University of Alberta

Influence of Site Quality and Overstory Age on the Growth of Understory White Spruce in Boreal Mixedwood Stands

by ©

Melanie Lois Kalischuk

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 2004

Your file Votre référence
ISBN: 0-612-96498-1
Our file Notre référence
ISBN: 0-612-96498-1

Abstract

The first objective of this thesis was to evaluate the influence of site quality, tree size and competition in explaining understory white spruce growth in NE British Columbia. Regression techniques were used to develop a height growth model that used crown surface area, an interaction between aspen site index and diffuse non-interceptance light (DIFN) and an interaction between crown surface area and DIFN to explain 51.7% of the variation in height growth. A basal area increment model was developed and used initial tree diameter, deciduous basal area, aspen site index and an interaction between aspen site index and deciduous basal area to explain 90.2% of the variation in spruce growth. Site series and age class were also important variables to consider when modelling growth. The second objective was to evaluate the relationships between white spruce site index and periodic mean annual height growth. Results show that white spruce site index can be predicted from periodic mean annual height growth of understory trees provided there is an adjustment for competition.

Acknowledgements

First of all, I would like to thank my supervisors Dr. Stephen Titus and Dr. Peter Blenis for their dedication and support on this project. Their support and dedication to this project is greatly appreciated. I would also like to acknowledge Keith Thomas from the B.C. Ministry of Forests for initiating and funding this research. I would also like to thank field staff that worked on this project, Michele Elston, Jocylene Read and Forsite Forestry Services Ltd.. I would also like to thank my parents, Victor and Ruth Kalischuk for their support throughout my degree. I would also like to thank my siblings, Lisa and Wilco Tymenson, V.R.J. (Rocky) and Kathi Kalischuk, and Andrea Kalischuk for encouraging me throughout my degree. I would like to thank my uncle Ron Grant for giving me the inspiration to write the thesis. I would also like to thank my uncle George Kalischuk for sparking my interest in working in the forest.

Financial support provided by Forest Productivity Council of British Columbia and Forest Renewal B.C.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (continued)

LIST OF APPENDICES

Chapter 1: Introduction

Mixtures of trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* {Moench} Voss) are a major component of the boreal forest in Western Canada and are abundant in the Boreal White and Black Spruce zone in British Columbia (DeLong et al. 1990; Meidinger and Pojar 1991). After disturbance, trembling aspen regenerates prolifically by root suckering with densities ranging between 10 000 and 40 000 stems per hectare (Peterson and Peterson 1992). Rapid initial growth rates enable aspen to dominate sites for the first 40-60 years (Navratil et al. 1994). Mixedwood stands arise when white spruce develops in the understory. The age structure of white spruce can be even aged with white spruce becoming established at the same time as aspen or uneven aged with the recruitment of white spruce occurring gradually over 15-20 years (Lieffers et al. 1996). After age 60, aspen dominated stands reach maturity and if not harvested the stand goes through a period of stand breakup. If white spruce is growing in the understory during break-up, the site shifts to a conifer-dominated site for the next 20-40 years (Navratil et al. 1994).

Many benefits have been identified for growing mixtures of trembling aspen and white spruce together, and they include amelioration of environmental extremes, control of herbaceous competitors, reduction in insect pests and pathogens, stability from wind and improved litter decomposition and nutrient cycling (Comeau 1996; Man and Lieffers 1999). Although these benefits may enhance the growth of understory spruce, competition for light and other resources may reduce white spruce growth rates (Shirley 1945; Lautenschlager 1995).

The objectives of this thesis are to 1) evaluate the influence of site quality, understory tree size and competition in explaining understory white spruce growth and to determine which initial tree size variable and competition variable are the most useful for estimating growth. 2) to determine if site series and age class are important variables for explaining understory white spruce growth in mixedwood stands and 3) to determine if white spruce site index can be predicted from understory white spruce periodic annual height growth and to determine if competition is a necessary variable for developing these predictive equations.

The Light Environment Beneath the Aspen Canopy

Many studies have focused on the light dynamics of boreal mixedwood stands (Lieffers and Stadt 1994; Lieffers et al. 1999; Messier et al. 1999a; Comeau 2001). Although the light dynamics in mixedwood stands tend to be variable, it can be generalised that white spruce growing in the understory of aspen experience a bottle neck effect when in competition for light (Lieffers et al. 2002) and possibly other resources (Shirley 1945). As aspen establish during the first 10-15 years after disturbance, understory white spruce recruitment tends to be gradual, and understory growing conditions are adequate for white spruce growth. At 15-25 years post-disturbance, aspen stands reach maximum leaf area and light availability for white spruce tends to be minimized (Lieffers et al. 2002). After 25 years and until the spruce become the dominant species, light levels increase as deciduous stems are lost through self-thinning.

Influences of Light on Growth of White Spruce in the Understory

Given that light is more easily measured than soil moisture and nutrients (Lieffers et al. 1999; Comeau 2000) and light has been considered the most important limiting factor influencing growth of understory trees in mixedwood stands (Canham 1988; Coates and Burton 1999), relationships between understory growth and light penetrating the overstory have been recorded. Appreciable height growth rates of understory white spruce can occur provided that approximately 40% of light is transmitted through the overstory (Logan 1969; Lieffers and Stadt 1994; Wright et al. 1998). For survival, the minimum transmittance tolerated by white spruce is 8% (Lieffers and Stadt 1994) and height growth is expected to increase linearly with transmittance between 10 and 40% of full sunlight (Wright et al. 1998).

Numerous studies indicate diameter growth is more responsive to competition than height growth (Wagner and Radosevich 1991; Lautenschlager 1995). This may result from trees assigning higher priority to maintenance of height growth rather than diameter growth (Lanner 1985; Drew and Farrell 1997) when under competition. Although maximum height growth is achievable at 40% transmittance, diameter growth tends to be greatly reduced at this light level, and it is suggested that maximum diameter growth rates may only be attainable in full sunlight (Logan 1969; Jobidon 2000).

The response of crown length and width to light gradients for various species with different shade tolerances has received considerable study (Greis and Kellomaki 1981; Messier et al. 1999b). Under shaded conditions, tolerant species such as *Abies* maximize the efficiency of overhead light interception by producing a plate-like crown structure through increasing lateral branch growth relative to height growth (Oliver and Larson 1990). Shade intolerant species lack morphological plasticity and height growth continues under limited light conditions producing a narrow and deep crown with sparse foliage (Bazzaz and Carlson 1982). White spruce follows the growth trends of a tolerant species and has the capability of altering crown and height morphological growth responses relative to light gradients (Gries and Kellomaki 1981). For example, white spruce show strong interactions between tree height and the light environment (Claveau et al. 2002) and between crown volume and the light environment under paper birch stands (Comeau et al. 2003).

