta

In Alberta, tree improvement programs were started in 1975, with eight out of 28 native tree species being incorporated into 24 controlled parentage programs (CPPs), including white spruce (*Picea glauca* (Moench) Voss), lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.), black spruce (*Picea mariana* (Mill.) B.S.P), jack pine (*Pinus banksiana* Lamb.), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mirb.) Franco), western larch (*Larix occidentalis* Nutt.), and more recently, balsam poplar (*Populus balsamifera* L.) and trembling aspen (*Populus tremuloides* Michx.) (ATISC 2008, 2010, 2011). Each program has a corresponding CPP region and typically an independent seed orchard (production facilities) and associated progeny testing trials (AAF 2016a). CPP refers to a program, usually a breeding program, geared to produce *Stream 2* material for deployment within the associated CPP region, and a CPP region is defined as a geographic area with ecological and geographical proximity (usually consisting of several *seed zones*, which refer to the geographic area for deployment of *Stream 1* material) to produce and deploy the *Stream 2* material (AAF 2016a). *Stream 2* material refers to registered or registerable seed or vegetative material produced from an approved *production population* or *production unit* (e.g. a seed orchard), and *Stream 1* material refers to seed or vegetative material collected from wild or artificially regenerated stands (including *Stream 1* seed orchards) of native species within a given *seed zone* (AAF 2016a).

The seeds produced from an orchard in a breeding program constitute an improved seedlot. For each improved seedlot, a genetic worth (GW) value is used as an important attribute to represent its expected genetic gain of a trait of interest (usually height) at a designated rotation age when the seedlot is used for reforestation (AAF 2016a). Currently, GW is estimated as the mean breeding value (BV) of all families in a seedlot weighted by the proportion of gametes contributed by each family (AAF 2016a). BV refers to a genetic value of an individual at a specific age and is usually expressed as a percent deviation from the population mean, and genetic gain refers to the heritable change in the population mean for a specified trait as a result of selection and breeding (AAF 2016a).

1.3 Major challenges for Alberta's forestry and tree improvement programs

1.3.1 Challenge of estimating genetic gain at rotation age

Alberta's forestry has been facing a shrinking forest land-base in the past few decades, which is associated with land deletions for recreation, habitat, energy and other uses (Schneider and Dyer 2006). In addition, multiple studies have reported rapid climate change and its associated increases in mortality, age-independent growth reduction (Mbogga *et al.* 2009; Fettig *et al.* 2013; Wang *et al.* 2014; Hogg *et al.* 2017). The decrease in forest landbase and reduced forest productivity are likely to have a significant impact on

Alberta's forestry sector.

Tree improvement shows great potential for forest-based ecological and economic benefits and is recognized as one of the most efficient approaches in addressing the issues raised above through the application of forest genetics principles in developing high yielding, healthy and sustainable plantation forests (White *et al*. 2007). Tree improvement programs can contribute to an increase in growth rate (e.g. height and diameter growth), better wood quality (e.g. wood density and stiffness) (Carlisle 1970; Vargas-Hernandez and Adams 1990; Isik and Li 2003; White *et al.* 2007; Fundova *et al.* 2019; Hassegawa *et al.* 2019). resistance to insects and disease (Zobel and Talbert 1984; White 1987; Burdon 2001), and adaptability to environmental variation (e.g. drought resistance) (Daniel and Kenneth 1998; Harfouche *et al.* 2014).

Due to the cold climate and slow growth rate of trees in the boreal forest, progeny trials in Alberta, which were recently established, only have tested trees up to approximately 30 years old and are not able to provide sufficient measurements to reach rotation ages. Lack of direct measurement at rotation (e.g. approximately 70 years for lodgepole pine and approximately 100 years for white spruce) makes it challengeable to estimate yield of improved seedlots at rotation. Currently, the selection of families occurs at an age considerably younger than the anticipated rotation age. However, given that genes functioning at an early age may not be the same as those functioning at an older age, genetic gain of selected families may diminish with increasing age (Xie and Yanchuk 2003). The diminishing gain with increasing age also requires a minimum selection age, for example, with an anticipated rotation of 100 years, selections can be made at no less than age 14 following the Alberta Forest Genetic Resource Management and Conservation Standards (AFGRMs) 2016 standards (AAF 2016b).

1.3.2 Challenge of understanding the interaction between climate change and tree improvement

Alberta has become warmer and somewhat drier in the past century (Wang *et al.* 2014; Jiang *et al.* 2015). According to a 50-km resolution dataset, from the Canadian Grid Climate Data (CANGRD) in 1900-2011, the trend of warming and drying has already been observed in Alberta, especially in central and southern Alberta. In northern Alberta, although 13 to 22% of observed precipitation showed a significant increasing trend, most temperature observations also showed a significant increasing trend of up to 0.05 °C year^{-1} in winter (Jiang *et al.* 2015). From the 2020s to 2080s, temperature is projected to increase at the provincial scale, with the largest increase in winter, and variable change precipitation between -25 and +35% is projected (Jiang *et al.* 2015). These findings indicate that water resources will become more critical in the future. For long-lived tree species, due to their relatively slow rate of growth and migration, the probability of a mismatch between populations and their most adaptive climate condition will increase, and as a consequence, lead to a decrease in distribution area, tree growth, and survival (Mbogga *et al.* 2009; Fettig *et al.* 2013). A relevant study has reported that all major tree species across North America have been under stress from increasing drought, and the associated mean mortality has increased from 1.1% yr^{-1} in 1951 to 2% yr^{-1} in 2014 across North America (Hember *et al.* 2017). In Alberta, climate change has accounted for a large amount of variation in mortality, growth and distribution area for major tree species, such as white spruce (Hogg *et al.* 2017), trembling aspen (Chen *et al.* 2018; Cortini and Comeau 2019), and lodgepole pine (Monserud *et al.* 2008), and the current trend of climate change effects is projected to continue in the future.

Provenance trials, which do not typically retain any family structure, focus on the growth variation attributed to environmental differences across populations (Morgenstern 1996; Weber and Montes 2012). Using data from provenance trials, previous studies have developed Universal Response Functions (URF) and Universal Transfer Functions (UTF) to investigate the response of different populations to variation in climate (O'Neill *et al.* 2008; Wang *et al.* 2010; O'Neill and Nigh 2011; Nigh 2014; Yang *et al.* 2015). However, neither URF nor UTF has yet to address the question about how improved seedlots will perform at rotation ages under various climate change scenarios. Using the meta-data from provenance trials of white spruce and hybrid spruce (*Picea engelmannii* Parry ex Engelmann x *Picea glauca* (Moench) Voss), Ahmed *et al*. (2016, 2020) developed a height trajectory meta-analysis model by using a random coefficient non-linear mixed effect model and has applied it in adjusting genetic gain estimates with an increasing age for white spruce and hybrid spruce. However, applying this method on other tree species, especially in Alberta, has not yet been tested.

1.3.3 Challenge of gain estimate for improved seedlots deployed in mixedwood stands

The boreal mixedwood forest, which refers to a tree community on a boreal mixedwood stand, in which no single species comprises 80% or more of the total basal area, is distributed across southern portions of Canada (MacDonald 1995). Under natural conditions, development of a boreal mixedwood stand is characterized by four stages: stand initiation, stem exclusion, canopy transition, and gap dynamics (Chen and Popadiouk 2002). Due to a higher frequency of disturbance (e.g. wild fire), mixedwood stands play a prominent role in the boreal forests of western Canada, and are characterized by major tree species: white spruce, balsam poplar, trembling aspen and paper birch (*Betula papyrifera* Marsh.) (Chen and Popadiouk 2002; Bergeron *et al.* 2014).

In forest management, mixtures of multiple tree species are considered an important approach for conservation of species biodiversity, especially at the landscape scale (Cavard *et al.* 2011), as well as forest productivity, and resistance and resilience to insect infestation, drought and temperature stresses (Ammer 2017; Brassard *et al.* 2010; Cavard *et al.* 2011; Zhang *et al.* 2012; MacLean and Clark 2021). However, selection of improved families in progeny trials does not account for inter and intra-specific competition effects. Due to the complexity and uncertainty in mixedwood stands, in Alberta, current policy only considers genetic gain of improved seedlots that are deployed in pure species managed stands (AAF

2016b).

Realized gain trials, which consider the comparative environments (e.g. ecosites) and deployment strategies (e.g. planting density) between improved (from an orchard breeding program) and unimproved seedlots (from wild stand seed zones), and timing that permits interpretation of rotation age outcomes with reasonable confidence, are typically used to corroborate estimates of gain from progeny trials (Weng *et al.* 2008). The realized gain trials in Alberta, however, were only initiated in 2016 (internal report of Alberta Operational Tree Improvement Monitoring Subcommittee 2018), and data are not yet available to verify realized gain estimates for improved seedlots in either mixedwood or pure stand. Therefore, data from progeny trials are used for estimating genetic gain.

1.4 Importance of white spruce and lodgepole pine

White spruce is a mid-late successional conifer species and has a transcontinental range in North America, with a distribution area across Canada along the northern limit of trees (approximately latitude 69ºN) and extending south to South Dakota (approximately latitude 44ºN) (Burns and Honkala 1990). Lodgepole pine is a ubiquitous, early successional conifer tree species that grows throughout the Rocky Mountains and Pacific coast region, extending north to Yukon area (approximately latitude 64ºN) and south to latitudes around 31º N (Burns and Honkala 1990).

White spruce and lodgepole pine are the two most important commercial tree species in

Alberta, with approximately 80 million seedlings planted each year, and over 90% accounted for by white spruce (with 17% improved seed historical use) and lodgepole pine (with 13% improved seed historical use). In 2019, 65% of reforested white spruce and 21% of reforested lodgepole pine were derived from genetically selected (improved) seed sources (pers. Comm. A. Benowicz, 2019, Govt. of Alberta).

1.5 General objective and thesis structure

Considerable investments have been made in tree improvement in Alberta, resulting in the development of 24 CPPs across the province (ATISC 2008, 2010, 2011), and an increasing percentage of improved seedlots for white spruce and lodgepole pine (pers. Comm. A. Benowicz, 2019, Govt. of Alberta). The economic potential from tree improvement was highlighted in recent financial analyses in Alberta (Schreiber and Thomas 2017; Chang *et al.* 2018), and use of improved seed, as long as available, is currently required (AAF 2016b). However, a fixed percentage gain throughout the rotation was assumed by previous research (Schreiber and Thomas 2017; Chang *et al.* 2018), while there is still a lack of information on predicting the effect of tree improvement on growth and yield with a consideration of diminishing genetic gain with increasing age. Given the rapid climate change and corresponding effect on forest productivity, climate variables are becoming more important when estimating growth and yield of trees, and the effect of climate change on tree improvement programs needs to be determined. In addition, the important role of mixedwood stands in the boreal forests of Alberta makes it imperative to understand performance of improved seedlots when deployed in mixedwood stands. Therefore, the general objective of this program was to provide a tool to estimate yield information of improved seedlots of white spruce and lodgepole pine, with or without climate change effects, and to support forest management decisions to maximize both economic and ecological benefits from tree improvement programs.

To achieve this general objective described above, this thesis is organized into five chapters, including three data chapters (Chapters 2-4). Chapter 1 is the general introduction of this thesis; Chapter 2 focuses on estimating genetic gain at rotation age and corresponding growth and yield for improved white spruce and lodgepole pine; Chapter 3 focuses on climate change effects on improved white spruce and lodgepole pine; Chapter 4 focuses on early growth of improved white spruce in mixedwood stands in northeastern Alberta; and Chapter 5 is the general conclusions from the research presented in this thesis.

Chapter 2: An analysis of age-age correlations in white spruce and lodgepole pine and how it applies to the growth and yield projection system (GYPSY) in Alberta

2.1 Introduction

Alberta forestry is facing an unoptimistic trend with a shrinking forest land-base resulting from land conversion, creation of reserves, climate change and the impact of fire and insects (Schneider and Dyer 2006; Mbogga *et al.* 2009; Fettig *et al.* 2013; Wang *et al.* 2014). A shrinking operational land-base and a continued drying trend is proving detrimental to both forest ecosystems and the forest industry in Alberta (Hogg *et al.* 2017). Tree improvement shows great potential for forest-based ecological and economic benefits and is recognized as one of the most efficient approaches in addressing the issues raised above through the application of forest genetics principles in developing high yielding, healthy and sustainable plantation forests (White *et al.* 2007). Tree improvement programs have been underway in Alberta since 1975 (ATISC 2008, 2010, 2011), and improved seed originating from Controlled Parentage Programs (CPP) (e.g., tree breeding programs) is required in artificial reforestation whenever availabe (AAF 2016b). Therefore, there is considerable need for quantifying the amount of volume gain anticipated at harvest in order to provide reasonable estimates for a company's annual allowable cut (AAC) calculation (SRD 2016).

The growth and yield projection system (GYPSY) model is commonly used in Alberta to predict the forest growth and yield as a function of age, site index (SI) and stand density (Huang *et al.* 2009). In GYPSY, site index refers to top height at total age 50. Top height, used to describe the productivity of a site, comes with multiple definitions, such as mean height of dominant and codominant trees over the life of the stand, the average height of the 100 trees with the largest diameter at breast height (1.3m) per hectare of the last measurement taken, etc. (Sharma *et al.* 2002; Skovsgaard and Vanclay 2008). In Alberta, the top height refers to the average height of 100 trees with the largest diameter at breast height per ha. GYPSY is reliable for, and built using, wild stands. However, fitting GYPSY to improved stands is still at a preliminary stage, and one important challenge is the lack of growth information of improved trees at rotation age.

Previous studies have suggested applying an age-age correlation to growth and yield models (Xie and Yanchuk 2003; Newton 2015). The age-age correlation refers to, in the case of tree improvement, the correlation of the same trait (e.g. height) at different ages, and it is based on a very important quantitative concept: the expectation of a correlated response to selection (Falconer and Mackay 1989). The genetic gain at rotation age (e.g. 100 years) is predicted through an age-age correlation with the genetic gain measured at a much younger selection age (e.g. 10-20 years). Top height and SI are the main drivers of GYPSY, therefore, one option for incorporating genetic gain into GYPSY could be to modify the top height functions through adjustment of genetic worth (GW) values (the average level of genetic gain expected for the trait of interest for a seedlot) and the age-age correlation.

The model from Lambeth's (1980) is a commonly used simple linear regression model to estimate age-age correlation, based on the age ratio between selection age and rotation age, and was used in Alberta (AAF 2009) until 2016. Since yield predictions prior to or after the designated rotation age could be under- or over-estimated, Rweyongeza (2016) modified the age-age correlation to non-linear regression models and developed separate correlation models for different selection ages, specifically for interior lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.) and white spruce (*Picea glauca* (Moench) Voss) in Alberta. Even though several studies have reported that the model from Lambeth (1980) may under- or over-estimate genetic gain in some circumstances (Kung 1993; Gwaze *et al.* 2000; Osorio *et al.* 2003; Isik *et al.* 2007), it is still considered an effective model for predicting age-age correlation and is used for all species in British Columbia (details available at https://www.for.gov.bc.ca/hti/projects/geneticworth.htm accessed on June 8th 2020).

A single reference population is a key concept for estimating genetic correlations, since genetic correlations are strongly influenced by allele frequencies, which are different in each population (Falconer and Mackay 1989). Differences in allele frequencies are therefore expected to influence the corresponding parameter estimates and may affect the age-age correlation predictions. However, Lambeth's (1980) model has a constant intercept and regression coefficient for all species with no adjustment between populations. According to the Alberta Forest Genetic Resource Management and Conservation (AFGRMs) 2016 Standards (AAF 2016b), seed produced from an approved seed orchard cannot be transferred to other CPP regions (a geographic area with ecological and geographical proximity for a specific CPP) except for testing (AAF 2016a). These key concepts and policies are not completely consistent with how Rweyongeza (2016) developed his age-age correlation estimates, as they were based on a combination of both progeny and provenance trials. For example, seedlots originating from different CPP regions should be taken as independent populations with their own age-age correlation matrices, and therefore should be excluded from current within-region age-age correlation models. In addition, several provenance trial sites used in the model from Rweyongeza (2016) were located outside of their designated CPP breeding regions (Pine Ridge, Hangingstone and Calling Lake for lodgepole pine) and therefore should also be excluded from the development of the age-age correlation equations.

White spruce and lodgepole pine are the two most important commercial tree species in Alberta (ATISC 2008, 2010, 2011). Therefore, Chapter 2 focuses on the question: what is the quantitative method that could be used to estimate the yield of improved stands for white spruce and lodgepole pine at rotation age? Using the latest measurements from all progeny trials for white spruce and lodgepole pine in Alberta, Chapter 2 addressed this question by: 1) adjusting the age-age correlation equations developed by Lambeth (1980) and Rweyongeza (2016); 2) exploring other potential methods for establishment of a robust age-age correlation; and 3) modifying the top height-age curve based on an adjusted age-age correlation and predict the volume per hectare from improved seedlots with different genetic worth values.

2.2 Materials and Methods

2.2.1 Data Resources

In Alberta, there are nine white spruce CPPs (breeding regions) (Gray *et al.* 2016a) and six lodgepole pine CPPs (Gray *et al.* 2016b) each with their own set of progeny trial tests. Since realized gain trials are not yet able to provide sufficient data, serial height measurements, available from most of the progeny trials associated with these 15 tree improvement programs of lodgepole pine and white spruce, were used for the analyses. All progeny trial data[1] were provided by the government of Alberta, with approval from the program owners.

Only trial series with at least three height measurements were used for age-age correlation estimation, and therefore this limited me to first-generation progeny trials only. In addition, only families tested within their parent origin CPP regions were selected (Table 2.1).

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[1] Serial height measurement

Table 2.1 Species, trial series code, controlled parentage program (CPP) region codes and age of available height measurements for six white spruce (Sw) and five lodgepole pine (Pl) progeny trial series in Alberta used for analysis in this study

Species	Trial Series	CPP regions	Number of sites	Age of height measurements
Sw	G132	D1	2	8, 10, 15, 16, 21, 24, 30
	G133	D1, G2, H	3	11, 12, 18, 21, 24, 31
	G135	G1, G2	2	10, 11, 15, 16, 18, 21
	G156	E	3	10, 11, 15, 18, 24
	G157	D1, H	2	10, 11, 15, 18, 25
	G352	G2	3	4, 7, 10, 16
Pl	G127	B1	4	11, 15, 19, 27
	G128	C	4	9, 23, 30
	G154	B2	2	6, 11, 14, 20
	G293	K1	2	6, 11, 14, 20
	G346	J	3	6, 9, 15

2.2.2 Fitting and comparing alternative age-age correlation equations

2.2.2.1 Fitting of age-age correlation equations

Equations (2.1) and (2.2) represent the models of Lambeth's (1980) and Rweyongeza's (2016), respectively.

$$\hat{r}_{si,ri} = a + b * LAR \tag{2.1}$$

$$\hat{r}_{si,ri} = \beta_0 * \exp{(\beta_1 * LAG)} \qquad (2.2)$$

Where $\hat{r}_{si,ri}$ is the age-age correlation between selection age and rotation age ; $LAR = log_e(selection\ age/rotation\ age)$; $LAG = ri - si$; ri is rotation age; si is selection age; a, b, β_0, β_1 are parameters with no biological interpretation.

Following the single reference population principles, parameters from Lambeth's (1980) model were re-estimated separately for white spruce and lodgepole pine based on the latest progeny trial data in Alberta, and parameters from Rweyongeza's (2016) model were re-estimated excluding the provenance trial data. The models with estimated parameters were named as the 'adjusted Lambeth equations' and 'adjusted Rweyongeza equations' respectively. To avoid confusion, the original Lambeth (1980) and Rweyongeza (2016) models are typically named 'Lambeth's (1980) equation' and 'Rweyongeza's (2016) equation' in a conventional way. Following this logic, the models for age-age correlation estimates will be referred to as 'age-age correlation equations' in this thesis. All age-age correlation equations were developed to predict age-age correlation coefficients and the results from these equations were compared.

2.2.2.2 Age-age correlation matrix establishment for adjusted Lambeth and adjusted Rweyongeza equations

Given that the minimum selection age in years=4+0.1*(midpoint of rotation age class ±5 years), according to Table 30.1 in AFGRMs (AAF 2016a), measurements of trees < 5 years old and the combinations of height at different ages, which do not meet the standard, were excluded from the analysis. Trees recorded as being significantly crooked or affected by insects or disease were also excluded from the analysis. Bulk family seedlots in progeny trials, which are a mix of multiple families, were not included in the calculation of the age-age correlations. The height measurements of individual trees that met these criteria were retained for further analysis, and a Pearson's correlation coefficient was used to build a separate age-age correlation matrix for each CPP region.

The age-age correlation matrix for the adjusted Rweyongeza equations was established following the methods proposed by Rweyongeza (2016). Since LAG (difference between selection age and rotation age) was used as the explanatory variable, which requires more data points than currently available to establish age-age correlation curves for separate selection ages, Rweyongeza (2016) used a combination of a power function and logistic function to extrapolate the height-age curves until expected rotation ages assuming the same asymptote as for wild trees (Meng and Huang 2010), as shown in Equations (2.3) and (2.4). Next, a hybrid dataset, which consisted of both observed height measurements from progeny and provenance trials and estimated heights from Equations (2.3) and (2.4), were used to establish an age-age correlation matrix. The same method was repeated for the adjusted Rweyongeza equations by using the most recent and comprehensive progeny trial data excluding provenance trial data and families tested outside their parent origin CPP regions. Since height at an older age could be shorter than height at a younger age in the hybrid dataset, only the estimated heights from Equations (2.3) and (2.4) were used to calculate the age-age correlation.

$$HT_i = k/(1 + q * exp(R * i)) \tag{2.3}$$

$$HT_i = A * i^B \tag{2.4}$$

Where HT_i is the tree height at total age i; k is the height asymptote in the logistic curve; i is total age of the tree; R is the growth rate in the logistic curve; q, A, B are the shape parameters. Since Lambeth's (1980) equation was originally developed based on observed height measurements, the adjusted Lambeth equations were also based on available height measurements from the progeny trials and not based on the hybrid dataset that Rweyongeza's (2016) equations used.

2.2.2.3 Non-asymptotic sigmoid curves vs. asymptotic sigmoid curves in the establishment of the age-age correlation matrix

The asymptote of forest trees varies with site productivity. According to observed growth data from Meng and Huang's (2009) research, white spruce and lodgepole pine, in some of Alberta's wild forest stands, showed no asymptote beyond 120 years. A similar trend has also been shown in some of boreal forests of Europe (Bontemps and Duplat 2012), where no clear asymptote was reached. Bontemps and Duplat (2012) have developed a sigmoidal curve with an upper oblique asymptote, called the sigmoid with parabolic branch (SPB) equation. This method includes a first-order autonomous differential model with four parameters, and its numeric integration, as shown in Equation (2.5). To explore other potential methods for age-age correlations, I also used an SPB function and its numeric integration to replace the logistic curve used in the establishment of Rweyongeza's (2016) equations.

$$dHT/di = (R_m * (h/K_R)^{m1*m2})/(1 - m1 + m1 * (h/K_R)^{m2}) \qquad (2.5)$$

Where HT is tree height; i is total age; R_m the maximum growth rate in SPB; K_R is the tree height when growth rate reaches the maximum; $m1$ and $m2$ are the shape parameters. Since Equation (2.5) has no analytical closed-form solution, the Runge-Kutta 4 (RK4) method of numerical integration was used to estimate height curves (Bontemps and Duplat 2012). Unlike the logistic curve, SPB does not have a clear asymptote. Therefore, instead of assuming identical asymptotes as for wild trees as proposed by Rweyongeza (2016), I assumed that the mean values from the progeny trees have similar height curves with top height trees as found in the fire origin stands.

The first step in developing the SPB function was to use the mean height of progeny trees at three ages as the reference points to look for the appropriate top height (the average height of 100 trees with the largest diameter at breast height per ha) curves from the wild trees. This method of selecting mean height of progeny trees is assuming trees in progeny trials were under optimum conditions and equivalent to top height trees as in wild forests. The values used were 1.85m at age 10, 3.01m at age 15, and 8.35m at age 31 for all white spruce progeny, and 2.26m at age nine, 3.66m at age 15 and 10.77m at age 30 for all lodgepole pine progeny. Among all SI (top height at total age 50) values from the ‘Field Guide to Ecosites of West-central Alberta’ and ‘Field Guide to Ecosites of Northern Alberta’ (Beckingham and Archibald 1996a, b), the mean height curves of progeny trees were approximate to the SI (at total age 50) of 12.6m for white spruce and 12.9m for lodgepole pine. Age 120 was selected as the benchmark to estimate height curves for progeny trees even though the typical rotation age for both white spruce and lodgepole pine in Alberta is shorter (Rweyongeza 2013). However, by selecting age 120, I was able to ensure that the age-age correlations calculated based on these estimated curves would cover all possible rotation age scenarios. Consequently, the average height estimated would be approximately 23m for white spruce and 25m for lodgepole pine at age 120 according to the top height curves predicted by GYPSY. In addition, the mean height of the three ages selected from progeny trees, allowed for the assignment of four reference points for each species as the surrogates of logistic asymptotes.

In step two, the SPB function was fitted to the annual increment of progeny trees. Since directly fitting SPB was not feasible due to insufficient annual increment information, a power function and a logistic function were fitted to the progeny trial data to estimate total height at each age until 30-years-old. A logistic function was used in this step since an inflection point is required to fit the SPB function. A power function was used in step two since the mean height of progeny trees was underestimated using only a logistic function. A power function was used to estimate total height for each individual tree up to 13-17 years old. Next, a logistic function was fitted to the estimated heights from a power function and continue to estimate all height values until age 30. This method made the curves of estimated mean height approximate to the three selected heights from the first step, and also guaranteed an inflection point after 30-years-old to avoid underestimation of individual tree heights. The annual height increments up to 30-years-old were then calculated and were fitted by the SPB function. The annual height increments until age 120 were projected using the SPB function, and corresponding total heights were calculated using the Runge-Kutta 4 (RK4) method of numerical integration. In addition, to make the estimated curves approximate to the selected top height curves of wild trees (from the first step) beyond the latest measurement age, constant values for shape parameters $m1$ and $m2$ in the SPB function were assigned for all trees to force the curves to align as closely as possible with the top height tree curves.

In step three, the age-age correlation matrix was then built on estimated height curves of individual progeny trees. The corresponding models developed were named the ‘SPB age-age correlation equations’ in the following sections. Logarithm and exponential models were both used to fit the estimated age-age correlation, and the corresponding SPB age-age correlation equations were denoted as SPB (log) and SPB (exp).

2.2.3 Model validation

Since the phenotypic age-age correlation is an approximate of the genetic age-age correlation (Falconer and Mackay 1989), and typically underestimates the genetic correlations (Hodge and White 1992; Gwaze *et al.* 1997; Lambeth and Dill 2001), the genetic age-age correlation was calculated for each CPP region, based on the observed height measurements, and used the genetic age-age correlation for validation in this study. The family breeding values were estimated at different measurement ages and the corresponding genetic age-age correlation matrix was established (Lambeth and Dill 2001). A linear mixed effects model was used, as shown in Equation (2.6), with blocks nested within sites, and families were replicated across blocks and sites. The breeding value of each family was multiplied by two for the corresponding best linear unbiased predictions (BLUPs). The block effect, in most cases, is taken as a random effect in a mixed effect linear model. However, some studies argue that the block effect is not orthogonal to treatment and should be taken as a fixed effect when estimating BLUPs for families (Dixon 2016; Gezan 2020). Following the method of Gezan (2020), in my study, the block effect was taken as a fixed effect in Equation (2.6). Equation (2.6) was run separately for each measurement age.

$$H_{ikjln} = \mu + S_i + B_{k(i)} + F_j + S_i F_j + P_{l(ij)} + \varepsilon_{ikjln} \tag{2.6}$$

Where H_{ikjln} is the height measurement of individual n in plot l for family j in block k installed in site i; μ is the overall mean of all families installed in the same CPP region from the same progeny trial series; S_i is the fixed effect of site; $B_{k(i)}$ is the fixed block within site effect following the method of Gezan (2020), since the block effect is not orthogonal to treatment and the block effect in the progeny trials is not a random sample from a larger population (Dixon 2016); F_k is the random effect of family; $S_i F_j$ is the interaction between family and site, which is a random effect; $P_{l(ij)}$ is the random plot effect within family; and $\varepsilon_{ikjln} \sim iid(0, \sigma^2)$ is the error following a normal distribution.

Average model bias (AMB) eq (2.7), relative model bias percentage (RMB) eq (2.8) and efficiency (EF) eq (2.9) are commonly used validation metrics and were applied in this study (Loague and Green 1991; Vanclay and Skovsgaard 1997; Huang *et al.* 1999; Bokalo *et al.* 2013).

$$AMB = 1/n * \sum(Y - \hat{\hat{Y}}) \qquad \text{eq (2.7)}$$

$$RMB = 100/n * \sum((Y - \hat{Y})/\bar{Y}) \qquad \text{eq (2.8)}$$

$$EF = 1 - \sum(Y - \hat{Y})^2 \,/\, \sum(Y - \bar{Y})^2 \qquad \text{eq (2.9)}$$

Where n is the number of genetic age-age correlation values calculated from observed tree height (observed genetic age-age correlation values); Y is the genetic age-age correlation value; $\hat{Y}$ is the predicted phenotypic age-age correlation value; $\bar{Y}$ is the average of the genetic age-age correlation values.

Since the data from five CPP regions of white spruce and five CPP regions of lodgepole pine were used, a leave-one-group-out cross-validation approach was used to combine measures of fitness in prediction. Five iterations were conducted and the average of all validation metric values from the iterations were used. In each iteration, the phenotypic age-age correlations from four CPP regions, with corresponding selection ages and rotation ages, were taken as the training set, the genetic age-age correlation from one CPP region, with corresponding selection ages and rotation ages, were taken as the validation set. The training set used for the adjusted Rweyongeza equations and SPB age-age correlation equations were based on the phenotypic age-age correlations calculated from corresponding estimated individual tree heights in each CPP region. The validation set was based on the genetic age-age correlations calculated from observed height measurements. The training sets for adjusted Lambeth equations were based on the phenotypic age-age correlation calculated from observed height measurements and corresponding validation sets were based on the genetic age-age correlation values calculated from observed height measurements. Validation was also conducted for Lambeth's (1980) and Rweyongeza's (2016) equations, and only test sets that consisted of genetic age-age correlations were used since parameter estimation was already provided for the Lambeth's (1980) and Rweyongeza's (2016) models. The explanatory variable LAR was used for validation of Lambeth's (1980) and adjusted Lambeth equations while explanatory variable LAG was used for validation of all other models. After validation, the final adjusted Lambeth equations were built on the whole dataset of phenotypic age-age correlations calculated from observed height measurements, the adjusted Rweyongeza and SPB equations were built based on the whole dataset of phenotypic age-age correlations calculated from corresponding estimated individual tree heights.

2.2.4 Incorporation of genetic gain into GYPSY

The top height functions for unimproved white spruce and lodgepole pine are shown in Equations (2.10) and (2.11) respectively and published in Huang *et al.* (2009). Both functions were adjusted for incorporation of improved trees through GW values and the age-age correlation (eq 2.12).

$$\widehat{HT_{i.Sw}} = SI * (1 + \exp\left(b_1 + b_2\sqrt{\ln(1 + 50^2)} + b_3[\ln(SI)]^2 + b_4\sqrt{50}\right))/(1 + \exp\left(b_1 + b_2\sqrt{\ln(1 + totage_i^2)} + b_3[\ln(SI)]^2 + b_4\sqrt{50}\right)) \qquad (2.10)$$

$$\widehat{HT_{i.Pl}} = SI * (1 + \exp\left(f_1 + f_2\sqrt{\ln(1 + 50)} + f_3[\ln\,(SI)] + f_4\sqrt{50}\right))/(1 + \exp(f_1 + f_2\sqrt{\ln(1 + totage_i)} + f_3[\ln\,(SI)] + f_4\sqrt{50})) \qquad (2.11)$$

$$\widehat{Hgw_{i.Sw}} = \left(\left((GW/100) * r_{si,i} + 1\right)\right) * HT_{i.Sw} \qquad (2.12)$$

$$\widehat{Hgw_{i.Pl}} = \left(\left((GW/100) * r_{si,i} + 1\right)\right) * HT_{i.Pl} \qquad (2.13)$$

Where $\widehat{HT_{i,Sw}}$ and $\widehat{HT_{i,Pl}}$ are the estimated top height (m) at a given total age *i* for unimproved trees (*GW*=0) of white spruce (Sw) and lodgepole pine (Pl), respectively; *SI* is in meters; totage=total age from the point of germination; $\widehat{Hgw_{i.Sw}}$ and $\widehat{Hgw_{i.Pl}}$ are the estimated improved top height at total age (totage) i; *GW* is the genetic worth at selection age expressed as a %, and is the ratio of the weighted average breeding value in an improved seedlot to the average height of all families; $r_{si,i}$ is the genetic or phenotypic age-age correlation coefficient; *si* is selection age; $b_1, b_2, b_3, b_4, f_1, f_2, f_3, f_4$ = parameters with no biological interpretation.

Xie and Yanchuk (2003) suggested that GW at rotation age should be added into the top height of unimproved trees, resulting in the improved tree volume being predicted by the adjusted top height at a given rotation age. The stand density (stems ha^{-1}) in GYPSY is a function of total age, SI at breast height age 50 and a stand density factor (stems ha^{-1} at total age 50). Breast height age refers to the age measured at 1.3m from the ground (Huang *et al.* 2009). Therefore, the SI of improved seedlots (SI adjusted by GW value and age-age correlation) was also used to produce the stand density curves for improved seedlots. The basal area increment in GYPSY is also predicted including SI as a predictor (Huang *et al.* 2009), therefore, the SI of improved seedlots was also used to modify the basal area increment in GYPSY. The modified top height curves, modified stand density curves and modified basal area increment for improved white spruce and lodgepole pine, were then inputted into GYPSY instead of modifying the top height at rotation age as proposed by Xie and Yanchuk (2003).

