INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI

A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor MI 48106-1346 USA
313/761-4700 800/521-0600

UNIVERSITY OF ALBERTA

INGROWTH MODELS AND JUVENILE MIXEDWOOD STAND DYNAMICS

BY

YANGUO QIN ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of **MASTER OF SCIENCE** in Forest Biology and Management.

DEPARTMENT OF RENEWABLE RESOURCES

EDMONTON, ALBERTA
SPRING 1998

0-612-28978-8

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **INGROWTH MODELS AND JUVENILE MIXEDWOOD STAND DYNAMICS** submitted by **YANGUO QIN** in partial fulfillment of the requirements for the degree of **MASTER OF SCIENCE**. in Forest Biology and Management.

Dr. Stephen J. Titus (supervisor)

Dr. Victor J. Lieffers

Dr. Yanhong Wu

Dr. Bruce P. Dancik

December 18, 1997

To my parents

Qin, Tianwen and Zao, Peifen

Abstract

Based on a data set from 937 Alberta Land and Forest Services permanent sample plots, two sets of stand-level, two-stage ingrowth models were developed to predict periodic annual ingrowth for white spruce (Picea glauca (Moench) Voss), trembling aspen (Populus tremuloides Michx), lodgepole pine (Pinus contorta var. latifolia Engelm), and black spruce (Picea mariana (Mill.) Britton) grown in the boreal mixed-species stands in Alberta. One set was developed based on all trees with DBH$\geq$1.1 cm, and another one based on all trees with DBH$\geq$9.1 cm. The first stage predicts the probability of the ingrowth occurrence, and the second stage model predicts the annual amount of ingrowth, given that it is known to occur. Both were modeled as a function of tree diameter at breast height, stand density, species composition, and site productivity. Fitted models are highly significant for all species and the general shape of the response surface is biologically realistic. The results of the Hosmer-Lemeshow goodness-of-fit test on the ingrowth probability models and validation on ingrowth amount models show that the average prediction biases are not significant at the $\alpha = 0.05$ level, indicating that the models appropriately describe the data and perform well when predictions are made.

Modeling juvenile growth of white spruce and aspen in mixedwood is important to advance our understanding of the whole process of mixedwood stand development and to schedule appropriate silvicultural treatment for young stands. The second part of this study evaluated the effects of site productivity and density on white spruce and aspen growth and survival, and presented models for the early growth of planted white spruce and naturally regenerated aspen at the first 5 years after field planting. Using the data from 90 permanent sample plots, the statistical analyses were conducted to discuss site productivity and test density effects on young tree growth and survival rate. It was shown that aspen regeneration density had significant influence, and spruce density effect was negligible, and the differences of growth and survival for both species between high site and median site exist. The fitted models can be used to predict juvenile white spruce and aspen growth and distribution of root collar diameter and height given the tree age, health indicator, stand density, site productivity. The curve-fitting method was to first select an appropriate equation as the base function, and then incorporate other tree and stand level variables such as health indicator, stand density, and site productivity to predict the parameters of the base function, using the parameter prediction method.

Acknowledgments

I would like to thank all the individuals and institutions that made this study possible.

I will be perpetually indebted to Dr. Stephen J. Titus, my supervisor, for his guidance, encouragement, understanding, patience, and continuing support throughout the entire period of my graduate studies at the University of Alberta. Dr. Titus read the manuscripts countless times and provided much needed editorial and technical review. To Dr. Titus, I offer my greatest professional gratitude. It was fortunate for me to have this opportunity to learn from him and work with him.

I would like to gratefully acknowledge the members of my thesis supervisor committee, Dr. Victor J. Lieffers and Dr. Bruce P. Dancik of the Department of Renewable Resources, and Dr. Yanhong Wu of the Department of Mathematical Science, for reviewing the thesis draft and provided constructive criticism and guidance.

This project was supported by the Western Boreal Growth and Yield (WESBOGY) cooperative. The Timber Management Branch of Alberta Land and Forest Service and Daishowa-Marubeni International Ltd. provided the data for this project. Special thanks go to Mr. David J. Morgan and Ms. Teresa Stokes of Alberta Land and Forest Service and Ms. Florance Niemi of Daishowa-Marubeni International Ltd. for providing valuable help and cooperation.

I am grateful to the Department of Renewable Resources, University of Alberta for providing such an excellent learning environment.

Dr. Xiaohong Yao and Dr. Yue Wang, with whom I was blessed as an office mate deserve special commendation for the invaluable assistance they rendered in the area of computer programming and companionship, and for their instantaneous responses to my questions. I want to particularly thank Dr. Shongming Huang, Dr. Zhiming Wang and Dr. Ron J. Hall for their valuable advice and encouragement. I am also thankful to my friends, Mr. John Kornelsen and Mrs. Leona Kornelsen, for their assists and friendship.

On a personal note, I wish to express gratitude to my parents, who instilled in me from a very young age the desire for knowledge and wisdom. My final and most deeply felt gratitude goes to my wife, Qing Lin, my son, Wang Qin, and all my family. Their love and continuing encouragement and support gave me the endurance to see this project through to its completion.

Table of Contents

List of Tables

List of Figures

Chapter 1

Introduction

Ingrowth is defined as the number or volume of trees that periodically grow into the smallest measured size class of a forest stand (Beers 1962). In the data of Alberta Land and Forest Services permanent sample plots (PSP), ingrowth is defined as the number of the new trees growing past the smallest measured diameter, DBH=9.1 cm. The three basic components of stand growth are survivor growth, mortality, and ingrowth (Husch, Miller and Beers 1972, Adams and Ek 1975). There is little empirical information documenting the number or species composition of ingrowth trees for boreal mixedwood stands in Alberta. Ingrowth becomes a problem when the period of prediction is so prolonged, or the growth of individual trees so rapid, that trees of very small size or even which are currently nonexistent will appear in future-stand tables (Spurr 1952). Many models of forest dynamics estimate survivor growth, mortality, and ingrowth separately. Of these, ingrowth estimation has received the least attention, and many forest growth projection systems in widespread use make no provision for estimating ingrowth (Shifley et al. 1993).

The boreal mixedwood association of western Canada is widespread and contains some of the most productive forest lands of the boreal forest (Kabzems et al. 1986; Drew 1988). The most important commercial species are white spruce and aspen. After clearcut harvesting, aspen quickly dominates sites by regenerating from root sprouts (Schier 1981). White spruce is shade tolerant and in natural stands grows slowly in the understory of aspen for 50 or more years before achieving dominance. Yield tables from the Alberta Phase 3 Inventory (Anonymous 1985) show that mixedwood stands outproduce pure stands of either hardwoods or white spruce. The utilization of aspen resource has accelerated in the last decade and it is now of some economic importance (Bella 1975), the development of a spruce understory could be regarded as a means of increasing total site productivity, since its presence may not inhibit aspen production. Pure deciduous stands do not attain the yield benefits of growing shade tolerant conifer in the understory of intolerant hardwoods (Anonymous 1985; Kelty 1989; Burkhart and Tham 1992) nor will pure stands achieve the biodiversity values of mixed stands (Burton et al. 1992). Selection harvesting of aspen, without damaging the spruce, is now possible using new harvesting technology. This, coupled with the potential and ecological advantages of mixtures demands further research on mixed stands. The optimum mix of spruce and aspen is certainly not clear. Efforts to manage mixedwood stands for better stocking and growth of the spruce have been only marginally successful (Drew 1988). Most growth models focus on simulating stand or tree growth after canopy closure when competition among trees is thought significant. Belli and Ek indicated (1988) that most forest growth models developed in the past have dealt exclusively with established stands, while ignoring the regeneration process leading up to successful establishment. While modeling of juvenile growth has not been comparably addressed (Avila 1993), there is a need to model juvenile growth in order to gain a better understanding of the whole process of stand development and for scheduling proper silvicultural treatment for young stands (Zhang et al. 1996).

Therefore, in Alberta boreal mixedwood forests, the following two questions need to be addressed:

(1) What are the relationships between ingrowth and site and stand conditions? What factors affect ingrowth? What is the pattern of ingrowth process? Ingrowth is difficulty to predict in the mixedwood stands due to its complexity and variability. However, it is an essential component in any growth and yield model system. A well-behaved ingrowth model for the four major Alberta's species trees is desirable.

(2) How do the juvenile trees grow in mixedwood stands under different species density combinations with the passage of time? Are the growth and survival of these juvenile trees affected by age, site quality and density? What is the trend of individual tree growth in juvenile stands in terms of age, site quality and density? What are distributions of aspen root collar diameter and height? During the last several decades, extensive natural stands have been harvested and replaced by stands with naturally regenerated aspen and planted spruce in western Canada. Therefore, our understanding of the regenerated juvenile mixedwood stand dynamic becomes increasingly important. The evaluation of the effects of site productivity and density on white spruce and aspen growth and survival in juvenile stand is expected, and based on this, a juvenile stand growth model is presented for the early growth of planted white spruce and naturally regenerated aspen at the first 5 years after field planting.

Based on the questions above, the two primary objectives of this study are: (1) to develop a stand-level ingrowth model for the four major Alberta's species trees; (2) to evaluate the effects of site productivity and density on growth and survival of planted white spruce and naturally regenerated aspen, and to develop a model for the early growth of both species, in regenerated juvenile mixedwood stands at the first 5 years after field planting.

To meet the first objective, a two-stage approach was used. Modelling or data analysis of a two-state system is frequently inappropriately done with a single model or analysis. Hamilton and Brickell (1983) indicated that data drawn from two-state system is most effectively dealt with by separate but related models or analysis - a two-stage model. One of the difficulties in modelling ingrowth is the great variability in ingrowth. Much of the variability associated with ingrowth is due to the fact that during any period some ingrowth may or may not occur, and that if the data are partitioned into a two-state system, the ability to predict the amount of ingrowth is greatly enhanced. With a two-stage approach, the first equation estimates the probability that some ingrowth will occur, usually with a logistic function with presence (or absence) of ingrowth as the response variable. The second stage is a conditional function to predict the amount of ingrowth, given that ingrowth is known to occur, and can be estimated using ordinary linear regression (Vanclay 1992) or nonlinear regression. The effects of stand density, species composition, and site productivity on ingrowth process were evaluated. This analysis was based on the permanent sample plot data collected by Alberta Land and Forest Services (Alberta Forest Services 1994).

To meet the second objective, the effects of site productivity and density on growth and survival of white spruce and aspen were evaluated, and models for the early growth of planted white spruce and naturally regenerated aspen were also presented. The model expressed tree height and root collar diameter as a function of tree age, damage agents, stand density, and site quality. To exhibit the aspen size structure of the newly regenerated stands, height and root collar diameter distributions at 1, 2, 3, 4, and 5 years after harvesting were simulated. Using an appropriately selected unimodal-shaped base function, and the method of parameter prediction used by Clutter et al. (1983), the distribution model was constructed as a function of aspen density and average height or root collar diameter.

Evaluation of predictions made by a simulation model is essential before forest managers can rely on predictions to examine implications and consequences of forest policy options and management strategies. Model validation is very important in terms of detecting faults and limitations, and avoiding unreliable predictions. For each component relationship developed in this study, due to the limited amount of data, model validation was not adequately discussed.

This thesis is written in a paper-format with each chapter describing a separate part of the research. Chapter 2 develops two sets of stand-level, two-stage ingrowth models for the major tree species in Alberta mixedwood stands. Chapter 3 analyzes the effects of site productivity and density on the growth and survival of spruce and aspen, and develops a model for the early growth of both species, and summarizes the aspen height and root collar diameter distributions at 1, 2, 3, 4, and 5 years after harvesting, in regenerated juvenile mixedwood stands. Chapter 4 provides the general discussion and conclusion.

References

Adams, D.M. and Ek, A.R. 1975. Derivation of optimal management guides for individual stands. P.132-147 in System analysis and forest resource management. Meadows, J.C., B.B. Bare, K.D. Ware, C. Row (eds). Society of American Foresters, Bethesda, MD.

Alberta Environmental Protection. 1994. A Permanent Sample Plot Field Procedures Manual. Forest Inventory Section, Land and Forest Service, Alberta Environmental Protection, Edmonton, Alberta.

Anonymous. 1985. Alberta phase 3 forest inventory: yield tables for unmanaged stands. Alberta Energy and Natural Resources, Edmonton, Alberta, ENR Rep. 60a.

Avila, O.B. 1993. Modelling growth dynamics of juvenile loblolly pine plantations. Ph.D. Dissertation, Virginia Polytechnic Institute and State University.

Beers, T.W. 1962. Components of forest growth. J. For., 60:245-248.

Bella, I.E. 1975. Growth-density relations in young aspen sucker stands. Environment Canada, Canadian Forestry Service, Northern Forestry Research Centre, Edmonton, Alberta, Inf. Rep. NOR-X-124. 12p.

Belli, K.L. and Ek, A.R. 1988. Growth and survival modeling for planted conifers in the Great Lakes Region. For. Sci. 34(2): 458-473.

Burkhart, H.E. and A. Tham. 1992. Prediction from growth and yield models of the performance of mixed species stands. pp.21-34. *In* The ecology of mixed species stands. M.G.R. Cannell, D.C. Malcolm, and P.A. Robertson (Eds.). Blackwell Scientific, London.

Drew, J.J. 1988. Managing white spruce in Alberta's mixedwood forest: the dilemma. In J.K. Samoil (Ed.) Management and utilization of northern mixedwood. Forestry Canada Inf. Rep. NOR-X-296. Pp. 35-40.

Clutter, R.G., Fortson, J.C., Pienaar, L.V., Brister, G.H., and Beiley, R.L. 1983. Timber management: a quantitative approach. John wiley & sons.

Hamilton, D.A. and Brickell, J. E. 1983. Modeling methods for a two-state system with continuous responses. Can. J. For. Res. 13:1117-1121.

Husch, B., Miller, C.I. and Beers, T.W. 1972. Forest mensuration. 2nd edition. Ronald Press, New York, N.Y.

Kabzems, A., Kosawan, A.L., and Harris, W.C. 1986. Mixedwood section in an ecological perspective: Saskatchewan. Can. For. Serv. and Sask. Parks Renew. Res., For. Div. Tech. Bull. 8, Second Edition.

Kelty, M.J. 1989. Productivity of New England hemlock/hardwood stands as affected by species composition and canopy structure. For. Ecol. Manage. 28: 237-257.

Schier, G.A. 1981. Physiological research on adventitious shoot development in aspen roots. U.S.D.A. For. Serv. Gen. Tech. Rep. INT-107.

Shifley, S.R., Ek, A.R. and Burk, T.E. 1993. A generalized methodology for estimating forest ingrowth at multiple threshold diameters. Forest Science, 39:776-798.

Shifley, S.R. 1990. Analysis and modeling of patterns of forest ingrowth in the North Central United State. Ph.D. Diss., Univ. of Minnesota, St. paul. 178 p.

Spurr S.H. 1952. Forest inventory. The Ronald Press Company. New York.

Vanclay J.K. 1992. Modelling regeneration and recruitment in a tropical forest. Can. J. For. Res. 22:1235-1248.

Zhang, S., Burkhart, H.E., and Amateis, R.L. 1996. Modeling individual tree growth for juvenile loblolly pine plantations. For. Ecol. Manage. 89: 157-172.

Chapter 2

Ingrowth models for the major species in Alberta

2.1 Introduction

The three components of stand growth are survivor growth, mortality, and ingrowth (Husch, Miller and Beers 1972, Adams and Ek 1975). Ingrowth is defined as the number or volume of trees that periodically grow into the smallest measured size class of a forest stand (Beers 1962). It is standard practice to measure only trees that are larger than some minimum (threshold) size, usually a minimum breast height diameter (DBH). As trees in small size classes tend to have low survival rates, are costly to measure, and are of little or no commercial value, the ingrowth threshold is generally set at the minimum merchantable size or the largest size possible without overlooking information necessary for forest management decisionmaking (Shifley 1990). In the data of Alberta Land and Forest Services permanent sample plots (PSP), ingrowth is defined as the number of the new trees growing past the smallest measured diameter, DBH=9.1 cm.

Many models of forest dynamics estimate survivor growth, mortality, and ingrowth separately. Of these, ingrowth estimation has received the least attention, and many forest growth projection systems in widespread use make no provision for estimating ingrowth (Shifley et al. 1993). Vanclay (1994) indicated that even though many plantation growth models disregard any ingrowth, the assumption, that ingrowth for the models for uneven-aged forests is negligible or will not influence short term estimates of yield, is unsatisfactory for longer simulations of natural forests, as ingrowth may contribute substantially to future stand basal area and thus influence growth and yield forecasts. Consequently, application of forest growth projection systems must be restricted to situations where ingrowth is presumed to be unimportant or situations where users are willing to accept the unknown element of error resulting from failure to account for ingrowth (Shifley 1990).

Ingrowth becomes a problem when the period of prediction is so prolonged, or the growth of individual trees so rapid, that trees of very small size or even which are currently nonexistent will appear in the future stand table (Spurr 1952). In ponderosa pine, as in other forest types, an important factor affecting board foot growth is the number of small trees that grow into merchantable size during the growth period (Davis 1966). Working in uneven-aged Appalachian hardwoods, Buell (1945) has presented a method of growth estimation based on the diameter distribution of the stand. By means of multiple regression equations, the net growth in board feet per tree per year for any diameter class was determined as a combination of (1) growth of surviving trees, (2) mortality of trees dying during the growth estimation period, and (3) growth of trees entering the diameter class during the period--the ingrowth.

Shifley (1990) stated that from a broad perspective, the problem of forecasting ingrowth is a problem of forecasting small tree dynamics based upon limited information about the forest overstory. Husch et al. (1972) and Shifley (1990) indicated that ingrowth in one remeasurement interval may contribute fifty percent or more of the total cubic foot volume growth, and that ingrowth is variable from one interval to another, so the contribution of ingrowth to the change in volume or value of a stand depends upon the species, threshold DBH, the stand history, and the stage of stand development.

Based on a data set from 937 Alberta Land and Forest Services permanent sample plots, two sets of stand-level, two-stage ingrowth models were developed in this study for white spruce (Picea glauca (Moench) Voss), trembling aspen (Populus tremuloides Michx), and lodgepole pine (Pinus contorta var. latifolia Engelm), and black spruce (Picea mariana (Mill.) Britton) grown in the boreal mixed-species stands in Alberta. The relationships are compatible with individual-tree-based forest growth projection systems. One set was developed based on all trees with DBH≥1.1 cm, and another one based on all trees with DBH≥9.1 cm. The first stage model predicts the probability of the ingrowth occurrence, and the second stage model predicts the annual amount of ingrowth, given that it is known to occur. Both were modeled as a function of stand average tree diameter at breast height, stand density, species composition, and site productivity.

2.2 Ingrowth models

McTague and Stansfield (1994) thought that the modeling of ingrowth is a difficult task, and past effects of directly modelling ingrowth or the instantaneous change in ingrowth (Ek 1974, Moser 1972, Hann 1980, Hyink and Moser 1983, Lynch and Moser 1986) have not explained a high percentage of variation, and some of the ingrowth models contain predictor variables that are well correlated with ingrowth but fall short as causal mechanisms of ingrowth.

Vanclay (1992) suggested two approaches to predict ingrowth, static approaches and dynamic approaches. Static approaches predict a constant amount of ingrowth each year irrespective of stand condition, whereas dynamic approaches respond to stand condition, predicting ingrowth as a function of stand density, composition and other parameters.

McTague and Stansfield (1994) developed a system of algebraic difference equations for projecting number of pole trees, survivor number of merchantable trees, and survivor basal area. In their models, the ingrowth component is obtained indirectly as the arithmetic difference of two difference projection equations, ingrowth trees are then classified by species with a simple ratio of frequency by species and a habitat series code.

Moser (1972, 1974) and Ek (1974) predicted the periodic number of ingrowth trees per acre in northern hardwood stands as a function of the number of trees and/or basal area per acre of trees larger than the ingrowth threshold (the factors of site and cultural treatments were not considered). They found that number of ingrowth trees increased as the number of trees per acre increased, as the basal area per acre decreased, and the mean size of trees in the stand decreased. Shifley et al. (1982) obtained similar results for elm-ash-cottonwood stands in Indiana. Hann (1980) developed an ingrowth model based on site index and on basal area of trees above a 3-inch DBH ingrowth threshold. Burk (1978) developed a model to predict ingrowth for Lake States aspen, and the dependent variable in his model was the number of ingrowth trees expressed as a percentage of number of trees larger than the 5-inch threshold diameter. Hyink and Moser's (1983) diameter distribution model applied to uneven-aged northern hardwoods included a submodel to forecast the number of ingrowth trees per unit area as a function of the number and the sum of diameter per acre of all trees larger than the 7-inch DBH ingrowth threshold.

The Prognosis model (Ferguson et al. 1986) and NORM model (Vanclay 1994) used a two-stage approach to predict ingrowth. They thought one of the difficulties in modelling ingrowth is the great variability in regeneration, and much of the variability associated with regeneration is due to the fact that during any period some regeneration may or may not occur, and that if the data are partitioned into a two-stage system, the ability to predict the amount of ingrowth is greatly enhanced. With this approach, the first equation estimates the probability that some ingrowth will occur, usually with a logistic function with presence (or absence) of ingrowth as the response variable. Then a conditional function can be used to predict the amount of ingrowth, given that ingrowth is known to occur. But the two-stage approach introduces some complications when the data represent different time intervals. Longer intervals will have a greater probability of ingrowth, and there may be more ingrowth if it occurs. Thus it may be necessary to adjust for the time interval in both functions, to obtain a satisfactory fit to the data.

In McTague et al.'s (1995) study, total ingrowth was computed with a stand-level projection equation, the presence or absence of ingrowth for a given species was determined with a discriminant function, while the proportion of total ingrowth allocated to a species is predicted with a logistic function.

Vanclay (1989) predicted the total ingrowth at 20 cm diameter in Queensland rainforests as a linear function of stand basal area and site quality. Although simplistic, this model allowed sufficient flexibility for species group dynamics to emerge and provided reasonable results.

Vanclay (1994) indicated that where data permit, a better approach is to predict ingrowth as a function of site and stand condition. Several such models have been published, and range from the highly empirical to those with a biological basis. Variables commonly used include site productivity, stand density (e.g. stand basal area, stem number, competition indices), and time since nature of harvesting.

Botkin et al. (1972) established an ecological approach to modelling ingrowth at 0.5 cm diameter on their 10 × 10 m plots. They assumed that a seed source was available for each of the major species considered by their model and compiled a list of possible species for the plot being modelled, on the basis of shade tolerance, growing season, and soil moisture. Shugart and West (1977) followed a similar approach, but identified the requirements of each species for mineral soil or leaf litter, introduced stochastic elements of variable weather and animal browsing, and also modelled sprouting from dead trees. Reed (1980) followed an approach somewhat similar to that of

Botkin et al. (1972), but introduced alternate seed years and "off years" and imposed a maximum stocking of 2500 stems/ha, irrespective of size, above which no ingrowth could occur.

In this study we developed two sets of stand-level, two component ingrowth models to predict periodic annual ingrowth for the four major species in mixedwood stands of Alberta in order to satisfy different needs. Ingrowth is modeled as a function of stand average tree diameter at breast height, stand density, species composition, and site productivity.

2.3 Dynamics of mixedwood stands

The boreal forests in Alberta commonly have a mixed-species composition. White spruce, trembling aspen, lodgepole pine and black spruce are the four major species. Most natural mixedwood stands originated after fire (Rowe and Scotter 1973), and can range from pure stands of white spruce to pure aspen, and mixtures of the two in the varying proportions (Corns, and Annas 1986). Complexity in stand development for boreal mixedwoods arises because of differences in recruitment strategies, shade tolerance, juvenile growth rates, and lifespan/time to maturity of the main species. The structure and composition of mixedwood also are influenced strongly by time since disturbance, amount of forest floor removal, survival of root stocks, and seed sources. These factors can be categorized as stand history (McCune and Allen 1985, Lieffers et al. 1996a).

In the early developmental stage of a mixed spruce-aspen stand, the shade-intolerant aspen has the competitive advantage over white spruce and exhibits faster early height growth. As a result, aspen tends to rapidly establish dominance on the site by occupying the upper layer of the canopy. Shade-tolerant white spruce is often established a short but distinct time after the overstorey aspen and exhibits slow juvenile height growth. As time progresses, the competitiveness of aspen is reduced relative to that of white spruce as individual aspen stems start to die at 60-80 years of age, giving dominance gradually to the more shade-tolerant and long-lived white spruce. This dynamic process results in changes both in whole stand density and the proportions of the species in the stand.

In most circumstances, fire will return older mixedwood stands to early successional stage before there is any further species replacement (Rowe 1961; Achuff and La Roi 1977; Cogbill 1985).

However, overmature mixedwood stands do occur in various forms. Old aspen stands tend to be gradually dominated by shrubs and remain a relatively stable community (Rowe 1961) or occasionally there is some rejuvenation of the aspen component in the stands (Dix and Swan 1971; Carleton and Maycock 1978). In white spruce stands, the very shade tolerant balsam fir will establish in the understory if there are seed sources available (Lieffers et al. 1996a). If undisturbed, the overstory white spruce will decline gradually because of litter buildup and reduction in nutrient cycling (Pastor et al. 1987), or more rapidly by spruce budworm attack (Cogbill 1985; Bergeron and Dubuc 1989). These spruce will be replaced by uneven-aged, low density mixtures of balsam fir and white spruce (Achuff and La Roi 1977), sometimes mixed with birch and shrubs (Cogbill 1985; Bergeron and Dubuc 1989).

Ingrowth and regeneration are intimately related; ingrowth is the direct result of past patterns of regeneration (Shifley 1990). Lieffers et al. (1996b) indicated that in some circumstances white spruce recruitment occurs immediately after the disturbance and in others the recruitment will occur some years later, so in most of the stands there was a wide range in the age of the white spruce, reflecting nearly continuous recruitment. The period of recruitment may be relatively short, i.e., 15-20 years, or continue for decades, producing an uneven-aged understory.

2.4 Data

The data of permanent sample plots (PSP), which the Alberta Land and Forest Services provided, were used in this study. The PSP plots were established and remeasured since the early sixties, and most of them were initially 30 years or older. Over 900 permanent sample groups have been established and measured. PSP groups were located throughout the inventory area of the province to provide representative information for a variety of stand density, species composition, and site condition. Each PSP group consists of 1 or 4 plots. Each plot has been remeasured up to 5 times over different time intervals. A sapling/regeneration plot with size 62 to 125 m^2 was established within each PSP's tree plot. All standing trees$\geq$9.1 cm DBH within the tree plot were tagged, remeasured, and tallied. In the sapling/regeneration plot, all sapling (DBH$\geq$1.1 and <9.1 cm) were measured and tallied. All trees$\geq$0.16 m in height up to a DBH of 1.0 cm inside the sapling/regeneration plot were tallied as regeneration. A description of the development and data collection can be found in the *Permanent Sample Plots Field Procedures Manual* (Alberta Land and Forest Service 1994).

The original PSP data were summarized to provide additional variables such as the number of trees per hectare, basal area per hectare, average height, and average diameter, both for all species combined and by individual species in the stand. The stand statistics were calculated respectively based on all trees with DBH≥1.1 cm and based on all trees with DBH≥9.1 cm. The advantage of the stand statistics based on all trees with DBH≥1.1 cm is that the data that contain the information of small trees in the stands would not be lost for developing models. But this may limit the utility of the models for extrapolating inventory data, as such data (sapling trees) may not be recorded during operational inventory. Therefore, both stand statistics were used to develop models in this study. A detailed description of the method of compiling plot level variables can be found in the *Permanent and Temporary Sample Plot Compilation Procedures* (Alberta Land and Forest Service 1995).

Site index could not be estimated for some plots, and omission of these plots left 155 PSPs for white spruce, 314 for lodgepole pine, 317 for aspen, and 281 for black spruce in the present study. Pairs of consecutive remeasurements (i.e., all nonoverlapping intervals) were selected from the data base and formatted to provide a data file suitable for analysis. Each non-overlapping growth period from the remeasurements defined a growth interval, that is, the growth intervals are obtained from measurements between first and second, second and third, but not first and third. A total number of 1478 growth intervals were obtained for white spruce, 2593 for lodgepole pine, 2247 for aspen, and 2121 for black spruce.

Analysis of the present data has been complicated by the different plot sizes (varying from 0.02 to 0.34 ha.) and remeasurement intervals (varying from 2.2 to 19.0 years). To provide a consistent basis for analysis, amounts of ingrowth have been standardized to number of stems per hectare per year. The periodic annual ingrowth was calculated as: number of ingrowth trees within each growth interval divided by the length of the interval. The length of interval was computed as: $L = Year_2 - Year_1 + (Adj_2 - Adj_1)$, where $Year_1$ and $Year_2$ are consecutive measurement years, and Adj_1 and Adj_2 are consecutive month adjustments. The month adjustment was defined according to the biological growth period in the boreal mixedwood stands (Huang 1992). It was equal to 0.0, 0.2, 0.5, 0.9, and 1 when month was ≤ 4, = 5, = 6, = 7, ≥ 8, respectively.

Descriptive statistics including the mean, minimum, maximum, and standard deviation of periodic annual ingrowth and stand characteristics at the beginning of the growth period are displayed in Table 2-1 and Table 2-2.

2.5 Methods

2.5.1 Explanatory variables

The ingrowth models discussed in the previous section indicated that the ingrowth occurrence probability and the number of ingrowth trees were related to stand density and size structure and site productivity. Based on the preliminary analysis, the following characteristics (refer Table 2-1, Table 2-2) and dynamics are found to influence the occurrence and the quantity of ingrowth and were considered in the development of ingrowth models. The correlation coefficients (Table 2-3) between the amount of ingrowth and some independent variables are low, indicating either that these independent variables are inappropriate predictors of the number of ingrowth trees, that the relationships are strongly nonlinear, or that there is a high degree of natural variability in the ingrowth process. Preliminary graphical analyses provided substantial evidence for this third explanation.

2.5.1.1 Stand average diameter at breast height

The average diameter at breast height (DBH) of all trees (both greater than 1.1 cm dbh and greater than 9.1 cm dbh) in the stand was one of the most important factors influencing ingrowth process; it is also indicative of stand maturity and is almost universally available. Maturity of stands is closely related to the ingrowth process. In juvenile stands there may be more ingrowth trees than in mature stands. But stands in Alberta commonly have a mixed species composition with an irregular age structure, so stand age is often less meaningful in this situation (Wykoff 1990). The correlation coefficients between the amount of ingrowth and stand age are lower than that between the ingrowth and stand DBH (Table 2-3). Age also is the most expensive, time consuming, and difficult variable to measure (Huang and Titus 1992). Moser (1972) indicated that even though age is a parameter commonly utilized in the study of stand development, its interpretation is at best nebulous for the uneven-aged stand. Therefore, stand average DBH was chosen as the primary explanatory variables in this study. Larger mean DBH's in well-stocked stands often indicate that most of the trees are larger than the ingrowth threshold (Shifley et al. 1993). An observation was made by Moser (1972) for the uneven-age stand: greater ingrowth expectancy was associated with stands that have a high proportion of trees in the smaller diameter classes. A similar conclusion was obtained by Shifley et al. (1993): high ingrowth rates are associated with stands that have a large proportion of trees near the threshold DBH.

2.5.1.2 Total number of trees and total basal area

Shifley (1990) proposed that the combination of the number of trees per unit area and the overall size structure of the forest stand are clearly important factors in controlling the number of ingrowth trees. Density is closely related to growing space and availablity of resources for trees. It is anticipated that the amount of ingrowth will be related to stand density, and specifically to the amount of available growing space to support ingrowth trees. Ingrowth trees are expected to occur in greater numbers when more growing space is avalable. Both the total number of trees (Nha) and total basal area per hectare (BA), for all species combined in the stand are used as mixed-species stand density measures. The use of these two stand level attributes as simple and objective measures of stand density has been widespread (Clutter et al. 1983), and for reasons described by Spurr (1952), they should be particularly suitable for mixed-species stand with irregular age structures (Huang and Titus 1995). Shifley (1990) discussed the importance of selection of suitable indices of competition. He indicated that ingrowth trees are those which survive long enough and grow large enough to reach the threshold diameter, and there is a clear link between growth and competition (Hilt 1985, Shifley 1987) and between survival and competition (Monserud 1976, Buchman et al. 1983), so estimates of the level of competition impacting trees at or below the ingrowth threshold should be correlated with the number of ingrowth trees. He stated that sites that are understocked have potential space for ingrowth trees, and that crown competition factor was a good density indictor for evaluating available growing space, and being able to accommodate stands with multiple species and irregular size or age distributions. The crown competition factor, although commonly used as a measure of stand density in growth and estimation (Stage 1973; Arney 1985; Wykoff 1990), was not used because the measurements of crown areas from open-grown trees were not available. In general, large numbers of trees per area are associated with stands comprised of individuals of small mean size, leading to higher rate of ingrowth (Shifley et al. 1993), and several previous researchers found that the number of ingrowth trees increased as the number of trees per acre increased. In this study, the total number of trees and total basal area per hectare by species and by all species combined were used.