Measuring Competition in Boreal Mixedwood Stands

To provide quantitative methods for assessing competition in an operational setting, numerous studies have focused on relating easily measurable stand attributes to light transmittance. Basal area of hardwoods has been correlated with transmittance of light to the understory (Comeau 2001; Lieffers et al. 2002). Lorimer's index, the ratio of the sum of all the aspen diameters located in a fixed area plot to the diameter of a subject tree has been strongly correlated with understory light levels measured over the entire growing season (Comeau et al. 1998). Lorimer's index is useful as a competition index because it takes into account the density and size of competitors relative to the size of the subject tree (Lorimer 1983). These findings suggest that easily measurable stand attributes may be capturing similar species interactions in mixedwood stands and therefore could potentially be useful for predicting tree growth. Although there are more complicated competition indices such as distance dependent or spatial indices, these types of indices require timely proximity measurements between competitors and a subject tree and therefore, are less likely to be used in an operational setting. Distance independent indices such as hardwood basal area or Lorimer's index are much less time consuming to measure, are easily computed and therefore potentially more operationally suitable as competition measurements. As far as performance of the types of competition indices, studies have suggested there is little or no benefit to incorporating inter-tree distances into an index (Lorimer 1983; MacDonald et al. 1990; Holmes and Reed 1991; Wagner and Radosevich 1991).

Interaction between Site Quality, Competition and Tree Growth

Relationships between site quality and competition have been identified in the forest. Relationships between site and competition were found in stands comprised of Douglas-fir and western red cedar where competition influenced the growth of trees more at low light and site influenced the growth of trees more at high light (Drever and Lertzman 2001). In boreal mixedwood forests, aspen and white spruce grow together across a range of sites but it is unknown if there are site and competition interactions influencing the growth of understory white spruce.

In British Columbia, the province's biogeoclimatic classification system is widely used by forest managers to make decisions about harvesting activities and silviculture treatments (DeLong et al. 1990; Meidinger and Pojar 1991; British Columbia, Ministry of Forests 2002). The system of classification uses climatic conditions, soil properties and indicator vegetation to classify sites into zones, subzones and site series (Pojar et al 1987). The zone and subzone are indicative of factors such as elevation, accumulation of precipitation, as well as soil and atmospheric temperatures. Site series is determined on a more local scale and is based on soil moisture regime and nutrient status. Soil moisture regime (SMR) is defined as the amount of soil water available for evapotranspiration by vascular plants and should approximate a yearly average taken over several years. Soil nutrient regime (SNR) is defined as the amount of essential nutrients available to vascular plants and is also based on a yearly average taken over several years. Together, the SMR and SNR are placed onto an edatopic grid with grid positions corresponding to site series.

Predicting White Spruce Site Index in Boreal Mixedwood Stands

Site productivity includes the sum of all possible uses of a geographical area and in the context of forestry, site productivity is the amount of timber a site can produce within a certain time. Because there are difficulties with measuring the actual productivity of site, foresters estimate productivity using site quality. Site index is the most common method for estimating site quality and is defined as the average total height of dominant and co-dominant trees at a specified reference age. Site index is important in forestry because it is used as an input variable for most growth and yield models. It is also essential for making decisions about the opportunities and magnitude of silviculture treatments.

When dominant and co-dominant trees are absent in a stand or trees are suppressed due to competition, disease or insect problems, alternative methods are required for estimating site quality. In the Boreal White and Black Spruce zone (BWBS) of British Columbia, mixtures of trembling aspen and white spruce are common and widespread. Due to its rapid initial growth rates, trembling aspen commonly overtops the slower growing white spruce for the first 40-60 years after stand establishment. Consequently, dominant overstory white spruce site trees (i.e. trees that have grown free of the effects of competition over their lifetime) are rarely available for site index determination and therefore, the boreal mixedwood stand structure requires alternative methods for estimating the productivity potential of white spruce.

Other than traditional site indices, there are at least three methods for estimating site quality including: 1) the use of existing vegetation, environmental indicators and physiographic land features 2) conversion equations and 3) the use of periodic height growth (growth intercept methods).

Ecological variables such as site quality factors (soil moisture and nutrient availability), environmental conditions (climate, precipitation, seasonal temperatures, duration of the growing season), physiographic land classifications (topography, aspect, slope gradient, elevation) and understory vegetation have been used alone or in multiple factor analyses for estimating site index (Barnes et al. 1998 pp.306-328). Climate, topography, edatope and soil properties have been used to predict aspen site index in the BWBSwm sub-zone in British Columbia (Chen et al. 1998a). In the sub-boreal spruce (SBS) zone, Wang (1995) found soil properties, foliar nutrients and understory vegetation composition accounted for a substantial amount of variation in white spruce site index. It has been determined that site quality potentials for both aspen and white spruce are responsive to edatope where values increase from dry, nutrient poor sites to moist, nutrient rich sites (Wang 1993; Wang 1995; Chen et al. 1998a; Chen et al. 1998b).

When suitable site trees are absent in a stand, site index for one species may be predicted from that of a second species by the use of conversion equations. One-way or two-way prediction equations may be developed from stands when both species are present using linear regression or geometric mean regression (Nigh 1995a). Linear regression techniques were used to develop one-way prediction models that suggested yellow poplar (*Liriodendron tulipifera*) located at superior sites in Indiana, Ohio and West Virginia, had a consistently higher site index than oak (*Quercus velutina*, *Q. alba, Q. coccinea, Q. prinus and Q. rubra*) (Carmean and Hahn 1983). In northern Alberta forests, Hostin and Titus (1996) used linear regression to predict white spruce site index from a trembling aspen site index, with and without other ecological variables. Alone, site index of trembling aspen was a poor predictor (r^2=0.09), however, combined with aspen diameter, density, elevation and soil nutrient regime, the coefficient of multiple determination was 0.79. Two-way conversion equations have been developed for lodgepole pine and white spruce (Nigh 1995b; Wang 1998) and Douglas-fir and western hemlock (Nigh 1995) with R^2 values between 0.82 and 0.94.

Periodic height growth has been used in young plantations to predict site index (Wakeley and Marrero 1958; Ferree et al. 1958; Day et al. 1960; Gunter 1968; Beck 1971; Brown and Stires 1981; Nigh 1999; Huang et al. 2001 p.31-32). This method is known as the growth intercept method and is designed specifically for estimating site quality in juvenile stands (Warrack and Fraser 1955; Wakeley and Marrero 1958; Ferree et al. 1958). A number of methods have been used to determine growth intercepts (Huang 1996). For example, the fixed growth intercept method uses an average of a certain number of growth intervals (3,4,5 and 10 years) above a fixed base height (0.3, 0.5, 0.75, 1.0, 1.3 and 2.0 m above ground level) to determine site index. In red pine plantations, site index was predicted from five-year height growth increments above breast height (Wakeley and Marrero 1958; Ferree et al. 1958; Day et al. 1960). Gunter (1968) predicted site index with five-year height growth one growing season after red pine was released from suppression. Beck (1971) predicted white pine site index from three and five-year height growth above breast height level. Brown and Stires (1981) predicted white pine site index from five-year growth increment from two years above breast height. Alban (1972) suggested the accuracy of predicting red pine site index was doubled when five-year height increments were taken from the first node above 8 feet rather than from breast height. Although growth intercept models have been developed for many species there is no standard for the number of height growth increments to include in the equation and contrary to Husch (1956) who suggested that the base height should be at breast height, there are no universal standards for the level of the base height.