To produce and compare the top height and stand volume of improved white spruce and lodgepole pine under different GW values, the selection age was set at 15 years. To present the effect of a gradient of GW values, GW height of seedlots was set as 4%, 5%, 6%, 7%, 8%, 9% and 10% at a selection age of 15. The stand volume curves from age 20 to age 250 for white spruce and lodgepole pine were also produced and compared by setting GW values at 5% and 10% at age 15. The non-spatial version of GYPSY, without basal area adjustment, was used. The planting density was set at 2,000 stems ha^{-1}, which corresponds to the ‘high density’ class in the ‘Guidelines for Operational Growth & Yield Monitoring of Improved Seed Deployment & Forest Management Plan Yield Projections’ (internal report of the Alberta Operational Tree Improvement Monitoring Subcommittee 2020). All stands were assumed to be pure species (>80% of the stand area is accounted for by a single tree species) (MacDonald 1995) managed stands.

2.2.5 Software for analysis

All analysis in Chapter 2, models and data were run in the R environment (R Core Team 2018), non-linear functions were run using the packages ‘nlme’ (Pinheiro *et al.* 2020). Graphs were plotted using the package ‘ggplot2’ (Wickham 2016). Equation (2.6) was run in ASReml (Isik *et al.* 2017; Butler *et al.* 2018) under *R* conditions (R Core Team 2018), which is a commercial software that provides considerable flexibility and utility in analyzing breeding program data (Isik *et al.* 2017; Butler *et al.* 2018; R Core Team 2018).

2.3 Results

2.3.1 Age-age correlation

2.3.1.1 Adjusted Lambeth equation

The preliminary results showed that models developed at the individual CPP regional scale had limited residual degrees of freedom. In addition, Some CPPs, such as region J with trial series G346 for lodgepole pine, have limited measurement at very young ages, thus relying on the age-age correlation predicted from the data of other CPPs. Therefore, , data was ultimately analyzed at the provincial scale, combining CPP regions. A generalized linear model following a Gamma distribution with the identity link function was used since the age-age correlation coefficients calculated from observed height measurements did not follow a normal distribution. Lodgepole pine has a larger regression coefficient and intercept than white spruce, indicating that white spruce has higher age-age correlation estimates than lodgepole pine at the same selection age (Table 2.2).

Table 2.2 Parameter estimate, pseudo R^2, and residual degrees of freedom (df) of adjusted Lambeth's equations for white spruce and lodgepole pine (Species) at the provincial scale in Alberta

Species	Equation[a]	R^{2b}	df
White spruce	$\hat{r}_{si,ri} = 0.993 + 0.255(LAR)$	0.761	65
Lodgepole pine	$\hat{r}_{si,ri} = 1.017 + 0.445(LAR)$	0.723	22

[a]: $LAR = log_e(younger\ age/older\ age)$ for those ages used in the calculation of $\hat{r}_{si,ri}$, they would be selection age and rotation age in the final model.

[b]: $R^2 = 1 - (residual\ deviance/null\ deviance)$

2.3.1.2 Adjusted Rweyongeza equation

The mean asymptote value for the estimated individual tree height is 21.84m (±9.01m standard deviation) for white spruce and 22.70 (±10.86m standard deviation) for lodgepole pine, the inflection points are approximate to the 30th year of growth for both species, and the root mean square error (RMSE) of the estimated individual tree height is 0.316m for white spruce and 0.481m for lodgepole pine (Figure 2.1).

Both the pseudo R^2 and the RMSE decrease with an increase in selection ages from fitting an exponential function to the age-age correlation matrix established on the estimated individual tree heights, which suggests that the average deviation from the established age-age correlations matrix decreases when larger selection ages were chosen to predict the age-age correlation; however, this also results in an increased fraction of unexplained variation (Table 2.3).

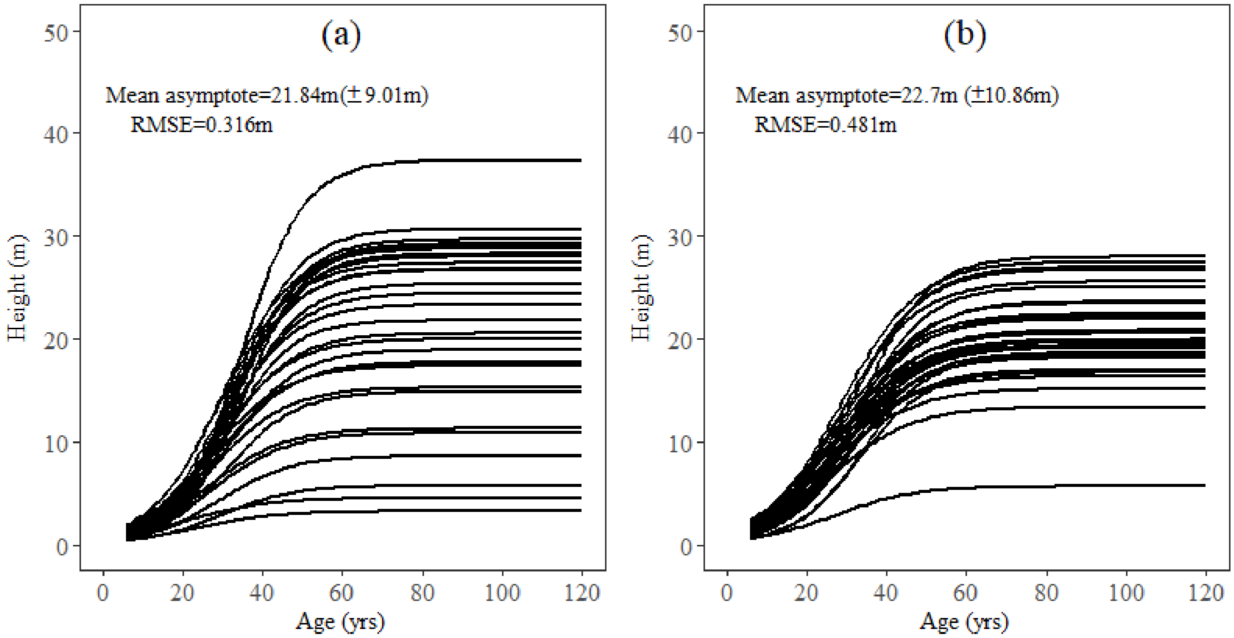

Figure 2.1 Estimated individual tree heights (m) based on Equations (2.3) and (2.4) for white spruce (a) and lodgepole pine (b) up to age 30, data points in the figure are from 30 randomly sampled individuals from the whole dataset of estimated individual tree heights

Table 2.3 Parameter estimates, pseudo R^2 and root mean square error (RMSE, m) based on selection age (yrs) from six to 40, of adjusted Rweyongeza equations[a] for white spruce and lodgepole pine at the provincial scale in Alberta

Selection age	White spruce				Lodgepole pine			
(yrs)	[b] β_0	[b] β_1	[c] R^2	[d] RMSE	[b] β_0	[b] β_1	[c] R^2	[d] RMSE
6	0.87966	-0.00709	0.496	0.13333	1.19803	-0.03640	0.866	0.11330
10	0.88611	-0.00732	0.581	0.11288	0.98893	-0.02189	0.739	0.13459
15	0.86746	-0.00724	0.535	0.11634	0.84373	-0.01006	0.478	0.15152
20	0.84527	-0.00518	0.328	0.13411	0.83922	-0.00465	0.270	0.14120
25	0.87389	-0.00267	0.207	0.10778	0.88954	-0.00203	0.158	0.10206
30	0.93156	-0.00112	0.165	0.05724	0.94404	-0.00080	0.109	0.05328
35	0.97263	-0.00041	0.159	0.02226	0.97835	-0.00027	0.091	0.02024
40	0.99095	-0.00014	0.158	0.00746	0.99325	-0.00008	0.082	0.00603

[a]: $\hat{r}_{si,ri} = \beta_0 * \exp(\beta_1 * LAG)$
[b]: β_0, β_1 = constants with no biological interpretation
[c]: R^2 = pseudo R square
[d]: RMSE = root mean square error

2.3.1.3 Sigmoid with parabolic branch (SPB) age-age correlation equations

The constant shape parameters $m1$=0.39 and $m2$=2.32 were assigned to white spruce and $m1$=0.131 and $m2$=2.57 assigned to lodgepole pine for the SPB function. Shape parameters R_m and K_R were estimated from each tree. The estimated heights after numeric integration then approximated to the top height curves, resulting in a mean height of 21.00m (±13.20m standard deviation) for white spruce and 22.70m (±10.90m standard deviation) for lodgeople pine at age 120. The RMSE of the estimated individual tree height is 0.936m for white spruce and 2.204m for lodgepole pine (Figure 2.2). The larger RMSE indicates that, compared to the logistic function, the individual tree height estimated by the SPB has a larger deviation from the observed height measurement.

With both the logarithm and exponential models, RMSE decreased with an increase in selection ages from fitting an exponential or logarithm function to the age-age correlation matrix established on the estimated individual tree height, suggesting that the average deviation from the established age-age correlations matrix decreased when a higher selection age was chosen to predict the age-age correlation (Tables 2.4 and 2.5).

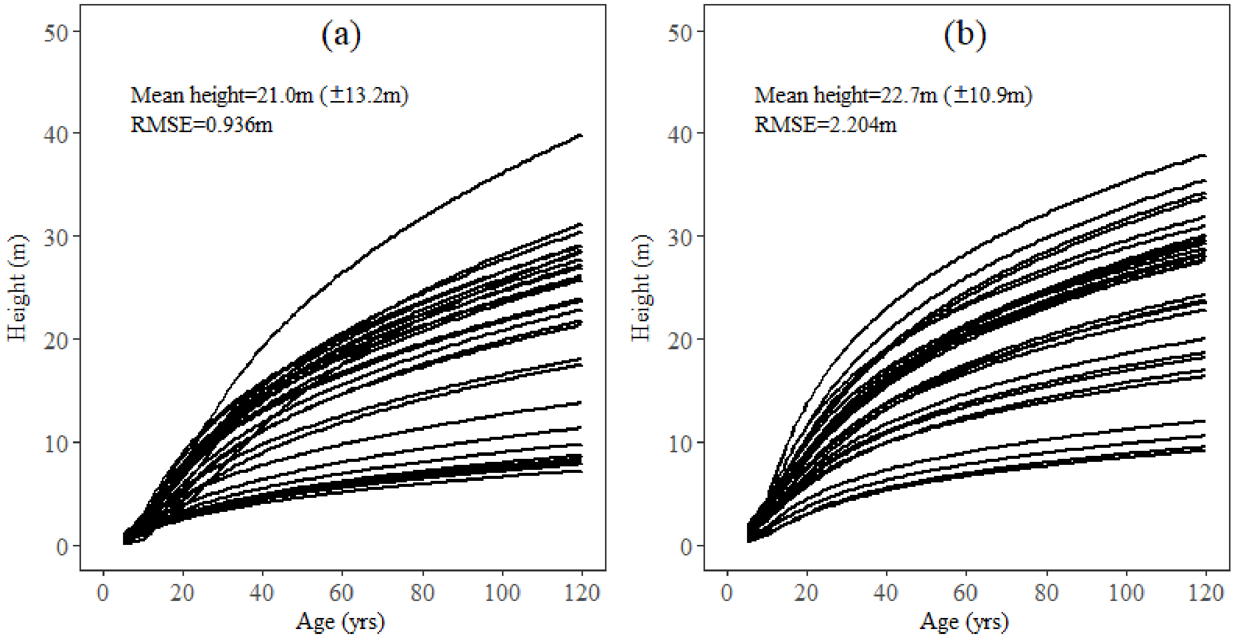

Figure 2.2 Estimated individual tree heights (m) b based on Equations (2.3) to (2.5) for white spruce (a) and lodgepole pine (b) up to age 30, data points in the figure are from 30 randomly sampled individuals from the whole dataset of estimated individual tree heights

Table 2.4 Parameter estimate, pseudo R^2 and root mean square error (RMSE) based on selection age (yrs) from six to 40, of sigmoid with parabolic branch age-age correlation equations exponential version, denoted as SPB (exp)[a], for white spruce and lodgepole pine at the provincial scale in Alberta

Selection age	White spruce				Lodgepole pine			
(yrs)	[b] β_0	[b] β_1	[c] R^2	[d] RMSE	[b] β_0	[b] β_1	[c] R^2	[d] RMSE
6	0.77540	-0.00457	0.177	0.18910	0.64595	-0.00267	0.178	0.10211
10	0.84037	-0.00709	0.214	0.24171	0.93281	-0.00211	0.251	0.09529
15	0.93172	-0.00679	0.293	0.20668	0.98577	-0.00197	0.341	0.07346
20	0.97368	-0.00536	0.353	0.15504	0.99550	-0.00164	0.367	0.05689
25	0.99462	-0.00420	0.392	0.11651	1.00019	-0.00132	0.376	0.04377
30	1.00422	-0.00338	0.399	0.09281	1.00248	-0.00106	0.377	0.03386
35	1.00826	-0.00277	0.389	0.07646	1.00339	-0.00086	0.373	0.02647
40	1.01008	-0.00230	0.370	0.06384	1.00358	-0.00070	0.366	0.02086

[a]: $\hat{r}_{si,ri} = \beta_0 * \exp{(\beta_1 * LAG)}$

[b]: β_0, β_1 = constants with no biological interpretation

[c]: R^2 = pseudo R square

[d]: RMSE = root mean square error

Table 2.5 Parameter estimate, pseudo R^2 and root mean square error (RMSE) based on selection age (yrs) from six to 40, of sigmoid with parabolic branch age-age correlation equations logarithm version, denoted as SPB (log)[a], for white spruce and lodgepole pine at the provincial scale in Alberta

Selection age	White spruce				Lodgepole pine			
(yrs)	[b] β_0	[b] β_1	[c] R^2	[d] RMSE	[b] β_0	[b] β_1	[c] R^2	[d] RMSE
6	1.01384	-0.10899	0.236	0.18213	0.82660	-0.07182	0.352	0.09068
10	1.12109	-0.14440	0.242	0.23727	1.05899	-0.06094	0.264	0.09451
15	1.19670	-0.14439	0.296	0.20635	1.09263	-0.05512	0.318	0.07478
20	1.19083	-0.12064	0.334	0.15738	1.07840	-0.04426	0.327	0.05866
25	1.16380	-0.09629	0.352	0.12034	1.06195	-0.03415	0.322	0.04559
30	1.13479	-0.07652	0.344	0.09701	1.04805	-0.02617	0.313	0.03555
35	1.10854	-0.06081	0.324	0.08043	1.03702	-0.02008	0.302	0.02793
40	1.08643	-0.04818	0.298	0.06737	1.02841	-0.01546	0.289	0.02208

[a]: $\hat{r}_{si,ri} = \beta_0 + \beta_1 * log_e(LAG)$
[b]: β_0, β_1 = constants with no biological interpretation
[c]: R^2 = pseudo R square
[d]: RMSE = root mean square error

2.3.1.4 Age-age correlation curves

To compare between the different LAG based age-age correlation equations in the same plots, Lambeth's (1980) and adjusted Lambeth equations were transformed with LAG as the explanatory variable in Figures 2.3 and 2.4 at the same selection ages. This allows for the presentation of non-linear logarithm curves. The adjusted Lambeth equations predict higher age-age correlation coefficients than Lambeth’s (1980) equation for white spruce across all selection ages, while the adjusted Lambeth equations predict lower age-age correlation coefficients than Lambeth’s (1980) equation for lodgepole pine. The adjusted Rweyongeza equations predict higher age-age correlation coefficients than Rweyongeza’s (2016) equations for white spruce across all selection ages, and both adjusted Rweyongeza equations and Rweyongeza’s (2016) equations predict higher age-age correlation coefficients than the adjusted Lambeth equations for lodgepole pine. Both SPB (log) and SPB (exp) equations show higher predictions than the adjusted Lambeth equations for lodgepole pine.

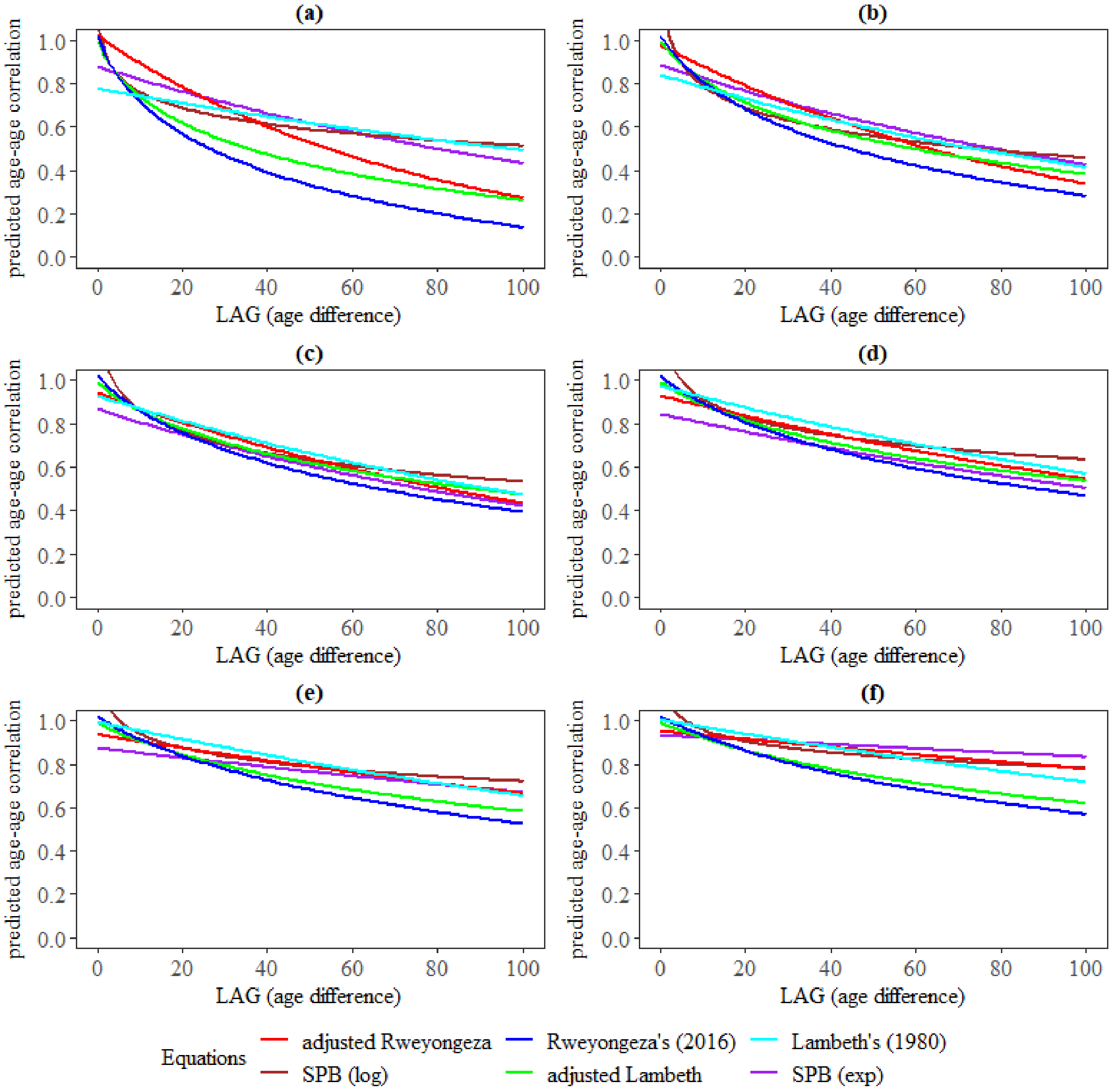

Figure 2.3 Selection age-specific regression plots of age-age correlations using the equations of Lambeth's (1980), adjusted Lambeth, Rweyongeza's (2016), adjusted Rweyongeza, sigmoid with parabolic branch age-age correlation equations exponential version (SPB, exp) and logarithm version (SPB, log) for white spruce at selection age 6 (a), 10 (b), 15 (c), 20 (d), 25 (e) and 30 (f); Lambeth's (1980) and adjusted Lambeth equations were transformed with LAG as the explanatory variable

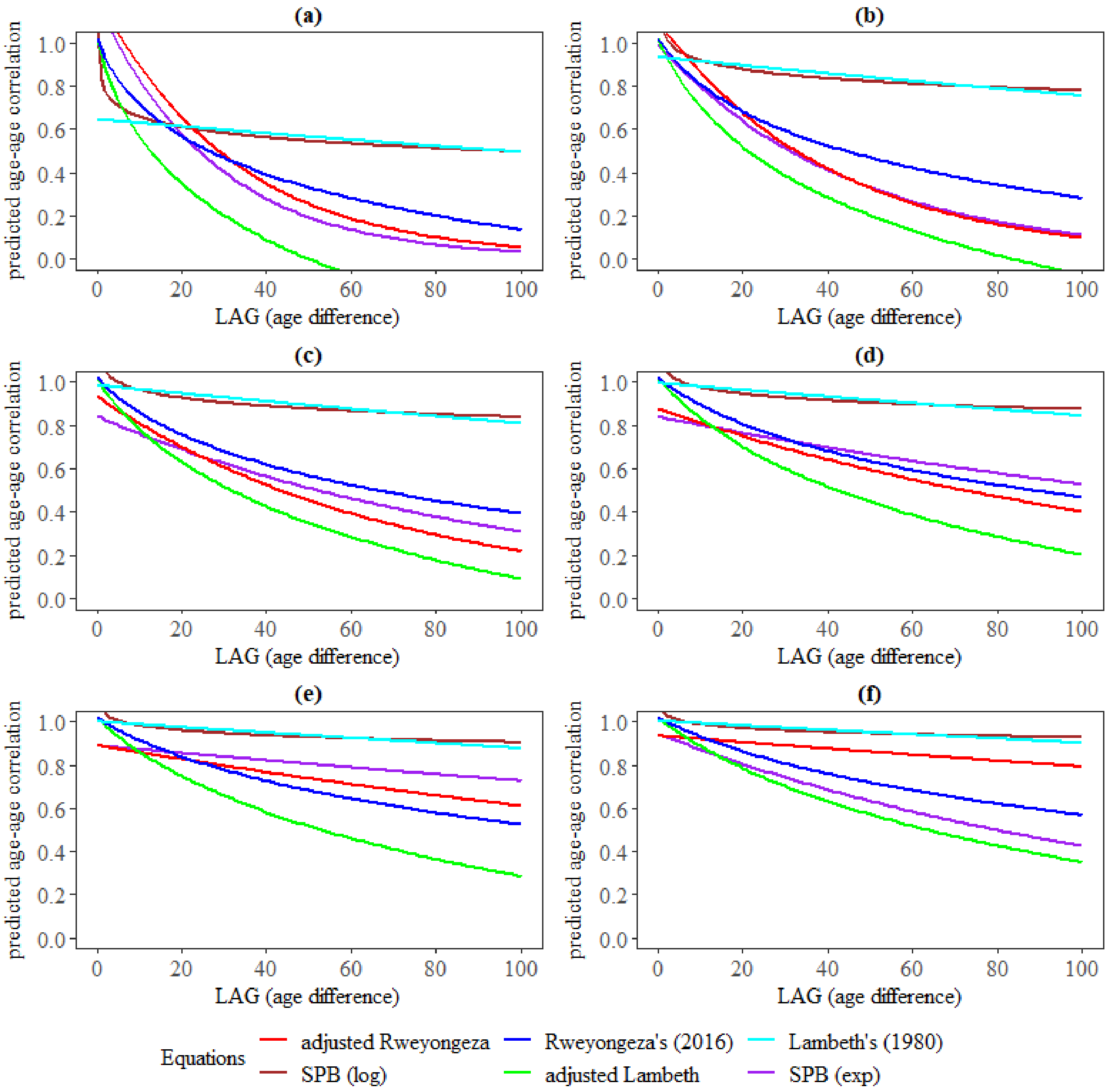

Figure 2.4 Selection age-specific regression plots of age-age correlations using the equations of Lambeth's (1980), adjusted Lambeth, Rweyongeza's (2016), adjusted Rweyongeza, sigmoid with parabolic branch age-age correlation equations exponential version (SPB, exp) and logarithm version (SPB, log) for lodgepole pine at selection age 6 (a), 10 (b), 15 (c), 20 (d), 25 (e) and 30 (f); Lambeth's (1980) and adjusted Lambeth equations were transformed with LAG as the explanatory variable

2.3.1.5 Validation of age-age correlation equations

The adjusted Lambeth equations showed the smallest absolute values of AMB and RMB for both white spruce and lodgepole pine. The t-test showed no significant difference between the observed and predicted age-age correlation for the adjusted Lambeth equations (Table 2.6). Although a t-test does not guarantee that there is no lack of fit, an EF value of 0.561 for white spruce and 0.482 for lodgepole pine indicated a good fit of the adjusted Lambeth equations (a zero or minus EF value indicates a poorer model fit compared with using the overall mean of all observations).

The adjusted Rweyongeza equations showed significant bias for age-age correlation estimations for both white spruce and lodgepole pine (Table 2.6). The minus EF value of adjusted Rweyongeza equations for white spruce and lodgepole pine indicated a poorer model fit compared with simply using the overall mean of observed age-age correlations (Table 2.6).

The exponential version of the SPB age-age correlation equations showed significant bias for prediction of white spruce and lodgepole pine. The logarithm version of SPB age-age correlation equations showed no significant bias in prediction for white spruce. However, a minus EF value indicates a poorer model fit than simply using the overall mean of age-age correlations from the training sets. Fitting the SPB age-age correlation equations to lodgepole pine showed poor validation results regardless of the version, exponential or logarithm (Table 2.6 and Figures 2.6c to 2.6f).

Lambeth's (1980) equation produced a good estimate of the age-age correlation for both white spruce and lodgepole pine. Although the p-value in the t-test showed that the age-age correlations estimated for lodgepole pine from Lambeth's (1980) equation was not significantly different from the observed (Table 2.6), it was still possible for the age-age correlation to be overestimated at older ages since most predictions were above the diagonal (Figures 2.6a and 2.6b). Rweyongeza's (2016) equations ahd minus EF values and a nearly horizontal distribution of data points, indicating a poorer model fit compared with the adjusted Lambeth equations (Table 2.6 and Figures 2.5e and 2.5f).

Overall, the adjusted Lambeth equations showed the most accurate predictions and indicated a higher age-age correlation for white spruce than lodgepole pine at all ages of selection.

Table 2.6 Validation statistics for age-age correlation equations based on progeny trial data of white spruce and lodgepole pine (Species), AMB (average model bias), RMB (relative model bias, percent %) and EF (efficiency) show the average over validation indices in five iterations, p-value is from the t-test between observed and predicted age-age correlations with significant difference marked with an asterisk (*)

Species	Age-age correlation equation	AMB	RMB (%)	EF	p-value
White spruce	Adjusted Lambeth	0.009	1.067	0.561	0.561
	Lambeth's (1980)	0.015	1.453	0.275	0.361
	Adjusted Rweyongeza	0.043	4.764	-0.740	0.002*
	Rweyongeza's (2016)	-0.002	-0.299	0.284	0.547
	SPB (exp)	0.044	4.807	-0.889	0.025*
	SPB (log)	-0.001	-0.132	-1.787	0.976
Lodgepole pine	Adjusted Lambeth	-0.009	-1.472	0.482	0.903
	Lambeth's (1980)	-0.048	-6.536	0.493	0.109
	Adjusted Rweyongeza	-0.086	-11.518	-0.268	0.002*
	Rweyongeza's (2016)	-0.076	-10.156	-0.036	0.007*
	SPB (exp)	-0.084	-11.915	-1.151	0.027*
	SPB (log)	-0.097	-13.581	-0.937	0.008*

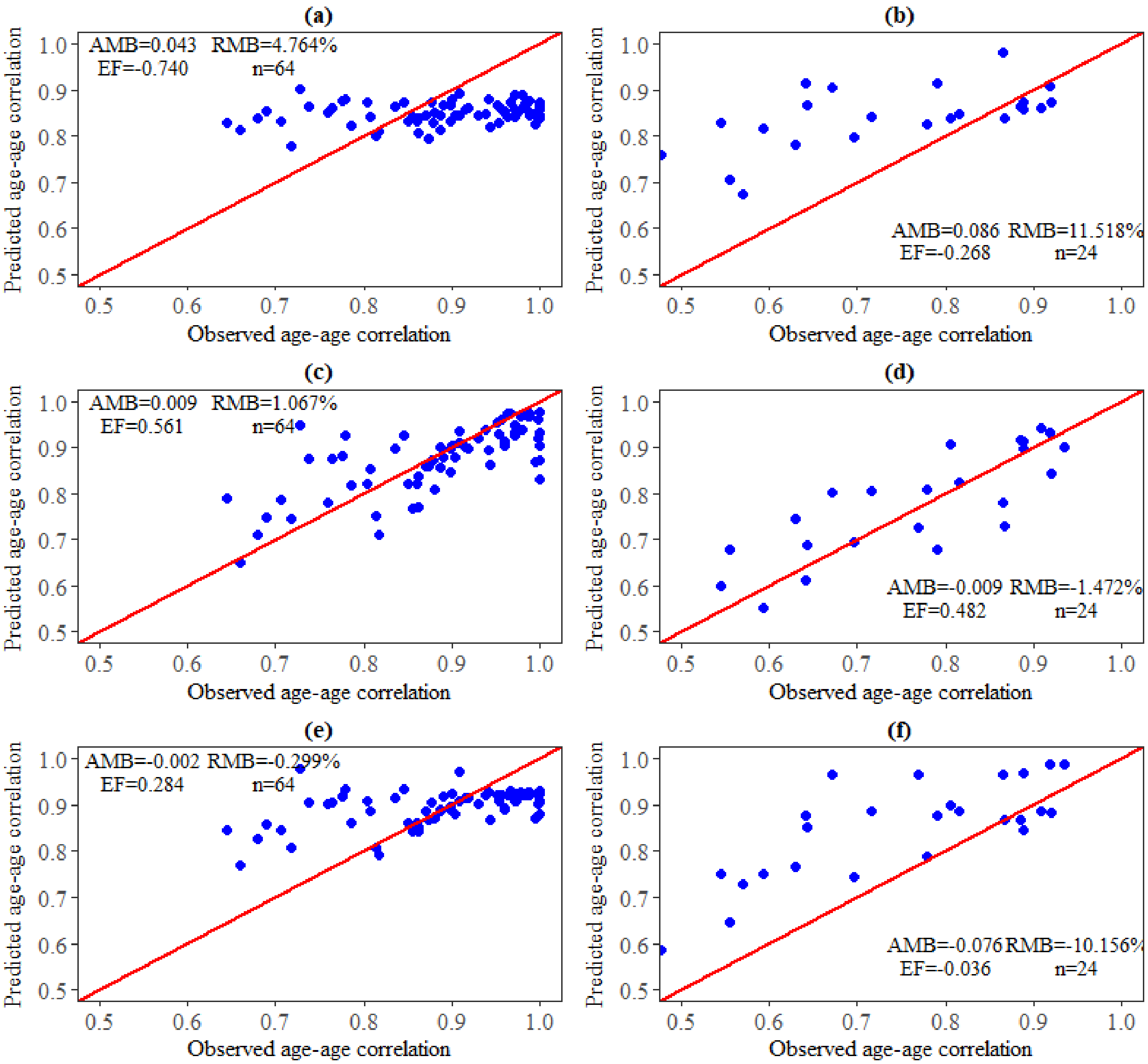

Figure 2.5 Predicted age-age correlations versus observed age-age correlations for white spruce (Sw) and lodgepole pine (Pl) across different selection ages, based on adjusted Rweyongeza equations (Sw, a; Pl, b), adjusted Lambeth equations (Sw, c; Pl, d), and Rweyongeza's (2016) equations (Sw, e; Pl, f)

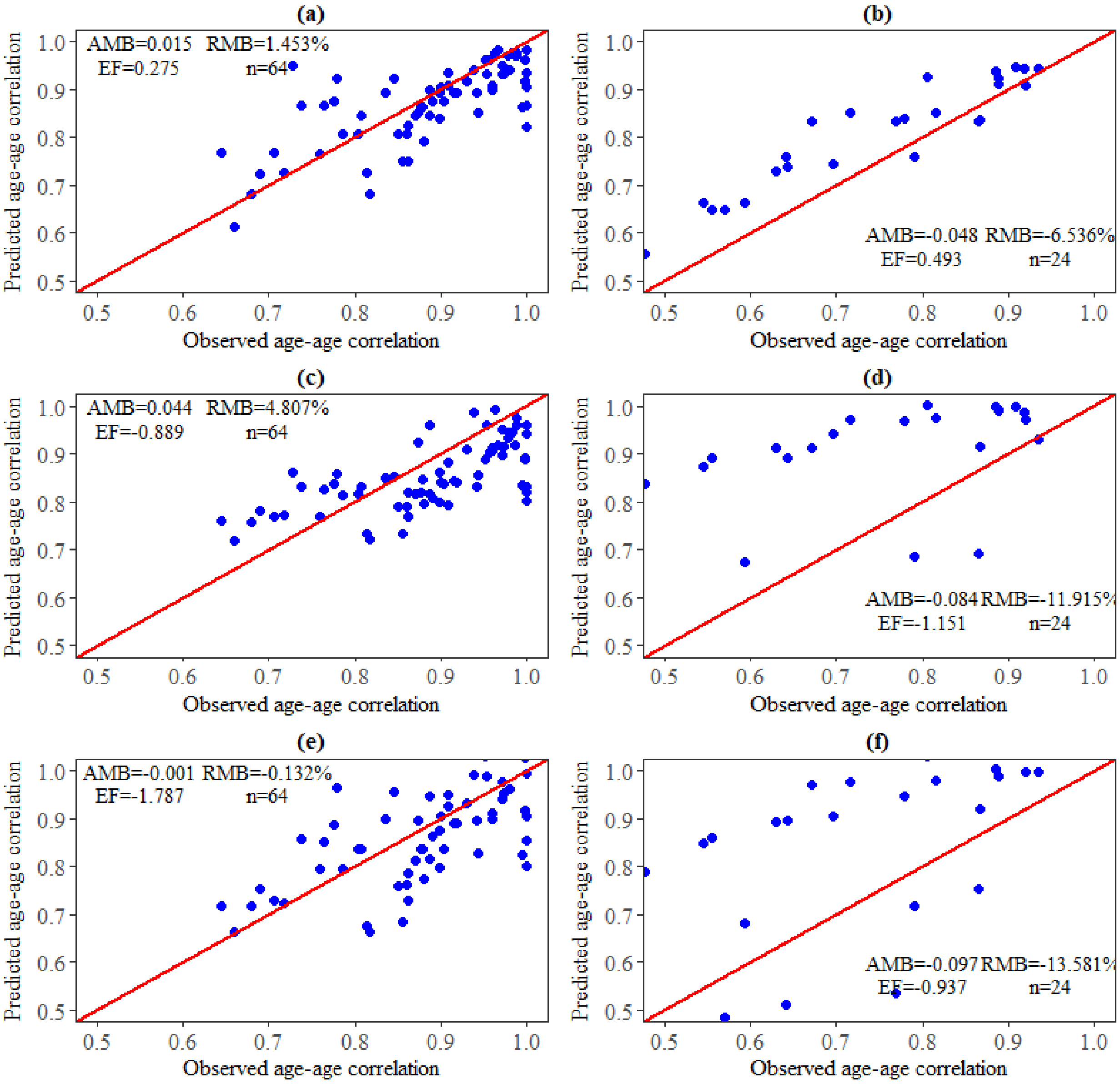

Figure 2.6 Predicted age-age correlations versus observed age-age correlations for white spruce (Sw) and lodgepole pine (Pl) across different selection ages, based on Lambeth's (1980) equations (Sw, a; Pl, b), sigmoid with parabolic branch age-age correlation equations for the exponential version (SPB, exp) (Sw, c; Pl, d), and logarithm version (SPB, log) (Sw, e; Pl, f)

2.3.2 Incorporation of genetic gain into growth and yield models

The adjusted Lambeth equations were used to build the top height tables for white spruce

(Table 2.7) and lodgepole pine (Table 2.8). Rather than seek out a higher yield at pre-determined rotation ages, an alternative is to reduce the rotation age to achieve the same yield as unimproved seedlots would have provided, at the longer rotation/harvest age. Due to the lower age-age correlations for lodgepole pine, the higher GW value was more important in reducing the number of years needed to reach the same top height (Table 2.8). Using GYPSY and assuming a SI of 15m at age 50 and a planting density of 2,000 stems ha^{-1}, lodgepole pine reached the stand volume asymptote earlier than white spruce, while white spruce had a higher stand volume gain at older rotation ages (Figures 2.7 to 2.10).

