UNIVERSITY OF ALBERTA

CALIBRATING THE MIXEDWOOD GROWTH MODEL (MGM) FOR LODGEPOLE PINE (*Pinus contorta*) AND ASSOCIATED SPECIES IN ALBERTA

BY

THOMPSON KWAKU NUNIFU ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of **DOCTOR OF PHILOSOPHY**

IN

FOREST BIOLOGY AND MANAGEMENT

DEPARTMENT OF RENEWABLE RESOURCES

EDMONTON, ALBERTA

SPRING 2003

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ISBN: 0-612-82147-1
Our file Notre référence
ISBN: 0-612-82147-1

UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR: **THOMPSON KWAKU NUNIFU**

TITLE OF THESIS: **CALIBRATING THE MIXEDWOOD GROWTH MODEL (MGM) FOR LODGEPOLE PINE AND ASSOCIATED SPECIES IN ALBERTA**

DEGREE: **DOCTOR OF PHILOSOPHY**

YEAR THIS DEGREE GRANTED: **2003**

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April 14, 2003

UNIVERSITY OF ALBERTA

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The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled CALIBRATING THE MIXEDWOOD GROWTH MODEL (MGM) FOR LODGEPOLE PINE (*Pinus contorta*) AND ASSOCIATED SPECIES IN ALBERTA submitted by THOMPSON KWAKU NUNIFU in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in FOREST BIOLOGY AND MANAGEMENT.

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Abstract

The Mixedwood Growth Model (MGM) was developed in the Department of Renewable Resources at the University of Alberta by Morton and Titus (1984). Initially, the emphasis was on trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench)). However, because of the interest in managing lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm) and some application problems identified by model users, there was the need to re-calibrate MGM. Four issues were considered; 1) the applicability of MGM for long-term projection applications, 2) the performance of MGM for predicting the effect of species interaction on tree growth, 3) compatibility between the component growth models and 4) the biological significance of predictor variables.

Empirical tree diameter growth models were developed for lodgepole pine, trembling aspen and white spruce using the modified three-parameter Weibull probability density function (pdf) as the base function of tree DBH (surrogate for age). Other variables reflecting competition, tree vigor and site productivity were included as modifiers. Fit and validation statistics indicated that all models were unbiased and fitted the data reasonably well. However, tree DBH seemed to be a poor substitute for tree age. This was attributed to lack of data balance across all DBH classes and possibly, unfavorable interaction of the growth predictor variables. The second study developed individual tree height growth models for each of the three species using the site index curve as the potential height growth. The modifier was assumed to be a function of basal area in larger trees and the species relative quadratic mean diameter. The models were unbiased and satisfactorily accounted for the effects of species interaction on tree height growth.

The third study developed a compatible system of height and diameter growth functions, linking tree height growth, diameter growth and the site curve, for each of the three species. The results of simulation tests using various forest stand conditions showed a significant improvement in the long-term projection accuracy of MGM. It was concluded that linking site curve to tree diameter and height growth was a reasonable approach to achieving compatibility between these growth components.

Acknowledgement

I am greatly indebted to Dr. Stephen J. Titus, my supervisor for accepting me as a graduate student and securing the much needed funding for my studies. I wish to thank Dr. Titus for his continued support, guidance, encouragement and patience throughout the entire period of my graduate studies at the University of Alberta. Dr. Titus has been very supportive to me in many ways that go beyond that of an academic mentor. I enjoyed a very cordial relationship with Dr. Titus, which offered me the most memorable and rewarding career at the University of Alberta; a very rich academic experience I will forever cherish. Dr. Titus read the manuscript a number of times and offered very constructive criticisms, suggestions and corrections; an effort that has greatly improved the quality of this thesis. To Dr. Titus, I offer my gratitude and feel very fortunate that I got the opportunity to study under your supervision.

I will like to acknowledge with profound gratitude, members of my thesis supervisory committee, Dr. Victor J. Lieffers and Dr. Ellen MacDonald of the Department Renewable Resources, Dr. Shongming Huang of the Alberta Lands and Forest Division for reviewing the draft thesis and making constructive criticisms and suggestions. Their input has made this a much better thesis. My thanks also go to the members of my thesis examination committee, Dr. Peter Blenis of the Department of Renewable Resources, who served as the chairman and Dr. Douglas P. Wiens of the Department of Mathematical Sciences for the valuable time they spent ensuring a successful thesis defense.

I am very grateful to Dr. Peter Marshall of the Faculty of Forestry at the University of British Columbia for serving as my external examiner, and for his careful, detailed and extensive review of the manuscript.

Weldwood Canada Ltd, Hinton is the major source of funding for this project through the Forest Resources Improvement Association of Alberta (FRIAA), and also provided their permanent sample plots data. Their help is greatly acknowledged. Special thanks to Thomas Braun, who served as a liaison between the Company and I, and provided me with the needed support and assistance to make this work a success. I wish to acknowledge the assistance of Alberta Lands and Forest Division for allowing me to use

their permanent sample plot data. I am particularly grateful to Dave Morgan for his assistance in this regard.

I will like to thank the WESBOGY for the funding support and the numerous opportunities they offered me during my studies. I have had excellent exposure to forest industry and can say, am a better forester today because of their support. I will like to thank Dr. Yuqing Yang; it has been a pleasure working and collaborating with you; a partnership that produced a much improved MGM.

My next thanks go to the Department of Renewable Resources for giving me an excellent opportunity for graduate studies and providing me with a favorable learning and research environment. The department also provided me with several funding assistance in the form of scholarships and graduate assistantship. For that, I will forever be grateful. Sandy Nakashima has been a very wonderful graduate secretary and I highly appreciate her numerous assistances.

Finally, on a much personal note but not the least, I will like to express my sincere and profound gratitude to me wife, Ruth and my children, Yobaat, Suguru and Yalinan for the support I enjoyed from them throughout my graduate studies at the University of Alberta. There are many friends who have been very helpful to me in diverse ways; I cannot list all of them here, but will like to say thanks to all.

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Chapter 1. Introduction

Forests are complex, long-lived dynamic biological systems, which are constantly changing in structure, composition and functioning. These changes are difficult to predict but are important for providing the necessary information about the future of the forests to assist in critical management decision-making. Growth and yield modeling is an attempt at simulating or predicting these changes or the effects of these changes over time so as to enable forest managers to predict the future conditions of the forests. This information is necessary in all facets of forest management including updating forest inventories, exploring management alternatives and evaluating silvicultural options against preset goals. As societal demands in terms quantity, quality and diversity of forest products continue to increase, growth and yield models are becoming increasingly important tools for assisting foresters in choosing management options that will satisfy these demands without jeopardizing the future conditions of the forest.

Forest growth and yield models have been developing ever since the beginning of forest management. As the forest management paradigm continues to change in response to changing societal demands from forests, growth and yield modeling philosophies continue to change in response to changes in management information needs. Models of whole-stand dynamics have been in use for several centuries in the form of growth and yield tables. The publication of the first yield tables in Germany in 1787 (Vuokila 1965) marked the birth of the seemingly interesting and sometimes, controversial field of growth and yield modeling. Yield tables, which present the anticipated yields from an even-aged stand at various ages, persisted as the *status quo* for growth and yield modeling until the 1950s. Models focusing on individual tree behavior began in the 19th century and have been developing rapidly since the 1960s (Vanclay 1994, 1995, Peng 2000) with advances in information technology.

The focus of this thesis is on individual tree level models within a non-spatial framework. The aim of this chapter is to provide some background and identify the problems associated with individual tree models, and the approaches past research work have adopted to mitigate these problems. The chapter ends with a brief outline of the remaining chapters on the approaches, the findings and conclusions

The most apparent reason for the introduction of the individual tree level models was the need to provide much more detailed information about stand composition and dynamics (Avery and Burkhart 1994). Today, there are many individual tree growth models in forest science and management. Dale et al. (1985) noted that there were several hundred computer models that project changes in forest stands by simulating the growth, and possibly dynamics, of individual trees. In spite of their perceived poor performance in estimating stand level yield compared to their stand level counterparts (Vanclay 1994), individual tree growth and yield models are still very popular in forest science. Several examples of individual tree growth and yield models exist, including, FOREST (Ek and Monserud 1974), PROGNOSIS with its several regional variants (Stage 1973, Wykoff et al. 1982), STEMS (Belcher et al. 1982), TWIGS (Miner et al. 1988) and the Forest Vegetation Simulator (FVS) based on PROGNOSIS and using STEMS/TWIGS model architecture (Teck et al. 1996).

Variance propagation due to the accumulation of error when individual tree level yield predictions are aggregated to obtain stand level yield (Mowrer 1991) or when multi-year projections are made (Gertner 1987) and internal inconsistency among component models are the two major problems of individual tree models (Vanclay 1994). Historical attempts to overcome these problems have been commendable. The focus has been mainly on increased precision at the individual tree level (e.g. Amateis et al. 1989) and compatibility among component models (Burkhart and Sprinz 1984, Huang 1992, Huang and Titus 1999). Increased precision of the individual tree level models should obviously reduce the error of stand level yield estimate whilst ensuring compatibility of component models will guarantee internal consistency in model prediction.

After Clutter (1963) pioneered the study of compatibility among growth and yield models, many researchers have studied compatibility among models. Furnival and Wilson (1971) specified and estimated growth and yield component equations as a system of simultaneous equations using econometric techniques as a way of achieving compatibility. Many other researchers have used simultaneous equation techniques to ensure that model components are compatible either within the same level of resolution (Burkhart and Sprinz 1984, Huang 1992, LeMay 1990, Huang and Titus 1999) or among different levels of resolution (e.g. Borders 1989, Zhang et al. 1997). This simultaneous equation approach recognizes the fact that the internal arrangement of components of a forest growth and yield model is hierarchical such that outputs of some component models also serve as inputs to some other component (Robinson and Ek 2000). Besides, individual tree and stand characteristics are interdependent and analytically related. The overall dynamics of a forest stand is driven by changes at the individual tree level (Oliver and Larson 1999) and changes in conditions at the forest stand level will in turn affect the growth and survival of individual trees. With such an interactive arrangement, constraining individual tree models with stand level models or parameters for instance can ensure that cumulative errors resulting from using individual tree level models to predict stand level growth and yield is reduced (Zhang et al. 1997). Achieving compatibility between individual tree diameter and height growth models may also ensure that predictions at the individual tree level are reasonable.

Although specifying and fitting component models as a system of equations is a statistically sound analytical procedure for achieving some form of compatibility among component models, the central issue in growth and yield modeling is to ensure that models are ecologically logical and model predictions have meaningful biological interpretation. If a model is ecologically illogical it will not perform well for any data set other than the one used for model development (Hamilton 1986). After constraining an individual tree mortality model in a system of seemingly unrelated regressions, Zhang et al. (1997) realized no improvement in the mortality prediction. They argued that the lack of improvement was due to limited mortality data.

The intrinsic biological relationship between individual tree growth and the individual tree and stand level predictor variables is usually not known and forest growth and yield modelers tend to rely on trends depicted by permanent sample plot data for specifying these relationships. However, typical permanent sample plot programs do not usually capture stands within certain extremes of conditions (e.g. extremely low or high density) and do not last long enough to cover the entire live of a stand in order to be able to adequately depict these relationships. Consequently a combination of incomplete time series of individual tree growth data collected from trees of different ages, site productivity classes and density is used for model fitting (e.g. Vanclay 1991, Huang 1992, Yao 1997). Obviously the assumption has been that these data are representative of individual trees growing in the forest ecosystem being modeled. In practice, this assumption is difficult to meet and therefore, extrapolating the model beyond the empirical data used may be erroneous.

The model fitting and applications problems identified above are typical of individual tree models and the Mixedwood Growth Model (MGM) is no exception. MGM (Morton and Titus 1984) is an example of a deterministic, empirical, distance-independent (non-spatial), individual tree-based growth model. This model uses an empirical approach where individual tree growth rate and survival probability are predicted in one-year time steps using tree and stand characteristics and/or non-spatial competition indices. The output is made up of summaries in the form of yield tables portraying averages and totals for the coniferous and deciduous tree species.

MGM has provided reliable short-term growth and yield projections for the boreal mixed species multi-aged stands in Alberta and northeastern British Columbia regions (Titus 1998). However, a long-term validation test conducted using simulated stands of varying densities and species mixtures showed serious projection problems suspected to be due to internal inconsistencies in the model (Craig Farnden, Consulting Forester, personal communication). The long-term growth trends and species interactions were poorly predicted. However, the performance of MGM in predicting long-term stand dynamics is crucial for constructing yield tables for use in timber supply analysis. Also, lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm) was given less attention in the initial development of MGM, in part due to data limitations. However, there has been a tremendous interest in the management of lodgepole pine particularly in the Weldwood

Canada Ltd. Forest Management Agreement Area (FMA), hence the need to re-calibrate of MGM for modeling lodgepole pine growth and yield in mixtures.

The over all objective of this thesis is to address the problems above, so as to improve both the short- and long-term projection accuracy of MGM for boreal mixedwood stands in Alberta, particularly lodgepole pine. The main objectives were: 1) to specify and estimate average periodic diameter and height growth models for the three major boreal species in Alberta, 2) to evaluate and model the effects of species interaction on diameter and height growth of the major boreal species, 3) to evaluate and model the relationship between the average periodic diameter and height growth, and 4) incorporate these models into the MGM framework and test them for projection accuracy and internal consistency.

In order to achieve these objectives, three studies were carried out and presented in the next three chapters. Empirical functions of individual tree diameter growth for lodgepole pine trembling aspen and white spruce were developed using a combined dataset from Weldwood Canada Ltd and the Alberta Land and Forest Division. The objective was to take advantage of this larger and more representative dataset than the one originally used to improve the fit of the basic functions in MGM. The emphasis of this chapter was on selecting good predictors of individual tree diameter growth, selecting functional relationships between these predictors and diameter growth that are biologically interpretable and achieve satisfactory statistical fits of the models. The fit and test statistics and the biological significance and interpretation of the predictor variables are presented and discussed in Chapter 2. The parameters associated with some of the predictor variables were counter to ecological expectations. It was concluded that data problems were partly responsible for that observation although the complex interrelationships among the growth predictors themselves may have a negative feedback on the model fit.

Chapter 3 presents individual tree height growth functions fitted using the potential-modifier approach, an alternative to directly relating individual tree growth to stand, site and tree variables. Species site index curves were used to define species maximum height growth. The upper limit restriction on the height growth prediction by site index was found to be a reasonable approach to control individual tree growth predictions and make extrapolations easier and safe. The modifier was assumed to be a function of one-sided competition defined by basal area in larger trees, and the species relative dominance, defined as the ratio of the species quadratic mean diameter to the stand quadratic mean diameter. The fit statistics and goodness of fit test statistics are presented and discussed. It turned out that assuming tree height growth relative to the site curve is a function of one-sided competition was reasonable and biologically consistent with species interactions, judging from the fit and validation statistics and evidence from the literature.

Chapter 4 presents an extension of the approach adopted in Chapter 3 to include individual tree diameter growth models in a compatible system of height and diameter growth functions for aspen, white spruce and lodgepole pine. These functions were based on the assumption that there is a fixed relationship between tree diameter growth and height growth such that: 1) at any time in the life of the tree, the diameter growth (DI) and height growth (HI) are directly proportional (Ek 1971, Sievänen 1993), 2) the proportionality constant is a function of competition, resources availability and the tree's ability to respond to reduction in competition (vigor) and 3) the proportionality constant is higher for the dominant and/or open grown trees than suppressed trees and/or trees in high density stands. The height growth model is formulated as in Chapter 3 and estimated together with the diameter growth model as a system of equations. These models have been tested for goodness of fit and their simulation results are presented and discussed. This approach provided a significant improvement on the long-term projection accuracy of MGM as evidenced from the result of MGM validation results.

Chapter 5 presents a general discussion, summary and conclusions of the thesis.

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Chapter 2. Individual Tree Diameter Growth Models for Major Boreal Species in Alberta

2.1 Introduction

Individual tree diameter (or basal area) growth models are important components of individual tree growth models such as SPS (Arney 1985), FOREST (Ek and Monserud 1974), Stand PROGNOSIS (Stage 1973, Wykoff et al. 1982, Wykoff 1990) and MGM (Morton and Titus 1984). Apart from contributing to individual tree volume or biomass growth predictions, tree diameter growth is used as an indicator of tree vigor to predict individual tree mortality or survival probability (Monserud 1976, Buchman et al. 1983, Hamilton 1986, Hamilton 1990, Yao 1997, Yang 2002).

Although diameter growth is a complex physiological process, there are two general procedures for fitting diameter growth models. One approach calculates individual tree periodic annual growth rates and then directly relates these growth rates to other tree and stand variables using functions with suitable properties. Huang (1992) used the Box-Lucas function, one of the solutions of Von Bertalanffy's (1957) quantitative laws in metabolism and growth for organisms, for modeling individual tree diameter growth for white spruce. The modified three-parameter Weibull (1951) probability density function has also been used extensively for modeling individual tree diameter or basal area growth (e.g. Wykoff et al 1982, Wykoff 1990, Vanclay 1991, Yao 1997). Other functions of similar shapes used in modeling individual tree growth are the three-parameter beta function (e.g. Alder 1995) and the two-parameter gamma function (Lessard et al 2001). Tree growth is assumed to increase to a maximum dictated by the species genetic potential, the site carrying capacity and competition, and then decline asymptotically to zero as age or size increases. Forest ecology literature support and provide biological justification for this growth trend (e.g. Oliver and Larson 1996).

In most studies individual tree diameter (DBH) is used as a surrogate variable for tree age (e.g. Huang 1992, Huang and Titus 1995), such that diameter growth increases with increasing diameter but only to a maximum and then declines asymptotically to 0 as diameter increases. Further, substituting tree DBH for age seems reasonable for several reasons. Among these reasons are: (1) the ecology literature suggests that tree size is closely related to both photosynthetic leaf area, net photosynthetic production available for growth and the amount of energy spent on maintenance (maintenance respiration) (e.g. Oliver and Larson 1996, Barnes et al. 1998); (2) in multi-species uneven-age stands, individual tree ages are difficult to determine but may be highly correlated with size, (3) individual tree size may be an indication of how competitive the tree is relative to its neighbors; and (4) DBH is easy to measure and tends to correlate quite closely with other tree characteristics such as height, volume or biomass, which are good indicators of tree size. Although some researchers have proposed the use of dominant stand age (e.g. Quicke et al. 1994), this variable has been found to be a poor substitute for individual tree age in multi-species uneven aged stands (Schröder et al. 2002).

The other approach uses the potential-modifier method to model individual tree diameter growth (e.g. Daniels and Burkhart 1975, Ek and Monserud 1974, Shao 1985, Hasenauer 1994, Shao and Shugart 1997). First, a function that defines the potential diameter growth of competition-free trees is selected, and then a competition adjustment (the modifier) is used to reduce the potential. The major advantages of this approach are: (1) individual tree diameter growth can be safely extrapolated beyond the range of data used for model calibration and (2) diameter growth predictions are always kept within bounds, i.e. individual tree growth rates will always be positive provided the modifying function is positive and tree growth cannot be greater than the potential growth rates (Shao 1985, Shao and Shugart 1997). The application of this procedure for modeling diameter growth has been difficult because of the difficulty in defining and estimating potential growth. Lessard et al. (2001) indicated that the application of this procedure precludes accurate estimation of parameter covariance and model prediction uncertainties for: (1) no estimates of the covariance between the parameters of the potential and modifier components are possible, (2) bias in the model prediction may occur because the potential component parameters are not allowed to vary in response to the totality of observed data and (3) the uncertainty of model predictions cannot be accurately obtained because the parameter covariance structure is incomplete. Lessard et al. (2001) proposed the use of the mean – modifier approach in which the parameters of both the mean and the modifier functions are estimated simultaneously. This approach expresses individual tree diameter growth as the product of the mean growth and the modifier. The mean part is a function of tree DBH whilst the modifier is expressed as a function of other tree and stand characteristics that reflect individual tree competitiveness, stand and tree level competition, site productivity and resource availability. A closer look at the approach reveals some close similarities with the approach adopted by Huang (1992), Huang and Titus (1993) and many others except that in the mean – modifier approach average stand conditions are determined and fixed, such that anytime these mean conditions are met the effect of the modifier function reduces to 0, and model prediction is strictly based on the mean function (Lessard et al. 2001).

In this study a procedure similar to that of Lessard et al. (2001) is used without the mean stand condition restriction. The objective is to fit individual tree diameter growth models for the major boreal species in Alberta – trembling aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* (Moench) Voss) and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm) within the Mixedwood Growth Model (MGM) framework (Morton and Titus 1984, Huang 1992, Yao 1997). Because prediction variables and their proper integration are important determinants of the performance of MGM, the focus of this chapter is on: (1) selecting the appropriate variables to cover the most important determinants of tree growth including vigor, resource availability and competition and (2) selecting the most appropriate and biologically interpretable functional relations between these variables and diameter growth.

2.2 The Data

The data used in this study came from two sources, Weldwood Canada Ltd and Alberta Land and Forest Division (ALFD). The ALFD data were collected over the past four decades from about 1755 permanent sample plots (PSPs) located throughout the inventory area of the province to provide representative information on forest growth and yield. The Weldwood Canada Ltd data, perhaps the largest database in the province covers just over 3000 PSPs, most of which are found in lodgepole pine stands, throughout their forest management agreement area (FMA). A detailed description of the Alberta Land and Forest Division (ALFD) database is found in the PSP Field Procedure Manual (ALFD 2000). The two datasets were combined to take advantage of the greater representation and much bigger sample size.

A subset of the combined dataset was selected for this study. Plots with at least three re-measurements were selected for analysis. This criterion was adopted to ensure that individual trees with multiple observations were included in the model calibration data. In spite of the statistical consequences of autocorrelation associated with multiple observations per tree, selecting only trees with multiple observations will ensure that individual tree growth trends are manifested in the overall trend of the dataset. This way, a least squares fit of the data will describe a more realistic average individual tree growth pattern. Plot selection was also based on the availability of other information, such as site tree measurements, which are also relevant for the curve fitting.

Since the measurement intervals of these plots are more that one-year, instantaneous annual diameter growth cannot be estimated. Rather, periodic average annual diameter growth rates were computed as DIN = (DBH2 - DBH1)/L. Where DBH1 and DBH2 are any two consecutive measurements of individual tree diameter such that DBH2 > DBH1 and L is the interval length between the measurements DBH1 and DBH2. Trees with obvious measurement errors were excluded from the analyses. DBH measurements that appear to shrink with time were assumed to be in error if they shrunk more than 1 cm in 10 years or more. Trees with excessive growth rates were also excluded.

Data from the selected plots were summarized to provide information on individual tree and stand characteristics, which were suitable for use as covariates in the model estimation. Summaries of these variables are provided in Table 2.1.