A second method for determining growth intercepts is the variable growth intercept procedure. In British Columbia, Nigh (1995b, 1996a, 1996b, 1996c, 1997) has used this procedure to predict site index for most commercial species and it is particularly useful for species that do not produce distinct annual whorls. This method predicts site index from measurements of tree height and breast height age. The variable growth intercept method differs from the fixed growth intercept method by the number of growth intercepts being used to determine site index. The variable growth intercept method averages all the growth increments above breast height level. An advantage of the variable growth intercept method includes a reduction in the influence of abnormal growth years. It also avoids having to find annual height growth whorls that can be difficult to identify with certainty, in some cases.

Thesis Organisation

This thesis is arranged in three chapters and a research summary at the end. Chapter 2 of the thesis focuses on developing a height growth model and a basal area increment model from tree size variables, site quality and overstory competition variables. Chapter 3 focuses on determining if site series and overstory age are important variables when predicting the growth of understory trees. The fourth chapter attempts to predict white spruce site index using conventional growth intercept equations with an adjustment for competition.

References

Alban, D.H. 1972. An improved growth intercept method for estimating site index of red pine. USDA For. Ser. Res. Pap. NC-80.

Barnes, B.V., D.R. Zak., S.R. Denton., S.H. Spurr. 1998. Forest ecology, 4th edition. John Wiley & Sons, Inc., New York. 774 pp.

Bazzaz, F.A., R.W. Carlson. 1982. Photosynthetic acclimation to variability in the light environment of early and late successional plants. Oecologia 54: 313-316.

Beck, D.E.1971. Growth intercept as an indicator of site index in natural stands of white pine in the Southern Appalachians. USDA For. Serv. Res. Note SE-154.

British Columbia, Ministry of Forests. 2002. Stocking and free growing survey procedures manual. B.C. Min. For., Forest Practices Br. Victoria, B.C..

Brown, J.H., J.L. Stires. 1981. A modified growth intercept method for predicting site index in young white pine stands. For. Sci. 27(1): 162-166.

Canham, C.D. 1988. An index for understory light levels in and around canopy gaps. Ecology 69(5): 1634-1638.

Carmean, W.H., J.T. Hahn. 1983. Site comparison for upland oaks and yellow popular in the central States. J. For. 81: 736-739.

Chen, H.Y.H., K. Klinka., R.D. Kabzems. 1998a. Site index, site quality, and foliar nutrients of trembling aspen: relationships and predictions. Can. J. For. Res. 28: 1743-1755.

Chen, H,Y,H., K.Klinka., R.D. Kabzems. 1998b. Height growth and site index models for trembling aspen (*Populus tremuloides* Michx.) in northern British Columbia. For. Ecol. Manage. 102: 157-165.

Claveau, Y. C. Messier., P.G. Comeau., K.D. Coates. 2002. Growth and crown morphological responses of boreal conifer seedlings and saplings with contrasting shade tolerance to a gradient of light and height. Can. J. For. Res. 32: 458-468.

Coates, K.D., P.J. Burton. 1999. Growth of planted tree seedlings in response to ambient light levels in northwestern interior cedar-hemlock forests in British Columbia. Can. J. For. Res. 29: 1374-1382.

Comeau, P.G., J.R. Wang., T. Letchford. 2003. Influences of paper birch competition on growth of understory white spruce and subalpine fir following spacing. Can. J. For. Res. 33: 1962-1973.

Comeau, P.G. 2001. Relationships between stand parameters and understory light in boreal aspen stands. B.C. Journal of Ecosystem Management. 1(2): 1-8.

Comeau, P.G. 2000. Measuring light in the forest. B.C. Ministry of Forests., Res. Br. Victoria, Extension Note 42. 7 pp.

Comeau, P.G., F. Gendron., T. Letchford. 1998. A comparison of several methods for estimating light under a paper birch mixedwood stands. Can. J. For. Res. 28: 1843-1850.

Comeau, P.G. 1996. Why Mixedwoods? *In* Silviculture of boreal and temperate broadleaved-conifer mixtures. P.G. Comeau and K. Thomas (editors) B.C. Ministry of Forests, Victoria, B.C., Land Management Handbook No. 36, pp.1-7.

Day, M.W., C.F. Bey., V.J. Rudolph. 1960. Site index for planted red pine by the 5-year growth intercept method. J. For. 58: 198-202.

Delong, C., A. MacKimmon., L. Jang. 1990. A field guide for identification and interpretation of ecosystems of the Northeast portion of the Prince George Forest Region. B.C. Ministry of Forests, Res. Br., Victoria, British Columbia. Land Management Handb. 22.

Drever, C.R., K.P. Lertzman. 2001. Light-growth responses of coastal Douglas-fir and western redcedar saplings under different regimes of soil moisture and nutrients. Can. J. For. Res. 31: 2124-2133.

Drew, A.P., W.K. Ferrell. 1977. Morphological acclimation to light intensity in Douglas-fir seedlings. Can. J. Bot. 55:

Ferree, T., D. Shearer., E.L. Stone, Jr. 1958. A method of evaluating site quality in young red pine plantations. J. For. 56: 328-332.

Greis, I., S. Kellomaki. 1981. Crown structure and stem growth of Norway spruce undergrowth under varying shading. Silv. Fenn. 15: 306-322.

Gunter, J.E. 1968. Site index for released red pine plantations. J. For. 66: 862-863.

Holmes, M.J. and D.D. Reed. 1991. Competition indices for mixed species northern hardwoods. For. Sci. 37(5): 1338-1349.

Hostin, P.J., S.J. Titus. 1996. Indirest site index models for white spruce in Alberta's boreal mixedwood forest. For. Chron. 72: 73-79.

Huang, S., D. Morgan, G. Klapstein., J. Heidt., Y. Yang., G. Greidanus. 2001. Gypsy: A Growth and yield projection system for natural and regenerated stands within an ecologically based, enhanced forest management framework. Land and Forest Division, Alberta Sustainable Resource Development. Edmonton.

Huang, S. 1996. Growth intercept models for assessing the site potential of young lodgepole pine stands in Alberta. Alberta Land and Forest Service, Tech. Rep. Pub. No. T/339, Edmonton, Alberta. 97pp.

Husch. B. 1956. Use of age at D.B.H. as a variable in the site index concept. J. For. 54: 340.

Jobidon, R. 2000. Density-dependent effects of northern hardwood competition on selected environmental resources and young white spruce (*Picea glauca*) plantation growth, mineral nutrition and stand structure development-15-year study. For. Ecol. Manage. 130: 77-97.

Lanner, R.M. 1985. On insentivity of height growth to spacing. For. Ecol. Manage. 13: 143-148.

Lautenschlager, R.A. 1995. Competition between forest brush and planted white spruce in north-central Maine. NJAF 12(4): 163-167.

LI-COR. 1992. LAI-2000 plant canopy analyzer. Instructions manual. LI-COR, Inc., Lincoln, Nebr.

Lieffers, V.J., B.D. Pinno., K.J. Stadt. 2002. Light dynamics and free-to-grow standards in aspen-dominated mixedwood forests. For. Chron. 137-145.

Lieffers, V.J., C. Messier, K.J. Stadt, F. Gendron, P.G. Comeau. 1999. Predicting and managing light in the understory of boreal forests. Can. J. For. Res. 29: 796-811.

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

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

Logan, K.T. 1969. Growth of tree seedlings as affected by light intensity IV. Black spruce, white spruce, balsam fir and eastern white cedar. Dept. of Fisheries and Forestry, Canadian Forest Service. Publication 1256.