2.5.1.3 Species composition

BA assumes that all species exert equal competition influence, but in mixedwood stands some species could exert a greater influence than others. Species composition (SCsp) is considered as an additional explanatory variable indicative of mixedwood competition. It is demonstrated that the species found in the overstory are powerful indicators of the future ingrowth species. Shifley (1990) reported that on average, 65 percent of the ingrowth trees are of the same species as one of the trees present in the overstory of the parent stand in his study. Two measures of species composition were used, one is the proportion of total density, one is the proportion of total basal area. They were defined respectively as follow:

$$(2.1)\quad SCsp1 = Nhasp/Nha$$

$$(2.2)\quad SCsp2 = BAsp/BA$$

where Nhasp is the total number of trees per hectare for the species under consideration, and Nha is the total number of trees per hectare for all species, BAsp is the total basal area per hectare for the species under consideration, and BA is the total basal area per hectare for all species. Trees of different species may differ in their contribution to the level of competition impacting ingrowth trees. The species composition as defined in equations (2.1) and (2.2) has a range of zero to one, with zero indicating there is no specific species in the stand and one indicating a pure species stand.

2.5.1.4 Site productivity

Site index, defined as the average height of the dominant (or dominant and codominant) trees in the stand at a specified reference age, is probably the most widely used site productivity measure in North America (Carmean 1975, Alemdag 1991). One of the main drawbacks regarding the use of site index as a measure of forest productivity is that it is not well suited for uneven-aged, mixed species stands or stands with competition in juvenile phases. Avery and Burkhart (1994) indicated that in spite of the foregoing limitations, site index is a useful tool because it provides a simple numerical value that is easily measured and understood by the practicing forester. They believed that its use will apparently be continued until the day when the varied factors affecting the productivity of forests can reduced to an equally simple and quantitative measurement. Therefore, a species specific site index (SI) based on stand age and height was used in this study.

2.5.1.5 Length of re-measurement interval

Longer intervals (L) will have a greater probability of ingrowth occurrence. For any individual plot, there is always an interval L long enough for us to observe ingrowth occurrence. The length of re-measurement interval (L) was used as an explanatory variable in the ingrowth occurrence probability models.

2.5.2 Model development

An important consideration in selecting a model to predict ingrowth is the need to impose biologically realistic constraints on model predictions. Shifley et al. (1993) indicated that the amount of ingrowth cannot be negative and should not be so great that it causes a stand to exceed biological limits of stand density, and when other factors being equal, the number of ingrowth trees should decrease as levels of competition and threshold diameter increase.

Burk (1978) reported that linear forms are not appropriate for the amount prediction of ingrowth because there are possibilities that predicted number of ingrowth trees may be negative. To avoid this problem, exponential models are commonly used.

Hamilton and Brickell (1983) described the most general two-state system by two conditions: (1) observations cannot be placed with certainty in either of the two states and (2) the relationship between the dependent variable and potential independent variable is different for each of the two states. For a more limited two-state system and situation that initiated this work, the second condition can be said that the dependent variable is a constant value (frequently zero) for one state. Modelling or data analysis of such a system is frequently inappropriately done with a single model or analysis. Data drawn from a two-state system is most effectively dealt with by separate but related models or analysis (Hamilton and Brickell 1983). One of the difficulties in modelling ingrowth is the great variability in ingrowth. Much of the variability associated with ingrowth is due to the fact that during any period some ingrowth may or may not occur, and that if the data are partitioned into a two-state system, the ability to predict the amount of ingrowth is greatly enhanced. In this study, more than half of the observations in the data sets shows no ingrowth. With a two-stage approach, the first equation estimates the probability that some ingrowth will occur, usually with a logistic function with presence (or absence) of ingrowth as the response variable. The second stage is a conditional function to predict the amount of ingrowth, given that ingrowth is known to occur, and can be estimated using ordinary linear regression (Vanclay 1992) or nonlinear regression. Hamilton and Brickell (1983) gave an example of such a two-stage approach applied to the prediction of defective volume in standing trees, which can be applied equally well to ingrowth modelling (Vanclay 1992).

This method of analysis is similar to one frequently applied in decision theory (Raiffa and Schlaifer 1961). An event can have one of two possible outcomes. Each outcome occurs with known (or estimable) probability. For each outcome there is a known (or estimable) response. The equation (2.3) of the predicted response when the event occurs and when the response for one of the two states is zero was expressed as (Hamilton and Brickell 1983)

(2.3) $\hat{Y}_i = \hat{P}_i \hat{C}_{1i} + (1 - \hat{P}_i)0 = \hat{P}_i \hat{C}_{1i}$

where $\hat{Y}$ is equal to the predicted response (ingrowth) when the event occurs for the i-th observation; $\hat{P}_i$ is equal to the estimated probability that the i-th observation falls in the first state; $(1 - \hat{P}_i)$ is equal to the estimated probability that the i-th observation falls in the second state, $\hat{C}_{1i}$ is equal to the estimate of the response of the dependent variable for i-th observation, given the i-th observation falls in the first state.

A classification may be needed when this approach is fitted into a general growth simulator process such as mixedwood growth model (MGM), which was developed in the University of Alberta (Morton and Titus 1984, Huang 1992, Huang and Titus 1995, Yao 1997). This usually involves establishing a probability level (cut-off point) to segregate observations into "likely events" (stands with ingrowth) and "unlikely events" (stands without ingrowth). This probability level is customarily set at 0.5 (the midpoint of the logistic distribution) and is the cut-off point used to categorize the observations. If it is possible to categorize all observations either as stands with ingrowth or as stands without ingrowth, then simulation for the amount of ingrowth may be confined to stands with ingrowth. In that case equation (2.3) simplifies to $\hat{Y}_i = \hat{P}_i\hat{C}_{1i}$ if the stand has some ingrowth trees, otherwise $\hat{Y}_i = 0$.

Nevertheless, the cut-off point is arbitrary, and ultimately depends on the objectives for the model or the goals of the user (Jamnick and Beckett 1987). A decision about the "best" probability level involves a trade-off between predicting correctly both true events (ingrowth presence) and false events (ingrowth absence) (Schuster 1983, Jamnick and Beckett 1987). Schuster (1983) suggested this problem is similar to the Type I/II errors, which can occur in statistical hypothesis testing. For example, a 0.02 probability level was defined in the study of fire occurrence prediction (Garcia et al. 1995).

2.5.2.1 Probability of ingrowth occurrence

2.5.2.1.1 Model specification

Assume that there are k explanatory variables $x=(x_1, x_2, \ldots, x_k)$ at the beginning of a growth period. L denotes the length of the growth period (or remeasurement interval). The response variable y is a binary variable to indicate the presence status of ingrowth trees in a plot at the end of the period, where $y=1$ if ingrowth occurs, and $y=0$ if ingrowth does not occur. The plot of the response versus explanatory variable based on the data falls into two parallel lines. It depicts the dichotomous nature of the response variable clearly, but does not provide a clear picture of the relationship between ingrowth occurrence and the explanatory variables. In this situation, a special technique, called a generalized linear model (McCullagh and Nelder 1983, Hinkley et al. 1991), is needed.

Let $\pi(x)$ be the mathematical expectation of y under condition x, $E(y|x)$. This conditional mean is also the ingrowth occurrence probability (p) of the individual plot, where $p=\text{Probability}(y=1|x)=\pi(x)$. The idea of the generalized linear model is based on an assumption that a function of p may be expressed as a linear combination of x. The formulation of the model is

$$g(p) = g(\pi(x)) = \beta_0 + \beta_1 x_1 + \cdots + \beta_k x_k$$

where g(.) is a one-to-one differential function, called a link function, and $\beta_0, \beta_1, \cdots \beta_k$ are unknown parameters (McCullagh and Nelder 1983). The link function relates the ingrowth occurrence probability with the linear combination of the variables. Different link functions indicate different formulations of the model. The choice of a link function is usually made based on aptness to the data, model interpretation, and simplicity of the corresponding statistics (Hinkly et al. 1991). The most frequently used link function is the logistic link $g(p)= \log\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 x_1 + \cdots + \beta_k x_k$, and the corresponding generalized linear model is the logistic model:

(2.4) $p=[1+\exp(-(\beta_0 + \beta_1 x_1 + \cdots + \beta_k x_k))]^{-1}$

The logistic model is the cumulative distribution function of the logistic distribution, which is bounded by zero and one, the potential range of probability of ingrowth occurrence. It has been widely used for individual tree mortality modelling (Hamilton 1974, Hamilton and Edwards 1976, Monsured 1976) and fire occurrence prediction modelling (Martell et al. 1987, Loftsgaarden and Andrews 1992, Chou et al. 1993). With a selection of the proper set of variables and transformations, the model should be able to describe most natural occurring patterns of ingrowth.

In this study, the length of re-measurement intervals (L) varied considerably (2.2-19.0 years). Longer measurement interval had a higher probability of ingrowth occurrence. Thus it is necessary to adjust for the time interval to obtain a satisfactory fit to the data. Three methods to accommodate unequal the length of re-measurement intervals were considered. The first one was that the logistic model (2.4) is adapted to handle unequal growing period lengths by weighting the regression analysis by 1/L (Hamilton and Edwards 1976, Vanclay 1992). Vanclay's logistic model was fitted using maximum likelihood estimation weighted by the inverse of the measurement interval (1/L) to compensate for the differing measurement intervals and provide annual probabilities of ingrowth occurrence. The second was a generalized logistic model (2.5) proposed by Monserud (1976), to predict individual overstory tree mortality:

(2.5) $p=[1+\exp(-(\beta_0 + \beta_1 x_1 + \cdots + \beta_k x_k))]^{-L}$

In model (2.5), (L is as an exponent), the survival probability can be projected for a variable time interval rather than a fixed yearly interval (Yao 1997).

The third method was that L is as a concomitant independent variable like other independent variable (model (2.6)), not as an exponent like that in model (2.5). This method was used in an individual tree mortality model by Moran-Palma et al. (1997). They indicated that the modelling of individual tree mortality has traditionally been conducted on an annual basis using a time interval of $t = 1$ (Hamilton and Edwards 1976), then standard compound interest formulas may be used to calculate the probability of survival over any desired time interval. Moran-Palma et al. (1997) also indicated that Efron (1988), using data of a cancer study, demonstrated the efficiency of using the variable t as a predictor variable in a logistic regression model over that of a discrete survival function which is compounded forward for t interval.

$$(2.6)\quad p=[1+\exp(-(\beta_0+\beta_1x_1+\cdots+\beta_kx_k+\beta_{k-1}L))]^{-1}$$

Vanclay's (1992) method, by which the model (2.4) was fitted by weighting 1/L using maximum likelihood estimation, resulted in a double correction that underestimates the expected ingrowth, because in his study, the probabilities of ingrowth occurrence have been adjusted to annual probability by weighting by the inverse of the remeasurement interval, and amounts of ingrowth have been standardized to stems per hectare per year. Both these adjustments are necessary for variance stabilization, but result in a double correction that underestimates the expected ingrowth. Thus the parameter of the constant in his second model was adjusted to provided unbiased estimates of ingrowth (Vanclay 1992). Monserud (1976) indicated that although the differences between model (2.5) and (2.6) were not dramatic, classification was improved by using the L as an exponent rather than as another concomitant x variable, and using L as an exponent in a function defined on the unit interval allows for interpreting the "base" as an annual probability of survival (e.g., model (2.4) is the "base" in model (2.5)). So the Monserud method was preferred and was used in Yao's mortality models. Yao (1997) indicated for a live tree, at the beginning of a growth interval, i.e., L=0, the tree is definitely alive and p=1, and with increasing L, the survival probability p decreases and gradually approaches zero, and the survival probability model should satisfy that the p=1 when L=0, and p=0 when $L\rightarrow+\infty$. In Yao's survival probability model, the exponent is the interval (L). However, longer measurement interval will have a higher probability of ingrowth occurrence, that means ingrowth occurrence probability increases as length of interval increases, so the ingrowth occurrence probability model should satisfy that the $p\rightarrow0$ when $L\rightarrow0$, and p=1 when $L\rightarrow+\infty$, this is contrary to Yao's survival probability model. Therefore, the model

(2.7), in which the exponent is inverse of the interval (1/L), was chosen in the ingrowth occurrence probability model in this study.

$$(2.7)\quad p=[1+\exp(-(\beta_0+\beta_1x_1+\cdots+\beta_kx_k))]^{-1/L}$$

In this model, the ingrowth occurrence probability can be projected by a variable time interval rather than a fixed yearly interval. For a plot, at the beginning of a growth interval, L=0, there are definitely no ingrowth trees in the plot and p=0, and with increasing L, the ingrowth occurrence probability p increasing and gradually approaches 1. In model (2.7), L was restricted to values greater than zero. At L=0, probability (p) was explicitly set at zero, since the model was not designed to address the current year. The link function for model (2.7) can be written as

$$(2.8)\quad g(\pi(x))=\log\left(\frac{\pi(x)^L}{1-\pi(x)^L}\right)=\beta_0+\beta_1x_1+\cdots+\beta_kx_k$$

A binary response such as this can be studied through several analysis techniques (Garcia et. al., 1995). Common choices for models with dichotomous dependent variables are discriminant analysis, the linear probability model, the probit model, and the logistic model (Ben-Akiva and Lerman 1985, Cox and Snell 1989).

The discriminant function approach requires that the explanatory variable, x, follows a normal distribution for two groups y=1 and y=0 having different mean and the same variance (Cornfield 1962). If there are any dichotomous explanatory variables, the discriminate function estimates will overestimate the magnitude of the association (Hosmer and Lemeshow 1989). The discriminate analysis was not preferred because the growth interval L was scheduled close to 2, 5, 10 and 20 years, which was not a normal distribution (Yao 1997). The linear probability model is not well suited for this application, mainly because the predictions are not restricted to the interval (0, 1) (Maddala 1983, Cox and Snell 1989). Maddala (1983) and Yao (1997) concluded that the probit model and logistic model are equal in predictive power, but logistic model offers computational advantage and has broad application and acceptance. Furthermore, logistics model have been successfully used in similar applications. Therefore, the logistic model (2.7) was chosen to describe the relationship between ingrowth occurrence (a dichotomous dependent variable) and a set of independent variables in this study.

2.5.2.1.2 Model fitting

The method to fit the generalized logistic model (2.7) is an extension of the logistic regression for model (2.4). To fit the logistic model (2.4), Hosmer and Lemeshow (1989) gave a detailed discussion, and many statistics software packages provide the specific procedures, such as the procedure PROC LOGISTIC and the procedure PROC PROBIT on SAS (SAS Institute Inc. 1992) and GLM on S-plus (Statistics Science 1993). However, the estimates of parameters for model (2.7) are slightly different and the log likelihood function was derived as below.

The ingrowth present status code y is a binary response following a Bernoulli distribution when given a value of the input variable x, thus for the i-th observation,

(2.9) $\mathrm{Prob}(y_i = 1|x_i) = \pi(x_i)$,

(2.10) $\mathrm{Prob}(y_i = 0|x_i) = 1 - \pi(x_i)$,

where y_i is the response variable for the i-th observation, x_i is the vector of the explanatory variable for the i-th observation. From (2.9) and (2.10), the probability distribution function of y_i can be written as:

(2.11) $f(y_i, \pi(x_i)) = \pi(x_i)^{y_i}(1 - \pi(x_i))^{1-y_i}$

There are n independent observations. The likelihood function is equal to

(2.12) $L(y, \pi(x)) = \prod_{i=1}^{n} \pi(x_i)^{y_i}(1 - \pi(x_i))^{1-y_i}$

After a logarithmic transformation of (2.12), the log likelihood function is

(2.13) $l(y, \pi(x)) = \log(L(y, \pi(x))) = \sum_{i=1}^{n} \{y_i \log(\pi(x_i)) + (1 - y_i)\log(1 - \pi(x_i))\}$

From the link function (2.8), it can be derived that

(2.14) $\pi(x_i) = [1+\exp(-(\beta_0 + \beta_1 x_{i1} + \cdots + \beta_k x_{ik}))]^{-1/L_i}$

Substitute (2.14) into the log likelihood function (2.13). It becomes

(2.15)

$$l(y,\beta)=\sum_{i=1}^{n}\left\{-y_i\left(1\ \ L_i\right)\log\left[1+\exp\left(-\left(\beta_0+\beta_1x_{i1}+\cdots+\beta_kx_{ik}\right)\right)\right]+\left(1-y_i\right)\log\left[1-\left(1+\exp\left(-\left(\beta_0+\beta_1x_{i1}+\cdots+\beta_kx_{ik}\right)\right)\right)^{-1\ \ L_i}\right]\right\}$$

$$=\sum_{\substack{i=1\\ y_i=1}}^{n}\left(1\ \ L_i\right)\log\left[1+\exp\left(-\left(\beta_0+\beta_1x_{i1}+\cdots+\beta_kx_{ik}\right)\right)\right]+\sum_{\substack{i=1\\ y_i=0}}^{n}\log\left[1-\left(1+\exp\left(-\left(\beta_0+\beta_1x_{i1}+\cdots+\beta_kx_{ik}\right)\right)\right)^{-1\ L_i}\right]$$

The log likelihood function contains the unknown parameter β. Maximizing the log likelihood function (2.15), the maximum likelihood estimates $\hat{\beta}$ for model (2.7) can be obtained. Different link functions provide different presentations of $\pi(x_i)$ in (2.14) and lead to different log likelihood function. Function (2.15) is not the same as the log likelihood function for model (2.4). This is why we cannot use the procedures built for fitting model (2.4) to fit model (2.7).

In this study, the S-plus statistics language (Statistical Science 1993) was used to obtain the maximum likelihood estimates for model (2.7). In S-plus, by specifying the log likelihood function (2.15) and providing the starting estimates for β, a nonlinear minimizer, *nlmin*, was used to minimize -l(y, β), and then to obtain the estimates $\hat{\beta}$ which maximized the log likelihood function -l(y, β). The nonlinear minimizer *nlmin* was based on a general quasi-Newton method. The detailed computation steps can be found in Dennis and Mei (1979) and Dennis et al. (1981). Different starting values were given to ensure the converge point was global.

Monserud (1976) used a re-weighted least square method to obtain the weighted nonlinear regression estimates for model (2.5). Vanclay (1992) used GLIM (generalized linear interactive modelling) on NAG (Numerical Algorithms Group) to obtain maximum likelihood estimates for model (2.4). In GLIM model, the maximum likelihood estimates can be computed by iteratively reweighted least squares, where the weights are the reciprocals of the variances (p1168, SAS Institute Inc. 1994). Hamilton (1974) used a re-weighted least squares method to obtain the weighted least squares estimates for model (2.4) in the RISK computer program. Monserud (1976) and Yao (1997) concluded that the maximum likelihood estimates and the weighted least squares estimates should be identical except for computational errors. Yao (1997) indicated that the maximum likelihood estimation is equivalent to the re-weighted least squares estimation, and is better than the discriminant analysis and the weighted linear regression to fit model (2.5). Therefore, the *nlmin* in S-plus was used in this study because it is more accessible for us.

2.5.2.1.3 Variable selection

An appropriate biological interpretation of the ingrowth process is essential in considering variable selection. In addition, statistical tests provide a useful tool when the relationships of some variables are not known. Therefore, both biologically meaningful selection and statistically significant selection were considered. The procedure PROC LOGISTIC (SAS Institute INC. 1994) provide various variable selection methods, and one of them is a stepwise procedure. Because the differences between model (2.6) and (2.7) should not be dramatic, information obtained from stepwise selection by fitting model (2.6) using the procedure PROC LOGISTIC on SAS was combined with the understanding of the process of ingrowth to primarily select a set of variables as candidates for model (2.7). Following this, the inclusion of additional explanatory variables was investigated and further variable selection was evaluated when fitting model (2.7) using *nlmin* in S-plus.

The stepwise procedure is based on a likelihood ratio test which checks for the importance of variables. Hosmer and Lemeshow (1989) explained the selection is that at any step in the procedure the most important variable will be one that produces the greatest change in the likelihood relative to a model not containing the variable. In the model fitting, the parameter significance, or the importance of the corresponding parameter, was also assessed through the likelihood ratio test. For example, for the j-th variable with corresponding parameter β_j, the null hypothesis is that the variable can be eliminated, that is, H_0: $\beta_j = 0$. The likelihood ratio statistic is

$$(2.16)\quad \Lambda = -2\log\left(\frac{L\left(y,\left(\tilde{\beta}_0,\tilde{\beta}_1,\ldots,\tilde{\beta}_{j-1},0,\tilde{\beta}_{j+1},\ldots,\tilde{\beta}_k\right)'\right)}{L\left(y,\left(\hat{\beta}_0,\hat{\beta}_1,\ldots,\hat{\beta}_{j-1},\hat{\beta}_j,\hat{\beta}_{j+1},\ldots,\hat{\beta}_k\right)'\right)}\right)$$

where $\left(\tilde{\beta}_0,\tilde{\beta}_1,\ldots,\tilde{\beta}_{j-1},0,\tilde{\beta}_{j+1},\ldots,\tilde{\beta}_k\right)$ are the maximum likelihood estimates under H_0, and $\hat{\beta} = \left(\hat{\beta}_0,\hat{\beta}_1,\ldots,\hat{\beta}_k\right)$ are the maximum likelihood estimates under the full model. The likelihood ratio statistic Λ compares the likelihood without variable β_j and the likelihood with variable β_j. In large sample, Λ is approximately distributed as a chi-square distribution with degree-of-freedom 1 under H_0. A large Λ value will provide evidence to against H_0.

2.5.2.1.4 Goodness-of-fit test

Once the model was fitted, the Hosmer and Lemeshow test, commonly employed in the logistic regression, was used to test the goodness-of-fit for the model. In the Hosmer and Lemeshow test, first, observations were sorted in an increasing order of their estimated ingrowth occurrence probability, then the observations were divided into g groups. As in the procedure PROC LOGISTIC (SAS Institute INC. 1994), ten groups were used in this study. The Hosmer and Lemeshow statistic was obtained by calculating the Pearson chi-square statistic from the 2×g table of observed and expected frequencies (Hosmer and Lemeshow, 1989):

$$(2.17) \quad x_{HW}^2 = \sum_{i=1}^{g} \frac{\left(o_i - n_i\bar{p}_i\right)^2}{n_i\bar{p}_i\left(1-\bar{p}_i\right)}$$

where n_i was the number of the observations in the i-th group, o_i was the number of the observations with ingrowth occurrence at the end of the growth interval in the i-th group, and $\bar{p}_i$ was the averaged predicted ingrowth occurrence probability for the i-th group. Under the assumption that no significant difference exits between the actual and predicted ingrowth occurrence, the Hosmer and Lemeshow statistic should be approximately distributed as a chi-square distribution with degree-of-freedom g-2 = 8.

2.5.2.2 Amount of ingrowth

2.5.2.2.1 Model specification

A subset of the data base provided estimates of the amount of ingrowth, given that it was known to occur. Approximately 75% of observations of this subset data were randomly selected for model fitting and the remaining 25% were used for model testing. Graphical inspection of the data suggested that the amount of ingrowth was strongly related to stand average dbh. For the data based on trees with DBH≥1.1 cm, the amount of ingrowth increases quickly to reach the maximum at around 7 cm DBH, and then decreases dramatically as stand average DBH increases (see Figure 2-1). The following function, used as a increment function in Wykoff (1990) and

Vanclay (1991), was considered as a base function, because the trend of ingrowth with size is similar in shape to this function.

(2.18) $I_{1.1} = \alpha DBH^{\beta} \exp(-\gamma DBH)$

where I is number of ingrowth trees per year per hectare, DBH is stand average DBH by species or by all species combined, α, β, and γ are unknown parameters. This curve begins at value zero, increases with increasing DBH, reaches the maximum value at β/γ, and then decreases and approaches 0 as DBH $\rightarrow +\infty$. In equation (2.18), with increasing DBH, simultaneously DBH^{β} increases and $\exp(-\gamma DBH)$ decreases. When DBH is less than β/γ, the increasing DBH^{β} term dominates the curve. After that, the decreasing $\exp(-\gamma DBH)$ becomes more and more dominant, and drives the curve asymptotically towards zero. The parameter α does not impact on the turning point, but it influences the slope of the curve, and affects the magnitude of the maximum.

For the data based on trees with $DBH \geq 9.1$ cm, the amount of ingrowth decreases as stand average DBH increases (see Figure 2-2), so the following exponential function was considered as a base function:

(2.19) $I_{9.1} = \alpha \exp(-\beta DBH)$

In equation (2.18), the amount of ingrowth increases as either α or β increases, and decreases as γ increases, and in equation (2.19), the amount of ingrowth increases as α increases, and decreases as β increases. This property makes them easy to modify and interpret the model according to the stand dynamic pattern. An additional noteworthy aspect of the equations described above is that they are amenable to logarithmic transformations to a linear form for fitting via standard multiple linear regression procedures. With a log transformation, the equations above become:

(2.20) $\log(I_{1.1}) = \log(\alpha) + \beta \log(DBH) - \gamma DBH$

(2.21) $\log(I_{9.1}) = \log(\alpha) - \beta DBH$

In this study, the linear models (2.20) and (2.21) were fitted to provide the initial guesses of the parameters α, β, and γ, and then nonlinear technique was used to fit the nonlinear models (2.18) and (2.19).

Several other base functions such as Box-Lucas function and Weibull-type function, which curves are compatible with the sigmodial S-shaped yield curves, were also examined. Preliminary analyses indicated that equations (2.18) and (2.19) were superior to these two models so equations (2.18) and (2.19) were used as the based function to model the amount of ingrowth in this study.

Other stand variables representing competition, species composition, and site productivity were also found to significantly affect the amount of ingrowth. These variables were incorporated into equations that predict the parameters of equations (2.18) and (2.19). This procedure is similar to the method of parameter prediction commonly used for a Chapman-Richards or Weibull-type function in which the parameters of the function are related to other tree and stand characteristics but the form of the original function remains the same (Clutter et al. 1983).The final models were formulated as

(2.22) $I_{1.1} = \alpha DBH^{\beta}\exp(-\gamma DBH)$

with $\alpha = f$ (other variables)

$\beta = g$ (other variables)

$\gamma = h$ (other variables)

and

(2.23) $I_{9.1} = \alpha\exp(-\beta DBH)$

with $\alpha = f$ (other variables)

$\beta = g$ (other variables)

and the fitting was accomplished using the procedure PROC REG and procedure PROC NLIN on SAS/STAT software (SAS Institute Inc. 1992).

2.6 Results

2.6.1 Probability of ingrowth occurrence

From the PSP data, 1475 and 1455 observations for white spruce, 2593 and 2582 for lodgepole pine, 2247 and 1960 for aspen, and 2123 and 1996 for black spruce were used to fit model (2.7) respectively. The summary statistics for the data both based on trees with DBH≥1.1 cm and trees with DBH≥9.1 cm by ingrowth presence and absence are list Table 2-1 and 2-2 for each species respectively.

A preliminary summary of the data showed that BA, Nha, DBH, SCsp and SI were the important variables. A number of interaction terms based on these variables were also considered to obtain a good fit and rational interpretations. In addition, all species specific variables (e.g., DBHsw vs. DBHaw) were potentially included in equations for each species. Based on the likelihood ratio test and the criteria that a rational interpretation is more important than the model precision, the significant explanatory variables and transformations for the four species were:

White spruce (DBH≥1.1 cm):

BA, log(Nhasw), DBHsw, SI, (DBHsw)×(DBH)

White spruce (DBH≥9.1 cm):

BA, Nhasw, DBHsw, SI, (DBHsw)×(DBH)

Lodgepole pine (DBH≥1.1 cm and DBH≥9.1 cm):

BA, DBHpl, SCpl1

Aspen (DBH≥1.1 cm):

BA, log(BAaw), DBHaw, SCaw1

Aspen (DBH≥9.1 cm):

BA, log(BAaw), log(DBHaw), SCaw1

Black spruce (DBH≥1.1 cm):

log(BA), log(Nhasb), DBHsb, log(DBHsb)

Black spruce (DBH≥9.1 cm):

log(BA), log(Nhasb), DBHsb, DBH^2sb

The significant variables and interaction terms were different for the four species, which indicates that the factors influencing ingrowth process are not identical, and the relations between ingrowth occurrence and explanatory variables differ considerably. The corresponding models were:

white spruce model (2.24) (DBH≥1.1 cm)

$$P = \left[1 + \exp\left(-\left(\beta_0 + \beta_1 BA + \beta_2 \log(Nhasw) + \beta_3 DBHsw + \beta_4 SI + \beta_5 (DBHsw * DBH)\right)\right)\right]^{-1/L}$$

white spruce model (2.25) (**DBH≥9.1 cm**)

$$P = \left[1 + \exp\left(-\left(\beta_0 + \beta_1 BA + \beta_2 Nhasw + \beta_3 DBHsw + \beta_4 SI + \beta_5 (DBHsw * DBH)\right)\right)\right]^{-1/L}$$

lodgepole pine model (2.26) (**DBH≥1.1 cm**)

$$P = \left[1 + \exp\left(-\left(\beta_0 + \beta_1 BA + \beta_2 DBHpl + \beta_3 SCpl1\right)\right)\right]^{-1/L}$$

lodgepole pine model (2.27) (**DBH≥9.1 cm**)

$$P = \left[1 + \exp\left(-\left(\beta_0 + \beta_1 BA + \beta_2 DBHpl + \beta_3 SCpl1\right)\right)\right]^{-1/L}$$

aspen model (2.28) (**DBH≥1.1 cm**)

$$P = \left[1 + \exp\left(-\left(\beta_0 + \beta_1 BA + \beta_2 DBHaw + \beta_3 \log(BAaw) + \beta_4 SCaw1\right)\right)\right]^{-1}$$

aspen model (2.29) (**DBH≥9.1 cm**)

$$P = \left[1 + \exp\left(-\left(\beta_0 + \beta_1 BA + \beta_2 \log(DBHaw) + \beta_3 \log(BAaw) + \beta_4 SCaw1\right)\right)\right]^{-1}$$

black spruce model (2.30) (**DBH≥1.1 cm**)

$$P = \left[1 + \exp\left(-\left(\beta_0 + \beta_1 \log(BA) + \beta_2 \log(Nhasb) + \beta_3 DBHsb + \beta_4 \log(DBHsb)\right)\right)\right]^{-1/L}$$

black spruce model (2.31) (**DBH≥9.1 cm**)

$$P = \left[1 + \exp\left(-\left(\beta_0 + \beta_1 \log(BA) + \beta_2 \log(Nhasb) + \beta_3 DBHsb + \beta_4 (DBHsb * DBHsb)\right)\right)\right]^{-1/L}$$

The fit statistics for the above eight models are listed in Table (2-4) to Table (2-11) for white spruce, lodgepole pine, aspen and black spruce. All parameters are significant. The Hosmer-Lemeshow test was used to test the goodness-of-fit. The observed ingrowth occurrence number and predicted ingrowth occurrence number for each group are also listed in Table (2-4) to Table (2-11). At level α=0.05, there was no significant difference between the predicted and actual ingrowth occurrence probability.

The inverse of interval (1/L) was not used in the aspen models (2.28) and (2.29) as an exponent like other species' models. When 1/L was used for aspen models as exponent, there was significant difference between the predicted and actual ingrowth occurrence probability when goodness-of-fit test was conducted. Further analysis showed that ingrowth occurrence probability for aspen was not changed as the length of re-measurement interval increased (see Figure 2-3), and parameter was not significant when model (2.28) and (2.29), in which L was as a concomitantly independent variable instead of as an exponent, was fitted. These facts shows us that ingrowth occurrence probability for aspen does not increase as the length of re-measurement interval increases. This may be explained by following argument:

(1) shorter recruitment period of aspen. After disturbance such as fire or clearcut harvesting, aspen quickly dominates sites by regenerating from root sprouts (Schier 1981). Most of aspen suckers occur within the first couple years after disturbance. Conifer species are usually regenerated from seed and some seeds can come from a relatively long distance. This may suggest that conifer species regeneration continues for a relatively longer period than aspen. Ingrowth and regeneration are intimately related; ingrowth is the direct result of past patterns of regeneration (Shifley 1990).

(2) high understory mortality of aspen. Ingrowth trees are those which survive long enough and grow large enough to reach the threshold diameter and there is a clear link between growth and competition (Hilt 1985, Shifley 1987) and between survival and competition (Monserud 1976, Buchman et al. 1983). Kowalski (1993) found that the young generation has differentiated with time in height regard, creating three groups of trees: seedlings, small saplings and tall saplings. Part of the tallest group trees has became ingrowth trees to the main stand, while the remaining trees have been subject to succumbing. He indicated that during the observation period half of ingrowth trees died and the intensity of succumbing was lowest in shade-tolerant species such as hornbean, and highest in shade-intolerant species such as aspen. The small existing numbers of ingrowth trees of shade-intolerant species have been reduced so that at the end observation period some of them did not exist any more and some others were represented by rare single trees (Kowalski 1993). There have been few ingrowth trees of shade-intolerant species and trees of shade-intolerant species have rarely produced ingrowth in stands dominated by hornbean and spruce (Kowalski 1993). Aspen is shade-intolerant and usually occupies the upper layer of the canopy. The mortality of understory aspen increases as the size of aspen increases, because the larger aspen trees need more light and competition for light between trees increases. White spruce and black spruce are relatively shade-tolerant and can survive in the understory of stand. In most of the stands there was a wide range in the age of the white spruce, reflecting nearly continuous recruitment. The period of white spruce recruitment may be relatively short, i.e., 15-20 years, or continue for decades, producing an uneven-aged

understory (Lieffers et al. 1996b). The PSP plots were established and remeasured since the early sixties, and most of them were initially 30 years or older. This means that most aspen ingrowth trees should come from understory. The mortality of understory aspen may increase as the length of interval increases, so the aspen ingrowth occurrence probability should not increase as the length of interval increases.