2.3 Model Specification

To specify the individual tree diameter growth models, it was hypothesized that the conditional mean of individual tree diameter growth DIN_{it} of tree i of a species at a particular time t in the life of a stand is a negative exponential decay function of the competition indices $AGGR_C$ and $AGGR_D$ defined as the ratios of basal area in coniferous and deciduous trees larger than the subject tree[1] to the stand spacing factor:

$$[2.1] \quad DIN_{it} = \beta * e^{\left(-\left(\theta_6 AGGR_C + \theta_7 AGGR_D\right)\right)} + \varepsilon_{it}$$

Parameters β, θ_6, and θ_7 are to be estimated such that β estimates the diameter growth of the largest tree of the species in the stand at a particular point in time, incorporating the mean effects of other variables in the stand and θ_6 and θ_7 are the slopes associated with $AGGR_C$ and $AGGR_D$ respectively, and the term ε_{it}, is the random error term associated with the prediction of DIN_{it}. For now, ε_{it} is assumed to be a normal random variable with mean = 0 and constant variance (σ^2). In order to be consistent with biological principles of tree growth, which will dictate that tree diameter growth will decline with increasing competition, the parameters θ_6, and θ_7 cannot be negative (see Figure 2.1 b). $AGGR_C$ and $AGGR_D$ are calculated as;

$$[2.2] \qquad AGGR_{(k)} = \frac{1}{SF} * \sum_{DBH_j > DBH_i}^{n_j} \lambda * P * BA_j.$$

SF is the spacing factor, λ is an expansion factor for converting the tree basal area (BA_j) to meters per hectare, DBH_i is the diameter at breast height of the subject tree, DBH_j is the diameter at breast height of any tree bigger than the subject tree (i), and n_j is the number of trees with diameters larger than the subject tree diameter. The parameter k is the species type designation; C for coniferous and D for deciduous, P is a dummy variable such that if k = C then P=1 for every coniferous tree and 0 for every deciduous tree, if k=D then P=0 for all coniferous trees and 1 for every deciduous. The spacing factor is defined here as the average inter-tree spacing in the stand (regardless of species) expressed as a percentage of the stand dominant or top height. Analytically, these competition indices are similar to the competition index presented in Schröder and Gado (1999), which accounts for the basal area percentiles of the subject tree and a spacing

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[1] A tree whose growth is being predicted

factor. Accounting for basal area is reasonable in the sense that the overall competition in the stand is also accounted for instead of only the one-sided competition, which depends only on tree basal area percentile. The spacing factor tends to standardize the effect of this variable across all stand types and ages. Furthermore, computing the competition by species groups is an innovative way to help account for species differences in competition and their possible interaction when they occur in mixedwoods (e.g. Man and Lieffers 1999).

Competition among neighboring trees is a combination of one-sided and two-sided competition (Weiner 1990). Two-sided competition implies that competition is symmetric, and trees interfere with one another in proportion to their size. In contrast, one-sided competition or resource depletion is asymmetric; larger trees are able to capture a greater share of a limiting resource than would be expected from their size (Weiner 1990). Light is normally the major limiting resource in one-sided competition in plants (Weiner 1990, Nilsson 1994, Newton and Jolliffe 1998). However it is possible to envisage one-sided competition below ground, if the soil is heterogeneous and larger trees are proportionately more successful in relation to their size in obtaining pockets of limiting resources (Thomas and Weiner 1989, Weiner et al 1997, Nilsson et al. 2002). Thus both one-sided and two-sided competitions are likely omnipresent in stands, but $AGGR_C$ and $AGGR_D$ capture the effect of mostly the one-sided competition. The formulation of $AGGR_C$ and $AGGR_D$ suggests that the diameter growth of the biggest tree in the stand is competition free, which is not necessarily the case.

Furthermore, the concept of competition among trees (one- and two-sided alike) suggests that larger trees will capture more growth resources than their smaller neighbors. However, this may not translate into superior growth because, larger trees have higher maintenance cost. The relative growth rate of plants decreases with size; the competitive advantages of large trees are reduced by their intrinsic growth disadvantage (Schwinning and Weiner 1997). Consequently, the relationship between growth and size may be two ways: increasing growth with increasing size in juvenile trees and decreasing growth with increasing size in older trees. Using tree size as a covariate will capture the increasingfollowed-by-decreasing individual tree growth trend suggested in the forest ecology literature (e.g., Assmann 1970, Oliver and Larson 1996, Barnes et al. 1998). Thus the relationship between β (and for that matter, DIN) and tree size (DBH) is hypothesized to be a nonlinear function, defined by Equation 2.3 (as in Yao 1997):

$$\beta = \alpha * DBH^{\theta_4} e^{\left(-\theta_5 * DBH^2\right)}; \tag{2.3}$$

Where α, θ_4 and θ_5 are parameters to be estimated such that $\alpha, \theta_4, \theta_5 > 0$. This function is made up of two parts, which combine to define the shape of the curve, the increasing (power) function of DBH (DBH^{θ_4}) and the decreasing (exponential decay) function of DBH ($e^{-\theta_5 * DBH^2}$). In juvenile trees, the impact of the power function on the value of β is greater than the exponential decay function. This leads to a net increase in β with increasing DBH up to a maximum at DBH = $\sqrt{\theta_4 / 2\theta_5}$ after which the effect of the exponential decay function exceeds the effect of the power function causing a net decrease in β asymptotically towards 0 with increasing DBH.

Finally, the parameter α (or DIN) is allowed to vary as a function of site productivity and stand basal area per hectare, i.e.,

$$\alpha = \theta_1 * e^{(\theta_2 SI + \theta_3 BAHA)} \tag{2.4}$$

where θ_1, θ_2 and θ_3 are parameters to be estimated such that $\theta_1, \theta_2 > 0$ and $\theta_3 < 0$; SI is the species site index and BAHA is the stand basal area in m^2 per hectare. Species site index is an indirect measure of site productivity and an indirect indicator of the availability of favorable resources for growth. Stand basal area is a measure of competition in the stand and may also be indicative of the availability of growth resources per tree in the stand. Figure 2.1 (c) and (d) show the relationships of tree diameter growth with site index and stand basal area respectively. From these graphs, it is reasonable to assume an exponential functional relationship of tree DIN with SI and BAHA.

Individual tree crown dimensions (e.g., the ratio of crown length to total tree height (crown ratio)) are usually used as indicators of tree vigor (e.g. Wykoff et al 1982, Wykoff 1990, Schröder et al. 2002). Tree crown dimensions correlate well with the amount of foliage (and hence photosynthetic leaf area) the tree carries and is a good indicator of the tree's ability to synthesize food for growth. Information on the crown dimensions of the trees used in this study was limited and could not be used. However, studies have shown that tree crown information correlate well with tree size, tree social rank and stand density (e.g. Monserud and Marshall 1999). It is therefore reasonable to assume that the association of tree DIN with tree vigor is well captured by the variables included in this model.

Putting Equations 2.1, 2.3 and 2.4 together, the diameter increment function is given by Equation 2.5 below. It is assumed here that the effects of the various components are multiplicative.

$$[2.5] \quad DIN_{it} = \theta_1 * e^{(\theta_2 SI + \theta_3 BAHA)} * DBH^{\theta_4} * e^{\left(-\theta_5 DBH^2\right)} * e^{(-(\theta_6 AGGR_C + \theta_7 AGGR_D))} + \varepsilon_{it}.$$

It is important to note that there are two trends in the data: the time dependent individual tree growth trend and the trend depicted by the mass of the individual tree data. In Equation 2.5, these trends are identified by the subscripts i and t. However, it is impossible to model individual tree growth patterns in this dataset. To satisfactorily model individual tree diameter growth patterns, there must be a sufficient number of measurements per tree to enable good estimates of the seven parameters (θ_1 - θ_7). In the dataset used for this study, the maximum number of measurements per tree is about six. This data problem eliminates the possibility of employing a nonlinear mixed modeling approach (Hall and Bailey 2001). It was therefore assumed that these two trends will coincide and that a mean curve fitted to the data will represent both trends. Specifically, it is assumed that a tree growing from one diameter class into another will grow the same way as a tree in that diameter class given that all the other conditions are the same. In other words, it is assumed that the trees in the older age (or bigger size) classes are growing, on average, at the same rates as those in the younger age (smaller size) classes will grow when they get older (or bigger). This assumption is very important and if it is not met, long-term projection of the model may be biased.

2.4 Model Fitting

2.4.1 Parameter Estimation

A preliminary nonlinear least squares fit of Equation 2.5 to the dataset of each species was done using the Model Procedure on SAS/ETS software (SAS Institute Inc. 1988). The Marquardt iterative method was used (Marquardt 1963). The ease of getting convergence for nonlinear regression estimation process and largely, whether the solution so obtained is global rather than a local solution depends very much on the starting values. This problem becomes increasingly severe when the nonlinear model being fitted is complex. Alternative methods of getting suitable starting values for nonlinear regression estimation have been dealt with in most standard nonlinear regression textbooks (e.g. Draper and Smith 1981, Gallant 1987 p29-30). The most simple and logical approach is to transform the nonlinear regression model into a linear model and use the parameter estimates obtained from the linear least squares fit of this model as the starting values. Clearly, taking natural logarithms of both sides can linearize Equation 2.5 into Equation 2.6. Equation 2.6 was fitted using the REG Procedure on SAS software (SAS Institute Inc. 1992). The parameter estimates of this fit were used as starting values for the nonlinear regression fit of Equation 2.5.

$$[2.6] \quad \ln DIN = \ln\theta_1 + \theta_2 SI + \theta_3 BAHA + \theta_4 \ln DBH - \theta_5 DBH^2 - \theta_6 AGGR_C^2 - \theta_7 AGGR_D^2 .$$

The asymptotic fit statistics and the parameter estimates of the nonlinear regression fit where obtained for all the three species (Tables 2, 3 and 4).

2.4.2 Model Diagnostics

Three of the major statistical considerations in regression model fitting are multicollinearity, heteroskedasticity and autocorrelation. Multicollinearity is a problem when the explanatory variables used in fitting the models are themselves correlated with each other. It was tested for using fit statistics called condition numbers. The condition number of a model is defined as the square root of the ratio of the largest eigenvalue to the smallest eigenvalue of the correlation matrix of the explanatory variables included in the model (Belsley et al. 1980). Specifying the option COLLIN at the fit section of the PROC MODEL produces these statistics. The condition number must be less than 30 to indicate little or no collinearity (Belsley et al. 1980). The condition numbers for all the three species were smaller than or almost equal to 30 indicating multicollinearity was not a problem.

Although, the ordinary nonlinear least square estimator of parameters is asymptotically unbiased and consistent even if autocorrelation and heteroskedasticity are present (Gallant 1987) and may not affect the unbiasedness of model prediction, inferences about the model parameters may not be valid. Heteroskedasticity diagnostics was limited to only the examination of the residual graphs of the preliminary fitted model. Although there are statistically more rigorous tests for heteroskedasticity such as the Goldfield-Quandt test (Judge et al. 1988), the residual plot was used because of its simplicity and clarity in illustrating the problem. For all species, the residuals graphs plotted against predicted diameter increment showed that residual variances were relatively stable with increasing predicted tree diameter growth (Figure 2.2).

Diagnostics for autocorrelation was limited only to the first order autocorrelation since non-overlapping measurements may not show autocorrelation (Borders 1987). The Durbin-Watson statistic was used. According to Seber and Wild (1988 pp. 318-319), the Durbin-Watson test is approximately valid for nonlinear regression if the sample size is large. The Durbin-Watson Statistics of 1.5052 for aspen, 1.5136 for lodgepole pine and 1.0742 for white spruce (Tables 2.2, 2.3 and 2.4 respectively) are particularly on the lower size when compared to the critical values for seven parameter models (e.g. see Judge et al. 1988) and thus indicate the presence of first order autocorrelation. Autocorrelation may result from multiple observations being taking on the same tree leading to intra-tree dependency of the error terms of the diameter increments. This was to be expected particularly in this study where trees with multiple observations were purposively selected for modeling. The consequences of autocorrelation are that the standard errors and the confidence interval of the parameter estimates are incorrect and any inferences based on them may be wrong (Judge et al. 1988).

Assuming that the error terms for the preliminary fit of Equation 2.5 follow a first order autoregressive (AR (1)) process such as shown in Equation 2.7 below, the procedure summarized by Huang et al. (1997) for generalized nonlinear least squares (GNLS) fit of models with first order autocorrelated error terms was adopted.

[2.7] $DIN_{it} = f(\theta, X) + \varepsilon_{it} \quad \varepsilon_{it} = \rho * \varepsilon_{i(t-1)} + d_i;$

DIN_{it} is the tree annual diameter growth at the current growth period, ε_{it} is the corresponding error term, $\varepsilon_{i(t-1)}$ is the error term of the tree height growth in the previous growth period, X_i is a set of explanatory variables at the current growth period, ρ is the coefficient of first order autocorrelation and d_i are the uncorrelated residual terms, which are assumed to be normally distributed with mean = 0 and uniform variance ω^2.

The estimates of the set of parameters θ were obtained as follows;

1. Estimate θ by nonlinear least squares and estimate the predicted diameter growth $DI_{it} = f(X_t, \theta)$ and the residual $\varepsilon_{it} = DIN_{it} - DI$;
2. Estimate the coefficient of autocorrelation ρ by fitting $\varepsilon_{it} = \rho * \varepsilon_{i(t-1)} + d_i$;
3. Re-estimate θ by fitting the equation: $DIN_{it} - \rho DIN_{i(t-1)} = f(X_i, \theta) - \rho f(X_{(i-1)}, \theta) + d_i$ and estimate new ε_{it}'s and DI_{it}'s as in step 1, where $DIN_{i(t-1)}$ and $X_{(t-1)}$ are the diameter increment and the set of explanatory variables for the previous growth period;
4. Repeat steps 2 to 3 until the estimates of the set of parameters θ stabilizes.

This four step iterative re-fitting procedure is equivalent to minimizing:

[3.9] $S(\theta) = \left[DI - f(X_i, \theta)\right]' \Sigma^{-1} \left[DI - f(X_i, \theta)\right]$

where Σ is the generalized variance-covariance matrix incorporating the coefficients of autocorrelation (Gallant 1987). Since Σ is not known, its structure is estimated and re-estimated when ρ changes after every iteration. The parameter estimates of the final fit are given in Tables 2.2 for aspen, 2.3 for lodgepole pine and 2.4 for white spruce. Much improved Durbin-Watson statistics were obtained; 2.1025 for aspen, 2.1936 for white spruce and 2.0601 for lodgepole pine. Apart from the statistically more appealing Durbin-Watson statistics, all parameter estimates of the fits with autocorrelation adjustments were significant at 5% probability level. Unfortunately however, the parameters θ_4 and θ_5 were negative for the aspen and lodgepole pine models, which is counter to the original hypothesis in Equation 2.3.

2.4.3 Model Validation

Using the final parameter estimates, a validation test was conducted to determine the precision and/or unbiasedness of the diameter growth model. The focus of the validation test was on unbiasedness. Bias is the average of the difference between observed and predicted diameter growth and the percent bias is the bias expressed as a percentage of the observed mean diameter growth. The overall bias values for all the three species were not statistically significantly different from 0 at the 5% probability level. Figure 2.3 presents graphs of the percentage prediction bias for all the three species by 10-cm diameter classes. Average bias expressed as a percentage of the average predicted growth seems more reasonable in this case since average bias alone may be small and may mask the true magnitude of the bias.

2.5 Discussion

Empirical regression fits of forest growth and yield models rely primarily on the association rather than cause-effect relationship between tree growth and/or yield and the predictor or explanatory variables. The cause-effect relationships between forest variables are rather complex and difficult to understand. The exact nature of these relationships is usually not well understood and most often is speculative. Depending on the data used, the estimate of the association may not have logical biological interpretation. This may stem from model misspecification (using the wrong functional form), insufficient calibration data to adequately depict the theoretical biological trends hypothesized, or improper statistical fit of the function to the data. These problems are further compounded by the fact that most biological relationships are non-linear in functional form with parameter estimates being highly data sensitive (Gallant 1987). Biased estimation of these parameters can lead to a biologically illogical model (Hamilton 1986).

In this study, individual tree diameter growth models were developed for three major boreal species - trembling aspen, lodgepole pine and white spruce. In discussing the model parameter estimates and their asymptotic statistics, the intention is to give biological justification for the association of the explanatory variables with tree diameter growth and not to imply causality. The interpretations of the fit statistics are similar to the linear regression case because the sample size for each dataset was quite large (over 4000). These statistics suggest that the models are reasonable. The coefficients of determination are comparable to values reported in other studies (e.g. Huang 1992, Huang and Titus 1995, Yao 1997) although they are generally low, explaining less than 50% of the variation in the data (adjusted R^2). In addition, the asymptotic statistics indicate that model parameter estimates are all statistically significant at 5% probability level. It also appears that all models are relatively unbiased throughout the entire range of tree sizes (DBH) used in this study. Even for the high variability associated with individual tree growth data, the percentage prediction bias is relatively low (Figure 2.3).

Although the fit statistics look very reasonable, the biological interpretation of some of the parameters is rather odd. The parameters for DBH and DBH^2 are negative for the aspen and lodgepole pine models (Tables 2.2 and 2.3). This appears to contradict the original hypothesis that tree diameter growth will increase to a maximum at DBH = $\sqrt{\theta_4/2\theta_5}$ and then decline asymptotically to 0 as size increases. The current relationship between DIN and DBH, as predicted by the model (for aspen and pine), implies that the DIN will decline up to a point (probably at DBH = $\sqrt{\theta_4/2\theta_5}$) and then begins to increase, a directly opposite scenario than the original hypothesis (see Figure 2.4). Figure 2.1 (a) seems to depict this trend for lodgepole pine. This problem may be due to lack of data balance across all DBH, site and density classes. However, because nonlinear least-squares fits usually follow the center of the data mass, the individual tree growth trends did not coincide with the fitted models for aspen and lodgepole pine. Lessard et al. (2001) encountered a similar problem when fitting diameter growth models using the mean-modifier approach; a two parameter gamma function that they used to fit tree diameter growth as a function tree DBH was reduced to a power function implying a monotonic increase in diameter growth with increasing tree DBH.

Individual tree level growth data pose one of the biggest challenges to individual tree growth and yield modeling. Growth measurement at the individual tree level is so erratic and can vary quite substantially from one year to another in response to random environmental shocks. Although biological theory prescribes a generalized trend in tree growth in relation to its size (Oliver and Larson 1996), trees are usually not measured long enough to portray this generalized trend. The consequence is that it becomes extremely difficult to isolate the effects of these random environmental shocks from the generalized growth pattern. To be able to do this, there is the need for much longer-term measurements of individual tree annual growth rates. Alternatively, it may be possible to model the effects of short-term environmental shocks by including the environmental variables as covariates (e.g., Reed 1980). Unfortunately, the dynamics of these environmental variables are difficult to predict and incorporate in the empirical growth and yield model framework. Models fitted to individual tree growth data (e.g. Huang 1992, Yao 1997) therefore tend to rely on the assumption that the mean growth rates of trees in the sample tend to follow the general trend described in forest ecology and that variations about the mean curve are caused by competition, individual tree vigor and site productivity. Unfortunately, this assumption did not hold in this study at least for lodgepole pine and aspen. The consequence of not meeting this assumption is that the model will project increases in individual tree diameters with no upper limit. This problem was observed in one of the older versions of MGM particularly for pure lodgepole pine.

Stand basal area and site index parameters are of the appropriate sign (negative for basal area and positive for site index) for all the three species. The positive sign associated with the site index parameter reflects the positive effect of site index on tree diameter growth. It is also reasonable to expect that inter-tree competition will increase with increasing density (basal area) resulting in a decrease in individual tree growth.

Tree diameter growth is particularly affected by competition as compared to height growth and this has been well documented in many thinning studies. Increase in tree diameter is the result of lateral cambial activity. The ecophysiology literature suggests that cambial growth shows no elements of preformation; the amount of cambial activity being dependent on the environmental flux and its effect on the tree's internal physiology at the time growth is occurring (Fritts 1976). The cessation of cambial growth is not governed by a fixed number of cell divisions that must first take place, but by the exhaustion of soil moisture, growth substances or needed assimilates and the accumulation of inhibitors (Fritts 1976, Zimmermann and Brown 1971). This is perhaps the reason why individual tree diameter growth appears to vary so much from year to year, increasing sharply in response to availability of favorable growth conditions and declining sharply in years with less favorable growth conditions.

The variables $AGGR_C$ and $AGGR_D$ also had positive coefficients, an indication that tree diameter growth decreases with increasing amount of suppression (i.e., dominant and co-dominant trees have superior diameter growth than suppressed trees of the same age. For all species, the coefficient of $AGGR_C$ is greater than that of $AGGR_D$. This was interpreted to mean that coniferous competition on individual tree diameter growth is more severe than deciduous competition. In aspen-lodgepole pine mixtures, this interpretation may be difficult to justify biologically since both species are shade intolerant and fast growing. Suffice it to say, when light is the limiting resource, the ability of the tree crown to allow light through may be of significant influence on the growth of smaller trees. Deciduous trees may be able to transmit more light through their crowns by virtue of their crown characteristics. That apart, it is more likely that lodgepole pine-aspen mixtures occur in low-density stands. Table 2.1 seems to support this assertion. The conditions necessary for successful regeneration of lodgepole pine may preclude the successful establishment of aspen on the same site. For instance, fire is needed to open pinecones and expose the seeds to mineral soil for successful regeneration. However, the fire may be severe enough to kill the propagules of aspen (Smithers 1961), resulting in very high-density establishment of pine with little or no aspen. Aspen – lodgepole pine mixtures may occur when lodgepole pine regeneration is low. In that case, the effect of the hardwood component on lodgepole pine growth may be compensated for by the reduction in competition associated with such low density.

The interpretation of the coefficients of $AGGR_C$ and $AGGR_D$ for aspen-white spruce mixtures may be quite straight forward; the dense crowns of white spruce may be more detrimental to the growth of other trees regardless of species; intercepting more photosynthetically active radiation and water (Constabel and Lieffers 1996). The degree to which this effect is felt may depend on the level of tolerance of the subject tree. The coefficient of $AGGR_C$ is comparatively smaller in the white spruce model (Table 2.4), perhaps because white spruce is more tolerant than the other species.

These results may have significant implications on the results of the model projections for mixedwood stands. It may be possible due to the differences in magnitude of the coefficients of $AGGR_C$ and $AGGR_D$ to successfully project the dynamics of aspen – white spruces mixtures. However, because most lodgepole pine stands are pure, the presence of the two variables in the lodgepole pine model may not be necessary.

2.6 Summary and Conclusions

Individual tree diameter growth models were developed for aspen, white spruce and lodgepole pine. The emphasis of the modeling approach was on selecting suitable predictor variables for individual tree diameter growth and selecting the most appropriate functional relationship between the growth predictors and diameter growth. Trees with multiple measurements were purposively selected to enhance individual tree growth trajectories in the data. Model parameters were estimated using the MODEL procedure in SAS and the models were tested for prediction bias. All parameter estimates were significantly different from 0 at the 5% probability level. However, the coefficients for

DBH and DBH^2 were negative in the aspen and lodgepole pine models, suggesting that individual tree diameter growth would increase without limit as tree size increased. This is not biologically realistic. Although the coefficients of the other variables had logical biological interpretations, the illogical DBH and DBH^2 coefficients may affect the model prediction performance. The mean component of the model will predict a monotonic increase in diameter growth with DBH (Figure 2.4). It is concluded that using this approach with permanent sample plot data may not necessarily give the appropriate model fit and that there is the need to look for alternative approaches to model fitting. These may include sacrificing statistical expediency for options that will produce models that are biologically logical. Some of these options are explored in the subsequent chapters.

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Table 2-1. Summary statistics of tree and stand variables relevant for data preparation and model fitting.