Table 2.7 Predicted top height for improved white spruce planted in different ecosites, subregions and associated site indexes, pre-determined rotation age set at 80 years with genetic worth values of 4%, 5%, 6%, 7%, 8%, 9% and 10% with a selection age of 15 and an age-age correlation estimated by the adjusted Lambeth equation

			Top height (m) at age 80 for different height gain selected at age 15						
Subregion	Ecosite	SI[a]	4%	5%	6%	7%	8%	9%	10%
Boreal Highland	e	15.0	22.1(2)[b]	22.2(3)	22.3(4)	22.4(4)	22.6(5)	22.7(5)	22.8(6)
	d	15.7	22.9(2)	23.0(3)	23.1(4)	23.2(4)	23.4(5)	23.5(6)	23.6(6)
	f	16.5	23.7(2)	23.9(3)	24.0(4)	24.1(4)	24.3(5)	24.4(6)	24.5(6)
Boreal Mixedwood	h	12.9	19.6(2)	19.7(3)	19.8(3)	19.9(4)	20.1(4)	20.2(5)	20.3(5)
	f	16.4	23.6(2)	23.8(3)	23.9(4)	24.0(4)	24.2(5)	24.3(6)	24.4(6)
	d	16.8	24.1(2)	24.2(3)	24.3(4)	24.5(5)	24.6(5)	24.7(6)	24.9(7)
	b	17.5	24.8(3)	25.0(3)	25.1(4)	25.2(5)	25.4(5)	25.5(6)	25.7(7)
	e	17.8	25.1(3)	25.3(3)	25.4(4)	25.6(5)	25.7(6)	25.8(6)	26.0(7)
Canadian Shield	c	6.4	10.8(1)	10.9(2)	10.9(2)	11.0(3)	11.0(3)	11.1(4)	11.2(4)
	b	12.0	18.5(2)	18.6(2)	18.7(3)	18.8(4)	18.9(4)	19.0(5)	19.1(5)
Lower Foothills	j	10.8	17.0(2)	17.1(2)	17.2(3)	17.3(3)	17.4(4)	17.5(4)	17.6(5)
	d	12.6	19.3(2)	19.4(2)	19.5(3)	19.6(4)	19.7(4)	19.8(5)	19.9(5)
	h	14.7	21.7(2)	21.9(3)	22(3)	22.1(4)	22.2(5)	22.3(5)	22.5(6)
	i	15.8	23.0(2)	23.1(3)	23.2(4)	23.4(4)	23.5(5)	23.6(6)	23.7(6)
	e	17.1	24.4(2)	24.5(3)	24.7(4)	24.8(5)	24.9(5)	25.1(6)	25.2(7)
	f	18.5	25.9(3)	26.0(3)	26.2(4)	26.3(5)	26.5(6)	26.6(6)	26.7(7)
Montane	g	5.3	9.1(1)	9.1(2)	9.2(2)	9.2(3)	9.3(3)	9.3(3)	9.4(4)
	f	6.2	10.5(1)	10.6(2)	10.6(2)	10.7(3)	10.7(3)	10.8(4)	10.8(4)
	b	12.1	18.6(2)	18.7(2)	18.8(3)	18.9(4)	19.1(4)	19.2(5)	19.3(5)
	c	12.8	19.5(2)	19.6(3)	19.7(3)	19.8(4)	19.9(4)	20.0(5)	20.1(5)
	d	14.3	21.3(2)	21.4(3)	21.5(3)	21.6(4)	21.7(5)	21.9(5)	22.0(6)
Subarctic	d	10.4	16.5(2)	16.6(2)	16.6(3)	16.7(3)	16.8(4)	16.9(4)	17.0(5)
	b	15.0	22.1(2)	22.2(3)	22.3(4)	22.4(4)	22.6(5)	22.7(5)	22.8(6)
Upper Foothills	d	10.5	16.6(2)	16.7(2)	16.8(3)	16.9(3)	17.0(4)	17.1(4)	17.1(5)
	c	14.7	21.7(2)	21.9(3)	22.0(3)	22.1(4)	22.2(5)	22.3(5)	22.5(6)
	j	15.0	22.1(2)	22.2(3)	22.3(4)	22.4(4)	22.6(5)	22.7(5)	22.8(6)
	f	16.1	23.3(2)	23.4(3)	23.6(4)	23.7(4)	23.8(5)	24.0(6)	24.1(6)

[a]: Site index of ecosite across subregion is from 'Field Guide to Ecosites of Northern Alberta' and 'Field Guide to Ecosites of West-central Alberta' (Beckingham and Archibald 1996a, b)

[b]: The number in the parenthesis indicates how many years earlier for improved seedlots to reach the same top height of unimproved seedlots under a presumed rotation age of 80

Table 2.8 Predicted top height for improved lodgepole pine planted in different ecosites, subregions and associated site indexes, pre-determined rotation age set at 80 years with genetic worth values of 4%, 5%, 6%, 7%, 8%, 9% and 10% with a selection age of 15 and an age-age correlation estimated by the adjusted Lambeth equation

			Top height (m) at age 80 for different height gains selected at age 15						
Subregion	Ecosite	SI[a]	4%	5%	6%	7%	8%	9%	10%
Lower Foothills	b	13.2	19.8(1)[b]	19.8(1)	19.9(1)	19.9(1)	20.0(2)	20.0(2)	20.1(2)
	h	15.0	22.4(1)	22.5(1)	22.5(1)	22.6(1)	22.6(2)	22.7(2)	22.8(2)
	d	15.3	22.8(1)	22.9(1)	23.0(1)	23.0(1)	23.1(2)	23.1(2)	23.2(2)
	i	16.7	24.9(1)	25.0(1)	25.0(1)	25.1(1)	25.2(2)	25.2(2)	25.3(2)
	e	17.7	26.4(1)	26.4(1)	26.5(1)	26.6(1)	26.6(2)	26.7(2)	26.8(2)
	c	18.4	27.4(1)	27.5(1)	27.5(1)	27.6(1)	27.7(2)	27.8(2)	27.8(2)
	f	19.9	29.6(1)	29.7(1)	29.7(1)	29.8(1)	29.9(2)	30.0(2)	30.1(2)
Montane	b	10.9	16.4(1)	16.4(1)	16.4(1)	16.5(1)	16.5(2)	16.6(2)	16.6(2)
	c	19.6	29.1(1)	29.2(1)	29.3(1)	29.4(1)	29.5(2)	29.5(2)	29.6(2)
Subalpine	b	8.4	12.7(1)	12.7(1)	12.7(1)	12.8(1)	12.8(2)	12.8(2)	12.9(2)
	g	10.3	15.5(1)	15.5(1)	15.6(1)	15.6(1)	15.6(2)	15.7(2)	15.7(2)
	d	10.8	16.2(1)	16.3(1)	16.3(1)	16.3(1)	16.4(2)	16.4(2)	16.5(2)
	f	11.9	17.8(1)	17.9(1)	17.9(1)	18.0(1)	18.0(2)	18.1(2)	18.1(2)
	c	13.4	20.0(1)	20.1(1)	20.2(1)	20.2(1)	20.3(2)	20.3(2)	20.4(2)
Subarctic	a	12.1	18.1(1)	18.2(1)	18.2(1)	18.3(1)	18.3(2)	18.4(2)	18.4(2)
	c	9.3	14(1)	14(1)	14.1(1)	14.1(1)	14.1(2)	14.2(2)	14.2(2)
Upper Foothills	b	11.4	17.1(1)	17.1(1)	17.2(1)	17.2(1)	17.3(2)	17.3(2)	17.4(2)
	d	12.9	19.3(1)	19.4(1)	19.4(1)	19.5(1)	19.5(2)	19.6(2)	19.6(2)
	j	14.2	21.2(1)	21.3(1)	21.3(1)	21.4(1)	21.5(2)	21.5(2)	21.6(2)
	c	14.7	22.0(1)	22.0(1)	22.1(1)	22.1(1)	22.2(2)	22.3(2)	22.3(2)
	h	14.7	22.0(1)	22.0(1)	22.1(1)	22.1(1)	22.2(2)	22.3(2)	22.3(2)
	f	16.9	25.2(1)	25.3(1)	25.3(1)	25.4(1)	25.5(2)	25.5(2)	25.6(2)

[a]: Site index of ecosites across subregion is from ‘Field Guide to Ecosites of Northern Alberta’ and ‘Field Guide to Ecosites of West-central Alberta’ (Beckingham and Archibald 1996a, b)

[b]: The number in the parenthesis indicates how many years earlier for improved seedlots to reach the same top height of unimproved seedlots under presumed rotation age 80

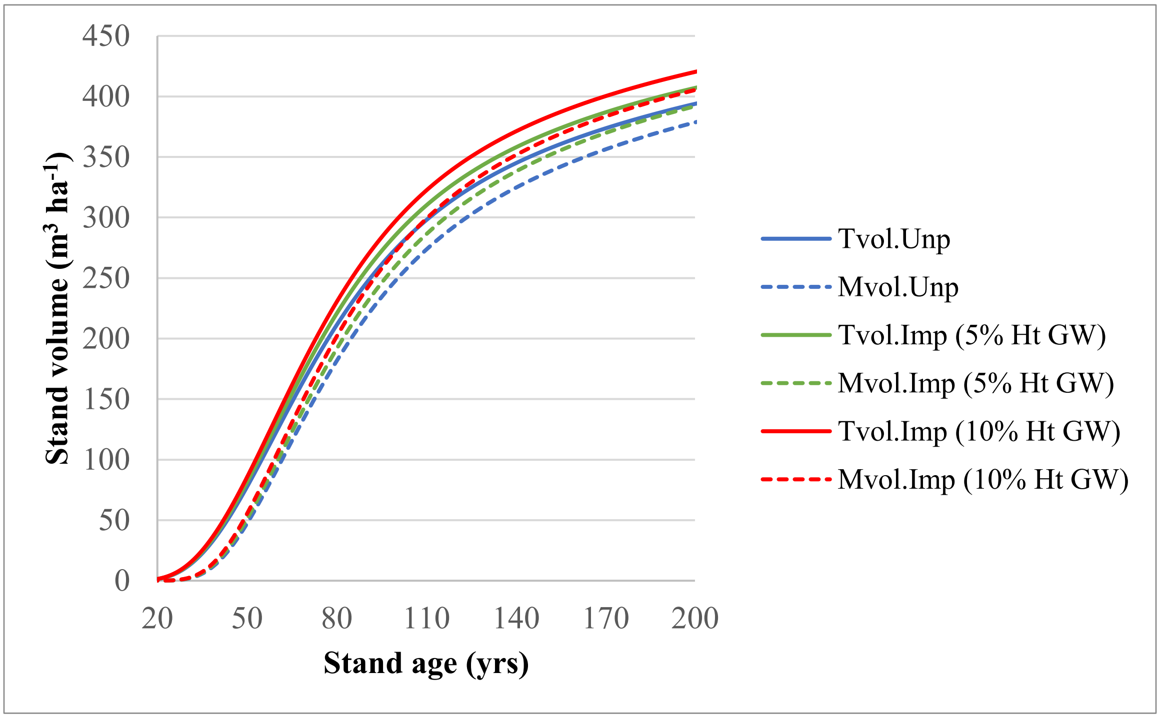

Figure 2.7 Total stand volume (Tvol) and merchantable stand volume (Mvol) under '7/13 utilization standard' (top diameter should be no less than 7cm and diameter at 0.3m tall from the ground should be no less than 13cm) in m^3 ha^{-1}, for unimproved (Unp), and improved (Imp) white spruce with 5% and 10 % genetic worth for height with a selection age of 15 and planting density of 2,000 stems ha^{-1} with a site index of 15m from 20-200 years of age

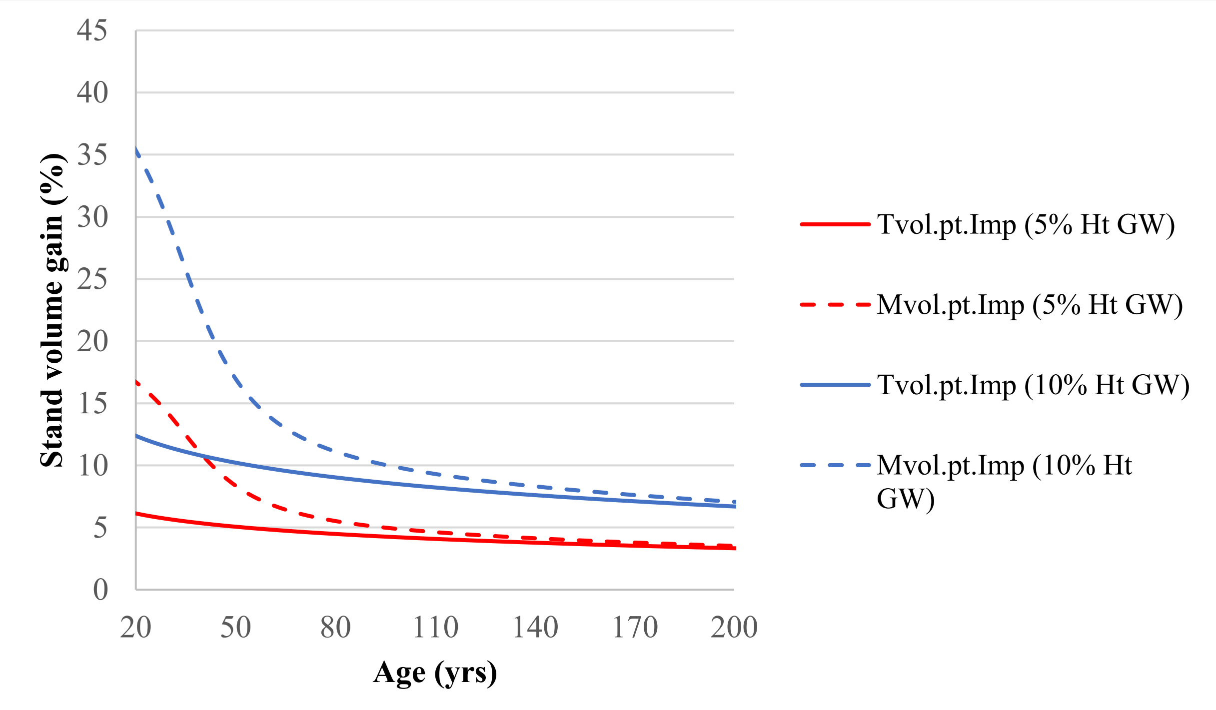

Figure 2.8 Total stand volume gain (Tvol.pt) and merchantable stand volume gain (Mvol.pt) under '7/13 utilization standard' (top diameter should be no less than 7cm and diameter at 0.3m tall from the ground should be no less than 13cm) in percent (%) for improved (Imp) white spruce with 5% and 10 % genetic worth for height with a selection age of 15 and planting density of 2,000 stems ha^{-1} with a site index of 15m from 20-200 years of age

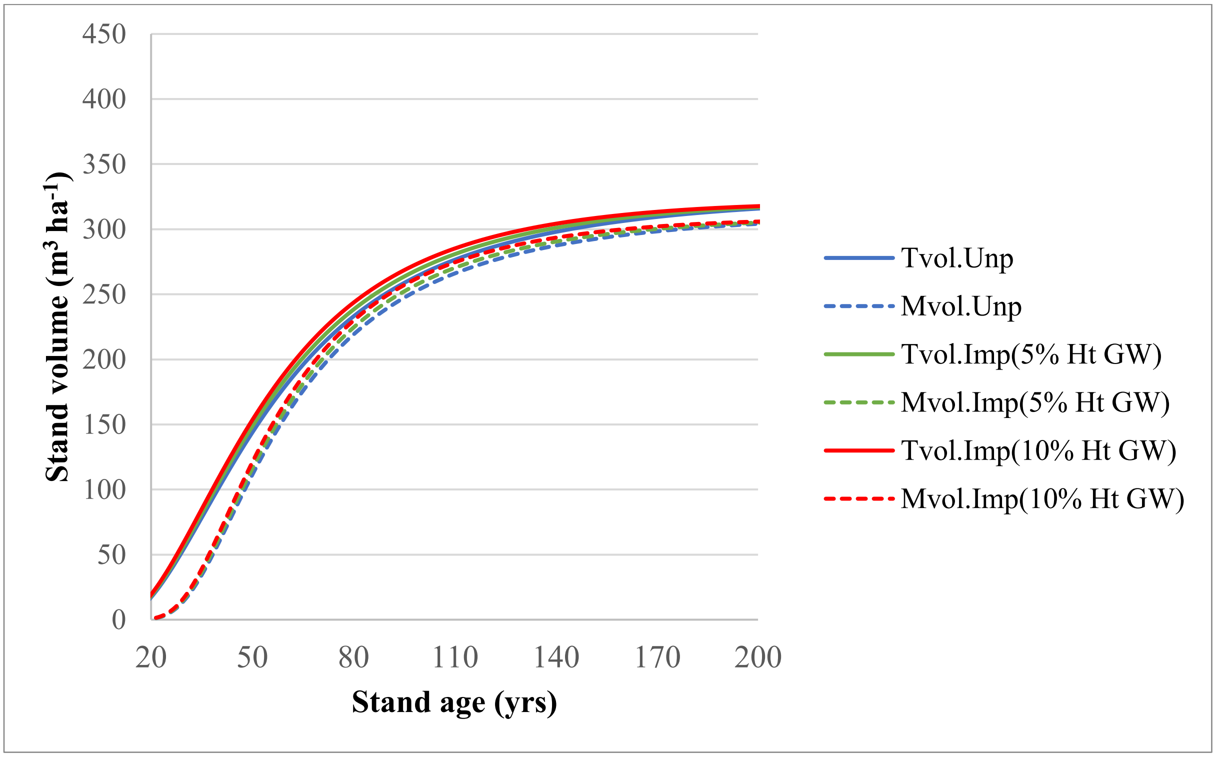

Figure 2.9 Total stand volume (Tvol) and merchantable stand volume (Mvol) under '7/13 utilization standard' (top diameter should be no less than 7cm and diameter at 0.3m tall from the ground should be no less than 13cm) in m^3 ha^{-1}, for unimproved (Unp), and improved (Imp) lodgepole pine with 5% and 10 % genetic worth for height with a selection age of 15 and planting density of 2,000 stems ha^{-1} with a site index of 15m from 20-200 years of age

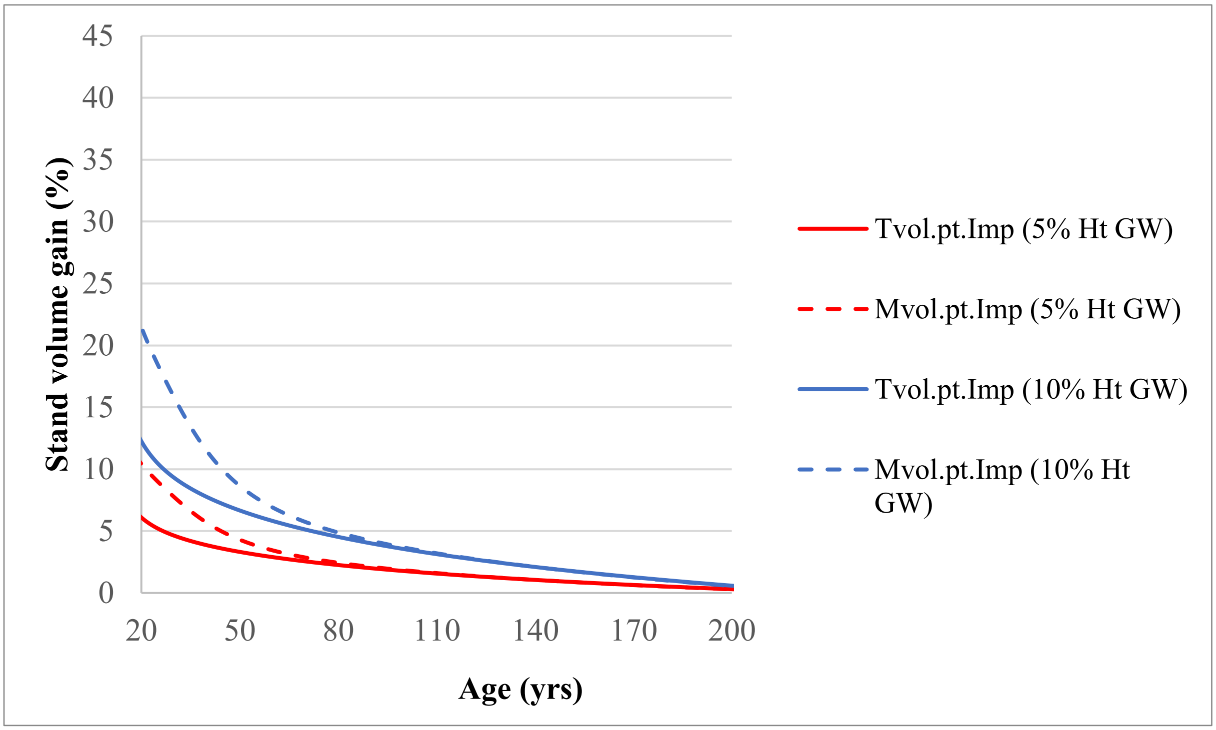

Figure 2.10 Total stand volume gain (Tvol.pt) and merchantable stand volume gain (Mvol.pt) under ‘7/13 utilization standard’ (top diameter should be no less than 7cm and diameter at 0.3m tall from the ground should be no less than 13cm) in percent (%) for improved (Imp) lodgepole pine with 5% and 10 % genetic worth for height with a selection age of 15 and planting density of 2,000 stems ha^{-1} with a site index of 15m from 20-200 years of age

2.4 Discussion

2.4.1 Age-age correlation

2.4.1.1 Non-asymptotic sigmoidal curves vs. asymptotic sigmoidal curves

The purpose of non-asymptotic sigmoidal curves is to capture a more realistic trend of age-age correlations along a wider range of ages. According to the shape of non-asymptotic curves (Bontemps and Duplat 2012), the height growth rate will reach the peak at young ages and then decrease slowly. The corresponding height curves, which represent the accumulation of height growth, are expected to be shorter before the inflection point, and taller after the inflection point, compared to heights estimated from a logistic function. Therefore, the age-age correlations predicted by the SPB age-age correlation equations were expected to be higher at the mid-rotation age and lower at the rotation age, compared to equations developed by Lambeth (1980) and Rweyongeza (2016). However, the SPB age-age correlation equations did not pass the cross validation assessment.

Both asymptotic sigmoidal curves and non-asymptotic curves were built with the limitation that application of LAG is difficult when extrapolating to real rotation ages. However, estimating height growth based on age-age correlations which are derived from estimated height is a 'self-fulfilling prophecy'. Since mature rotation age measurements from improved trees were not available, extrapolation was necessary. Certain assumptions were made in this study for adjusting Rweyongeza's (2016) equations and exploring the possibility of applying non-asymptotic curves for establishment of age-age correlation matrices. However, additional assumptions were also made for non-asymptotic curves to make the shape of the curve more natural. Compared to the asymptotic curves, the additional assumptions may have caused a larger deviation from the real height curves, and therefore increase the derivation from the real age-age correlations. In comparison, adjusting Lambeth's equations only needed observed height measurements.

2.4.1.2 Comparison between age-age correlation equations

Lambeth's (1980) equations have been used and discussed in many previous studies, and a common critique is that using a simple linear regression with LAR as an explanatory variable does not reflect characteristics of growth phases (Kung 1993; Gwaze *et al.* 1997; Lambeth and Dill 2001; Xie and Yanchuk 2003; Rweyongeza 2016). However, in practical terms, with a specified selection age, Lambeth's (1980) equation can be converted to a logarithm equation with the formula written as $r_{si,ti} = a + b * \log(si) - b * \log(ti)$. Because si is a specified selection age, and the only explanatory variable is rotation age ti. When LAG is used as the explanatory variable, Lambeth's (1980) equation can be written as $r_{si,ti} = a + b * \log(si) - b * \log(si + LAG)$. The corresponding curves present similar characteristics with other LAR models, when selection age is greater, and the same age difference will have a larger age-age correlation. Therefore, to criticize the disadvantages of this simple linear regression may not be warranted.

Following the idea of Rweyongeza's (2016) equations, non-asymptotic curves were used to build a new SPB age-age correlation matrix. However, this new method did not pass the model validation assessment.

Given that the adjusted age-age correlations were established and compared based on the first-generation progeny trials in Alberta, and data from realized gain trials will be used in the future, whether phenotypic age-age correlations could be used as the surrogate for genetic age-age correlations was also tested. Previous studies have shown that Lambeth's (1980) equations underestimate genetic age-age correlation (Hodge and White 1992; Gwaze *et al.* 1997; Lambeth and Dill 2001) by using the phenotypic age-age correlation. However, relevant research also suggests that the genetic age-age correlation does not warrant better prediction accuracy than building models based on phenotypic age-age correlations (Burdon 1989; Hodge and White 1992). Rweyongeza (2016) concluded that phenotypic correlations could be taken as a good substitute for genetic correlation since high levels of similarity between a genetic and phenotypic correlation should be expected due to autocorrelation, and higher standard errors were found with genetic age-age correlations (Lambeth *et al.* 1983; Tauer and McNew 1985). The results indicate that the phenotypic age-age correlations from the adjusted Lambeth equations are not significantly different from the genetic age-age correlations. Although directly using the genetic age-age correlation is a more accurate option, fitting a model to phenotypic age-age correlations is simpler. Therefore, the phenotypic age-age correlation, instead of the genetic age-age correlation, was used for the age-age correlation equations in this study, and the phenotypic age-age correlation is expected to be an ideal surrogate of genetic age-age correlation once sufficient realized gain trial data is available.

Following the principles of a single reference population, the adjusted Lambeth equations, adjusted Rweyongeza equations, and SPB age-age correlation equations were all built on a combined dataset consisting of separate correlation matrices from each CPP region.

Separate parameter estimates for each CPP region was not applicable to the adjusted Lambeth equations due to limited observations. However, the adjusted Lambeth equations at the provincial scale showed the best prediction accuracy. Separating models by CPP region was also not applicable to the adjusted Rweyongeza and SPB age-age correlation equations due to the limited number of height-age observations that could be used in validating the model.

2.4.1.3 Comparison in age-age correlations between white spruce and lodgepole pine

Overall, lodgepole pine shows a lower age-age correlation compared to white spruce. Lodgepole pine is a more shade-intolerant and fast-growing species compared to white spruce at a young age (Burns and Honkala 1990). This faster growth at the measurement ages was observed in the lodgepole pine progeny trials in this study. The higher growth rates and shade-intolerance may have led to increased intra-specific competition due to earlier canopy closure, and therefore larger growth variance among families, compared to the white spruce progeny trial datasets. These differences confirm the need for the development of unique age-age correlation equations for both white spruce and lodgepole pine in Alberta.

2.4.2 Incorporating genetic gain into growth and yield models in Alberta

The top height and stand volume generated from GYPSY, using the adjusted Lambeth equations, showed conclusively, that higher genetic gain will produce either greater yield at the same rotation age or the same yield at an earlier rotation age, based on the most current progeny trial datasets available. When the predictive ability of genetic gain is compromised by a lower age-age correlation, to assure the benefits from deploying improved seedlots, a higher GW at selection age becomes more important. Even though lodgepole pine has a lower age-age correlation, which requires an older selection age, by reducing the rotation age, the time interval between the selection age and the rotation age will be reduced and the associated age-age correlation increased.

2.4.3 Limitation of Chapter 2

The variation in diameter is larger than height when a stand has greater variation in site quality (Wang *et al.* 1998; Sharma *et al.* 2016), species composition (Groot and Carlson 1996; Pritchard and Comeau 2004; Voicu and Comeau 2006; Filipescu and Comeau 2007; Nunifu 2009), density and subsequent competition (Sjolte-Jørgensen 1967; Rich *et al.* 1986; Wang *et al.* 1998). Whether improved trees have a larger diameter, given the same height and therefore greater volume, is not addressed in this study as currently there is no realized gain trial data available yet in Alberta. Therefore, I assumed that improved and unimproved seedlots had an identical height-DBH (diameter at breast height) relationship.

The effect from silviculture practices in both pure and mixedwood stands have been discussed in many studies (Pitt *et al.* 2004; Landhäusser 2009; MacIsaac and Krygier 2009; Bergeron *et al.* 2014; Comeau 2014; Grover *et al.* 2014; Kabzems *et al.* 2015; Kabzems *et* *al.* 2016). However, Chapter 2 does not address silviculture and mixedwood stand factors. There is still a necessity to test the interaction between tree improvement and silviculture (e.g. mechanical preparation, commercial thinning) in the growth and yield models in Alberta.

The Mixedwood Growth Model (MGM) (Huang and Titus 1993; Bokalo *et al.* 1996; Huang *et al.* 1997; Huang and Titus 1999; Bokalo *et al.* 2007) is another growth and yield model used in Alberta, and is able to simulate stand growth based on the height and diameter data of individual trees. This flexibility will allow for the prediction of volume yield under different silvicultural practices. The performance of age-age correlation in MGM should be further discussed in future studies.

2.5 Conclusion

Chapter 2 adjusted Lambeth's (1980) and Rweyongeza's (2016) age-age correlation equations based on the most recent and comprehensive datasets available from progeny trials in Alberta, for white spruce and lodgepole pine. A new method called sigmoid with parabolic branch (SPB) age-age correlation equations based on non-asymptotic curves was also tested and compared with the four other equations. The adjusted Lambeth equations with re-estimated parameters were the most accurate for predicting the age-age correlation for both white spruce and lodgepole pine in Alberta. The long trend predictions from the adjusted Lambeth equations indicate that the age-age correlation is higher for white spruce compared to lodgepole pine at a given selection age and rotation age. Separate parameter estimates for these two species are also necessary.

The results of incorporating genetic gain into GYPSY showed that greater benefit is expected from improved seedlots of white spruce at older rotation ages than lodgepole pine. An older selection age may be necessary to increase the accuracy of yield prediction for improved lodgepole pine, however, an earlier rotation age of lodgepole pine, could ultimately reduce the selection age. The adjusted Lambeth equations should be considered for inclusion into GYPSY for stand volume prediction of improved seedlots for white spruce and lodgepole pine.

Chapter 3: Incorporation of climate change to estimate improved white spruce and lodgepole pine growth: a new perspective for tree improvement programs in Alberta, Canada

3.1 Introduction

The maladaptation of trees caused by climate change has been observed in Alberta, Canada, and this trend is predicted to continue in the future (Fettig *et al.* 2013; Schneider 2013; Wang *et al.* 2014; Hogg *et al.* 2017). Tree improvement programs in Alberta have highlighted and investigated the feasibility of seedlots being moved between breeding regions through the establishment of progeny and provenance trials (Gray and Hamann 2015).