(3) relatively even age/size distribution. Aspen stands usually present relatively uniform size and even-aged distribution comparing conifer species stands. The shade-intolerant aspen shows faster juvenile growth and the conifer species exhibits slow juvenile growth. Aspen grows past the DBH=9.1 cm over a shorter time period than the conifer species. So the aspen ingrowth occurrence probability is less influenced by the length of interval. Kowalski (1993) found that the process of hornbean ingrowing has been still occurring and suggested that this may be seen a consequence of slow growing rates of the species. As described previously, most of PSP plots were initially 30 years or older and the length of remeasurement interval varies from 2.2 to 19 years. Therefore, the aspen models (2.28) and (2.29) may only be suitable for adult stands with a relatively short length of remeasurement interval. For juvenile stands, aspen ingrowth occurrence probability may increase as the length of interval increases and this should be easily shown once the data of the juvenile stands are available.

An example of the model application is given here. The objective of this study is to predict the annual amount of ingrowth trees, so L=1 is used usually. For a plot with white spruce average DBH 16cm and density 1200 trees/ha with total basal area 30 m^2/ha and site index 16 m, based on the fitted generalized logistic model (2.24), the estimate of the one-year ingrowth occurrence probability for white spruce is equal to

$$P = \left[1 + \exp\left(-\left(2.20586 - 0.28227BA + 1.93020\log(Nhasw) - 0.78553DBHsw + 0.10910SI + 0.01348(DBHsw * DBH)\right)\right)\right]^{-1}$$

$$=0.618111$$

2.6.2 Amount of ingrowth

2.6.2.1 Model fitting

First, the linearized model (2.20) and (2.21) were fitted. The linear least squares fits of equation (2.20) and (2.21) were accomplished using the PROC REG procedure on SAS software (SAS

Institute Inc. 1992). Nhasp, BA, SCsp, SIsp and DBH^2 were also incorporated into intercept term $\log(\alpha)$ of the linear model (2.20) and (2.21). Since using stepwise regression analysis to select variables often includes an unnecessarily large number of variables, and the fitted model may perform poorly when it was used near the limits of the data (Vanclay 1994), the maximum R^2 improvement technique (MAXR) developed by Goodnight (1979) was utilized in variable selection (SELECTION=MAXR). The MAXR method did not select a single model. Instead, it tried to give the best one-variable model, the best two-variable model, and so forth (SAS Institute Inc. 1992). Checking all the models, the one with most reasonable statistical and biological properties was selected. The selected linear model for white spruce was

$$(2.32)\quad \log(I_{1.1}) = [\log(\alpha_1) + \alpha_2\, Nhasw + \alpha_3\, BA + \alpha_4\, SIsw + \alpha_5\, DBHsw^2\,] \\ +\beta \log(DBHsw) - \gamma\, DBHsw$$

and

$$(2.33)\quad \log(I_{9.1}) = [\log(\alpha_1) + \alpha_2\, Nhasw + \alpha_3\, BA + \alpha_4\, SIsw + \alpha_5\, DBHsw^2\,] - \beta DBHsw$$

where α_1, α_2, α_3, α_4, α_5, β, and γ were parameters (see Table 2-12 to Table 2-19 for estimates). Comparing equation (2.20) to (2.18) and equation (2.21) to (2.19), the final relationship between parameter α and other variables was

$$(2.34)\quad \alpha = \alpha_1\ exp\ (\alpha_2\, Nhasw + \alpha_3\, BA + \alpha_4\, SIsw + \alpha_5\, DBHsw^2)$$

With the initial estimates for the parameters from the linear fit, the nonlinear regression was used to fit the model

$$(2.35)\quad I_{sw1.1} = \alpha DBHsw^{\beta} \exp(-\gamma DBHsw)$$

$$\text{with } \alpha = \alpha_1\ exp\ (\alpha_2\, Nhasw + \alpha_3\, BA + \alpha_4\, SIsw + \alpha_5\, DBHsw^2)$$

$$\beta = \beta_1$$

$$\gamma = \gamma_1$$

and

$$(2.36)\quad I_{sw9.1} = \alpha \exp(-\beta DBHsw)$$

$$\text{with } \alpha = \alpha_1\ exp\ (\alpha_2\, Nhasw + \alpha_3\, BA + \alpha_4\, SIsw + \alpha_5\, DBHsw^2)$$

$$\beta = \beta_1$$

to the data set again. Furthermore, some explanatory variables were also tried to form the parameters β and γ of (2.35) and (2.36) for any further improvement of the fit. A positive sign of α_1, α_2, α_3, α_4, α_5, and β_1 in equation (2.35) and α_1, α_2, α_3, α_4, α_5 in equation (2.36) indicated a positive effect on ingrowth, and a negative sign of γ_1 in equation (2.35) and β_1 in equation (2.36) indicated a negative effect on ingrowth.

With the similar analysis, the final ingrowth amount models for lodgepole pine were found as

(2.37) $I_{pl1.1} = \alpha DBHpl^{\beta} \exp(-\gamma DBHpl)$

with $\alpha = \alpha_1 \; exp\,(\alpha_2\, Nhapl + \alpha_3\; BA + \alpha_4\, SCpl2)$

$\beta = \beta_1$

$\gamma = \gamma_1$

and

(2.38) $I_{pl9.1} = \alpha \exp(-\beta DBHpl)$

with $\alpha = \alpha_1 \; exp\,(\alpha_2\, Nhapl + \alpha_3\; BA)$

$\beta = \beta_1$

The final models for aspen were:

(2.39) $I_{aw1.1} = \alpha DBH^{\beta} \exp(-\gamma DBH)$

with $\alpha = \alpha_1 \; exp\,(\alpha_2\, Nhaaw + \alpha_3\; BA + \alpha_4\, SCaw1 + \alpha_5\, DBH^2)$

$\beta = \beta_1$

$\gamma = \gamma_1$

and

(2.40) $I_{aw9.1} = \alpha \exp(-\beta DBH)$

with $\alpha = \alpha_1 \; exp\,(\alpha_2\, BA + \alpha_3\, SCaw2 + \alpha_4\, DBH^{3\,2})$

$\beta = \beta_1$

The final models for black spruce were:

(2.41) $I_{sb1.1} = \alpha DBHsb^{\beta} \exp(-\gamma DBHsb)$

with $\alpha = \alpha_1 \; exp\,(\alpha_2\, log(Nhasb) + \alpha_3 Nhasb + \alpha_4\, BAsb + \alpha_5\, SCsb2 + \alpha_6\, DBHsb^2)$

$\beta = \beta_1$

$$\gamma = \gamma_1$$

and

(2.42) $I_{sb9.1} = \alpha \exp(-\beta DBHsb)$

$$\text{with } \alpha = \alpha_1 \exp(\alpha_2 \log(Nhasb) + \alpha_3 BAsb + \alpha_4 SCsb2 + \alpha_5 DBHsb^{3/2})$$

$$\beta = \beta_1$$

In model (2.37) to (2.42), SI were not included because it did not contribute significantly to explain the variation in ingrowth.

The fits of equation (2.35) to (2.42) were accomplished using procedure PROC NLIN on SAS/STAT software (SAS Institute Inc. 1992). The nonlinear least squares method minimizing the sum squared error was used to estimate the parameters. The Marquardt iterative method METHOD=MARQUARDT (Marquardt 1963) was applied to solve the nonlinear least square equations. To ensure the solution was global rather than local, multiple starting values for parameter estimates were provided.

By examining plots of the studentized residuals against predicted ingrowth, no definite pattern was seen, indicating that the model is appropriately identified and fitted. The residual plot for white spruce is shown in Figure 2-4. The fit statistics including the nonlinear least square estimates for the parameters, the mean squared error (MSE), and the coefficient of determination (R^2) are listed in Table 2-12 to Table 2-19. The R^2 was calculated as

$$(2.43)\quad R^2 = 1 - \frac{\sum_{i=1}^{n} (Ii - \hat{Ii})^2}{\sum_{i=1}^{n} (Ii - \bar{I})^2}$$

where Ii was the observed amount of ingrowth and $\hat{Ii}$ was the predicted amount of ingrowth for the i-th plot (i= 1, 2, ..., n), and $\bar{I}$ was the average observed amount of ingrowth.

All the parameter estimates corresponding to each independent variable were significant at $\alpha = 0.05$ level. The coefficients of determination (R^2) are from 0.3136 to 0.7157 for the ingrowth amount models. Some of them are not high. This reflects the variability in the ingrowth process itself.

2.6.2.2 Model testing

The remaining data, which were not used to fit the model, were used for testing the model performance. The test data included 178 and 177 observations for white spruce, 173 and 169 for lodgepole pine, 135 and 117 for aspen, 265 and 250 for black spruce. For the four species, the actual amount of ingrowth from the test data was compared with the amount of ingrowth predicted by model (2.35) to (2.42) using the estimated coefficients in Table 2-12 to Table 2-19. The difference between the predicted amount of ingrowth and actual amount of ingrowth was calculated for each observation. The mean and the standard deviation of the difference were computed and listed in Table 2-20 for each species. A t-test of the null hypothesis that the mean of the difference was zero was conducted according to the method described by Rawling (1988). The t statistics were equal to -1.2645 and -1.3781 for white spruce models, 0.7961 and 0.8472 for lodgepole pine models, 0.8621 and -0.2417 for aspen models, and 0.0371 and 0.9622 for black spruce models. The corresponding p-values for the t-test were 0.2077 and 0.1699, 0.4271 and 0.3981, 0.3902 and 0.8094, and 0.9704 and 0.3369, respectively. There was no evidence to against the null hypothesis at $\alpha = 0.05$ level. This infers that the prediction was an unbiased estimate of the actual amount of ingrowth. The results of the model testing indicate that the models appropriately describe the data and perform well when predictions are made.

The ingrowth amount models as expressed by equation (2.35) to (2.42) provide predictions of number of ingrowth trees per year, per hectare for white spruce, lodgepole pine, aspen, and black spruce given that ingrowth was known to occur. Asymptotic fit statistics in Table 2-12 to Table 2-19 show that the models agrees reasonably well with the ingrowth data. The model parameters corresponding to each independent variable in the models are all significant at $\alpha = 0.05$ level. The models were developed on appropriately chosen base functions and have the flexibility to assume various shapes with different parameter values and produced satisfactory curves under most circumstances.

An example of the model application is given here. For a plot with white spruce average DBH 16 cm and density 1200 trees/ha with total basal area 30 m^2/ha and site index 16 m, based on the fitted nonlinear model (2.35), the estimate of number of ingrowth trees per year, per ha for white spruce, given that it is known to occur, is equal to

$$I_{sw1\,i} = 0.34100 * EXP(0.00024 Nhasw - 0.02065 BA + 0.03723 SIsw + 0.00920 DBHsw^2)\, DBHsw^{3.69665} \exp(-0.65308 DBHsw)$$
$$= 3.853405$$

The equation (2.3) for this example may be written as

$$(2.44)\quad \hat{A}_i = \hat{P}_i \hat{I}_i + (1 - \hat{P}_i)0 = \hat{P}_i \hat{I}_i$$

where $\hat{A}_i$ is the estimated amount of ingrowth per year per ha for the i-th plot; $\hat{P}$ is the estimated probability that ingrowth occurs in the i-th plot; and $\hat{I}_i$ is the estimated amount of ingrowth per year per ha for the i-th plot given it occurs. So the average number of white spruce ingrowth trees per year per ha for the plots with white spruce average DBH 16 cm and density 1200 trees/ha with total basal area 30 m^2/ha and site index 16 m is estimated as,

$$\begin{aligned}\hat{A}_i &= \hat{P}_i \hat{I}_i \\ &= 0.618111 \times 3.853405 \\ &= 2.381831\end{aligned}$$

2.7 Discussion

The generalized logistic models for ingrowth occurrence probability as expressed by equations (2.24) to (2.31) and the nonlinear models for amount of ingrowth as expressed by equations (2.35) to (2.42) provide stand level predictions of ingrowth for white spruce, lodgepole pine, aspen, and black spruce grown in Alberta. The models for these four species confirm some commonly held beliefs and trends about ingrowth. While the following discussion attempts to address the effect of some individual variables, it is important to recognize that ingrowth is jointly predicted by the combination of all the variables.

For all models, the negative coefficients of DBH and positive coefficients of DBH^2 or DBH$^{3\,2}$ indicate that ingrowth occurrence probability and the amount of ingrowth are relatively lower when stand average DBH is large. With increasing DBH, ingrowth occurrence probability and the amount of ingrowth become smaller, then increase again for white spruce and black spruce, and continue decreasing for lodgepole pine. But for aspen, with increasing DBH, ingrowth occurrence probability and the amount of ingrowth become smaller, then only the amount of ingrowth begins to go up again. This may indicate that in mature stage, aspen ingrowth seldom occurs, and probably most of them occurs in the pure even-aged aspen stands, not in mixedwood stands. Burk (1978) indicated that the average size of aspen trees is larger in mature pure even-aged aspen stands, and that larger aspen trees are contributing more to the stocking level and for a given stocking level, there are fewer number of trees per acre, so more "space" is available for saplings to grow and reach the threshold DBH. He reported that this could also be related to the size of root systems on these larger trees, since the root systems probably cover large areas, reproduction from sucking is enhanced. Therefore, as stands get mature an increase of the number of aspen ingrowth trees should be expected in the pure aspen or aspen-dominated stands. White spruce and black spruce are relatively shade-tolerant and can survive in the understory of a stand. The uneven age distribution of juvenile stands indicated that recruitment of spruce continued for some time (Yao 1997). The longer period of white spruce recruitment can produce an uneven-aged understory (Lieffers et al. 1996b). This may indicate that more sapling trees in the understory will grow past over the threshold DBH and results in more ingrowth trees available as the stands get mature and some old trees die. In natural and seeded pine stands, lodgepole pine relies only on germination of seeds to reestablish, and most lodgepole pine trees appeared within 2-15 years after scarification. Over time the range of ages remained narrow indicating little or no ongoing lodgepole pine recruitment. Unlike white spruce, lodgepole pine shows a classic even-aged distribution. This may explain why ingrowth occurrence probability and the amount of ingrowth become smaller and smaller for lodgepole pine with increasing DBH.

The effect of total basal area is negative, as presented by negative coefficients in the models. The stand basal area measures stand competition. There is less growing space available for ingrowth trees in the stands where basal area is larger. At the same time, light transmission decreases as increasing stand basal area, which may suggest that effects of shrubs or grass on ingrowth trees are not critical because shrubs or grass are greatly reduced when stand basal area is large. Lieffers et al. (1993) observed that the cover and height of *C. canadensis* and *E. angustifolium* decreased with decreasing light transmission; at 40% light, both species were greatly reduced compared with open-grown conditions and both were virtually eliminated form stands with less than 10% light, in the stands which overstories were dominated by *Populus tremuloides* Michx., *P. glauca*, or were a mixture of these two species. With other factors being equal, the number of ingrowth trees should decrease as levels of competition increase (Shifley 1993).

In general, large number of trees per area are associated with stands comprised of individuals of small mean size, leading to a higher rate of ingrowth (Shifley et al. 1993). The positive coefficient for total number of trees by species indicates that the ingrowth occurrence probability and the number of ingrowth trees increased as the number of the same species trees per acre increased. Several previous researchers obtained the similar conclusion (Moser 1972, Ek 1974, Vanclay 1993, McTague et al. 1994, McTague et al. 1995).

Species composition has positive coefficients in equations (2.26), (2.27) and (2.37) for lodgepole pine, in equations (2.28), (2.29), (2.39) and (2.40) for aspen, and in equations (2.30), (2.31), (2.41) and (2.42) for black spruce. This indicates that the species composition positively impacts ingrowth for these three species. The ingrowth occurrence probability and the number of ingrowth trees should be positively associated with the number of the same species trees in the parent stand.

Site index was used as an explanatory variable only in white spruce models. The positive coefficients of site index in equations (2.24), (2.25), (2.35) and (2.36), may indicate that the site productivity has a positive impact on ingrowth. Site index was not included in ingrowth models of lodgepole pine, aspen and black spruce because it did not contribute significantly to explain the variation in ingrowth. The relationships between site productivity and number of ingrowth trees may be influenced by many factors simultaneously and further research is needed. Ek (1974) reported no significant relationship between site quality and the number of ingrowth trees. Hann (1980), working with ponderosa pine, developed an ingrowth model based on site index and on the basal area of trees above the 3 inches ingrowth threshold DBH. His model predicted increased ingrowth at higher site indices, but he noted that modifications of his initial model were required because the sign of the site index coefficient was not considered reasonable. In Shifley's study, he found that the relationship between site index and the number of ingrowth trees was positive for the 5- and 9-inch threshold DBH, but negative for the 1-inch threshold DBH, and found that addition of the site index term did not significantly improve the regression ($\alpha=0.05$) and therefore it was not used in his ingrowth model. Huang and Titus (1995) indicated that the boreal mixed species regions in Alberta, although covering a wide range of areas, have relative similar site conditions, so site variations might not be very large. In Burk (1978)'s study modelling lake states aspen ingrowth, site index was not included in his model because of the narrow range of site index. The fact that all correlation coefficients between ingrowth and site index are low and some not significant (Table 2-2) may contribute to a better understanding between site index and number of ingrowth trees. Theoretically, height growth is sensitive to differences in site quality, little affected by varying density levels and species compositions, relatively stable under varying thinning intensities, and strongly correlated with volume (Avery and Burkhart 1994). The fact, that site index is based on the average height of the dominant (or dominant and codominant) trees in the stand at a specified reference age, may tell us that it is little affected by stand density. So site index may not be a good indicator to reflect the change of stand density, and furthermore understory growing space and light. Therefore, site index may not be expected to be a good explanatory variable in ingrowth models. Huang and Titus (1995) recognized that defining a measure of site for uneven-aged and mixed-species stands and incorporating it into a model is a rather difficult problem. Therefore, further research regarding the methodologies for evaluating site productivity in uneven-aged and mixed-species stands may help improve the understanding of the real site effect on ingrowth.

The two-stage model shows a marked advantage over single model. The residuals about a single model are rarely either normally distributed or homogeneous, so the usual confidence intervals and tests of hypotheses that are based on the assumption of a normal, homogeneous distribution of residuals may not be adequate approximations (Hamilton and Brickell 1983). However, statistically sound approximations to confidence intervals and tests of hypotheses for the parameters of each of the components of the probabilistic two-stage method may be computed (Hamilton and Brickell 1983). The second major advantage is that the two-stage model is a much higher resolution model than single model. Hamilton and Brickell (1983) indicated that by using the knowledge that the process of interest is a two-state system in model development, the modeler is able to more completely describe the process than would be possible with a single model, regardless of its functional form. The estimation of amount of ingrowth discussed in the previous section provides a good example of this difference in model resolution. With a single model, we would only know that a plot with white spruce average DBH 16 cm and density 1200 trees/ha with total basal area 30 m^2/ha and site index 16 m would have an average of 2.38 white spruce ingrowth trees per year per ha. Each plot with white spruce average DBH 16 cm and density 1200 trees/ha with total basal area 30 m^2/ha and site index 16 m in the stand would be predicted to have this amount of white spruce ingrowth trees. However, we know that white spruce ingrowth will not occur in some plots with the same stand conditions. This information is used as part of the two-stage probabilistic model. The model predicts that there will be an average of 2.38 white spruce ingrowth trees per year per ha in a plot with white spruce average DBH 16 cm and density 1200 trees/ha with total basal area 30 m^2/ha and site index 16 m. However, the model also tells us that only 68.81% of the plots can be expected to have any ingrowth trees and that those plots with ingrowth trees can be expected to have 3.85 white spruce ingrowth trees per year per hectare. Thus, the higher resolution two-stage probabilistic model more fully describes the ingrowth process.

While the two-stage ingrowth models reveal the effects of the stand conditions and site quality on ingrowth occurrence probability and the number of ingrowth trees for each species, and this may provide some useful information about ecology and silviculture of these four major species growing in boreal mixed stands in Alberta, the models are mainly developed for stand-level ingrowth predictions in natural stands. The linear relationships between ingrowth and stand conditions such as stand average DBH, density and total basal area, may not exist forever because of stand succession. In Shifley et al. (1993) study, they found that ingrowth increases as CCF increases, up to a CCF of about 100, then decreases with CCF of above 100, and that the ingrowth increases with increasing density (number of trees or basal area) for stands with low CCF values (understocked stands), and decreases with increasing density for stands with high CCF values (full-stocked stands).

The precision of the ingrowth models is not as high as expected on an absolute scale. This is reflected in the low R-squared values and in the magnitude of the residual error variance. The R-squared values are relatively low, indicating that the number of ingrowth trees is highly variable. This variability in ingrowth is due in part to factors that are not account for in the models (e.g. ecoregion and forest type) and in part to the stochastic nature of the ingrowth process. The coefficients of variation for the number of ingrowth trees are relatively high (169-352%), further emphasizes the extreme variability inherent in this data set and reflects the variability in the ingrowth process itself. Even though precision of some models in an absolute sense is not high, the amount of variation accounted for by these models relative to the total variation in ingrowth is significant.

Ingrowth is a highly variable process. Ingrowth at any given time is the cumulative result of events and conditions over several previous years, including the factors of seed source, regeneration success, weather, and anthropogenic disturbance. Shifley et al. (1993) reported that the number and species of ingrowth trees are characterized by large stochastic elements and all these factors contribute to the difficulty of estimating ingrowth.

Vanclay indicated (1991) that ingrowth is a rather unpredictable process, and specific predictions (i.e., individual plot, single occasion) remain poor, but stand-level trends can be predicted with greater confidence. Shifley (1993) stated that significant increases in precision of ingrowth predictions seem unlikely without expanding the suite of independent variables considered or recalibrating the model for a more limited set of forest conditions, but improved predictions may be possible by incorporating additional site-specific information (e.g., site index, habitat type, or soils), or by performing the analysis on a more geographically or ecologically restricted data set. He thought that first approach is feasible, but second may not because geographical and ecological information is not available in most inventory data.

The analyses conducted in this study have raised a number of issues that merit further investigation.

1. Developing different ingrowth models for different ecoregions or forest types. The data sources in this study span all province and include stands representing a wide range of ecoregions, forest types and stand conditions and stand histories. The diversity of ecoregions and forest types complicated the analyses and introduce sources of variation that may obscure subtle trends associated with individual ecoregion or forest type. Within a particular data set (e.g. a particular ecoregion or forest type), it is likely that the accuracy of estimates could be improved by incorporating additional independent variables, because stands from the same ecoregion or forest type usually have similar stand history and site condition, therefore the variance of ingrowth may be low. Because no enough data are available for each individual

ecoregion or forest type, ingrowth models were not developed based on ecoregions or forest types in this study.

2. Using more suitable measures for density, competition and available growing space. Because number of ingrowth trees is highly correlated with available growing space and competition, an accurate measure of available growing space and competition is an important component of any growth prediction model. CCF may be a good candidate to evaluate available growing space for boreal mixed-species stands in Alberta. Shifley (1990) reported that CCF, based on crown widths of open-grown trees, can be widely applied to evaluate the degree of crowding in a stand, including stands with mixed-species and multiple size classes.
3. Considering the relationships between ingrowth and species shade tolerance level. The ratios of ingrowth presence against absence, which are 1.30:1 for black spruce, 1.00:1 for white spruce, 0.44:1 for lodgeppole pine, and 0.36:1 for aspen, show that ingrowth process is influenced strongly by species shade tolerance. Jones et. al. (1994) found that shade tolerance species, especially small tree life forms, had the greatest ratios of ingrowth to mortality in seven South Carolina mixed-species forests. They reported the flux data showed that shade tolerant species may achieve high ingrowth to mortality ratios in two distinct ways: by high survival rates in a shaded forest understory (low flux species) and by rapid replacement of dead stems (high flux species). Higher rates of ingrowth occurrence should associated with more shade tolerant species.
4. One of the best ways to gauge the quality of a model is to compare model predictions with independent data. Such comparisons are especially important in multistage models such as present one. The goodness-of-fit test with the raw data used in model fitting for logistic models and model testing with the raw data, which was not used in model fitting, for nonlinear models were conducted in this study. Independent validation should be made when independent data become available.

In summary, two sets of stand-level, two-stage ingrowth models were developed to predict periodic annual ingrowth for the four major species in mixedwood stands of Alberta. The first stage predicts the probability of ingrowth occurrence from stand basal area, density, DBH, species composition and site productivity in the existing stand. The second stage indicates the expected amount of ingrowth, given that it is known to occur, and employs stand basal area, density, DBH, species composition and site productivity. The generalized logistic models developed in this study can obtain a satisfactory predictions for data with unequal length of remeasurement interval and avoid double correction that will underestimate the expected ingrowth. Using appropriately selected base functions, and the method of parameter prediction (Clutter et al. 1983, Huang and Titus 1995), the ingrowth amount models were elaborated as functions of explanatory variables. The selected exponential base function prevented the predicted ingrowth values from being negative in some situations. The data were from Alberta Land and Forest Services permanent sample plots. Both stand statistics based on all trees with DBH≥1.1 cm and all trees with DBH≥9.1 cm were used to develop the models. Input variables of the models are simple stand variables that are readily obtainable from ordinary inventories, and compatible with the data-collection process in Alberta.

Table 2-1. Summary statistics (1) for stand characteristics by ingrowth present status (based on all trees with DBH ≥1.1 cm)

Species	Ingrowth	N	Variable	Mean	Std. Dev.	Minimum	Maximum
White spruce	Presence	740	INGROWTH	3.7460811	4.6380258	0.3000000	46.7000000
			BA	39.1168127	8.5987483	11.5494000	69.0042000
			Nhasw	978.5486486	892.5839815	10.0000000	7210.00
			DBH	18.1809459	5.8524391	5.4000000	37.9000000
			DBHsw	18.1025676	6.4800375	4.3000000	39.9000000
			SIsw	16.8779730	4.1697946	4.9000000	34.9000000
			L	9.9340541	3.7898022	2.2000000	18.9000000
	Absence	735	BA	42.2591638	9.3015327	8.6541000	87.9113000
			Nhasw	572.3360544	477.3278196	10.0000000	3459.00
			DBH	20.8223129	5.7554587	6.2000000	39.7000000
			DBHsw	24.2190476	7.1002565	8.5000000	58.0000000
			SIsw	16.6575510	4.4146733	3.8000000	27.1000000
			L	8.0857143	3.6882389	1.2000000	17.1000000
Lodgepol pine	Presence	800	INGROWTH	13.3226250	20.5972889	0.3000000	146.4000000
			BA	34.8204157	9.9580681	1.3229000	59.2516000
			Nhapl	2721.31	2231.62	39.0000000	18366.00
			DBHpl	13.1656250	4.2150610	4.0000000	32.2000000
			SCpl1	0.8104757	0.2414361	0.0248000	1.0000000
			SCpl2	0.8766574	0.1853409	0.0311000	1.0000000
			L	10.0416250	3.4253132	2.2000000	19.0000000
	Absence	1793	BA	40.0915797	9.1020121	8.5138000	64.8399000
			DBHpl	22.7922476	7.0489488	9.6000000	47.8000000
			SCpl1	0.4369375	0.3584027	0.0030000	1.0000000
			L	9.0128834	3.6132563	1.5000000	19.0000000
Aspen	Presence	601	INGROWTH	7.1948419	18.2961560	0.3000000	228.7000000
			BA	32.5124532	8.5667864	1.6866000	61.1295000
			BAaw	18.6104188	12.0460317	0.0050000	50.7070000
			Nhaaw	921.7254576	1284.85	5.0000000	14980.00
			DBHaw	18.0633943	8.0895936	3.3000000	59.9000000
			DBH	18.2615641	6.5413584	3.3000000	40.0000000
			SCaw1	0.5962880	0.3471131	0.0052000	1.0000000
			L	8.7396007	3.8033576	2.2000000	18.9000000
	Absence	1646	BA	39.9619980	9.4867741	0.5554000	87.9113000
			BAaw	11.7854670	11.2674909	0.000900000	54.0136000
			DBHaw	22.7821993	8.1966339	1.5000000	54.2000000
			SCaw1	0.2749910	0.2870627	0.0010000	1.0000000
			L	9.1719927	3.8787911	1.2000000	18.9000000
Black spruce	Presence	1199	INGROWTH	12.7804003	39.6126737	0.3000000	699.5000000
			BA	39.0209931	10.5967421	1.8502000	83.8685000
			BAsb	10.5299712	11.1869549	0.0030000	58.3243000
			Nhasb	1466.86	1974.37	5.0000000	13762.00
			DBHsb	10.2925771	4.2271169	2.2000000	28.4000000
			SCsb2	0.2679669	0.2708174	0.000100000	1.0000000
			L	9.4844871	3.7945409	1.2000000	19.0000000
	Absence	924	BA	39.1745389	9.8815573	1.3863000	87.9113000
			Nhasb	305.9783550	597.2442562	5.0000000	6557.00
			DBHsb	15.0777056	5.9644778	1.7000000	42.1000000
			L	8.5634199	3.6005031	2.2000000	18.9000000

Table 2-2. Summary statistics (2) for stand characteristics by ingrowth present status (based on all trees with DBH ≥9.1 cm)

Species	Ingrowth	N	Variable	Mean	Std. Dev.	Minimum	Maximum
White spruce	Presence	728	INGROWTH	3.7788462	4.6678381	0.3000000	46.7000000
			BA	37.5328117	8.2273436	11.5329000	65.1335000
			Nhasw	608.9107143	466.0480626	10.0000000	2815.00
			DBHsw	22.5940934	5.8683593	12.1000000	41.0000000
			SIsw	16.8986264	4.1417820	4.9000000	34.9000000
			L	9.9410714	3.7877167	2.2000000	18.9000000
	Absence	727	BA	41.7043188	9.3994697	12.8480000	87.0983000
			Nhasw	496.4346630	368.8675930	10.0000000	2628.00
			DBHsw	25.7156809	6.7965051	13.5000000	58.0000000
			SIsw	16.6583219	4.4166239	3.8000000	27.1000000
			L	8.1057772	3.6916956	1.2000000	17.1000000
Lodgepol pine	Presence	785	INGROWTH	13.5355414	20.7334627	0.3000000	146.4000000
			BA	29.6856009	10.5017768	0.2491000	56.1696000
			Nhapl	1657.35	791.9360103	30.0000000	3630.00
			DBHpl	14.7073885	3.6003538	9.6000000	32.2000000
			SCpl1	0.8915599	0.1717414	0.0506000	1.0000000
			L	10.0541401	3.4353633	2.2000000	19.0000000
	Absence	1797	BA	38.6887258	8.8422203	8.4860000	64.4733000
			DBHpl	23.0616027	6.8648199	11.1000000	47.8000000
			SCpl1	0.4971955	0.3702833	0.0040000	1.0000000
			L	9.0119087	3.6125019	1.5000000	19.0000000
Aspen	Presence	512	INGROWTH	6.9451172	18.5398280	0.3000000	228.7000000
			BA	31.1750559	9.0194653	1.2750000	61.1295000
			BAaw	17.5273303	11.5524627	0.0321000	50.7070000
			DBHaw	24.8308594	11.5081025	9.1000000	132.3000000
			DBH	22.3779297	6.7886778	9.7000000	40.7000000
			SCaw1	0.5763225	0.3523061	0.0077000	1.0000000
			SCaw2	0.5817979	0.3535511	0.000800000	1.0000000
			L	8.3035156	3.7883366	2.2000000	18.9000000
	Absence	1448	BA	39.5293061	9.5049123	5.8496000	87.0983000
			BAaw	11.7433445	10.9841657	0.0343000	54.0025000
			DBHaw	26.3158840	9.8827394	9.3000000	122.2000000
			SCaw1	0.2802537	0.2840344	0.0039000	1.0000000
			L	9.0204420	3.9246598	1.2000000	18.9000000
Black spruce	Presence	1133	INGROWTH	13.3338041	40.6690540	0.3000000	699.5000000
			BA	35.8167547	10.8065214	0.3695000	83.1717000
			BAsb	6.6350372	8.5022960	0	51.5583000
			Nhasb	549.1076787	678.2532797	5.0000000	3654.00
			DBHsb	15.1120035	4.9636609	9.1000000	58.0000000
			SCsb2	0.2014147	0.2605048	0	1.0000000
			L	9.4437776	3.7779966	2.2000000	19.0000000
	Absence	863	BA	39.0779476	9.2330355	11.5329000	87.0983000
			Nhasb	187.6848204	322.1167812	5.0000000	2871.00
			DBHsb	18.1431054	5.5196313	9.1000000	44.8000000
			L	8.5703360	3.5813257	2.2000000	18.9000000

Table 2-3. Pearson correlation coefficients between the number of ingrowth trees and predictor variables (based on all trees with DBH ≥1.1 cm)

	INGROWTH			
	White spruce	**Lodgepole pine**	**Aspen**	**Black Spruce**
Nhasp	0.5401	0.6562	0.5633	0.6298
Nha	0.4576	0.4902	0.2566	0.5407
Basp	-0.0243*	0.0697	0.1810	0.3499
BA	-0.1673	-0.1316	-0.2413	-0.0208*
Htsp	-0.3381	-0.4725	-0.2439	-0.2986
Ht	-0.2893	-0.4459	-0.2363	-0.3634
SC_{SP1}	0.2062	0.2059	0.3284	0.4734
SC_{SP2}	0.0709	0.1911	0.2937	0.3776
SIsp	0.0232*	-0.1958	0.0747*	-0.2190
DBHsp	-0.4676	-0.4378	-0.2324	-0.3705
DBH	-0.3959	-0.4082	-0.2256	-0.4680
AGEsp	-0.1737	-0.2707	-0.1971	-0.1734

Note: * indicates the correlation is not significant at α=0.05 level.