Aspen			
Variable	Mean	Minimum	Maximum
DBH (cm)	26.37	1.80	59.00
Height (m)	23.27	8.60	31.70
PSP measurement interval (years)	6.70	2.20	14.00
Annual tree DBH growth (cm)	0.16	-0.05	0.64
Total stand Basal area (m^2/ha)	39.81	13.29	56.89
Site Index (m) at age 50	18.05	14.40	21.86
$AGGR_C$	0.00	0.00	0.08
$AGGR_D$	0.03	0.00	0.09
Lodgepole pine			
DBH (cm)	20.40	4.80	49.80
Height (m)	16.19	6.40	30.80
PSP measurement interval (years)	8.18	2.20	26.00
Annual tree DBH growth (cm)	0.12	-0.05	0.82
Total stand Basal area (m^2/ha)	38.79	4.24	51.60
Site Index (m) at age 50	16.61	11.75	25.98
$AGGR_C$	0.03	0.01	0.07
$AGGR_D$	0.00	0.01	0.08
White spruce			
DBH (cm)	23.21	1.50	70.70
Height (m)	22.96	5.20	35.20
PSP measurement interval (years)	7.25	1.20	14.60
Annual tree DBH growth (cm)	0.15	-0.04	1.25
Total stand Basal area (m^2/ha)	41.97	4.24	58.83
Site Index (m) at age 50	16.03	5.52	25.22
$AGGR_C$	0.02	0.00	0.15
$AGGR_D$	0.02	0.00	0.08

$AGGR_C$ and $AGGR_D$ are the modifier basal areas in larger coniferous and deciduous trees respectively. They are calculated as the ratios of actual basal area in larger coniferous and deciduous trees to their respective stand spacing factors. Stand spacing factor is the ratio of average inter-tree spacing to stand dominant height expressed as a percentage.

Table 2-2. Parameter estimates and asymptotic statistics of the trembling aspen diameter growth model.

Variable	Parameter	Estimate	Std Error	t-stat.	Prob.> |t|	RMSE	Adj. R^2	DW
(a) No Adjustment for autocorrelations								
Const.	θ_1	0.072134338	0.01240	5.83	<0.0001	0.0871	0.1813	1.5052
SI	θ_2	0.060723686	0.00703	8.64	<0.0001			
BAHA	θ_3	-0.011120434	0.00137	-8.12	<0.0001			
DBH	θ_4	-0.009092949	0.03520	-0.26	0.7962			
DBH^2	θ_5	-0.000287271	0.00003	-10.51	<0.0001			
$AGGR_C$	θ_6	5.830563931	1.28900	4.52	<0.0001			
$AGGR_D$	θ_7	2.944462907	0.57170	5.15	<0.0001			
(b) Adjusted for autocorrelation								
Const.	θ_1	0.127283292	0.03060	4.16	<0.0001	0.0812	0.2508	2.1025
SI	θ_2	0.057885980	0.01080	5.35	<0.0001			
BAHA	θ_3	-0.018289293	0.00193	-9.50	<0.0001			
DBH	θ_4	-0.080296994	0.04110	-1.95	0.0510			
DBH^2	θ_5	-0.000261036	0.00004	-7.44	<0.0001			
$AGGR_C$	θ_6	7.711584231	1.78340	4.32	<0.0001			
$AGGR_D$	θ_7	3.943299899	0.72530	5.44	<0.0001			
	ρ	0.293741555	0.01710	17.17	<0.0001			

Table 2-3. Parameter estimates and asymptotic statistics of the lodgepole pine diameter growth model.

Variable	Parameter	Estimate	Std Error	t-stat.	Prob. > |t|	RMSE	Adj. R^2	DW
(a) No Adjustment for autocorrelations								
Const.	θ_1	0.177462599	0.03140	5.65	<0.0001	0.0705	0.4091	1.5136
SI	θ_2	0.062668326	0.00234	26.84	<0.0001			
BAHA	θ_3	-0.026361618	0.00136	-19.39	<0.0001			
DBH	θ_4	-0.103955689	0.06930	-1.50	0.1335			
DBH^2	θ_5	-0.000378107	0.00006	-6.28	<0.0001			
$AGGR_C$	θ_6	14.081770682	0.78900	17.85	<0.0001			
$AGGR_D$	θ_7	10.669186650	1.17070	9.11	<0.0001			
(b) Adjusted for autocorrelation								
Const.	θ_1	0.2838898982	0.06000	4.73	<0.0001	0.0687	0.4486	2.0601
SI	θ_2	0.0640189588	0.00316	20.28	<0.0001			
BAHA	θ_3	-0.0247992272	0.00160	-15.53	<0.0001			
DBH	θ_4	-0.2772415761	0.07950	-3.49	0.0005			
DBH^2	θ_5	-0.0004151468	0.00007	-5.67	<0.0001			
$AGGR_C$	θ_6	16.1479861136	0.99940	16.16	<0.0001			
$AGGR_D$	θ_7	13.1346878158	1.35790	9.67	<0.0001			
	ρ	0.2779423043	0.01980	14.03	<0.0001			

Table 2-4. Parameter estimates and asymptotic statistics of the white spruce diameter growth Model.

Variable	Parameter	Estimate	Std Err	t-stat.	Pr > |t|	RMSE	Adj. R^2	DW
(a) No Adjustment for autocorrelations								
Const.	θ_1	0.182536189	0.02530	7.20	<0.0001	0.1082	0.3061	1.0742
SI	θ_2	0.043768801	0.00253	17.28	<0.0001			
BAHA	θ_3	-0.039152062	0.00095	-41.31	<0.0001			
DBH	θ_4	0.241827484	0.04830	5.00	<0.0001			
DBH^2	θ_5	-0.000000105	0.00004	0.00	0.9978			
$AGGR_C$	θ_6	1.836846698	0.87630	2.10	0.0361			
$AGGR_D$	θ_7	-0.491818592	0.82350	-0.60	0.5504			
(b) Adjusted for autocorrelation								
Const.	θ_1	0.149211750	0.02680	5.57	<0.0001	0.0961	0.4668	2.1936
SI	θ_2	0.041804480	0.00428	9.76	<0.0001			
BAHA	θ_3	-0.035634652	0.00119	-30.03	<0.0001			
DBH	θ_4	0.367007298	0.06050	6.07	<0.0001			
DBH^2	θ_5	0.000236326	0.00005	4.52	<0.0001			
$AGGR_C$	θ_6	3.137200206	0.94900	3.31	0.0010			
$AGGR_D$	θ_7	2.876077837	0.97710	2.94	0.0033			
	ρ	0.470662668	0.01530	30.77	<0.0001			

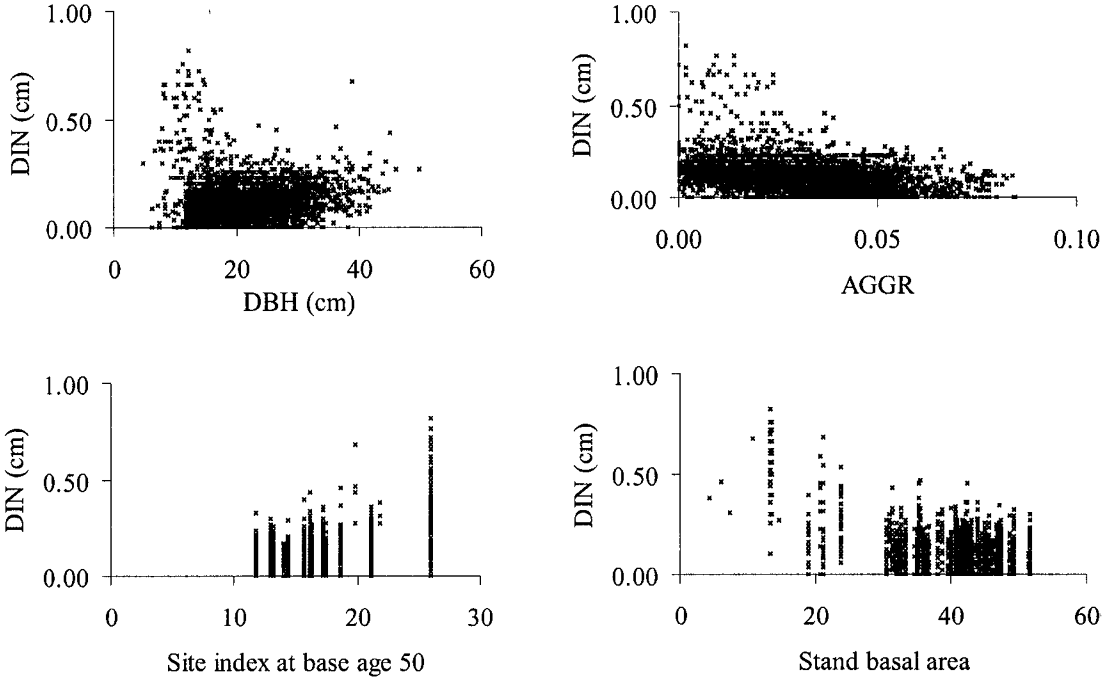

Figure 2-1. Scatter graphs of diameter growth (DIN) against diameter at breast height (DBH), modified basal area in larger trees (AGGR), site index and total stand basal area for lodgepole pine.

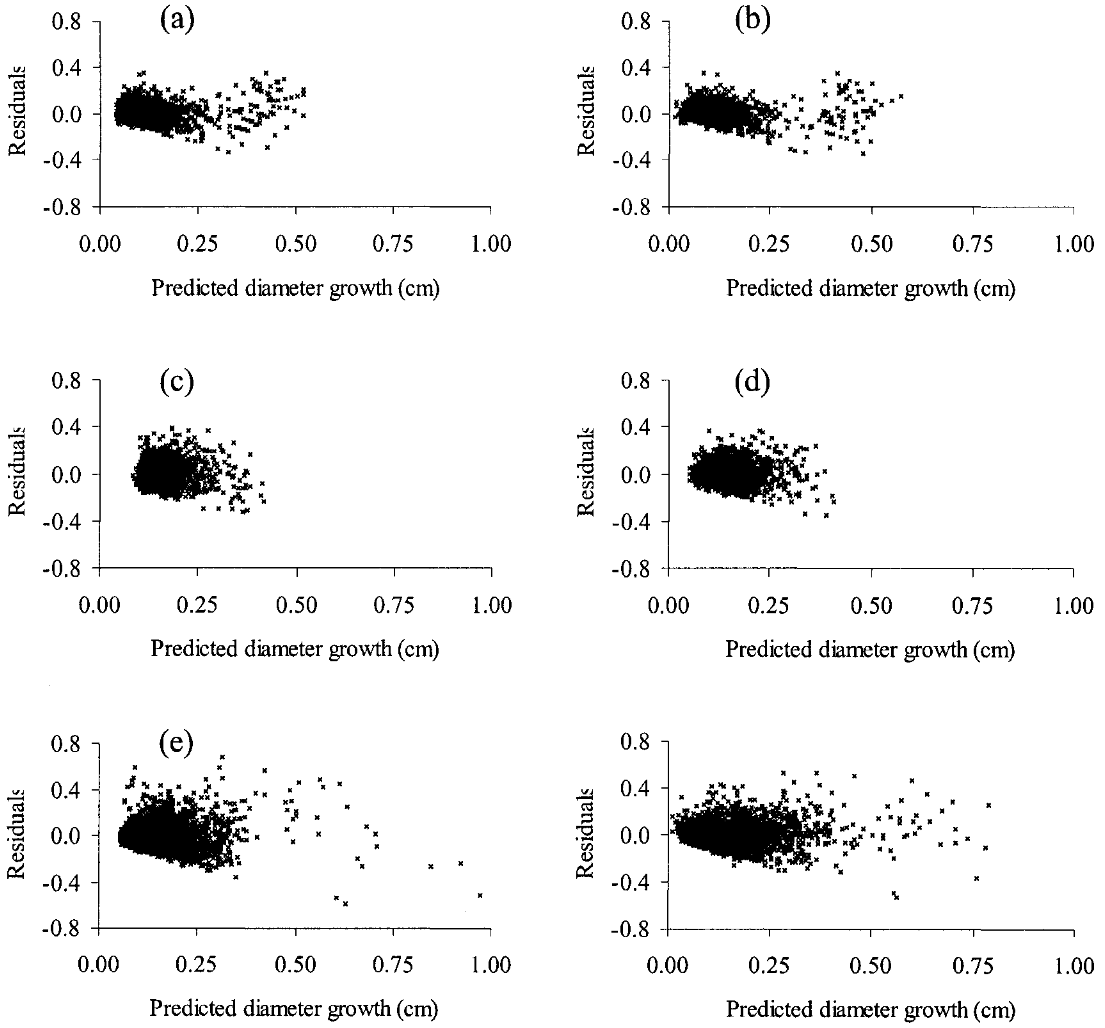

Figure 2-2. Residual Graphs of diameter growth models for lodgepole pine (a) and (b); aspen (c) and (d) and white spruce (e) and (f), fitted with and without the autocorrelation adjustment, respectively.

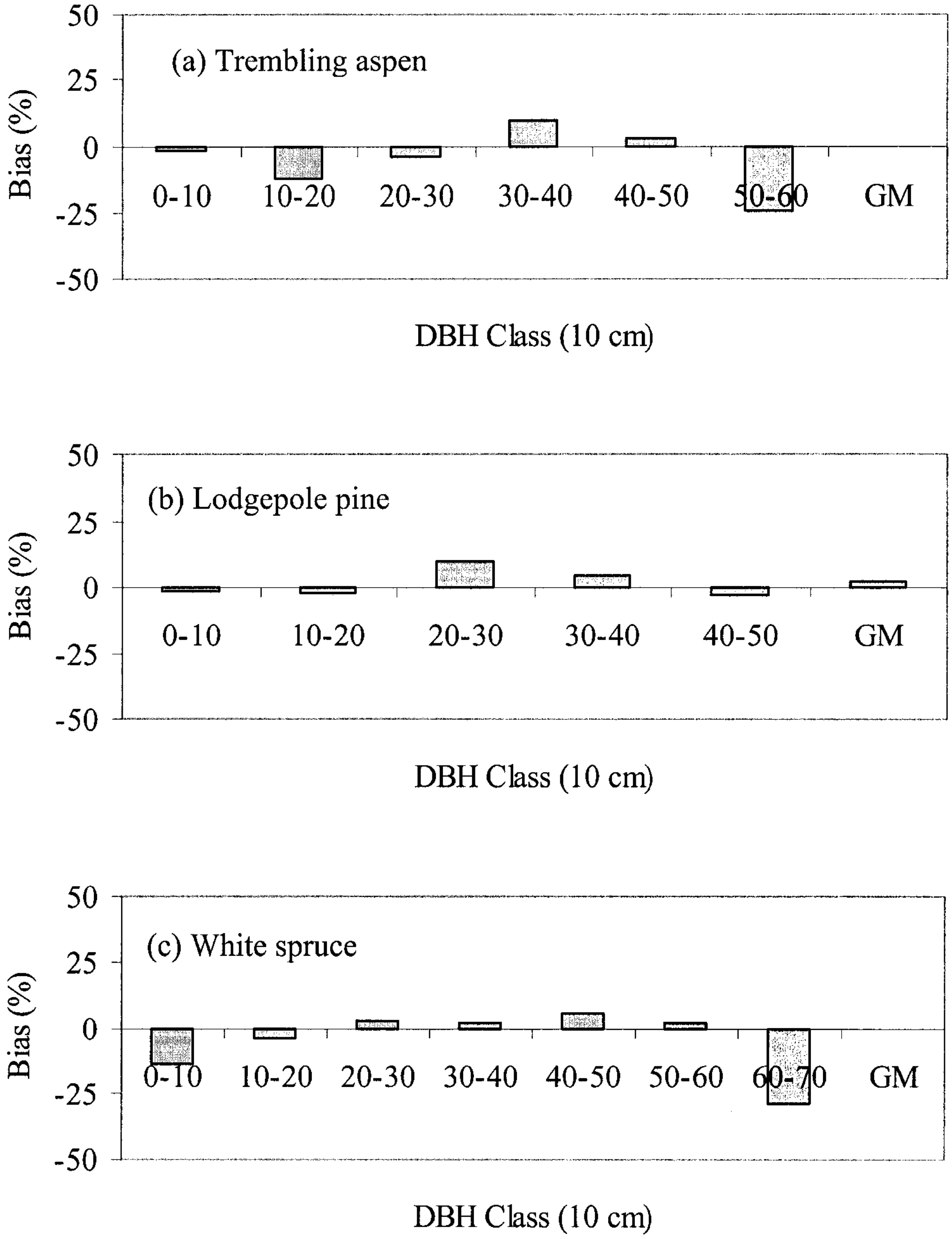

Figure 2-3. Individual tree diameter growth prediction bias as a percentage of mean plotted by 10-centimeter DBH classes for trembling aspen (a), lodgepole pine (b) and white spruce (c). GM is the overall bias.

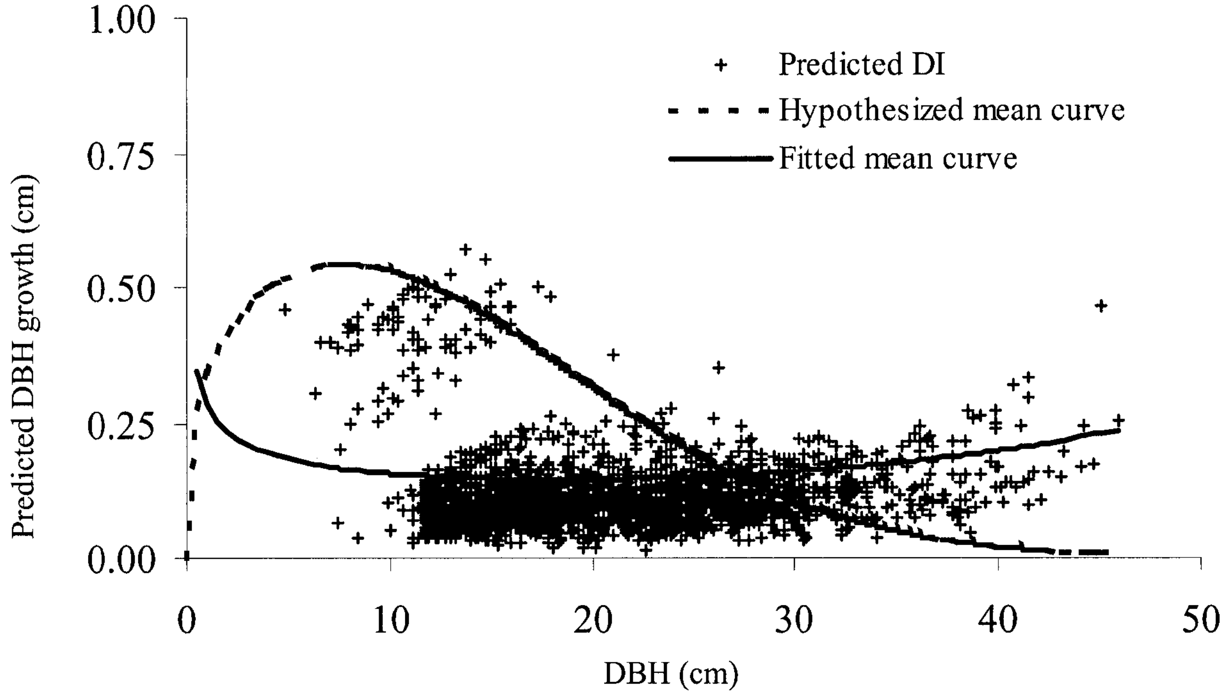

Figure 2-4. An overlay of predicted individual tree diameter growth patterns on the fitted and the hypothesized mean curves for lodgepole pine.

Chapter 3. Modeling Height Growth of Major Boreal Species in Alberta Using the Site Curve as the Maximum Height

3.1 Introduction.

Predicting individual tree height growth is an important component of forest growth and yield simulations. This is largely because tree height growth is highly correlated with individual tree and/or stand volume growth (Avery and Burkhart 1994), which are useful in making critical management decisions. Tree increment in height enhances the ability of the tree to expose its organs (leaves) to facilitate gaseous exchange and to capture light for photosynthetic activities and avoid over-topping by its neighbors (Oliver and Larson 1996). The height growth of dominant and co-dominant trees is widely used as an index of site productivity. Thus, tree height growth is an important aspect of forest dynamics.

A major drawback to effectively modeling and predicting tree height growth in mixedwood stands is measurement error. Height growth models are usually fitted by relating the instantaneous rate of change in height to individual tree and stand characteristics which reflect resources availability and/or the level of competition the tree is experiencing (e.g. Huang 1999). Because instantaneous rate of change cannot be observed directly and must be estimated from two observations, the noise (measurement error) to signal (growth) ratio is often high as it is argued that the noise in the data is usually doubled whilst the signal is reduced (Leary 1979).

In practice, instantaneous growth rate is usually measured as the ratio of change in tree height between two successive measurements to the time interval between the two measurements. The growth rates so obtained rather measures average annual growth rate between the two measurements rather than instantaneous annual growth rate. In most permanent sample plot schemes used for modeling, tree annual growth rate is calculated this way for practical reasons. McDill and Amateis (1993) argued that models fitted to such growth data could have serious growth prediction biases. There are two reason for this: 1) instantaneous annual tree growth rate is never constant over the entire measurement interval particularly when the interval long, but the average growth rate is constant over the entire measurement length and 2) as is always the case, the tree and stand variables measured at the initial measurement, are assumed to be good predictors of the average annual growth rate, which may not be the case; these variables may correlate better with instantaneous growth rate than with the average annual growth rate. The seriousness of this bias will depend on the difference between the true instantaneous growth rate and its estimate, the average periodic growth rate. The effect of this bias on model projection can be quite large when it gets propagated, particularly when the model is used for making long-term growth projections (Gertner 1987).

Some researchers have suggested that the averages of the observed tree and stand variables at the two successive measurements should be used as the independent variables for model fitting (Vanclay 1994). They argue that the average periodic growth rate will better approximate the actual instantaneous growth rate of the tree at the midpoint of the measurement interval. McDill and Amateis (1993) pointed out that the average periodic growth rate may not necessarily represent the growth rate at the midpoint of the measurement interval and recommended two other methods of interpolation based on iterative re-fitting, to improve parameter estimates of individual tree height growth models. Cao (1999) and Cao *et al.* (2002) presented a version of this method for improving the parameter estimates of an individual tree diameter growth and survival models. Whereas these interpolation methods have been shown to greatly improve individual tree growth models, their use requires knowledge of individual tree ages, which are often absent in permanent sample plot (PSP) data. Besides, the effects of the measurement error may be significant enough to seriously bias the model fit.

An alternative method for fitting individual tree height growth functions is the potential-modifier approach. A potential growth curve is defined and a modifying function based on some measure of competition is developed to adjust the potential height growth for predicting individual tree height growth (e.g. Ek and Monserud 1974, Daniels and Burkhart 1975, Mitchell 1975). The potential growth could be the growth of an open grown tree if the species has relatively strong epinastic control (Oliver and Larson 1996), or the growth of site curve. The use of this approach for fitting height growth models looks quite attractive because of the concept of site index. Daniels and Burkhart (1975) expressed the average dominant height as a simple function of age and site index. The first derivative of this equation with respect to age was taken as the maximum annual height increment function and then a modifier function was defined to adjust the maximum increment to obtain predicted tree height growth. Mitchell (1975) used a similar approach in which the modifying function was a negative exponential function of an index expressed as the ratio of the subject tree foliar volume to the potential foliar volume in the absence of competition. This approach appears to be more biologically reasonable and offers two advantages: (1) the model is flexible enough to enable safe extrapolation within the range of site conditions represented by the data; and (2) the model will be able to keep height growth within bounds (i.e., predicted minimum height growth rate cannot be negative and the maximum cannot be greater than the potential) (Shao 1985).