Lorimer, C.G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. For. Ecol. Manage. 6:343-360.

MacDonald, B., D.M. Morris., P.L. Marshall. 1990. Assessing components of competition indices for young boreal plantations. Can. J. For. Res. 20: 1060-1068.

Man, R., V.J. Lieffers. 1999. Are mixtures of aspen and white spruce more productive than single species stands? For. Chron. 75(3): 505-513.

Meidinger, D., J. Pojar. 1991. Ecosystems of British Columbia. B.C. Ministry of Forests, Res. Br. Victoria, B.C. Special Report Series 6.

Messier, C., R. Doucet, J.C. Ruel Y. Claveau., C. Kelly., M.J. Lechowicz. 1999a. Functional ecology of advance regeneration in relation to light in boreal forests. Can. J. For. Res. 29: 812-823.

Messier, C., S. Parent., M. Chengaou., J. Beaulieu. 1999b. Juvenile growth and crown morphological plasticity of eastern white pine (Pinus strobus L.) planted along a natural light gradient: results after 6 years. For. Chron. 75: 275-279.

Navratil, S., L.G. Brace., E.A. Squder., S. Lux. 1994. Silviculture and harvesting options to favor immature shite spruce and aspen regeneration in boreal mixedwoods. Canadian For. Serv., Info. Rep. NOR-S-337.

Nigh, G.D. 1999. Revised growth intercept models for coastal western hemlock, Sitka spruce, and interior spruce. B.C. Min. For., Res. Br., Victoria, B.C. Exten. Note 37. 8 pp.

Nigh, G.D. 1997. A growth intercept model for coastal Douglas-fir. B.C. Min. For., Res. Br. Victoria, B.C. Res. Rep. 10. 20pp.

Nigh, G.D. 1996a. A variable growth intercept model for spruce in the Sub-Boreal Spruce and Englemann Spruce-Subalpine Fir biogeoclimatic zones of British Columbia. B.C. Min. For., Res. Br., Victoria. B.C. Res. Rep. 05, 20pp.

Nigh, G.D. 1996b. A variable growth intercept model for Sitka spruce. B.C. Min. For., Res. Br. Victoria, B.C. Ext. Note 03. 7pp.

Nigh, G.D. 1996c. Growth intercept models for species without distinct annual branch whorls: western hemlock. Can. J. For. Res. 26: 1407-1415.

Nigh, G.D. 1995a. The geometric mean regression line: a method for developing site index conversion equations for species in mixed stands. For. Sci. 41: 84-98.

Nigh , G.D. 1995b. Variable growth intercept models for lodgepole pine in the sub-boreal spruce biogeoclimatic zone, British Columbia. B.C. Min. For., Res. Br., Victoria, B.C. Res. Rep. 02. 23 p.

Oliver, C.D., B.C. Larson. 1990. Forest stand dynamics. McGraw-Hill. Inc., New York, 673 pp.

Peterson, E.B., N.M. Peterson. 1992. Ecology, management, and use of aspen and balsam popular in the prairie provinces. For. Can. Northwest Reg. North. For. Cent. Spec. Rep. 1.

Pojar, J., K.Klinka, D.V. Meidinger. 1987. Biogeoclimatic Ecosystem Classification in British Columbia. For. Ecol. Manage. 22: 119-154.

Shirley, H.L. 1945. Reproduction of upland conifers in the lake states as affected by root competition and light. Am. Mid. Nat. 33(3): 537-552.

Wagner, R.G., S.W. Rodesevich. 1991. Interspecific competition and other factors influencing the performance of Douglas-fir saplings in the Oregon Coast Range. Can. J. For. Res. 21: 829-835.

Wakeley, P.C. J. Marrero. 1958. Five-year intercept as site index in southern pine plantation. J. For. 56: 332-336.

Wang, G.G. 1998. An ecologically based model for site index conversion among species. can. J.For. Res. 28: 234-238.

Wang, G.G. 1995. White spruce site index in relation to soil, understory vegetation, and foliar nutrients. Can. J. For. Res. 25: 29-38.

Wang, G.G. 1993. Ecological site quality, site index, and height growth of white spruce stands in the Sub-boreal Spruce Zone of British Columbia. Ph.D. thesis, University of British Columbia, Vancouver.

Warrack, G.C., A.R. Fraser. 1955. Estimation of site quality in juvenile Douglas-fir stands. B.C. For. Serv. Res. Note 28. 5pp.

Wright, E.F., K.D. Coates., C.D. Canham., P. Bartemucci. 1998. Species variability in growth response to light across climatic regions in northwestern British Columbia. Can. J. For. Res. 28: 871-886.

Chapter 2: Influence of site quality, overstory competition and tree size on the growth of understory white spruce

Introduction

Mixtures of trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* {Moench} Voss) are a major component of the boreal forest in Western Canada and are particularly abundant throughout the Boreal White and Black Spruce zone in British Columbia (DeLong et al. 1990; Meidinger and Pojar 1991). Aspen is a shade intolerant species and with rapid initial growth rates it can dominate a site right after disturbance (Haeussler and Coates 1986 pp.97-100). White spruce is initially slower growing, but as a moderately shade tolerant species, it has the adaptive capabilities to survive and grow in the understory of hardwoods (Chen 1997; Wright et al. 1998; Messier et al. 1999a). Many benefits have been associated with growing mixtures of white spruce and aspen, including amelioration of environmental extremes, control of herbaceous competitors, reduction in insect pests and pathogens, stability from wind and improved litter decomposition and nutrient cycling (Comeau 1996; Man and Lieffers 1999). Although the benefits of growing mixtures may enhance the growth of understory spruce, competition for light and other resources may reduce white spruce growth rates (Shirley 1945; Lautenschlager 1995).

There has been increasing interest in developing individual tree growth models that use measurements of climate, site quality and competition to describe the interactions among species growing in mixtures (Haung and Titus 1994; Golser and Hasenauer 1997). These models provide the basis for predicting sustainable harvests over a landscape and become instrumental in developing optimal timing and intensity of treatments that are used to regenerate the forest (Pinno 2000; Comeau 2003). The best models are those that use the necessary variables for explaining a reasonable proportion of the variation in the response variable, have biologically meaningful interpretations of the relationships between the variables and closely fit the data.

Given that light is more easily measured than soil moisture or nutrients (Lieffers et al. 1999; Comeau 2000) and light has been considered the most important factor influencing understory tree growth in mixedwood stands (Canham 1988; Coates and Burton 1999), relationships between understory growth and light penetrating the overstory have been recorded. Appreciable height growth rates of understory white spruce can occur between 40 and 100 percent of light transmittance (Logan 1969; Lieffers and Stadt 1994; Wright et al. 1998). For survival, the lowest transmittance tolerated by white spruce is 8% (Lieffers and Stadt 1994) and height growth is expected to increase linearly with transmittance between 10-40% of full sunlight (Wright et al. 1998).