Table 2-4. Parameter estimates for white spruce ingrowth probability model (2.24) (based on all trees with DBH ≥1.1 cm)

Variable	Degree-of-freedom	Parameter	Parameter estimate
INTERCEPT	1	β_0	2.20585675
BA	1	β_1	-0.28226727
log(Nhasw)	1	β_2	1.93020085
DBHsw	1	β_3	-0.78552514
SIsw	1	β_4	0.10909703
DBHsw*DBH	1	β_5	0.01347665

Log likelihood function is -799.1074

Log likelihood function ($\beta_0=\beta_1=\beta_2=\beta_3=\beta_4=\beta_5=0$) = -1829.299

Hosmer and Lemeshow goodness-of-fit test

		Number of ingrowth occurrence	
Group	Total number of observation	Observed	Expected
1	148	15	10.53429
2	148	34	28.29182
3	148	50	42.42686
4	148	54	57.80644
5	148	58	70.59791
6	148	74	81.50212
7	148	85	93.27918
8	148	107	106.2935
9	148	124	124.7324
10	146	141	142.1975

Hosmer and Lemeshow statistic = 14.02248 (p-value = 0.0811814)

Table 2-5. Parameter estimates for white spruce ingrowth probability model (2.25) (based on all trees with DBH ≥9.1 cm)

Variable	Degree-of-freedom	Parameter	Parameter estimate
INTERCEPT	1	β_0	19.025314453
BA	1	β_1	-0.363669917
Nhasw	1	β_2	0.004160624
DBHsw	1	β_3	-1.068804430
SIsw	1	β_4	0.066429341
DBHsw*DBH	1	β_5	0.020252160

Log likelihood function is -826.573

Log likelihood function ($\beta_0=\beta_1=\beta_2=\beta_3=\beta_4=\beta_5=0$) = -1807.811

Hosmer and Lemeshow goodness-of-fit test

		Number of ingrowth occurrence	
Group	Total number of observation	Observed	Expected
1	146	12	12.98722
2	146	38	31.60633
3	146	59	45.65349
4	146	61	57.70702
5	146	59	69.11558
6	146	72	78.94967
7	146	91	89.90207
8	146	93	100.5762
9	146	110	115.4555
10	141	133	133.2161

Hosmer and Lemeshow statistic = 14.97198 (p-value =0.0596926)

Table 2-6. Parameter estimates for lodgepole pine ingrowth probability model (2.26) (based on all trees with DBH ≥1.1 cm)

Variable	Degree-of-freedom	Parameter	Parameter estimate
INTERCEPT	1	β_0	22.0868453
BA	1	β_1	-0.2048297
DBHpl	1	β_2	-1.7573640
SCpl1	1	β_3	4.9600518

Log likelihood function is -906.683

Log likelihood function ($\beta_0=\beta_1=\beta_2=\beta_3=0$) = -4584.756

Hosmer and Lemeshow goodness-of-fit test

		Number of ingrowth occurrence	
Group	Total number of observation	Observed	Expected
1	259	1	0.1433036
2	259	3	2.536428
3	259	16	9.326323
4	259	25	21.72087
5	259	36	39.02296
6	259	50	61.16653
7	259	88	92.89154
8	259	132	134.4884
9	259	193	198.8214
10	262	256	257.5231

Hosmer and Lemeshow statistic = 15.40689 (p-value =0.05170026)

Table 2-7. Parameter estimates for lodgepole pine ingrowth probability model (2.27) (based on all trees with DBH ≥9.1 cm)

Variable	Degree-of-freedom	Parameter	Parameter estimate
INTERCEPT	1	β_0	16.4687141
BA	1	β_1	-0.2511109
DBHpl	1	β_2	-1.5415561
SCpl1	1	β_3	10.0363528

Log likelihood function is -919.5264

Log likelihood function ($\beta_0=\beta_1=\beta_2=\beta_3=0$) = -4593.536

Hosmer and Lemeshow goodness-of-fit test

		Number of ingrowth occurrence	
Group	Total number of observation	Observed	Expected
1	258	0	0.1483407
2	258	1	2.516563
3	258	15	9.555104
4	258	24	21.60322
5	258	31	39.10799
6	258	54	61.0133
7	258	95	92.66318
8	258	131	131.8438
9	258	187	188.1813
10	260	247	250.1334

Hosmer and Lemeshow statistic =8.78553 (p-value = 0.3607104)

Table 2-8. Parameter estimates for aspen ingrowth probability model (2.28) (based on all trees with DBH ≥1.1 cm)

Variable	Degree-of-freedom	Parameter	Parameter estimate
INTERCEPT	1	β_0	1.69462888
BA	1	β_1	-0.07039176
DBHaw	1	β_2	-0.07366143
log(BAaw)	1	β_3	0.40950987
SCawl	1	β_4	1.11044585

Log likelihood function is -1005.758

Log likelihood function ($\beta_0=\beta_1=\beta_2=\beta_3=\beta_4=0$) = -1557.502

Hosmer and Lemeshow goodness-of-fit test

Group	Total number of observation	Number of ingrowth occurrence Observed	Expected
1	225	9	6.668313
2	225	10	12.46621
3	225	20	18.90349
4	225	27	26.47274
5	225	36	35.75549
6	225	46	48.81852
7	225	65	67.50576
8	225	91	93.08856
9	225	131	126.4577
10	222	166	164.8632

Hosmer and Lemeshow statistic = 2.263664 (p-value =0.9718428)

Table 2-9. Parameter estimates for aspen ingrowth probability model (2.29) (based on all trees with DBH ≥9.1 cm)

Variable	Degree-of-freedom	Parameter	Parameter estimate
INTERCEPT	1	β_0	2.20321351
BA	1	β_1	-0.08908806
log(DBHaw)	1	β_2	-0.38234161
log(BAaw)	1	β_3	0.27178860
SCaw1	1	β_4	1.31466401

Log likelihood function is -895.7765

Log likelihood function ($\beta_0=\beta_1=\beta_2=\beta_3=\beta_4=0$) = -1358.568

Hosmer and Lemeshow goodness-of-fit test

		Number of ingrowth occurrence	
Group	Total number of observation	Observed	Expected
1	196	6	7.253569
2	196	14	13.15626
3	196	18	19.14227
4	196	22	24.85925
5	196	31	31.64252
6	196	51	41.5653
7	196	55	54.08434
8	196	74	75.29969
9	196	102	103.4412
10	196	139	141.555

Hosmer and Lemeshow statistic = 3.734995 (p-value =0.8802068)

Table 2-10. Parameter estimates for black spruce ingrowth probability model (2.30) (based on all trees with DBH ≥1.1 cm)

Variable	Degree-of-freedom	Parameter	Parameter estimate
INTERCEPT	1	β_0	-24.9788087
log(BA)	1	β_1	-0.9356382
log(Nhasb)	1	β_2	1.6951429
DBHsb	1	β_3	-1.9691353
log(DBHsb)	1	β_4	15.5156363

Log likelihood function is -1017.326

Log likelihood function ($\beta_0=\beta_1=\beta_2=\beta_3=\beta_4=0$) = -2384.763

Hosmer and Lemeshow goodness-of-fit test

		Number of ingrowth occurrence	
Group	Total number of observation	Observed	Expected
1	212	21	14.94836
2	212	42	43.9082
3	212	63	67.90618
4	212	77	91.06637
5	212	119	112.7417
6	212	136	135.6115
7	212	152	159.382
8	212	179	181.3033
9	212	200	197.5922
10	213	208	208.7259

Hosmer and Lemeshow statistic = 9.953009 (p-value =0.2683396)

Table 2-11. Parameter estimates for black spruce ingrowth probability model (2.31) (based on all trees with DBH ≥9.1 cm)

Variable	Degree-of-freedom	Parameter	Parameter estimate
INTERCEPT	1	β_0	23.48176012
log(BA)	1	β_1	-6.32573505
log(Nhasb)	1	β_2	2.26168009
DBHsb	1	β_3	-1.58324619
DBHsb^2	1	β_4	0.02999485

Log likelihood function is -1037.596

Log likelihood function ($\beta_0=\beta_1=\beta_2=\beta_3=\beta_4=0$) = -2230.752

Hosmer and Lemeshow goodness-of-fit test

		Number of ingrowth occurrence	
Group	Total number of observation	Observed	Expected
1	200	29	21.45692
2	200	58	49.84217
3	200	63	71.77085
4	200	88	89.94597
5	200	107	107.1044
6	200	109	124.4209
7	200	141	143.7958
8	200	163	165.9618
9	200	181	185.9889
10	196	194	194.6872

Hosmer and Lemeshow statistic = 14.33143 (p-value =0.07352553)

Table 2-12. Fit statistics for white spruce amount model (2.35)
(based on all trees with DBH ≥1.1 cm)

Parameter	Estimate	Asymptotic Std. Error	Asymptotic 95% Confidence Interval Lower	Upper	MSE	R^2
α_1	0.33662560	0.27410372	-0.20180763	0.875058841	8.640969	0.5226
α_2	0.00025289	0.00002543	0.00020294	0.00030284		
α_3	-0.01792562	0.00333806	-0.02448270	-0.01136853		
α_4	0.03924509	0.00518572	0.02905856	0.04943162		
α_5	0.00939836	0.00158109	0.00629256	0.01250415		
β_1	3.65126482	0.70741023	2.26166973	5.04085992		
γ_1	-0.65639556	0.10102329	-0.85483978	-0.45795134		

Model (2.35): $I_{sw1.1} = \alpha DBHsw^{\beta} \exp(-\gamma DBHsw)$

with $\alpha = \alpha_1 \; exp\,(\alpha_2\, Nhasw + \alpha_3\, BA + \alpha_4\, SIsw + \alpha_5\, DBHsw^2)$

$\beta = \beta_1$

$\gamma = \gamma_1$

Table 2-13. Fit statistics for white spruce amount model (2.36)
(based on all trees with DBH ≥9.1 cm)

Parameter	Estimate	Asymptotic Std. Error	Asymptotic 95% Confidence Interval Lower	Upper	MSE	R^2
α_1	329.810280	154.236968	26.8250162	632.7955433	12.346352	0.3136
α_2	0.0002934	0.00006897	0.00015789	0.00042885		
α_3	-0.0481681	0.00483011	-0.05765647	-0.03867977		
α_4	0.0184392	0.00741705	0.00386902	0.03300932		
α_5	0.0034521	0.00085707	0.00176844	0.00513573		
β_1	-0.2301176	0.04005106	-0.30879443	-0.15144070		

Model (2.36): $I_{sw9.1} = \alpha \exp(-\beta\, DBHsw)$

with $\alpha = \alpha_1\ exp\ (\alpha_2\, Nhasw + \alpha_3\, BA + \alpha_4\, SIsw + \alpha_5\, DBHsw^2)$

$\beta = \beta_1$

Table 2-14. Fit statistics for lodgepole pine amount model (2.37) (based on all trees with DBH ≥1.1 cm)

Parameter	Estimate	Asymptotic Std. Error	Asymptotic 95% Confidence Interval Lower	Upper	MSE	R^2
α_1	0.00105452	0.00152035	-0.00193188	0.00404091	87.56296	0.6519
α_2	0.00022812	0.00001854	0.00019170	0.00026454		
α_3	-0.04230614	0.00373910	-0.04965082	-0.03496147		
α_4	1.46257860	0.32011262	0.83378576	2.09137143		
β_1	8.80402295	1.18291592	6.48043745	11.12760845		
γ_1	-1.11802288	0.13432975	-1.38188496	-0.85416079		

Model (2.37): $I_{pl1.1} = \alpha DBHpl^{\beta}\exp(-\gamma DBHpl)$

with $\alpha = \alpha_1 \ exp\ (\alpha_2\ Nhapl + \alpha_3\ BA + \alpha_4\ SCpl2)$

$\beta = \beta_1$

$\gamma = \gamma_1$

Table 2-15. Fit statistics for lodgepole pine amount model (2.38)
(based on all trees with DBH ≥9.1 cm)

Parameter	Estimate	Asymptotic Std. Error	Asymptotic 95% Confidence Interval Lower	Upper	MSE	R^2
α_1	117.836101	42.6911464	33.97543979	201.69676276	72.65697	0.7257
α_2	0.0013980	0.00010491	0.00119189	0.00160405		
α_3	-0.1486555	0.01021244	-0.16871638	-0.12859461		
β_1	-0.0768177	0.03297792	-0.14159813	-0.01203730		

Model (2.38): $I_{pl9.1} = \alpha \exp(-\beta \mathit{DBHpl})$

with $\alpha = \alpha_1 \ exp\ (\alpha_2\ \mathit{Nhapl} + \alpha_3\ \mathit{BA})$

$\beta = \beta_1$

Table 2-16. Fit statistics for aspen amount model (2.39)
(based on all trees with DBH ≥1.1 cm)

Parameter	Estimate	Asymptotic Std. Error	Asymptotic 95% Confidence Interval Lower	Upper	MSE	R^2
α_1	0.1374636	0.1190040	-0.0964343	0.3713615	34.102676	0.4922
α_2	0.0000840	0.0000274	0.00003025	0.0001378		
α_3	-0.0211178	0.0065927	-0.0340755	-0.0081601		
α_4	1.5301190	0.2481779	1.0423348	2.0179033		
α_5	0.0127328	0.0016176	0.0095534	0.0159122		
β_1	4.9491302	0.7006351	3.5720584	6.3262020		
γ_1	-0.8791816	0.0960668	-1.0679972	-0.6903661		

Model (2.39): $I_{aw1.1} = \alpha DBH^{\beta} \exp(-\gamma DBH)$

with $\alpha = \alpha_1 \; exp\,(\alpha_2\, Nhaaw + \alpha_3\, BA + \alpha_4\, SCaw1 + \alpha_5\, DBH^2)$

$\beta = \beta_1$

$\gamma = \gamma_1$

Table 2-17. Fit statistics for aspen amount model (2.40)
(based on all trees with DBH ≥9.1 cm)

Parameter	Estimate	Asymptotic Std. Error	Asymptotic 95% Confidence Interval Lower	Upper	MSE	R^2
α_1	418.28642	237.15153	-47.768842	884.341689	42.779087	0.3888
α_2	-0.0266002	0.0059133	-0.0382212	-0.0149791		
α_3	1.0049360	0.1436203	0.7226902	1.2871818		
α_4	0.0634579	0.0140154	0.0359146	0.0910012		
β_1	-0.5060693	0.0970201	-0.6967353	-0.3154034		

Model (2.40): $I_{aw9.1} = \alpha \exp(-\beta DBH)$

with $\alpha = \alpha_1 \; exp \; (\alpha_2 BA + \alpha_3 SCaw2 + \alpha_4 DBH^{3/2})$

$\beta = \beta_1$

Table 2-18. Fit statistics for black spruce amount model (2.41)
(based on all trees with DBH ≥1.1 cm)

Parameter	Estimate	Asymptotic Std. Error	Asymptotic 95% Confidence Interval Lower	Upper	MSE	R^2
α_1	0.0005404	0.0005349	-0.0005093	0.0015902	55.39631	0.5332
α_2	0.4881194	0.0598039	0.3707417	0.6054972		
α_3	-0.0000578	0.0000225	-0.0001021	-0.0000136		
α_4	-0.0080267	0.0040373	-0.0159508	-0.0001027		
α_5	0.9364895	0.0970767	0.7459561	1.1270228		
α_6	0.0397347	0.0073072	0.0253927	0.0540766		
β_1	9.6624022	1.2532509	7.2026360	12.1221685		
γ_1	-2.0002860	0.2790964	-2.5480710	-1.4525010		

Model (2.41): $I_{sb1.1} = \alpha DBHsb^{\beta} \exp(-\gamma DBHsb)$

with $\alpha = \alpha_1 \exp(\alpha_2 \log(Nhasb) - \alpha_3 Nhasb - \alpha_4 BAsb - \alpha_5 SCsb2 - \alpha_6 DBHsb^2)$

$\beta = \beta_1$

$\gamma = \gamma_1$

Table 2-19. Fit statistics for black spruce amount model (2.42)
(based on all trees with DBH ≥9.1 cm)

Parameter	Estimate	Asymptotic Std. Error	Asymptotic 95% Confidence Interval		MSE	R^2
			Lower	Upper		
α_1	131.60558	51.536765	30.4474202	232.7637482	76.69054	0.3685
α_2	0.3273916	0.0327417	0.2631250	0.3916582		
α_3	-0.0161016	0.0043698	-0.0246787	-0.0075245		
α_4	0.7770506	0.1091372	0.5628324	0.9912689		
α_5	0.0713473	0.0072753	0.0570671	0.0856275		
β_1	-0.6077871	0.0537356	-0.7132613	-0.5023129		

Model (2.42): $I_{sb9.1} = \alpha \exp(-\beta DBHsb)$

with $\alpha = \alpha_1 \; exp\,(\alpha_2 \, log(Nhasb) + \alpha_3 \, BAsb + \alpha_4 \, SCsb2 + \alpha_5 \, DBHsb^{3.2})$

$\beta = \beta_1$

Table 2-20. The t-test statistics for the model testing

Species	**N**	**Mean**	**Std. Error.**	**T**	**Prob>|T|**
White spruce (DBH ≥1.1 cm)	178	-0.2619055	0.2071213	-1.2645025	0.2077
White spruce (DBH ≥9.1 cm)	177	-0.3150830	0.2286358	-1.3780996	0.1699
Lodgepole pine (DBH ≥1.1 cm)	173	0.5040359	0.6331518	0.7960744	0.4271
Lodgepole pine (DBH ≥9.1 cm)	169	0.5123612	0.6047505	0.8472275	0.3981
Aspen (DBH ≥1.1 cm)	135	0.3946927	0.4578462	0.8620641	0.3902
Aspen (DBH ≥9.1 cm)	117	-0.1051217	0.4348219	-0.2417580	0.8094
Black spruce (DBH ≥1.1 cm)	265	0.0173440	0.4672330	0.0371206	0.9704
Black spruce (DBH ≥9.1 cm)	250	0.5521899	0.5738723	0.9622173	0.3369

Figure 2-1. Plot of number of white spruce ingrowth trees against stand average DBH

(based on all trees with DBH ≥1.1 cm)

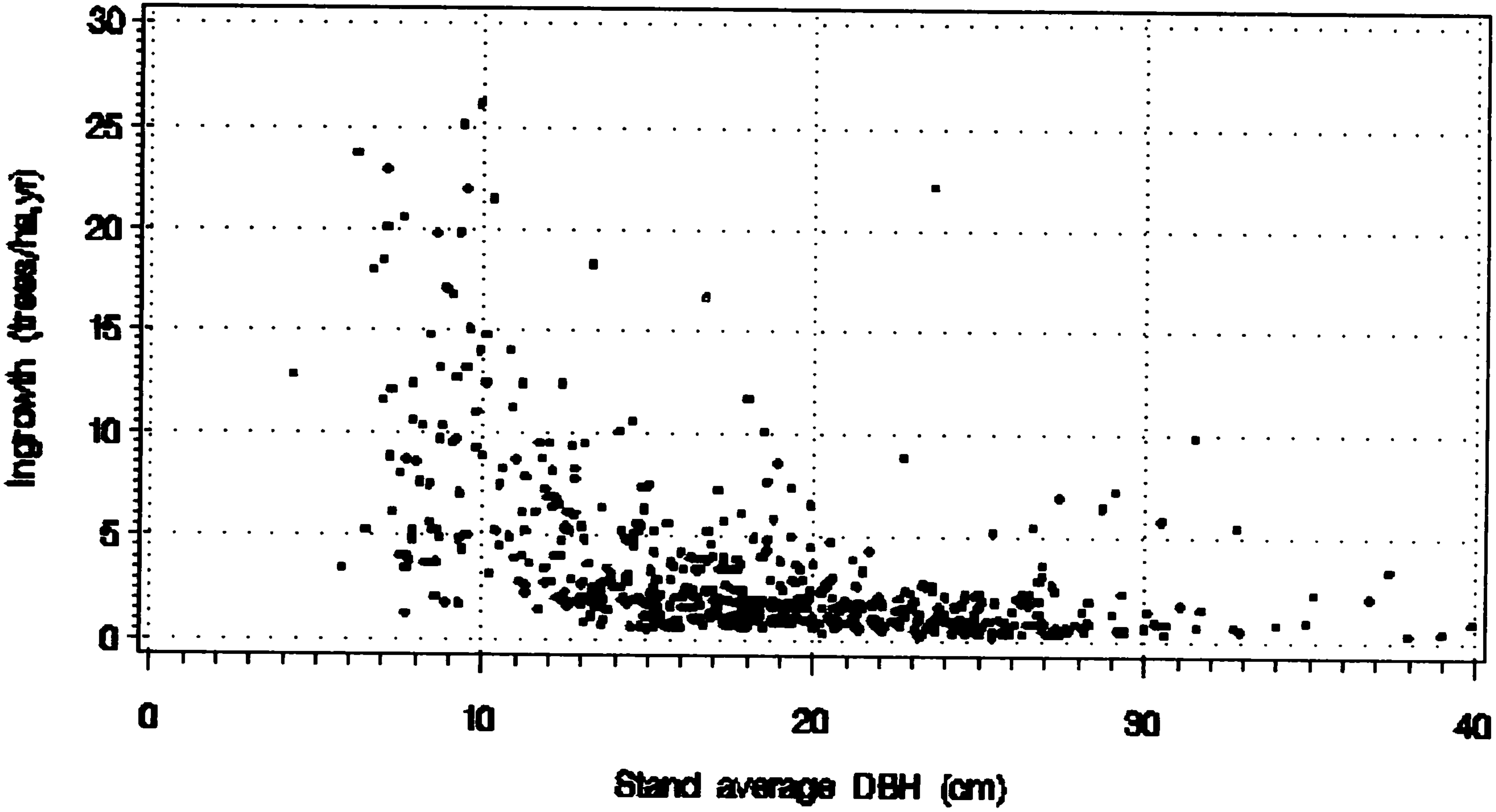


Figure 2-2. Plot of number of lodgepole pine ingrowth trees against stand average DBH

(based on all trees with DBH ≥9.1 cm)

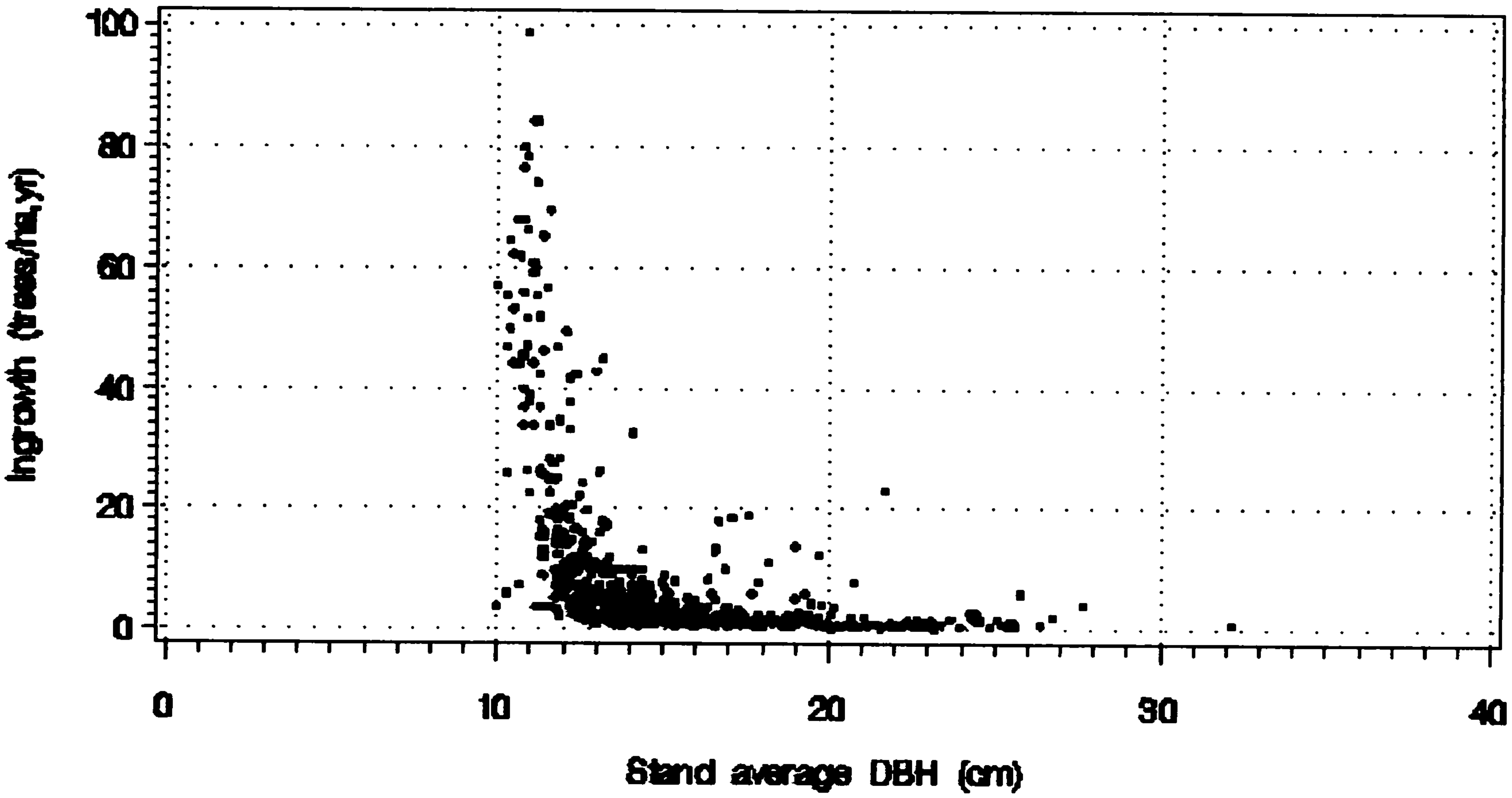


Figure 2-3. Plot of ingrowth occurrence probability against interval class

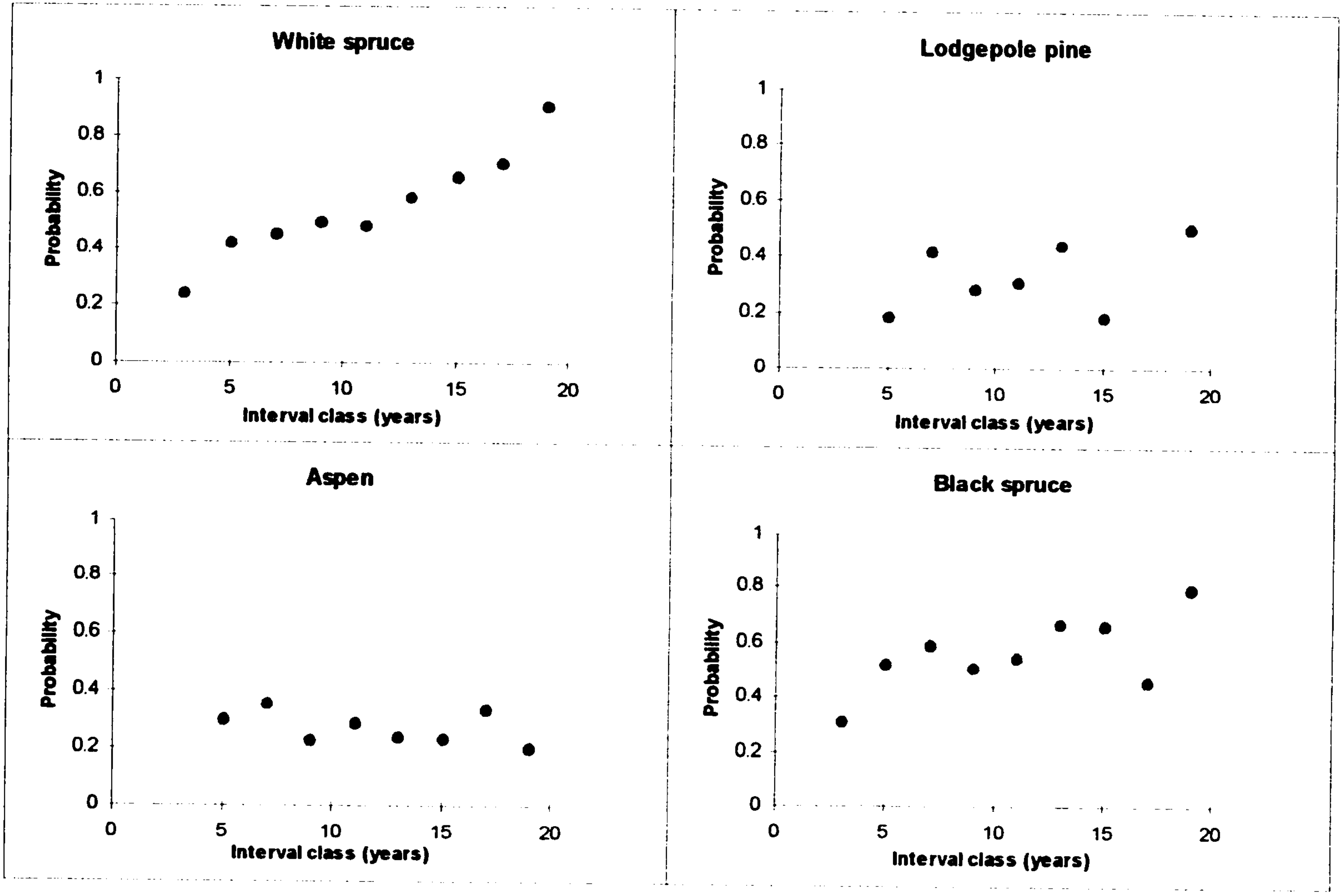


Figure 2-4. Plot of studentized residual against predicted ingrowth tree number for white spruce model (2.35)

(based on all trees with DBH ≥1.1 cm)

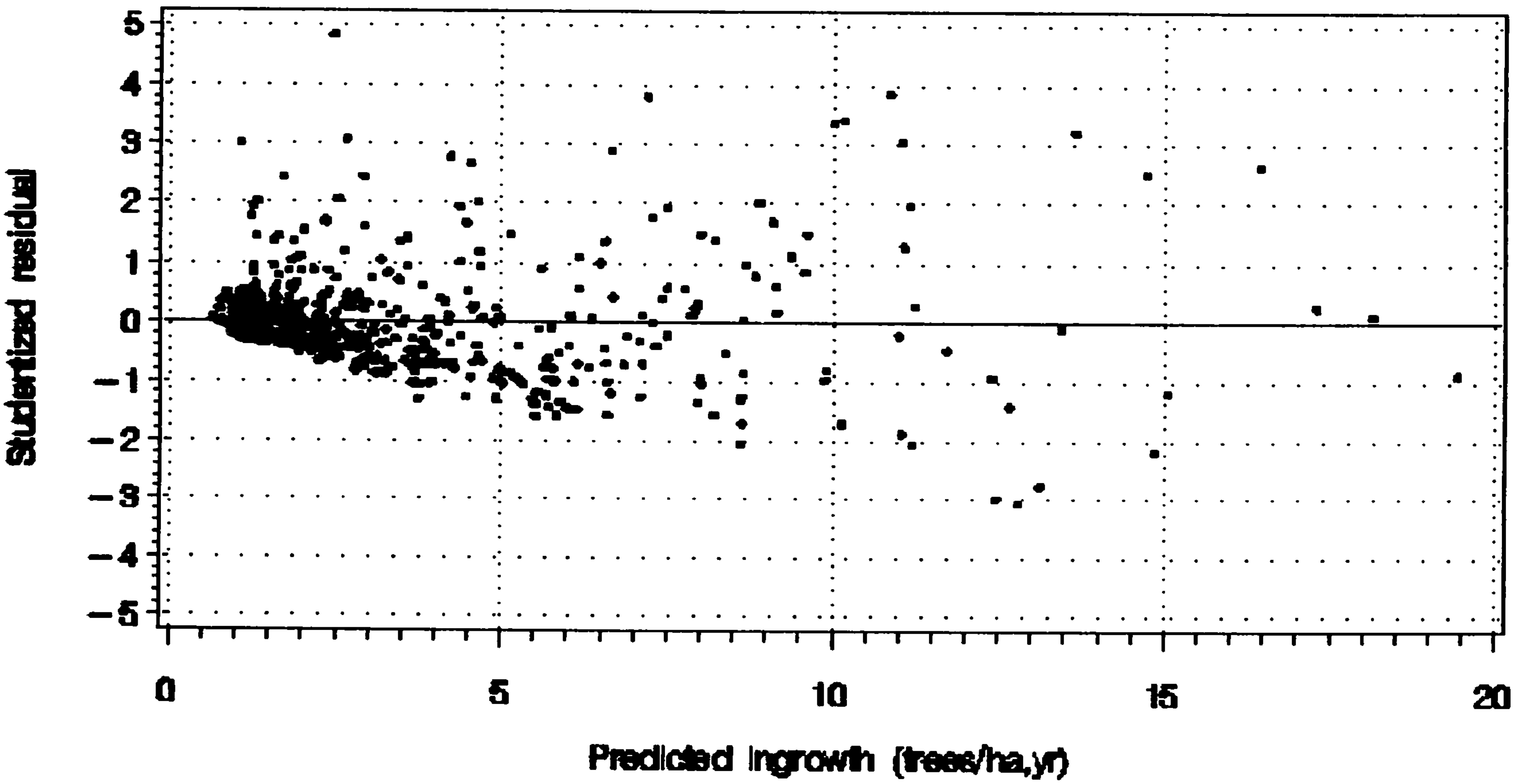


Figure 2-5. Typical graphs of ingrowth occurrence probability for SW

(based on all trees with DBH ≥1.1 cm)