In this chapter, the potential-modifier approach was adopted and used to fit an individual tree height growth function for use in Mixedwood Growth Model (MGM) (Morton and Titus 1984). The objectives are: 1) to explore the possibility of fitting a fairly simple height growth function using the site curves as the maximum; 2) to test the hypothesis that individual tree height growth relative to the site curve is a function of one-sided competition defined by basal area of trees larger than the subject tree; and 3) to test and model the effect of species composition (coniferous versus deciduous) on individual tree height growth. Achieving the above objectives will ensure that: 1) model predictions of long-term individual tree height growth trajectories are biological reasonable and interpretable; 2) species interaction is adequately modeled to ensure that predictions of long-term dynamics of mixedwood stands are within acceptable limits set by ecological theory; and 3) there is overall improvement in the predictive ability of the MGM. It was expected that this approach will reduce the effect of measurement error on model prediction bias and facilitate the adjustment of tree height growth predictions in response to changes in site index due to repression and/or in regenerated stands. The parameter estimates, fit statistics and tests results of the new height increment functions are presented and discussed.

3.2 The Data

The data for constructing this model came from two sources; Weldwood Canada Ltd and Alberta Land and Forest Division (ALFD). The ALFD data were collected over the past four decades from about 1755 permanent sample plots (PSPs) located throughout the inventory area of the province to provide representative information on forest growth and yield (ALFD 2000). The Weldwood Canada Ltd data, perhaps the largest database in the province covers just over 3000 PSPs, most of which are found in lodgepole pine stands, throughout their forest management agreement area (FMA).

About 300 and 180 PSPs from the Weldwood and ALFD databases respectively were selected for this study. Plot selection was based on the availability of information such as site tree measurements, which were deemed important for this study. Since most plots had no site index tree information, a significant portion of the data was not suitable for this study. In addition, most trees had no height measurements, requiring that a large number of sample plots be selected to obtain enough data on each species for modeling.

Individual tree height growth was computed as the ratio of the observed change in tree height between two successive height measurements on the same tree to the interval length of the two successive measurements. Data from the selected plots were summarized to provide information on individual tree and stand characteristics, which are suitable for use as variables in the model estimation. Summaries of these variables are provided in Table 3-1. The final dataset for model fitting was divided into two parts, about 75% for model fitting and 25% for model testing.

3.3 Model Development

3.3.1 Potential Height Growth

By definition, site index is the average height of dominant and co-dominant trees or the largest (by DBH) specified number of trees per unit area at a reference age and is an index of the production potential of a site. Theoretically, site index trees are selected on the assumption that they are little affected by varying density levels or competition, but sensitive to site quality differences and strongly correlated with stand volume growth. In even-aged, single species stands, the dominant and co-dominant trees are assumed to have these properties and are often selected as the site index trees. Site curves estimate the average heights of dominant and co-dominant trees, as functions of age and site indices (e.g. Huang 1997a, 1997b). The instantaneous rate of change of the site curve, given by its first derivative with respect to age, measures the rate at which a theoretical site index tree grows and can be used as the potential growth rate of all trees of the same species in the stand. Alternatively, average periodic rate of change of the site curve can be used as potential height growth. The average periodic rate of change is computed as the ratio of the difference between the average height of dominant and co-dominant trees predicted from the site curves at two successive measurement occasions to the interval length between the two successive measurements. The average periodic rate of change of the site curve matched the individual tree height growth computed in section 3.2 better, was easier to compute than the instantaneous rate of change, and was therefore used as the potential height growth estimate.

The application of site index to mixed species, multi-aged stands, is difficult and sometimes controversial as it is difficult to isolate the influence of trees of other species on the growth of trees selected as site trees. The selection of site trees in such stands is often very difficult. Besides, the use of the site curve to predict the potential height growth presupposes that trees of the same species in the stand are of the same age, which is often not the case in uneven-aged stands. Potential height growth calculated based on a site tree selected from a particular age cohort might not necessarily be the maximum for trees of the same species, which are far younger or older than the age of the site tree. For instance, Yao (1997) reported an age range of 0 to 15 years for spruce regeneration with an average age of 7 years. At such juvenile ages when growth rates are relatively high and varied, potential height growth from a site tree of age 15 will most likely be significantly different from the same rate computed using a tree of age 7 years.

Ek and Monserud (1974) dealt with this problem by using a simple function to predict the potential height growth given an individual tree's height and site index. In their formulation, the potential height growth of a tree is defined as the growth rate of a site tree of the same height and growing on the same site as the subject tree. A similar idea was used in this study. A simple function relating the average periodic rate of change of the site curve to the site index tree height at the initial measurement, site index and some measure of crowding was used for estimating the potential height growth for each species. The initial height of the site tree was taken as the height of the site tree at the earlier of the two consecutive measurements used for height growth rate computation. For instance, if the first and second measurements are used for height growth rate calculations, the site tree height at the first measurement was used as the independent variable in addition to site index. This approach eliminated the need for tree age in computing the potential height growth for individual trees.

The function represented by Equation 3.1 was found to be suitable for describing the height growth pattern of a typical tree. This function provides a reasonable description of tree height growth as described in most forestry literature (e.g. Barnes et al. 1998, Oliver and Larson 1996). Tree height growth is slow at first when the tree is young and too small to accumulate energy for rapid terminal growth, but becomes more rapid as more energy becomes available for terminal shoot growth as tree size and the amount of foliage increases. Height growth eventually reaches a maximum and begins to decline as a result of a number of factors. These factors may include stress due to the difficulty in conducting water and mineral salts through the entire length of the tree height to the leaves, increased maintenance cost and the achievement of crown size limit permitted by the growing space (Oliver and Larson 1996, page 60).

$$[3.1] \quad PHI = A_1 \exp(A_2 SI + A_3 CR) Ht^{A_4} \exp(-A_5 Ht^2)$$

PHI is the potential height increment, $A_1 - A_5$ are parameters to be estimated, Ht is the site tree height, SI is the site index and CR is an index for measuring crowding in the stand.

To predict individual tree potential height growth rate, the site tree heights in Equation 3.1 were replaced by the individual tree heights. The crowding index CR was calculated using an extension of Czarnowski's (1961) theory of height growth density relationships, presented by Cieszewski and Bella (1993). This theory states that in fully stocked stands, the product of squared stand height and number of trees per unit area remains constant during the stands life. Mathematically, Equation 3.2 represents this index.

$$[3.2] \quad CR = Ht^2 * Dens * 10^{-4}$$

where Dens is the number of stems per hectare, Ht is the stand height (preferably, top height) and 10^{-4} is a factor that converts area in hectares to meters. The inclusion of CR in the model was an attempt to account for the effect of density on site index.

The variable CR was not included in the model for predicting site tree growth for aspen and white spruce. Since aspen and white spruce typically occur in mixtures of varying combinations of species age and proportions, the implementation of this crowding index may not be suitable. Besides, repression associated with excessive stand densities, which results in the reduction of dominant tree height growth rate, may not be a serious problem in aspen and spruce.

The site indices used in this study were based on site curves from Huang (1997a, 1997b). Site indices and site index tree height growth were computed by natural sub regions of Alberta and where the natural sub region of a PSP or PSP group was not indicated, the Provincial average curve was used. The results of the fit of Equation 3.1 using the potential height growth data computed from the site trees measurements are presented in Table 3.2. The coefficients of the explanatory variables are all of the appropriate signs. For example, the positive sign for the site index coefficients indicates that potential height growth increases with increasing site index and the negative sign on the CR coefficient translates into a reduction in potential height growth when stand density is excessive.

3.3.2 Individual tree Height Growth Adjustment

Each individual tree (j) in the stand was given a height growth adjustment A_j, which was related to the potential height growth (PHI) and the height growth (HI_j) attained by tree (j) by:

$$[3.3] \quad HI_j = A_j * PHI .$$

Tree physiology literature suggests that tree height growth rates are relatively stable across a range of densities compared to diameter growth (Sjolte-Jørgensen 1967, Dahms 1973 Schmidt et al 1976, Seidal 1984). Although differences of opinion exist as to the physiological basis of this stability, there appears to be a general agreement of the fact that trees tend to put on more height growth than diameter growth when faced with extreme competition and resource limitation. Therefore, a suitable function for A_j should allow trees to grow in height close to their potential until competition is relatively intense forcing a substantial reduction in height growth rate. A modified version of the semi-Gaussian (normal) function (Ratkowsky 1990), given in Equation 3.4 was found to be more suitable for this purpose.

$$[3.4] \quad A_j = \alpha + \beta \exp\left(-\left(\theta_1 X_1^2 + \theta_2 X_2^2 + \theta_3 X_3^2 \ldots + \theta_n X_n^2\right)\right)$$

Where $X_1, X_2, X_3, \ldots X_n$ are a set of explanatory variables, comprising individual tree and stand characteristics, which define the level of competition and the competitiveness of the subject tree for growth resources and $\alpha, \beta, \theta_1, \theta_2, \theta_3, \ldots \theta_n$ are parameters to be estimated. The parameter α is the minimum value A_j can take and the biological maximum of A_j (i.e. when all terms in the exponent add up to 0) has been constrained in this study to be $\alpha+\beta$, although mathematically, A_j can be greater than $\alpha+\beta$ when the terms in the exponent add up to a value less than 0. When α is set to 0, indicating that the tree height growth adjustment is zero under extremely intense competition, and β is set to 1 then the best trees in the stand are growing at a rate equal to the site curve. Alternatively, Equation 3.4 can be fitted with a restriction that α and β add up to 1, to constrain the maximum growth adjustment to be 1 whilst allowing the minimum height growth for the most suppressed tree in the stand to be greater than 0. In this study, the parameter α was set to 0 and β set to 1 after a preliminary analysis indicated that the estimate of the parameter β was not statistically significantly different from 1 for all the three species.

3.4 Variable Selection

The variables to be included in the model (Equation 3.4) were selected within the framework of individual tree non-spatial models. Several non-spatial competition indices have been published (e.g. see Clutter et al. 1983, Vanclay 1994, Biging and Dobbertin 1995). The non-spatial indices based on crown measurements have been shown to be better for predicting individual tree growth than the non-crown based variables (Biging and Dobbertin 1995). However tree crown-based competition indices were not used in this study because of lack of crown measurements for most trees in the data used for the study. Non-crown competition indices are also effective predictors of tree growth and most of them are based on tree and stand characteristics such as stand density, tree DBH and height that are strong predictors of tree crown-based information.

The basal area in larger DBH trees (GGR) has been shown to be a good predictor of individual tree growth (Wykoff 1990, Vanclay 1991, Yao 1997, Schröder and Gadow 1999). GGR is one of the common competition indices, based on individual tree size difference. Calculated by Equation 3.5, this variable combines an individual tree's basal area percentile and the stand basal area (Wykoff et. al. 1982, Wykoff 1990, Schröder and Gadow 1999). The variable GGR has been shown to behave well under all types of thinning (Schröder and Gadow 1999).

$$[3.5] \quad GGR = (1 - p_i)BAHA.$$

p_i is the basal area percentile of the subject tree and expresses the relative social rank of the tree and $BAHA$ is the basal area of the stand expressed in square meters per hectare.

Past applications of GGR have failed to recognize that species characteristics and growth habits of both the subject tree and its competitors can affect the influence of this variable on tree growth prediction. The level of tolerance of the subject tree and the crown morphology of the trees over-topping the subject tree are important determinants of the level of competition the subject tree experiences. Studies on light, temperature and moisture conditions under aspen stands and their comparison to the physiological requirements of white spruce (Lieffers and Stadt 1994, Man and Lieffers 1999) for instance, suggested that a suitable micro-environment for white spruce growth is created under aspen. The general expectation is that a white spruce tree over-topped by a given basal area of aspen may grow better than when it is over-topped by white spruce trees of the same basal area. This suggests that effects of species interaction on height growth in mixed species and mixedwoods stands may be better modeled if GGR is calculated by species. This is however not possible if there are many species. For this study, species were grouped into deciduous and coniferous categories for computing GGR (i.e. Deciduous GGR=DGGR and coniferous GGR=CGGR) to take advantage of the differences in the crown characteristics, rooting habits and resource use efficiency between coniferous and deciduous trees.

Another variable, which was considered biologically significant for modeling species interaction, was the ratio of species quadratic mean DBH to the stand quadratic mean DBH (QMDR). This variable measures the relative dominance of the species in the stand in terms of both composition and size. For a single species stand, this ratio is 1 and competition is strictly intra-specific. The ratio will be less than 1 for a mixed species stand where the species is in the understory, and greater than 1 where the species is mainly in the overstory. For a particular species the sign of and whether the coefficient of QMDR is significantly different from 0 is an indication of whether the average size of the species relative to others species in the stand affects the species height growth. The final model is given by:

$$[3.6] \quad HI_j = PHI * \exp\left(-\left(\theta_1 CGGR^2 + \theta_2 DGGR^2 + \theta_3 QMDR^2\right)\right) + e_j .$$

The random error term e_j is assumed to be normally distributed with mean 0 and uniform variance σ^2.

3.5 Model Fitting

3.5.1 Parameter Estimation

The preliminary nonlinear least squares fit of Equation 3.6 to the dataset of each species was done using the Model Procedure on the SAS/ETS software (SAS Institute Inc. 1988). The Marquardt iterative method was used (Marquardt 1963). The ease of getting convergence for nonlinear regression, and largely, whether the solution so obtained is a global rather than a local solution, depends very much on the starting values. This problem becomes increasing severe when the nonlinear model being fitted is complex. Alternative methods of getting suitable starting values for nonlinear regression have been dealt with in most standard nonlinear regression textbooks (e.g. Draper and Smith 1981, Gallant 1987 p29-30). The most simple and logical approach is to transform the nonlinear regression model into a linear model and use the parameter estimates obtained from the least squares fit of this linear model as the starting values. Using this approach, Equation 3.6 was first transformed into a linear function by taking the natural logarithms of both sides (Equation 3.7) and fitted using the REG Procedure on SAS software (SAS Institute Inc. 1992). The parameter estimates of this fit were used as starting values for the nonlinear regression fit of Equation 3.6.

[3.7] $$\ln\left(HI_j\right) = \ln(PHI) - \theta_1 CGGR^2 + - \theta_2 DGGR^2 + - \theta_3 QMDR^2$$

The asymptotic fit statistics and the parameter estimates of the nonlinear least-squares fits for the aspen, white spruce and lodgepole pine data are listed in Table 3.3. The asymptotic statistics have the same interpretation as those in the linear regression case because of the large sample size. At the preliminary stage, model parameters were estimated using potential height growth predictions from both Equation 3.1 and the potential height growth calculated from the site curve. Both approaches yielded similar results and so the potential height growth calculated from the site curve was used for further analysis.

3.5.2 Model Diagnostics

Model diagnosis was done for multicollinearity, heteroskedasticity and autocorrelation. Multicollinearity was tested for using the condition numbers of the explanatory variables included in the model. Specifying the option COLLIN at the fit section of the PROC MODEL produces these statistics. The condition number must be less than 30 to indicate little or no collinearity (Belsley et al. 1980). The condition numbers for all the three species were far smaller than 30 (all less than 2) (Table 3.3) indicating multicollinearity was not a problem.

Although the ordinary nonlinear least square estimator is asymptotically unbiased and consistent even if autocorrelation and heteroskedasticity are present (Gallant 1987) and may not affect the unbiasedness of model prediction, inferences about the model parameters may not be valid. Heteroskedasticity diagnostics was limited to only the examination of the residual graphs of the preliminary fitted model. Although there are statistically more rigorous tests for heteroskedasticity such as the Goldfield-Quandt test (Judge et al. 1988), the residual plot was used because of its simplicity and clarity in illustrating the problem. For all species, the graphs of studentized residual against predicted height increment showed that residual variances increased with increasing predicted tree height growth (e.g. see Figure 3.2). Diagnostics for autocorrelation were limited only to the first order autocorrelation because only a few trees included in the data had more than two successive height growth measurements. The Durbin-Watson statistics in Table 3.3 were used for first order autocorrelation diagnostics. According to Seber and Wild (1988 pp. 318-319), the Durbin-Watson test is more appropriate for linear regression but is also approximately valid for nonlinear regression if the sample size is large. The Durbin-Watson Statistics of 1.5257 for aspen, 1.6157 for white spruce and 1.4224 for lodgepole pine (Table 3.3) are lower than the critical values for three parameter models and thus indicate the presence of first order autocorrelation. Autocorrelation may result from multiple observations being taking on the same tree leading to the intra-tree dependency of the error terms of the height increments.

The common solution for heteroskedasticity is to use weighted nonlinear least squares using the inverse of an appropriate variance function as weights. Here it was assumed that the off diagonal elements of the variance covariance matrix are zeros and the diagonal elements are dependent on some explanatory variables in the form of a variance function. In the presence of both heteroskedasticity and autocorrelation, this assumption is not applicable because the off diagonal elements of the variance–covariance matrix can no longer be zero because of the correlation that exists between error terms of the same tree. For this study, a variance function relating the squares of the residuals as estimates of the residual variance to predicted tree height growth was used for weighting. After studying the residuals from the preliminary fits for all the three species, the exponential function, $r_i^2 = \beta_1 * exp(\beta_2 * h_i)$ was found to be the most appropriate variance function for all the three species. The weighting factor was therefore $w_i = 1/(\beta_1 * exp(\beta_2 * h_i))$; where β_1, and β_2 are parameters to be estimated, and h_i is the predicted annual height growth. The most appropriate way of using a variance function that uses predicted values as a dependent variable to correct a model for heteroskedasticity is by iterative refitting until the model parameter estimates converge (Dr. S Lele, Associate professor of statistics, Department of Mathematical Science, University of Alberta, Edmonton, personal communication). This is because both predicted height growth and the error terms change each time the model parameters change.

Based on the assumption that the error terms for the preliminary fit of Equation 3.6 follow a first order autoregressive (AR (1)) process as shown in Equation 3.8 below, the procedure summarized by Huang et al. (1997) for generalized nonlinear least squares (GNLS) fit of models with first order autocorrelated error terms was adopted and modified for use to correct for both heteroskedasticity and first order autocorrelation.

[3.8] $HI_i = f(\boldsymbol{\theta}, X) + r_i \qquad r_i = \rho * r_{i-1} + d_i;$

where HI_i is the annual height growth for a tree in the current growth period, r_i is the corresponding error term, r_{i-1} is the error term in the previous growth period, X_i is a set of explanatory variables for the current growth period, ρ is the coefficient of first order autocorrelation and d_i are the uncorrelated residual terms, which are assumed to be normally distributed with mean 0 and uniform variance σ^2.

Using the variance functions specified above and the fact that the residual follow a first order autoregressive process, the estimate of the set of parameters $\boldsymbol{\theta}$ were obtained as follows:

1. Estimate $\boldsymbol{\theta}$ by nonlinear least squares and estimate the predicted height growth $h_i = f(Xi, \boldsymbol{\theta})$ and the residual $r_i = HI_i - f(Xi, \boldsymbol{\theta})$;

2. Fit the variance function; $r_i^2 = f(\boldsymbol{\beta}, h_i) + e_i$, where e_i's are the errors and $\boldsymbol{\beta}$ is vector of parameters of the variance function;

3. Estimate the coefficient of autocorrelation ρ by fitting $r_i = \rho^* r_{i-1} + d_i$;

4. Re-estimate $\boldsymbol{\theta}$ by fitting the Equation: $HI_i - \rho HI_{(i-1)} = f(X_i, \boldsymbol{\theta}) - \rho f(X_{(i-1)}, \boldsymbol{\theta}) + d_i$ using the estimated variance function as the weighting factor and estimate new r_i's and h_i's as in step 1; where $HI_{(i-1)}$ and $X_{(i-1)}$ are the height increment and the set of explanatory variables for the previous growth period;

5. Repeat steps 2 to 4 until the parameters converge.

This five step iterative re-fitting procedure is equivalent to minimizing:

$$[3.9] \quad S(\theta) = [HI - f(X_i, \theta)]' \Sigma^{-1} [HI - f(X_i, \theta)];$$

where Σ is the generalized variance-covariance matrix incorporating the heteroskedastic variance function and the coefficients of autocorrelation (Gallant 1987). Since Σ is not known, its structure is estimated when ρ and the coefficient of the variance function change after every iteration. The parameter estimates of the generalized nonlinear least squares estimate of Equation 3.6 are given in Table 3.4. The Durbin-Watson statistics are 2.1614 for aspen, 2.0619 for white spruce and 2.1611 for lodgepole pine; these values satisfactorily indicate autocorrelation has been removed. However, the coefficients for DGGR for lodgepole pine and QMDR for aspen were not statistically significantly different from 0 at α=0.05. Consequently, height adjustment models for aspen and lodgepole pine were refitted without these variables and the fit statistics are given in Table 3.5. The asymptotic statistics such as R-square, root mean square error and Durbin-Watson statistics did not change with the refit (Table 3.4 and 3.5). The residual graph of the GNLS fit for white spruce is given in Figure 3.2. The graph shows that the residual variance has been stabilized by this approach.

3.5.3 Model Validation

Using the validation data and parameter estimates in Tables 3.4 and 3.5, a validation test was conducted to determine the precision and bias of the height growth model. Table 3.6 presents the goodness of fit statistics calculated for each species by 4m height classes using the independent dataset. Bias is the average of the difference between observed and predicted height growth and the percent bias is the bias expressed as a percentage of the observed mean height growth. The over all bias values for aspen and white spruce were not statistically significantly different from 0. Lodgepole pine had the worse fit with a bias significantly different from 0. This statistical significance was probably due to the large sample size for pine, which made the test more sensitive. In terms of percentage bias, the lodgepole pine model was similar to the other species (Table 3.6). Also computed was the mean squared error of prediction (MSEP), which includes the variance of the prediction error and the square of the prediction bias and measures the precision of the model prediction. Smaller MSEP values indicate the model has a higher precision. The MSEP values showed that the white spruce model had the best fit and lodgepole pine model had the worst fit.

3.6 Discussion and Conclusion

The height increment models given by Equations 3.4 and 3.6 were fitted to provide individual tree height growth for the three major boreal species in Alberta, namely aspen, white spruce and lodgepole pine. The fit statistics for the potential height growth function generally show close to a perfect fit and all the model parameters are significant at $\alpha = 0.05$. This indicates that the model is a reasonable predictor of potential height growth of individual trees when site index is known (for aspen and white spruce) and when site index and the degree of crowding are known (for lodgepole pine). Although the fit results of the modifier function obtained at the preliminary stage by using this curve to predict potential height growth were similar to the results obtained using estimates from the site curve, this equation is important. In forest stands with multiple cohorts of trees of the same species, where age can differ substantially, the use of this equation is advised.

The asymptotic t-statistics for the parameters of the modifier function (Equation 3.6) are all significant at $\alpha = 0.05$ except for basal area in larger deciduous trees (DGGR) in the lodgepole pine model and the quadratic mean DBH ratio in the aspen model (Table 3.5). However, approximately 40% of the height increment variation for aspen, 17% for white spruce and 29% for lodgepole pine were explained by the model. Although these figures are relatively low, they reflect the large variation in height increments observed in mixed boreal forests. Preliminary data screening (not reported here) did show that measurement errors could be a major contributory factor to this larger variation. Nevertheless, the coefficients of determination observed here are comparable to similar studies done for boreal mixedwoods (e.g., Huang 1992, Huang and Titus 1999, Yao 1997).

The lodgepole pine and white spruce height models were, on average, slightly negatively biased whereas the aspen model was slightly positively biased. The bias for lodgepole pine and aspen models appeared to decline from positive to negative with increasing tree height. A negative bias is an indication that the model will over predict individual pine tree heights whilst the reverse is true for positive bias. The bias could be due to the restriction placed on the maximum height growth to be equal to the site curve growth. A preliminary analysis to test the hypothesis that the parameter β in Equation 3.4 is equal to 1 produced a value of the parameter β to be slightly less than 1 (about 0.86 and 0.94 for lodgepole pine and white spruce respectively) and slightly bigger than 1 (about 1.03) for aspen. The small difference between 1 and the values of α estimated without any restriction could have contributed to the bias.