Although provenances of white spruce (*Picea glauca* (Moench) Voss) and lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.) transferred from warmer and lower elevation environments to cooler and higher elevation environments were found to outgrow local provenances (Gray *et al.* 2016a; Gray *et al.* 2016b), relevant research indicates that "local is best" is still a valid assumption in the near future since local provenances in most breeding regions still outgrow seedlots that have been obtained from neighbouring regions (Mbogga *et al.* 2009; Fettig *et al.* 2013; Wang *et al.* 2014; Gray *et al.* 2016a; Gray *et al.* 2016b). Therefore, it is expected that improved seed orchard seedlots from improvement programs that consist of local provenances will remain an appropriate option, at least in the short term. However, to what degree growth superiority of local populations at a young age will be maintained over non-local populations at older ages under climate change, has yet to be determined.

Alberta's Growth and Yield Projection System (GYPSY) model predicts growth and yield of naturally established (fire origin) forest stands and planted stands with wild seeds as a function of age, site index (SI) and stand density for several species (Huang *et al.* 2009). Applying GYPSY to improved seedlots consisting of local provenances has also been studied (see Chapter 2). To date, however, GYPSY has not been applied to growth and yield prediction of improved seedlots under climate change. Using data from provenance trials of lodgepole pine across British Columbia and southern Yukon, Canada, previous studies have investigated the feasibility of applying a Universal Transfer Function (UTF) (O'Neill *et al.* 2008) or a Universal Response Function (URF) (Wang *et al.* 2010) to predict growth responses of various provenances to a range of climate conditions. A URF has also been developed for black spruce and eastern white pine (*Pinus strobus* L.) across Canada (Yang *et al.* 2015), and a UTF has been developed for Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mirb.) Franco) in the western United States (Leites *et al.* 2012b). However, the UTF and URF have several limitations in predicting the impact of climate change or seed transfer on forest growth and yield. First, the UTF and URF functions use data from a single age, requiring the assumption that population responses to climate do not vary with tree age. Second, these functions are usually developed from short-term (e.g., 5-20 years-old) provenance tests, and growth of the tested populations represents the impact of climate change on population *growth rate* at their test climate instead of on the *cumulative growth* of local populations at rotation age (O'Neill and Nigh 2011). Third, since values of tree height or stand volume at a young age were used as the response variable for the UTF and URF, the results have had limited use in predicting the growth and yield of improved seedlots at rotation age. Using the meta-data from provenance trials of white spruce and hybrid spruce (*Picea engelmannii* Parry ex Engelmann x *Picea glauca* (Moench) Voss), a height trajectory meta-analysis model was developed by Ahmed *et al*. (2016, 2020) and was applied in adjusting genetic gain estimates with an increasing age for white spruce and hybrid spruce. However, this method has not yet been applied to other tree species, or other regions such as Alberta. For the purpose of further improving the climate risk management strategy for forestry in Alberta, it is of great interest and necessity to explore a potential method of incorporating climate change into the predictions of growth and yield of improved seedlots.

Taking advantage of the latest measurements from a comprehensive dataset of provenance and progeny trials of white spruce and lodgepole pine in Alberta, in Chapter 3, I: 1) explored potential methods to incorporate both climate change and genetic gain into GYPSY; 2) investigated the effect of climate change on the growth and yield of improved (seed orchard) and unimproved (wild stand) seedlots consisting of local provenances; and 3) compared the effect of climate change on growth and yield of white spruce and lodgepole pine.

3.2 Materials and Methods

3.2.1 Data resources

White spruce trees were derived from 554 open-pollinated families associated with six progeny trial series that were tested at 17 sites in Alberta, Canada. In addition, 50 white spruce populations from three provenance trials tested at five sites were also included in the analysis (Figure 3.1, Table 3.1). Lodgepole pine trees were derived from 1,162 open-pollinated families associated with five progeny trial series tested at 14 sites across Alberta, Canada. A further 44 lodgepole pine populations from four provenance trials tested at four sites were also included in the analysis (Figure 3.1, Table 3.1). The white spruce provenances represented populations from Alaska (USA) to southern Quebec (Canada), while the lodgepole pine provenances originated from Alberta and British Columbia (Canada). All test sites are located within Alberta (Figure 3.1). A randomized complete block design with multiple tree plots (several trees of a single family or population) or a randomized incomplete block design with multiple tree plots was utilized for both the progeny and provenance trials for both species. Hereafter, for simplicity, both families and populations are referred as ‘populations’, and I use the term ‘provenance’ to refer to the geographic origin of a population. Progeny and provenance trials were established in well managed sites with early competition control and fencing to exclude herbivores. Therefore, I refer to the top heights of populations from progeny and provenance trials as their mean top heights.

Table 3.1 Species, trial type, trial series code and age of available height measurements for white spruce (Sw) and lodgepole pine (Pl) progeny and provenance trial series in Alberta, Canada, used for analysis in this study

Species	Trial type	Trial series code	Number of sites	Age of height measurements
Sw	Progeny trial	G132	3	8, 10, 15, 16, 21, 24, 30
		G133	3	11, 12, 18, 21, 24, 31
		G135	2	10, 11, 15, 16, 18, 21
		G156	3	10, 11, 15, 18, 24
		G157	3	10, 11, 15, 18, 25
		G352	3	4, 7, 10, 16
	Provenance trial	G276	3	10, 15, 18, 25
		G277	1	7, 10, 15, 18
		G366	1	3, 7, 11
Pl	Progeny trial	G127	4	11, 15, 19, 27
		G128	4	9, 23, 30
		G154	1	6, 11, 14, 20
		G293	2	6, 11, 14, 19
		G346	3	6, 9, 15
	Provenance trial	Berland 3	1	3, 6, 9, 12, 15
		Berland 5	1	4, 7, 10, 13, 16
		Marlboro 7	1	4, 7, 10, 13, 16
		Embarrass	1	4, 7, 10, 13, 16

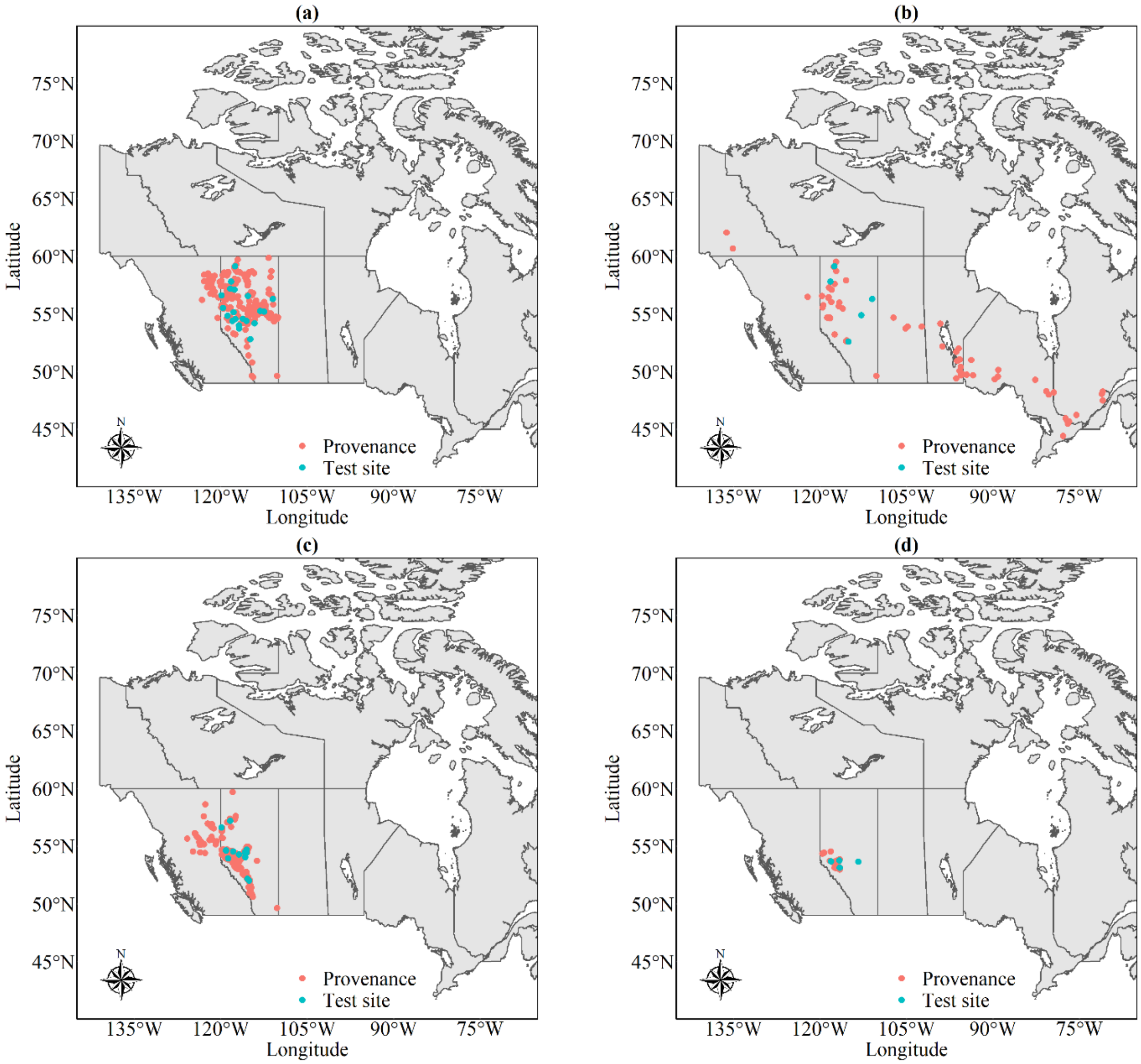

Figure 3.1 Test sites and provenances of the families in the white spruce progeny (a) and provenance trials (b), and in the lodgepole pine progeny (c) and provenance trials (d). Cyan dots show test sites within Alberta, and orange dots show the provenances from different provinces and Yukon territory of Canada.

3.2.2 Climate data

Climate data in this study was derived from ClimateNA V6.22, software used to generate scale-free historical and future climate data for annual, seasonal and monthly periods (Wang *et al.* 2012; Wang *et al.* 2016). This software package is freely available at http://climatena.ca/ (accessed on June 1st, 2020). Values of 21 annual climate variables were generated from ClimateNA for all test sites and provenances (Table 3.2), and mean annual precipitation (MAP) and mean annual temperature (MAT) of provenances and test sites for both species are shown in Figure 3.2

Table 3.2 Climate variables generated by ClimateNA (version V6.22)

Climatic abbreviations	Explanation	Unit
AHM	Annual Heat-Moisture index	°C mm^{-1}
CMD	Hargreaves Climatic Moisture Deficit	mm
DD_0	Degree-Days below 0 °C	°C days
DD_18	Degree-Days below 18 °C	°C days
DD18	Degree-Days above 18 °C	°C days
DD5	Degree-Days above 5 °C	°C days
EMT	Extreme Maximum Temperature over 30 years	°C
Eref	Hargreaves reference evaporation	mm
EXT	Extreme minimum temperature over 30 years	°C
FFP	Frost-Free Period	days
bFFP	The day of the year on which FFP begins	day
eFFP	The day of the year on which FFP ends	day
MAP	Mean Annual Precipitation	mm
MAT	Mean Annual Temperature	°C
MCMT	Mean Coldest Month Temperature	°C
MSP	May to September Precipitation	mm
MWMT	Mean Warmest Month Temperature	°C
NFFD	Number of Frost-Free Days	days
PAS	Precipitation As Snow	mm
SHM	Summer Heat-Moisture index	°C mm^{-1}
TD	Continentality	°C

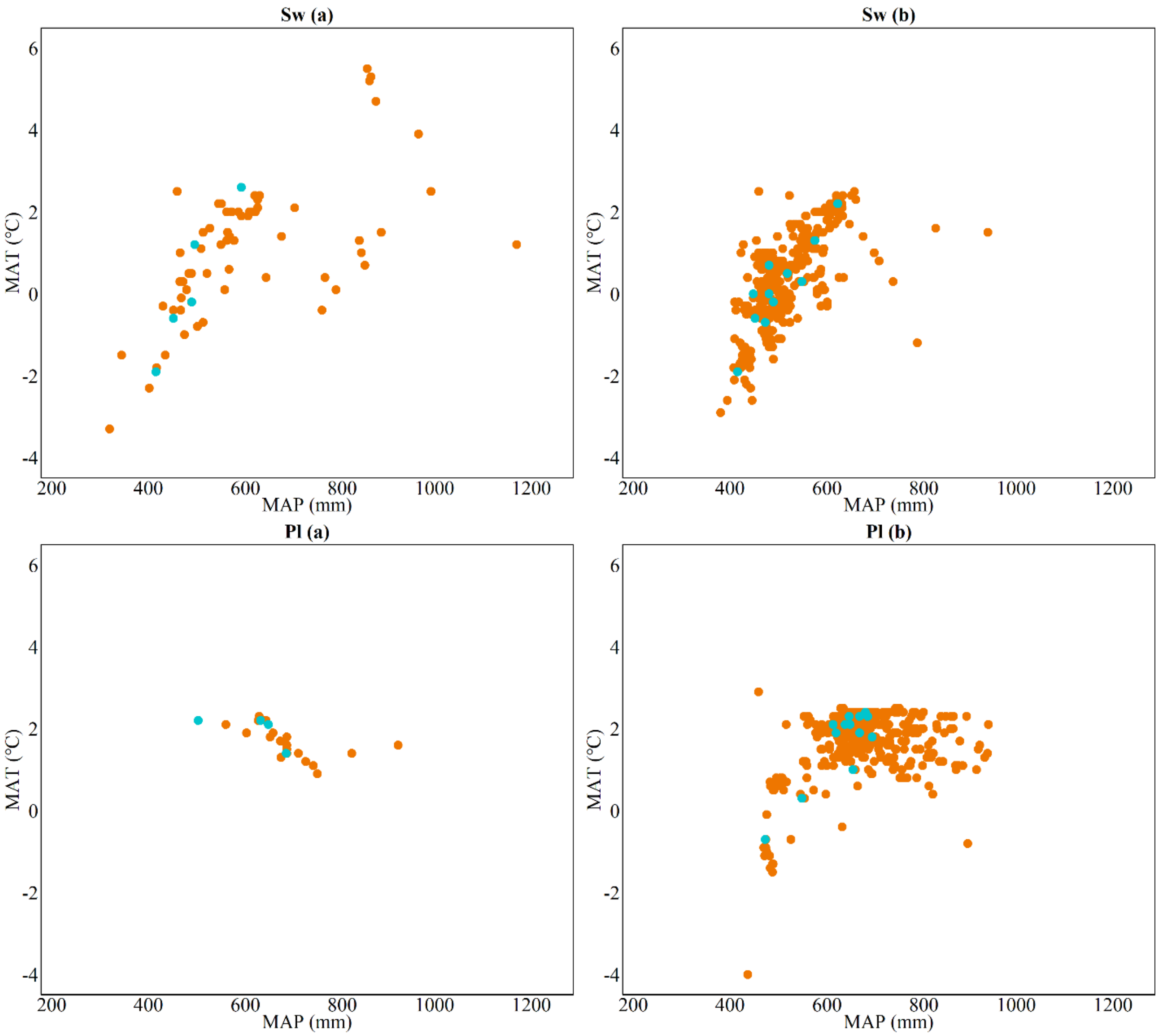

Figure 3.2 Scatterplot of climatic origins of white spruce (Sw) and lodgepole pine (Pl) provenances and test sites (mean annual precipitation (MAP) and mean annual temperature (MAT) from 1961-1990) used in this analysis. Populations tested in provenance trials (a) and families tested in progeny trials (b) are displayed with orange dots for their provenances, and with cyan dots for test sites

Three Representative Concentration Pathways (RCP), RCP2.6, RCP4.5, and RCP8.5, corresponding to three possible greenhouse gas concentration trajectories (e.g. atmospheric CO_2 equivalent concentration) (Taylor *et al.* 2012) were used to predict the effect of climate change on the improved and unimproved seedlots in the future. RCP2.6, RCP4.5 and

RCP8.5 refer to a "low scenario", "intermediate scenario", and "high scenario" with radiative forcing reaching 2.6 Watts per square meter (W m^{-2}), 4.5 W m^{-2}, and 8.5 W m^{-2} by the end of the 21st century, respectively (Taylor *et al.* 2012).

3.2.3 Growth and yield predictions for improved and unimproved seedlots under climate change

3.2.3.1 Response of population mean height to climate change

In Alberta, top height refers to the average height of 100 trees with the largest diameter at breast height (1.3m) per ha. Top height at total age 50 is defined as the site index (SI). These two terms are the main drivers of GYPSY (Huang *et al.* 2009). Therefore, I took the following steps to modify the top height growth model for improved and unimproved seedlots under climate change, thereby incorporating climate change into the growth and yield projections.

First step: Taking advantage of the randomized block design in each test site, the mean height of each population at each measurement age was estimated using Equation (3.1).

$$HT_{ijln} = \mu + B_i + F_j + P_{l(j)} + \varepsilon_{ijln} \tag{3.1}$$

Where, at each age, HT_{ijkl} is the height of individual n, in plot l, population j, and block i; μ is the overall mean of all populations installed in the site; B_i is the random effect of block; F_j is the fixed effect of population; $P_{k(j)}$ is the random effect of plot within population; and $\varepsilon_{ijkl}{\sim}iid(0,\sigma^2)$ is the error following a normal distribution.

Second step: Separate (univariate) URFs were fitted for each of the 21 climate variables using the estimated population mean in the first step as the dependent variable, and then using climate values for test site, population, test site by population interaction, and measurement age, as the independent variables. Following the approach of Nigh (Nigh 2014), climate variables were divided into three categories: temperature (temp) -related variables, precipitation (precip) -related variables, and temp/precip-related variables (Table 3.3), and the climate variable with the lowest Akaike's Information Criterion (AIC) was selected from each category for univariate URFs. A bivariate URF with climate variables selected from temp-related and precip-related categories was also built and compared with three selected univariate URFs. Preliminary analysis showed that the population mean height datasets (with all measurement ages) followed a Gamma distribution, and the log link function had the lowest AIC regardless of the climate variables. Therefore, the URF was revised as shown in Equation (3.2), and data from progeny and provenance trials were pooled for climate variable selection. Provenance climate was considered as a long-term environment which shaped the genotype, while the test site climate was considered a short-term environment which reflected the genetic by environment interaction (Monserud and Rehfeldt 1990; Leites *et al.* 2012b). Since most height measurements were after 1990, following the methods of Yang *et al.* (2019), climate variables at test sites were averaged over a time period (five years were selected given young ages of all trees) prior to each measurement age, and provenance climate variables were averaged from the normal period

1961-1990.

$$HT_{jti} = exp\big(a_1 * x_j + a_2 * x_{ti} + a_3 * x_j^2 + a_4 * x_{ti}^2 + a_5 * x_j{:}x_{ti} + a_6 * age + a_7 * age^2\big) + \varepsilon_{jti} \qquad (3.2)$$

Where HT_{jti} is the estimated jth population mean height (from Equation 3.1) at a specific $age\ i$ tested in site t; x_j is the climate variable at the provenance (averaged during 1961-1990 normal period); x_{ti} is the climate variable at the test site (averaged from five years prior to each measurement age); a_1–a_7 are the parameters to be estimated.

Third step: Given that majority of populations were not tested in extreme environments, 'anchor points', which are height estimates of tested populations when grown in extreme environments, were imputed in order to 'tie down' the tails of the URF (Wang *et al.* 2006). For each species, sites having the minimum and maximum climate values for 1961-1990 for the climate variables selected in the second step, were identified. Individual Genecology Functions (IGFs) were constructed for both species to predict population mean height from their provenance climate at those four anchor sites (Equation 3.3). After excluding sites without squared climate terms in their IGFs (Equation 3.3), provenance trial sites G133a (MCMT = -23°C) and G276d (MCMT = -11.9°C), and progeny trial site G132d (MCMT -10.9°C) were selected as 'anchor sites' from which to generate 'anchor points' for white spruce. Provenance test site Berland 5 (MAP = 657mm), and progeny test sites G127b (MAP = 657mm) and G346a (MAP = 445mm) were selected as 'anchor sites' from which to generate 'anchor points' for lodgepole pine (data not shown).

$$HT_{ji} = exp\left(a_1 * x_j + a_2 * x_j^2 + a_3 * age + a_4 * age^2\right) + \varepsilon_{ji} \qquad (3.3)$$

Where HT_{ji} is the estimated jth population mean height (from Equation 3.1) at a specific age i tested in the selected 'anchor site'; x_j is the climate variable at the provenance (time period 1961-1990); a_1–a_4 are the parameters to be estimated. The height of the populations not tested in the selected 'anchor sites' was then estimated and added to the dataset.

Fourth step: Non-climatic site factors can play a large role in site productivity. Consequently, to account for non-climatic site factors in the predictions of population height, a site-specific non-climatic index was included in the URF (O'Neill *et al.* 2007). Local populations were identified at each test site as those populations that originated within 3° latitude, 2.0 °C MAT, and 300 mm MAP of the test sites (O'Neill *et al.* 2007). The population mean height (from Equation 3.1) of each site's local population were modeled using multiple regression (Equation 3.4) with stepwise selected climate variables and age as predictors.

$$HT_{ti.local} = exp(d_0 + d_1 * x_{1ti} + d_2 * x_{1ti}^2 + d_3 * x_{2ti} + d_4 * x_{2ti}^2 + d_5 * x_{3ti} + d_6 * x_{3ti}^2 + d_7 * age + d_8 * age^2) + e_{ti} \qquad (3.4)$$

Where $HT_{ti.local}$ is the estimated population mean height (from Equation 3.1) at a specific $age\ i$ and defined as the local population tested in site t; x_{ti} is the climate variable at the test site (averaged from five years prior to each measurement age), x_{1ti}, x_{2ti} and x_{3ti}

are the three selected climate variables; d_0–d_8 are the parameters to be estimated; e_{ti} is the residual.

To ensure that e_{ti} values were independent of population mean height used in subsequent analysis, a site height regression for each test site was established using data from all other sites and excluding the local provenance of the site (O'Neill *et al.* 2007). Given the limited number of test sites (22 for white spruce and 18 for lodgepole pine), provenance and progeny trials were combined in Equation (3.4) with seedlot type (improved from progeny trials and unimproved from provenance trials) included as an independent variable, and three climate variables with the lowest AIC (from the second step) were selected: MCMT, TD and DD_18 for white spruce, and MAP, EMT and DD18 for lodgepole pine.

Fifth step: The population mean height (from Equation 3.1) was adjusted by removing the non-climatic effect, and the URF was then re-fitted separately for improved and unimproved seedlots using the adjusted population mean height. Equation (3.2) was revised as Equation (3.5), where e_{ti} is the non-climatic index from step four and the other variables remain unchanged. In this step, e_{ti} was not used as a covariate, since height measurements at the provenance origin for each population was not available. An exponential function was used and e_{ti} could then be cancelled out in the calculation of Htp. However, e_{ti}, which is not SI, varies with age at each test site. Therefore, for simplicity, the BLUEs were adjusted directly (from eq 3.1) with e_{ti} and re-fitted the URF (eq 3.5).

$$HT_{jti} - e_{ti} = exp\big(a_1 * x_j + a_2 * x_{ti} + a_3 * x_j^2 + a_4 * x_{ti}^2 + a_5 * x_j{:}x_{ti} + a_6 * age + a_7 * age^2\big) + \varepsilon_{jti} \quad (3.5)$$

Sixth step: For the purpose of combining genetic gain and climate change impacts into growth and yield projections, population mean height, excluding any non-climatic effect predicted in Equation (3.5), was converted to a height proportion (Htp) by dividing population mean height at the test site by its estimated mean height at its provenance location. Impacts of seed source climate and climate change, reflected by Htp, could then be integrated into the growth and yield models by annually adjusting heights in the top height functions by Htp. Since test sites, and therefore height measurements at the locations where the seeds were collected, were not available, the modified URF (Equation 3.5) was used to estimate the provenance population mean height by setting x_j equal to x_{ti}. Htp was then calculated for each population, at each test site, and at each age.

Seventh step: Finally, Htp was fitted with age and selected single climate variables (Equation 3.6). The preliminary results indicated that adding age did not significantly reduce the root mean square error of prediction (RMSEP) (Table 3.4). Therefore, age was later removed from Equation (3.6). The climate transfer distance ($x_{dist.jti}$) was used and calculated as $x_{ti} - x_j$, therefore the Htp would equal to 1 when $x_{dist.jti}$ is zero, as Equation (3.6) was revised as Equation (3.7) by removing x_j. The selected function in the seventh step is named the adjusted Pooled Transfer Function (adjusted PTF) in the following analysis, and the adjusted PTF was built separately for improved and unimproved seedlots for each species.

$$Htp_{jti} = exp(c_1 * x_j + c_2 * x_{dist.jti} + c_3 * x_j^2 + c_4 * x_{dist.jti}^2 + c_5 * x_j{:}x_{dist.jti} + c_6 * age + c_7 * age^2) + \varepsilon_{jti} \quad (3.6)$$

$$Htp_{jti} = exp(c_1 * x_{dist.jti} + c_2 * x_{dist.jti}^2 + c_3 * x_j{:}x_{dist.jti}) + \varepsilon_{jti} \quad (3.7)$$

Where Htp_{jti} is the estimated height proportion for the jth population at age i tested in site t; x_j is the provenance climate variable for the jth population (averaged during 1961-1990 normal period); $x_{dist.jti}$ is the climate transfer distance calculated as $(x_{ti} - x_j)$ and x_{ti} is the climate variable in the tth test site (averaged from five years prior to each site measurement age) for the jth population at age i; age is the total age of the even-aged family; $c_1 -$ c_7 are the parameters to be estimated.

Eighth step: Since the Htp was later used in predicting the growth and yield under climate change in the future, average model bias (AMB) (Equation, 3.8), relative model bias percentage (RMB) (Equation, 3.9), efficiency (EF) (Equation, 3.10) and p_value from t-tests between observation and prediction in a 10-fold cross validation (Loague and Green 1991; Vanclay and Skovsgaard 1997; Bokalo *et al.* 2013) were applied in step eight to check the performance of the final adjusted PTF. Given that mean height at provenance location was estimated by modified URF (equation 3.5) and IGF (equation 3.4) and was used to calculate Htp, Equation (3.8) to Equation (3.10) and p_values were also applied to check the performance of the Equations (3.4) and (3.5).

$$AMB = 1/n * \sum(Y - \hat{Y}) \tag{3.8}$$

$$RMB = 100/n * \sum((Y - \hat{Y})/\bar{Y}) \tag{3.9}$$

$$EF = 1 - [\sum(Y - \hat{Y})^2 / \sum(Y - \bar{Y})^2] \tag{3.10}$$

Where n is the number of observed values; Y is the observed value; $\hat{Y}$ is the predicted value; $\bar{Y}$ is the average of the observed values.

Although Cauchy and Weibull functions were used in relevant studies (O'Neill *et al.* 2008; O'Neill and Nigh 2011; Nigh 2014), the preliminary analysis performed here indicated that Cauchy and Weibull functions did not perform better than the polynomial function (not shown) when only one climate variable was included as the predictor. In addition, preliminary results showed that convergence was unsuccessful when a second climate variable was added (along with age) as the predictors, and extra restrictions were needed to force Htp to equal 1 when x_{dist} is zero. Therefore, Cauchy and Weibull functions were not used in the next analysis.

3.2.3.2 Adding both genetic gain and climate change into GYPSY

Age-age correlation has been proposed as a mechanism to predict the growth and yield of improved trees consisting of local provenances (Xie and Yanchuk 2003; Newton 2015). Incorporation of genetic gain for height into growth and yield estimates was achieved by applying age-age correlations to top height functions for white spruce and lodgepole pine in GYPSY, as shown in Equations (3.11 to 3.13).

$$\widehat{HTgw_{\iota.or\iota}} = \left(\left((GW/100) * r_{si,i} + 1\right)\right) * \widehat{HT_{\iota.or\iota}} \quad (3.11)$$

$$\widehat{HT_{\iota.or\iota.Sw}} = SI * (1 + \exp\left(b_1 + b_2\sqrt{\ln(1 + 50^2)} + b_3[\ln(SI)]^2 + b_4\sqrt{50}\right))/(1 + \exp\left(b_1 + b_2\sqrt{\ln(1 + totage_i^2)} + b_3[\ln(SI)]^2 + b_4\sqrt{50}\right)) \quad (3.12)$$

$$\widehat{HT_{\iota.or\iota.Pl}} = SI * (1 + \exp\left(f_1 + f_2\sqrt{\ln(1 + 50)} + f_3(\ln(SI)) + f_4\sqrt{50}\right))/(1 + \exp\big(f_1 + f_2\sqrt{\ln(1 + totage_i)} + f_3(\ln(SI)) + f_4\sqrt{50}\big)) \quad (3.13)$$

Where $\widehat{HTgw_{\iota.or\iota}}$ is the estimated improved top height at total age (totage) i under no climate change; GW is the genetic worth at selection age under no climate change, expressed as a %, and is the average breeding value weighted by gametic contributions of selected families in an improved seedlot; $r_{si,i}$ is the age-age correlation coefficient between selection age si and rotation age ri or total age i estimated from adjusted Lambeth equations (see Chapter 2, section 2.3.1.1), $r_{si,i} = 0.993 + 0.255(LAR)$ for white spruce, $r_{si,i} = 1.017 + 0.445(LAR)$ for lodgepole pine, $LAR = \log(si/i)$; $\widehat{HT_{\iota.or\iota}}$ is the top height (m) at a given total age for unimproved trees (GW=0) assuming no climate change for white spruce ($\widehat{HT_{\iota.or\iota.Sw}}$) and lodgepole pine ($\widehat{HT_{\iota.or\iota.Pl}}$); SI is in meters, assuming no climate change; totage=total age from the point of germination; $b_1, b_2, b_3, b_4, f_1, f_2, f_3, f_4$ = parameters with no biological interpretation.

Climate change impacts were incorporated into the growth and yield modelling of improved seedlots by adding Htp into Equation (3.11), as shown in Equation (3.14), and therefore the relative top height of improved seedlots under climate change could be calculated using Equation (3.15).

$$\widehat{HTgw_{\iota.cl\iota}} = \left(\left((GW/100) * r_{si,i} + 1\right)\right) * \widehat{HT_{\iota.or\iota}} * \widehat{Htp} \tag{3.14}$$

$$\widehat{Htp.GW} = \left(\left((GW/100) * r_{si,i} + 1\right)\right) * \widehat{Htp} \tag{3.15}$$

Where $\widehat{HTgw_{\iota.cl\iota}}$ is the esimated top height (m) of an improved seedlot at a given total age i under climate change condition; $\widehat{Htp}$ is the estimated height proportion for a population under climate change; $\widehat{Htp.GW}$ is the estimated top height proportion for an improved seedlot with genetic worth as GW under climate change.

To examine the impact of climate change and genetic gain on forest productivity, top height curves were generated with and without a changing climate, and with and without genetic gain. Each set of curves was developed for four white spruce test sites and four lodgepole pine test sites that covered the range of the selected climate variables (MCMT for white spruce and MAP for lodgepole pine, Table 3.3) in all test sites within Alberta. Finally, test sites G276d, G276a, G156a and G133a were selected for white spruce, and test sites Berland 3, Berland 5, G346b and G346a were selected for lodgepole pine.

To make the results of predicted heights comparable between white spruce and lodgepole pine, planting year for all curves was set at 2011 (year 1) and run for 80 years. Mean height and measurement age of a predefined local population (in the fourth step) was used to determine SI, which was inputted into GYPSY (Equations 3.12 and 3.13) to produce the top height curves of unimproved seedlots under no climate change for selected sites.

Annual climate values for the selected climate variables were obtained from ClimateNA (Wang *et al.* 2012; Wang *et al.* 2016) for each year from 2011 to 2090 at all eight test locations. Future values were generated from the second-generation Canadian Earth System global circulation model (CanSEM2) for all three RCPs. Values of the five-year-average climate variables (MCMT for white spruce and MAP for lodgepole pine, Table 3.3) prior to each site measurement age from year 2011 to 2090 were calculated for each population. To capture the long-term trend of climate change in the future and to produce smooth top height curves, a simple linear regression was fitted to five-year-average climate data. Selection age was set at 15 for white spruce and 25 for lodgepole pine to make the age-age correlation between selection age and age-80 close to 0.5 for both species (see Chapter 2, section 2.3.3.1, and Appendix Tables A-1 and A-2).

3.2.3.3 Spatial application of the adjusted Pooled Transfer Function (adjusted PTF)

To illustrate the effect of climate change on growth and yield at a provincial scale, I modelled *in situ* Htp of 484 white spruce and 491 lodgepole pine populations from throughout the natural range of these species in Alberta from 2011 (year of planting) to 2090. ClimateNA's ensemble climate projection, which is an averaged prediction from 15 General Circulation Models (GCMs), was used to generate future climate data for three time periods: 2020s (2011-2040), 2050s (2041-2070) and 2080s (2071-2100) (henceforth referred to by their mid-period year – 2025, 2055 and 2085, respectively). RCP8.5 was selected since it is the 'high scenario' and represents the maximum potential effect of climate change. Equations (3.7) and (3.15) were used to estimate Htp and Htp.GW at each seed source location. A GW of 10% for top height, which is the maximum GW from Chapter 2, was applied at years 2025, 2055 and 2085. To compare the relative heights of unimproved and improved seedlots, the difference in Htp between the two types of seedlots was also mapped across the selected sites. The estimated Htp values were presented with coloured heat-maps and added into the vector map of Alberta (Figures 3.9 to 3.11).