Numerous studies indicate diameter growth is more responsive to competition than height growth (Wagner and Radosevich 1991; Lautenschlager 1995). This may result from trees assigning higher priority to maintenance of height growth rather than diameter growth (Lanner 1985; Drew and Farrell 1997) under competition. Although maximum height growth is achievable at 40% transmittance, diameter growth tends to be greatly reduced at this light level, and maximum diameter growth rates may only be attainable in full sunlight (Logan 1969; Jobidon 2000).

To provide quantitative methods for assessing competition in an operational setting, numerous studies have focused on relating easily measurable stand attributes to transmittance. Basal area of hardwoods has been correlated with transmittance of light to the understory (Comeau 2001; Lieffers et al. 2002). Lorimer's index, the ratio of the sum of all the aspen diameters located in a fixed area plot to the diameter of a subject tree has been strongly correlated with understory light levels measured over the growing season (Comeau et al. 1998). Lorimer's index is useful as a competition index because it takes into account the density and size of the competitors relative to the size of the subject tree (Lorimer 1983). These findings suggest that easily measurable stand attributes may be capturing similar species interactions in mixedwood stands and therefore could be useful for predicting tree growth. Although there are more complicated competition indices such as distance dependent or spatial indices, these indices require timely proximity measurements between competitors and a subject tree and therefore are less likely to be used in an operational setting. Distance independent indices such as hardwood basal area or Lorimer's index are much less time consuming to measure, are easily computed and therefore, are potentially more operationally suitable as competition measurements. Moreover, studies have suggested that there is little or no benefit to incorporating intertree distances into an index (Lorimer 1983; MacDonald et al. 1990; Holmes and Reed 1991; Wagner and Radosevich 1991).

When competition is used alone as a predictor of tree growth, the resulting explanation of variation tends to be low (Burton 1993; Bell et al. 2000). This may be because other variables such as site quality, overstory age, prior conditions experienced by the tree or other factors have a substantial influence on growth. Including an initial tree size variable with a competition index improves the performance of growth predictions (Daniels et al. 1986; MacDonald et al. 1990; Bell et al. 2000). The value of including initial tree size in a growth equation is that size is an indicator of past stand effects and prior conditions experienced by a tree and includes the inherent capability of a species to adapt to long term environmental conditions. The response of crown length and width to light gradients for various species with different shade tolerances has received considerable study (Greis and Kellomaki 1981; Messier et al. 1999b). Under shaded conditions, tolerant species such as *Abies* maximize the efficiency of overhead light interception by producing a plate-like crown structure through increasing lateral branch growth relative to height growth (Oliver and Larson 1990). Intolerant species lack morphological plasticity and height growth continues under limited light conditions, producing a narrow and deep crown with sparse foliage (Bazzaz and Carlson 1982). White spruce follows the growth trends of a tolerant species and has the capability of altering crown and height morphological growth responses relative to light gradients (Gries and Kellomaki 1981). For example, there were strong interactions between tree height and light (Claveau et al. 2002) and between crown volume and light under paper birch stands (Comeau et al. 2003). Currently there are no models for predicting understory white spruce growth in boreal forests as a function of the array of complex interactions that manifest from different tree sizes and competition variables.

Including tree size in a growth model is beneficial because size is correlated with age. In boreal mixedwood forests, white spruce typically become established beneath an overstory, persist in the understory while growing slowly, and then rapidly respond when sunlight increases following death of the shorter lived overstory. In natural mixedwood stands, understory white spruce age may not be a valuable indicator of growth because spruce establishment may be irregular and occur over many decades (Lieffers et al. 1996) or the light environment in the understory may be uneven with gaps providing favorable growing conditions for some individuals and a thick overstory providing harsh growing conditions for others (Canham 1988). Uneven competitive effects suggest that understory white spruce age may not be a useful variable for predicting growth in mixedwood stands.

Studies that have focused on relationships between site quality and above and below ground biomass accumulation have strongly suggested that higher quality sites support greater leaf area than lower quality sites (Keys and Grier 1981). It has been observed that on high quality sites, Douglas-fir produced more above ground biomass whereas trees growing at lower quality sites had greater production in below ground biomass accumulation (Keyes and Grier 1981). Shifting allocation between above and below ground biomass is essential to avoid moisture and nutrient deficiencies on low quality sites. Species that are responsive to site quality usually have lower maximum height growth rates at dry and/or poor soil nutrient sites. This has been observed in temperate hardwoods (Hix and Lorimer 1990). For mixtures of Douglas-fir and western red cedar, site quality and light environment studies suggested that radial growth was not responsive to site quality except when light transmittance was over 60%, whereas height growth was more influenced by site quality than competition (Drever et al. 2001). The relationship between site quality and height growth response may be species specific, with some species not responding to all components of site quality. For example, Nigh (1997) suggested juvenile lodgepole pine height growth was not responsive to changes in soil moisture availability. In boreal mixedwood stands, few studies have focused on the influence of site quality as a predictor of understory white spruce growth and therefore the role of site quality is unknown.

The objective of this study was to evaluate the influence of site quality, tree size and competition in explaining understory white spruce growth and to determine which combination of tree size and competition were the most useful variables for estimating growth.

Methods

Data for this study were collected during July and August of 2000 and 2001 from 27 aspen dominated mixedwood stands ranging in age from ten to 60 years located in the moist warm Boreal White and Black Spruce subzone (BWBSmw1) (DeLong et al. 1990) near Dawson Creek and Fort St. John, British Columbia. Stands were intentionally selected to cover a wide range of site productivity levels with large amounts of variation in site characteristics and stand attributes. Stands originated following either natural disturbance or clear-cut harvesting and had not been treated with the exception of a few younger stands that had been planted.

In each stand, three fixed area plots with a radius of 5.64 meters were established (Fig. 2-1). Depending on the size of the mixedwood stand, the first plot was placed 80-125 meters at a random bearing from the stand edge or access trail, the second plot was positioned 30 meters away at a bearing of 150 degrees from the first plot, the third plot was placed 30 meters 270 degrees from the second plot. At the time of the selection, the cluster of plots in each stand were placed at locations to avoid influences such as wind from permanent access structures and large openings; stands with insect outbreaks or pathogen problems were avoided.

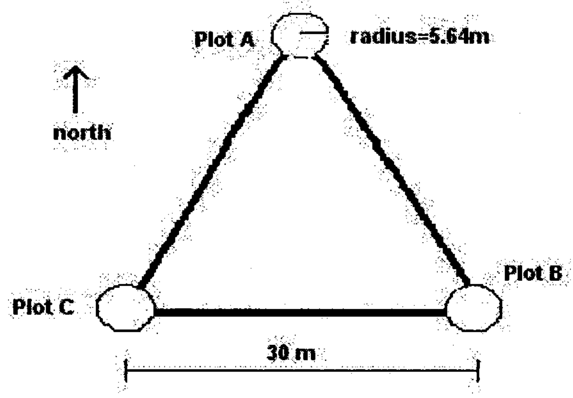

Figure 2-1: Schematic diagram of the plot layout. Understory white spruce and competition measurements were taken from the three fixed area plots. Site quality data were obtained from the 0.039 ha triangle.