The age of trees selected as site trees could also have some influence on the site curve and hence the potential height growth function. If the selected site trees are in the younger age classes, the potential height growth curve could be over-estimated. On the other hand if site trees are older trees, the potential height growth curve could be seriously under-estimated. It was observed during data screening that the lodgepole pine site trees, particularly from the Weldwood Canada Limited PSP data, were mostly younger trees. As a consequence, the potential height growth function estimated from this data could over estimate the potential growth for older trees resulting in the over estimation of older tree heights. Site tree selection is as important in this modeling approach as it is in fitting site index curves. Data balance is very important to ensure unbiasedness in estimating the potential height growth.

In spite of these limitations, the approach used in fitting these models appears to be a reasonable description of competition and individual tree height growth. In this chapter, it has been assumed that competition for light is asymmetric (Weiner 1990) with the smaller, less vigorous trees receiving less photosynthetically active radiation (PAR) than the bigger more vigorous neighbors. Observation by Mitchell (1975) and Reukema (1970, 1979) may suggest that tree height growth is relatively independent of its degree of crowding and the amount of foliage except at extremely narrow spacing. This means all trees are expected to be growing in height close to their potential unless they are heavily suppressed, causing a severe reduction in tree crown size and the amount of foliage.

The species type, number and size of trees larger than the subject tree largely determines the amount of side shading and in turn, may affect the size of the tree crown, the amount of foliage carried, and the amount of light received by the subject tree. Larger trees will tend to be the least affected by shading. The extent of lateral extension of roots, which may be indicative of the relative competitiveness of the tree, may also be related to the size of tree; larger trees may have more extensive root systems and may be more successful in obtaining pockets of limited growth resources than their smaller counterparts of the same species (Thomas and Weiner 1989). These are all pointers to the fact that one-sided competition, measured by basal area in larger trees, is a good predictor of individual tree height growth if site quality is known.

The signs of the coefficients of basal area in larger coniferous and deciduous trees are all positive, indicating that tree height growth will tend to decline as coniferous and deciduous competition increases. The rate of decline will depend on the magnitude of the coefficients of these variables. Since CGGR and DGGR are measured in the same units, differences in the magnitudes of their respective coefficients may be indicative of which variable affects the height growth of the species most. In a typical aspen–white spruce mixture, it will be expected that basal area in larger coniferous trees will have the biggest coefficient. However, in this study, the coefficients of CGGR and DGGR were similar, with that of DGGR slightly larger for white spruce and aspen (Table 3.4 and 3.5). It must be noted here that there were deciduous and coniferous species other than aspen and white spruce in the data used for this study. The contribution of these species to the deciduous and coniferous competition on aspen and white spruce could be different.

The coefficient for basal area in larger deciduous trees for the lodgepole pine model was not statistically significant. The possible explanation of this could be that stands containing lodgepole pine in mixtures with hardwoods are generally low in density and hence the hardwood component had very little effect on the pine tree height growth. It appears the hardwood component in lodgepole pine stands was very low (Table 3.1). For this modeling approach, it might be safer to use basal area in larger trees without the distinction between deciduous and coniferous tree species for predicting lodgepole pine tree height growth (Table 3.5). This is because the magnitude of the coefficient for basal area in larger deciduous trees was far larger than that of the coniferous component although it was not significant. The inclusion of this variable may tend to exaggerate the effect of deciduous tree on pine height growth.

The model presented in this chapter is a simple, and yet effective predictor of individual tree height of the major boreal species. Since the site curve defined the upper bound of individual tree height growth and is formulated to always approach an asymptote, long term projections which will require extrapolation beyond the age of the data used will produce a much more reasonable prediction. By separating competition into coniferous and deciduous, species interaction is better accounted for in predicting individual tree height growth. The major requirement for the success of this approach is the selection of site trees to cover a major part of the rotation of the species in the stand. This will reduce the possibility of any prediction bias. It must be added here that the fitted potential height growth curve (Equation 3.1) and the potential height growth obtained directly from the species site curve gave similar results. However the use of the fitted potential height growth is encouraged, particularly in multi-cohort stands.

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Table 3-1. Summary statistics for tree and stand characteristics for aspen, White spruce and Lodgepole pine used for model fitting.

	Mean	Minimum	Maximum
Aspen			
Conifer GGR (m2/ha)	3.42	0.00	38.72
Deciduous GGR (m2/ha)	10.34	0.00	42.08
Quadratic mean DBH ratio	0.82	0.11	1.38
Site index (m)	17.49	6.15	23.57
Tree height growth (m)	0.20	0.00	0.83
Number of trees/ha	1341.56	232.33	5000.00
Tree height (m)	16.79	3.70	32.70
White Spruce			
Conifer GGR (m2/ha)	17.89	0.00	57.98
Deciduous GGR (m2/ha)	4.43	0.00	47.40
Quadratic mean DBH ratio	0.89	0.08	2.30
Site index (m)	16.04	4.38	26.50
Tree height growth (m)	0.16	0.00	1.00
Number of tree/ha	1156.94	86.49	4932.01
Tree height (m)	18.85	1.60	35.90
Lodgepole Pine			
Conifer GGR (m2/ha)	17.61	0.00	57.68
Deciduous GGR (m2/ha)	0.33	0.00	27.85
Quadratic mean DBH ratio	0.96	0.07	2.28
Site index (m)	16.06	7.42	25.98
Tree height growth (m)	0.14	0.00	0.99
Number of tree/ha	1802.74	24.71	6584.16
Tree height (m)	15.69	1.40	30.80

GGR is the basal area in trees larger than the subject tree.

Table 3-2. Parameter estimates for the potential height growth function (Equation 3.1)

Parameter	Estimate	Asymptotic Std. Error	Asymptotic t-value	Prob. > |t|	RMSE	R^2
Aspen						
A1	0.050475	0.002090	24.1600	<0.0001	0.00313	0.9933
A2	0.082606	0.000638	129.4400	<0.0001		
A4	0.313324	0.017100	18.3100	<0.0001		
A5	0.002808	0.000025	113.0500	<0.0001		
White Spruce						
A1	0.096656	0.003360	28.7300	<0.0001	0.01390	0.9399
A2	0.075648	0.001470	51.3700	<0.0001		
A4	0.022943	0.011400	2.0200	0.0437		
A5	0.001454	0.000034	43.3500	<0.0001		
Lodgepole Pine						
A1	0.073654	0.001130	65.4700	<0.0001	0.01430	0.9547
A2	0.089323	0.000550	162.3700	<0.0001		
A3	-0.000390	0.000120	-3.2800	0.0010		
A4	0.060953	0.008460	7.2100	<0.0001		
A5	0.002402	0.000042	56.7500	<0.0001		

Table 3-3. Parameter estimates of the nonlinear ordinary least squares fit for the aspen, white spruce and lodgepole pine height adjustment model (Equation 3.6).

Parameter	Estimate	Asymptotic Std Err	t-Value	Pr > |t|	MSE	Adj. R-Sq	Durbin Watson
Aspen *(Condition Number =1.6246)*							
θ_1	0.000612	0.000170	3.60	0.0003	0.0178	0.3673	1.5257
θ_2	0.000977	0.000134	7.31	0.0001			
θ_3	0.025103	0.019300	1.30	0.1937			
White Spruce *(Condition Number = 1.7597)*							
θ_1	0.000339	0.000026	12.87	<0.0001	0.0121	0.1381	1.6157
θ_2	0.000467	0.000068	6.88	<0.0001			
θ_3	0.136569	0.013800	9.88	<0.0001			
Lodgepole Pine *(Condition Number = 1.5788)*							
θ_1	0.000547	0.000023	23.90	0.0001	0.0104	0.2252	1.4224
θ_2	0.000472	0.000658	0.72	0.4732			
θ_3	0.192860	0.009340	20.65	0.0001			

Table 3-4. Parameter estimates of the generalized least squares fit for the aspen, white spruce and lodgepole pine height adjustment model (Equation 3.6).

Parameter	Estimate	Asymptotic Std Error	t-Value	Pr > |t|	RMSE	Adj R-Sq	Durbin Watson
Aspen							
θ1	0.000472689	0.000172	2.75	0.0060	0.1296	0.4031	2.1614
θ2	0.000923405	0.000139	6.66	<0.0001			
θ3	0.002300412	0.022600	0.10	0.9191			
ρ	0.247200000	0.029200	8.47	<0.0001			
White Spruce							
θ1	0.000342828	0.000029	12.01	<0.0001	0.1080	0.1673	2.0619
θ2	0.000488424	0.000078	6.23	<0.0001			
θ3	0.127310000	0.015800	8.05	<0.0001			
ρ	0.193246000	0.017800	10.87	<0.0001			
Lodgepole Pine							
θ1	0.000467472	0.000024	19.18	<0.0001	0.0978	0.2901	2.1611
θ2	0.001696675	0.001000	1.70	0.0901			
θ3	0.202571000	0.011900	17.05	<0.0001			
ρ	0.294256000	0.011700	25.18	<0.0001			

Table 3-5. Parameter estimates for the refit of Equation 3.6 for aspen without QMDR and lodgepole pine with only GGR and DGGR.

Variable	Parameter Estimate	Asymptotic Std Error	t-Value	Pr > |t|	RMSE	Adj R-sq	Durbin Watson
Aspen							
CGGR	0.000475280	0.000170	2.79	0.0054	0.1296	0.4037	2.1618
DGGR	0.000931179	0.000127	7.34	<0.0001			
ρ	0.247727622	0.029000	8.55	<0.0001			
Lodgepole pine							
GGR	0.000456938	0.000024	19.28	<0.0001	0.0978	0.2902	2.1617
QMDR	0.203585533	0.011900	17.16	<0.0001			
ρ	0.295098000	0.011700	25.29	<0.0001			

Table 3-6. Model accuracy and precision test statistics by tree height classes

Tree height class (m)	Mean height growth (m/yr)	Prediction Bias (m)	Std. dev. pred. bias	Percent pred. bias	Mean square Error of pred.
Aspen					
0 – 3	0.494776	0.127779	0.181802	25.83	0.0492147
4 – 7	0.454090	0.067324	0.163530	14.83	0.0311342
8 – 11	0.343048	-0.064529	0.126103	-18.81	0.0200374
12 – 15	0.104048	-0.025050	0.053622	-24.08	0.0129299
16 – 19	0.107227	-0.020358	0.065106	-18.99	0.0093441
20 – 23	0.087752	-0.015074	0.061139	-17.18	0.0058971
All	0.359402	0.023849	0.168844	6.64	0.0294578
Lodgepole pine					
0 – 3	0.432115	0.065817	0.140298	15.23	0.0346472
4 – 7	0.325022	0.064835	0.114741	19.95	0.0155565
8 – 11	0.134320	0.025724	0.127886	19.15	0.0340312
12 – 15	0.142371	-0.013847	0.186300	-9.73	0.0665095
16 – 19	0.145472	-0.025651	0.220530	-17.63	0.0890991
20 – 23	0.151836	-0.035781	0.350342	-23.57	0.1264419
≥ 24	0.142857	-0.025872	0.593281	-18.11	0.1206408
All	0.165589	-0.014741	0.224992	-8.90	0.0676946
White Spruce					
0 – 3	0.263200	-0.0514413	0.0821569	-19.54	0.0093885
4 – 7	0.282340	-0.0192927	0.1426553	-6.83	0.0207004
8 – 11	0.199920	-0.0279850	0.1384655	-14.00	0.0199348
12 – 15	0.179580	-0.0055553	0.1293986	-3.09	0.0167565
16 – 19	0.163010	-0.0004335	0.1051812	-0.27	0.0110511
20 – 23	0.168200	0.0216179	0.1085596	12.85	0.0122396
≥ 24	0.147090	0.0174839	0.0984654	11.89	0.0099905
All	0.193113	-0.0086547	0.1250825	-4.48	0.0157033

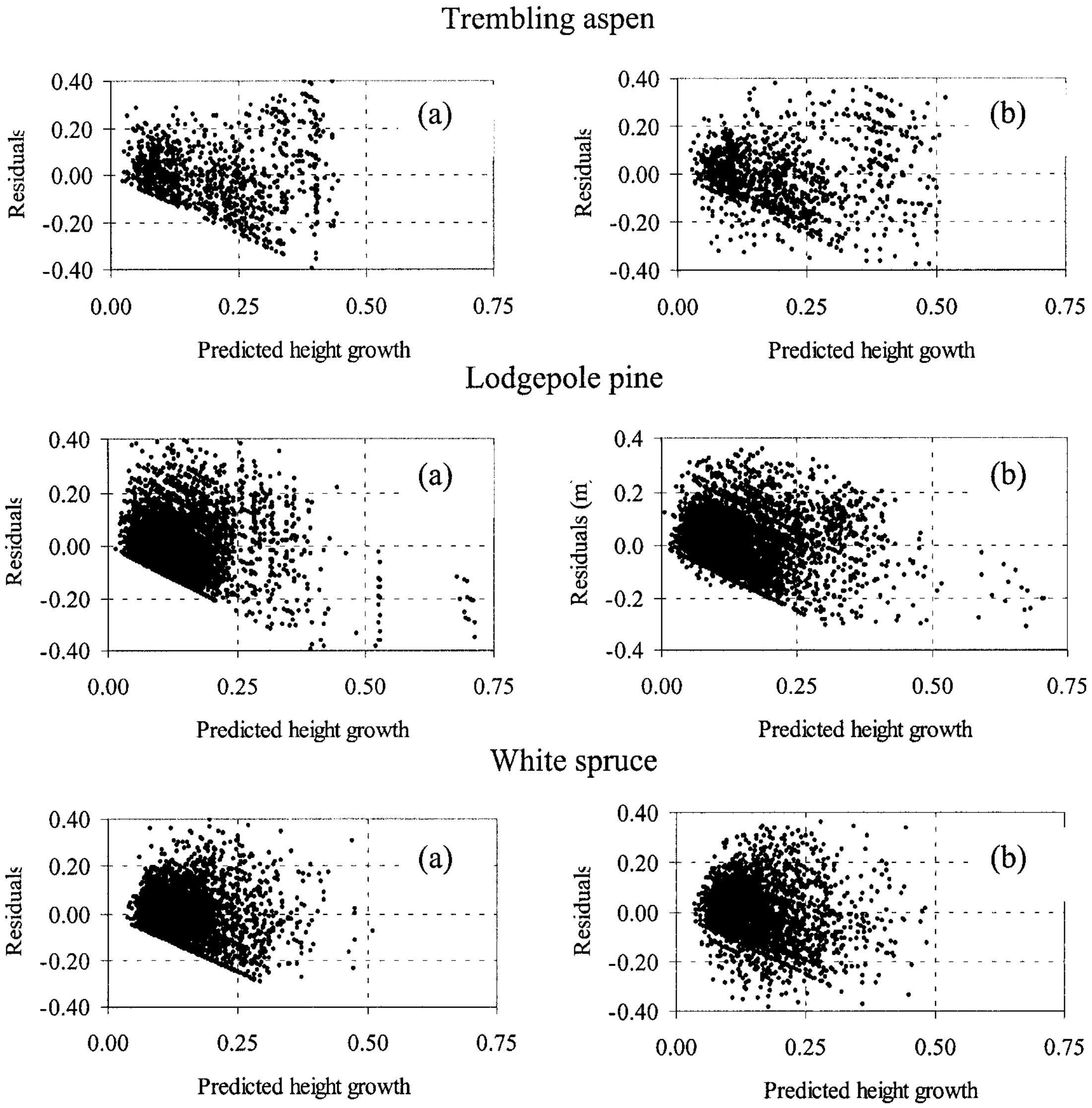

Figure 3-1. Residual graphs for trembling aspen, lodgepole pine and white spruce height growth models fitted with ordinary nonlinear least squares (a) and generalized non-linear least squares (b)

Chapter 4. Compatible Individual Tree Diameter and Height Growth Functions for Major Boreal Species in Alberta

4.1 Introduction

The various components of individual tree growth and yield models are connected together hierarchically for making projections. Individual tree diameter and height growth models are used to increment individual tree sizes at fixed time steps and the mortality or survival probability models determine the number of surviving trees whose yields must be aggregated to obtain the stand level yield. The importance of fitting these functions such that they are compatible with each other has long been recognized in the forest growth and yield literature (Furnival and Wilson 1971).

Buckman (1962) and Clutter (1963) pioneered the study of compatibility among growth and yield models. Furnival and Wilson (1971) specified and estimated growth and yield component equations as a system of simultaneous equations using well established econometrics techniques. Many other researchers have used simultaneous equation techniques to ensure that model components are compatible either, within the same level of resolution (Burkhart and Sprinz 1984, Huang 1992, Huang and Titus 1999) or among different levels of resolution (e.g. Borders 1989, Zhang et al. 1997). Compatibility between individual tree height and diameter growth models, for instance, will ensure that individual trees projected by the model have forms that are ecologically realistic and consistent with the stand conditions. It is desirable to ensure that individual tree diameter growth predictions are compatible with height growth predictions, to ensure that there are no much larger than expected trees in a crowded stand, as this may seriously inflate stand level volume estimate. A useful connection between individual tree diameter and height growth models has been identified to be the tree height – diameter at breast height (DBH) relationship (Ek 1971, Sievänen 1993, Huang 1992, Huang and Titus 1999)

The relationship between tree DBH and tree height has been studied extensively in the forestry literature apparently because of the mensurational advantage of being able to predict tree height which is much more difficult and/or expensive to measure accurately. The height – DBH relationship has also been found to be of ecological significance, determining the stability of the tree to damage from wind and snow (e.g. Cremer *et al.* 1982, Nykänen *et al.* 1997) and reflecting the amount of competition the tree is experiencing (e.g. Opio *et al.* 1999). These ecological properties are the results of factors that influence the relative allocation of photosynthate by individual trees in the stand to increments in girth and height respectively.

Huang (1992) compared several functions for fitting individual tree height - DBH relationships. These functions are generally concave in shape portraying asymptotic increases in tree height with respect to tree DBH. This trend appears to be consistent with the common biomechanical models in the ecology literature. These models predict that as trees must maintain their growth in height to be able to expose their leaves to light, increase the shading of competitors and elevating reproductive or dispersal organs (Rich *et al.* 1986, Aarssen 1995), trees must maintain a strong structural support either through increased wood density or increased diameter to prevent them from elastic deformation or buckling under their own weight or breakage by wind.

For a single tree monitored over time, this relationship may be affected by various factors including competition effects from neighbors, which are constantly changing in response to some dynamics of the ecosystem. Neighbor effects may include shading and/or reducing the subject tree wind sway (Henry and Aarssen 1999). Under crowded conditions for instance, trees may allocate stem growth biomass preferentially to height growth over diameter growth in order to minimize over-topping by neighbors and thus maximize exposure to light (Rich *et al.* 1986) thereby becoming relatively slimmer (Assmann 1970). Reduced wind sway in dense stands has also been shown to increase height – diameter ratios of trees (Jacobs 1954, King 1986).

A typical tree growing in a stand will constantly experience changes in neighborhood effects and may respond accordingly by modifying its growth pattern resulting in jagged, inconsistent height – DBH trajectories rather than a smooth curve implied by the static data (Sumida et al. 1997, Henry and Aarssen 1999), although Ek (1971) found a linear relationship between diameter growth and height growth in open grown red pine trees. Cross-sectional survey data collected on trees of different ages, stand densities and site productivity have been used to fit tree height - DBH curves. With the assumption that all age, density and site classes are well represented, a common interpretation given to the usual concave height – DBH curve fitted to such data has been that trees tend to slow down in height growth faster than diameter growth as they age. Physiologically this may be true (e.g. see Ryan and Yoder 1997). However, using one-time survey data to arrive at such conclusion, as some studies have done (e.g. Rai 1979, Rich *et al.* 1986, King 1990, O'Brien *et al.* 1995), may not be appropriate. In fact, the concave height – DBH curve from cross-sectional data may be the result of two ecological facts: 1) the smaller suppressed trees in the stand are relatively thinner than the dominant trees (Assmann 1970) and 2) faced with competition, tree height growth relative to diameter growth is higher for the suppressed trees (Sjolte-Jørgensen 1967, Dahms 1973, Schmidt et al 1976, Seidal 1984). Although the individual tree height – DBH relationship at the stand level is concave, recent studies have noted that the parameters tend to vary for different stands (Zakrzewski and Bella 1988) and with age (Lappi 1997) thus suggesting that neighborhood effects vary with age and other stand characteristics such as density.

Nevertheless, it is reasonable to conclude that the height – DBH relationship expressed either as a ratio of height to diameter or as the slope of a height – DBH equation is a very important determinant of how the tree grew in the past. It is therefore important that individual tree diameter and height growth be modeled to function in such a way that this unique relationship is maintained and reflect competition, tree vigor and site productivity.

In this chapter, compatible individual tree diameter and height growth functions are developed for the three major boreal species in Alberta namely trembling aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* (Moench) Voss), and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), as system of nonlinear seemingly unrelated regression equations. The relationship between tree height and tree DBH is used as a reflection of the pattern of growth allocation of photosynthate by the individual trees in the stand. It is assumed that there is a definite relationship between the amount of growth allocated to diameter and height in each tree depending on competition and site productivity. The fit statistics of the simultaneous equations are presented and discussed. These models were then coded into the Mixedwood Growth Model (MGM) (Morton and Titus 1984) and tested using both simulated pure species stands of varying initial density and site index, and real permanent sample plot data.

4.2 The Data

The data used in this study came from two sources: Weldwood Canada Ltd and Alberta Land and Forest Division (ALFD). The ALFD data were collected over the past four decades from about 1755 permanent sample plots (PSPs) located throughout the inventory area of the province to provide representative information on forest growth and yield (ALFD 2000). The Weldwood Canada Ltd data, perhaps the largest database in the province covers just over 3000 PSPs, most of which are found in lodgepole pine stands, throughout their forest management agreement area (FMA) located in west-central Alberta. The two datasets were combined to take advantage of the much larger sample size. Also, there were more remeasurements in the present dataset than the previous ones used for calibrating the old version of MGM.

A subset of the combined datasets from the Weldwood and ALFD databases were selected for this study. Selection was based on the availability of information on site index tree measurement, which is relevant to the curve fitting. Since most plots had no site tree information, a significant portion of the data was not suitable for this study. Data from the selected plots were summarized to provide information on individual tree and stand characteristics, which were used as covariates in the model estimation. Since the data were intended to be used for simultaneous equation fits, it was necessary to choose only trees with both diameter and height measurements. Summaries of these variables are provided in Table 4.1. A random selection of 75% of the data for each species was taken for model fitting and the remaining were used 25% for validation testing.

4.3 Model Development

4.3.1 Model specification

Diameter Growth Model

The allometric growth characteristics of individual trees have been used as a basis for modeling the relationship between the sizes or weight of individual component of trees (e.g. Huxley and Teissier 1936, Parde 1980, Monserud and Marshall 1999). In forestry, it has been long recognized that there is proportionality between the relative increments of two parts (X and Y) of a plant (Monserud and Marshall 1999):

4.1 $$\frac{dY}{Y} = b\left(\frac{dX}{X}\right)$$

Integrating Equation 4.1 with respect to X gives the allometric relationship:

4.2 $$Y = \eta * X^{b},$$

Equation 4.2 is widely used in forestry particularly for modeling the individual tree height-DBH relationship. Equation 4.2 is very flexible and can be used to model the relationship between tree height and tree DBH with either one of the variables being the dependent variable. The flexibility of Equation 4.2 stems from the ability of the model to take any form depending on the value of the parameter b. In most applications of this function for modeling tree height – DBH relationships, the parameter b is less than 1 (often closer to 0.6) when height is used as a dependent variable. This has been interpreted to mean that tree height growth declines faster than diameter growth. A special case is when b=1 making the relationship between Y and X a straight line that passes through the origin (X=0, Y=0) with the slope η. Ek (1971) showed that this special case is true for open grown red pine. Sievänen (1993) also used this assumption and added that the slope is a function of tree's ability to put on diameter growth.