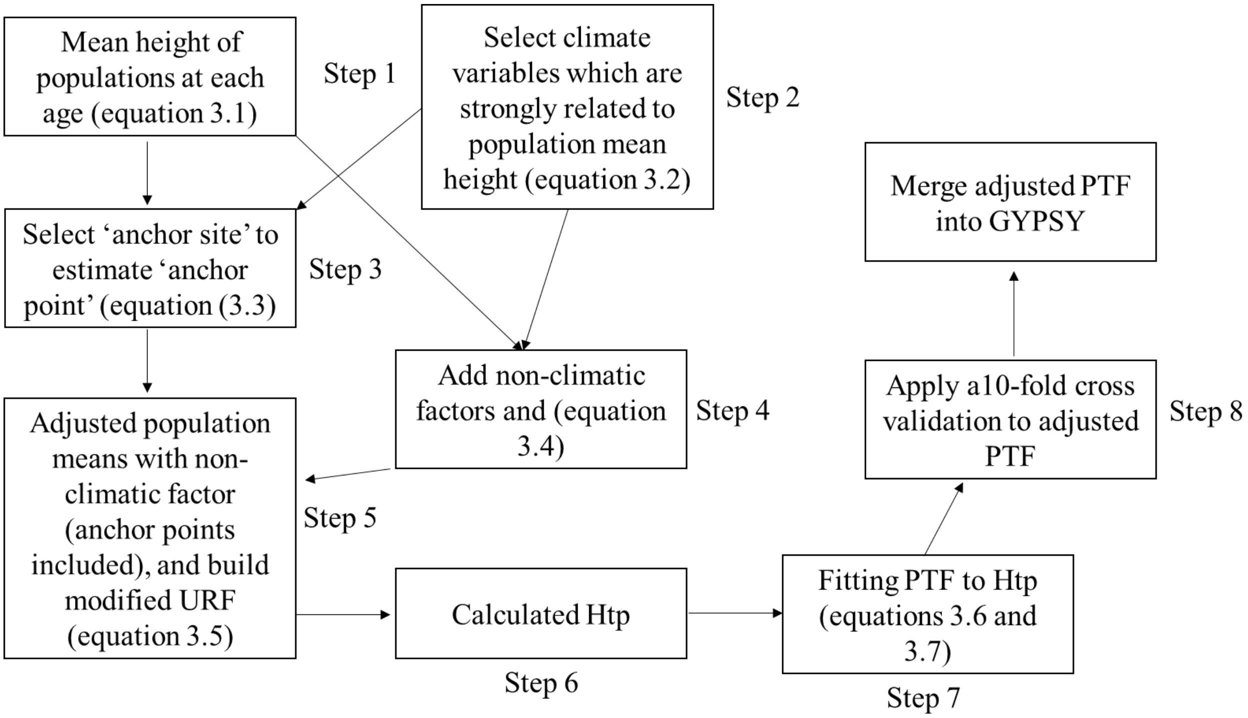

Figure 3.3 Flow chart for data analysis and development of the adjusted Pooled Transferred Function (adjusted PTF)

3.2.4 Software for analysis

All analysis in Chapter 3, models and data were run in the R environment (R Core Team 2018), using the packages ‘nlme’ (Pinheiro *et al.* 2020). Graphs were plotted using the package ‘ggplot2’ (Wickham 2016).

3.3. Results

3.3.1 Response of population mean height to climate change

The results of univariate URF (Equation 3.2) selection indicated that MCMT, MSP and SHM had the lowest AIC among temp, precip, and temp/precip variables, respectively, for white spruce, while EMT, MAP, and CMD had the lowest AIC for lodgepole pine (Table 3.3). For both species, bi-variate URFs using these climate variables showed lower AIC values than either univariate model (Table 3.3). However, a response surface plot with provenance climate as the y-axis and test site climate as the x-axis was expected to have a single height peak on the z-axis and therefore be biologically meaningful, as each provenance should have an optimum climate transfer distance to reach its physiological optimum (O'Neill *et al.* 2008; Nigh 2014; Rehfeldt *et al.* 2018). Response surface plots for MSP for white spruce and EMT for lodgepole pine, did not show a biologically meaningful single peak in preliminary analyses (data not shown), and were therefore removed in subsequent analyses and a univariate URF was selected.

Table 3.3 Model evaluation statistics (Akaike's Information Criterion (AIC) and pseudo R^2) for univariate and bivariate Universal Response Functions (eq 3.2) for temperature, precipitation and temperature/precipitation-related climate variables for white spruce (Sw) and lodgepole pine (Pl). Insignificant parameters were excluded; bolding refers to the variable with the lowest AIC in each category

Climate variable	AIC (Sw)	Pseudo R^2 (Sw)	AIC (Pl)	Pseudo R^2 (Pl)
Single variable - temperature related				
Mean annual temperature (MAT)	104213	0.882	158352	0.913
Mean coldest month temperature (MCMT)	**103219**	**0.894**	158655	0.911
Mean warmest month temperature (MWMT)	106551	0.849	158457	0.912
Continentality (TD)	103949	0.886	158872	0.909
Degree-days below 0 °C (DD_0)	104390	0.880	157550	0.917
Degree-days above 5 °C (DD5)	106665	0.847	160038	0.902
Degree-days below 18 °C (DD_18)	104177	0.883	158310	0.913
Degree-days above 18 °C (DD18)	106657	0.847	157525	0.918
Number of frost-free days (NFFD)	105784	0.861	158880	0.909
Frost-free period (FFP)	106353	0.852	159466	0.906
The day of the year on which FFP begins (bFFP)	106322	0.853	159093	0.908
The day of the year on which FFP ends (eFFP)	106857	0.844	158987	0.909
Extreme maximum temp over 30 y (EMT)	105290	0.868	**157125**	**0.920**
Extreme minimum temp over 30 y (EXT)	106315	0.853	157638	0.918
Single variable-precipitation related				
Mean annual precipitation (MAP)	106413	0.851	**157092**	**0.920**
Mean summer precipitation (MSP)	**106001**	**0.858**	158108	0.914
Precipitation as snow (PAS)	106725	0.846	159019	0.909
Single variable-temperature/precipitation related				
Annual heat-moisture index (AHM)	106278	0.853	159015	0.909
Summer heat-moisture index (SHM)	**105746**	**0.861**	159415	0.906
Hargreaves climatic moisture deficit (CMD)	105982	0.858	**158073**	**0.915**
Two-climate-variable model				
MCMT&MSP	**102899**	**0.897**	-	-
EMT&MAP	-	-	**150787**	**0.941**

Fitting a model to local population mean height (Equation 3.4) showed an accurate prediction (Figure 3.4), with low RMBs of 3.38% and 1.33% for white spruce and lodgepole pine, respectively, and an efficiency of 0.70 and 0.92 for white spruce and lodgepole pine, respectively. Cross validation results indicate that fitting a modified URF (Equation 3.5) to population mean height adjusted with a non-climatic index resulted in an accurate prediction, as shown in Figure 3.5. Although a significant bias was shown in improved lodgepole pine, population mean height was only overestimated by 3.8% (Figure 3.5d). Also, efficiencies were higher than 0.88 for both species, and for both unimproved and improved seedlots (Figure 3.5).

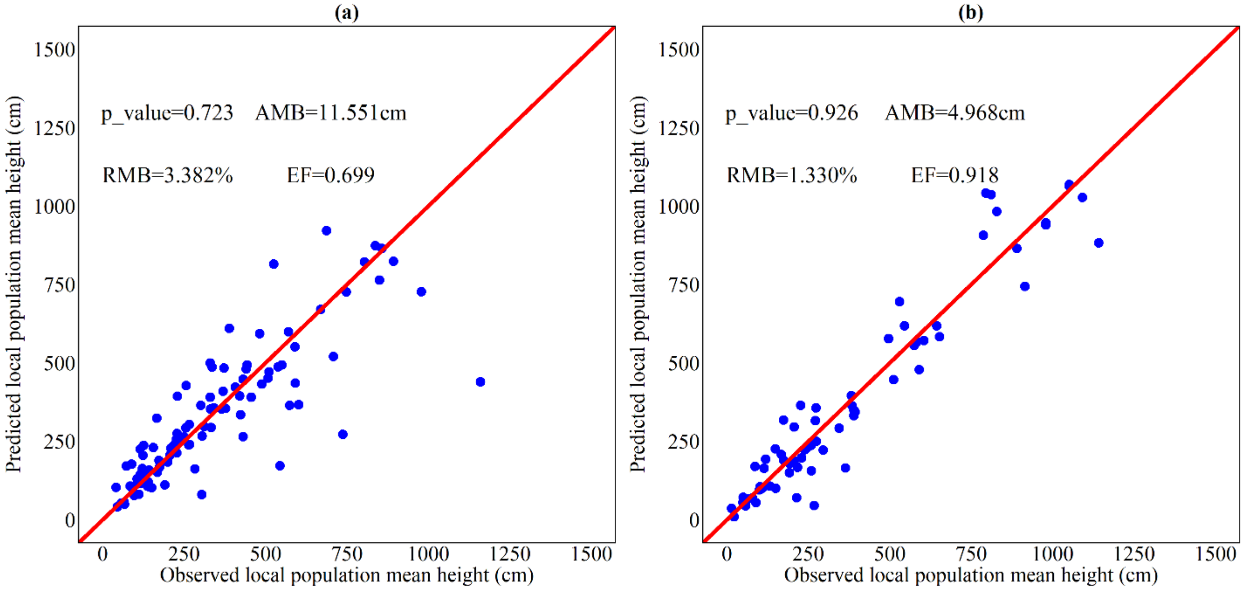

Figure 3.4 Scatterplot of observed local population mean height value vs. predicted local population mean height for white spruce (a) and lodgepole pine (b). The p_value was obtained from t-tests between observed and predicted population mean height, AMB is the average model bias, RMB is the relative model bias, EF is the efficiency, and a minus EF value indicates a poorer model fit than using the overall mean of the observations

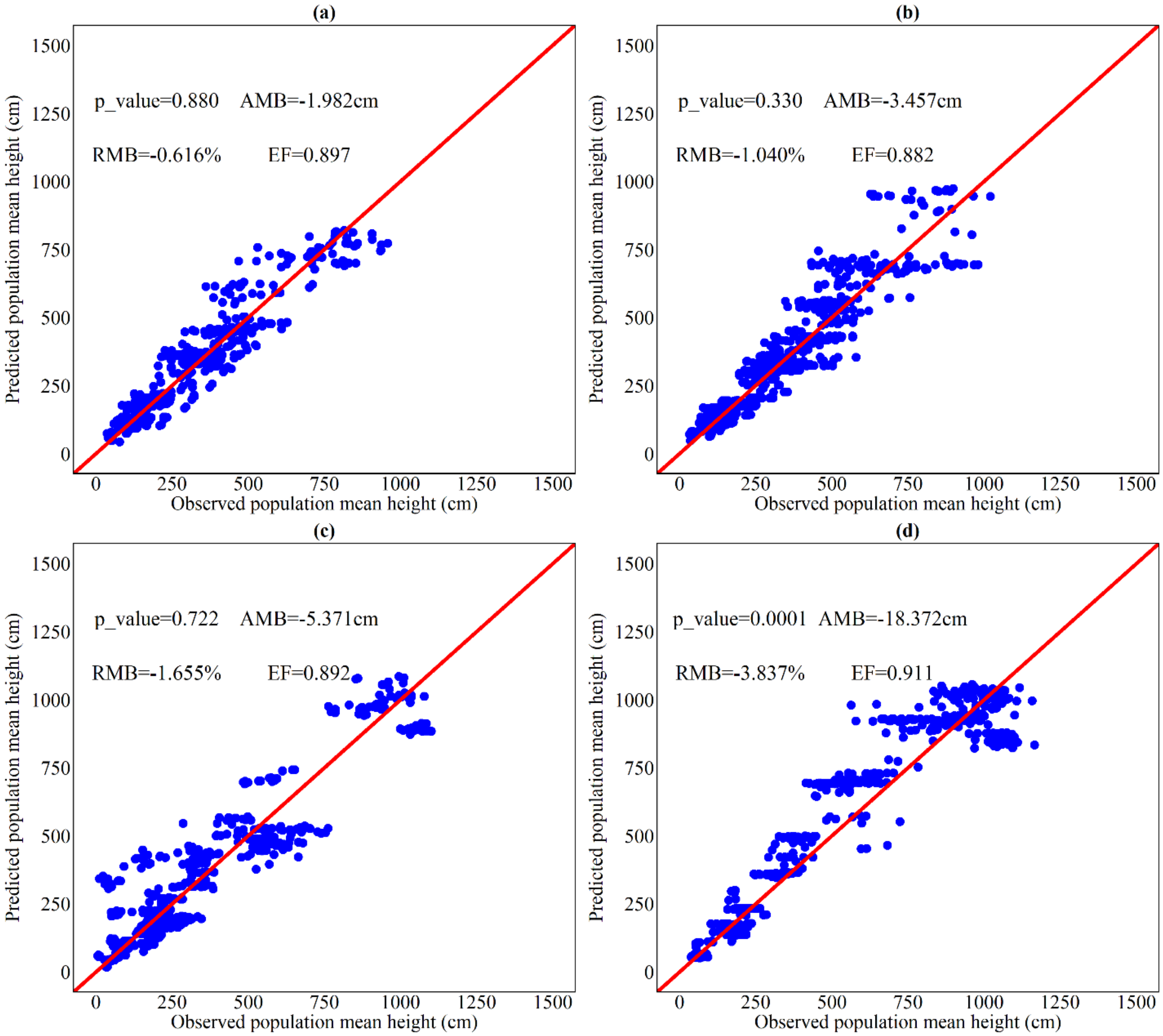

Figure 3.5 Scatterplot of observed population mean height value vs. predicted population mean height for unimproved (a) and improved (b) white spruce seedlots, and for unimproved (c) and improved (d) lodgepole pine seedlots. The p_value was obtained from t-tests between observed and predicted population mean height, AMB is the average model bias, RMB is the relative model bias, EF is efficiency, and a minus EF value indicates a poorer model fit than using the overall mean of the observations

Adding age into the 2nd degree polynomial function did not significantly change the RMSEP (Table 3.4). Therefore, the adjusted PTF using a single climate variable was used (Table 3.5) and a 10-fold cross validation for the final adjusted PTF is shown in Figure 3.6.

The results of cross validation indicated that the predicted Htp values were not significantly biased for white spruce and lodgepole pine regardless of seedlot type and EF values were between 0.33 and 0.84 (Figure 3.6).

Table 3.4 Results of a 10-fold cross validation on the height proportion (Htp) for seedlot type (improved and unimproved) of white spruce (Sw) and lodgepole pine (Pl) with a polynomial function. 2nd is the 2^{nd} degree polynomial, RMSEP.lsm is least square mean of root mean square error of prediction, SE is standard error of RMSEP, p_value was obtained from t test between selected models, MCMT is mean coldest month temperature, and MAP is mean annual precipitation

Species	Seedlot Type	Model	RMSEP.lsm	SE	p_value
Sw	Unimproved	2nd MCMT	0.245	0.00681	0.883
		2nd MCMT & age	0.247	0.00681	
	Improved	2nd MCMT	0.218	0.00155	0.985
		2nd MCMT & age	0.218	0.00155	
Pl	Unimproved	2nd MAP	0.641	0.0301	0.798
		2nd MAP & age	0.630	0.0301	
	Improved	2nd MAP	0.291	0.00229	0.845
		2nd MAP & age	0.292	0.00229	

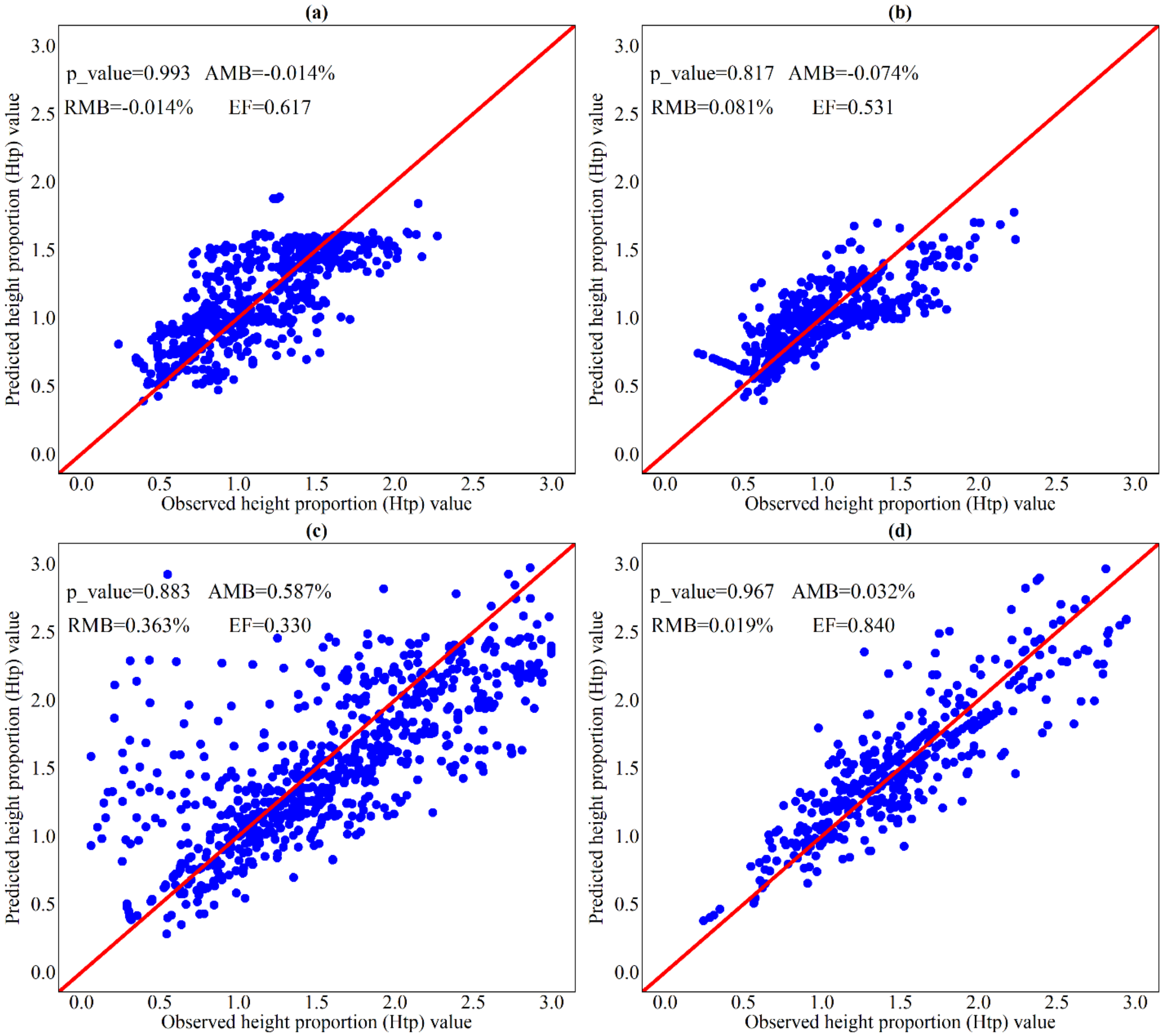

Figure 3.6 Scatterplot of observed height proportion (Htp) value vs. predicted Htp value for white spruce unimproved seedlots (a) and improved seedlots (b), and for lodgepole pine unimproved (c) and improved seedlots (d). The p_value was obtained from t-tests between observed and predicted Htp, AMB is the average model bias, RMB is the relative model bias, EF is efficiency, and a minus EF value indicates a poorer model fit than using the overall mean of the observations

Table 3.5 Parameter estimates for white spruce (Sw)[a] and lodgepole pine (Pl)[b] by seedlot type (improved and unimproved) for c_1, c_2, and c_3, for the adjusted Pooled Transfer Function (adjusted PTF, eq 3.7)

Species	Seedlot type	c_1	c_2	c_3
Sw	Unimproved	-0.513722	-0.017885	-0.031722
	Improved	-0.344	-0.01372	-0.0217
Pl	Unimproved	0.04447	-0.00004891	-0.00008799
	Improved	0.02092	-0.0000284	-0.00004565

[a]: $Htp = exp(c_1 * MCMT_{dist} + c_2 * MCMT_{dist}^2 + c_3 * MCMT_{ori}: MCMT_{dist})$

[b]: $Htp = exp(c_1 * MAP_{dist} + c_2 * MAP_{dist}^2 + c_3 * MAP_{ori}: MAP_{dist})$

Results showed that both improved and unimproved white spruce populations from provenances colder than -16 °C are expected to display their greatest height when grown in climates warmer than their origin, whereas populations from provenances warmer than -16 °C are expected to display their greatest height when grown in climates colder than their origin (Figure 3.7 a-b). Likewise, populations from provenances colder than -16 °C are expected to show an increase in height from climate warming, whereas those from provenances warmer than -16 °C are expected to show a decrease in height from climate warming (Figure 3.7 a-b). For lodgepole pine, both improved and unimproved populations from provenances with a MAP < 500 mm are expected to display their greatest height when grown in climates wetter than their origin, whereas populations from provenances with an MAP > 500 mm are expected to display their greatest height when grown in climates drier than their origin (Figure 3.7 c-d). Likewise, populations from provenances with MAP <

500 mm are expected to show an increase in height from increased precipitation, whereas those from provenances with MAP > 500 mm are expected to show a decrease in height from increased precipitation (Figure 3.7 c-d).

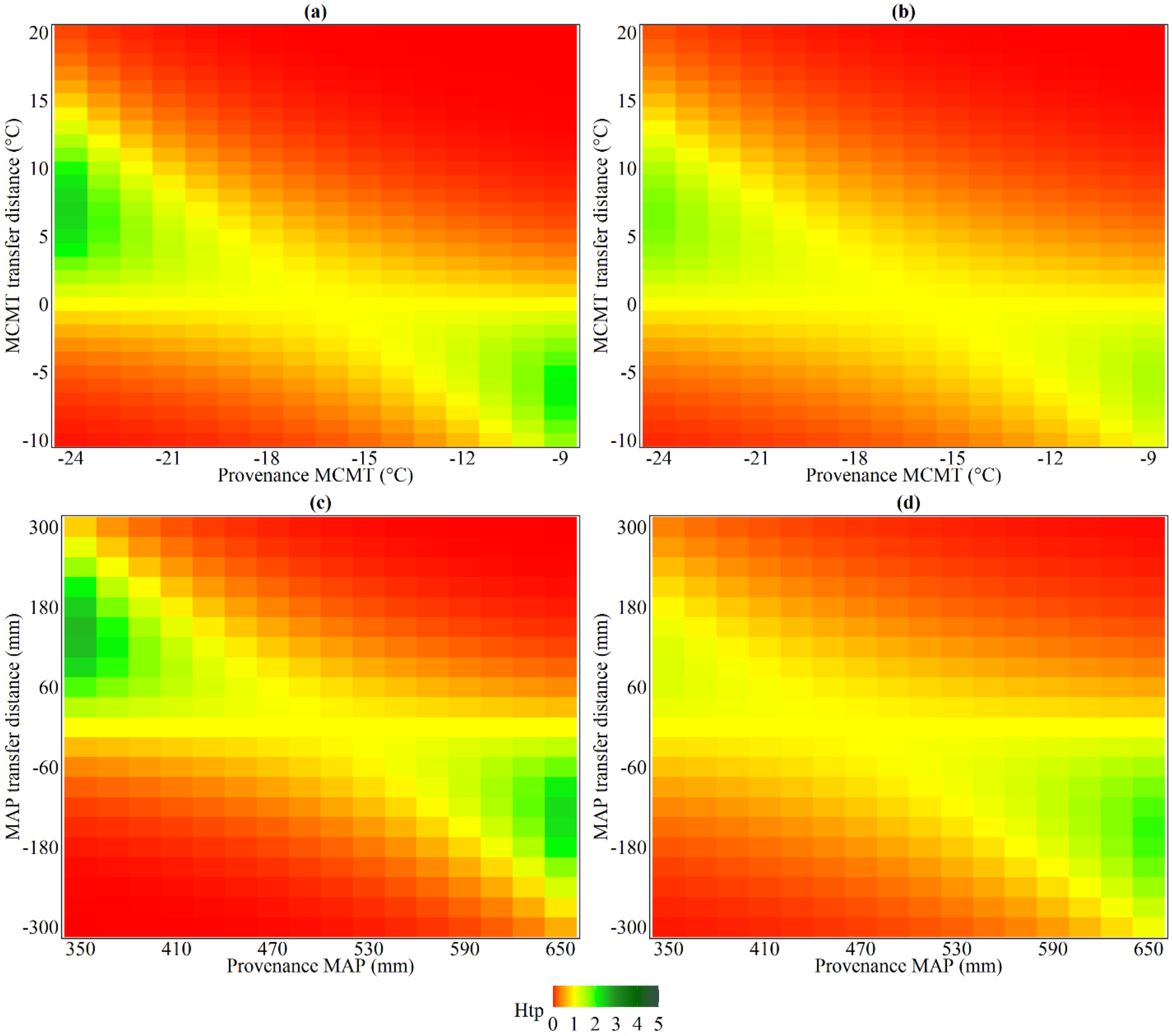

Figure 3.7 Height proportion (Htp) as a function of provenance mean coldest month temperature (MCMT) and MCMT transfer distances for unimproved (a) and improved (b) white spruce seedlots; Htp as a function of provenance mean annual precipitation (MAP) and MAP transfer distances for unimproved (c) and improved (d) lodgepole pine seedlots; value 1 (yellow) indicates no change of Htp

3.3.2 Growth and yield of improved and unimproved seedlots under climate change

The white spruce improved seedlots with a warmer provenance origin MCMT and greater top height values (e.g. G276d in Figure 3.8) showed a decrease in top height in the future with an increase in MCMT. An increase in MCMT showed a positive effect on the height of white spruce seedlots with a colder provenance origin MCMT (e.g. G133a in Figure 3.8). The lodgepole pine, from the four test sites, showed a negative height response to future MAP regardless of seedlot type (improved vs. unimproved) (Figure 3.9). For both white spruce and lodgepole pine, when certain climate change parameters showed a positive effect on height, unimproved seedlots were expected to gain more height (Figures 3.8 and 3.9). Furthermore, when climate change parameters showed a negative effect on height, improved seedlots were expected to retain superiority over the unimproved seedlots (Figures 3.8 and 3.9).

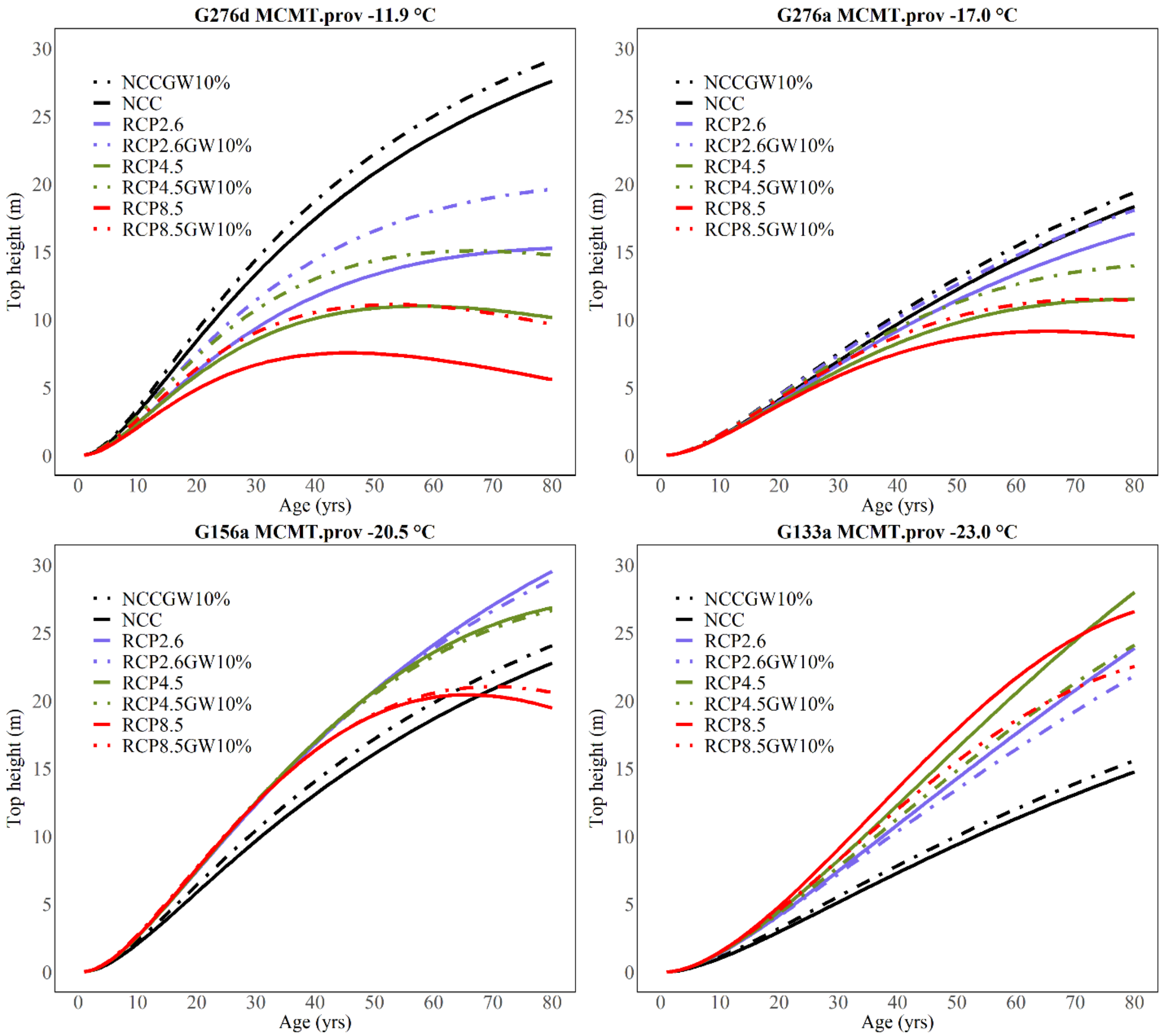

Figure 3.8 Expected top height curves of unimproved (solid lines) and improved (dashed lines) populations of white spruce with 10% genetic worth for height selected at age 15 in sites G276d (elevation = 998m), G276a (elevation = 572m), G156a (elevation = 499m) and G133a (elevation = 334m) under a No Change in Climate Condition (NCC) and under three Representative Concentration Pathways (RCPs) (RCP2.6, RCP4.5 and RCP8.5). MCMT.prov refers to provenance mean coldest month temperature (MCMT)

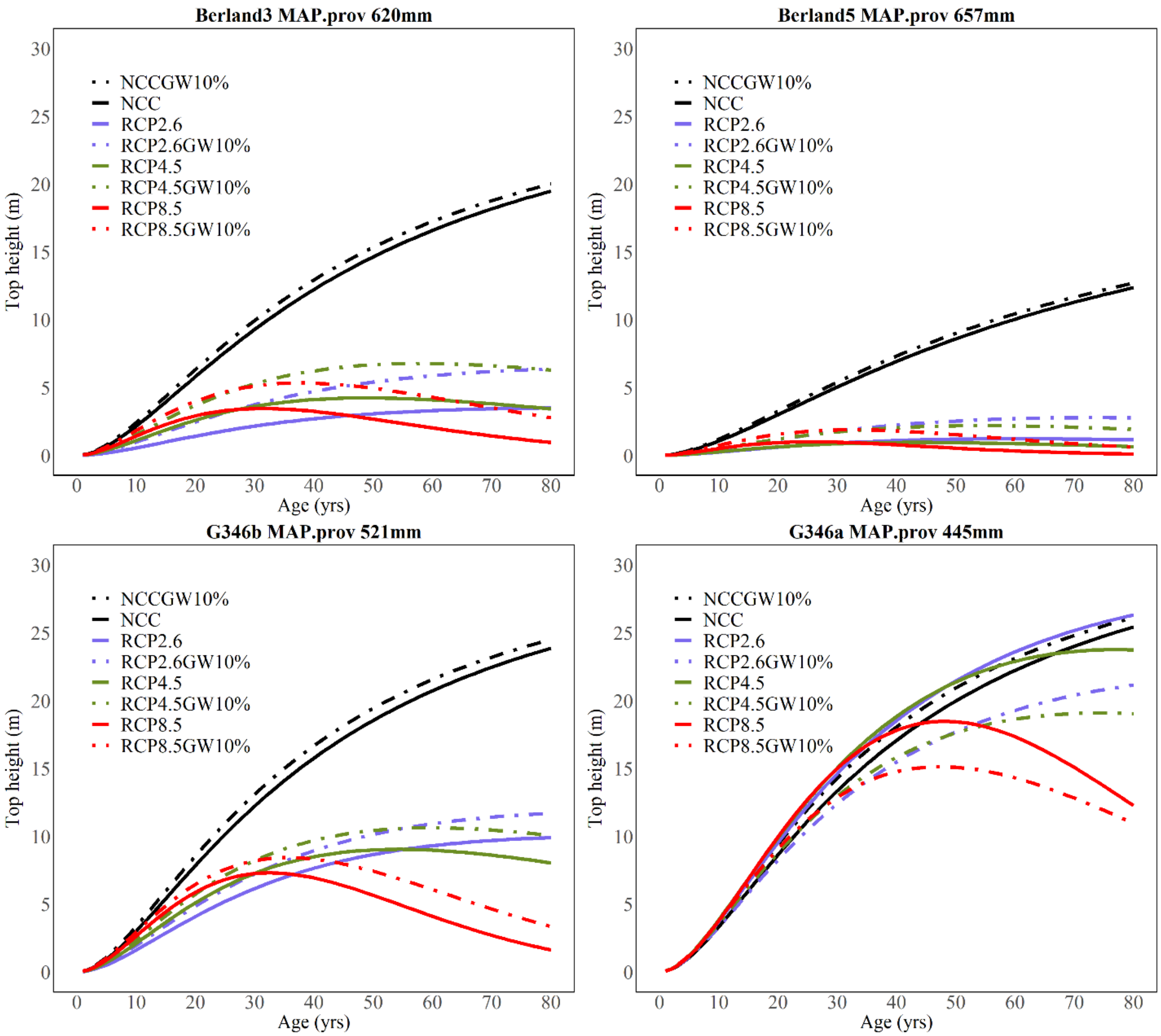

Figure 3.9 Expected top height curves of unimproved (solid lines) and improved (dashed lines) lodgepole pine with 10% genetic worth for height selected at age 25 in sites Berland3 (elevation = 1074m), Berland5 (elevation = 956m), G346b (elevation = 932m) and G346a (elevation = 750m) under a No Change in Climate Condition (NCC) and three Representative Concentration Pathways (RCPs), including RCP2.6, RCP4.5 and RCP8.5. MAP.prov refers to provenance origin mean annual precipitation (MAP)

3.3.3 Spatial application of the adjusted Pooled Transfer Function (adjusted PTF)

The results suggest that white spruce will show an increase in height in northern Alberta (green dots, Figure 3.10) and a decrease in height in the middle to southwestern Alberta (scarlet and red dots, Figure 3.10) due to climate change (RCP 8.5) in years 2025, 2055 and 2085, regardless of seedlot type. On the other hand, lodgepole pine will show a decrease in height due to climate change on most sites (scarlet and red dots, Figure 3.11), except for some sites in northern Alberta where an increase of height is expected (light green dots, Figure 3.11). Under RCP8.5, the most severe climate change scenario, the analyses predicted that improved white spruce seedlots established in 2011 will be shorter at age-80 than unimproved seedlots in northern Alberta (scarlet and red dots, Figure 3.12, upper graphs), but will be taller than the unimproved seedlots in the middle to southwestern Alberta (light green dots, Figure 3.12, upper graphs). For lodgepole pine, improved seedlots are expected to be taller than unimproved seedlots throughout most stands (green dots, Figure 3.12, lower graphs), with some regions showing no difference in performance between improved and unimproved seedlots (orange dots, Figure 3.12, lower graphs).