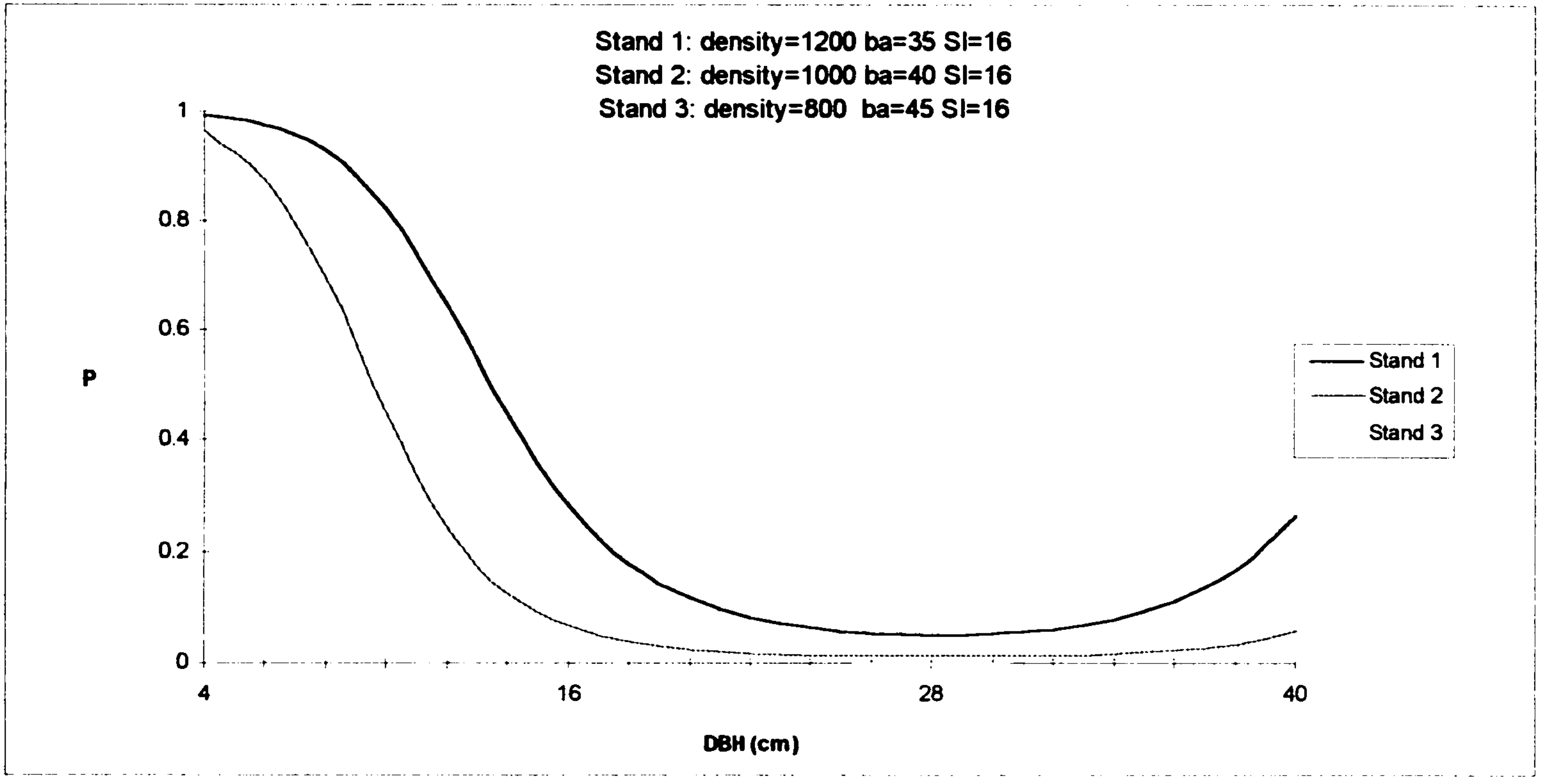


Figure 2-6. Typical graphs of ingrowth occurrence probability for PL

(based on all trees with DBH ≥9.1 cm)

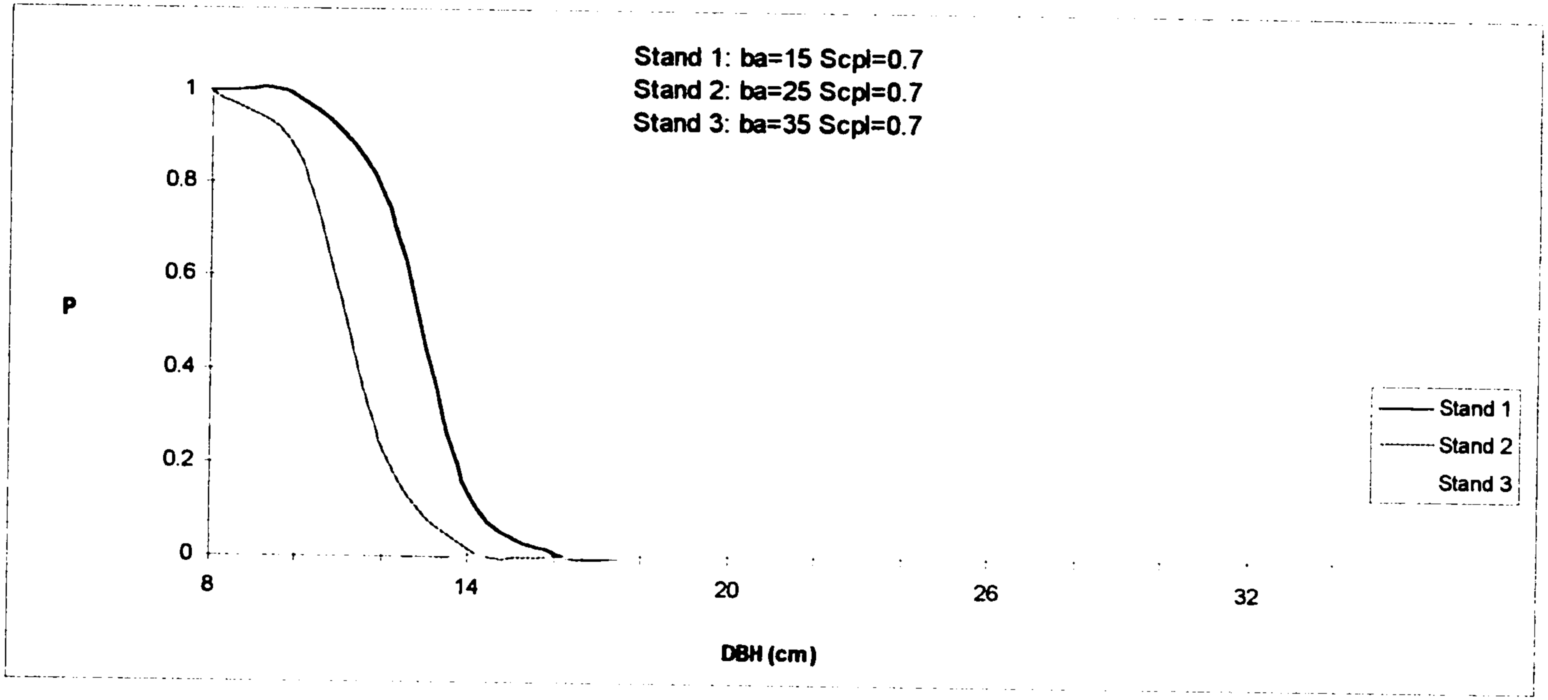


Figure 2-7. Typical graphs of amount of ingrowth for SW, given that it is known to occur

(based on all trees with DBH ≥1.1 cm)

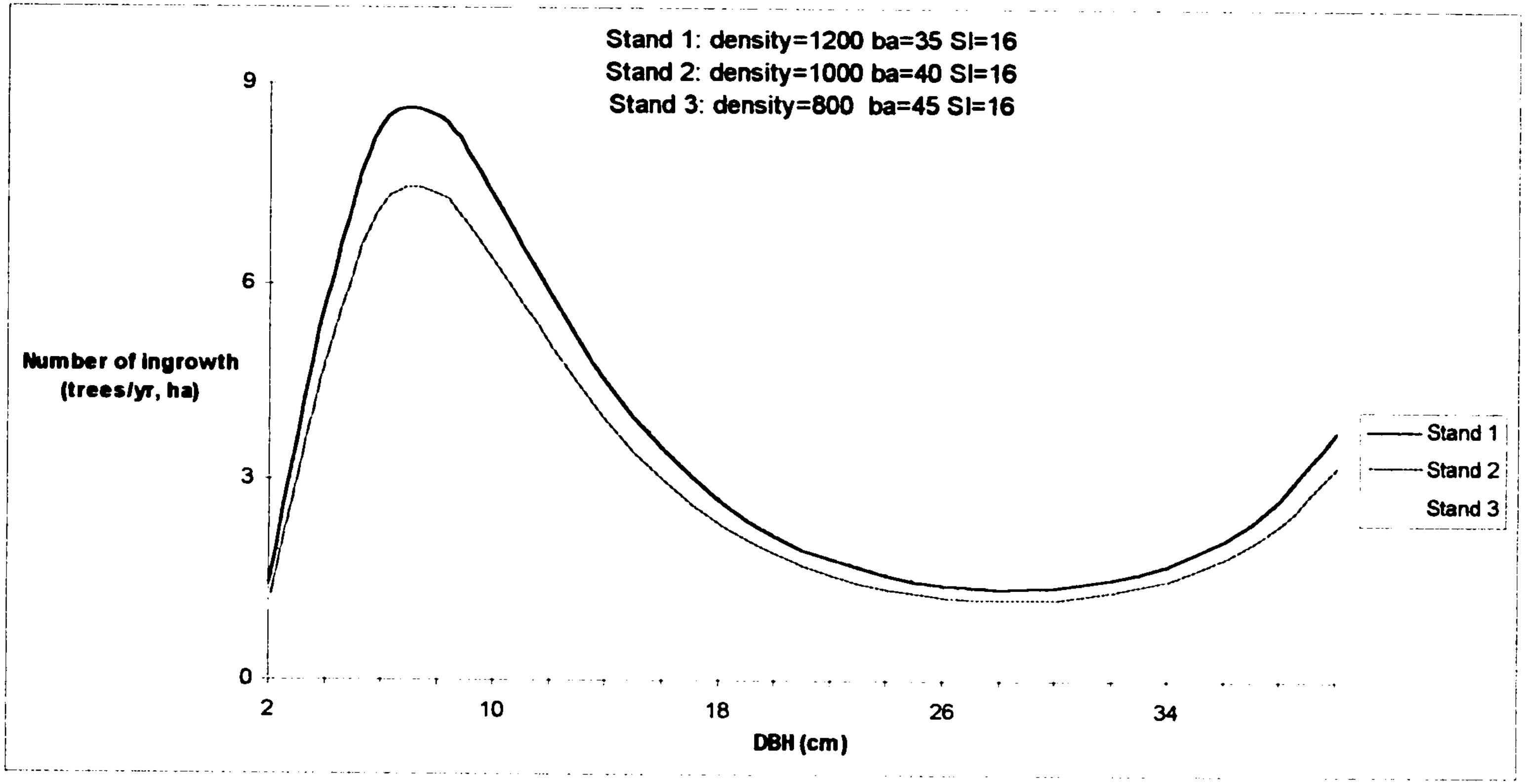
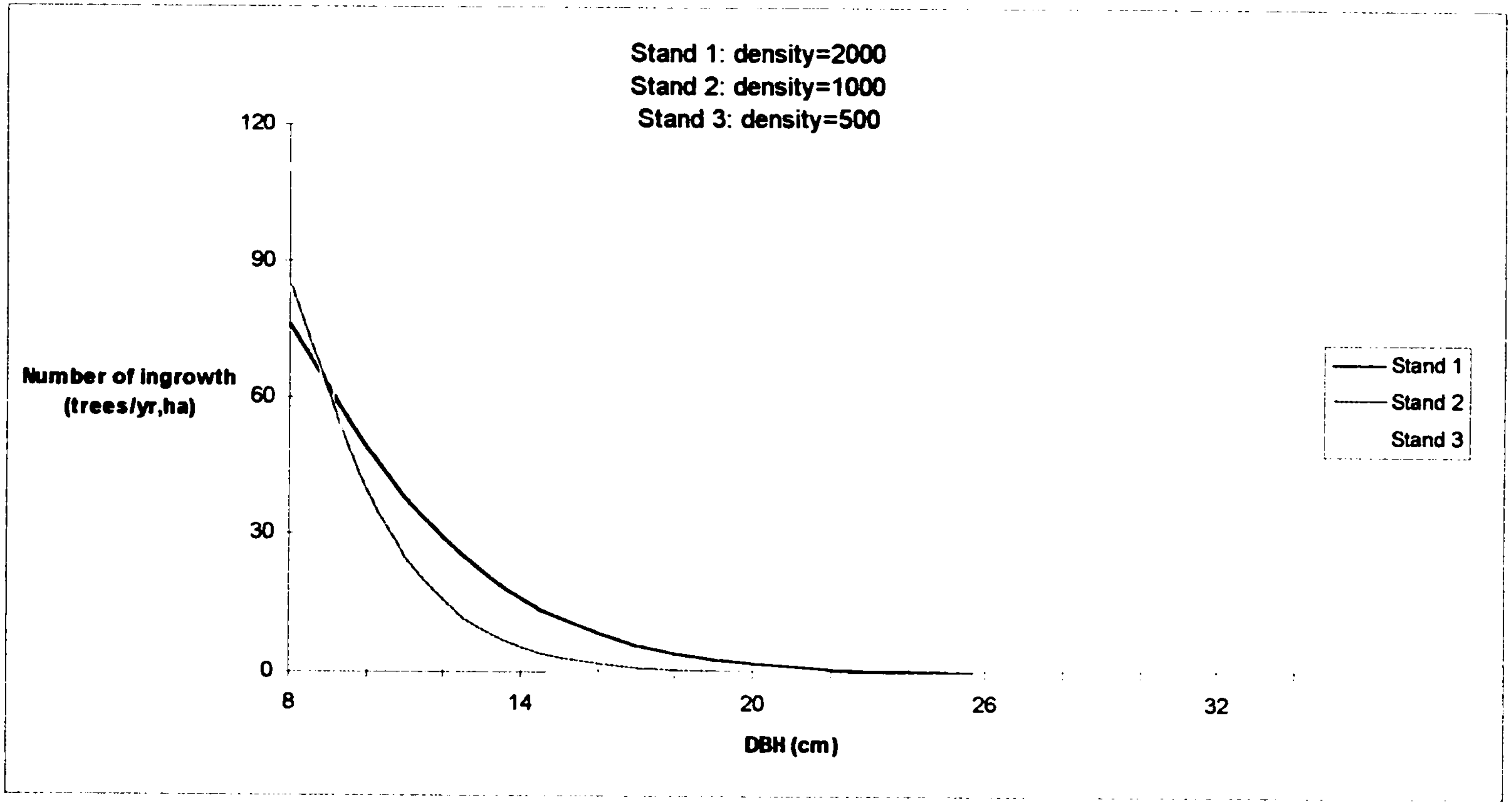


Figure 2-8. Typical graphs of amount of ingrowth for PL, given that it is known to occur

(based on all trees with DBH ≥9.1 cm)



2.8 References

Adams, D.M. and Ek, A.R. 1975. Derivation of optimal management guides for individual stands. P.132-147 in System analysis and forest resource management Meadows, J.C., B.B. Bare, K.D. Ware, C. Row (eds). Society of American Foresters, Bethesda, MD.

Alberta Environmental Protection. 1994. A Permanent Sample Plot Field Procedures Manual. Forest Inventory Section, Land and Forest Service, Alberta Environmental Protection, Edmonton, Alberta.

Alberta Environmental Protection. 1995. Permanent and Temporary Sample Plot Compilation Procedures. Resource Information Branch, Land and Forest Service, Alberta Environmental Protection, Edmonton, Alberta.

Arney, J.D. 1985. A modelling strategy for the growth projection of managed stands. Can. J. For. Res. 15: 511-518.

Avery, T.E. and Burkhart, H.E. 1994. Forest measurements. 4th ed. McGRAW-HILL, INC.

Beers, T.W. 1962. Components of forest growth. J. For., 60:245-248.

Ben-Akiva, M. and Lerman, S.R. 1985. Discrete choice analysis: theory and application to travel demand. The MIT Press, Cambridge, Massachusetts, USA. 390 pp.

Buell, J. H. 1945. The prediction of growth in uneven-aged timber stands on the basis of diameter distributions. Duke Univ. Sch. For. Bull. 11. 70 p.

Botkin, D.B., Janak, J.F. and Wallis, J.R. 1972. Some ecological consequences of a computer model of forest growth. J. Ecol. 60:847-872.

Buchman, R. G. and Shifley, S.R. 1983. Guide to evaluating forest growth projection systems. J. For. 81: 232-234.

Burk, T.E. 1978. Characterizing the growth dynamics of Lake States aspen. M.S. Thesis, Univ. of Minnesota, St. paul. 90 p.

Chou, Y.H., Minnich, R.A., and Chase, R.A. 1993. Mapping probability of fire occurrence in San Jacinto Mountains, California, USA. Environmental Management. 17:129-140.

Clutter, R.G., Fortson, J.C., Pienaar, L.V., Brister, G.H., and Beiley, R.L. 1983. Timber management: a quantitative approach. John wiley & sons.

Corns, I.G.W. and Annas, R.M. 1986. Field guide to forest ecosystems of west-central Alberta. Northern Forestry Centre, Canadian Forestry Service, Edmonton, Alta.

Cornfield, J. 1962. Joint dependence of the risk of coronary heart disease on serum cholesterol and systolic blood pressure: A discriminant function analysis. Federation proceedings, 21, 58-61.

Cox, D.R. and Wermuth, N. 1992. A comment on the coefficient of determination for binary responses. American Statistician. 46(1): 1-4.

Cox, D.R. and Snell, E.J. 1989. Analysis of binary data. Second Edition. Chapman and Hall, New York, N.Y., USA. 236 pp.

Crow, G.R. and Hicks, R.R. Jr. 1990. Predicting mortality in mixed oak stands following spring insect dafoliation. Forest Science, 36 (3): 831-841.

Davis, K. P. 1966. Forest management. McGRAW-HILL BOOK COMPANY.

Dennis, J.E., Gay, D.M., and Welsch, R.E. 1981. An adaptive nonlinear least-squares algorithm. ACM Transactions on Mathematical Software. 7:348-383.

Dennis, J.E. and Mei, H.H.W. 1979. Two new unconstrained optimization algorithms which use function and gradient values. Journal of Optimization Theory and Applications. 28:453-483.

Draper, N.R. and Smith, H. 1981. Applied regression analysis. John Wiley & Sons, Inc.

Efron, B. 1988. Logistic regression, survival analysis, and the Kaplan-Meier Curve. J. Am. Stati. Assoc. 83: 414-425.

Ek, A.R. 1974. Nonlinear models for stand table projection in Northern hardwood stands. Can. J. For. Res., 4:23-27.

Ferguson, D.E., Stage, A.R. and Boyd, R.J. 1986. Predicting regeneration in the grand fir-cedar-hemlock ecosystem of the northern rocky mountains. For. Sci. Monogr. 26.

Freund, J.E. and Walpole, R.E. 1980. Mathematical statistics. Third edition. Prentice-Hall Inc., Englewood Cliffs, New Jersey 07632.

Garcia, C.V., Woodard, P.M., Titus, S.J., Adamowicz, W.L. and Lee, B.S. 1995. A logit model for predicting the daily occurrence of human caused forest fires. Int. J. Wildland Fire. 5(2):101-111.

Goodnight, J.H. 1979. A tutorial on the sweep operator. American statistician, 33: 149-158.

Hamilton, D.A. 1990. Extending the range of applicability of an individual tree mortality model. Canadian Journal of Forest Research, 20:1212-1218.

Hamilton, D.A. 1986. A logistic model of mortality in thinned and unthinned mixed conifer stands of Northern Idaho. Forest Science, 32:989-1000.

Hamilton, D.A. and Brickell, J. E. 1983. Modeling methods for a two-state system with continuous responses. Can. J. For. Res. 13:1117-1121.

Hamilton, D.A. and Edwards, B.M. 1976. Modelling the probability of individual tree mortality. U.S.D.A. For. Serv. Res. Pap. INT-185.

Hamilton, D.A. 1974. Event probability estimated by regression. U.S.D.A. For. Serv. Res. Pap. INT-152, 18 p.

Hann, D.W. 1980. Development and evaluation of an even- and uneven-aged ponderosa pine / Arizona fescue stand simulator. U.S.D.A. For. Serv. Res. Pap. INT-267.

Harms, W.R. 1983. An empirical function for predicting survival over a wide range of densities. Proc. Second Biennial South Silv. Res. Conf., Atlanta, Ga, Nov 4-5, 1982. USDA Forest Serv. Gen.Tech. Rep. SE-24, p 334-337.

Hilt, D.W. 1985. OAKSIM: An individual-tree growth and yield simulator for managed, even-aged, upland oak stands. USDA For. Serv. Res. Pap. NE-562. 21p.

Hinkley, D.V., Reid, N., and Snell, J. 1991. Statistical theory and modelling. Chapman and Hall Ltd.

Hosmer, D.W. and Lemeshow, S. 1989. Applied logistic regression. John Wiley & Sons. New York. USA.

Huang, S, and Titus, S.J. 1995. An individual tree diameter increment model for white spruce in Alberta. Can. J. For. Res. 25:1455-1465.

Huang, S, and Titus, S.J. 1993. An index of site productivity for uneven-aged and mixed-species stands. Canadian Journal of Forest Research, 23:558-562.

Huang, S. 1992. Diameter and height growth models. Ph.D. Thesis, Department of Forest Science, University of Alberta.

Husch, B., Miller, C.I. and Beers, T.W. 1972. Forest mensuration. 2nd edition. Ronald Press, New York, N.Y.

Hyink, D.M. 1979. A generalized method for the prediction of diameter distributions applied to uneven-aged stands. Ph.D. Diss., Purdue Univ., W. Lafayette, IN. 161 p.

Hyink, D.M. and Moser, J.W. 1983. A generalized framework for prejecing forest yield and stand structure using diameter distributions. For. Sci. 29:85-95.

Jamnick, M.S. and Beckett, D.R. 1987. A logit analysis of private woodlot owner's harvesting decisions in New Brunswick. Can. J. For. Res. 18: 330-336.

Jones, R.H., Sharitz, R.R., James, S.M. and Dixon, P.M. 1994. Tree population dynamics in seven South Carolina mixed-species forests. Bulletin of the Torrey Botanical Club. 121(4):360-368.

Kowalski, M. 1993. Stand structure dynamics of a young forest generation in the Bialowieza national park. Folia Forestalia Polonica. Ser.A, 35:15-33.

Lee, Y.J. 1971. Predicting mortality for even-aged stands of lodgeploe pine. The For. Chron. 47:29-32

Lieffers, V.J., Macmillan, R.B., MacPherson, D., Branter, K. and Stewart, J.D. 1996a. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. For. Chron. 72:286-292.

Lieffers, V.J., Stadt, K.J. and Navratil, S. 1996b. Age structure and growth of understory white spruce under aspen. Can. J. For. Res. 26:1002-1007.

Lieffers, V.J. and Stadt, K.J. 1994. Growth of understory *Picea glauca*, *Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstory light transmission. Can. J. For. Res. 24:1193-1198.

Loftsgaarden, D.O. and Andrews, P.L. 1992. Constructing and testing logistic regression models for binary data: Applications to the national fire danger rating system. USDA For. Serv. Gen. Tech. Rep. INT-286. 36 pp.

Lynch, T.B., and Moser, J.W. 1986. A growth model for mixed species stands. For. Sci. 32:697-706.

Maddala, G.S. 1988. Introduction to econometrics. Macmillan Publishing Co., New York, USA.

Maddala, G.S. 1983. Limited-dependent and qualitative variables in econometrics. Econometric Society Monographs; 3. Cambridge University Press, New York, N.Y. USA. 401 pp.

Marquardt, D.W. 1963. An algorithm for the estimation of non-linear parameters. J. SIAM, 11, 431-441.

Martell, D.L., Otukol, S., and Stocks, B.J. 1987. A logistic model for predicting daily people-caused fire occurrence in Ontario. Can. J. For. Res. 17:394-401.

McCullagh, P. and Nelder, J.A. 1983. Generalized linear models. Chapman and Hall Ltd.

McCune, B. and Allen, T.F.H. 1985. Will similar forests develop on similar sites? Can. J. Bot. 63: 367-376.

McTague, J.P. and Stansfield, W.F. 1995. Stand, species, and tree dynamics of an uneven-aged, mixed conifer forest type. Can. J. For. Res. 25:803-812.

McTague, J.P. and Stansfield, W.F. 1994. Stand and tree dynamics of uneven-age ponderosa pine. Forest Science, 40:289-302.

Monserud, R.A. 1976. Simulation of forest tree mortality. Forest Science, 22:438-444.

Moran-Palma, P. and McTague, J.P. 1997. Stand dynamics of the spruce-fir forest in east-central Arizona. West. J. Appl. For. 12(2):55-61.

Morton, R.T. and Titus, S.J. 1984. The development of a mixedwood stand growth model. Final report to Forest Research Branch, Alberta Forest Service.

Moser, J.W. 1972. Dynamics of an uneven-aged forest stand. For. Sci. 18:184-191.

Moser, J.W. 1974. A system of equations for the components of forest growth. P. 260-287 in Growth models for tree and simulation, Fries, J.(ed). Proc. 1973 IUFRO meeting, working party S4.01-4, Stockholm. Royal Coll. of For. Res. Notes 30. 379 p.

Peterson, E.B. and Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces. Forestry Canada.

Raiffa, H. and Schlaifer, R. 1961. Applied statistical decision theory. Division of research graduate school of business administration, Harvard University, Boston.

Rawling, J.O. 1988. Applied regression analysis - a research tool. Wadsworth, Belmont, CA.

Reed, K.L. 1980. An ecological approach to modelling the growth of forest trees. For. Sci. 26:33-50.

Rowe, J.S. and Scotter, G.W. 1973. Fire in the boreal forest. Quat. Res. 3: 444-464.

SAS Institute Inc. 1994. SAS/STAT user's guide: statistics. Version 6. 4th ed., Cary, NC 27513.

SAS Institute Inc. 1992. SAS/STAT user's guide: statistics. Version 6. first ed., Cary, NC 27512-8000.

SAS Institute Inc. 1992. SAS technical report P-229, SAS/STAT software: Changes and enhancement. Cary, NC 27513.

Schuster, E.G. 1983. Evaluating nonindustrial private land-owners for forestry assistance programs: a logistic regression approach. USDA For. Ser., Res. Pap. INT-320. 7 pp.

Schier, G.A. 1981. Physiological research on adventitious shoot development in aspen roots. U.S.D.A. For. Serv. Gen. Tech. Rep. INT-107.

Shapiro, S.S. and Wilk, M.B. 1965. An analysis of variance test for normality. Boimetrika. 52 (3 *and* 4): 591-611.

Shifley, S.R., Ek, A.R. and Burk, T.E. 1993. A generalized methodology for estimating forest ingrowth at multiple threshold diameters. Forest Science, 39:776-798.

Shifley, S.R. 1990. Analysis and modeling of patterns of forest ingrowth in the North Central United State. Ph.D. Diss., Univ. of Minnesota, St. paul. 178 p.

Shifley, S.R. 1987. A generalized system of models forecasting Central States growth. USDA For. Serv., Res. Pap. NC-279. 10 p.

Shifley, S.R., Moser, J.W. and Brown, K.M. 1982. Growth and yield model for the elm-ash-cottonwood type in Indiana. USDA For. Serv. Res. Pap. NC-218. 16 p.

Shugart, H.H. and West, D.C. 1977. Development of an Appalachian deciduous forest succession model and its application to assessment of impact of the chestnut blight. J. Environ. Manage. 5:161-180.

Smalley, G.W. and Bailey, R.L. 1974. Yield tables and stand structure for shortleaf pine plantations in Tennessee, Alabama, and Georgia highlands. U.S.D.A. For. Serv. Res. Paper SO-97.

Somers, G.L., Oderwald, R.G., Harms, W.R. and Langdon, O.G. 1980. Predicting mortality with a Weibull distribution. Forest Science, 26:291-300.

Spurr S.H. 1952. Forest inventory. The Ronald Press Company. New York.

Stage, A.R. 1973. Prognosis model for stand development. For. Serv. Res. Pap. INT-137.

Statistical Science. 1993. S-PLUS Guide to statistical and mathematical analysis, version 3.2. Seattle: StatSci, a division of mathsoft Inc.

Tait, D.E., Cieszewski, C.J. and Bella, I.E. 1988. The stand dynamics of lodgepole pine. Canadian Journal of Forest Research. 18:1255-1260.

Vanclay J.K. 1994. Modelling forest growth and yield - Applications to mixed tropical forest. CAB international, Wallingford, Oxon OX10 8DE, UK.

Vanclay J.K. 1992. Modelling regeneration and recruitment in a tropical forest. Can. J. For. Res. 22:1235-1248.

Vanclay J.K. 1991. Aggregating tree species to develop diameter increment equations for tropical rainforests. For. Ecol. Manage. 42: 143-168.

Vanclay J.K. 1989. A growth model for north Queensland rainforests. For. Ecol. Manage. 27:245-271.

Wykoff, W.R. 1990. A basal area increment model for individual conifers in the northern Rocky Mountains. For. Sci. 36: 1077-1140.

Yao, X. 1997. Modeling Juvenile growth and mortality. Ph.D. Diss., Univ. of Alberta.

Chapter 3

Dynamics of juvenile white spruce and aspen mixedwood stands

3.1 Introduction

The boreal mixedwood association of western Canada is widespread and contains some of the most productive forest lands of the boreal forest (Kabzems et al. 1986; Drew 1988). The most important commercial species are white spruce and aspen. After clearcut harvesting, aspen quickly dominates sites by regenerating from root sprouts (Schier 1981). White spruce is shade tolerant and in natural stands grows slowly in the understory of aspen for 50 or more years before achieving dominance. Efforts to manage mixedwood stands for better stocking and growth of the spruce have been only marginally successful (Drew 1988). Indeed, many plantations of spruce have suffered mortality and slow juvenile growth because of competition (Drew 1988).

In many areas of Canada, the tendency has been to describe the mixedwood land base as either deciduous or coniferous and after cutting, the sites are either allowed to regenerate to aspen or planted to white spruce. There is extreme pressure on the forested land base in the Canadian boreal forest to produce conifer and hardwood products, and at the same time to provide areas for agriculture, range, recreation, and wildlife. These competing interests on the land base, along with some difficulties with white spruce regeneration after clearcutting, and public demands for more ecologically based management, has led to the demand for better silvicultural systems for mixedwood stands (Lieffers and Beck 1994). Silvicultural and harvesting operations as well as forest management planning are much easier with single species stands, but monocultures may be less productive than mixed species stands (Savill and Evans 1986; Vandermeer 1989). This may occur because of better utilization of space during the rotation, reduced pests and diseases (Gibson and Jones 1977) or better nutrient cycling (Vandermeer 1989) in mixed stands. The biggest gains in productivity are usually achieved when species have very different crown shape, different phenologies and tolerances to shade (Kelty 1989). The deciduous, intolerant aspen associated with tolerant spruce might be such a combination. Also, aspen contributes to rapid mineral cycling (Fowells 1965) and is considered necessary for maintaining fertility of luvisolic soils (Valentine et al. 1978).

The enhancement of total production (up to 50%) in mixed stands as compared to pure stands has been demonstrated many times in long-term studies of plantations of various species in Europe (Assman 1970 cited in Kelty 1989). If aspen have commercial value, the development of a spruce understory could be regarded as a means of increasing total site productivity, since its presence may not inhibit aspen production. Yield tables from the Alberta Phase 3 Inventory (Anonymous 1985) show that mixedwood stands outproduce pure stands of either hardwoods or white spruce. Selection harvesting of aspen, without damaging the spruce, is now possible using new harvesting technology. This, coupled with the potential and ecological advantages of mixtures demands further research on mixed stands. The optimum mix of these species is certainly not clear. The dynamics of these stands are poorly understood in natural conditions and almost no data exist on stand characteristics under controlled density for both species.

During past decades, a number of stand-level and individual tree growth models and simulators have been developed (Stage 1973, Ek and Monserud 1974, Danials and Burkhart 1975, Burkhart et al. 1987, Amateis and Burkhart 1989, Huang and Titus 1995). Most growth models focus on simulating stand or tree growth after canopy closure when competition among trees is thought significant. While modelling of juvenile growth has not been comparably addressed (Avila 1993), there is a need to model juvenile growth in order to gain a better understanding of the whole process of stand development and to schedule proper silvicultural treatment for young stands (Zhang et al. 1996). Belli and Ek indicated (1988) that most forest growth models developed in the past have dealt exclusively with established stands, while ignoring the regeneration process leading up to successful establishment. The reforestation is often the most expensive and risky phase of management. The risk of losing such an investment is increased by a failure to understand and manage for the complexity of the artificial regeneration system (Belli and Ek 1988).