As in Ek (1971), it is assumed that for every tree in the stand, the DBH is linearly related to the height H. However, unlike Ek (1971), the slope parameter η, is not assumed to be constant but allowed to vary with changes in tree and stand conditions. Replacing X and Y in equation 4.2 with height and respectively DBH, a partial derivative of DBH with respect to height (H) produces:

$$[4.3] \quad \frac{\partial(DBH)}{\partial(H)} = \eta$$

It was therefore assumed that: 1) Equation 4.3 holds for annual diameter growth DI and height growth HI (e.g. Sievänen 1993), 2) the proportionality constant η, is a function of competition and 3) the proportionality constant is higher for dominant and/or open grown trees than for suppressed trees and/or trees in high density stands. As the status of a tree in the stand approaches that of an open grown tree, η is assumed to approach an unknown constant value, ***Θ***, typical for each species and site index. These assumptions are made to ensure that the concave relationship between individual tree height and DBH projected by the model is maintained.

The proportionality constant could be greater than or less than one depending on the individual tree's relative competition. Sievänen (1993) used the ratio of height to crown base to total tree height as a measure of an individual tree's ability to put on growth in diameter. This ratio is 0 when height to crown base is 0 implying proportionately more diameter growth than height growth. In this study, crown information was not available and so a surrogate variable had to be found. The modified basal area in trees with larger DBH than the subject tree (AGGR) was used as an index of the tree's ability to put on diameter growth, with the assumption that the ratio of height to crown base to total height is highly correlated with stand density and the tree social rank. This may be expressed as:

$$[4.4] \qquad AGGR_{(k)} = \frac{1}{SF} * \sum_{DBH_j > DBH_i}^{n_j} \lambda * P * BA_j .$$

where SF is the spacing factor, λ is an expansion factor for converting the tree basal area (BA_j) to meters per hectare, DBH_i is the diameter at breast height of the subject tree,

DBH_j is the diameter at breast height of any tree bigger than the subject tree, n_j is the number of trees with diameters larger than the subject tree diameter, subscript k is the species type designation (C for coniferous and D for deciduous) and P is a dummy variable such that if $k = C$ then $P=1$ for every coniferous tree and 0 for every deciduous tree, if $k=D$ then $P=0$ for all coniferous trees and 1 for every deciduous tree bigger than the subject tree.

Basal area in larger trees has been shown to be an effective predictor of individual tree growth (e.g. Stage 1973, Wykoff et al 1982, Wykoff 1990, Yao 1997, Schröder and Gado 1999). Basal area in larger trees accounts for the social status (basal area percentile) of the tree in the stand and competition in the form of stand density (stand basal area). The spacing factor is defined here as average tree spacing in the stand expressed as a percentage of the stand dominant height. Analytically, the basal areas in large coniferous and deciduous trees ($AGGR_C$ and $AGGR_D$) are similar to the competition index presented in Schröder and Gado (1999), which accounts for the basal area percentile of the subject tree and the spacing factor. Computing the competition by species groups will help account for differences in composition, interaction and the possible differential resource utilization capacities when they occur in mixedwoods (see Man and Lieffers 1999).

Using stand basal area as a non-spatial competition index is very popular in forest growth and yield. This variable incorporates both the total number and size of trees in the stand (Clutter et al. 1983). This way, stand basal area effectively accounts for competition in the stand. More importantly, the modified basal area in larger trees accounts for one-sided competition only. Individual tree diameter growth relative to height growth seems to be affected by both one-sided and two-sided competition. Individual tree DBH was used as a variable for overall tree size and can act as a surrogate variable for tree age. However, because tree size is also dependent on other variables, the correlation between tree size and age may not be strong. Moreover, tree size is indirectly accounted for in the variables AGGR, $AGGR_C$ and $AGGR_D$. Therefore, tree DBH was not a very strong predictor of diameter growth relative to height growth.

Equations 4.5 to 4.7 present the final functions selected for η for lodgepole pine, aspen and white spruce respectively:

$$[4.5] \quad \eta_{PL} = \beta_0 + \beta_1 \ln(1 + DBH) + \beta_2 \ln(1 + AGGR) + \beta_4 \ln(1 + AGGR_D) + \beta_5 \ln(1 + BA)$$

$$[4.6] \quad \eta_{AW} = \beta_0 * Exp(-(\beta_3 AGGR_C + \beta_4 AGGR_D))$$

$$[4.7] \quad \eta_{SW} = \beta_0 * Exp(-(\beta_1 DBH + \beta_2 AGGR + \beta_4 AGGR_D + \beta_5 BA))$$

where $\beta_0 - \beta_5$ are parameters to be estimated for each equation.

Height Growth Model

In developing the height growth model the potential – modifier approach was used (Mitchell 1975, Golser and Hasenauer 1997, Hasenauer and Kindermann 2002). Each individual tree (j) in the stand was given a height growth adjustment A_j, which is related to the potential height increment (PHI) and the achieved height growth (HI_j) attained by tree (j) by;

$$[4.8] \quad HI_j = A_j * PHI\,.$$

Potential height growth is the growth rate of the site index tree given by the site curve. This was calculated by first assuming that the site trees in the data will grow according to the site curve. With this assumption and using the height (H_P) and age (A_p) measurements of the site trees in the data and the permanent sample plot measurement interval lengths (L), future site tree heights (H_F) were computed using the site index curves developed by (Huang 1997a, 1997b). Site tree height growth rates are computed as $(H_f - H_p)/L$.

The application of the concept of site index to mixed species multi-aged stands is difficult and sometimes controversial. I anticipated this controversy for the concept of potential height growth as defined in this work. This is partly because individual tree growth rates vary with age and competition. Juvenile trees have relatively faster growth rates than mature trees. In uneven aged stands, this could be a potential set back to the use of site curve as the potential height growth and can seriously affect the quality of model fit. For instance, the use of the site curve to predict the potential height growth presupposes that trees of the same species in the stand are of the same age, which is often not the case in uneven-aged stands. The regeneration of white spruce under an aspen overstory for instance, may produce multiple age cohorts of white spruce trees. In that case, potential height growth calculated based on a site tree selected from a particular age cohort might not necessarily be the maximum for trees of the same species, which are in much younger or older age cohorts. Moreover, selecting a tree that was previously suppressed as the site index tree may be erroneous.

Ek and Monserud (1974) fitted a simple function to predict the potential height growth given an individual tree's height and site index. In their work, the potential height growth of a tree was defined as the growth rate of a site tree of the same height and growing on the same site as the subject tree. A similar idea was used in this study to help improve the quality of fit of the height growth model. A simple function relating the computed site tree growth rates to the current site index tree height, species site index and some measure of crowding (for lodgepole pine only) was used for estimating the potential height growth for each species. The function represented by Equation 4.9 was found to be suitable for describing the height growth pattern of a typical tree. This function provides a reasonable description of tree height growth as described in most forestry literature (e.g. Barnes et al. 1998, Oliver and Larson 1996). Tree height growth is slow at first when the tree is young and too small to accumulate energy for rapid terminal growth, but becomes more rapid as more energy becomes available for terminal shoot growth as tree size and the amount of foliage increases. Height growth eventually reaches a maximum and begins to decline as a result of a number of factors. These factors may include stress due to the difficulty in conducting water and mineral salts through the entire length of the tree height to the leaves as tree height increases (Ryan and Yoder 1997), increased maintenance cost or the achievement of crown size limit permitted by the growing space (Oliver and Larson 1996, page 60).

$$[4.9] \quad PHI = \alpha_1 \exp(\alpha_2 SI + \alpha_3 CR) H_p^{\alpha_4} \exp\left(-\alpha_5 H_p^{\,2}\right)$$

In Equation 4.9, PHI is the potential height growth, α_1 – α_5 are parameters to be estimated, H_p is the site tree height, SI is the site index and CR is an index for measuring crowding in the stand, determined as (TH^2Dens)/10000 (Cieszewski and Bella1993). CR is based on Czarnowski (1961) stand dynamics theory. The variable TH is species top or dominant height and DENS is the number of stems per hectare. The factor 10000 is for converting the square meters in TH^2 into hectares. CR is used to account for the effects of density on dominant height growth in lodgepole pine (Mitchell and Goudie 1980, Cieszewski and Bella1993). CR has the property of remaining fairly constant at limiting stand density (Czarnowski 1961). This way, it is possible to compare crowding in stands of different ages. To predict tree potential height growth, the site tree height (H_p) in Equation 4.9 is replaced by the subject tree height.

Finally a suitable function for A_j was defined, which allowed trees to grow in height close to their potential until competition is relatively intense forcing a substantial reduction in height growth rate (e.g. see Mitchell 1975, Mitchell and Goudie 1980, Arney 1985, Hann and Ritchie 1988). Equations 4.10, 4.11 and 4.12 were selected for modeling the height growth adjustment (A_j) for lodgepole pine, aspen and white spruce respectively.

$$[4.10] \quad A_{jPL} = \theta_0 + \theta_1 * SPHT^{0.5} + \exp\left(-\left(\theta_2 GGR^2\right)\right) + \theta_5 \ln(QMDR) + \theta_6 \ln(CR)$$

$$[4.11] \quad A_{jAW} = Exp\left(-\left(\theta_1 * SPHT^2 + \theta_2 GGR^2 + \theta_3 CGGR + \theta_5 QMDR + \theta_6 CR\right)\right)$$

$$[4.12] \quad A_{jSW} = Exp\left(-\left(\theta_3 CGGR^2 + \theta_4 DGGR^2 + \theta_6 CR\right)\right)$$

where GGR, CGGR and DGGR are the total, coniferous and deciduous basal area in trees larger than the subject tree, respectively; QMDR is the ratio of species quadratic mean DBH to the stand quadratic mean DBH; SPHT is the average height of all trees of the species in the stand; and CR is as defined before. As usual, θ_1 - θ_6 are parameters to be estimated separately for each equation. Although, the concept of CR is more of pure species phenomenon and its usage in height growth modeling was more suitable for lodgepole pine, which typically occurs in pure stands, the variable was also found to be a useful predictor for aspen and white spruce height growth.

Variable selection for the height growth model was based on three premises: (1) size hierarchies are more of the result of one-sided competition for light where larger trees tend to overtop smaller ones (Weiner 1990, Nilsson 1994, Newton and Jolliffe 1998), (2) in mixed stands, the relative size of the species may determine the amount of inter-specific competition affecting trees of that species; and (3) the number, size and species type of the trees larger than the subject trees are important in determining the amount of side shading and to a very large extent, the amount of leaf area a tree can carry (Oliver and Larson 1996).

4.3.2 Parameter Estimation

The parameters of Equation 4.9 were first estimated with site tree height growth data using the MODEL procedure in the SAS/ETS software (SAS Institute Inc. 1988) and used as inputs for fitting the height growth model in a system of nonlinear simultaneous equations for each species. A preliminary analysis showed that the differences in terms of height growth parameter estimates, between using the potential height growth computed from the site curve and those predicted by the model in Equation 4.9, were only marginal for lodgepole pine. Therefore, Equation 4.9 was not used in the subsequent analysis for lodgepole pine. For each species, the diameter and height growth models were considered as a system rather than as individual equations for two reasons:

(1) the dependent variable η in Equations 4.5 to 4.7 is a ratio of diameter growth to height growth, which is also part of the dependent variable Aj in Equations 4.10 to 4.12 and so, there is some evidence of cross equation dependency; and

(2) the random errors for the diameter and height growth models can be correlated. A major reason to expect a cross-equation correlation of the error terms in this study is the fact that each DI - HI pair comes from the same tree and are therefore interdependent.

Applying nonlinear ordinary least squares to estimate the parameters of simultaneous equations will produce biased and inconsistent parameter estimates. This is called simultaneous equation bias (Judge *et al.* 1982). A method to remove simultaneous equation bias is to replace the endogenous variables on the right-hand side of the equations with predicted values that are uncorrelated with the error terms. These predicted values could be obtained through a preliminary, or "first stage," instrumental variable regression. Instrumental variables, which are uncorrelated with the error term, are used as regressors to model the predicted values. The parameter estimates are obtained by a second stage regression using the predicted values as the regressors. This process is called two-stage least squares. Nonlinear two-stage least squares is one of several instrumental variables methods available in the MODEL procedure of SAS/ETS (SAS Institute Inc. 1988) to handle simultaneous equation bias. However, in this study, because the ratio of diameter growth to height growth was used as the dependent variable with no HI appearing on the right hand side of the diameter growth model, simultaneous equation bias was not considered a problem and was thus ignored.

In its place, generalized least squares method that takes the cross-equation correlations of the error terms into account was used (SAS Institute Inc. 1988). With the assumption that the equations are not simultaneous (no dependent regressors), seemingly unrelated regression (SUR) was used (Zellner 1962). The SUR method requires an estimate of the cross-equation error covariance matrix, Σ with dimension (m x m), where m is the number of individual models in the system. The usual approach is to first fit the equations using OLS, compute an estimate $\hat{\Sigma}$ from the OLS residuals as:

$$[2.13] \quad \hat{\Sigma} = \frac{1}{n} \mathrm{E}'\mathrm{E}$$

where **E** is a matrix (n x m) of model residuals with each column representing a vector of residuals from an individual model, and n is the sample size. Based on $\hat{\Sigma}$ the SUR estimation is performed by minimizing:

$$[2.14] \quad Z(\theta) = [y - f(\theta)]' \left(\Sigma^{-1} \otimes I\right) [y - f(\theta)]$$

where y is the vector of observed responses, *I* is a unit matrix (m x m) and $\otimes$ denotes the Kronecker product. The assumption here is that Σ is a symmetric positive definite matrix (m x m).

The MODEL procedure of the SAS/ETS software was used to fit the system as nonlinear SUR equations. Several different functions of tree DBH and height were used iteratively for correcting for heteroskedasticity in the DI and HI models respectively. For HI, the inverse of tree height was enough, while for DI, ($DBH^{-0.2}$) was enough to substantially decrease the problem. The coefficients of first order autocorrelation for the diameter and height growth models in the system represented by ρ_1 and ρ_2 respectively, were first estimated and incorporated into the generalized variance-covariance matrix and the model parameters re-estimated. The process was repeated until convergence was achieved. The procedure is summarized below from Huang (1997a):

1. Estimate model parameters $\boldsymbol{\theta}$ by nonlinear least squares and estimate the predicted growth $g_i = f(Xi, \boldsymbol{\theta})$ and the residual $r_i = G_i - f(Xi, \boldsymbol{\theta})$; where G_i is the observed diameter or height growth rate;

2. Estimate the coefficient of autocorrelation ρ by fitting $r_i = \rho^* r_{i-1} + d_i$;

3. Re-estimate $\boldsymbol{\theta}$ by fitting the equation: $G_i - \rho G_{(i-1)} = f(X_i, \boldsymbol{\theta}) - \rho f(X_{(i-1)}, \boldsymbol{\theta}) + d_i$ and estimate new r_i's and G_i's as in step 1; where $G_{(i-1)}$ and $X_{(i-1)}$ are the tree diameter or height growth and the set of explanatory variables for the previous growth period;

4. Repeat steps 2 and 3 until the parameters converge.

The parameter estimates of the diameter and height growth models for lodgepole pine, aspen and white spruce, with and without first order autocorrelation adjustment are given in Tables 4.3, 4.4 and 4.5 respectively

4.3.3 Model Validation

Model validation was carried out in two ways; at the individual tree level using approximately 25% of each species individual tree growth data and at the stand level using stand level projections from MGM with the new model coefficients. At the individual tree level, each diameter or height growth function was used to predict individual tree growth. The mean difference between predicted and observed growth (increments) was computed for each model as the model prediction error. The student t-test was used to test the hypothesis that these mean differences are not statistically significantly different from 0.

At the stand level, PSP data independent of the data used for model fitting were used as initial yield conditions and the future yields projected using revised version of MGM incorporating the new diameter and height growth models reported in this study. New mortality models reported in Yang (2002) were used together with the new diameter and height growth models in the revised. Predicted stand level variables were compared with the observed data for possible bias. Stand level averages compared were mean height and DBH, average basal area per hectare and total stand volume per hectare. This test was done using protocols developed by Bokalo (1994). In this protocol, if a PSP was made up of 75% or more of a particular species by basal area, the plot was assumed to be a pure stand of that species. Stands in which no particular species dominates were further classified as coniferous or deciduous. If the plot was made up of 75% or more of coniferous species by basal area, it was considered a coniferous stand. On the other hand, if it was made up of 75% or more deciduous by basal area, it was considered deciduous. To avoid the confounding effects of other species, the results of only the pure species stands are reported here. Predicted stand level yields using MGM were compared with real observed yields to determine the presence of any prediction bias.

Simulated stands of both pure and mixed species were established and projected until stand break-up to determine if the projected trends were consistent with expected trends of stand dynamics. The simulated stands were developed by Craig Fandern[2] (personal

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[2] Craig Farnden is a consulting forester with an office in Prince George, British Columbia.

communication). Projection results (graphs) for pure lodgepole pine, site index 18 m at breast height age 50, with varying initial densities from 600 to 70,000 stems per hectare and an aspen – white spruce mixture (spruce site index 16 and aspen site index 18) were chosen for illustrations. In the aspen – spruce stand, the initial density for spruce was fixed at 1000 stems while that of aspen varied from 600 to 40,000 stems per hectare. All yield estimates were based on total for the stand and did incorporate any merchantability standards. Model settings were based on the Upper Foothills Natural sub-regional settings.

4.4 Results and Discussion

4.4.1 Parameter Estimates and Fit Statistics

The parameter estimates and asymptotic fit statistics for the diameter and height growth models show that the variables included in the model are reasonable predictors of growth with only a few exceptions (Tables 3, 4 and 5). At a significance level of 5%, basal area in larger coniferous trees (CGGR) was not statistically significant in explaining aspen height growth. The variable $AGGR_D$ was not significant for explaining the variation in lodgepole pine diameter relative to height growth, and the crowding index (CR) was not significant in explaining variation in white spruce height growth. However, these variables were left in their respective models for two reasons: (1) the emphasis was more on model calibration (parameter estimation) than hypothesis testing of the significance of parameters; and (2) it made sense ecologically to leave these variables in the respective models. For instance, the coniferous component in aspen stands which is typically white spruce, may have a significant impact on aspen growth for two reasons: (1) the much denser crowns may intercept rain water and thus reduce aspen growth even if they are in the understory; and (2) the much denser crowns of spruce can effectively intercept light and subsequently reduce aspen growth. It is therefore misleading to exclude the coniferous component in aspen model predictions based on only fit statistics.

The standard errors of estimate for the models were substantially higher than similar statistics for the separate diameter and height growth models in Chapters 2 and 3 of this thesis. This might be because there were more variables in those models to explain the sources of variation, resulting in relatively smaller standard errors. The coefficients of determination were also relatively lower in this study than in Chapters 2 and 3, most probably for the same reason. Nevertheless, the simultaneous equation fit was thought to be preferable for two reasons: 1) the statistical advantage of lower standard error and higher coefficients of determination may not necessarily translate into better prediction; and 2) the restriction placed on the system by forcing diameter growth to depend on height growth is desirable to achieve compatibility between the two component growth models as shall be discussed in the section that follows.

The coefficients of basal area in larger trees (CGGR and DGGR) and modified basal area in larger trees ($AGGR_C$ and $AGGR_D$) are slightly smaller for white spruces than aspen and lodgepole pine. Although the differences in the parameter estimates my not be statistically significant, the effect of these difference on MGM performance in mixed stands of aspen and spruce is quite profound, as shall be illustrated in the next section. It is ecologically reasonable to expect these results since white spruce is relatively more tolerant than aspen and lodgepole pine. White spruce generally has very dense crowns, which can intercept and effectively utilize the smallest amount of light that may pass through the canopy (Man and Lieffers 1999). As expected, the coefficients for the basal area in larger coniferous trees are relatively bigger, reflecting a bigger influence on aspen and white spruce growth than the deciduous basal area in larger trees, except for diameter growth of aspen (Table 4.3). Ecological advantages associated with white spruce growing in the understory of aspen discussed in Man and Lieffers (1999) suggest that the effect of deciduous tree competition on spruce growth will be less severe than coniferous tree competition. The presence of larger coniferous trees with dense crowns may intercept more light and water than deciduous trees, resulting in a decrease in the subject tree growth rate and perhaps death. It is therefore reasonable to expect relatively bigger coefficients for coniferous basal area in larger trees.

4.4.2 Model Validation and Verification

The student t-test was used to test the hypothesis that the average prediction bias of the individual tree diameter and height growth models was zero. The test indicated that the average prediction biases for both the height and diameter growth models were not statistically significantly different from 0 for all the three species. This was assumed to be an indication that the diameter and height growth models are unbiased at the individual tree level. Not much emphasis was placed on this level of testing for the variability in individual tree growth data was quite substantial and may have prevented a more sensitive test.

Predicted stand level yields using MGM were compared with observed yields. Figure 4.1 presents the graphs of predicted stand level yield plotted (on the vertical axis) against the observed yields for lodgepole pine. Graphs of the other species are presented in Appendices 1 and 2. The relative scatter of the individual points (plots) about the diagonal line in each graph is taken as an indication of the presence or absences of bias and whether the bias is constant or varies with the magnitude of yield under study. If the plots are evenly scattered about the diagonal line, then the predictions are unbiased. Based on this interpretation, all yield estimates are fairly unbiased.

The type of mortality in the stand can affect stand level yield estimates. The mortality function determines the number of surviving trees in the stand. If the mortality function is such that smaller trees have relatively higher mortality rates, stand level averages will tend to go up even though individual tree growth rates may not be too high. At stand break-up, accelerated mortality in bigger trees or the in-growth of trees into smaller DBH classes may lower the stand average tree size and indeed stand basal area and volume. The mortality models used in MGM are from Yang (2002). A maximum basal area–average size limit is set for each species above which individual tree mortality is increased to force the density-average size combination of the stand to fall below the maximum. In addition, a set of constraining factors were setup such that: 1) a maximum basal area is set such that as this basal area is approached, more trees are killed to force the stand basal area to fall below this limit and 2) an average size limit is set such that when the species' average size exceeds the size limit of that species, trees of the species larger than the species average size are subjected to increased mortality (Yang 2002). These factors were put in place to control excessive volume growth associated with the low mortality rates predicted and to ensure that stands, particularly of lodgepole pine and aspen, break-up when they attain certain ages or average size.

As a consequence, increased mortality rates in bigger trees at stand break-up may result in lower mean DBH, stand basal area, and ultimately, lower stand volume predictions than the actual observed values. It is suspected that the slight positive bias (lower predictions) in the higher yield stands was a result of increased mortality of bigger trees in these stands, although this was not investigated further.

The simulation results of the pure pine stands are presented in Figure 4.2. Only stand density, stand volume, stand average DBH and stand average heights plotted against stand age are presented. These graphs look quite reasonable from a stand dynamics point of view, although there are certain irregularities particularly in the high-density classes. In general, stand volume and basal area all increase with increasing initial stand density, while average DBH and height decrease with increasing initial density. When these results are contrasted with those of the older version of MGM (Figure 4.3), it is clear that the new model gives much more reasonable yields (volume and basal area) when extrapolations are made to project higher density stands. The new model also gives ecologically reasonable height and DBH trajectories.