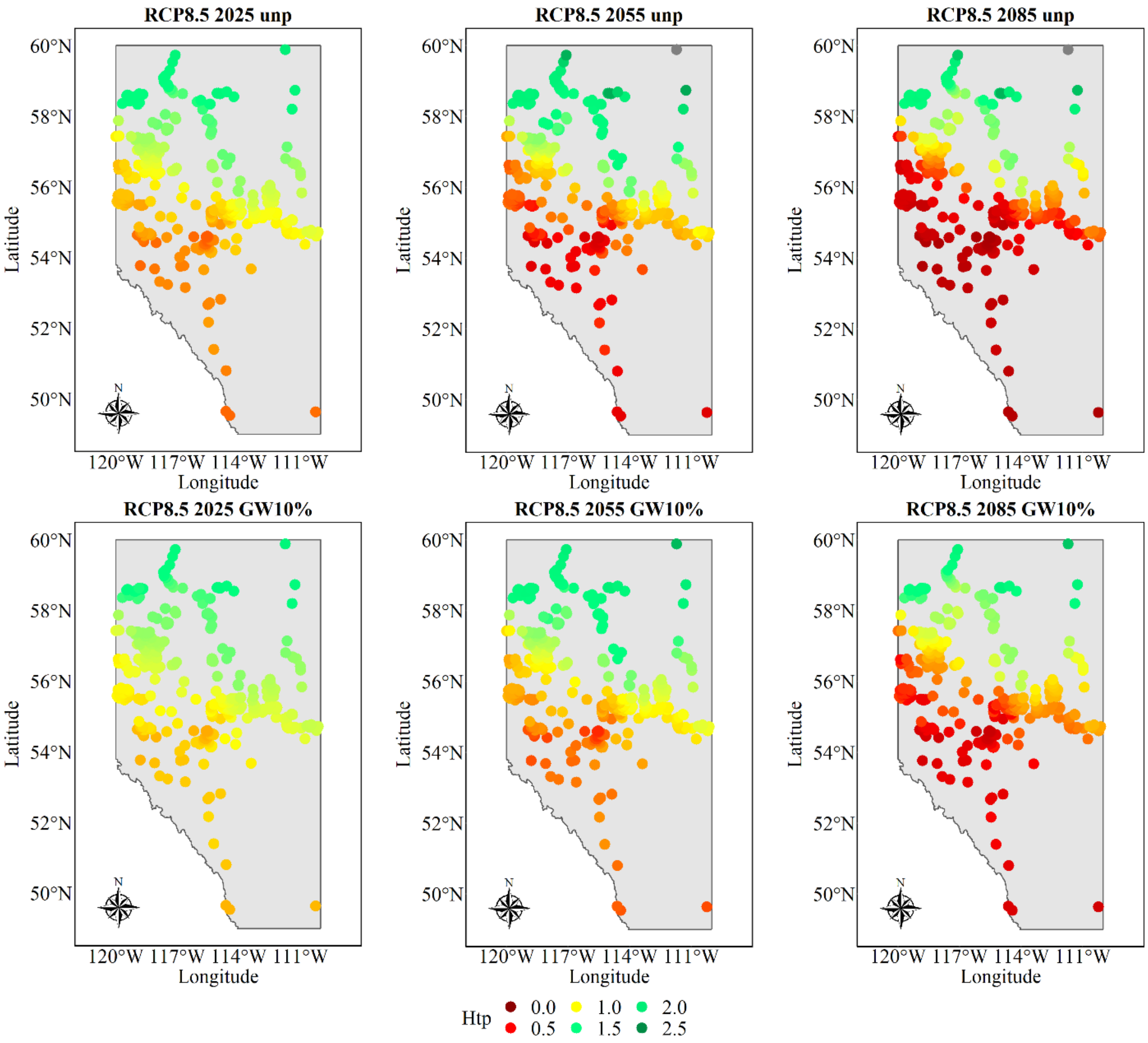

Figure 3.10 Expected impact of climate change on height of white spruce established in 2011 with unimproved (unp) and improved (genetic worth = 10%, GW10%) local seedlots in 2025, 2055 and 2085 under Representative Concentration Pathway (RCP) 8.5. Htp refers to the expected height under climate change relative to the expected height in the absence of climate change. Htp = 1 indicates no change in performance (yellow dots), Htp < 1 indicates a decrease in height (scarlet and red dots), and Htp > 1 indicates an increase in height due to climate change (green dots)

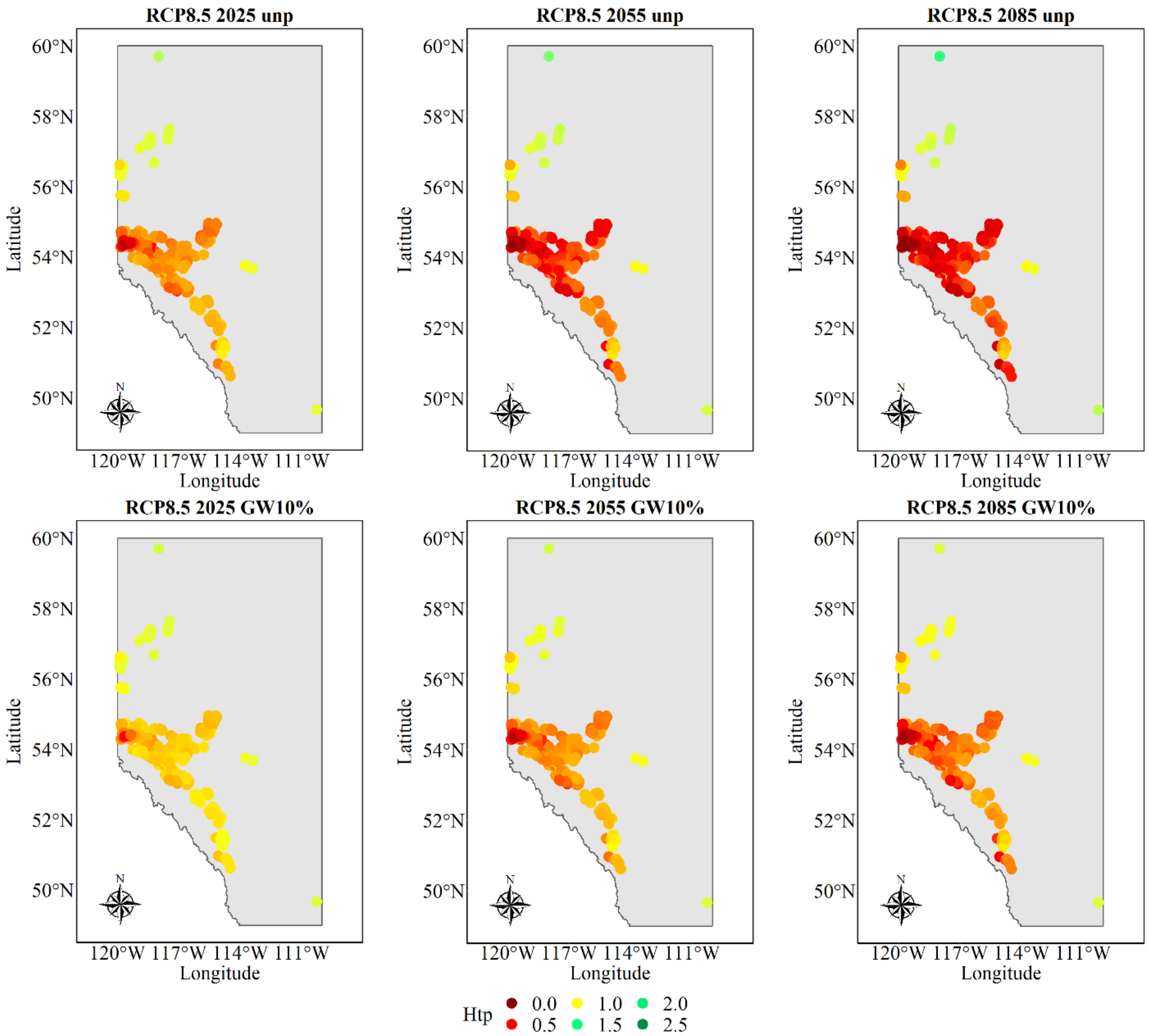

Figure 3.11 Expected impact of climate change on height of lodgepole pine established in 2011 with unimproved seedlots (unp) and improved (genetic worth = 10%, GW10%) local seedlots in 2025, 2055 and 2085 under Representative Concentration Pathway (RCP) 8.5. Htp refers to the expected height under climate change relative to the expected height in the absence of climate change. Htp = 1 indicates no change in performance (yellow dots), Htp < 1 indicates a decrease in height (scarlet and red dots), and Htp > 1 indicates an increase in height due to climate change (green dots)

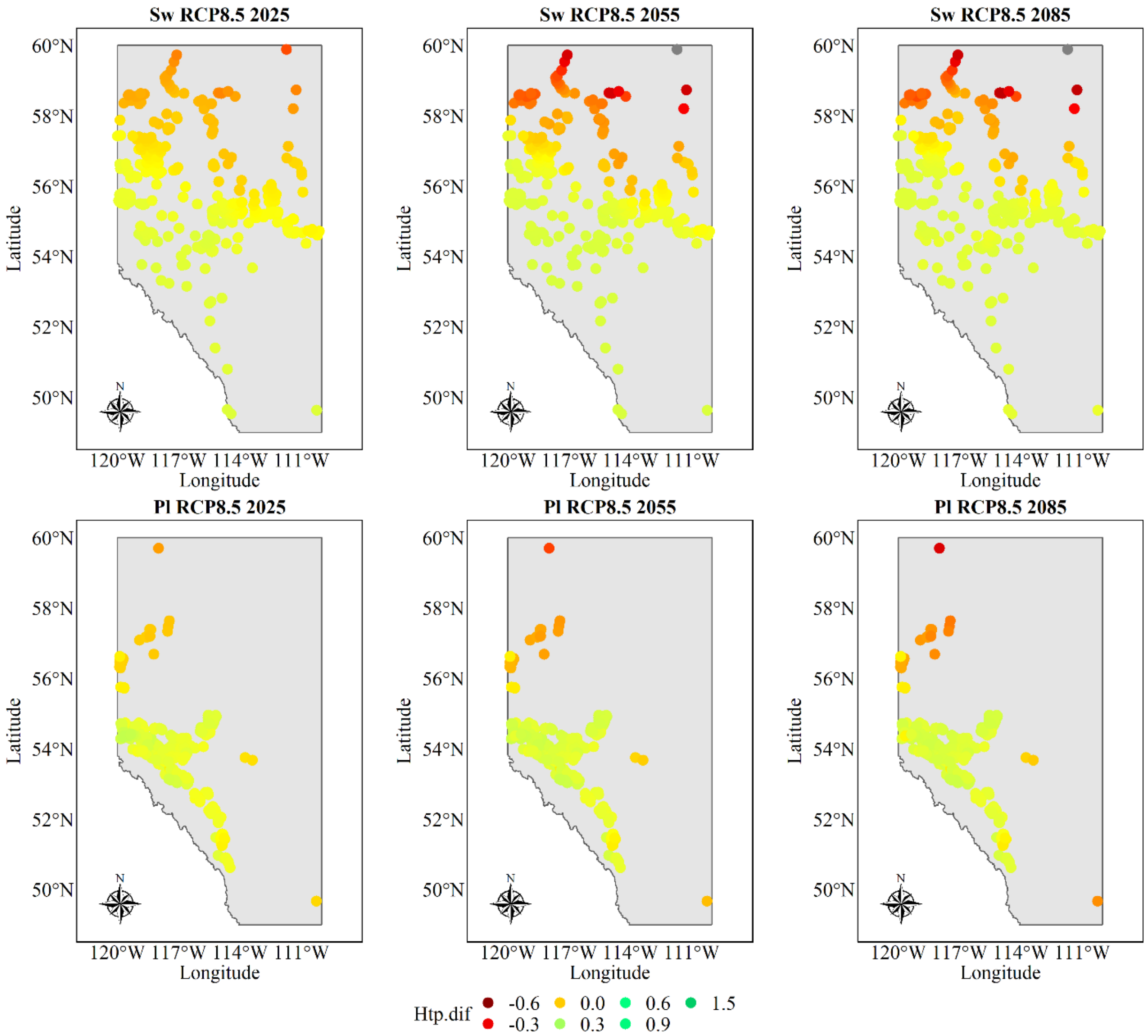

Figure 3.12 Height proportion difference (Htp.dif) between improved (genetic worth = 10%, GW10%) and unimproved local seedlots for white spruce (Sw) and lodgepole pine (Pl) across provenance and test sites in 2025, 2055 and 2085 under Representative Concentration Pathway (RCP) 8.5. Htp.dif = 0 indicates no difference between improved and unimproved seedlots (orange dots), Htp.dif < 0 indicates improved seedlots outgrown by the unimproved seedlots (scarlet and red dots), and Htp.dif > 0 indicates improved seedlots outgrow the unimproved seedlots (green and blue dots)

3.4. Discussion

3.4.1 The effect of climate change on improved and unimproved seedlots of white spruce and lodgepole pine in Alberta

Height proportion, Htp, the height of families in progeny trials and seedlots in provenance trials, relative to their expected height at their origin (i.e. provenance), was used in establishing models for estimating responses of seedlots (improved and unimproved) originating from a wide range of provenances to a variety of climate conditions. Growth responses of different populations to different climate conditions have also been investigated in previous studies. For example, in British Columbia, Canada, by using provenance trial data, losses in stand yield for lodgepole pine were predicted in most areas, with an exception of a stand yield increase in northern areas (O'Neil *et al*. 2008). In Alberta, by using stem analysis on trees from natural stands, a decreasing trend of aboveground biomass for white spruce was reported throughout most areas of the province, except in northern areas where an increase in aboveground biomass was observed (Hogg *et al*. 2017). These findings are similar to the results from unimproved seedlots in our current study (Figure 3.10). It is important to note that in previous work, both UTF's and URF's were unable to predict yield at rotation ages under a variety of climate change scenarios for improved seedlots (O'Neill *et al.* 2008; Wang *et al.* 2010). Therefore, by taking advantage of the seedlots moved and tested outside of their region of origin, in both progeny and provenance trials in Alberta, I was able to incorporate genetic gain, age-age correlation and the adjusted PTF into GYPSY to simulate the yield response for improved and unimproved seedlots under various climate change scenarios.

With the objective of being able to predict climate change impacts, the final adjusted PTF was selected based on the results of a 10-fold cross validation, which differs from the focus on AIC and residuals used in the development of earlier UTF (O'Neill *et al.* 2008) and URF (Wang *et al.* 2010) models. The validation results indicate that the adjusted PTF showed an accurate prediction in predicting the response of white spruce and lodgepole pine seedlots regardless of seedlot type (Figure 3.6). Therefore, the adjusted PTF was expected to be effective in adjusting yield curves for improved and unimproved seedlots under the various climate change scenarios tested. The addition of age, as a predictor in the adjusted PTF, does not improve the prediction accuracy, as shown by the cross-validation results, and therefore the Htp is independent of age and thus expected to represent a reasonable extrapolation to rotation age (Table 3.4).

The feature of a single peak for the relative height (Htp) along the transfer distance is captured in the adjusted PTF (Figure 3.7), and this peaked yield is not located near the zero-transfer distance for many populations. Previous studies have reported that populations seem to inhabit a variety of suboptimal climates, and the ecological optimum (competitively exclusive) of a provenance is often not equal to its physiological optimum (competitively excluded) (Leites *et al.* 2012a; Rehfeldt *et al.* 2018). This difference between 'ecological optimum' and 'physiological optimum' is consistent with the patterns found in Chapter 3, which is that the peak of Htp falls near a non-zero transfer distance for many provenances (Figure 3.7), especially for the provenances with a lower original SI (SI in the origin site assuming no climate change) growing under a suboptimal climate. However, the ecological optimum and physiological optimum for a provenance tend to have a smaller difference and even to overlap as the original SI increases, as shown in Figure 3.7. Therefore, the potential increase in yield under climate change is expected for provenances originating from a suboptimal climate and growing in the climate approaching these provenances 'physiological optima'.

The finding of non-local optimality also supports the idea of 'gene swamping' (Aitken *et al.* 2008), in which there exists a net flow of pollen from the center of a species' distribution where populations are dense (large numbers of trees/ha) toward peripheral populations where densities are lower. This flow results in an evolutionary lag among peripheral populations, such that their adaptation is more similar to the central populations than one would expect from their climate (Aitken *et al.* 2008).

3.4.2 The implication of climate change on tree improvement in Alberta

The results shown in this study highlight the importance of considering climate change in tree improvement programs. Improved populations adapted to current climates may be maladapted to climates in the near future. Adding both genetic gain and climate change into GYPSY enables the interaction between genotype and environment to be further delineated and explored in the long-term. The results of Chapter 3 indicate that improved populations may or may not retain a yield advantage over the unimproved seedlots under different climate change scenarios (Figures 3.8, 3.9, 3.12). The improved seedlots may be outgrown by the unimproved seedlots when climate change favours height growth (Figures 3.8, 3.9, 3.12), while improved seedlots are expected to retain their yield advantage over the unimproved seedlots in locations where climate will have a negative effect on height growth (Figures 3.8, 3.9, 3.12). In addition, the drop in top height for lodgepole pine appeared under RCP8.5, suggesting a decrease in the maximum height that could be supported by future climate and potential mortality of top height trees under an extreme climate change scenario (Figure 3.9). These long-term simulation results may have a considerable impact on tree improvement strategies and policy in Alberta. Program managers may need to adjust and refocus their breeding objectives, and a single strategy may not be appropriate in all regions for both white spruce and lodgepole pine. Other traits of adaptive importance such as drought or pest tolerance may become more important for tree growth under climate change scenarios, and should be considered, investigated and prioritized in future tree improvement program decisions.

The adage of 'local is best' was demonstrated in recent studies in Alberta, which indicates that seedlots moved to new regions, in most cases, may be outgrown by local populations (Gray *et al.* 2016a; Gray *et al.* 2016b). The height of a seedlot that is moved, relative to the average height of the local population in the 'new' target sites was also used in predicting the yield of a population under multiple climate change scenarios in British Columbia, Canada (O'Neill and Nigh 2011; Nigh 2014). Previous reports standardized a moving population site mean height value by dividing the population mean height at each site by the mean height of each site's local population (HT_L) (O'Neill and Nigh 2011; Nigh 2014). This step enabled data across sites of differing productivity to be pooled so that $HT_L = 1.0$, allowing seed transfer or climate change impacts to be expressed as a proportion of HT_L, a necessary prerequisite for adjusting growth and yield models with provenance test results (O'Neill and Nigh 2011; Nigh 2014). In contrast, I standardized a moving population site mean height value by dividing each population mean height at each site by the expected height of each population when grown at its origin. As non-climatic (site) effects on height were already accounted for in Step 6 (see Materials and Methods, section 3.2.3), I chose this standardization approach because it accounts for environmental differences rather than genetic differences. This difference in calculation may be contributing to the differences in my study compared with earlier studies, since in my study I focused on the effect of climate change on local populations, while earlier studies mentioned above focused on the effect of assisted migration. In other words, Chapter 3 did not focus on the optimum transfer distance, that is, the best location for a seedlot (physiological optimum) does not identify the best seedlot for a location (ecological optimum).

3.4.3 Limitations of Chapter 3

The results did not consider all possible factors associated with climate change, including mortality (Michaelian *et al.* 2011; Kweon and Comeau 2017), shifts in species distributions (Parmesan and Yohe 2003; Gray and Hamann 2011), forest fire frequency (Flannigan *et al.* 2000; Bergeron *et al.* 2004), the impact of insects (Pureswaran *et al.* 2018), or application of silviculture (Landhäusser 2009; MacIsaac and Krygier 2009; Comeau 2014; Kabzems *et al.* 2016). One should also consider that diameter variation is more sensitive than height when site quality differs, species composition changes, and competition varies (Rich *et al.* 1986; Wang *et al.* 1998; Pritchard and Comeau 2004; Voicu and Comeau 2006; Nunifu 2009; Sharma *et al.* 2016).

In this study, I assumed that natural migration will not occur, and that local populations will remain competitively exclusive until 2090. Whether this assumption will stand the test of time is yet to be seen. In addition, how to choose between selecting improved local families and using different provenances will also need further study.

The test sites available were not installed beyond the natural distribution range of the species nor where the effects of climate considered extreme to the growth of white spruce and lodgepole pine. Therefore, the ability of progeny and provenance trials to predict climate change impacts is mainly limited by the climate range of the test sites (Figure 3.2).

The number of observations available from provenance trials was considerably less than that available from progeny trials for lodgepole pine (Figures 3.1 and 3.2), which may impact the prediction accuracy. Ahmed *et al.* (2016, 2020) developed a height trajectory meta-analysis model for white spruce and hybrid spruce, based on provenance trials across the boreal forest in Canada, and applied this method in estimating genetic gain with an increasing age under climate effects for white spruce. The comparison between the height trajectory meta-analysis model and the adjusted PTF was done in this study.

Nonetheless, the results from my work provides a valuable new approach of combining genecology with growth and yield models in predicting climate change impacts on reforested plantation stands.

3.5. Conclusion

I explored a new method for estimating the effect of climate change on the growth and yield of improved and unimproved seedlots for white spruce and lodgepole pine in Alberta. Taking advantage of existing test sites where both wild stand seed zone seedlots (unimproved) and seed orchard breeding program seedlots (improved) were planted outside their region of origin, a height proportion of the moving seedlot to its height in its provenance was calculated and used in establishing a new model. The new adjusted pooled transfer function (adjusted PTF) model combined genetic gain and age-age correlation which was then incorporated into GYPSY to predict the growth and yield of improved and unimproved seedlots that consisted of local provenances under multiple climate change scenarios.

The cross-validation results indicated that the adjusted PTF was accurate for estimating the future yield of improved and unimproved seedlots for white spruce and lodgepole pine. White spruce height was strongly related to the mean coldest month temperature (MCMT) at provenances and test sites, while lodgepole pine height was found to be strongly related to the mean annual precipitation (MAP) at provenances and test sites. White spruce is projected to have improved height yield in northern Alberta and a decrease in height yield further south; lodgepole pine is projected to show a decrease in height across most of the species' range in Alberta. For both species, unimproved seedlots are expected to gain more benefit when climate change favours height growth, while improved seedlots are expected to retain their growth advantage over unimproved seedlots when climate change shows a negative effect on height.

Chapter 4: Effects of competition on early growth of improved white spruce in northeastern Alberta

4.1 Introduction

White spruce (*Picea glauca* (Moench) Voss) is one of the most important commercial tree species in Alberta and occurs in both mixedwood and pure stands in the boreal region of Alberta as well as in other parts of Canada. Boreal mixedwood forests are distributed across northern Canada and are characterized by canopy dominance of mixtures of boreal broadleaf and conifer trees (Bergeron *et al.* 2014). In western Canada in particular, mixedwood stands play a prominent role in the boreal forests due to the high wildfire frequency (Bergeron and Fenton 2012; Bergeron *et al.* 2014), with relatively large areas covered by white spruce and trembling aspen (Chen and Popadiouk 2002). In mixtures of white spruce and trembling aspen (*Populus tremuloides* Michx.), aspen cover can promote growth of young white spruce by reducing frost damage and suppressing growth of other competitive species, while facilitating carbon and nutrient cycling over the long-term to increase the efficiency of resource utilization in the stand (MacIsaac and Krygier 2009; Comeau 2014; Grover *et al.* 2014; Kabzems *et al.* 2015; Pitt *et al.* 2015).

Tree improvement is recognized as one approach to addressing a reduction in the operable forest landbase (Schneider and Dyer 2006; Mbogga *et al.* 2009; Fettig *et al.* 2013; Wang *et al.* 2014); White *et al*. 2007). However, in Alberta, only improved seedlots deployed in pure managed stands are currently considered for genetic gain in Forest Management Plans (FMP) and Timber Supply Analysis (TSA), due to current uncertainties in estimating and verifying operational gain where improved seedlots are deployed in mixed stands (AAF 2016b). This emphasizes the need for better understanding of the performance of improved seedlots in mixedwood stands.

Several studies have examined effects of competition in both naturally regenerated forest stands and artificially regenerated stands with unimproved seedlots under various silvicultural practices (Pitt *et al.* 2004; Filipescu and Comeau 2007; MacIsaac and Krygier 2009; Comeau 2014; Grover *et al.* 2014; Kabzems *et al.* 2015; Pitt *et al.* 2015; Kabzems *et al.* 2016). However, after an extensive literature search, limited information was found regarding the effects of inter- and intra-specific competition on growth of improved seedlots in Alberta.

Competition for light is widely considered to be the predominant mechanism by which aspen inhibits growth of white spruce (Burton 1993). However, aspen also has facilitative effects on white spruce, including reduced frost injury (Pritchard and Comeau 2004), reduced competition from shrubs and grass (Lieffers and Stadt 1994), reduced photorespiration and photoinhibition (Singsaas *et al.* 2000), and improved carbon and nutrient cycling (Kelty 1992).

Interactions between white spruce and aspen are commonly quantified using competition indices, and numerous competition indices have been proposed and tested in previous studies. For example, stand density and stand basal area are widely used due to their simplicity (Huang *et al.* 2013; Luo *et al.* 2017). However, stand density is limited in its ability to represent competitive effects since it only considers the number of trees and not their sizes (Filipescu and Comeau 2007), with basal area or similar indices often performing better for characterizing variation in tree growth. In addition, including the size ratio between subject tree and competitor trees has often been found to improve the usefulness of competition indices either without (Lorimer 1983; Holmes and Reed 1991) or with spatial information (Daniels 1976; Tomé and Burkhart 1989). To date no single competition index has shown consistently better performance than others under various conditions across a range of studies. In addition, when evaluating differences between wild and improved seedlots, I felt it was appropriate to utilize several different competition indices.

Estimate of gain from progeny trials is not completely representative of potential realized gain estimates due to lack of accounting for inter- and intra-specific competition as trees grow. Realized gain trials are typically used to corroborate gain estimate from progeny trials by setting comparisons of environments (e.g. ecosite) and deployment strategies (e.g. planting density) between improved and unimproved seedlots, and timing that permits interpretation of rotation age outcomes with reasonable confidence (Weng *et al.* 2008). However, the realized gain trials in Alberta were only initiated in 2016, and therefore not able to provide sufficient data (internal report of Alberta Operational Tree Improvement Monitoring Subcommittee 2018).

In this chapter, measurements from plantations established using improved and unimproved white spruce in northeastern Alberta were utilized, as a temporal substitute for realized gain trial data. The objectives of this chapter include: 1) to evaluate height and diameter growth of an improved white spruce seedlot compared to an unimproved seedlot at an early age; 2) to investigate the effects of intra- and inter-specific competition on improved white spruce at an early age; and 3) to select a competition index that accounts for most of the growth variation in height and diameter for improved white spruce.

4.2 Materials and Methods

4.2.1 Data sources

Four Forest Management Units (FMUs) managed by Alberta-Pacific Forest Industries Inc. (Al-Pac) were selected for this study, where FMU refers to an administrative unit of forest land designated by the Government of Alberta (GoA 2006). In each FMU, two stands of improved and unimproved white spruce were selected, for a total of 16 stands. Several criteria were required to be met in selecting the stands: 1) each stand had to contain both trembling aspen and white spruce; 2) each stand was at least 4 ha in area and the minimum width was 200m; 3) within each stand, there was a gradient of aspen density relative to white spruce; 4) all stands originated from a previously white spruce dominated stand and were harvested through clearcutting; and 5) total age (stock age included) differences of all selected seedlots planted in the stands was within two years (Table 4.1). The 16 stands used in this study were measured in 2019 (except the 4th stand in FMU L11, which was not accessible, as shown in Table 4.3), and were selected from 10 openings based on the above criteria, with FMU L03 and L08 each having only one opening that met study requirements, but with the openings in L03 and L08 including both wild and improved spruce. All selected openings were sprayed with herbicide (glyphosate, to remove aspen and shrub competition) in August 2017. Most openings were mounded during site preparation, and planting density was between 1260 and 1702 stems ha^{-1}. The seedlot types in all stands were categorized into unimproved and improved, as shown by genetic class codes AIa1 for unimproved and AIc9 for improved (AAF 2016a), as shown in Table 4.1. The selected AIc9 seedlot originated from an orchard in 2003, before roguing, and was assigned a 1.9% height gain at a 100-year rotation by the Government of Alberta (pers. Comm. A. Benowicz, 2019, Govt. of Alberta), and was equivalent to a 2.33% height gain at reference total age 50 for site index in Alberta (according to adjusted Lambeth equations in Chapter 2, Table 2.2).

In each stand, before sampling, a square with a width of 200m was superimposed, and nine parallel lines 20m apart were systematically installed. Along each line, four points were chosen, the first point was located randomly but no less than 30m away from the boundary, and the remaining three points were systematically selected 20m apart. The white spruce closest to each point was selected as the 'subject' spruce tree. When a potential subject tree showed effects of factors other than competition (e.g. top breakage, insect damage, sweep, or poor form), it was discarded and another white spruce (the secondly closest to the selected point) was selected to replace it. In each stand, 36 subject spruce trees were selected, with each tree located approximately 20 m apart to ensure sampling independence.

Total height (Ht) and stem diameter at stump height (DSH, diameter at 0.3m height above the ground) of subject spruce were measured. Stump height diameter was used in place of diameter at breast height (DBH) due to the limited number of trees that had reached 1.3m height. Annual height growth of the subject spruce was measured using distances between annual branch whorls, as well as the length of the current leader. To calculate competition indices for each subject spruce (Table 4.2), Ht, DBH and DSH of all competitor trees within a radius of 4m were recorded. Identity (species) of competitor trees was also recorded. The distance to subject spruce from the closest competitor tree in each of four quadrants was also measured. Given the young stand age and that most competitor trees were shorter than 8m, a radius larger than 4m was not used (Filipescu and Comeau 2007). All aspen within a radius of 4m were accounted for and measured as competitor trees. For spruce, only trees whose heights were larger than their distances to the subject spruce were considered as competitors. The subject spruce all had aspen as the closest competitor trees in all four quadrants. After measurement, subject spruces were harvested and a 3-5cm thick stem disk/cookie was collected at stump height. The harvested cookies were air dried and sanded, the stem cross-sections were scanned, and annual rings were measured using *WinDendro* software (Regent Instruments, Inc.). Each cookie was measured along three pathways from pith to cambium at 120º angles.

Site productivity of a forest characterizes the site's potential ability to affect tree growth, and site index (SI, average height of 100 trees with the largest diameter at breast height per ha) is usually used as the index of site productivity (Skovsgaard and Vanclay 2008). It is generally recognized that more realized gain can be obtained through deploying improved seedlots to better sites (McKeand *et al.* 2006; Weng *et al.* 2010). However, pre-harvest SI values were not available in our sampled sites, instead, ecosite of each stand was identified. In each sampled stand (at least 200m × 200m), six soil pits, which were 50m apart, were assigned, and at every sixth subject spruce, a corresponding soil pit was dug. At each pit, following the 'Field Guide to Ecosites of Northern Alberta', ecosite was identified (Beckingham and Archibald 1996a). Given the vegetation type might have changed after clearcutting, the ecosite identification was mainly based on edatope.