To advance our understanding of the dynamics of the juvenile mixedwood stands under controlled planting spruce density and natural aspen regeneration density with removal understory vegetation at the first five years after field planting, this study evaluated the effect of site and density on white spruce and aspen growth and survival, and developed models for the early growth of planted white spruce and naturally regenerated aspen. The data were from permanent sample plots in which all individual trees were measured for age, height, height increment and root collar diameter. The fitted models can be used to predict growth and distribution of root collar diameter and height given the tree age, health indicator, stand density, site productivity. The curve-fitting method was to first select an appropriate equation as the base function, and then incorporate other tree and stand level variables such as health indicator, stand density, and site productivity to predict the parameters of the base function, using the parameter prediction method (Clutter et al. 1983). The models were fitted using the nonlinear least squares regression.

3.2 Dynamics of juvenile mixedwood stands

In the natural development of mixedwood stands, aspen is usually the first species to dominate the site. However, depending upon spruce seed sources and seedbeds, spruce can establish immediately after disturbance or in the next several decades (Lieffers et al. 1996a). In the most cases, spruce grow in the understory of deciduous species during its early development. If there are no spruce seed sources, aspen may be the sole tree species for a long period. In most circumstances, however, the longer-lived and taller white spruce eventually becomes the dominant species (Lieffers et al. 1996a).

In Alberta the mixedwood land areas are currently designated as coniferous or deciduous landbase depending upon the volume of conifer in the stand at the time of inventory (Lieffers et al. 1996a). Currently, management has been biased towards white spruce and most of the silvicultural activities associated with these mixedwood systems have been aimed at establishing relatively pure stands of white spruce (Lieffers and Beck 1994). However, utilization of the aspen resource has accelerated in the last decade and it is now of some economic importance and furthermore its future is especially promising (Bella 1975). Pure deciduous stands do not attain the yield benefits of growing shade tolerant conifer in the understory of intolerant hardwoods (Anonymous 1985; Kelty 1989; Burkhart and Tham 1992) nor will pure stands achieve the biodiversity values of mixed stands (Burton et al. 1992).

Establishing a sufficient amount of regeneration is an essential first step in forest renewal. This can be secured either through artificial regeneration, natural regeneration installed after harvesting, or through the preservation of regeneration present underneath the harvested stand (Ruel et al. 1995). Clearcutting is the only harvesting method that will allow a satisfactory stand of suckers to develop

(Baker 1925; Graham et al 1963). Partial cuts result in fewer and less vigorous suckers and encourage invasion by more tolerant species. Relatively pure aspen stands can be regenerated successfully by clearcutting. Suckering should be prolific provided that the root systems are healthy and carbohydrate reserves are high (Peterson and Peterson 1992). Where possible, cutting should be avoided in spring and early summer when carbohydrate levels are at their lowest (Schier and Zasada 1973). Older and faster-growing clones may also have lower carbohydrate reserves (Schier and Johnson 1971). Relatively pure aspen stands could be underplanted with white spruce seedlings. Historically, mixed stands of hardwood and conifer species, especially aspen and white spruce were very common throughout the boreal forest (Rowe 1972). However, human settlement and repeated disturbances related forestry, agriculture or range management, have removed the spruce seed source and created pure hardwood stands (DeLong 1997). Underplanting these hardwood stands with white spruce may generate stands similar to natural mixedwood stands. Planting spruce under hardwood canopies has the potential advantages: (1) snowpress is less likely to occur in understory because of reduced snow and standing litter accumulation; (2) white spruce seedlings are also less exposed to drought because of reduced wind speeds and radiation loads under tree canopies; (3) summer frost damage to spruce seedlings is reduced by moderating night time minimum temperatures (Stathers 1989). On clear-cut sites in the boreal forest planted white spruce seedlings are frequently overtopped by such competitors as *Populus tremuloides* Michx. (aspen), *Calamagrostis canadensis* (Michx.) Beauv. (bluejoint), *Epilobium angustifolium* L. (fireweed), or a variety of shrubs (Drew 1988; Hogg and Liffers 1991). Probably understory site preparation would be needed to reduce shrub/herb vegetation, improve planter access and plantability (Lieffers et al. 1996a). The planting could be done relatively late in the life of the aspen stand, perhaps 10 to 20 years prior to harvesting of the aspen (Lieffers et al. 1996a). This would allow sufficient time for the spruce to grow 1 m in height and therefore be tall enough to be seen and avoided during the harvest of the aspen using understory protection techniques (two stage harvesting regime) (Brace and Bella 1988) and be taller than much of the developing shrub/herb layer. These trees would be above much of the developing shrub and herb vegetation after cutting the aspen, but not be so tall that they would windthrow (Lieffers et al. 1996a). If the white spruce were planted relatively early in the development of the aspen stand, it might afford a total yield advantage as the stand would be in a mixed state for a longer period of time (Kelty 1989). Also, these mixed stands may be more desirable for wildlife/diversity benefits. In the early planting, white spruce might be at a disadvantage relative to late planting because of lower light transmission by the young overstory aspen (Lieffers et al. 1994b). When the aspen overstory is removed and the tall understory spruce is protected from logging damage, it is more prone to blowdown unless the overstory is removed in patterns that afford wind protection to the understory spruce (Navratil et al. 1994).

3.3 Data

The data were from Alberta Forest Service (LFS) and Daishowa-Marubeni International Ltd. (DMI), respectively, and were part of the data for the Western Boreal Growth and Yield (WESBOGY) Cooperative long-term study. There were 60 permanent sample plots in 1 block from DMI and 30 permanent sample plots in 1 block from LFS. The major species of parent stands was aspen and the stands were clearcut in 1990's summer in LFS sites and 1991's summer in DMI sites. The white spruce seedlings were planted in 1992's summer in the clearcut areas where aspen was already established. The design is a randomized block experiment. Each block consists of two installations, one on a superior site and one on a median site. (Only one median installation was set up by LFS). The site productivity was determined from the site index of reserve stands adjacent to the WESBOGY cut-block because the reserve and cutover were in the same stand type and origin. Each installation consists of two replications of a series of 15 plots. Both replications for an installation were on a common soil type. Each replication had relatively uniform physical (slope and aspect) conditions.

White spruce 1-0 stock and 2-0 stock were planted respectively by LFS and DMI. Initial planting of spruce were at two densities (2000/ha and 1000/ha) corresponding to the high and low treatment densities for spruce. When a spruce seedling died, a new seedling was planted to replace the dead tree, therefore, spruce densities are 2000/ha in plots 1-6 and 1000/ha in plots 7-12 respectively, and aspen density was natural regeneration density levels, before year 5 (Table 3-1).

Square plots were used with buffers between plots. Plots are square 0.04 ha with 20 m sides and 28.3 m diagonal with corners and center permanently marked. This size can ensure adequate numbers of trees over the entire life of the study. During the period between establishment and thinning to treatment density (5 years after field planting), 0.0001 ha (1×1 m) subplots in plots 6, 12, and 15 were used to monitor dynamics of aspen where it was left at the natural density. All competing vegetation were removed once each year.

For each white spruce seedlings in plots 1-12 and aspen trees in the subplots in plots 6, 12, 15, following characteristics were measured and recorded each year: species, tree number, root collar diameter, height, height increment, condition code and other tree and site characteristics. Therefore, only the data from plots 6, 12 and 15 can be used for the statistical analysis and modeling in this study.

The juvenile trees were vulnerable to many damage agents. The damaged trees might show less growth and lower survival probability. In this study, a health indicator, H, was given to each tree. If a tree was not damaged, then H=1, otherwise H=0. Since a block was either on a superior site or on a median site, the site class only had two categories: good and medium. SITE=1 where the site class was good, and SITE=0 where the site class was medium. Because spruce densities were 2000/ha in plots 1-6 and 1000/ha in plots 7-12 respectively, SwN=0 where spruce density was 1000/ha; SwN=1 where spruce density was 2000/ha. The aspen density (AwN) was defined as the total number of aspen trees per ha.

3.4 The effects of site and density on stand dynamics

All available data were used to compare and test the site and density effects on tree growth and dynamics. The tests were conducted by age (time after clearcut or planting). The replanted spruce seedlings were not included when spruce growth were tested. The response variables considered were tree total height (Ht), height increment (Hti), root collar diameter (Rcd), survival rate and aspen density.

The spruce density effects on the survival and growth of spruce and aspen seedlings were not significant (Table 3.2 and Figure 3.1), indicating that the effects of white spruce density may be negligible prior to age 5, so only the effects of site and aspen density were discussed and tested.

The differences of white spruce height and root collar diameter between sites increases as time after planting. At first year, the averages of white spruce Ht are 22.69 cm on mediun site and

22.51 cm on high site respectively, their diffence only 0.79%, and the Rcd difference is -0.24%; however, at year 5, the averages of Ht are 61.25 cm on median site and 52.70 cm on high site respectively, their diffence is 16%, and the Rcd difference is 10.72%, both differences are greater than at first year (Figure 3.2). The differences of white spruce survival rate decreases as time after planting. At first year, the averages of white spruce survival rate are 94.69% on median site and 53.26% on high site respectively, and it is higher on median site than on high site; however, at year 5, they are 97.56% and 98.47% on median site and on high site respectively, and they are almost the same on both sites (Figure 3.2). Similar results of site effect on the growth and survival were also observed for aspen (Figure 3.3).

The aspen density effect on the response variables for spruce were significant (Table 3.2 and 3.3), but for aspen only significant on high sites where aspen density was very high, and not significant on median sites where aspen density was relatively low (Table 3.2 and 3.4). This may indicate that aspen density influence on spruce, and on aspen when aspen regeneration sucker density is much high, starts immediately since first year after harvesting and spruce planting, but its influence on aspen when aspen regeneration sucker density is lower starts relatively later. Aspen density was strongly related to site. There were much more aspen regeneration suckers in high site (130,416/ha) than median sites (67,500/ha) (see Figure 3.3) at the first year after clearcut. Spruce and aspen seedlings were larger and survival rates were higher in the median sites than high sites(see Figure 3.2 and 3.3), that may indicate that denser aspen stands in high site retarded the growth of understory spruce and the competition between aspen suckers was significantly high there. The spruce mortality of the first year was higher, especially in high sites where about half of spruce seedlings died, this mainly was due to the drought that occured on high sites. Then, spruce density decreased little and the mortality was low since year 2 (see Figure 3.2 and 3.3), indicating that the effects of site and aspen density in the first year after planting was critical for spruce survival.

The higher aspen density in high the site decreased dramatically with the time after harvesting, while the relatively lower density in median site decreased little with time, this suggested that juvenile stands with high initial density suffered heavy mortality in the first 5 years of their life. As time passed, the aspen densities decreased slowly, and the density difference between high site and median site became not significant at year 5, they were 93.21% at year 1, and only 1.44% at year 5, respectively (Figure 3.3). Sorenson (1968), Strothmann and Heinselman (1957) concluded that aspen sucker stands show a marked approach towards a common density level, with very dense stands suffering the highest mortality (simple self-thinning) and the least dense stands suffering little or no mortality. Bella et al (1972) found the same results as in this study, that aspen exhibits extremely high and variable mortality in young dense stands with a rapid reduction of initial difference in density. Therefore, the effects of denser aspen stands on high site will not exist several years later. The spruce and aspen seedlings in high sites may overgrow the trees in median sites, because both species usually grow fast in high sites. Steneker (1976) reported that aspen growth will generally be poor on the dry sites and wet clays, and best on fresh to moist clay loams and moist sandy loams that have good drainage and a groundwater table within reach of the roots. He found that aspen site index at age 70 will vary from about 16 m on poor sites to 24 m on good sites, with corresponding stand volumes and average breast height diameters (dbh) ranging from 175 m^3/ha and 15 cm to 280 m^3/ha and 23 cm respectively. In the Lake States, Carmean and Hahn (1981) reported that the time to reach breast height for natural white spruce depended on site quality, for example, 15 years for site index = 9.1 m, and 8 years for site index = 24.4 m (Rauscher 1984). Russell (1963) indicated the optimum growth for white spruce on soils with a slit plus clay content between 20 and 60 percent and with moisture-retaining bands of slit or clay.

3.5 Tree height and root collar diameter projection

Juvenile tree height and diameter prediction models are an essential component in a stand growth model. The descriptions of regenerated stand development rely heavily on accurate height and root collar diameter prediction. The height and root collar diameter versus age relationship predicts cumulative height growth and root collar diameter growth for both species based on age and other variables.

3.5.1 Growth function

Models of established forests, when representing cumulative tree growth over time, have relied on classic sigmodial functions such as the Johnson-Schumacher (Johnson 1935; Schumacher 1939), and the Chapman-Richards (Richards 1959), among others. When confronted with observations falling only in the regeneration phase, the opposite situation, a sigmodial expression, would prove to be unwieldy without major assumptions about the position of the inflection point asymptote (Belli and Ek 1988). If the entire regeneration phase were to precede the point of inflection in a sigmoid function, it would logically be characterized by an exponential curve, one that increases at an increasing rate (Belli and Ek 1988). In practice, scatter plots of the total seedling height (cumulative growth) over time consistently reflect an exponential pattern (see Figure 3.4). Therefore, a general requirement of the growth model to be developed for regeneration was that it allowed exponential growth for the entire establishment phase (Belli and Ek 1988), in this case defined as year 1 through 5 after planting.

Graphs of total height and root collar diameter observations over time revealed a tendency for white spruce, even for aspen, to grow very little in years one and two, followed by rapid increases in growth in years three, four and five (Figure 3.4). Furthermore, little variation in growth was apparent in the first year regardless of differences in critical factors such as site quality and density. Alternatively, fifth-year height and root collar diameter varied greatly, in correlation with these same critical factors. Consequently, the growth function needed to be flexible enough to handle this variability, while essentially remaining stable or fixed over the first two years.

Several additive and multiplicative functions were hypothesized that met the require attributes of exponential shape and flexibility. Two candidates for the height-age or diameter-age base function were considered in this study. The first one was:

(3.1) $\mathrm{Ht} = \alpha\, Age^{\beta}$

or

$\mathrm{Rcd} = \alpha\, Age^{\beta}$

where Ht is total tree height (cm) and Rcd is tree root collar diameter (cm), Age is the tree age (year after planting for spruce or clearcut for aspen, counted after each growing season), limited to Age = 1, 2, 3, 4, 5, and α and β are unknown parameter. The selection of function (3.1) was based on an examination of the height or root collar diameter and age relationships as revealed by plotting total tree height or root collar diameter against age for the two species.

The second candidate was the commonly used Chapman-Richards function:

(3.2) $Ht = a(1 - e^{-bAge})^{c}$

or

$$Rcd = a(1 - e^{-bAge})^{c}$$

where *Ht* is total tree height (cm) and *Rcd* is tree root collar diameter (cm), *Age* is the tree age, and *a*, *b*, and *c* are unknown parameters. It is a sigmoidal curve, with an inflection point occurring in the younger age and a maximum value *a* indicating the potential maximum growth.

The models were fitted by the nonlinear least squares regression accomplished utilizing the procedure PROC NLIN on SAS/STAT software (SAS Institute Inc. 1992). The nonlinear least squares method minimizing the sum squared error was used to estimate the parameters. The Marquardt iterative method METHOD=MARQUARDT as described in Bates (1988) was applied to solve the nonlinear least square equations. To ensure the solution was global rather than local, multiple starting values for parameter estimates were provided. Quality of the fitted model was evaluated using the mean squared error (MSE), the coefficient of determination (R^2), and plots of residuals. Model validation was not done due to the small amount of data available.

3.5.2 Results of growth fits

A total number of 1037 white spruce and 174 aspen trees in AFS datasets and 2347 white spruce trees and 64 observations of aspen average height and root collar diameter in DMI datasets were used to fit the height and root collar diameter prediction models. The models were developed based on the AFS's data and DMI's data, respectively. All white spruce trees were 1 to 5 years old, and all aspen trees were 1 to 6 years old in AFS and 1 to 5 years in DMI. Because the age of aspen was recorded as the same at each measurement based on time after cleartcut in DMI datasets, the average values of aspen height and root collar diameter at each year after harvesting in each plot were used when fitting the models.

In a preliminary analysis, both models were fitted to the data. It was found that the fitted curve (3.1) was closer to the data, with a lower mean squared error (MSE) and a higher coefficient of determination (R^2). Based on the fact that equation (3.1) had a better fit to the data, the function (3.1) was chosen as the base curve of the height and root collar diameter growth model.

On the basis of the base function, H, AwN, SITE were accommodated to parameters α and β by using the parameter prediction method (Clutter et al. 1983). The final fits for the growth models (3.4) to (3.10) are presented in Tables 3.5 to 3.11 for white spruce and aspen. The coefficients of determination (R^2) are 0.6296 to 0.7482 for white spruce, relatively lower for aspen, from 0.4417 to 0.5706, which are not as high as those commonly found for mature tree height or diameter and age relationships. This indicates that the juvenile tree height or diameter growth was quite variable. The variety probably was due to genetic and microsite differences.

3.6 Aspen height and root collar diameter distribution projection

Initial conditions for subjects are required in any stand growth simulation, including tree growth and yield models (Zhang et al. 1996). The initial status of seedlings significantly affects juvenile tree growth (Barnett, 1991; Pothier et al. 1995), so we may need to know initial tree attributes in modeling juvenile growth (Zhang et al. 1996).

The variability of aspen sucker growth was quite large, so the models for aspen tree height and root collar diameter distributions at each of first 5 years after clearcut (age=1, 2 , 3, 4, 5) were developed based on DMI data. The following function (3.3) was considered as a base function. The selection of function (3.3) was based on an examination of the plots of number of trees within each height class or within each root collar diameter class against the height class or root collar diameter class. The graphs of height distribution and root collar diameter distribution for aspen are shown in Figure 3.5 and 3.6.

(3.3) $DHt_{Aw} = \alpha Ht^{\beta} e^{(-\gamma Ht)}$

or

$$DRcd_{Aw} = \alpha Rcd^{\beta} e^{(-\gamma Rcd)}$$

where Dht_{Aw} or $DRcd_{Aw}$ is number of trees per hectare within a height class (10 cm) or within a root collar diameter class (0.4 cm), Ht is height class midpoint (cm) and Rcd is root collar diameter class midpoint (cm), and α, β, and γ are unknown parameters.

Other stand variables such as aspen density and average height or average root collar diameter were also found to significantly affect the height or root collar diameter distribution. These variables were incorporated into equations that predict the parameters of equations (3.3). This procedure is similar to the method of parameter prediction commonly used for a Chapman-Richards or Weibull-type function in which the parameters of the function are related to other tree and stand characteristics but the form of the original function remains the same (Clutter et al. 1983). The final models and the fit statistics are summarized in Table 3.12 and 3.13.

3.7 Discussion and conclusions

There are large differences of growth and survival for both species between high site and median site. Juvenile tree growth of spruce, and aspen on high site where aspen regeneration sucker density is higher, was significantly affected by aspen regeneration density. Stand density effects increase as tree develop. There were no significant differences of survival and growth of spruce and aspen seedlings between two level spruce density, 2000/ha and 1000/ha, indicating that they were not affected by spruce spacing interval prior to year 5 after field planting. Statistical analyses for juvenile spruce and aspen growth suggested that effects of aspen density on height and root collar diameter of spruce and aspen seedlings become significant soon after planting or clearcut. Spruce and aspen seedlings were larger and survival rates were higher in the median sites than high sites. Aspen density also impacted spruce height increment. Nienstaedt and Zasada (1990) reported that height increment of white spruce is reduced under dense canopies. Interspecific competition is a serious threat to the establishment of conifer seedling in young conifer plantations in many forest regions of North America (Eis 1981; Knapp et al. 1984; Chan and Walstad 1987). Bella (1975) indicated that there is already a substantial negative density effect on stem growth at around 5 years of age in dense aspen stands. Even at this early age, crowding may reduce diameter increment by as much as half of what it could be under more open stand conditions (Bella 1975). He suggested that thinning may be effective for improving diameter increment in similar stands at this early age. On forest sites, light, nutrient and water are the environmental resources, which often can not meet the need of tree growth. Competition between the trees or competition between subject trees and competing vegetation are unavoidable if these resources are in short supply.

White spruce is considered to tolerate shade (Spurr and Barnes 1980, Nienstaedt and Zasada 1990) but is not as tolerant as Abies balsamea (L) that is capable of growing on the same sites. For naturally occurring white spruce, Eis (1970) reported that at 25% transmitted light, white spruce seedlings grew 52% as tall as fully illuminated seedlings, and reported death of the seedlings at 15% light. Lieffers and Stadt (1994) reported that the length of leader decreased with decreasing transmitted light and generally white spruce saplings were not found in stands below 8%

transmitted light. Hardwood-dominated overstories transmitted between 14 and 40% of incoming light while white spruce canopies transmitted between5 and 11% of light, and at 40% transmitted light, height growth of white spruce was approximately equal to that attained in open-grown sites (Lieffers and Stadt 1994). These may be reflected by the negative coefficients of aspen density in models (3.7) and (3.8) and the positive coefficient of aspen density in model (3.3) and (3.4). The negative coefficients of aspen density in models (3.7) and (3.8) showed that the aspen density negatively impacts on spruce growth when aspen density is very high (The data were from DMI and the aspen density range was 20,000-290,000 trees/ha). The negative coefficients of aspen density in model (3.6) also showed that the intra-specific competition negatively impacts on the height growth of aspen. This is contradictionary to the mature stands where density positively stimulates height growth. But generally great density found in young stand leads either to heavy juvenile mortality or severe growth stagnation. However, the positive coefficient of aspen density in model (3.4) and (3.5) means that aspen has a positive impact on white spruce growth when aspen density is not too high (The data were from LFS and the aspen density range was 7,500-37,500 trees/ha.). As we mentioned in the earlier section, after havesting, reproduction by root suckering assists the shade intolerant aspen to achieve fast early growth and the domination of the site by occupying the upper layer of the canopy. Therefore aspen has the competitive advantage over shade tolerant white spruce that exhibits slow juvenile growth (Mueggler 1989). Russell (1963) found that white spruce planted under a nurse canopy of aspen providing about 30 percent shade for the first 10 to 12 years were usually taller than those in the open. Olson and Perala (1981) corroborated that shading of 1 to 4 year old white spruce seedlings had a positive effect on height growth. They also found that overhead cover helped protect the seedlings from attacks by the yellowheaded spruce sawfly (*Pikonema alaskensis*) without affecting height growth. Therefore, at least for the early stages of white spruce seedling establishment and growth, shading by a suitable aspen canopy has advantages. A suitable aspen overstory canopy may provide a suitable environment for spruce seedling growth by reducing competition, and ameliorating temperature and moisture conditions. DeLong (1997) recommended that the most suitable stands for underplanting spruce based on light regime are those with a density of less than 1200 stems/ha and basal area less than 35 m^2/ha. It is generally recognized that once the white spruce seedling is established, reductions in light intensity are detrimental (Johnson 1986).

The spruce mortality of the first year is higher, especially in high quality sites where about half of spruce seedlings died, the reason mainly was due to the drought occured on high sites at planting time. Similar results were reported by Eis (1981), after 5 growing seasons, survival of seedlings grown from seeds on plots at Davie Lake amounted to only 10%, 66% for 2+0 bare-root nursery stock, and 87% for bullet plugs, mainly as a result of summer drought. The number of spruce decreased little and survival rates were high after year 1 (Figure 3.2 and 3.3). It should be recognized that moisture stress may be a limiting factor (Morris and Forslund 1991), especially for newly planted seedlings because contact between seedling roots and soil is not well established (Morgolis and Brand 1990; Waring and Running 1978). So the establishment and first-year growth of white spruce seedlings is probably dependent on moisture conditions of the planting site (Burdett et al. 1984; Burdett 1990). Some research shows that grasses or shrubs compete with planted seedlings primarily for moisture (Burdett et al. 1984; Cole and Newton 1986; Eissenstat and Mitchell 1983; Ferguson 1958). Results from a monitoring of diurnal changes in water potential indicate that competing vegetation can pose a severe water stress on young trees (Carter and Miller 1983; Sands and Nambiar 1984). Water stress of seedlings caused by vegetative competition will increase on dry sites or during drought period (Ferguson 1958; Morris and Forslund 1991) and may decrease progressively with increasing tree age (Cole and Newton 1986; Stands and Nambiar 1984). In this study, excessive aspen density on high quality sites may have intensified competition for moisture and resulted in a higher mortality of spruce seedling at the first year. Spruce seedlings should be planted as early as possible in spring, to take advantage of early season moisture and higher light levels prior to full leaf emergence of deciduous species. After full leaf emergence of the aspen canopy, moisture levels drop significantly due to the relatively high moisture demand of this canopy. Thus, planting should be avoided after abnormally dry winters or during abnormally dry spring conditions to reduce the potential for drought induced seedling losses.

Competition for nutrients constitutes an important aspect of vegetation-young tree competition. Although many researches have revealed that competing vegetation can significantly reduce the nutrient level in the needles of seedlings or in the soil (Burdett et al. 1984; Carter and Miller 1983; Nambiar and Zed 1980; Reed et al. 1983), no report has identified nutrient stress as a dominant factor influencing early performance of conifer seedlings. This can be attributed mainly to the fact that nutrients are so abundant on the newly disturbed forest site that newly planted seedlings do not suffer any nutrient stress. Results from observations on the early growth of different stock type white spruce seedlings imply that as root establishment proceeds, shoot growth tends to be limited by the supply of environmental resources, first of water, then of mineral nutrients (Burdett et al.

1984). In eastern Ontario weed control significantly conserved soil moisture and produced highly significant increases in foliage nutrient concentrations in white spruce seedlings (Sutton 1975). Light would not be a limiting factor for the seedlings of shade tolerant species, especially in the first several years after planting. Early height growth of planted trees can be increased by fertilization (Carlson 1981) and by irrigation (Sutton 1968).

The density of the overstory canopy will play a major role in determining the growth rate of understory seedlings. In Manitoba mixedwood, total height of seven-year-old white spruce natural regeneration was strongly correlated with the basal area of the residual stand under which they were growing (Waldron 1966). Therefore, it may be necessary to keep a suitable aspen regeneration density level; at this density level, the intra-specific competition and inter-specific competition are not significant and spruce and aspen seedlings can grow well, and the competing vegetation can be effectively controlled. If aspen density is too low, some shrubs and grasses will invade the sites, which may increase the spruce mortality and reduce the growth of juvenile spruce and aspen. Coopersmith (unpublished, 1997) observed that the early plantation mortality of spruce was high at first year in his spruce-aspen autecology trial at Bear mountain, principally due to vegetation competition from *Calamagrostis canadensis*, especially in the plots where aspen was removed. The rich boreal mixedwood sites contain a large component of fast growing hardwoods and shrubs developed from root suckers or seed germination after clear cutting (Haeussler et al. 1990). Many grasses, such as *Calamagrostis canadensis*, are also abundant on the open site and taller than conifer seedlings, especially in the first several years after planting. *Calamagrostis canadensis* is particularly abundant and becomes a problem weed species in white spruce plantations (Eis 1981; Norokorpi 1986; Drew 1988) in mesic to subhygric mixed-wood sites and subhyric to hygric spruce sites in the boreal forests of western Canada (Corns and Annas 1986). Because of the large biomass of *C. canadensis* during the grasss-dominated stage, its competitive and inhibitory effects on white spruce are significant (Lieffers et al. 1993). Mortality of juvenile white spruce and aspen was greater and height growth lower when the trees were associated with grass rather than shrubs or other trees (John and Lieffers 1991). Eis (1981) reported that while density of vegetation kept incresing for several years, 3 years after logging the competition was already so intense that on plots where shrubs were not annually removed, height growth of spruce was usually less than 2 cm and mortality was severe. The survival and growth of juvenile white spruce and aspen can also be increased by weed control owing, apparently, to an increase in the availability of water and mineral nutrients.

Aspen suckers prolifically (up to 200,000/ha) following a severe disturbance such as fire or clearcutting (Schier and Smith 1979, Kemperman 1978, Debyle 1976, Steneker 1976, Bella and DeFranceschi 1972). After logging the density of suckers produced is proportional to the number of stems removed, with the best regeneration occurring after a total clearcut (Schier and Smith 1979, Bella and DeFranceschi 1972). A high aspen regeneration density is neither good for aspen growth and quality nor spruce survival and growth. Even for the early stage, higher aspen density reduces spruce growth because aspen competes with spruce for both moisture and light; however, relatively low aspen density enhances spruce growth by reducing grass competition, and ameliorating temperature and moisture conditions. Steneker (1976) reported that a stocking of 6000 evenly spaced suckers/ha during the third year after harvesting will be adequate, particularly for fiber production, and for lumber production the number of suckers per hectare should be around 2500. If sawlog material is desired, either selective or mechanical thinning can be carried out, and to be most effective, thinning should be done not later than age 15, but preferably earlier, because even at age 5 suppression of diameter increment due to competition is possible in dense sucker stands (Steneker 1976). Aspen clones can vary in growth rate (Zahner and Crawford 1965) and quality (Wall 1969). Therefore consideration may be given to management techniques that will reduce the number of inferior clones in a stand in favor of faster growing and better quality clones (see Steneker 1974 for details), to obtain a suitable aspen suckering density that is also beneficial to the survival and growth of spruce.

For spruce, health indicator is a significant factor affecting spruce growth. The positive coefficients of the variable H indicate that trees without any damage have higher height and root collar diameter predictions when other variables are the same.

Site productivity has a negative impact on the height growth due to too many aspen suckers or drought occuring at planting time on high sites, as indicated by the negative coefficient of site productivity. Much higher aspen density accelerates the competition between trees.

The frequency distributions of aspen height and root collar diameter, illustrated in Figure 3.5 and 3.6, indicated that throughout the 5 years of study, the stand contained a large number of seedlings less 50 cm height and 1 cm root collar diameter. The draft of the stem population into large classes was accompanied by increasing mortality: stand aspen density was about 99000/ha in 1992, 83000/ha in 1993, 67000/ha in 1994, 61000/ha 1995 and 41000/ha in 1996. Figure 3.5 and 3.6 may also indicated that the annual reductions in aspen stand density were largely a result of mortality of small seedlings, because the suppressed trees are prone to die. During the first few years of life many suckers die due to suppression or pathological factors (Bellar 1975, Bellar and DeFranceschi 1972, Anderson and Anderson 1968). Pollard (1971) reported that about 80% of aspen stems dying in the 3 years of study were less than 2 cm dbh (suppressed trees) and over a 3-year period very few individuals initially less than 1 cm dbh managed to outgrow their class; most died, and it is probable that all 4-year-old stems in that class were destined to die within a few years. He indicated that one class up (1-2 cm), the mortality rate was much lower, but the bulk of the stems still remained in their class and thus the increase in biomass of the stand as a whole depended entirely on development of the upper classes. Ruel et al. (1995) reported the similar conclusion in their study of mortality of balsam fir and black spruce advance growth 3 years after clear-cutting, first-year mortality was mostly concentrated in small stems of low quality. Steneker (1976) found that fast-growing suckers will form the upper canopy of the stand, whereas slower-growing ones will quickly become suppressed and die. The Figures 3.5, 3.6 and 3.7 showed that there was still a relatively more small aspen trees at the 5th growing season, this indicate either that suppressed trees can not grow well or that aspen sucking may last several years when aspen sucker regeneration density at the first year after clearcut is relatively low(see Figure 3.8). Even though, the size distributions become increasingly normal-like as the stand age increases and stand mortality concomitantly decreases. The similar results for the diameter distribution of even-aged stands were reported by Schnur (1937) and Dey (1990) and in numerous stand tables.

In summary, the height and root collar diameter versus age relationships were evaluated for white spruce and aspen in juvenile mixedwood Stands. A exponential function was used as a height-age or diameter-age base function, and the parameter prediction method was used to incorporate additional tree and stand level variables into the parameters of the base function. The models proposed here should provide foresters with a useful tool for predicting the height and root collar diameter based on tree age, damage agent, stand density, and site productivity. Also the aspen height distribution and root collar diameter distribution models were developed using a similar procedure. Model validation was not done due to not enough data available, and since the base growth curve is an exponential function, any extrapolation of the curve needs cautions and further studies.

Table 3-1. Plot numbers associated with spruce and aspen densities

before thinning[a]

Sw/Aw	Natural	Natural	Natural	Natural	Natural	Natural
2000	1	2	3	4	5	6
1000	7	8	9	10	11	12
0	x	x	x	13	14	15

after thinning[b]

Sw/Aw	0	200	500	1500	4000	Natural
1000	1	2	3	4	5	6
500	7	8	9	10	11	12
0	x	x	x	13	14	15

Note:

1. plot numbers (1-15);
2. empty cells (x) for extreme density combinations that are not of interest;
3. row headers show spruce (Sw) density; column headers show aspen (Aw) density;
4. for each installation 30 individual plots are required;
5. [a] spruce and aspen density combinations before thinning which were the data used in this study;
6. [b] spruce and aspen density combinations after thinning which data will be used in WESBOGY long term study.