The results for lodgepole pine height may be disputable in that the general expectation may be that the effect of repression in higher initial density stands would result in a bigger reduction in stand average height, thereby leading to a much wider spread in the mean height curves than what is observed in Figure 4.2. Although, a theoretically more stable stand density measure, the crowding index based on the modified Czarnowski's (1961) theory of stand dynamics of height growth density relationships (Cieszewski and Bella 1993) used to model the effect of initial stand density on potential height growth of lodgepole pine did not appear to be effective. One possible reason could be that the stand average dominant co-dominant height – density combinations projected by the model for all the initial density classes gave crowding indices that are quite similar, leading to less variation in potential height growth rates and hence mean height. This can happen when the mortality trend is such that stands are not allowed to reach the maximum density-dominant height combinations permitted by the site carrying capacity so as to cause a reduction in growth potential. Another reason for the failure could be that the data used for model fitting were from low to medium-density stands (Table 4.1b). Thus, the effect of excessive density on dominant height growth might not have been captured. Nevertheless, not much emphasis was placed on getting stands to respond in terms of dominant height growth to varying initial density, which is a rather complicated issue. However, the advantage of using site index as the potential height growth in this study may be exploited to accommodate the effect of repression by developing an appropriate site index adjustment function or factors for excessively higher density stands.

The dynamics of mixedwood stands, particularly the aspen-white spruce mixture, seem to be adequately predicted by the model (see Figure 4.4). The graphs show that increasing aspen density reduces the final average DBH and height only slightly. However, it does appear from Figure 4.4 that increasing aspen density results in an initial decline in spruce basal area and volume growth, which eventually picks up after the aspen break-up. Although an additional increase in aspen density beyond 12,000 stems per hectare does not appear to have any additional effect on spruce basal area and volume growth, more simulations are needed to confirm this. Mixedwood stand dynamics will dictate that aspen yield will peak at about age 80 years and begin to decline thereafter due to stand break-up, allowing growing space for the understory spruce to takeover. These dynamics seem to be clearly illustrated by Figure 4.4.

All simulation graphs look reasonable from a stand dynamics point of view, although there are certain limitations of this model. One obvious limitation is the lack of data in the higher densities. Forecasts for these densities are mere extrapolations, since the models were fitted using only low to medium density stands. A lot of uncertainty exists for these density classes and care must be taken when interpreting the results or making inference from the results.

4.5 Summary and Conclusions

In this study, compatible individual tree diameter and height growth models were developed for lodgepole pine, aspen and white spruce. The diameter growth models were based on the fact that tree growth in height and diameter is allometric, which results in a fixed linear relationship between diameter and height growth rates. This view is supported by the literature in ecology and ecophysiology. This biological relationship and the fact that both diameter and height growth components in MGM are interdependent suggest the need for the two component models to be formulated and estimated as a system of compatible equations. The height growth models were based on the potential - modifier approach, using the site curves to define the maximum height growth. The use of a site curve to define the maximum height growth was useful particularly for lodgepole to help deal with issues related to stand repression and differences in site productivity between regenerated stands and stands of fire origin. More work is needed to test this part and calibrate site index adjustment.

Model parameters were estimated using seemingly unrelated regression (SUR) techniques. Nearly all parameter estimates were statistically significant at the 5% probability level. Validation at both the individual tree and stand levels indicate that these models were unbiased and produced ecologically reasonable predictions of stand level yields. This approach achieved two things: 1) making individual tree diameter growth depend on height growth ensured that tree diameter and height projections were compatible with each other; and 2) some control on individual tree height growth was extend to individual tree diameter growth too. These results were reflected in the MGM simulation output given in the accompanying figures.

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Table 4-1a. Summary statistics of tree and stand characteristics for trembling aspen

	Mean	Minimum	Maximum
Tree height (m)	17.89	2.40	29.60
Tree DBH (cm)	21.19	1.60	56.40
Species composition (relative basal area)	0.73	0.04	0.99
Height growth (m/yr)	0.17	0.00	0.83
DBH growth (cm/yr)	0.23	0.00	1.16
Modified basal area in larger trees (m^2/ha)	0.87	0.00	4.24
Modified basal area in larger conifer trees (m^2/ha)	0.19	0.00	3.07
Modified basal area in larger deciduous trees (m^2/ha)	0.68	0.00	3.05
Basal area in larger trees (m^2/ha)	14.97	0.00	50.78
Basal area in larger coniferous trees (m^2/ha)	3.02	0.00	38.72
Basal area in larger deciduous trees (m^2/ha)	11.95	0.00	42.93
Number of stems per hectare	1516.97	232.33	5000.00
Potential height growth (m/yr)	0.22	0.05	0.47
Crowding index	33.88	1.72	97.38
Stand basal area (m^2/ha)	29.50	1.86	59.14

Table 4-1b. Summary statistics of tree and stand characteristics for lodgepole pine

	Mean	Minimum	Maximum
Tree height (m)	15.56	1.30	30.80
Tree DBH (cm)	16.86	0.50	51.70
Species composition (relative basal area)	0.88	0.04	1.00
Height growth (m/yr)	0.14	0.00	0.69
DBH growth (cm/yr)	0.13	0.00	1.18
Modified basal area in larger trees (m^2/ha)	1.26	0.00	5.86
Modified basal area in larger conifer trees (m^2/ha)	1.23	0.00	5.86
Modified basal area in larger deciduous trees (m^2/ha)	0.02	0.00	1.95
Basal area in larger trees (m^2/ha)	18.02	0.00	57.68
Basal area in larger coniferous trees (m^2/ha)	17.68	0.00	57.68
Basal area in larger deciduous trees (m^2/ha)	0.34	0.00	27.85
Number of stems per hectare	2103.84	24.71	11336.63
Potential height growth (m/yr)	0.20	0.04	0.75
Crowding index	46.94	0.02	162.44
Stand basal area (m^2/ha)	35.99	0.06	63.71

Table 4-1c. Summary statistics of tree and stand characteristics for white spruce

	Mean	Minimum	Maximum
Tree height (m)	18.95	1.60	35.80
Tree DBH (cm)	24.19	1.30	65.90
Species composition (relative basal area)	0.64	0.02	1.00
Height growth (m/yr)	0.16	0.00	0.78
DBH growth (cm/yr)	0.21	0.00	1.20
Modified basal area in larger trees (m^2/ha)	1.46	0.00	8.39
Modified basal area in larger conifer trees (m^2/ha)	1.11	0.00	5.40
Modified basal area in larger deciduous trees (m^2/ha)	0.35	0.00	4.97
Basal area in larger trees (m^2/ha)	22.15	0.00	70.84
Basal area in larger coniferous trees (m^2/ha)	17.07	0.00	55.99
Basal area in larger deciduous trees (m^2/ha)	5.09	0.00	47.40
Number of stems per hectare	1275.59	86.49	5975.31
Potential height growth (m/yr)	0.21	0.04	0.54
Crowding index	42.64	0.25	243.51
Stand basal area (m^2/ha)	38.51	0.48	87.91

Table 4-2. Parameter estimates of lodgepole pine diameter and height growth models

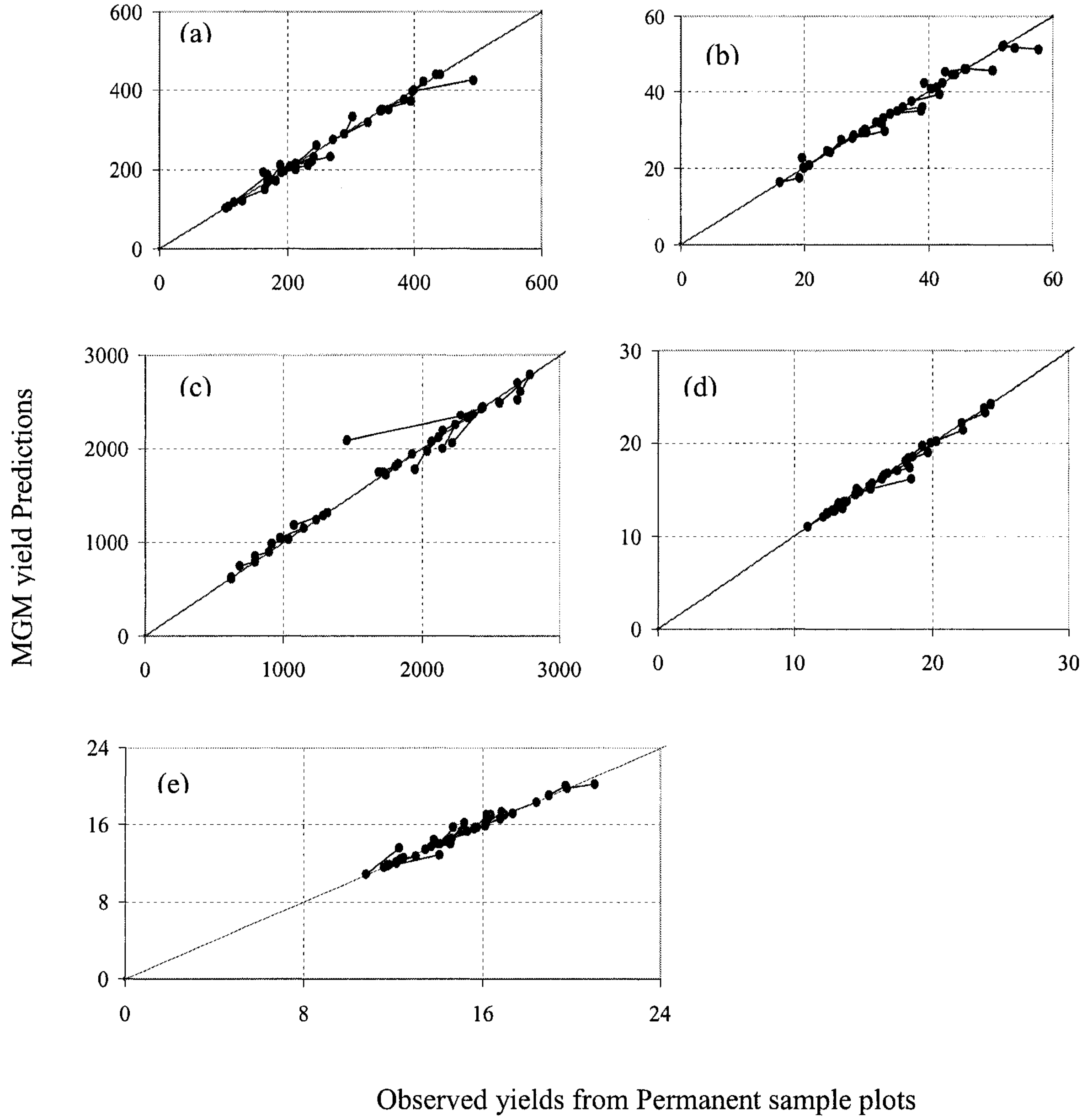
Parameter	Estimate	Std Error	t Value	Pr > |t|	RMSE	DW
(A) Diameter Growth Model (Equation 4.5)						
(1) Fit without Adjusting for Autocorrelation						
β_0	1.262793	0.16060	7.86	<0.0001	1.9321	1.8720
β_1	0.157894	0.07200	2.19	0.0425		
β_2	-0.529840	0.06960	-7.62	<0.0001		
β_4	1.089192	0.23200	4.69	0.0221		
β_5	-0.140420	0.06130	-2.29	<0.0001		
(2) Fit Adjusting for autocorrelation						
β_0	1.306883	0.17440	7.50	<0.0001	1.9546	1.9910
β_1	0.118405	0.04880	2.43	0.0183		
β_2	-0.554530	0.07450	-7.44	<0.0001		
β_4	1.131392	0.25220	4.49	0.0865		
β_5	-0.113690	0.06630	-1.71	<0.0001		
ρ	0.066321	0.00943	7.03	<0.0001		
(B) Height Growth Model (Equation 4.10)						
(1) Fit without Adjusting for Autocorrelation						
θ_0	0.094027	0.038400	2.45	0.0144	0.5046	1.3050
θ_1	-0.071490	0.014100	-5.06	<0.0001		
θ_2	0.000103	0.000013	8.20	<0.0001		
θ_5	0.742249	0.063000	11.79	<0.0001		
θ_6	-0.030110	0.009150	-3.29	0.0010		
(2) Fit Adjusting for Autocorrelation						
θ_0	0.142098	0.052900	2.69	0.0072	0.4730	2.1830
θ_1	-0.068880	0.019100	-3.61	0.0003		
θ_2	0.000102	0.000013	8.04	<0.0001		
θ_5	0.637897	0.082700	7.71	<0.0001		
θ_6	-0.045210	0.012000	-3.75	0.0002		
ρ	0.349460	0.009530	36.69	<0.0001		

Table 4-3. Parameter estimates of aspen diameter and height growth models

Parameter	Estimate	Std Err	t Value	Pr > |t|	RMSE	DW
(A) Diameter Growth Model (Equation 4.6)						
(1) Fit without Adjusting for Autocorrelation						
β_0	2.330053	0.143500	16.24	<0.0001	2.5024	1.5469
β_3	0.025520	0.008600	2.97	0.0082		
β_4	0.294882	0.079800	3.69	0.0002		
(2) Fit Adjusting for Autocorrelation						
β_0	2.295738	0.164100	13.99	<0.0001	2.4417	2.0420
β_3	0.115630	0.052000	2.22	0.0447		
β_4	0.258351	0.087900	2.94	0.0034		
ρ	0.221171	0.029400	7.51	<0.0001		
(B) Height Growth Model (Equation 4.11)						
(1) Fit without Adjusting for Autocorrelation						
θ_1	-0.002710	0.000174	-15.63	<0.0001	1.4981	1.6263
θ_2	0.000146	0.000072	2.01	0.0444		
θ_3	0.001199	0.000449	2.67	0.0077		
θ_5	0.387435	0.093900	4.12	<0.0001		
θ_6	0.006991	0.001630	4.30	<0.0001		
(2) Fit Adjusting for Autocorrelation						
θ_1	-0.002520	0.000198	-12.73	<0.0001	1.4709	2.0317
θ_2	0.000260	0.000085	3.04	0.0024		
θ_3	0.000687	0.000411	1.67	0.0945		
θ_5	0.268910	0.107600	2.50	0.0126		
θ_6	0.007304	0.001890	3.86	0.0001		
ρ	0.202594	0.028200	7.18	<0.0001		

Table 4-4. Parameter estimates of white spruce diameter and height growth

Parameter	Estimate	Std Error	t Value	Pr > |t|	RMSE	DW
(A) Diameter Growth Model (Equation 4.7)						
(1) Fit without Adjusting for Autocorrelation						
β_0	1.824633	0.10540	17.88	<0.0001	1.5255	1.8706
β_1	-0.008030	0.00187	-4.30	<0.0001		
β_2	0.091785	0.02940	2.43	0.0150		
β_4	-0.239080	0.04040	-5.92	<0.0001		
β_5	0.011113	0.00196	5.68	<0.0001		
(2) Fit Adjusting for Autocorrelation						
β_0	1.825006	0.11220	16.69	<0.0001	1.5180	2.0074
β_1	-0.003388	0.00196	-4.19	<0.0001		
β_2	0.091785	0.03060	2.25	0.0248		
β_4	-0.213220	0.04300	-5.41	<0.0001		
β_5	0.010862	0.00205	5.42	<0.0001		
ρ	0.057607	0.01640	3.51	0.0005		
(B) Height Growth Model (Equation 4.12)						
(1) Fit without Adjusting for Autocorrelation						
θ_3	0.000270	0.000024	11.17	<0.0001	0.0982	1.6990
θ_4	0.000587	0.000587	8.14	<0.0001		
θ_6	0.000091	0.000380	0.24	0.8111		
(2) Fit Adjusting for Autocorrelation						
θ_3	0.000242	0.000023	10.53	<0.0001	0.0975	2.0277
θ_4	0.000572	0.000067	8.53	<0.0001		
θ_6	0.000432	0.000356	1.21	0.2247		
ρ	0.155699	0.017100	9.08	<0.0001		



[3]Figure 4-1. MGM yield predictions against observed yields for lodgepole pine; (a) total stand volume (m^3/ha), (b) stand basal area (m^2/ha), (c) number of stems per ha, (d) quadratic mean DBH (cm) and (e) average height (m).

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[3] Points are connected to indicate the projections of individual PSP yields from initial values. Points on the diagonal line are the initial (observed) yield values and points off diagonal are the MGM projected yield estimates.

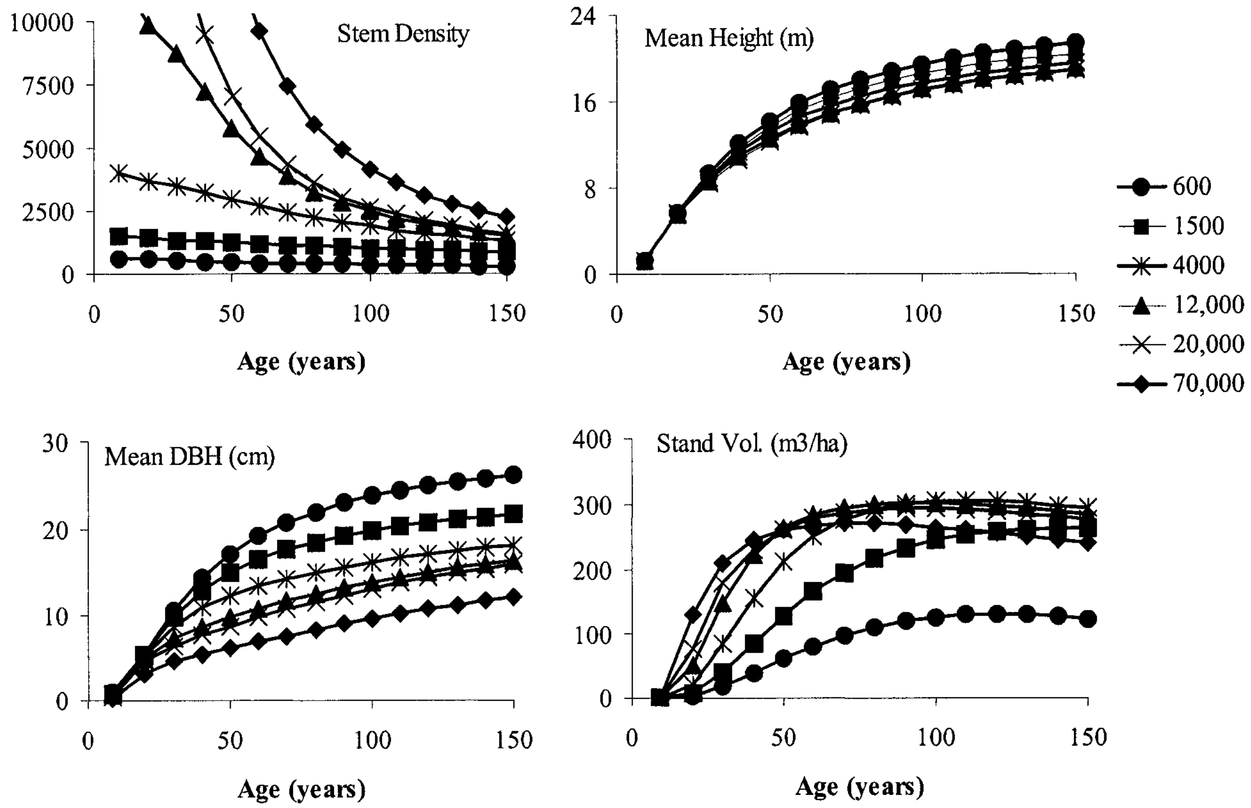

Figure 4-2. Simulation results for pure lodgepole pine stands of varying initial stand densities for site index 18m.

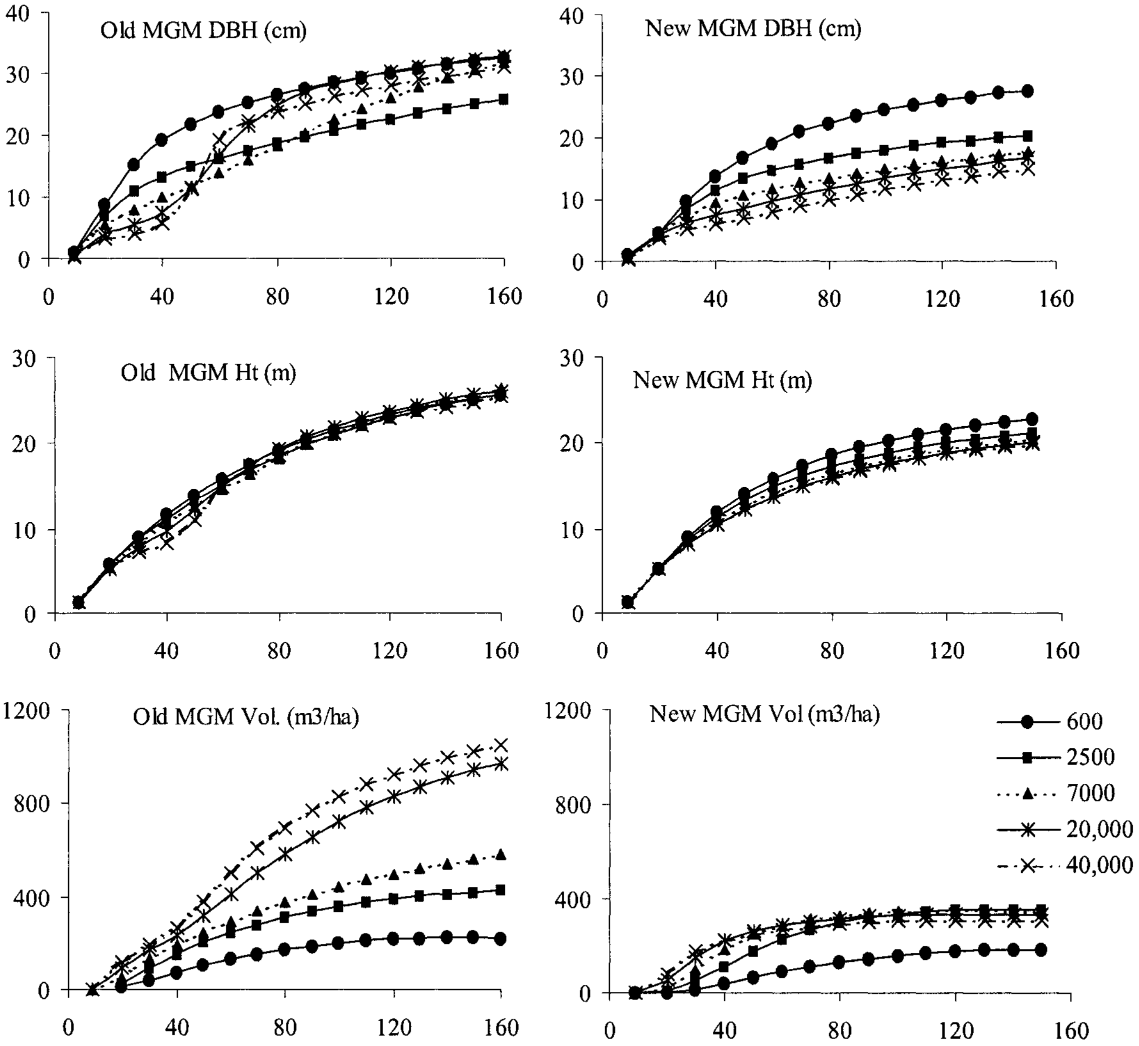

Figure 4-3. Comparison the new MGM with the old MGM for pure lodgepole pine stands (site index 18 m at breast height age 50) for varying initial stem densities.