Table 4.1 Forest Management Unit (FMU), opening number, latitude, longitude, number of stands, genetic class code, site preparation, stand age, stock type and planting density for sampling

FMU	Opening number	Latitude °N	Longitude °W	Number of stands and genetic class code[a]	Site preparation	Stand age[b]	Stock type[c]	Planting density (stems ha^{-1})
L03	4160773453	55°42'30"N	112°24'15"W	AIa1×2	None	10	S412A, S412B (1+9)	1600, 1462
				AIc9×2			S412A (1+9)	1600
L08	4140710594A	55°06'45"N	112°06'00"W	AIa1×2	Mounding	10	S412B (1+9)	1260
				AIc9×2			S412B (1+9)	1260
L01	4120691788	54°59'00"N	111°47'30"W	AIa1×1	Mounding	9	S412A (1+8)	1483
L01	4130712182	55°09'15"N	111°56'00"W	AIa1×1	Mounding	9	S412B (1+8)	1486
L01	4130710568	55°07'15"N	111°57'45"W	AIc9×1	Mounding	9	S412A, S412B (2+8)	1497
L01	4130713662	55°11'00"N	111°51'30"W	AIc9×1	Mounding	9	S412B (2+8)	1460
L11	4050830428	56°10'45"N	110°45'00"W	AIa1×1	Mounding	8	S412A, S412B (2+6)	1702
L11	4050831039	56°11'45"N	110°43'00"W	AIa1×1	Mounding	8	S412A (2+6)	1508
L11	4060802262	55°56'30"N	110°51'00"W	AIc9×1	Mounding, plow	8	S412B (2+6)	1425
L11	4060801557	55°56'15"N	110°51'30"W	AIc9×1	Plow	8	S412B (2+6)	1530

[a]: AIa1 is the genetic class code for unimproved white spruce seedlots; AIc9 is the genetic class code for improved white spruce seedlots; 2003 seedlot, assigned a 1.9% height gain at 100-year rotation, was used for AIc9 (AFF 2016a)

[b]: Stand age refers to the age from planting year until the end of the 2018 growing season, including stocking age

[c]: Stock type name is a shorthand method of specifying seedling morphology (BC.MofF 1998), number in parenthesis is stock age + years after transplanting

4.2.2 Competition index

Seven competition indices were selected for use in this study (Table 4.2): distance-independent competition indices including number of trees per ha (N) and basal area of competitor trees (BA); size-ratio distance-independent competition indices including: Lorimer’s 1 (LOR1, without accounting for subject spruce size) and Lorimer’s 2 (LOR2, which included subject spruce size); size-ratio distance-dependent competition index (Hegyi’s index based on four closest aspens (HEG4); spacing factors without accounting for subject white spruce size (SF_A) and including subject spruce size (SF_S). Crown surface area and light transmittance were not used as previous work has shown these factors were time consuming to measure and were poor predictors of variation in height or diameter growth of white spruce (Filipescu and Comeau 2007).

Although most competitor trees were aspen, other broadleaf species (balsam poplar and paper birch) were also observed as competitor trees within a radius of 4m. To simplify calculations, these other competing broadleaf species were counted as aspen.

Table 4.2 Competition index and corresponding formulas

Competition index	Formula
Number of competitor trees	N (stems ha^{-1})
Basal area of competitor trees	BA (m^2 ha^{-1})
Lorimer's 1	LOR1 $= \sum_{i=1}^{n} DBH_{AWi}$
Lorimer's 2	LOR2$= \sum_{i=1}^{n} DBH_{AWi}/DSH_{SW}$
Hegyi's (based on four closest aspen)	HEG4$= (\sum_{i=1}^{4} DBH_{AWi}/DSH_{SW} \times dist_i) \times BA/BA_4$
Spacing factor (aspen)	$SF_A = 10000/(Ht_{AW} \times \sqrt{N})(\%)$
Spacing factor (spruce mid-crown)	$SF_S = 10000/((Ht_{AW} - Ht_{SW}/2) \times \sqrt{N})(\%)$

Note: DBH_{Awi}, breast height diameter (cm) of the *i*th competitor aspen; DSH_{SW}, stem diameter (cm) of subject white spruce at stump height of 0.3m; LOR1 and LOR2 are extrapolated to the hectare level; $dist_i$, inter-tree distance (m) between subject white spruce and the *i*th competitor aspen; BA, aspen basal area (m^2) per ha; BA_4, basal area of the four closest competitor aspens (m^2); Ht_{AW}, top height of competitor aspen; Ht_{SW}, Height of subject white spruce

4.2.3 Tree ring analysis

In each sampled stand, stem cookies with the largest number of clear rings were selected to generate a 'master series', which was then used for visual cross-dating of the remaining stem cookies in the same stand. Intimately, all cookies were measured. Since early rings do not typically provide reliable information on climate responses (Fritts 1976), standardization was not applied to evaluate the relationship between inter-annual growth variation and climate. However, mean inter-series correlation coefficients ($\bar{r}_{bt}$) and expression population signals (EPS) were calculated to verify the measurement accuracy of the tree rings. $\bar{r}_{bt}$ indicates to what extent the common signal, such as the effect from the same silvicultural practice (e.g. herbicide spraying) and climatic conditions, are shared by all trees in the same site (Cook and Kairiukstis 1990). The EPS reflects the expected correlation between the sampled series and the hypothetical population average (Wigley *et al.* 1984).

4.2.4 Analysis of variation and competition effect

Given the limited range and variation in stand age (8-10 years), there were two components to the analysis in this study. First, the size of improved white spruce at age eight was compared to that of unimproved white spruce in each FMU with different ecosites, and a multiple comparison was conducted based on a randomized complete block design. For this analysis, stand density for competitor trees (N in Table 4.2, stems ha^{-1}) was categorized into three levels: low (<15,000), medium (15,000-30,000) and high (>30,000), and was included in the model (Equation 4.1). Secondly, using the average height growth (Htinc) and average diameter growth at stump height (DSHinc, geometric mean from three measurements for each tree) from 2016 - 2018, growth response of improved and unimproved white spruce seedlots to competition was compared using the various competition indices (Table 4.2). Initial size of seedlings (at end of growth season in 2015) was included in the models to account for the effects of variation in tree size (Equations 4.2 to 4.4). The competition indices were measured in 2018 and were assumed constant between 2016 and 2018.

$$y_{msdqn} = \mu + F_m + S_s + D_d + E_q + DE_{dq} + SE_{sq} + e_{msdqn} \tag{4.1}$$

Where y_{msdqn} is the nth tree observation (Ht or DSH at age eight) for the sth seedlot type (improved or unimproved) planted in dth density level of competitor trees (between 2016 and 2018) within the mth FMU and within qth ecosite; μ is the overall mean; F_m is the random effect of mth FMU; S_s is the fixed effect of the sth seedlot type; D_d is the fixed effect of dth density level; E_q is the fixed effect of qth ecosite; DE_{dq} is the fixed effect of interaction between ecosite and density level; SE_{sq} is the fixed effect of interaction between seedlot type and ecosite; e_{ijklq} is the random error.

$$y_{snq} = a_{sq} + \mathrm{b}_{sq} \times DI \times CI + e_{snq} \tag{4.2}$$

$$y_{snq} = a_{sq} + \mathrm{b}_{sq} \times DI \times \ln\ (CI) + e_{snq} \tag{4.3}$$

$$y_{snq} = b_{sq} \times CI^{c_{sq}} \times DI^{d_{sq}} + e_{snq} \tag{4.4}$$

Where y_{snq} is the average annual growth (Htinc or DSHinc) from 2016-2018 for the nth tree observation under the sth seedlot type in qth ecosite; CI is competition index from Table 4.2; DI is the initial size of height or DSH for subject spruce at the end of the 2015 growing season; e_{snq} is the residual error term; a_{sq}, b_{sq}, c_{sq}, d_{sq} are parameters specific to sth seedlot type in qth ecosite.

4.2.5 Software for analysis

All analysis in Chapter 4 was conducted under *R* 3.6.2 (R Core Team 2018). For tree ring analysis, both $\bar{r}_{bt}$ and EPS were calculated using the package 'dplR' (Bunn 2009, 2010). The non-linear functions were run using the packages 'nlme' (Pinheiro *et al.* 2020). Graphs were plotted using the package 'ggplot2' (Wickham 2016).

4.3 Results

4.3.1 Annual height and diameter growth

Based on the stump height stem cookies, the range of years that could measured were between 2012 and 2018 across sampled stands (2013-2018 for L11 Stand 3 due to a limited number of rings available for 2012). During this time period, $\bar{r}_{bt}$ was between 0.537 and 0.801 and EPS was between 0.958 and 0.990 across sampled stands (Table 4.3). An EPS value of 0.85 was considered the critical threshold for judging cross-dating quality (Wigley *et al.* 1984; Cook and Kairiukstis 1990) and a higher $\bar{r}_{bt}$ reflects a common signal shared by all trees, therefore the cross-dating results showed good measurement accuracy. Figures 4.1 and 4.2 show trends in the raw chronologies for ring width and annual height growth. Due to the young age of the collected subject spruce the annual height and diameter growth both increased with age and was primarily associated with increasing tree size.

Table 4.3 Statistics for annual radial growth for the raw chronology of white spruce in all selected Forest Management Units (FMUs) with stand number, seedlot type, inter-series correlation ($\bar{r}_{bt}$ $\pm$ standard deviation (sd)), expression population signal (EPS), range of years, range of age, number of sample trees (N_1) and number of measured pathways from pith to bark (N_2)

FMU	Stand	Seedlot type[a]	$\bar{r}_{bt}$ (±sd)	EPS[b]	Range of years	Range of age	N_1 (N_2)[d]
L08	1	Improved	0.751 (±0.202)	0.988	2012-2018	4-10	30 (89)
	2	Improved	0.662 (±0.320)	0.981	2012-2018	4-10	28 (81)
	3	Unimproved	0.664 (±0.184)	0.981	2012-2018	4-10	27 (78)
	4	Unimproved	0.625 (±0.245)	0.985	2012-2018	4-10	35 (102)
L03	1	Unimproved	0.630 (±0.276)	0.969	2012-2018	4-10	34 (91)
	2	Unimproved	0.662 (±0.240)	0.983	2012-2018	4-10	35 (105)
	3	Improved	0.706 (±0.187)	0.984	2012-2018	4-10	28 (83)
	4	Improved	0.694 (±0.160)	0.986	2012-2018	4-10	33 (101)
L01	1	Unimproved	0.727 (±0.259)	0.985	2012-2018	3-9	32 (87)
	2	Unimproved	0.744 (±0.205)	0.990	2012-2018	3-9	36 (98)
	3	Improved	0.801 (±0.170)	0.977	2012-2018	3-9	35 (93)
	4	Improved	0.800 (±0.191)	0.994	2012-2018	3-9	36 (102)
L11[b]	1	Unimproved	0.537 (±0.429)	0.958	2012-2018	2-8	36 (95)
	2	Improved	0.640 (±0.325)	0.988	2012-2018	2-8	33 (101)
	3	Improved	0.672 (±0.367)	0.984	2013-2018	3-8	35 (100)

[a]: Improved white spruce seedlot is a 2003 seedlot, with a 1.9% height gain at 100-year rotation

[b]: The 4th stand in L11 was not accessible and therefore no data is available

[c]: An EPS value of 0.85 is considered the critical threshold for judging cross-dating quality (Wigley *et al.* 1984; Cook and Kairiukstis 1990)

[d]: Some pathways were deleted due to blurred cross-sections, some cookies were deleted due to anomalous readings or a lack of sufficient subject spruce 20m apart in the selected stands

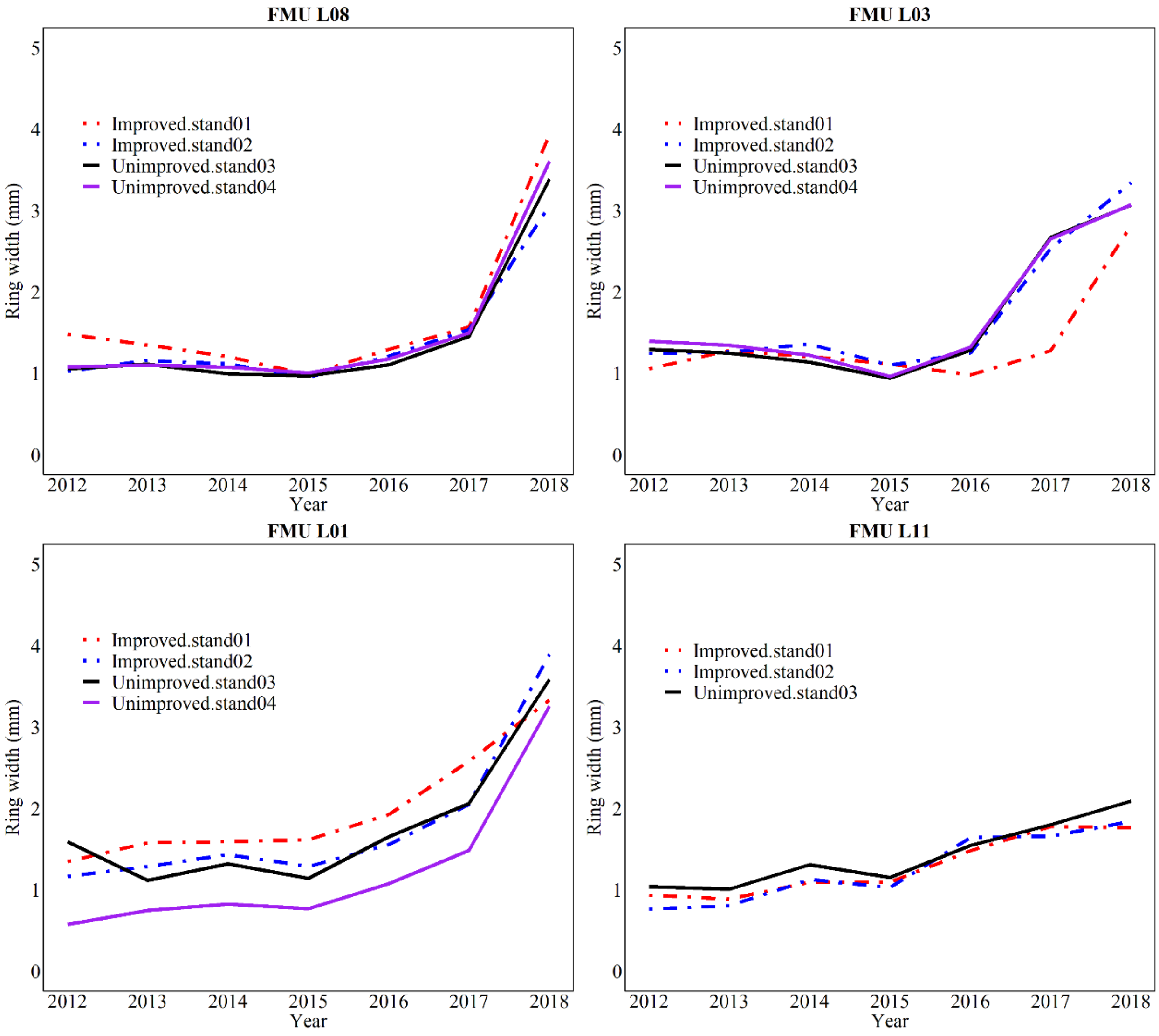

Figure 4.1 Raw chronology for ring-width at stump height (0.3m from the ground) for improved and unimproved white spruce in Forest Management Units (FMUs) L08, L03, L01 and L11

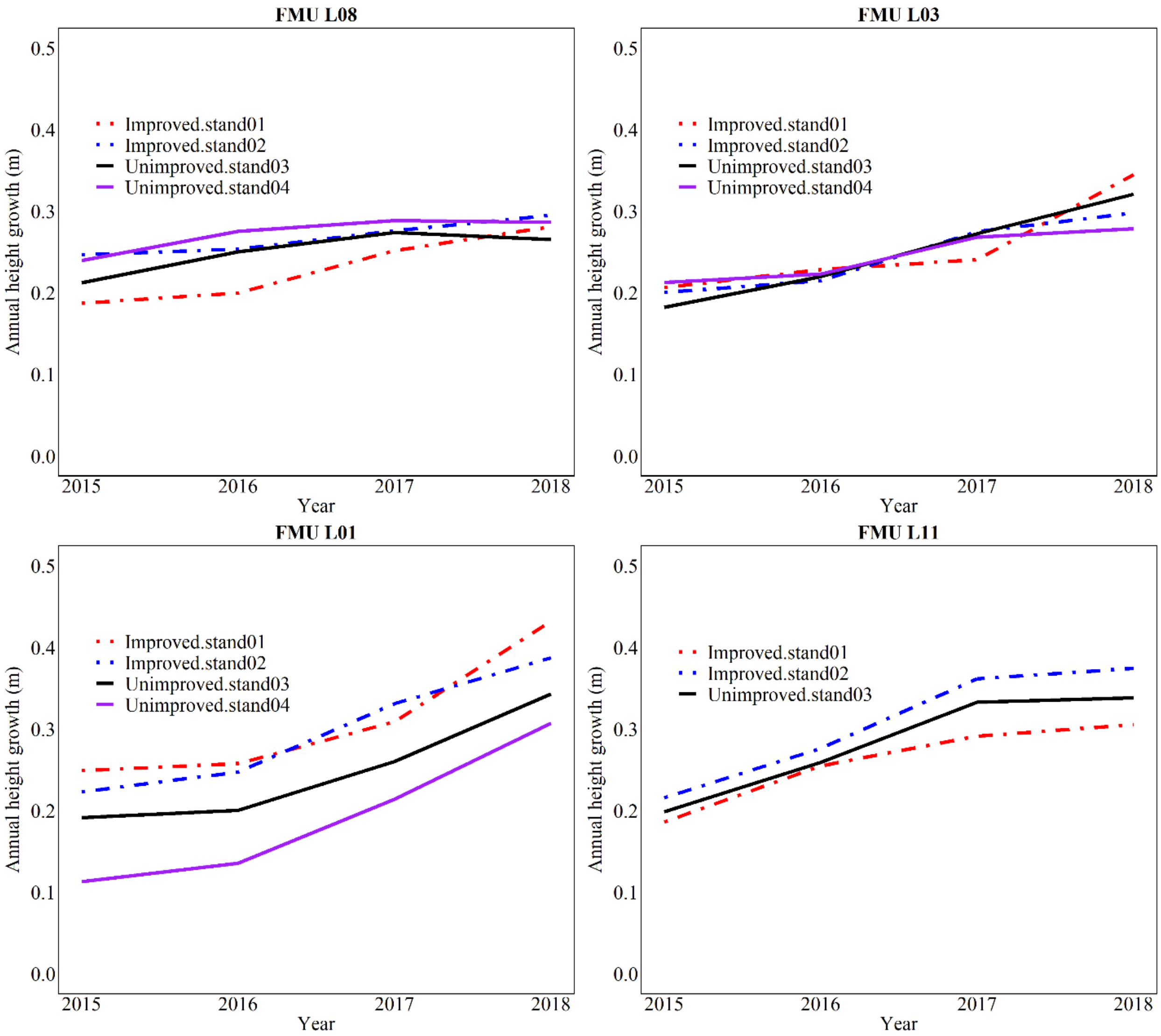

Figure 4.2 Annual height growth for improved and unimproved white spruce in Forest Management Units (FMUs) L08, L03, L01 and L11

4.3.2 Growth variation between improved and unimproved seedlots

The highest mean Ht and DSH measurements at age eight were obtained from those stands with the lowest density level of competitor trees between 2016 and 2018, regardless of FMU and seedlot type, as shown in Table 4.4. Based on the linear mixed effect model

(Equation 4.1), with unequal numbers of observations under each treatment, a type III ANOVA was conducted on least square mean (lsmean) (Table 4.5). Unimproved seedlots had significantly taller Ht at age eight compared to the improved under three density levels of competitor trees with lsmean difference around 0.1m (Figure 4.3). No significant differences were found for DSH at age eight between seedlot types under three density levels of competitor trees, while a low density level of competitor trees showed significant difference of DSH compared to medium and high density levels of competitor trees (Figure 4.3). Interaction between density level of competitor trees and ecosite and interaction between seedlot types and ecosite were significant for DSH. Unimproved seedlots showed larger DSH than improved seedlots across ecosite except b and h, and unimproved seedlots in ecosite a had the largest DSH at age eight (30.6mm, Figure 4.3). A low density level of competitor trees showed the largest DSH across ecosites, and a low density level of competitor trees within an ecosite showed the largest DSH regardless of seedlot type (30.5mm, Figure 4.3).

Table 4.4 Mean total height (Ht) and mean diameter at stump height (DSH) and their standard deviations (sd) at age eight for unimproved and improved white spruce seedlots with number of observations (n) under three stand density levels (of competitor trees): low (N<15,000), medium (15,000⩽N⩽30,000) and high (N>30,000) across Forest Management Units (FMUs) L08, L03, L01 and L11

FMU	Density level	Ht (m) ± sd (n)		DSH (mm) ± sd (n)	
		Unimproved	Improved	Unimproved	Improved
L08	low	1.28 ± 0.36 (26)	1.39 ± 0.29 (31)	24.55 ± 4.26 (73)	26.98 ± 4.11 (91)
	medium	1.33 ± 0.44 (28)	1.17 ± 0.30 (24)	24.43 ± 6.32 (84)	24.11 ± 5.00 (71)
	high	1.04 ± 0.26 (8)	1.21 ± 0.19 (3)	20.84 ± 4.46 (23)	18.96 ± 4.70 (8)
L03	low	1.48 ± 0.33 (22)	1.52 ± 0.36 (22)	27.46 ± 6.01 (61)	32.48 ± 7.30 (66)
	medium	1.32 ± 0.29 (36)	1.31 ± 0.23 (31)	25.07 ± 5.96 (105)	27.67 ± 6.06 (92)
	high	1.13 ± 0.18 (7)	1.05 ± 0.10 (6)	19.93 ± 2.30 (19)	24.09 ± 7.82 (20)
L01	low	1.62 ± 0.34 (41)	1.21 ± 0.33 (34)	31.23 ± 7.17 (108)	21.67 ± 7.37 (95)
	medium	1.45 ± 0.45 (21)	1.07 ± 0.24 (31)	25.08 ± 7.41 (58)	16.75 ± 4.71 (83)
	high	1.62 ± 0.26 (5)	1.02 ± 0.18 (6)	22.82 ± 5.78 (14)	14.90 ± 3.15 (17)
L11	low	1.63 ± 0.41 (17)	1.72 ± 0.28 (22)	20.79 ± 6.20 (47)	25.05 ± 6.67 (65)
	medium	1.50 ± 0.27 (16)	1.62 ± 0.24 (34)	20.27 ± 4.34 (40)	20.35 ± 4.73 (101)
	high	1.35 ± 0.14 (2)	1.58 ± 0.25 (11)	18.96 ± 2.22 (5)	19.32 ± 3.61 (32)

Table 4.5 Statistical summary for total height (Ht) and diameter at stump height (DSH) at age eight for two types of white spruce seedlots (improved and unimproved) under three stand density levels (of competitor trees): low (N<15,000), medium (15,000⩽N⩽30,000) and high (N>30,000), and in ecosite a, b, c, d and h; insignificant predictors were removed

Response variable	Predictor	Df	χ^2	p_value
Ht at age 8	Intercept	1	162.7618	2.20E-16*
	Seedlot type	1	9.8456	0.002*
	Density level	2	30.631	2.232e-07*
DSH at age 8	Intercept	1	89.835	2.20E-16*
	Seedlot type	1	99.925	2.20E-16*
	Density level	2	55.314	9.74E-13*
	Ecosite	4	12.688	0.013*
	Density level: ecosite	8	17.956	0.022*
	Seedlot type: ecosite	4	128.407	2.20E-16*

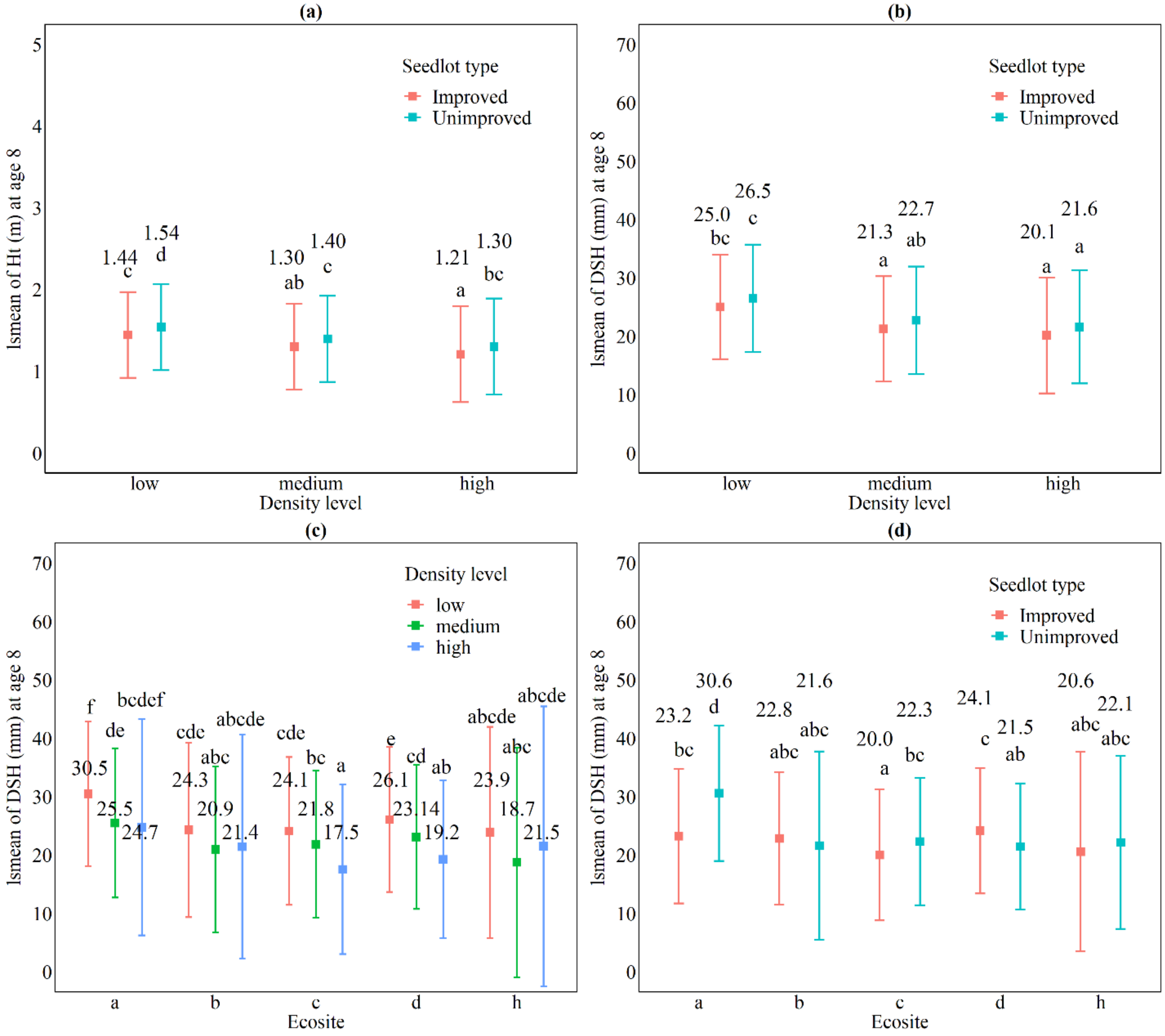

Figure 4.3 Multiple comparison of least square mean (lsmean) of height (Ht, m) at age 8 for improved and unimproved white spruce seedlots across density levels (of competitor trees) (a); multiple comparison of least square mean (lsmean) of diameter at stump height (DSH, mm) at age 8 for improved and unimproved white spruce seedlots across density levels (of competitor trees) (b); multiple comparison of least square mean (lsmean) of diameter at stump height (DSH, mm) at age 8 for across density levels and ecosite (c); multiple comparison of least square mean (lsmean) of diameter at stump height (DSH, mm) at age 8 for improved and unimproved white spruce seedlots across ecosite (d); error bars represent confidence intervals for lsmean, numbers indicate corresponding lsmean of Ht and DSH

4.3.3 Growth response to competition between improved and unimproved seedlots

Because there was little evidence of intra-specific competition among white spruce, spruce competition was excluded from further analysis. The variation of Htinc was less accounted for by competition (R^2_{adj} value 0.115 – 0.303) compared to the variation of DSHinc (R^2_{adj} value 0.399 – 0.620), as shown in Table 4.6. The LOR2 competition index using a power function on both CI and initial size (Equation 4.4) performed best for both Htinc and DSHinc. The interaction between competition indices, ecosite and seedlot type was checked and insignificant predictors were removed from the linear regression model (Equation 4.2). For non-linear regression models (Equations 4.3 and 4.4), the effect of pooling improved and unimproved seedlots and pooling of ecosite were checked using extra sum of squares tests based on F-tests in the R package 'nlshelper'. Pooling was not applicable when Equation (4.3) and Equation (4.4) were used to examine effects of competition on both height and diameter growth (Table 4.7).

Improved and unimproved white spruce seedlots have different relationships between LOR2 and Htinc, and different relationships between LOR2 and DSHinc in different ecosite (Tables 4.7 and 4.8, Figures 4.4 and 4.5). Initial tree size affected both Htinc and DSHinc significantly. A simple linear regression was fitted to Htinc and DSHinc with initial size as a predictor, and variation of DSHinc was more accounted for by initial size (R^2=0.502) compared to Htinc (R^2=0.114) (Figure 4.6). Since coefficient c in Equation (4.4) should be negative to be ecologically meaningful, and a decrease in average annual growth of height and diameter should occur with an increase in LOR2, unimproved seedlot in ecosite b and improved seedlot in ecosite h were removed (Table 4.8, in italic).

Table 4.6 Predictive ability (R^2_{adj}) and residual standard error (RSE) for average height growth (Htinc, m year $^{-1}$) and average diameter growth at stump height (DSHinc, mm year $^{-1}$) from 2016 - 2018 by model and competition indices; bolding indicates the highest R^2_{adj}

Response variable	Model	R^2_{adj} (RSE)						
		N	BA	LOR1	LOR2	HEG4	SFA	SFS
Htinc	eq (4.2)	0.210 (0.076)	0.162 (0.078)	0.183 (0.077)	0.238 (0.075)	0.185 (0.077)	0.173 (0.078)	0.196 (0.077)
	eq (4.3)	0.136 (0.081)	0.115 (0.082)	0.141 (0.081)	0.130 (0.081)	0.139 (0.081)	0.175 (0.079)	0.179 (0.079)
	eq (4.4)	0.264 (0.001)	0.230 (0.001)	0.249 (0.001)	**0.303 (0.001)**	0.245 (0.001)	0.230 (0.001)	0.252 (0.001)
DSHinc	eq (4.2)	0.551 (0.470)	0.563 (0.464)	0.571 (0.460)	0.595 (0.447)	0.522 (0.485)	0.570 (0.460)	0.577 (0.457)
	eq (4.3)	0.399 (0.548)	0.216 (0.626)	0.396 (0.549)	0.357 (0.567)	0.407 (0.545)	0.525 (0.487)	0.529 (0.485)
	eq (4.4)	0.562 (0.469)	0.589 (0.455)	0.588 (0.455)	**0.620 (0.437)**	0.540 (0.481)	0.570 (0.465)	0.577 (0.462)

Note: The interaction between competition index, ecosite and seedlot type was checked in Equation (4.2), the insignificant predictor was removed; pooling improved and unimproved seedlots was tested using extra sums of squares F test in R package 'nlshelper' for Equation (4.3) and Equation (4.4); Equation (4.3) and Equation (4.4) have separate parameter estimates for both Htinc and DSHinc for unimproved and improved regardless of competition indices; N is number of trees per ha; BA is basal area of competitor trees (m^2 ha^{-1}); LOR1 is Lorimer's 1 competition index; LOR2 is Lorimer's 2 competition index; HEG4 is Hegyi's competition index based on four closest aspens; SF_A is spacing factor without subject white spruce; SF_S is spacing factor with subject white spruce

Table 4.7 Statistical summary of F test based on extra sums of squares for average height growth (Htinc, m year^{-1}) and average diameter growth at stump height (DSHinc, mm year^{-1}) from 2016 – 2018 by models and competition indices

Model	Competition index	F	p_value	F	p_value
		Htinc (df1=5, df2=470)		DSHinc (df1=2, df2=1338)	
Eq (4.3)	N	3.525	1.69E-06	6.807	2.20E-16
	BA	3.267	7.87E-06	9.348	2.20E-16
	LOR1	3.577	1.24E-06	7.140	2.20E-16
	LOR2	3.584	1.18E-06	7.530	2.20E-16
	HEG4	3.569	1.30E-06	6.047	2.38E-14
	SFA	3.758	4.14E-07	6.004	3.23E-14
	SFS	3.748	4.39E-07	6.102	1.61E-14
Eq (4.4)	N	3.257	1.46E-07	5.195	2.96E-16
	BA	3.529	1.53E-08	5.682	2.20E-16
	LOR1	3.342	7.21E-08	5.317	2.20E-16
	LOR2	3.350	6.77E-08	5.223	2.24E-16
	HEG4	3.052	7.90E-07	6.215	2.20E-16
	SFA	3.125	4.33E-07	5.432	2.20E-16
	SFS	3.111	4.85E-07	5.683	2.20E-16

Note: df1 is the difference of residual degree of freedom between pooling model (pooling improved and unimproved seedlots) and non-pooling model; df2 is the residual degree of freedom of pooling; N is number of trees per ha; BA is basal area of competitor trees (m^2 ha^{-1}); LOR1 is Lorimer's 1 competition index; LOR2 is Lorimer's 2 competition index; HEG4 is Hegyi's competition index based on four closest aspen; SF$_A$ is spacing factor without subject white spruce; SF$_S$ is spacing factor with subject white spruce

Table 4.8 Selected models and parameter estimates for average height growth (Htinc, m year^{-1}) and average diameter growth at stump height (DSHinc, mm year^{-1}) for unimproved and improved seedlot in ecosite a, b, c, d and h from 2016 – 2018 period

Model	df	Seedlot type	Ecosite	b	c	d
$Htinc = b \times CI^{c} \times DI^{d}$	442	Unimproved	a	0.71910	-0.09239	0.36681
			*b**	*0.00341*	*0.42920*	*-0.39822*
			c	0.62389	-0.08401	0.35249
			d	1.16501	-0.15585	-0.10172
			h	7.61717	-0.35374	0.18285
		Improved	a	1.37793	-0.18377	0.18457
			b	1.56252	-0.17195	-0.06928
			c	1.36220	-0.17183	0.43087
			d	1.31120	-0.17009	-0.26327
			*h**	*0.08540*	*0.12049*	*-0.11258*
$DSHinc = b \times CI^{c} \times DI^{d}$	1310	Unimproved	a	0.78978	-0.11726	0.68236
			*b**	*0.17480*	*0.12663*	*0.37487*
			c	2.27604	-0.19230	0.54752
			d	3.88363	-0.22448	0.45966
			h	2.59618	-0.18909	0.50301
		Improved	a	9.02921	-0.20898	0.17437
			b	1.12397	-0.13007	0.61244
			c	22.53316	-0.28921	0.09679
			d	2.06051	-0.14249	0.43640
			*h**	*0.00901*	*0.06318*	*1.57810*