Site Quality Measurements

Within the interior of the plot cluster (0.039 hectares) three dominant trembling aspen were selected as measurement trees. These trees were healthy, showed no signs or indicators of stress such as insect damage, disease or major structural deformities. For each sample tree, total height was measured with a clinometer and measuring tape and two cores were taken 1.3 meters above ground level. Ground level was determined as the highest point on the tree where the ground met the main stem. Cores were stored frozen until inspected in a laboratory. In the laboratory, age was determined and annual rings inspected for suppressed growth periods using a dissecting scope. If suppressed growth periods were identified, the core was discarded and the tree was eliminated as a measure of site quality.

Understory White Spruce Measurements

Within the fixed-radius plot area, the tallest understory white spruce was selected for measurements. Selected understory trees were not overtopped by herbaceous vegetation or shrubs and did not display any signs of insect or pathogen damage. Measurements included total height, height increments from the previous 5 years, height to the base of the live crown, crown radius measured in cardinal directions, branch increments from the previous 5 years measured in cardinal directions, diameter outside the bark, age, and diameter increments of the main stem from the previous 5 years measured at 1.3 meters above ground level.

The understory trees varied substantially in size, and therefore different measuring techniques were used. For trees with a total height between one and four meters, height measurements were completed using a tape measure. A height pole was used to measure trees between four and 12 meters, and a clinometer and tape measure was used to obtain height data for trees taller than 12 meters. For a few of the tallest understory trees, an estimate of height growth was made rather than a measurement because the top of the tree was obscured by the aspen canopy. An estimate of height growth was made less than three percent of the time.

Subject trees were cored or sectioned to determine age and radial growth for the last 5 years. Trees with a diameter greater than 5 cm were cored once at 1.3 meters above ground level and subject trees with a smaller diameter were sectioned at the same location. Cores and sections were stored frozen until inspection. Age was determined and increment widths measured using a mechanical Parker micrometer mounted on a dissecting scope. Radial increments for the sections were based on measurements from four perpendicular axes with the first axis being the position on the main stem with the longest diameter. Four axes were used for measurements because most of the understory trees had highly variable ring widths with tension and compression wood being present. One age measurement was taken from trees that were cored (trees with a dbh >5).

Crown radius was measured as the horizontal distance from the bole of the tree to the drip line in each cardinal direction around each tree. Branch increments were measured on the longest branch in cardinal directions. If the longest branch was 2.5 meters or higher above ground level, it was removed from the tree for measurements. When the longest branch could not be reached with the 6.0-meter pruning pole, a shorter branch was measured for growth.

Competition Measurements

Within each of the three fixed area plots located at each site, all trees taller than 130 cm were classified according to species and canopy position (Smith et al. 1997 p.30). Measurements and calculations included total density by species, and for each tree diameter 130 cm above ground level, an estimate of total tree height and an estimate of the ratio between the height of live foliage to the total height of the tree were taken. The ratio between live foliage to the height of the tree was an ocular estimate. One tree per plot within each canopy position was measured for total height and height to the base of the crown using a clinometer and measuring tape. Height to the base of the crown was determined as the position on the main stem where 50% of the bole was surrounded by healthy foliage. A smaller sampling area was used when the fixed area plot had more than 50 trees. A 5.64 m transect was placed through the center of the fixed area plot with the direction based on a random bearing. Trees located within 1.0 m on either side of the transect were measured. When the transect method was used, density was determined on the entire 5.64 m length.

Diffuse non-interceptance was measured in the cardinal directions around each understory sample tree using a LAI-2000 light meter (LiCor Inc., Lincoln, Nebraska) during July and August of 2001 for all sites with the exception of three that were measured during 2000. Sampling points with the LAI-2000 measurements corresponded directly to the crown width measurements by marking the precise location with flagging tape. DIFN is the diffuse portion of incident light and under a canopy, is the portion of sky not blocked by foliage (Li-Cor 1992). When LAI-2000 measurements are taken under a hardwood canopy, without direct beam light and preferably in uniform and overcast sky conditions, the values can provide reasonable estimates of photosynthetic photon density flux (PPDF) measured throughout the growing season (Comeau et al. 1998). To avoid direct beam light interfering with the readings, the north and west sides of the tree were measured in the morning and the south and east sides of tree were measured in the late afternoon. LAI measurements were taken at mid canopy with the height determined by the understory subject tree. In comparison to measurements taken at the top of a tree, measurements taken at mid canopy provide a better estimation of the amount of light a subject tree receives. With the LAI-2000 having a 10-meter radius field of view, a 180-degree view restrictor cap was placed over the lens to avoid inclusion of the subject tree in the measurements. Two LAI-2000 instruments were calibrated together and used for sampling. One instrument was placed in a nearby opening and used for open sky readings and the second was used for measurements under the canopy. The open sky instrument was programmed to take readings every 30-seconds for the length of the time required to complete the measurements under the canopy. Diffuse non-interceptance was calculated with C2000 software and the resulting values interpreted as a ratio of below to above canopy readings.

Data Preparation

The dependent variables were based on a 3-year period of annual growth from 1997, 1998 and 1999. Dependent variables included height and basal area increment.
Height increment was calculated as:

$$HTG3Y = SHTI_i / 3$$

where HTG3Y was 3-year periodic annual height growth measured in cm/y and HTI_i was the height increment of the subject tree measured in cm during the ith year (1997, 1998, 1999).

Basal area increment was calculated as:

$$BA3Y = (p\ (DBH99/2)^2 - p\ (DBH96/2)^2)\ / 3$$

where BA3Y was 3-year periodic annual basal area increment measured in cm^2/y.

DBH99 was calculated as:

$$DBH99 = DBH_m - SDIAINC_i$$

where DBH99 was diameter 130 cm above ground level at the end of the growing season in 1999 measured in cm, DBH_m was diameter at the time of the field work, measured in cm outside of the bark at 1.3 meters above ground level, $DIAINC_i$ was diameter increment measured in micrometers and converted to centimeters for the growth seasons i (2001, 2000).

DBH96 was calculated as:

$$DBH96 = DBH_m - SDIAINC_i$$

where DBH96 was diameter 130 cm above ground level at the end of the growing season in 1996 measured in cm, DBH_m was diameter at the time of the field work, measured in cm outside of the bark at 1.3 meters above ground level, $DIAINC_i$ was diameter increment measured in micrometers and converted to centimeters for the growth seasons i (2001, 2000, 1999, 1998, 1997).

Site Quality Variable

Trembling aspen site index (ATSI) was used as the measurement of site quality and was determined from models generated by the Alberta Forest Service (1985). These curves were recommended for use in British Columbia by the Ministry of Forests.

Initial Tree Size Variables

To avoid spurious correlation between the explanatory and response variable, size variables were based on measurements determined at the beginning of the growth period. Variables used to estimate the initial size of the subject tree were total height, diameter, crown surface area, crown volume and age at 1.3 meters above ground level. Age was determined by observation and did not require computation.

TH96 was calculated as:

$$TH96 = TH_m - SHTI_i$$

where TH96 was tree height measured in cm at the beginning of the growth period, TH_m was tree height at the time of measurement measured in cm, HTI_i were height increments measured in cm during the growth seasons of i (2001, 2000, 1999, 1998 and 1997).

DBH96 was calculated as:

$$DBH96 = DBH_m - SDIAINC_i$$

where DBH96 was diameter measured in cm at the beginning of the growth period, DBH_m was diameter at the time of the field work, measured in cm outside of the bark at 1.3 meters above ground level, $DIAINC_i$ was diameter increment measured in micrometer and converted to cm for the growth seasons i (2001, 2000, 1999, 1998 and 1997).