Table 3-2. Significance level (p-value) for spruce and aspen density effects on white spruce and aspen juvenile development for each of 5 years since planting (based on the data from LFS)

Time	SW				AW			
	Ht		Rcd		Ht		Rcd	
(year)	SwN	AwN	SwN	AwN	SwN	AwN	SwN	AwN
1	-	0.0001	0.7191	0.0001	0.1563	0.1441	-	-
2	0.5607	0.0001	0.5271	0.0001	0.7997	0.4834	-	-
3	-	-	-	-	-	-	-	-
4	0.2508	0.0001	0.6822	0.0491	0.5868	0.2285	-	-
5	0.0100	0.0001	0.4512	0.0300	0.8456	0.0787	-	-

Note:

1. Time - growing seasons after white spruce planting for spruce, or after clearcut for aspen ;
2. SW - white spruce, AW - aspen;
3. Ht - tree height, Rcd - root collar diameter;
4. SwN - white spruce density (2000/ha in plots 1-6, 1000/ha in plots 7-12), AwN - number of aspen seedlings/ha;
5. - No observations;

Table 3-3. Significance level (p-value) for aspen density effects on white spruce juvenile development for each of 5 years since planting by site (based on the data from DMI)

Time	Ht		Rcd		Hti	
(year)	Median site	High site	Median site	High site	Median site	High site
1	0.1933	0.0352	0.0548	0.0184	-	-
2	0.6624	0.2023	0.0001	0.0001	0.4494	0.0616
3	0.0770	0.0062	0.2843	0.0001	0.0910	0.0001
4	0.0051	0.0022	0.1028	0.1505	0.0147	0.0512
5	0.0326	0.0023	0.0408	0.8519	0.3009	0.7326

Note:

1. Time - growing seasons after white spruce planting;
2. Ht - tree height, Hti - tree height increment, Rcd - root collar diameter;
3. - No observations.

Table 3-4. Significance level (p-value) for aspen density effects on aspen juvenile development for each of 5 years since harvesting by site

(based on the data from DMI)

Time	Ht		Rcd		Hti	
(year)	Median site	High site	Median site	High site	Median site	High site
1	0.2983	0.0003	-	-	-	-
2	0.2219	0.0001	0.6614	0.0033	0.3233	0.0001
3	0.9197	0.0211	0.8734	0.6216	0.7041	0.0001
4	0.3329	0.0068	0.9450	0.0018	0.4867	0.0001
5	0.8732	0.1029	0.2436	0.0013	0.6329	0.0607

Note:

1. Time - growing seasons after aspen harvesting;
2. Ht - tree height, Hti - tree height increment, Rcd - root collar diameter;
3. - No observations.

Table 3-5. Fit statistics for white spruce height model
(based on the data from LFS)

Parameter	Estimate	Asymptotic Std. Error	Asymptotic 95% Confidence Interval		MSE	R^2
			Lower	Upper		
α_1	13.2205555	0.39884018	12.43791291	14.00319822	72.2561	0.6296
α_2	0.00553795	0.00073211	0.004101342	0.006974567		
α_3	0.20530955	0.01740926	0.171147418	0.239471692		
α_4	0.61321779	0.01712958	0.579604470	0.646831117		

(3.4) Model : $Ht_{sw} = \alpha_1 e^{(\alpha 2 \cdot AwN \cdot \alpha 3 H)} Age^{\alpha 4}$

where: Ht - total tree height (cm)

AwN - number of aspen seedlings/ha (1000 trees/ha);

H - health indicator

Age - tree age (year after planting)

Table 3-6. Fit statistics for white spruce root collar diameter model
(based on the data from LFS)

Parameter	Estimate	Asymptotic Std. Error	Asymptotic 95% Confidence Interval		MSE	R^2
			Lower	Upper		
α_1	0.28186979	0.00756726	0.267020570	0.296719017	0.020543	0.6957
α_2	0.00308827	0.00064952	0.001813720	0.004362829		
α_3	0.05703392	0.01465495	0.028276569	0.085791282		
α_4	0.64419986	0.01587673	0.613045006	0.675354717		

(3.5) Model : $\mathrm{Rcd}_{sw} = \alpha_1\, e^{(\alpha 2\, AwN\, -\, \alpha 3 H)}\, Age^{\alpha 4}$

where: Rcd - root collar diameter (cm)

AwN - number of aspen seedlings/ha (1000 trees/ha);

H - health indicator

Age - tree age (year after planting)

Table 3-7. Fit statistics for aspen height model
(based on the data from LFS)

Parameter	Estimate	Asymptotic Std. Error	Asymptotic 95% Confidence Interval		MSE	R^2
			Lower	Upper		
α_1	55.3960987	6.60053221	42.36694641	68.42525108	1814.5806	0.4477
α_2	-0.00856259	0.00293131	-0.014348859	-0.002776312		
α_3	0.70535665	0.07166576	0.563891673	0.846821633		

(3.6) Model : $\mathbf{Ht}_{aw} = \alpha_1 e^{(\alpha_2 AwN)} Age^{\alpha_3}$

where: Ht - total tree height (cm)

AwN - number of aspen seedlings/ha (1000 trees/ha);

Age - tree age (year after harvesting)

Table 3-8. Fit statistics for white spruce height model
(based on the data from DMI)

Parameter	Estimate	Asymptotic Std. Error	Asymptotic 95% Confidence Interval		MSE	R^2
			Lower	Upper		
α_1	16.903012	0.3433002	16.2297966	17.5762284	50.5684	0.7306
α_2	-0.0005364	0.0001394	-0.00080984	-0.00026307		
α_3	0.0036556	0.0002386	0.00318769	0.00412368		
α_4	0.1020970	0.0082078	0.08600139	0.11819264		
α_5	0.4577791	0.0135025	0.43130031	0.48425779		

(3.7) Model : $Ht_{sw} = \alpha_1 \, e^{(\alpha 2 AwN + \alpha 3 Ht_{aw} + \alpha 4 H)} \, Age^{\alpha 5}$

where: Ht - total tree height (cm)

AwN - number of aspen seedlings/ha (1000 trees/ha);

Ht_{aw} - aspen average total height (cm)

H - health indicator

Age - tree age (year after planting)

Table 3-9. Fit statistics for white spruce root collar diameter model
(based on the data from DMI)

Parameter	Estimate	Asymptotic Std. Error	Asymptotic 95% Confidence Interval		MSE	R^2
			Lower	Upper		
α_1	0.27281621	0.00621785	0.260622898	0.285009523	0.01508929	0.7482
α_2	-.000903702	0.00015806	-.0012136607	-.0005937433		
α_3	0.00088861	0.00025609	0.000386411	0.001390817		
α_4	0.06924993	0.00879064	0.052011346	0.086488532		
α_5	0.68023367	0.01548169	0.6498873849	0.710593498		

(3.8) Model : $Rcd_{sw} = \alpha_1 e^{(\alpha 2AwN + \alpha 3Htaw + \alpha 4H)} Age^{\alpha 5}$

where: Rcd - root collar diameter (cm)

AwN - number of aspen seedlings/ha (1000 trees/ha);

Ht_{aw} - aspen average total height (cm)

H - health indicator

Age - tree age (year after planting)

Table 3-10. Fit statistics for aspen height model
(based on the data from DMI)

Parameter	Estimate	Asymptotic Std. Error	Asymptotic 95% Confidence Interval Lower	Asymptotic 95% Confidence Interval Upper	MSE	R^2
α_1	45.8317581	4.26136283	37.31063249	54.35288367	328.60960	0.5703
α_2	-0.15748035	0.05868319	-0.274824709	-0.040135993		
α_3	0.52964430	0.06809654	0.393476794	0.665811816		

(3.9) Model : $\mathrm{Ht}_{aw} = \alpha_1\, e^{(\alpha_2\, Site)}\, Age^{\alpha_3}$

where: Ht - total tree height (cm)

Site - site quality

Age - tree age (year after harvesting)

Table 3-11. Fit statistics for aspen root collar diameter model
(based on the data from DMI)

Parameter	Estimate	Asymptotic Std. Error	Asymptotic 95% Confidence Interval		MSE	R^2
			Lower	Upper		
α_1	5.25311036	1.20105959	2.839496071	7.666724662	18.3872492	0.4417
α_2	-0.36698323	0.09391935	-0.555720824	-0.178245643		
α_3	0.82455174	0.16232058	0.498357028	1.150746452		

(3.10) Model : $Rcd_{aw} = \alpha_1 \, exp^{(\alpha 2 \, Site)} \, Age^{\alpha 3}$

where: Rcd - root collar diameter (cm)

Site - site quality

Age - tree age (year after harvesting)

Table 3-12. Aspen height distribution model
(based on the data from DMI)

Year	Model	
1	$Dht_{Aw} = \alpha_1 Ht^{\alpha_2} e^{(\alpha_3 AwN + \alpha_4 AH + \alpha_5 Ht)}$ $R^2 = 0.7216$, MSE = 34.11, N = 116	$\alpha_1 = 0.792343235$ $\alpha_2 = 1.449333301$ $\alpha_3 = 0.006714913$ $\alpha_4 = -0.021049291$ $\alpha_5 = -0.055311806$
2	$Dht_{Aw} = \alpha_1 Ht^{\alpha_2} e^{(\alpha_3 AwN + \alpha_4 AH + \alpha_5 Ht)}$ $R^2 = 0.5879$, MSE =18.12, N = 135	$\alpha_1 = 0.476990731$ $\alpha_2 = 1.175597342$ $\alpha_3 = 0.008133881$ $\alpha_4 = -0.013150221$ $\alpha_5 = -0.029293843$
3	$Dht_{Aw} = \alpha_1 Ht^{\alpha_2} e^{(\alpha_3 AwN + \alpha_4 AH + \alpha_5 Ht)}$ $R^2 = 0.5461$, MSE = 9.29, N = 137	$\alpha_1 = 0.126735875$ $\alpha_2 = 1.554555720$ $\alpha_3 = 0.010200772$ $\alpha_4 = -0.017394093$ $\alpha_5 = -0.029516712$
4	$Dht_{Aw} = \alpha_1 Ht^{\alpha_2} e^{(\alpha_3 AwN + \alpha_4 AH + \alpha_5 Ht)}$ $R^2 = 0.5158$, MSE = 6.92, N = 138	$\alpha_1 = 0.100073241$ $\alpha_2 = 1.577714269$ $\alpha_3 = 0.007561312$ $\alpha_4 = -0.014684497$ $\alpha_5 = -0.023620180$
5	$Dht_{Aw} = \alpha_1 Ht^{\alpha_2} e^{(\alpha_3 AwN + \alpha_4 AH + \alpha_5 Ht)}$ $R^2 = 0.5387$, MSE = 7.16, N = 134	$\alpha_1 = 0.004131769$ $\alpha_2 = 2.192557519$ $\alpha_3 = 0.007530168$ $\alpha_4 = -0.005519104$ $\alpha_5 = -0.027362049$

where: $\mathrm{Dht}_{\mathrm{Aw}}$ - number of trees per hectare within a height class (10 cm);

Ht - height class (cm);

AH - aspen average height (cm);

AwN - number of aspen seedlings/ha (1000 trees/ha);

Table 3-13. Aspen root collar diameter distribution model
(based on the data from DMI)

Year	Model	
2	$DRcd_{Aw} = \alpha_1\, Rcd^{\alpha 2}\, e^{(\alpha 3\, AwN + \alpha 4\, AR + \alpha 5\, Rcd)}$ $R^2 = 0.8821.$ MSE =47.88. N = 58	$\alpha_1 = 3014.686$ $\alpha_2 = 2.802735$ $\alpha_3 = 0.009538$ $\alpha_4 = -0.998684$ $\alpha_5 = -5.121165$
3	$DRcd_{Aw} = \alpha_1\, Rcd^{\alpha 2}\, e^{(\alpha 3\, AwN + \alpha 4\, AR + \alpha 5\, Rcd)}$ $R^2 = 0.8562.$ MSE = 23.30. N = 74	$\alpha_1 = 639.46589$ $\alpha_2 = 2.7981341$ $\alpha_3 = 0.0117233$ $\alpha_4 = -0.4059147$ $\alpha_5 = -3.8794824$
4	$DRcd_{Aw} = \alpha_1\, Rcd^{\alpha 2}\, e^{(\alpha 3\, AwN + \alpha 4\, AR + \alpha 5\, Rcd)}$ $R^2 = 0.7981.$ MSE = 24.98. N = 78	$\alpha_1 = 3869.098$ $\alpha_2 = 4.177756$ $\alpha_3 = 0.011477$ $\alpha_4 = -0.837712$ $\alpha_5 = -5.068767$
5	$DRcd_{Aw} = \alpha_1\, Rcd^{\alpha 2}\, e^{(\alpha 3\, AwN + \alpha 4\, AR + \alpha 5\, Rcd)}$ $R^2 = 0.8479.$ MSE = 15.96. N = 79	$\alpha_1 = 653.3156$ $\alpha_2 = 3.8204420$ $\alpha_3 = 0.0111900$ $\alpha_4 = -0.2449982$ $\alpha_5 = -4.0523954$

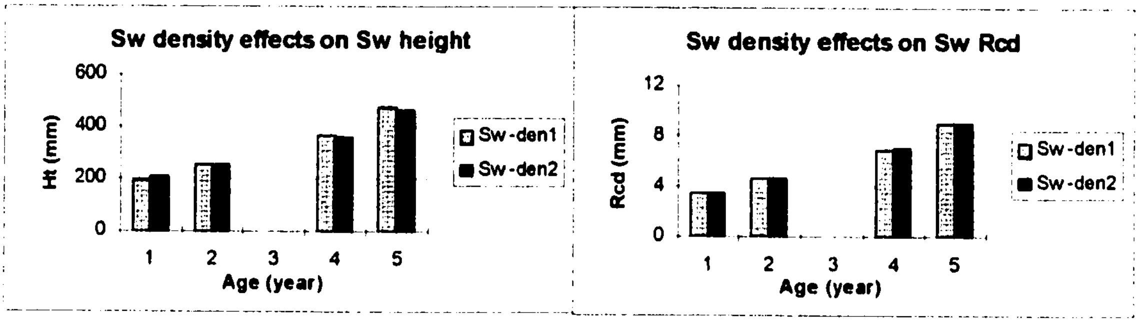
where: $DRcd_{Aw}$ - number of trees per hectare within a root collar diameter class (0.4 cm);

Rcd - root collar diameter class(cm);

AR - aspen average root collar diameter (cm);

AwN - number of aspen seedlings/ha (1000 trees/ha);

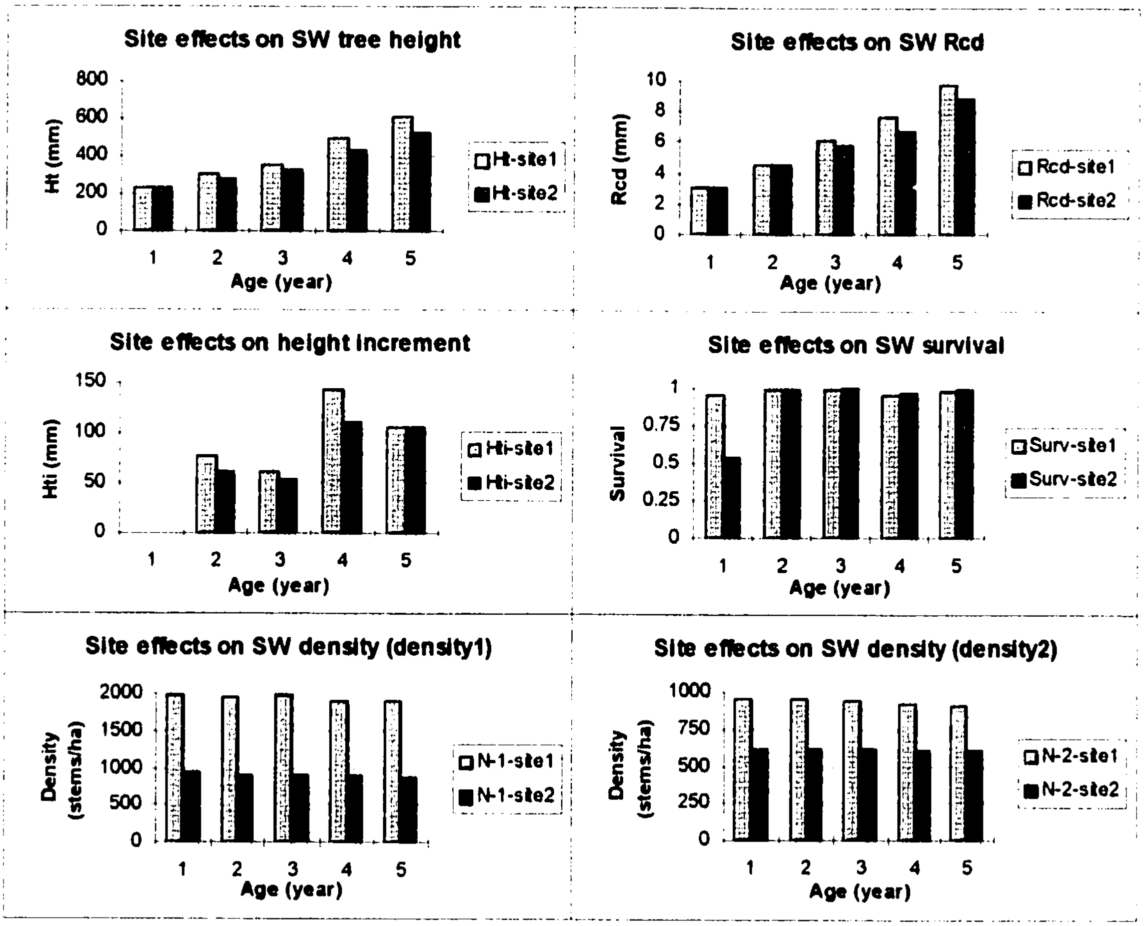
Figure 3-1. Effects of Sw density on white spruce height, root collar diameter (based on the data from LFS)



Note: 1. Sw-den1 = 2000 white spruce seedlings/ha in plots 1-6, Sw-den2 =1000 white spruce seedlings /ha in plots 7-12;

Figure 3-2. Effects of site on white spruce height, root collar diameter, height increment, survival rate and density

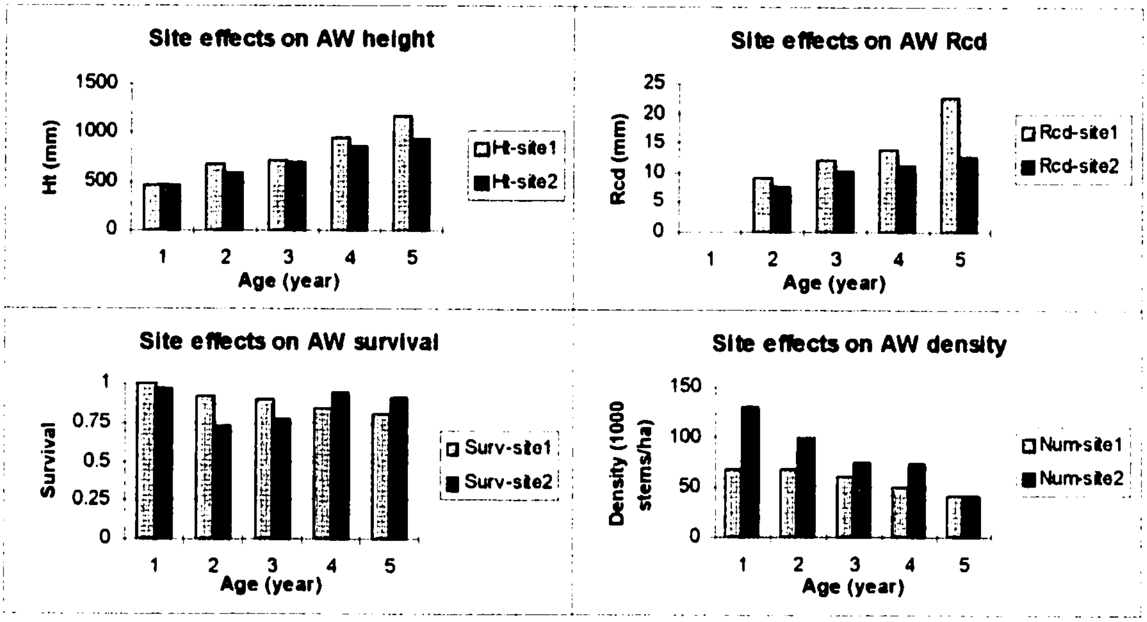
(based on the data from DMI)



Note: 1. Site 1 = median site; site 2 = high site,

2. density1 = 2000 white spruce seedlings/ha in plots 1-6, density2 = 1000 white spruce seedlings /ha in plots 7-12.

Figure 3-3. Effects of site on aspen height, root collar diameter, survival rate and density (based on the data from DMI)



Note: 1. Site 1 = median site; site 2 = high site.

Figure 3-4. Total height over time for white spruce seedlings

(based on the data from DMI)

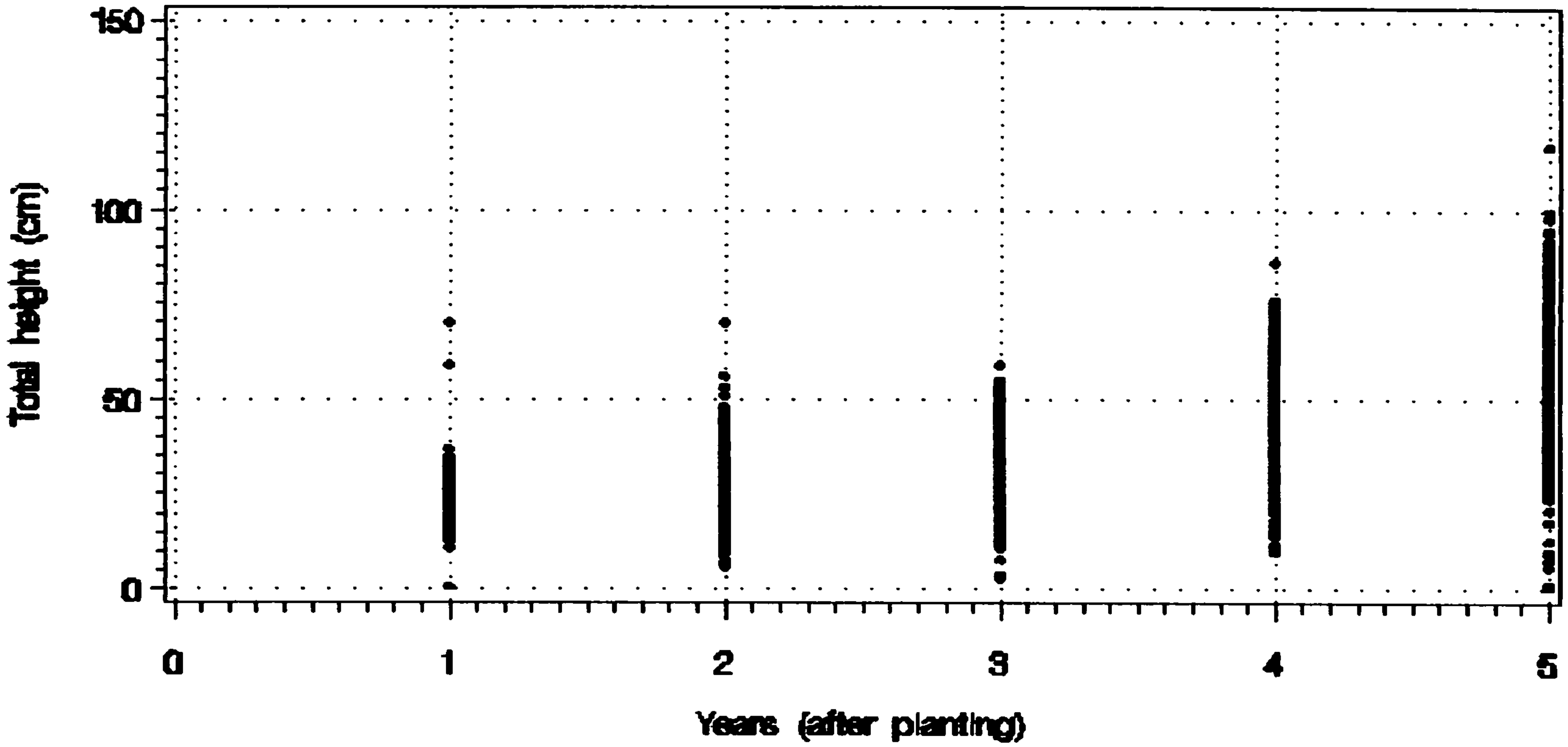
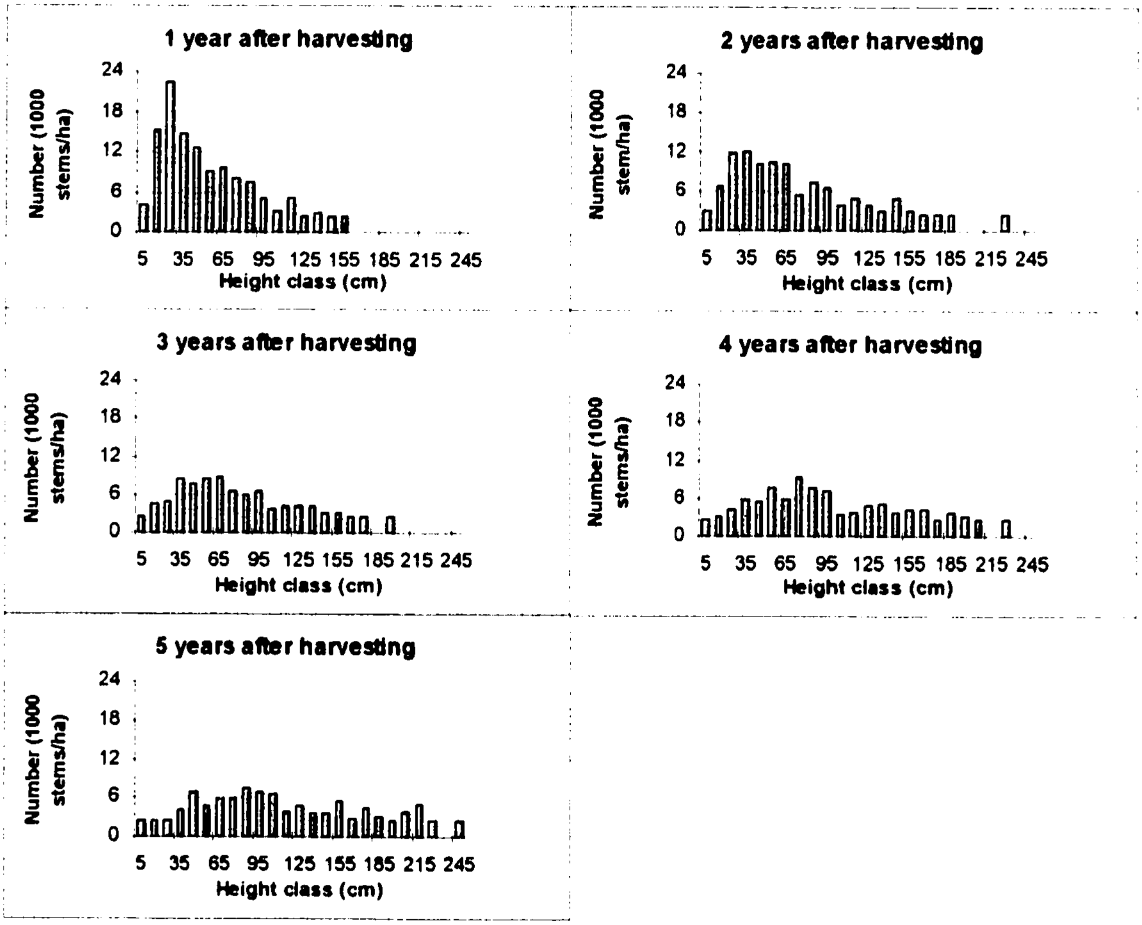


Figure 3-5. Height distribution for aspen in the first 5 years after harvesting (based on the data from DMI)



1 year after harvesting

2 years after harvesting

3 years after harvesting

4 years after harvesting

5 years after harvesting

Figure 3-6. Root collar diameter distribution for aspen at years 2-5 after harvesting (based on the data from DMI)

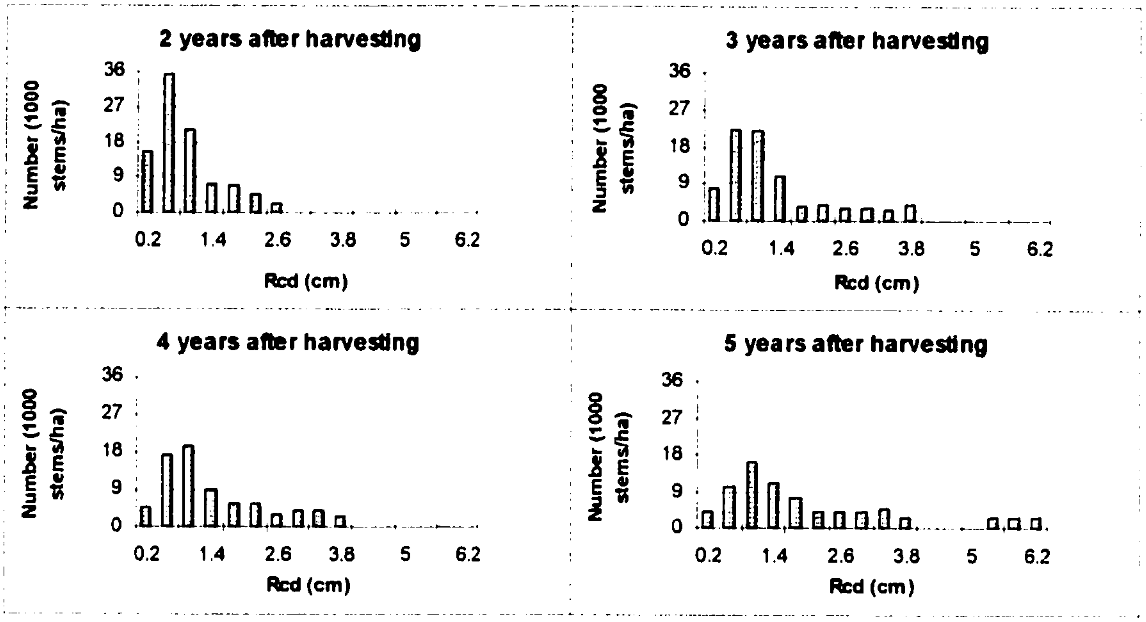


Figure 3-7. Typical graphs of aspen height distribution before year 5

(based on the model in table 3.11)

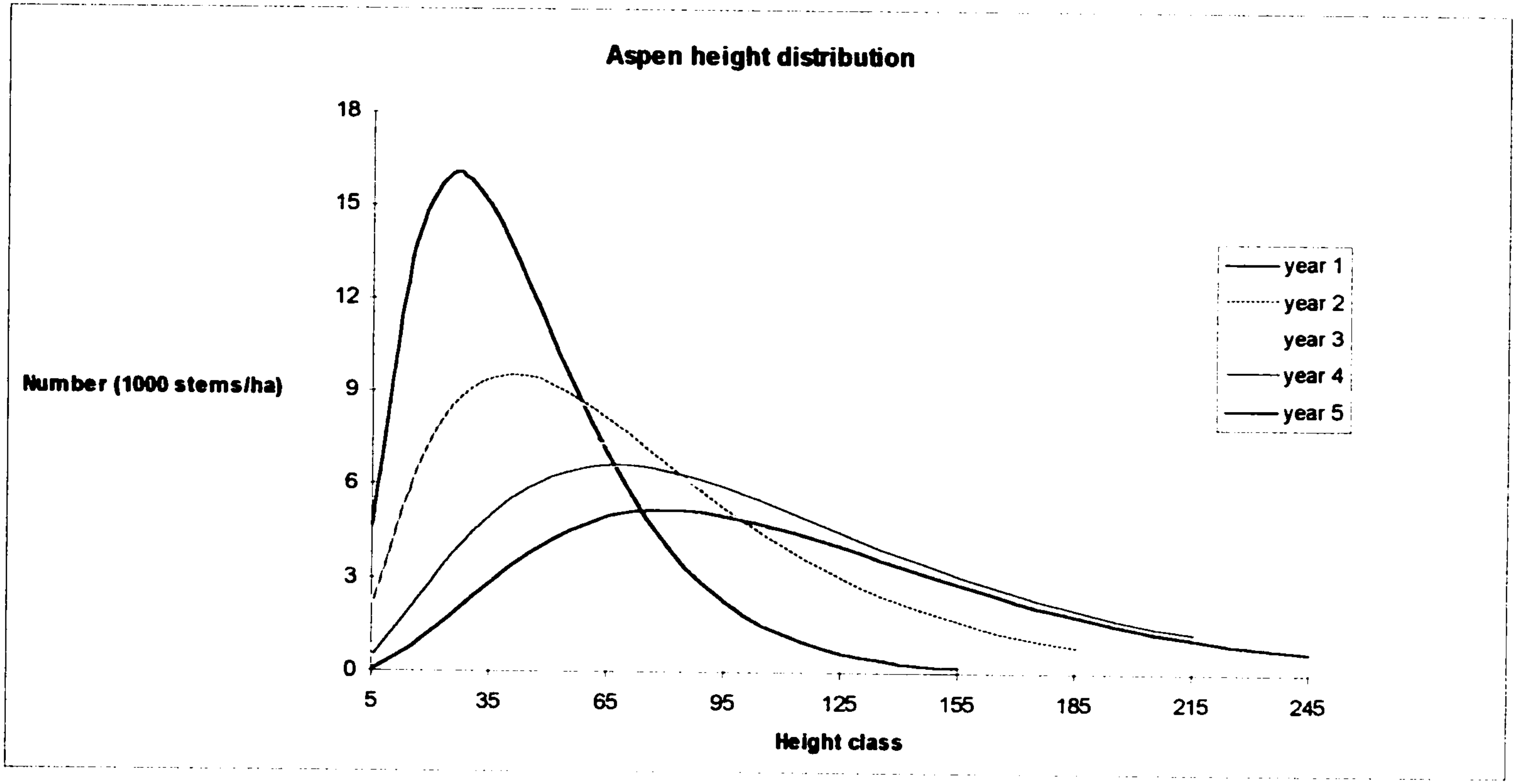
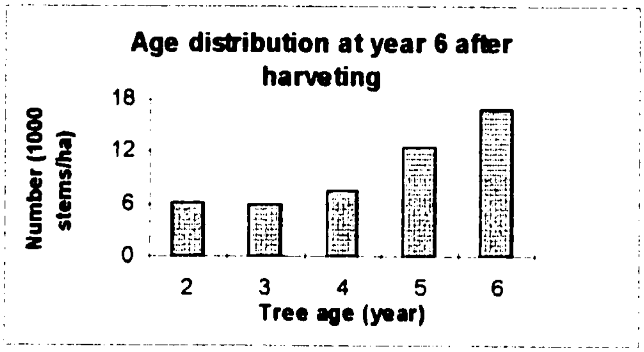


Figure 3-8. Age distribution for aspen at year 6 after harvesting (based on the data from LFS)



3.8 References

Anderson, G.W. and Anderson, R.L. 1968. Relationship between density of quaking aspen and incidence of Hypoxylon canker. For. Sci. 14(1):107-112.