Note: CI= Lorimer's 2 (LOR2);

*: Unimproved seedlot in ecosite b and improved seedlot in ecosite h were removed since positive value for coefficient c

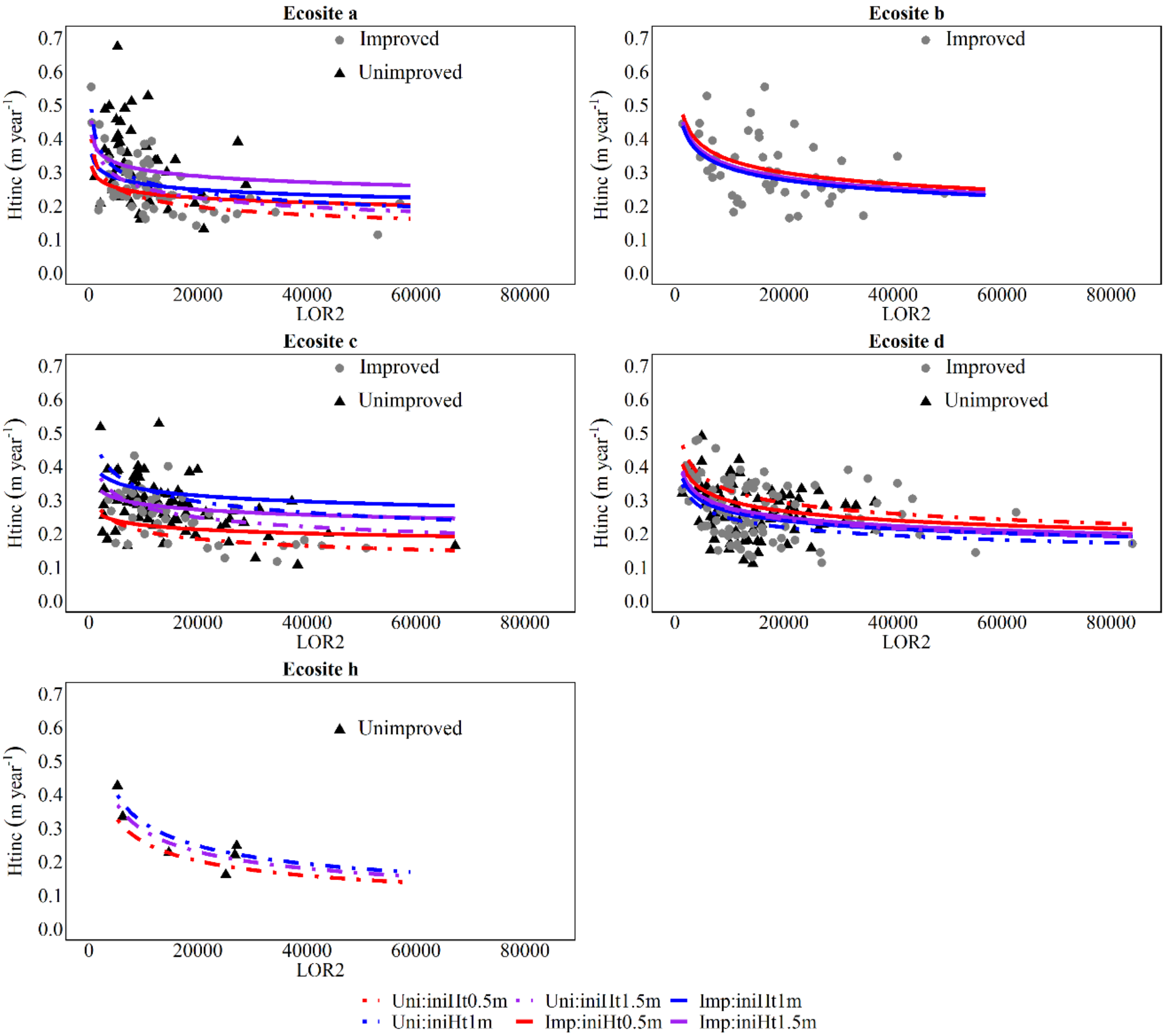

Figure 4.4 Relationship between average height growth (Htinc, m year^{-1}) from 2016-2018 and Lorimer's 2 (LOR2) for both unimproved (Uni) and improved (Imp) white spruce seedlots with initial (ini) tree height (Ht) of 0.5m, 1m and 1.5m at the end of growing season of 2015 in ecosite a, b, c, d and h; iniHt values of 0.5m, 1m and 1.5m are indicated by colour red, blue and purple respectively, Uni and Imp are indicated by dashed and solid lines respectively

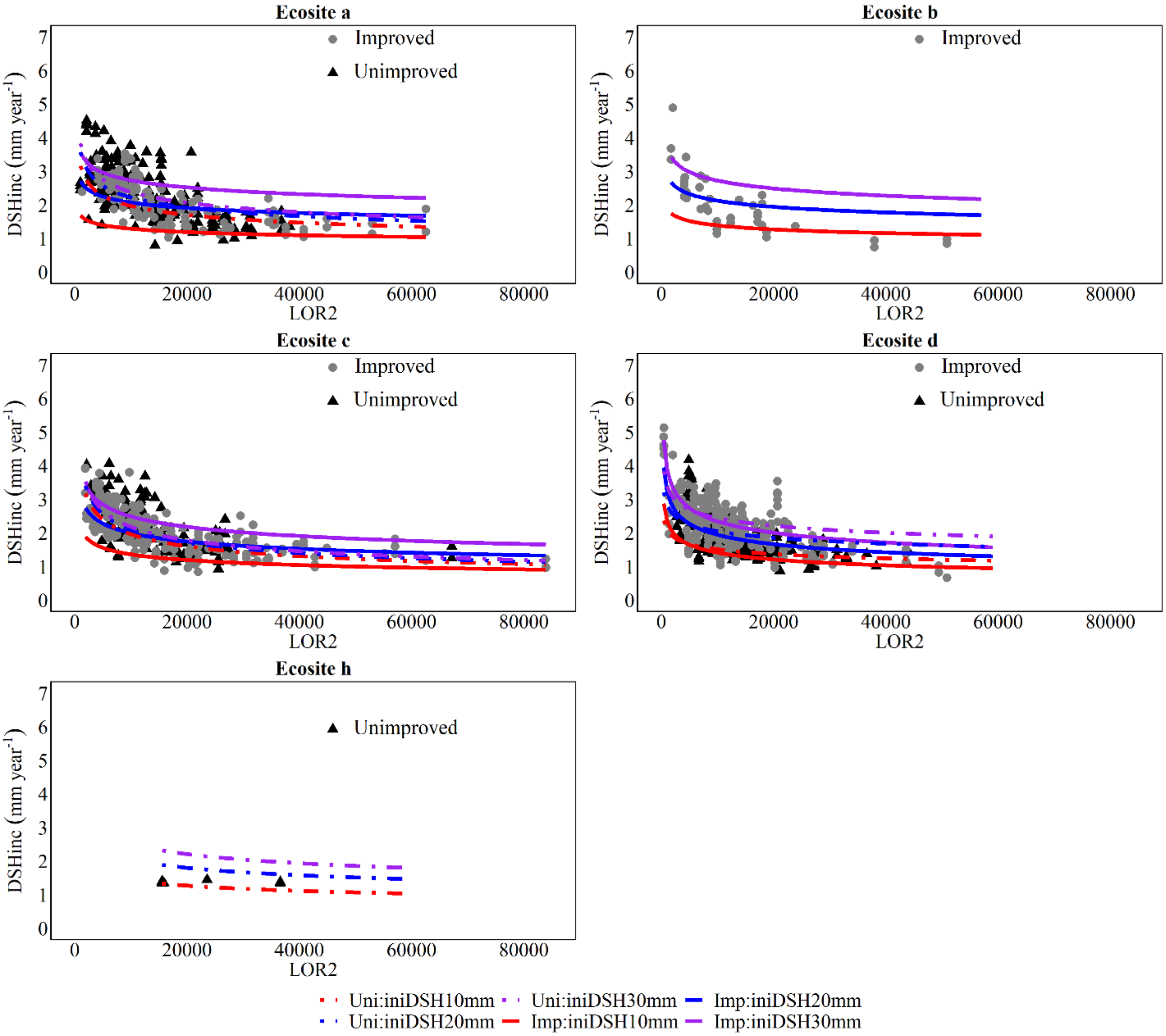

Figure 4.5 Relationship between average diameter at stump height growth (DSHinc, mm year^{-1}) from 2016-2018 and Lorimer's 2 (LOR2) for both unimproved (Uni) and improved (Imp) white spruce seedlots with initial (ini) diameter at stump height (DSH) of 10mm, 20mm and 30mm at the end of growing season of 2015 in ecosite a, b, c, d and h; iniDSH values of 10mm, 20mm and 30mm are indicated by colour red, blue and purple respectively, Uni and Imp are indicated by dashed and solid lines respectively

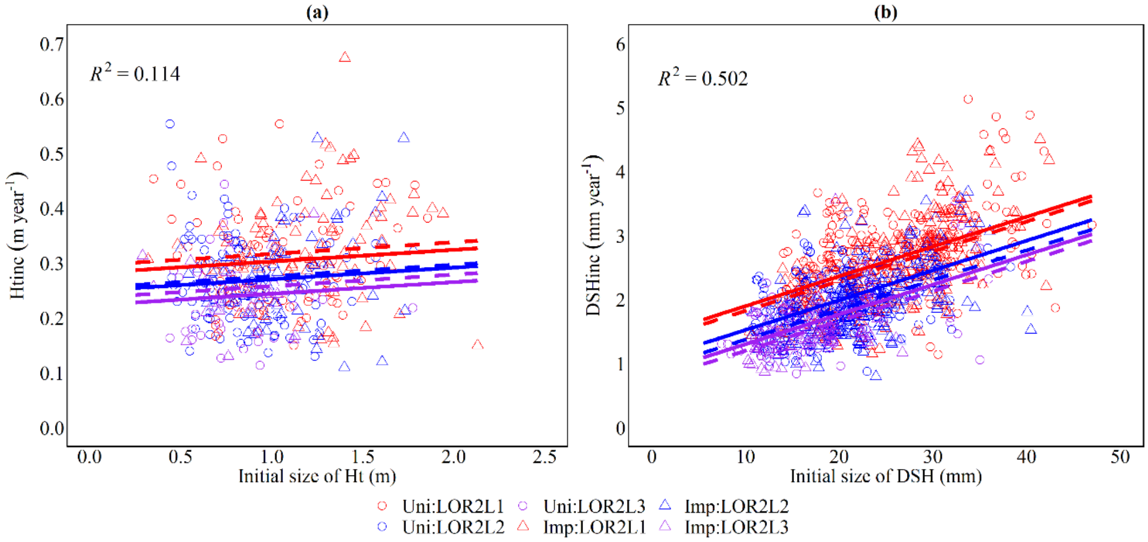

Figure 4.6 Relationship between average height growth (Htinc, m year^{-1}) from 2016-2018 (a), average diameter growth at stump height (DSHinc, mm year^{-1}) from 2016-2018 (b) and initial size at the end of growing season of 2015 for both unimproved (Uni) and improved (Imp) white spruce seedlots under three Lorimer's 2 (LOR2) levels: LOR2L1 (LOR2<10000), LOR2L2 (10000≤LOR2≤20000) and LORL3 (LOR2>30000); LOR2L1, LOR2L2 and LOR2L3 are indicated by colour red, blue and purple respectively, Uni and Imp are indicated by hollow circle and hollow triangle, and dashed and solid lines respectively

4.4 Discussion

4.4.1 The effect of competition on improved and unimproved white spruce in a mixedwood stand

Under crowded conditions tree growth may be restricted by increasing competition for resources, such as light, water, nutrients and physical space. This competition can affect growth and mortality rates, restricting access to resources and have a variable impact on trees of different sizes (Kunstler *et al.* 2011; Su *et al.* 2015).

Simple competition indices, such as density and stand basal area, were not accurate in accounting for growth variation regardless of height or diameter growth. Competition indices that included the size ratio between competitor aspen and subject spruce proved to be better predictors. The optimum competition index for both height and diameter growth was the distance-independent LOR2, which included initial subject tree size as well as competitor size. In general, distance-independent competition indices are easier to acquire and have been shown by other studies to be as accurate as distant-dependent competition indices, in terms of accounting for variation in growth of white spruce in mixtures with trembling aspen (Filipescu and Comeau 2007; Huang *et al.* 2013; Luo *et al.* 2017).

The power function (Equation 4.4) accounted for the greatest variation in tree growth and was therefore selected. Initial size was also significant in the non-linear realationship between diameter growth and competition, and between height growth and competition, consistent with other studies which emphasize the importance of cumulative growth under competition stress (Wyckoff and Clark 2005; MacFarlane and Kobe 2006; Filipescu and Comeau 2007).

Competition accounted for a larger amount of variation of annual diameter growth compared to annual height growth. These results could be explained by the relative insensitivity of height growth to competition compared to diameter growth, as previous research indicates that the variation in diameter is larger than height when a stand has a variety of competition levels (Sjolte-Jørgensen 1967; Rich *et al.* 1986; Wang *et al.* 1998).

In addition, the improved and unimproved white spruce showed different patterns of diameter and height growth response to competition in different ecosite. This result suggests that height–diameter relationships may differ between improved and unimproved white spruce under the same gradient of competition and ecosite. This difference highlights the need for further studies to examine effects of tree improvement on the relationships between height and diameter and between diameter growth and competition, most particularly at slightly older ages. Information on effects of competition on growth of seedlings, saplings and trees is needed for improved seedlots for use in growth and yield models, such as Mixedwood Growth Model (MGM) (Huang and Titus 1993; Bokalo *et al.* 1996; Huang *et al.* 1997; Wang *et al.* 1998; Huang and Titus 1999; Bokalo *et al.* 2007). Acquiring the data needed to develop these diameter growth functions for improved seedlots should be considered a priority in the future.

4.4.2 Growth of improved white spruce compared to the unimproved in mixedwood stands

The improved white spruce seedlots, which were assigned 1.9% height gain at a 100-year rotation and were planted in northeastern Alberta, did not show an advantage over the unimproved seedlots, in terms of tree height and diameter at age eight. In comparison, competition and ecosite played a more important role given the significant differences between density levels for height and diameter of individual spruce across three density levels and the five measured ecosite. The lack of difference between improved and unimproved seedlots, and even the significantly lower height and diameter values for improved seedlots, may be due to several factors. First, a wide range of factors may lead to variation in early growth of planted seedlings which may include competition from shrubs and herbs (Man *et al.* 2008) and planting microsite, in addition to effects of inter- and intra-specific competition from other trees. Second, the improved white spruce seedlot used that was from a first-generation orchard prior to any roguing had a relatively low genetic gain (1.9% height at rotation). The low genetic worth may influence growth to an insignificant extent under a gradient of competition, while seedlots with a higher genetic gain should still be expected to achieve a significant advantage over the unimproved seedlots in terms of height and diameter. In addition, seed collection for the unimproved white spruce is generally done from a helicopter given the difficulty of seed collection on the ground (pers. Comm. R. Buston, 2018, Al-Pac). Consequently, unimproved seedlots are likely to be collected from the tallest trees in each stand, and therefore a form of genetic selection for height was already made. Third, the genetic gain estimated from progeny trials did not account for inter-and intra-specific competition and could lead to biased estimates of forest growth in mixedwood stands (Magnussen 1989, 1993). This emphasizes the necessity of establishing well-designed realized gain trials, which has been recognized by industry and government of Alberta, and include a gradient of genetic gain values, planting density, competition, silvicultural practice and environment conditions since 2016 (internal report of Alberta Operational Tree Improvement Monitoring Subcommittee 2018).

4.4.3 Limitations of Chapter 4

Since sufficient realized gain trial data is not yet available in Alberta, my research provides only a preliminary substitute towards our understanding of how currently deployed improved white spruce performs in mixedwood stands at a coarse scale. The sampled stands, although distributed across northeastern Alberta, included relatively few cutblocks with improved and unimproved white spruce seedlots established in comparable adjacent areas. Uncontrolled variation between paired stands, however, limits direct comparisons.

The young stand age used also limited my understanding of how the improved seedlots perform under a gradient of competition with age. The stand species composition, which affects diameter growth and slenderness of individual trees through affecting the stand competition level, may also change with age of the stands, and therefore change the growth response to competition (Chen and Popadiouk 2002). In addition, intra-specific competition of spruce, which increases with the age of the stands, was not included in the analysis since no intra-specific competition was observed for young seedlings regardless of planting density. Interaction between planting density and genetic gain of improved spruce seedlots also need future study.

Nursery effect is another factor that can lead to variation in the size of seedlings. For example, larger container sizes and wider spacing when seeding the crop can produce seedlings with larger root collar diameter and generally greater height (BC.MofF 1998). In this study, however, two stock types with stock age one and two-years-old, were mixed and used for both improved and unimproved seedlots, between and within the selected openings. Therefore, the effect of stock type on the interaction between ecosite and genetic gain level of seedlots under a gradient of competition indices needs further analysis based on realize gain trials in the future.

4.5 Conclusion

Based on the available data from improved white spruce currently deployed in the boreal mixedwood stands in northeastern Alberta, I evaluated the relative height and diameter growth of improved white spruce compared to unimproved white spruce at a relatively young age. The effect of competition was also compared between the improved and unimproved white spruce at a young age. The results indicated that the improved white spruce from the orchard, before roguing, did not have an advantage over the unimproved local seed zone white spruce, in terms of height and diameter by age eight across several ecosite and density levels. The variation in annual height and diameter growth response to competition differed significantly between improved and unimproved white spruce, and annual height growth was found to be less sensitive to effects of competition compared to the diameter growth. Finally, the distance-independent Lorimer's 2 (LOR2) competition index, which included the size ratio between competitor aspen and subject spruce, showed the highest predictive ability when a power function, including initial size, was used. The results hightlight the need for ongoing research to support development of diameter growth functions needed for modeling growth and yield of improved white spruce deployed in a mixedwood stand.

Chapter 5: General Conclusion

5.1 Summary

Tree improvement has been used as a strategy to handle the challenges of Alberta's forestry. Assessing benefits from tree improvement programs through a quantitative approach is necessary. However, by 2017, the following knowledge gaps still limited the extent to which tree improvement could be applied. First, due to the typical young selection ages and long rotation ages in boreal forest species, and diminishing genetic gain found with increasing age, the lack of direct measurement at a given rotation age increases the uncertainty of estimate for growth and yield of improved seedlots. Second, the negative impact from rapid climate change on forest ecosystem has been observed and is predicted to continue into the future, however, the possible interaction between tree improvement and climate risk management has received little attention. Third, a lack of information on performance of improved seedlots in mixedwood stands increases the uncertainty of estimate when improved seedlots from an orchard (from a breeding program) are growing under the effects from inter-specific competition.

The major objective of this thesis was to investigate the effect of tree improvement on growth and yield, and the potential interaction between tree improvement and climate change. To address this objective, I explored a quantitative method for the purpose of improving forest management under climate change scenarios, by using the latest and most comprehensive data available from progeny and provenance trials of white spruce and lodgepole pine, with the approval by government of Alberta and program owners, as well as data collected from four Forest Management Units (FMUs) managed by Alberta-Pacific Forest Industries Inc. (Al-Pac).

The major findings of this thesis begin to fill the knowledge gaps mentioned above. The robust adjusted age-age correlation equations for white spruce and interior lodgepole pine (adjusted Lambeth equations) and adjusted Pooled Transfer Function (adjusted PTF), produced in this thesis, offer a quantitative method to estimate growth and yield of improved forest stands under different climate change scenarios, for the purpose of improving forest management strategies in the future.

5.1.1 Chapter 2: Research conclusions and implications

In Chapter 2, based on the latest height measurement from white spruce and lodgepole pine families tested within their origin Controlled Parentage Program (CPP) regions, I adjusted and compared two available age-age correlation equations developed previously by Lambeth (1980) and Rweyongeza (2016). I also explored a new method for building an age-age correlation based on a sigmoid parabolic branch (SPB) equation, named SPB age-age correlation equation. Age-age correlation equations based on a ‘leaving one out’ cross validation method was selected and then incorporated into Alberta’s Growth and Yield Projection System (GYPSY).

The results of Chapter 2 showed that: 1) the adjusted Lambeth equations, with the parameters re-estimated based on all the data available in Alberta, was the most accurate in estimating the age-age correlation coefficients for both tree species, according to the cross validation results (7-31 years for white spruce and 6-30 years for lodgepole pine); 2) the phenotypic age-age correlation was not significantly different from the genetic age-age correlation for white spruce and lodgepole pine in Alberta; and 3) white spruce, at the same selection and rotation ages, had a higher age-age correlation coefficient for height compared to lodgepole pine, and therefore will have a higher percentage height gain.

Chapter 2 provides the adjusted Lambeth equations, and confirms the feasibility of applying age-age correlation equations into GYPSY for growth and yield projections with improved materials. The greater benefit from improved growth is expected from improved white spruce seedlots at older rotation ages than from lodgepole pine. For lodgepole pine, in order to obtain the same age-age correlation coefficient as white spruce at the same rotation age, and therefore to achieve the same gain value, an older selection age will be needed. However, an earlier rotation age for lodgepole pine, could ultimately reduce the selection age and increase the age-age correlation.

5.1.2 Chapter 3: Research conclusions and implications

In Chapter 3, taking advantage of the latest height measurement from white spruce and lodgepole pine in both progeny and provenance trials, I developed an adjusted Pooled

Transfer Function (PTF), which relates standardized population height with population climate transfer distance and population climate. Merging adjusted PTF with GYPSY and using the newly adjusted Lambeth age-age correlation equations (Luo and Thomas, 2021) from Chapter 2, I predicted the growth and yield of improved (from orchard breeding programs) and unimproved (from wild seed zone collection) stands under three climate change scenarios: Representative Concentration Pathways (RCPs) 2.6, 4.5 and 8.5.

The results of Chapter 3 indicated that: 1) height growth was strongly influenced by the mean coldest month temperature (MCMT) for white spruce, and by the mean annual precipitation (MAP) for lodgepole pine; 2) regardless of RCPs and seedlot types (improved or unimproved), by 2090, white spruce stands are expected to have a decreased height growth in middle to southern Alberta, while having an increase in height growth in northern Alberta, and lodgepole pine stands are expected to show a decrease in height growth in most regions in Alberta; 3) for both species under all RCPs, improved seedlots are predicted to be outgrown by unimproved seedlots in locations where climate change favours height growth, while improved seedlots will retain their growth advantage over unimproved seedlots in locations where climate change shows a negative effect on height growth. These results indicate the necessity of incorporating climate change into estimating the benefits of tree improvement programs in Alberta where the trait of selection is height.

Chapter 3 provides a potential quantitative method: merging the adjusted PTF and adjusted Lambeth age-age correlation equations into GYPSY, to predict growth and yield of stands planted with both improved and unimproved seedlots under various climate change scenarios. The different growth responses to climate variation between improved and unimproved seedlots for both species highlights the importance of adjusting and refocusing breeding objectives accordingly, and one strategy may not be appropriate in all regions for both white spruce and lodgepole pine. The adjusted PTF developed in Chapter 3 showed accurate predictions according to the results from 10-fold cross validation and could be considered for climate risk management in the future.

5.1.3 Chapter 4: Research conclusions and implications

In Chapter 4, with the permission of Al-Pac, we collected stem cookies from subject white spruce trees in 8–10-year-old stands of improved and unimproved white spruce planted in northeastern Alberta, and competition data, as a temporary substitute of realized gain trials in Alberta. Making use of the collected data, I investigated the performance of improved white spruce compared to unimproved white spruce in mixedwood stands at an early age and analyzed the effect of competition on height and diameter growth for both improved and unimproved white spruce.

The results in Chapter 4 indicated that: 1) at age eight, the reforested improved white spruce seedlot from an orchard before roguing and assigned a 1.9% height gain at 100-year rotation age, showed no advantage over the unimproved seedlots for either height or diameter in these mixedwood stands; 2) a distance-independent competition index based on Lorimer's index, that included size ratio between competitor aspen and subject spruce, combined with a power function, accounted for most of the variation in diameter and height growth from 2016-2018; 3) height growth was less sensitive to competition compared to diameter growth for both improved and unimproved seedlots; and 4) the effects of competition on height and diameter growth differed significantly between unimproved and improved seedlots across ecosites.

Although considerable additional benefit is expected from being able to deploy improved materials over a much larger deployment area (CPP region) versus that of a seed zone, the findings in Chapter 4 highlight the importance of deploying improved seedlots with a higher genetic worth, particularly in mixedwood stands. In addition, the differential growth response to competition between improved and unimproved seedlots highlights the need for development of separate diameter growth functions for improved seedlots for use in estimating growth and yield (e.g. using Mixedwood Growth Model, a.k.a. MGM) of white spruce in mixedwood stands in Alberta.

5.2 Limitations and future research

The research conducted and presented in this thesis makes a contribution which could be considered for incorporating into forest management in Alberta by providing new information on understanding gain estimates at rotation age, the effect of climate change on improved seedlots, and an assessment of growth of improved and unimproved white spruce in mixedwood stands. Major gaps in knowledge include a lack of direct measurement at rotation age for improved seedlots, a lack of information on interactions between climate risk management and tree improvement programs, and a lack of information on performance of improved spruce in mixedwood stands, have been filled, however, there are still limitations that may affect application of the results from this thesis. Accordingly, a number of suggestions are presented below to further improve the studies conducted in this thesis.

First, diameter gain and corresponding age-age correlation for white spruce and lodgepole pine were not considered in all three data chapters. Since variation in diameter is usually larger than height, and is associated with site quality (Wang *et al.* 1998; Sharma *et al.* 2016), species composition (Groot and Carlson 1996; Pritchard and Comeau 2004; Voicu and Comeau 2006; Filipescu and Comeau 2007; Nunifu 2009), density and subsequent competition (Sjolte-Jørgensen 1967; Rich *et al.* 1986; Wang *et al.* 1998), lack of information of gain and age-age correlation coefficients for diameter will compromise the prediction accuracy of volume at the stand level. Therefore, building an independent age-age correlation equation for diameter will be necessary once enough diameter measurements from progeny or realized gain trials are available.

Second, it is widely recognized that current silviculture practices have had a significant effect on improving stand yield or reducing rotation age (Pitt *et al.* 2004; Landhäusser 2009; MacIsaac and Krygier 2009; Bergeron *et al.* 2014; Comeau 2014; Grover *et al.* 2014;

Kabzems *et al.* 2015; Kabzems *et al.* 2016; Pinno *et al.* 2021). However, there is currently insufficient data available in Alberta to understand the interaction among silviculture, tree improvement and climate change, hence, the effect of silviculture was not included in the data chapters. This issue has been recognized by both the industry and government in Alberta, and installation of realized gain trials was initiated in 2016, including a gradient of genetic worth values, planting density, competition, silvicultural practice and environment conditions (internal report of Alberta Operational Tree Improvement Monitoring Subcommittee 2018). Compared to height growth, diameter growth has greater variation, and the results of Chapter 4 also indicate the significantly different diameter growth response to competition between improved and unimproved seedlots. Therefore, development of separate diameter growth functions under different silvicultural practices, is expected to improve the accuracy in estimating growth and yield of improved seedlots, and should be considered as a priority in future studies.

Third, as mentioned in Chapter 3, a lack of test sites under extreme climate condition limits the prediction accuracy when future climate change is beyond the climate range of provenance and progeny test sites. In addition, climate associated factors, such as forest fire frequency (Flannigan *et al.* 2000; Bergeron *et al.* 2004) and the impact of insects (Pureswaran *et al.* 2018), were also not included in the analyses. Whenever possible, combining multiple datasets including larger climate transfer distances, information from forest fires, and the impacts of disease and insect attacks should be considered to extend the scope of application when modifying growth and yield models.

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Appendix

Table A-1 Age-age correlation table for selection age (yrs) and rotation age (yrs) for improved white spruce based on the adjusted Lambeth equations (Equation 2.1) at the provincial level in Alberta

Selection age	Rotation age (yrs)						
(yrs)	60	70	80	90	100	110	120
6	0.406	0.367	0.332	0.302	0.276	0.251	0.229
7	0.445	0.406	0.372	0.342	0.315	0.291	0.268
8	0.479	0.440	0.406	0.376	0.349	0.325	0.302
9	0.509	0.470	0.436	0.406	0.379	0.355	0.332
10	0.536	0.497	0.463	0.433	0.406	0.382	0.359
11	0.560	0.521	0.487	0.457	0.430	0.406	0.384
12	0.583	0.543	0.509	0.479	0.452	0.428	0.406
13	0.603	0.564	0.530	0.500	0.473	0.448	0.426
14	0.622	0.583	0.549	0.519	0.492	0.467	0.445
15	0.639	0.600	0.566	0.536	0.509	0.485	0.463
16	0.656	0.617	0.583	0.553	0.526	0.501	0.479
17	0.671	0.632	0.598	0.568	0.541	0.517	0.495
18	0.686	0.647	0.613	0.583	0.556	0.531	0.509
19	0.700	0.660	0.626	0.596	0.570	0.545	0.523
20	0.713	0.674	0.639	0.609	0.583	0.558	0.536
21	0.725	0.686	0.652	0.622	0.595	0.571	0.549
22	0.737	0.698	0.664	0.634	0.607	0.583	0.560
23	0.748	0.709	0.675	0.645	0.618	0.594	0.572
24	0.759	0.720	0.686	0.656	0.629	0.605	0.583
25	0.770	0.730	0.696	0.666	0.639	0.615	0.593
26	0.780	0.740	0.706	0.676	0.649	0.625	0.603
27	0.789	0.750	0.716	0.686	0.659	0.635	0.613
28	0.799	0.759	0.725	0.695	0.668	0.644	0.622
29	0.808	0.768	0.734	0.704	0.677	0.653	0.631
30	0.816	0.777	0.743	0.713	0.686	0.662	0.639
31	0.825	0.785	0.751	0.721	0.694	0.670	0.648
32	0.833	0.793	0.759	0.729	0.702	0.678	0.656
33	0.841	0.801	0.767	0.737	0.710	0.686	0.664
34	0.848	0.809	0.775	0.745	0.718	0.694	0.671
35	0.856	0.816	0.782	0.752	0.725	0.701	0.679
36	0.863	0.823	0.789	0.759	0.732	0.708	0.686
37	0.870	0.830	0.796	0.766	0.739	0.715	0.693

38	0.877	0.837	0.803	0.773	0.746	0.722	0.700
39	0.883	0.844	0.810	0.780	0.753	0.729	0.706
40	0.890	0.850	0.816	0.786	0.759	0.735	0.713

Table A-2 Age-age correlation table for selection age (yrs) and rotation age (yrs) for improved lodgepole pine based on the adjusted Lambeth equations (Equation 2.1) at the provincial level in Alberta

Selection age	Rotation age (yrs)						
(yrs)	60	70	80	90	100	110	120
6	-0.008	-0.076	-0.136	-0.188	-0.235	-0.277	-0.316
7	0.061	-0.008	-0.067	-0.119	-0.166	-0.209	-0.248
8	0.120	0.052	-0.008	-0.060	-0.107	-0.149	-0.188
9	0.173	0.104	0.045	-0.008	-0.055	-0.097	-0.136
10	0.220	0.151	0.092	0.039	-0.008	-0.050	-0.089
11	0.262	0.193	0.134	0.082	0.035	-0.008	-0.046
12	0.301	0.232	0.173	0.120	0.073	0.031	-0.008
13	0.336	0.268	0.208	0.156	0.109	0.067	0.028
14	0.369	0.301	0.241	0.189	0.142	0.100	0.061
15	0.400	0.332	0.272	0.220	0.173	0.130	0.092
16	0.429	0.360	0.301	0.248	0.202	0.159	0.120
17	0.456	0.387	0.328	0.275	0.228	0.186	0.147
18	0.481	0.413	0.353	0.301	0.254	0.212	0.173
19	0.505	0.437	0.377	0.325	0.278	0.236	0.197
20	0.528	0.460	0.400	0.348	0.301	0.258	0.220
21	0.550	0.481	0.422	0.369	0.323	0.280	0.241
22	0.571	0.502	0.443	0.390	0.343	0.301	0.262
23	0.590	0.522	0.462	0.410	0.363	0.321	0.282
24	0.609	0.541	0.481	0.429	0.382	0.340	0.301
25	0.627	0.559	0.499	0.447	0.400	0.358	0.319
26	0.645	0.576	0.517	0.464	0.418	0.375	0.336
27	0.662	0.593	0.534	0.481	0.434	0.392	0.353
28	0.678	0.609	0.550	0.497	0.451	0.408	0.369
29	0.693	0.625	0.565	0.513	0.466	0.424	0.385
30	0.709	0.640	0.581	0.528	0.481	0.439	0.400
31	0.723	0.655	0.595	0.543	0.496	0.453	0.415
32	0.737	0.669	0.609	0.557	0.510	0.468	0.429
33	0.751	0.682	0.623	0.571	0.524	0.481	0.443
34	0.764	0.696	0.636	0.584	0.537	0.495	0.456
35	0.777	0.709	0.649	0.597	0.550	0.507	0.469
36	0.790	0.721	0.662	0.609	0.562	0.520	0.481

37	0.802	0.733	0.674	0.621	0.575	0.532	0.493
38	0.814	0.745	0.686	0.633	0.586	0.544	0.505
39	0.825	0.757	0.697	0.645	0.598	0.556	0.517
40	0.837	0.768	0.709	0.656	0.609	0.567	0.528