CSA96 was calculated as:

$$CSA96 = (p*CR96*CSAL96) / 10000$$

where CSA96 was crown surface area measured in m^2 at the beginning of the growth period.

CR96 was calculated as:

$$CR96 = SCR_d / 4$$

where CR96 was crown radius measured in cm at the beginning of the growth period.

CR_d was calculated as:

$$CR_d = CW_d - SCRINC_{di}$$

where CR_d was crown radius at the end of the growing season in 1996 one direction (d=N,S,E or W) measured in cm, CW_d was crown radius measured in cm at the time of measurements in d defined as one of the cardinal directions (N,S,E or W), and $CRINC_{di}$ was the length of the branch increment measured in cm in d (one cardinal direction) for the ith year (2001, 2000, 1999, 1998, 1997).

CSAL96 was used to calculate CSA96 and is equivalent to the hypotenuse of a 90 degree angled triangle. CSAL96 was calculated as:

$$CSAL96 = (CR96^2 + CL96^2)^{1/2}$$

where CR96 is defined above and CL96 is defined below.

CVOL96 was calculated as:

$$CVOL96 = (p*CR96^2 *CL96)/3 * 1000000$$

where CVOL96 was initial crown volume measured in m^3, CR96 was defined above.

CL96 was calculated as:

$$CL96 = TH_m - (HTI_i + HTLC)$$

where CL96 is crown length at the beginning of the growth period, HTLC is the height to the base of the live crown at the time of the field measurement were taken measured in cm, TH_m was tree height at the time of measurement measured in cm, HTI_i were height increments measured in cm during the growth seasons of i (2001, 2000, 1999, 1998 and 1997). HTLC was assumed as not rising throughout the growth period.

Competition Variables

Competition indices were calculated from field measurements and include deciduous basal area (BADEC), Lorimers index (CI1), and a crown-based index (CI2). DIFN was calculated using C2000 software and did not require calculations. For plots measured using the transect method, DBH_{TT} and CI2 were multiplied by 4.43 to achieve sampling in 99.93 m^2.

Basal area of the deciduous was calculated as:

$$BADEC = S\ ((p*d^2 / 4*10000)/ pm*10000)$$

where BADEC was deciduous basal area per hectare (m^2/ha), d was diameter of the aspen measured 1.3 m above ground level in cm, pm was either 99.93 if the entire 5.64 meter radius plot was measured or 22.56 if the transect method was used for sampling

CI1 was calculated as:

$$CI1 = (S\ (DBH_{TT})) / DBH_s$$

where CI1 was Lorimers index, DBH_{TT} was diameter of an aspen tree measured 1.3 m above ground in cm within the 5.64 m radius plot or transect, DBH_s was diameter of the subject tree measured 1.3 m above ground level.

CI2 was calculated as:

$$CI2 = S\ (CL_{At} - TH_m)$$

where CI2 was the sum of all the aspen crown lengths above the height of the sample tree inside the 5.64 m radius plot where CL_{At} was crown length of the aspen measured in cm and TH_m is the tree height of the subject tree the year that measurements were completed measured in cm.

The crown based competition index was based on two linear regression equations used to predict crown length of the aspen. Appendix A shows the equations and describes the methods in the development of the index.

Data Analysis

Regression analysis was used for predicting height growth and basal area increment of understory trees using aspen site index, tree size, competition and interaction terms. The first step involved developing simple linear relationships between one independent and the dependent variables. When required, a logarithmic transformation of the dependent variable was used to achieve homogeneous variance of errors.

Variables were selected using the C(P) statistic (Mallows 1973) and the R-square selection method in the Proc Reg procedure in SAS (SAS Institute Inc. V8 1999). To determine the appropriate number of variables for explaining the variation in the dependent variable, the C(P) statistic was plotted against the number of independent variables (p) and the number of variables was determined where the C(P) approaches (p+1), starting with the model having the most variables (Mallows 1973). After determining the number of variables, the R-selection procedure was used to determine the combination of variables that would explain the largest amount of variation in the response variable with site quality, initial understory tree size and competition variable. The selection process was completed for each dependent variable using each combination of competition variables, tree size variables and aspen site index and this resulted in 20 equations (five size variables, four competition variables, one site quality variable) for each dependent variable. Models were evaluated by having significant parameter estimates (alpha=0.05), the lowest error sums of squares and homogenous variances when the residuals were plotted against the predicted values.

After the variable selection process and equations were developed, one equation was selected as the best model for explaining the variation in each of the dependent variables. The final equation for each dependent variable was selected on the basis of having the highest adjusted R^2, biologically meaningful interpretation of the relationships between the variables and parsimony. Scatter plots were used to illustrate the relationships between the variables by transforming the linear equation without correction (Baskerville 1972), into a non-linear form in order to provide an easy interpretation of the response variable.

The number of observations in this study was less than 81 (27 sites x three understory trees) because the absence of understory trees with at least five years increments above 130 cm and in a few cases, an understory white spruce tree was not available for measurement at the reference point.

Results:

For the range of data collected in this study (Table 2-1), height growth and basal area increment as a function of either overstory deciduous basal area, diffuse non-interceptance and aspen site index were described as linear relationships. Other competition variables required a logarithmic transformation. A second order polynomial or logarithmic transformation explained growth as a function of initial understory tree size.

Table 2-1: Descriptive statistics for the dependent and independent variables

Variable	Units	N	Mean	Std. Dev.	Minimum	Maximum
HTG3Y	cm/y	43	26.23	9.50	11.57	47.67
BA3Y	cm^2/y	43	1.23	1.15	0.06	4.38
CSA96	m^2	43	1.69	1.99	0.006	8.38
CVOL96	m^2	43	2.07	3.37	0.00014	17.25
DBH96	cm	43	3.99	3.34	0.057	13.20
TH96	cm	43	315	231	73	1115
BHAGE	y	43	12.84	7.06	5.0	31.0
BADEC	m^2/ha	43	24.54	12.78	4.17	51.41
DIFN	-	43	0.26	0.11	0.10	0.51
CI1	$cm/100m^2$	43	147.82	158.03	12.94	802.38
CI2	-	43	148	141	9.04	755
ATSI	m	43	20.22	4.31	11.35	28.6

The Height Growth Model

The best fit equation for predicting spruce height growth included spruce crown surface area and the interactions between crown surface area and diffuse non-interceptance and between aspen site index and diffuse non-interceptance (Equation 1 Table 2-2). This model had the highest adjusted R^2 (0.52) and the lowest RMSE (6.60). Initial tree height, diameter, crown volume and breast height age were also suitable as initial tree size variables but in this study the equation including crown surface area had the highest R^2 and lowest RMSE (Appendix G).

The interaction between aspen site index and DIFN and the interaction between crown surface area and DIFN were important variables in the equation. When either interaction was dropped or only one term from either of the interactions was retained, the parameter estimates were not significant and/or the adjusted R^2 was lower and the RMSE was higher (Table 2-2). As individual terms, DIFN explained the most variation in height growth (0.18) and the equations containing crown surface area and aspen site index had parameter estimates that were not significant (alpha>0.05) (Table 2-2). When the quadratic term was added to the equation, there was a substantial increase in the ability of the equation to predict height growth (Equation 8, Table 2-2). The correlation matrix shows the relationships between independent variables (Table 2-3).