Anonymous. 1985. Alberta phase 3 forest inventory: yield tables for unmanaged stands. Alberta Energy and Natural Resources, Edmonton, Alberta, ENR Rep. 60a.

Avila, O.B. 1993. Modelling growth dynamics of juvenile loblolly pine plantations. Ph.D. Dissertation, Virginia Polytechnic Institute and State University.

Baker, F.S. 1925. Aspen in the central Rocky Mountain region. U.S.D.A. Dep. Bull. 1291, 46p.

Barnett, J.P. 1991. Seedbed densities and sowing and lifting dates affect nursery development and field survival of longleaf pine seedings. Tree Planters' Note, 42(3): 28-31.

Bella, I.E. 1975. Growth-density relations in young aspen sucker stands. Environment Canada, Canadian Forestry Service, Northern Forestry Research Centre, Edmonton, Alberta, Inf. Rep. NOR-X-124. 12p.

Bella, I.E. and DeFranceschi, J.P. 1972. The effect of logging practices on the development of new aspen stands, Hudson Bay, Saskatchewan. Northern Forestry Research Centre, Inf. Rep. NOR-X-33. 20p.

Belli, K.L. and Ek, A.R. 1988. Growth and survival modeling for planted conifers in the Great Lakes Region. For. Sci. 34(2): 458-473.

Brace, L. and Bella, I.E. 1988. Understanding the understory dilemma and opportunity. pp. 69-86. *In* Management and utilization of northern mixedwoods. J.K. Samoil (Ed.). Can. For. Ser. Inf. Rep. NOR-X-296.

Burdett, A.N. 1990. Physiological processes in plantation establishment and the development of specifications for forest planting stock. Can. J. For. Res. 20: 415-427.

Burdett, A.N., Herring, L.J. and Thompson, C.F. 1984. Early growth of planted spruce. Can. J. For. Res. 14: 644-651.

Burkhart, H.E. and Tham, A. 1992. Prediction from growth and yield models of the performance of mixed species stands. pp.21-34. *In* The ecology of mixed species stands. M.G.R. Cannell, D.C. Malcolm, and P.A. Robertson (Eds.). Blackwell Scientific, London.

Burton, P.J., Balisky, A.C., Coward, L.P., Cumming, S.C. and Kneeshaw, D.D. 1992. The value of managing for biodiversity. For. Chron. 68: 225-237.

Carlson, W.C. 1981. Effects of controlled-release fertilizer on shoot and root development of outplanted western hemlock (*Tsuga heterophylla* Raf. Sarg.) seedlings. Can. J. For. Res. 11: 725-757.

Carmean, W.H. and Hahn, J.T. 1981. Revised site index curves for balsam fir and white spruce in the Lake States. U.S.D.A. For. Serv. Res. Note NC-269.

Carter, G.A. and Miller, G.H. 1984. Effect of vegetative competition on the moisture and nutrient status of loblolly pine. Can. J. For. Res. 14: 1-9.

Chan, S.S. and Walstad, J.D. 1986. Correlations between overtopping vegetation and development of Douglas-fir saplings in the Oregon Coast Range. West. J. Appl. For. 2: 117-119.

Clutter, R.G., Fortson, J.C., Pienaar, L.V., Brister, G.H., and Beiley, R.L. 1983. Timber management: a quantitative approach. John wiley & sons.

Cole, E.C. and Newton, M. 1986. Nutrient, moisture, and light relations in 5-year-old Douglas-fir plantation under variable competition. Can. J. For. Res. 16: 723-727.

Daniels, R.F. and Burkhart, H.E. 1975. Simulations of individual tree growth and stand development in managed loblolly pine plantations. FWS-5-75, Division of Forestry and Wildlife Research. Virginia Polytechnic Institute and State University.

DeByle, N.V. 1976. The aspen forest after harvest. In: Utilization and marketing as tools for aspen management in the Rocky Mountains, Proceedings of the Symposium, p.20-23. U.S.D.A. For. Serv. Gen. Tech. Rep. RM-29, Rocky Mountain Forest and Range Experiment Station, Fort Collin, Colo.

DeLong, C. 1997. Operational considerations for underplanting hardwood stands with white spruce. For. Can. And B.C. Min. For., Prince George, B.C. Note # PG-11.

Dey, D., P.S. Johnson, Garrett, H.E. and P.L. Speckman. 1990. Interfacing a regeneration model with growth and yield models. Paper presented at Sixth Biennial Southern Silvicultural Research Conference, Memphis, TN, Oct. 30 - Nov.1, 1990.

Drew, J.J. 1988. Managing white spruce in Alberta's mixedwood forest: the dilemma. In J.K. Samoil (Ed.) Management and utilization of northern mixedwood. Forestry Canada Inf. Rep. NOR-X-296. Pp. 35-40.

Eis, S. 1981. Effect of vegetative competition on regeneration of white spruce. Can. J. For. Res. 11: 1-8.

Eissenstat, D.M. and Mitchell, J.E. 1973. Effects of seeding grass and clover on growth and water potential of Douglas-fir seedlings. For. Sci. 29: 166-179.

Ek, A.R. and Monserud, R.A. 1974. FOREST: a computer model for simulating the growth and reproduction of mixed species forest stands. Publ. R2635, School of Natural Resources, University of Wisconsin, Madison.

Ferguson, E. R. 1958. Response of loblolly pines to reduction of competitions. J. For. 56: 29-32.

Fowells, H.A. 1965. Silvics of forest trees of the United States. USDA For. Serv. Handbook No 271.

Gibson, I.A.S. and Jones, T. 1977. Monocultures as the origin of major forest pests and diseases. In origins of pests, parasite, disease and weed problems. J.M. Cherrett and G.R. Sagar (Eds.) Blackwell Scientific Pub. Oxford. pp. 139-161.

Graham, S.A., Harrison, R.P. and Westell, C.E. 1963. Aspens: phoenix trees of the Great Lakes region. Univ. Mich. Press, Ann Arbor. 272 p.

Haeussler, S., Coates, D. and Mather, J. 1990. Autecology of common plants in British Columbia: A literature review. B. C. Ministry of northern Louisiana. For. Ecol. Manage. 15: 129-134.

Hogg, E.H. and Lieffers, V.J. 1991. The impact of *Calamagrostis canadensis* on soil thermal regimes after logging in northern Alberta. Can. J. For. Res. 21:382-394.

Huang, S. and Titus, S.J. 1995. An individual tree diameter increment model for white spruce in Alberta. Can. J. For Res. 25:1455-1465.

John, S.E.T and Lieffers, V.J. 1991. Analysis of monitor plot data for Alberta. Alberta Reforestation Branch, Alberta Forest Service, Edmonton.

Johnson, N.O. 1935. A trend line for growth series. J. Am. Stat. Assoc. 30: 717.

Johnson, H.J. 1986. The release of white spruce from trembling aspen overstorys: a review of available information and silvicultural guidelines. Manitoba Nat. Resouc., For. Branch, and Can. Forest. Serv., Winnipeg, Manitoba. 109 p.

Kabzems, A., Kosawan, A.L. and Harris, W.C. 1986. Mixedwood section in an ecological perspective: Saskatchewan. Can. For. Serv. and Sask. Parks Renew. Res., For. Div. Tech. Bull. 8, Second Edition.

Kelty, M.J. 1989. Productivity of New England hemlock/hardwood stands as affected by species composition and canopy structure. For. Ecol. Manage. 28: 237-257.

Kerperman, J.A. 1978. Sucker-root relationships in aspen. Ontario Ministry of Natural Resources, Forest Research Note No.12, 4p.

Knapp, W.H., Turpin, T.C. and Beuter, J.H. 1984. Vegetation control for Douglas-fir regeneration on the Siuslaw National Forest: a decision analysis. J. For. 82: 168-173.

Lieffers, V.J., Macmillan, R.B., MacPherson, D., Branter, K. and Stewart, J.D. 1996a. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. For. Chron. 72:286-292.

Lieffers, V.J., Stadt, K.J. and Navratil, S. 1996b. Age structure and growth of understory white spruce under aspen. Can. J. For. Res. 26:1002-1007.

Lieffers, V.J., and Beck, J.A. 1994. A semi-natural approach to mixedwood management in the prairie provinces. For. Chron. 70:260-264.

Lieffers, V.J. and Stadt, K.J. 1994. Growth of understory *Picea glauca, Calamagrostis canadensis,* and *Epilobium angustifolium* in relation to overstory light transmission. Can. J. For. Res. 24:1193-1198.

Lieffers, V.J., MacDonald, S.E. and Hogg, E.H. 1993. Ecology of and control strategies for *Calamagrostis canadensis* in boreal forest sites. Can. J. For. Res. 23:2070-2077.

Morgolis, H.A. and Brand, D.G. 1990. An ecophysiological basis for understanding plantation establishment. Can. J. For. Res. 20: 375-390.

Morris, D.M. and Forslund, R.R. 1991. A field-oriented competition index for young jack pine plantations and a computerized decision tool for vegetation management. New Forests 5 (2): 93-108.

Mueggler, W.F. 1989. Age distribution and reproduction of intermountain aspen stands. West. J. Appl. For. 4(2): 41-46.

Nambiar, E.K.S. and Zed, P.G. 1980. Influence of weeds on the water potential, nutrient content and growth of young radiata pine. Aust. For. Res. 10: 279-288.

Navratil, S., Brace, L.G., Sauder, E.A. and Lux, S. 1994. Silvicultural and harvesting options to favor immature white spruce and aspen regeneration in boreal mixedwood. Can. For. Ser. Inf. Rep. NOR-X-337.

Nienstaedt, H. and Zasada, J.C. 1990. *Picea glauca* (Moench) Voss (white spruce). *In* Silvics of North America. Vol. 1. Conifers. *Edited by* R.M. Burns and B.H. Honkala. U.S. Dep. Agric. Agric. Handb. 654.

Norokorpi, Y. 1986. White spruce vegetation options on fire-textured miniral soils of the boreal-mixed ecoregion in Alberta. Alberta Forest Service Reforestation and Reclamation Branch, Edmonton.

Olson, S.P. and Perala, D.A. 1981. Growth of planted white spruce in relation to soil texture, fertilization, and microenvironment. Final report to the CANUSA-East Spruce Budworm Program.

Pollard, D.F.W. 1971. Mortality and annual changes in distribution of above ground biomass in an aspen sucker stand. Can. J. For. Res., 1:262-266.

Peterson, E.B. and Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces. For. Canada. Northwest Reg., North. For. Cent., Edmonton, Alberta. Spec. Rep. #1.

Pothier, D., Doucet, R. and Boily, J. 1995. The effect of advanced regeneration height on future yield of black spruce stands. Can. J. For. Res., 25: 536-545.

Rauscher, H.M. 1984. Growth and Yield of white spruce plantations in the Lake States (A Literature Review). U.S.D.A. For. Serv. Res. Pap. NC-253.

Reed, K.C., Shumay, J. S., Walker, R.B. and Bledsoe, C. S. 1983. Evaluation of the interaction of two environmental factors affecting Douglas-fir seedling growth: light and nitrogen. For. Sci. 29: 193-203.

Richards, F.X. 1959. A flexible growth function for empirical use. J. Exp. Bot. 10:290-300.

Rowe, J.S. 1872. Forest regions of Canada. Dept. of Environment. Canadian Forestry Service Publ. 1300.

Ruel, J.-C., Doucet, R. and Boily, J. 1995. Mortality of balsam fir and black spruce advance growth 3 years after clear-cutting. Can. J. For. Res., 25: 1528-1537.

Russell, K.W. 1963. Plantation white spruce growth related to some forest soil-site characteristics. Plan B paper. St. Paul, MN: University of Minnesota, College of Forestry; 42p.

Sands, R. and Nambair, E.K.S. 1988. Water relations of *Pinus radiata* in competition with weeds. Can. J. For. Res. 14: 233-237.

SAS Institute Inc. 1992. SAS/STAT user's guide: statistics. Version 6. first ed., Cary, NC 27512-8000.

Savill, P.S. and Evans, J. 1986. Plantation silviculture in temperate regions. Clarendon Press. Oxford.

Schier, G.A. 1981. Physiological research on adventitious shoot development in aspen roots. U.S.D.A. For. Serv. Gen. Tech. Rep. INT-107.

Schier, G.A., and Smith, A.D. 1979. Sucker regeneration in a Utah aspen clone after clear cutting. U.S.D.A. For. Serv. Res. Note. INT-253, 6p.

Schier, G.A. and Zasada, J.C. 1973. Role of carbohydrate reserves in the development of root suckers in *Populus Tremuloides*. Can. J. For. Res. 3: 243-250.

Schier, G.A. and Johnston, R.S. 1971. Clonal variation in total non-structural carbohydrates of trembling aspen roots in three Utah areas. Can. J. For. Res. 1: 252-255.

Schnur, G.L. 1937. Yield, stand, and volume tables for even-aged upland oak forests. Tech. Bull 560. U.S.D.A., Forest Serv. 87 p.

Sorensen, R.W. 1968. Size of aspen crop trees little affected by initial sucker density. U.S.D.A. For. Serv. Res. Note NC-51, 4p.

Spurr, S.H. and Barnes, B.V. 1980. Forest Ecology. John Wiley & Sons, New York.

Stage, A.R. 1973. Prognosis model for stand development. U.S.D.A. For. Serv. Res. Pap. INT-137.

Stathers, R.J. 1989 Summer frost in young forest plantations. For. Can. And B.C. Min. For., Victoria, B.C. FRDA Rep. No.73.

Steneker, G.A. 1976. Guide to the silvicultural management of trembling aspen in the prairie province. Northern Forestry Research Centre, Inf. Rep. NOR-X-164. 6p.

Steneker, G.A. 1974. Factors affecting the suckering of trembling aspen. For. Chron. 2:32-34.

Strothmann, R.O. and Heinselman, M.L. 1957. Five-year results in an aspen sucker density study U.S.D.A. For. Serv. Lake States Forest Experiment Station, Tec. Note 490, 2p.

Sutton, R.F. 1975. Nutrition and growth of white spruce outplants: Enhancements by herbicidal site preparation. Can. J. For. Res. 5: 219-223.

Sutton, R.F. 1968. Ecology of young white spruce (Picea glauca [Moench] Voss). Ph.D thesis, Cornell University Microfilms 68-11, 645 (Ann Arbor, Michigan).

Valentine, K.W.G, Sprout, R.N., Barker, T.E. and Lavkulich, L.M. (eds.). 1978. The soil landscapes of British Columbia. B.C. Min. Environ., Resource Anal. Br., Victoria, B.C.

Vandermeer, J. 1989. The ecology of intercropping. Cambridge University Press. New York.

Waring, R.H. and Running, S.W. 1978. Sapwood water storage: its contribution to transpiration and effect upon water conductance through the stems of old-growth Douglas-fir. Plant Cell Environ. 1:131-140.

Waldron, R.M. 1966. Factors affecting natural white spruce regeneration on prepared seedbeds at the Riding Mountain Forest Experimental Area, Manitoba. Can. Dept. For. Rural Devel., For. Branch, Ottawa, Ontario, Publ. 1169. 41p.

Wall, R.E. 1969. Distribution of *Fomes igniarius* in aspen stands as affected by clonal variation. Can. Dep. Fish. Forest. Bi-monthly Res. Notes 25(1):5.

Zahner, R. and Crawford, N.A. 1965. The clonal concept in aspen site relations. In C. T. Youngberg (ed.) Forest-soil relationships. Oregon State Univ. Press, Corvallis, Ore. p. 230-243.

Zhang, S., Burkhart, H.E. and Amateis, R.L. 1996. Modeling individual tree growth for juvenile loblolly pine plantations. For. Ecol. Manage. 89: 157-172.

Chapter 4

General discussion and conclusions

This study has accomplished the two primary objectives stated in Chapter 1. First, two sets of stand-level, two-stage ingrowth models were developed for the four major species in mixedwood stands of Alberta. The effects of stand density, species composition, and site productivity on ingrowth process were evaluated, and the biological interpretation of the model was discussed. Secondly, the effects of site productivity and density on growth and survival of white spruce and aspen in regenerated juvenile mixedwood stands were evaluated, and models for the early growth of both species were also presented.

The two-stage approach is suitable to modelling ingrowth of the four major species in Alberta. The first stage predicted the probability of the ingrowth occurrence from stand basal area, density, DBH, species composition and site productivity in the existing stand, using the generalized logistic model. The second stage was a conditional function to predict the amount of ingrowth, given that ingrowth is known to occur, and was estimated using a nonlinear model. The generalized logistic models developed in this study can obtain satisfactory predictions for the data with unequal length of remeasurement interval and avoid double correction that will underestimate the expected ingrowth. Using appropriately selected base functions, and the method of parameter prediction, the ingrowth amount models were elaborated as functions of stand average DBH, stand density, species composition, and site productivity. The selected exponential base function prevented the predicted ingrowth values from being negative in some situations. Both stand statistics based on all trees with $DBH \geq 1.1$ cm and all trees with $DBH \geq 9.1$ cm were used respectively to develop two sets of the models. Input variables of the models are simple stand variables that are readily obtainable from ordinary inventories, and compatible with the data-collection process in Alberta.

Based on the permanent sample plot data collected from the regenerated stands with planted spruce and naturally regenerated aspen younger than 6 years, (1) statistical analyses were conducted to evaluate site productivity and density effects on juvenile tree growth and survival rate. It was shown that aspen regeneration density had significant influence, and spruce planting density effect was negligible, and the differences of growth and survival for both species between high site and median site exist. It was also found that spruce and aspen seedlings were smaller and survival rates were lower in the high sites where aspen regeneration density is much higher than median sites; (2) models to predict growth and distribution of root collar diameter and height, given the tree age, health indicator, stand density, site productivity, were developed. The curve-fitting method was to first select an appropriate equation as the base function, and then incorporate other tree and stand level variables such as health indicator, stand density, and site productivity to predict the parameters of the base function, using the parameter prediction method.

The quality of the ingrowth models is not as high as desired. The R-squared values are relatively low for some models, indicating that the number of ingrowth trees is highly variable. This variability in ingrowth is due in part to factors that are not accounted for in the models (e.g. ecoregion and forest type) and in part to the stochastic nature of the ingrowth process. Several issues associated with further ingrowth research were recommended in Chapter 2, which may contribute to the significant increases in precision of ingrowth predictions.

With more data available for regenerated stands, a suitable aspen regeneration density and the optimum combination of two species can be identified. Any suggestions and conclusions obtained from the further study will be helpful to guide regenerated stand management and silvicultural activities. Additional efforts on the validation of the models may also be conducted using independent data sets in order to detect any possible abnormalities of the models, developed for ingrowth and juvenile white spruce and aspen growth in this study, under different conditions.

The objectives of this study were met, and the models should be beneficial to the understanding of the ingrowth process in the boreal mixedwood stands, and the dynamics of the regenerated juvenile spruce and aspen mixedwood stands, and lead to better management of Alberta forest resources.

Appendices

Appendix 1. Splus code for fitting the generalized logistic model (ingrowth probability model) based on the maximum likelihood estimation

The following code provides an example for fitting the generalizes logistic model (2.7) based on the maximum likelihood estimation. The data file "sw1plus.dat", summarized from the original permanent sample data (PSP), contains ingrowth present status observation for white spruce, on each of which, the value of the explanatory variable DBH, DBHsw, BA, Nhasw, SI, L, and the binary response variable Y are listed. In this program, *beta0* must be given as initial estimates of the parameters, and *f* is defined as the negative log likelihood function. The call to the nonlinear minimizer, *nlmin*, minimizes the function *f*, and then obtains the maximum likelihood estimates for the generalized logistic model. The output results are listed in *mle*.

```
*****************************************************************************************
#Input data and abstract variables from the columns;
#DBH = average diameter at breast height for all species,
#DBHsw = average diameter at breast height by white spruce,
#BA = stand basal area per ha,
#Nhasw = number of white spruce trees per ha,
#SI = site index,
#L = length of the remeasurement interval,
#Y = ingrowth status at the end of the interval.
    data <- matrix (scan ("sw1plus3.dat"), ncol=10 , byrow=T)
    Y <- data[,10]
    L <- data[,9]
    DBHsw <- data[,6]
    BA <- data[,4]
    SI <- data[,8]
    Nhasw <- data[,5]
    DBH <- data[,7]
# Calculate DBH*DBHsw and logarithm of Nhasw;
    DSQUARE <-DBH*DBHsw
    LOGSDEN <-LOG(Nhasw)
#Form the matrix X
    x<-cbind(1, BA, LOGSDEN, DBH, SI, DSQUARE)
#Set the initial values for parameter vector β;
    beta0<-c(1.2, -0.1, 0.63, -0.2, 0.03, 0.003)
#Define the minus log likelihood function according to (2.9);
    f <- function(beta)
    { t(y*(1/l))%*%log(1+exp(-x%*%beta))-t(1-y)%*%log(1-(1/(1+exp(-x%*%beta))^(1/l))) }
#Minimize the minus log likelihood function, that is, maximize the log likelihood function;
    result <- nlmin(f, beta0, print.level=2, max.fcal=100, max.iter=50, ckfc=0.01)
```

```
#Assign the maximum likelihood estimate to mle;
     mle <- result$x
#Calculate the maximum likelihood function;
     llhf <- -f(mle)
#Print out the results;
     print (result)
     print (mle)
     print (llhf)
```

Appendix 2. SAS code for fitting the ingrowth amount model

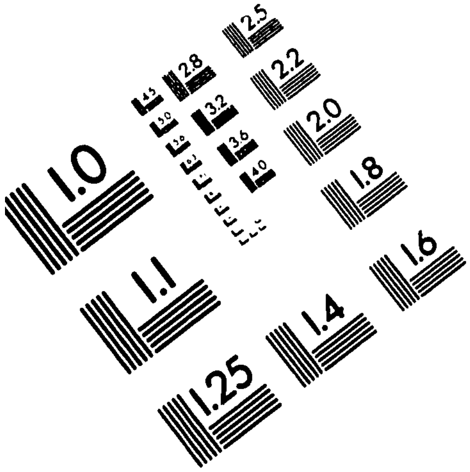
The following code illustrates the fitting procedure of the ingrowth amount model for white spruce, given the ingrowth is known to occur. Each observation is a record at the end of each remeasurement interval with the amount of ingrowth trees and corresponding stand characteristics such as stand basal area, density, species composition, site productivity, average diameter and average height. The call to the procedure PROC REG requests the maximum R^2 improvement technique for the explanatory variable selection in the linearized ingrowth amount model (2.26). The call to the procedure PROC NLIN illustrates the nonlinear regression for the model (2.29). The initial estimates of parameters are given (PARMS A1, ..., C1), and the partial derivatives of the model are listed (DER.A1, ..., DER.C1). The output data file "RESULT" from the nonlinear regression is used for residual analysis, which is accomplished by using the procedure PROC PLOT.

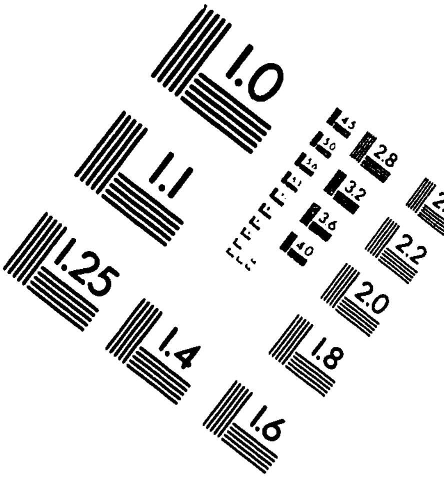
```
*****************************************************************************************
*Input the data;
*GRNUMB = group number;
*PLNUMB = plot number;
*SPCODEX = species code;
*MEASNU = measurement number;
*TOTDEN = total number of trees per ha (DBH≥1.1 cm);
*TOTDBH = average diameter at breast height (DBH≥1.1 cm);
*TOTBA = stand basal area per ha (DBH≥1.1 cm);
*AHTTOT = average total height (DBH≥1.1 cm);
*TREDEN = total number of trees per ha (DBH≥9.1 cm);
*TREDBH = average diameter at breast height (DBH≥9.1 cm);
*TREBA = stand basal area per ha (DBH≥9.1 cm);
*AHTTRE = average total height (DBH≥9.1 cm);
*SPDEN11 = total number of trees per ha by species (DBH≥1.1 cm);
*SPBA11 = stand basal area per ha by species (DBH≥1.1 cm);
*SPHT11 = average total height by species (DBH≥1.1 cm);
*SPDBH11 = average diameter at breast height by species (DBH≥1.1 cm);
*SPDEN91 = total number of trees per ha by species (DBH≥9.1 cm);
*SPBA91 = stand basal area per ha by species (DBH≥9.1 cm);
*SPHT91 = average total height by species (DBH≥9.1 cm);
*SPDBH91 = average diameter at breast height by species (DBH≥9.1 cm);
*SPSPI = species specific site productivity index;
*SPSI = species specific site index;
*INTVLEN = length of the remeasurement interval;
*DENRATE1 = species composition by density (DBH≥1.1 cm);
*DENRATE9 = species composition by density (DBH≥9.1 cm);
*COMPOSI1 = species composition by basal area (DBH≥1.1 cm);
```

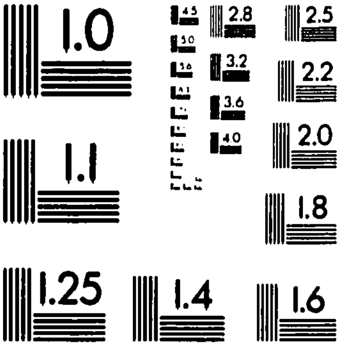
```
*COMPOSI9 = species composition by basal area (DBH≥9.1 cm);
*MING = annual ingrowth per ha by species;
    DATA SW;
    INFILE ' D:\DATASET.DAT ' MISSOVER LRECL=140;
      INPUT   GRNUMB 1-4 PLNUMB 5 SPCODEX 6 MEASNU 7 TOTDEN 8-12 TOTDBH
      13-17 .1 TOTBA 18-25 .4 AHTTOT 26-30 .1 TREDEN 31-35 TREDBH 36-40 .1 TREBA
      41- 48 .4 AHTTRE 49-53 .1 SPDEN11 54-58 SPBA11 59-66 .4 SPHT11 67-71 .1
      PDBH11 72-76 .1 SPDEN91 77-81 SPBA91 82-89 .4 SPHT91 90-94 .1 SPDBH91
      95-99  .1 NTVLEN 100-103 .1 DENRATE1 104-110 .4 DENRATE9 111-117 .4
     COMPOSI1 118-124 .4 COMPOSI9 125-131 .4 MING 132-139 .1;
*Only include observations for white spruce;
    IF  SPCODEX^=1 THEN DELETE;
*Only include observations with ingrowth;
    IF  MING=0 THEN DELETE;
*Compute possible variable transformations;
    LOGMING=LOG(MING);
    LOGSDBH1=LOG(SPDBH11);
    INSDBH1=1/SPDBH11;
    DBHSQU=(SPDBH11)*(SPDBH11);
    LOGSDEN1=LOG(SPDEN11);
    INSDEN1=1/(SPDEN11);
    LOGSBA1=LOG(SPBA11);
    INSBA1=1/SPBA11;
    LOGSI=LOG(SPSI);
    RUN;
/* An example for fitting the linearized model with the maximum R2 improvement technique for the
variable selection (2.26);                                                                      */
/* PROC REG DATA=SW;                                                                            */
/* MODEL LOGMING= LOGSDBH1 SPDBH11 SPDEN11 TOTBA SPSI LOGSI DBHSQU
                             DENRATE1 COMPOSI1 /LECTION=MAXR;                                   */
/* RUN;                                                                                         */
*Request PROC NLIN procedure on data SW using Marquardt method;
    PROC NLIN DATA=SW METHOD=MARQUARDT;
*Set the initial values for parameters;
    PARMS A1=0.6  A2=0.0002 A3=-0.02 A4=0.04 A5=0.01 B1=3.5 C1=-0.6 ;
*Calculate parameters as defined in (2.29);
    A=A1*EXP(A2*SPDEN11+A3*TOTBA+A4*SPSI+A5*DBHSQU);
    B=B1;
    C=C1;
*Specify the ingrowth amount base curve in (2.29);
    MODEL MING=A*(SPDBH11)**B*(EXP(C*SPDBH11));
*Calculate the partial derivative of the model (2.29) to each parameter;
    DER.A1=EXP(A2*SPDEN11+A3*TOTBA+A4*SPSI+A5*DBHSQU)*(SPDBH11)**B*
            (EXP(C*SPDBH11));
    DER.A2=SPDEN11*A*(SPDBH11)**B*(EXP(C*SPDBH11));
    DER.A3=TOTBA*A*(SPDBH11)**B*(EXP(C*SPDBH11));
    DER.A4=SPSI*A*(SPDBH11)**B*(EXP(C*SPDBH11));
    DER.A5=DBHSQU*A*(SPDBH11)**B*(EXP(C*SPDBH11));
    DER.B1=LOG(SPDBH11)*A*(SPDBH11)**B*(EXP(C*SPDBH11));
```

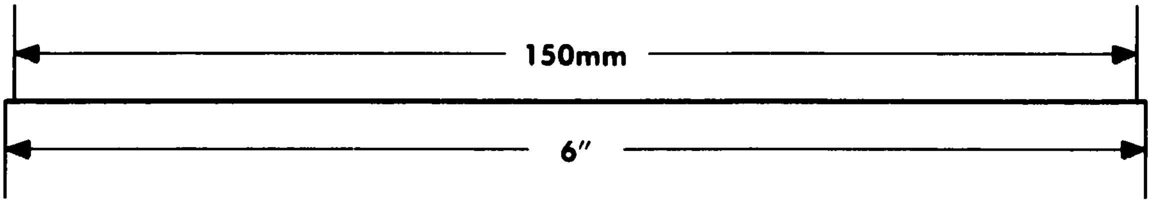
```
    DER.C1=(SPDBH11)*A*(SPDBH11)**B*(EXP(C*SPDBH11));
*Output the predicted ingrowth YHAT, residuals RESID, and studentized residuals STRESID;
    OUTPUT OUT=RESULT P=YHAT R=RESID STUDENT=STRESID;
    RUN;
*Plot scatter plots for residual examinations;
    PROC PLOT DATA=RESULT;
    PLOT MING*SPDBH11='A' YHAT*SPDBH11='P' /OVERLAY VPOS=25;
    PLOT RESID*SPDBH11 / VREF=0 VPOS=25;
    PLOT RESID*YHAT / VREF=0 VPOS=25;
    PLOT STRESID*YHAT / VREF=0 VPOS=25;
    RUN;
```

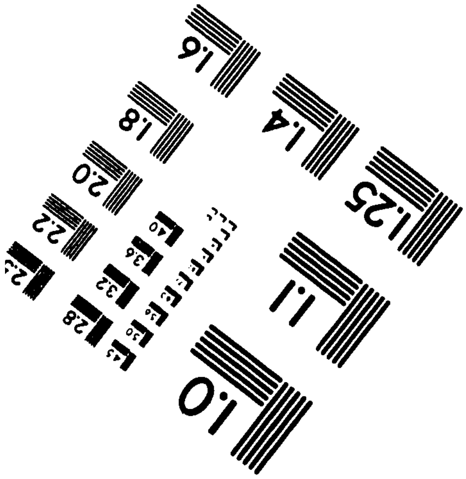
IMAGE EVALUATION
TEST TARGET (QA-3)

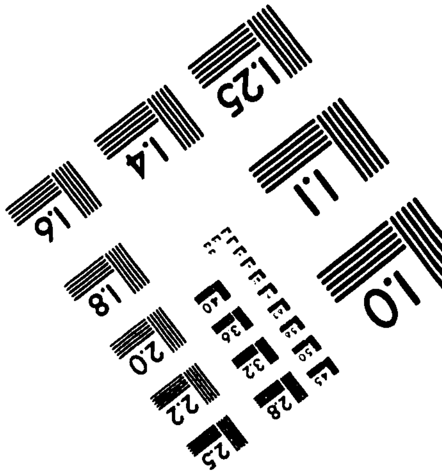












APPLIED IMAGE, Inc
1653 East Main Street
Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989