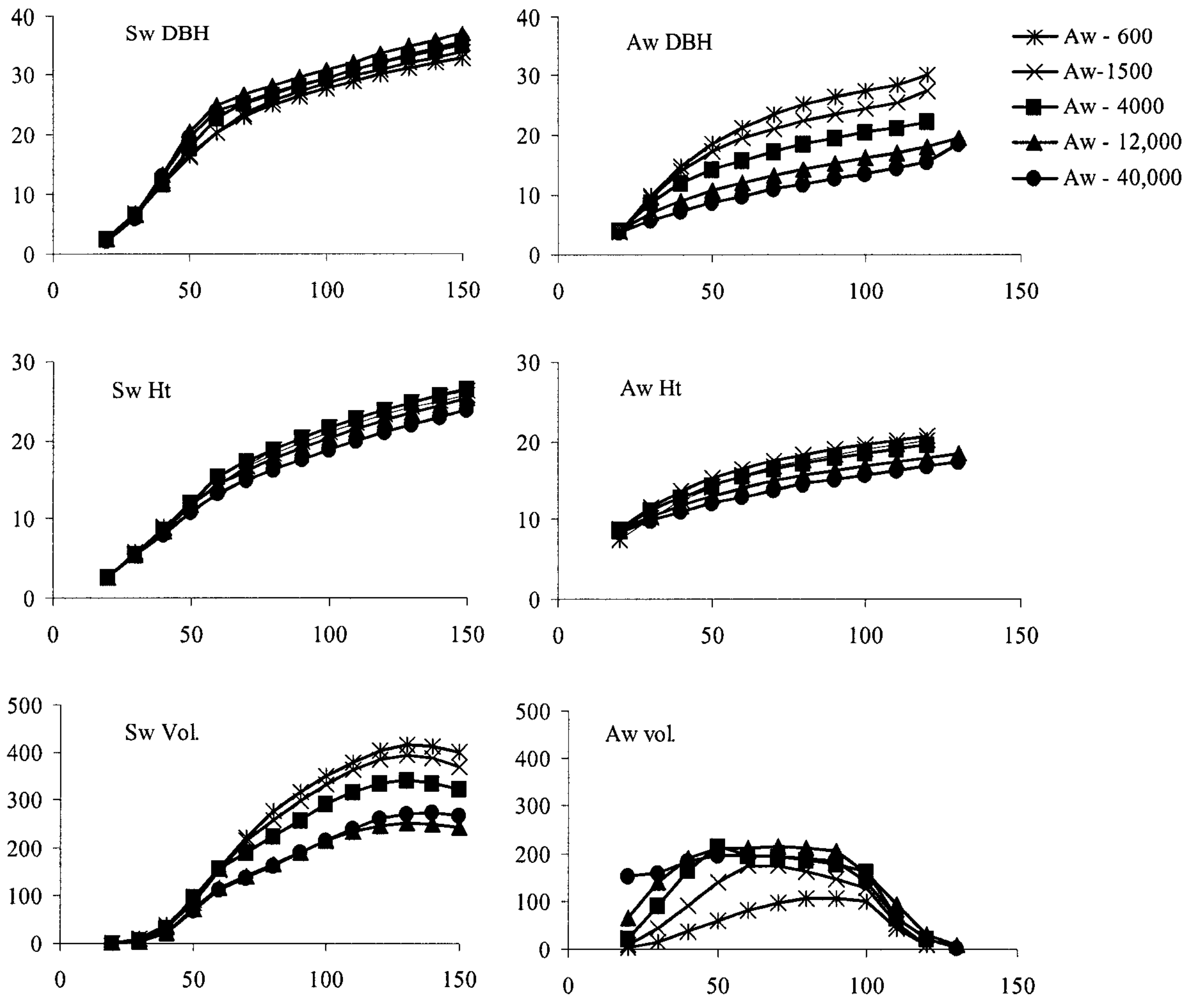

Figure 4-4. Simulation results for aspen (Aw) and white spruce (Sw) in mixed stands of varying initial aspen stem density; white spruce density is fixed at 1000.

Chapter 5. Discussions and Conclusions

Individual tree diameter and height growth models are the major components of most individual tree level stand growth simulation models. The estimation of these models poses a significant challenge to forest growth and yield modeling. The diversity in approaches, methodologies and philosophies is testimony to the complexity of modeling individual tree growth. The complexity stems from the fact that the growth and survival of individual trees are determined by extraordinarily complex interactions of various factors in the forest ecosystem.

Although complex, there are some general trends in tree growth based on which mathematical functions are fitted to relate tree growth with other factors or variables. In the long term, it is agreed that tree growth will increase as the tree age increases, but only up to a point and then begin to decline asymptotically to 0 (e.g. Oliver and Larson 1996, Barnes et al. 1998). In the short run, tree growth rate responds to short-term environmental shocks, such as short-term changes in microclimatic conditions, increase growing space due to mortality of other trees, or incidence of some natural hazards. These short-term shocks which are usually manifested in stand level characteristics tend to correlate well with individual tree growth and thus have more control on individual tree growth predictions than age related variables. The consequence is that traditional empirical modeling approaches which uses typical permanent sample plot data have often failed to satisfactorily model the hypothesized long term individual tree growth trajectories. Alternative approaches that emphasize the art and science and less statistics in model building are needed.

The focus of this thesis was on fitting individual tree diameter and height growth models for the three major species in the boreal forests of Alberta namely, trembling aspen, white spruce, and lodgepole pine. The study focus on four key issues: (1) selecting variables that are of ecological significance in predicting tree growth, (2) selecting appropriate functional relationships between tree growth and the ecological variables, (3) accounting for the effect of the interaction between species types and (4) ensuring compatibility between tree diameter and height growth. Although these issues are not new to forestry literature, they remain the most important problems in individual tree growth models. These issues in my opinion are very important determinants of the performance of individual tree growth and yield models.

Chapter 2, which sets the tone of the thesis, was designed to combine the use of additional and more representative sample data to improve diameter growth predictions. However, because individual tree annual growth rates are typically "noisy", the expected growth patterns did not match the fitted models for two of the species (aspen and lodgepole pine). This problem was related to the lack of balance in the data used for the model fitting across all variables. The model is therefore expected to perform satisfactorily in conditions that were represented well and poorly in others not well represented. However, it is possible using our understanding of the system to develop ways of ensuring that the model's performance is acceptable across a broader range of conditions. In forestry, it is common to estimate average bias for some stand conditions for adjusting the model output for those stand conditions.

Chapter 3 explored the use of the potential modifier approach for modeling individual tree height growth. The site curve was used as the maximum height growth. Although site index is technically only applicable to even-aged pure species stands, its use in multi-species uneven aged stands is widespread (e.g. Huang and Titus 1993). However, some studies in uneven-aged stands have avoided the use of site index (e.g. Schröder et al. 2002). As pointed out by Sjolte-Jørgensen (1967), tree height growth is relatively stable with varying density (competition). Therefore, it was assumed that tree height growth is affected by one-sided competition and the species' relative size in the stand. It was further assumed that the severity of the one-sided competition, measured by basal area in larger trees, depends on the species type. Two species groups were identified (coniferous and deciduous). This approach produced fit statistics similar to other studies involving boreal ecosystems (e.g., Huang 1992, Huang and Titus 1999, Yao 1997).

In my view, this approach to modeling individual tree height growth is attractive for several reasons. The most important of all is parsimony; the model is simple and biologically interpretable. Most studies modeling individual tree growth have included many variables to help explain variation in growth. Because individual tree growth is highly varied, including many variables to account for the larger number of factors that affect tree growth seems attractive. However, including many variables can cause problems both statistically and in model application. Statistically, multicolinearity may well become a problem. As pointed out in Chapter 1, forestry variables are correlated with each other and the effect of this correlation will be exacerbated when too many of them are included in the model as predictors. Including many variables in a model can sometimes be problematic in its application particularly for biological systems. Problems may arise from the complex interactions of these variables, which may adversely affect the prediction quality of the model.

Fitting individual tree diameter and height growth models as a system is desirable for the sake of achieving compatibility in model prediction behaviour. The rates at which trees grow in diameter relative to height determines the allometry between tree diameter and height at any given time. In other words, the present ratio of a tree's height to its diameter is a function of how the tree grew in the past in diameter and height. The allometric relationship between height and DBH has significant ecological interpretations and is largely a reflection of the conditions in the stand. Indeed, some researchers have used tree height-DBH ratios as measures of competition (e.g., Opio et al. 1999). The pipe-model theory (Shinozaki et al. 1964 a, b), used extensively in some mechanistic growth and yield model derivations (e.g. Mäkelä 1986, Valentine 1985, 1988, 1990, Valentine et al. 1997), uses some form of allometry in tree growth. The pipe model theory implies that the cross-sectional sapwood area should correlate with the leaf area of the tree. The amount of leaf area is also related to competition (Monserud and Marshall 1999). In crowded stands, competition for growing space may restrict the crown sizes, leaf area of the trees and by implication, the sapwood area. These allometric relationships in individual trees underscore the need for compatibility between tree diameter and height growth projections.

Chapter 4 of the thesis presents a compatible system of individual tree diameter and height growth models for each of the three species. The central argument is that tree diameter growth (DI) is in direct proportion with height growth (HI) and the proportionality constant is a function of competition and tree vigour at anytime in the life of the tree or stand. This way, a connection is established between diameter and height growth, such that diameter growth relative to height growth changes with changes in competition and tree vigour. Validation tests at both the individual tree and stand levels, and short- and long-term projections, showed that the model performance was reasonable.

The new Mixedwood Growth Model (MGM) calibrated in this thesis is indeed a much-improved model than the older version. The thesis contributes to the management of lodgepole pine and the associated species and provides a foundation for better prediction of lodgepole pine height growth. However, the success of the methodology used in this study is highly dependent on suitably calibrated site index curves. Using the site curve to define the upper limit to tree height growth and fitting tree height and diameter growth curves as a system of equations will be successful in improving model performance if the site curves are calibrated in such a way as to reflect the true productivity of the site for the species in question. Various attempts have been made in this regard to link site indices to biophysical properties of the site (e.g. Ung et al. 2001). In Alberta, attempts have also been made at fitting site curves by natural subregions (Huang et al 1997a, b) and ecosite types (Richard C. Yang, Research Scientist, Canadian Forest Service, Northern Forestry Centre, Edmonton, personal communication). These efforts will greatly improve the use of site index for predicting site productivity.

Linking tree diameter growth, tree height growth and species site index is particularly useful for modeling lodgepole pine growth, in that changes in site index with repressed or regenerated stands can be accommodated by applying an appropriate site index adjustment. However, more research is needed to determine the relationship between repression and changes in site index.

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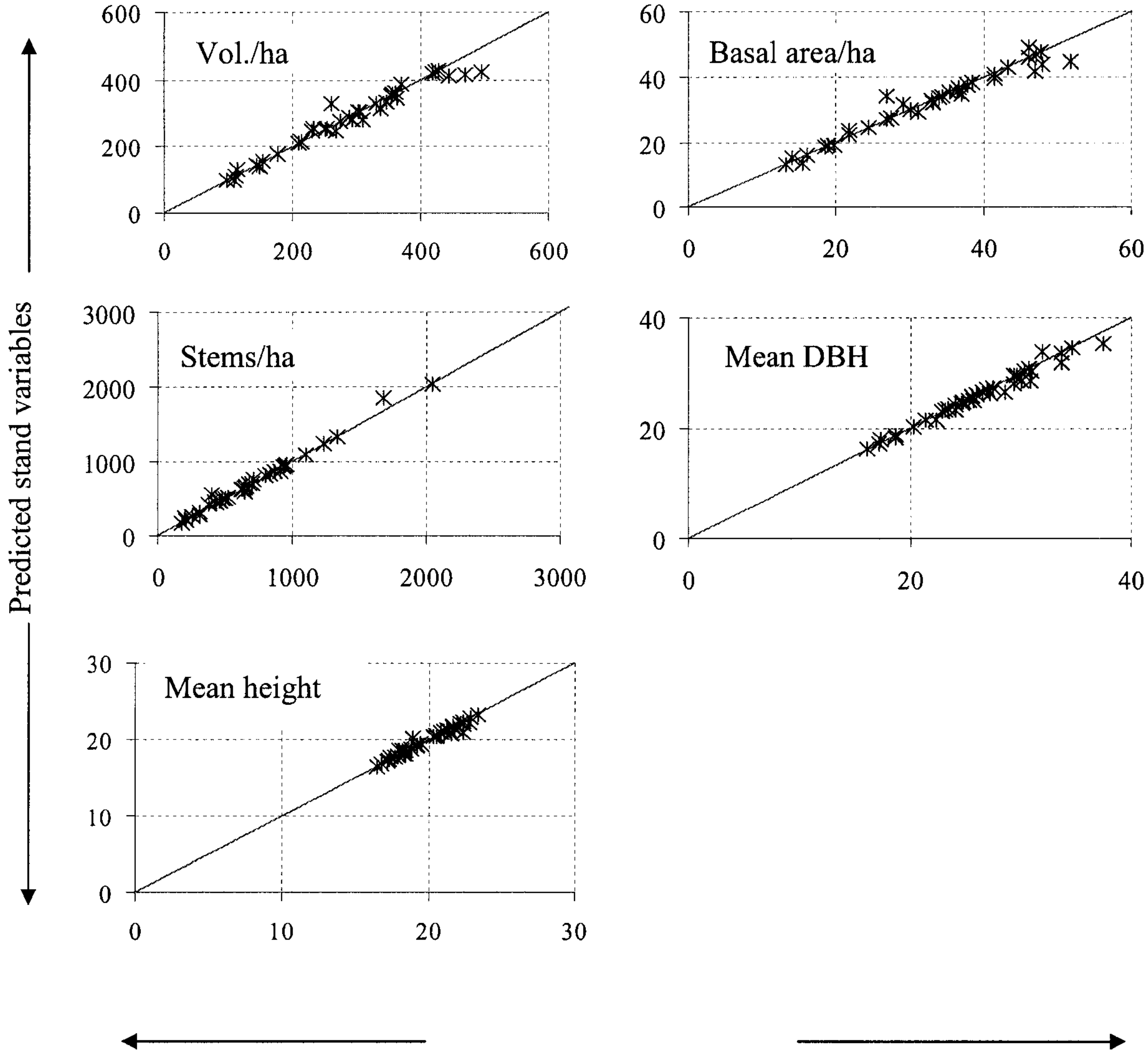
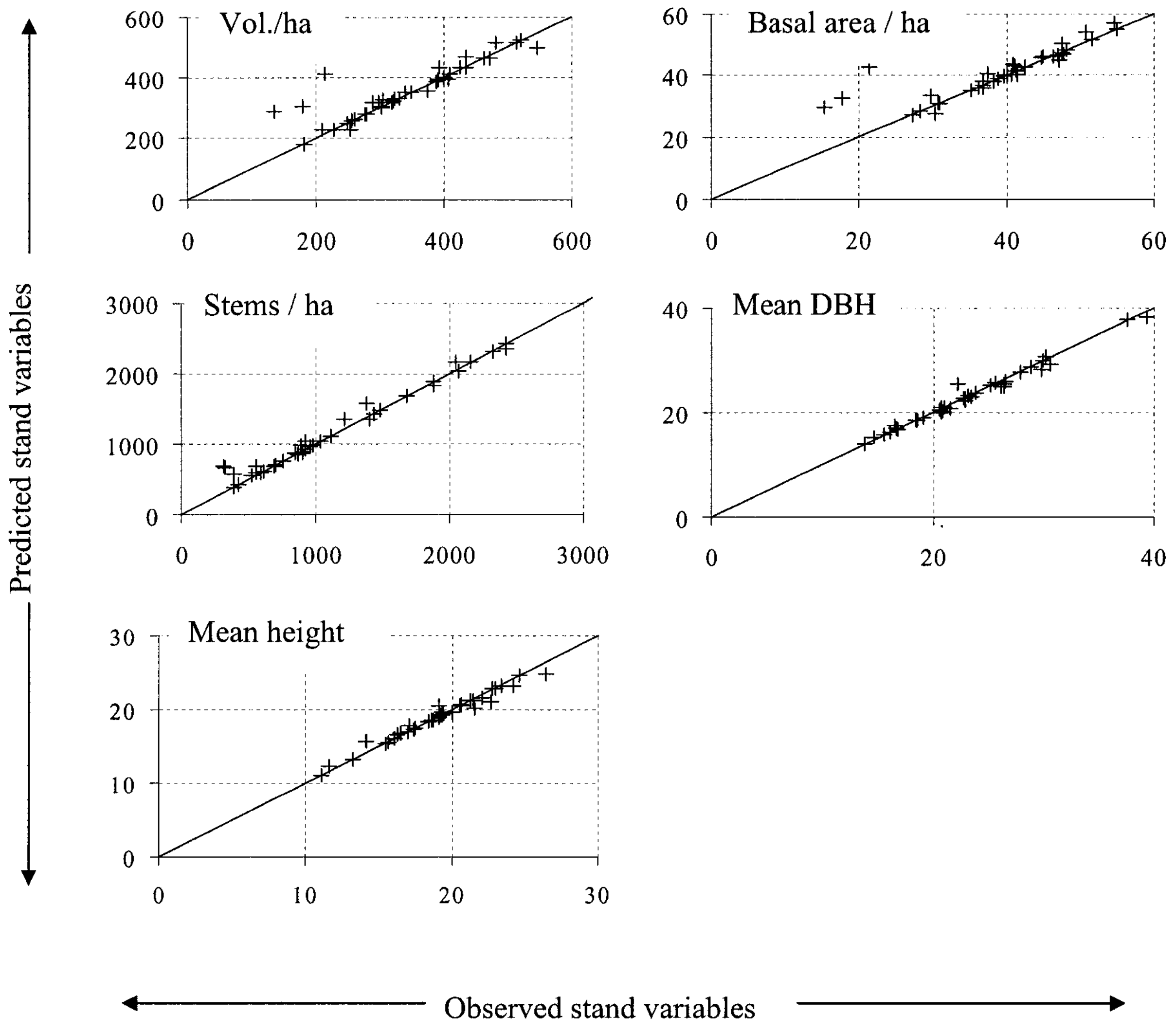
Appendix 1: MGM yield prediction for trembling aspen stands



Appendix 2: MGM yield predictions for white spruce stands



Appendix 3: SAS code for fitting empirical individual tree diameter growth models

```
*LIBNAME IN 'E:\THESIS\NEW BRIEFCASE\CHAPTER 2';
*OPTION LS=132 PS=120 FORMDLIM='-';
*DATA PL; SET IN.CH2_PL;
```

Calculating additional variables needed for model fitting;

```
*AGGR=GGR/(100*SF);
*CAGGR=CGGR/(100*SF);
*DAGGR=DGGR/(100*SF);
*SPD=SPQDBH/MQDBH;

*RUN;
```

Model fitting with no auto correlation adjustment;

```
*PROC MODEL DATA=PL MAXITER=1000 NDEC=9 OUTPARMS =
IN.PL_NAUTO;
*PARM A1=0.295651 A2=0.012392 A3=0.02 A4=5 A5=5 A6=0.3 A7=0.0002;
*A=A1*EXP(A2*SI+A3*BAHA);
*B=A*EXP(-(A4*CAGGR+A5*DAGGR));
*DIN=B*DBH**A6*EXP(-A7*DBH**2);
*FIT DIN/DW COLLIN OUT=NAOMI.PL_RES OUTRESID OUTPREDICT;
*_WEIGHT=DBH**0.2;
*RUN;
*QUIT;
```

Model fitting with autocorrelation adjustment;

```
*PROC MODEL DATA=PL MAXITER=1000 NDEC=9 *OUTPARMS=IN.PL_AUTO;
*PARM A1=0.295651 A2=0.012392 A3=0.02 A4=5 A5=5 A6=0.3 A7=0.0002 R=0.2;
*A=A1*EXP(A2*SI+A3*BAHA);
*B=A*EXP(-(A4*CAGGR+A5*DAGGR));
*PDIN=B*DBH**A6*EXP(-A7*DBH**2);
*DIN=PDIN+R*LAG(DIN-PDIN);
*FIT DIN/DW COLLIN OUT=NAOMI.PL_RES2 OUTRESID OUTPREDICT;
*_WEIGHT=DBH**0.2;
*RUN;
*QUIT;
```

Appendix 4: SAS code for fitting individual tree height growth models

```
*LIBNAME YAL 'G:\THOMPSON\DATA FILES\NEW DATA';
*DATA PL; SET YAL.PINE;
```

Calculating additional variables;

```
*CR=(1/SF)**2;
*SHIN1=0.073654*EXP(0.089323*SI-0.00039*CR)*HT**0.060953*EXP(-
0.002402*HT**2);
*IF CONGGR LT 0 OR CONGGR=. THEN CONGGR=0;
*QMDRATIO=SPQDBH/MQDBH;
*RUN;
*QUIT;
```

Parameter estimation without autocorrelation adjustment;

```
*PROC MODEL DATA=ASPEN OUTPARMS=PARAS METHOD=MARQUARDT
NDEC=12 CONVERGE=0.00000001;
*PARMS B1-B5;
*HTIN=SHIN1*EXP(-(B1*CONGGR**2+B2*DECGGR**2+B3*QMDRATIO**2));
*_WEIGHT=0.0011*EXP(7.0341*PHTIN);
*FIT HTIN /COLLIN DW OUT=PL_RES OUTPREDICT OUTRESID OUTACTUAL;
*RUN;
*QUIT;
```

Parameter estimation with autocorrelation adjustment;

```
*PROC MODEL DATA=ASPEN OUTPARMS=PARAS METHOD=MARQUARDT
NDEC=12 CONVERGE=0.00000001;
*PARMS B1-B5;
*PHTIN=SHIN1*EXP(-(B1*CONGGR**2+B2*DECGGR**2+B3*QMDRATIO**2));
*HTIN=PHTIN+R1*LAG(HTIN-PHTIN);
*_WEIGHT=0.0011*EXP(7.0341*PHTIN);
*FIT HTIN /COLLIN DW OUT=PL_RES OUTPREDICT OUTRESID OUTACTUAL;
*RUN;
*QUIT;
```

Appendix 5: SAS code for fitting a system of seemingly unrelated regression (SUR) models

```
*OPTIONS FORMDLIM='-';
*LIBNAME YAL 'G:\THOMPSON';
*DATA ASPEN; SET YAL.PINE;
```

Calculating additional variables needed for modeling;

```
*CR=(1/SF)**2;
*SHIN1=0.073654*EXP(0.089323*SI-0.00039*CR)*HT**0.060953*EXP(-
0.002402*HT **2);
*AGGR=GGR/(100*SF);
*RATIO=DIN/HTIN;
*RAT=HTIN/SHIN;
*QMDRATIO=SPQDBH/MQDBH;
*CONAGGR=CONGGR/(100*SF);
*DECAGGR=DECGGR/(100*SF);
```

Parameter estimation;

```
*PROC MODEL DATA=ASPEN NDEC=9 OUTPARMS=MIXFN;
*PARMS A0-A4  B0-B4 R1 R2;
*PRAT=A0+A1*SPHT**0.5+EXP(-
(A2*GGR**2))+A3*LOG(QMDRATIO)+A4*LOG(CR);
*RAT=PRAT+R1*LAG(RAT-PRAT);
*PRATIO=A0+A1*LOG(1.0+DBH)+A2*LOG(1.0+AGGR)+A3*LOG(1.0+BAHA)+A4
*LOG(1.0+DECAGGR);
*RATIO=PRATIO+R2*LAG(RATIO-PRATIO);
*FIT RAT RATIO/DW COLLIN ITSUR;
*RUN;
*QUIT;
```

Appendix 6: Sample managed yield curves for pure pine of site index 18 m at base age 50 years, minimum DBH of 9cm, minimum top diameter of 8cm and minimum piece length of 2 m.