Table 2-2 : Equations for predicting height growth together with the estimated values, observed significance level of parameter values, the adjusted R^2 values and the root mean square error of the model

Equation	Para-meters	Parameter Estimate	Parameter p-value	R^2adj	RMSE
1 HTG3Y=b_0+b_1*CSA96+b_2*(ATSI*DIFN)+b_3*($CSA96^2$* DIFN)	b_0	8.57	0.0036	0.52	6.60
	b_1	5.18	<0.0001		
	b_2	2.56	<0.0001		
	b_3	-2.57	0.0002		
2 HTG3Y=b_0+b_1*CSA96+b_2*DIFN+b_3*($CSA96^2$*DIFN)	b_0	7.71	0.0342	0.41	7.26
	b_1	5.53	<0.0001		
	b_2	53.02	<0.0001		
	b_3	-2.69	0.0004		
3 HTG3Y=b_0+b_1*CSA96+b_2*ATSI+b_3*($CSA96^2$*DIFN)	b_0	11.22	0.0959	0.14	8.79
	b_1	3.35	0.0226		
	b_2	0.58	0.0731		
	b_3	1.36	0.0868		

Table 2-2 (continued): Equations for predicting height growth together with the estimated values, observed significance level of parameter values, the adjusted R^2 values and the root mean square error of the model

Equation	Para-meters	Parameter Estimate	Parameter p-value	R^2adj	RMSE
4 $HTG3Y=b_0+b_1*CSA96+b_2*(CSA96^2*DIFN)$	b_0	22.81	<0.0001	0.09	9.05
	b_1	3.46	0.0219		
	b_2	1.39	0.0890		
5 $HTG3Y=b_0+b_1*CSA96+b_2*(DIFN*ATSI)+b_3*CSA96^2$	b_0	11.90	0.0001	0.41	7.25
	b_1	5.11	0.0019		
	b_2	1.90	0.0001		
	b_3	0.63	0.0079		
6 $HTG3Y=b_0+b_1*CSA96+b_2*(DIFN*ATSI)+b_3*DIFN$	b_0	14.68	<0.0001	0.30	7.91
	b_1	1.09	0.0849		
	b_2	2.42	0.0151		
	b_3	11.43	0.6034		
7 $HTG3Y=b_0+b_1*CSA96+b_2*(DIFN*ATSI)$	b_0	13.90	<0.0001	0.31	7.85
	b_1	1.11	0.0741		
	b_2	1.99	0.0002		
8 $HTG3Y=b_0+b_1*CSA96+b_2*CSA96^2$	b_0	21.36	<0.0001	0.20	8.68
	b_1	5.68	0.0034		
	b_2	-0.70	0.0126		
9 $HTG3Y= b_0+b_1*CSA96$	b_0	24.11	<0.0001	0.14	8.79
	b_1	1.25	0.0901		
10 $HTG3Y=b_0+b_1*DIFN$	b_0	16.69	<0.0001	0.18	8.71
	b_1	36.43	0.0046		
11 $HTG3Y=b_0+b_1*ATSI$	b_0	13.68	0.0512	0.08	9.22
	b_1	0.62	0.0670		

Table 2-3: Correlation matrix for independent variables and the dependent variable (HTG3Y) for the height growth equation. The upper number is the correlation coefficient, the number in parenthesis is the p-value. N=47

	DIFN	ATSI	CSA96	ATSI* DIFN	$CSA96^2$* DIFN	HTG3Y
DIFN	1	-0.09915 (0.5270)	0.00298 (0.9849)	0.8608 (<0.0001)	0.1910 (0.2199)	0.4237 (0.0046)
ATSI	-0.09915 (0.5270)	1	0.05350 (0.7333)	0.3836 (0.0111)	0.03713 (0.8131)	0.28191 (0.0670)
CSA96	0.00298 (0.9849)	0.05350 (0.7333)	1	0.05187 (0.7412)	0.8755 (<0.0001)	0.26167 (0.0901)
ATSI*DIFN	0.8608 (<0.0001)	0.3836 (0.0111)	0.05187 (0.7412)	1	0.1994 (0.1999)	0.5432 (0.0002)
$CSA96^2$*DIFN	0.1910 (0.2199)	0.03713 (0.8131)	0.8755 (0.0001)	0.19940 (0.1999)	1	0.10551(0.5020)
HTG3Y	0.4237 (0.0046)	0.28191 (0.0670)	0.26167 (0.0901)	0.54322 (0.0002)	0.1051 (0.5020)	1

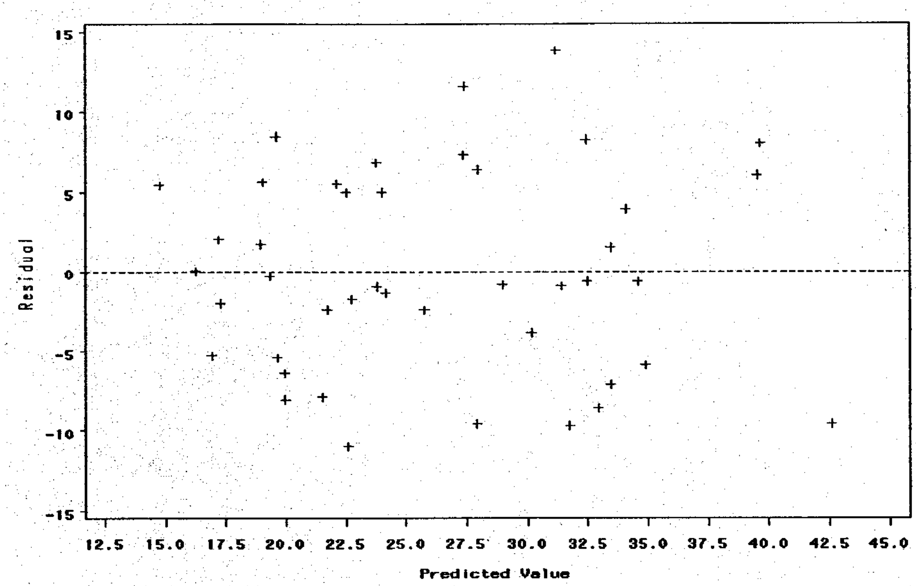

Figure 2-2: Plot of residuals versus predicted values for the height growth model

Along with the adjusted R^2 and the RMSE, the residual plot was also used to evaluate the height growth model. The residual plot showed that there were no model specification errors because there was a homogenous band of residuals plotted against the predicted values and they were centered on a mean error of zero (Fig. 2-2).

The model differentiated between trees growing under high (0.4) and low (0.1) DIFN (Fig. 2-3). Trees growing under low (0.1) DIFN increased height growth with larger crown surface areas, whereas trees growing under high (0.4) DIFN increased in height growth with larger crown surface areas up to the time that the tree reached a crown surface area of 3.0m^2. Once trees reach 3.0m^2 in crown surface area, growth rates did not increase but stay constant or slightly decreased.

The model predicted height growth increased with higher DIFN values (Fig. 2-4). Height growth was expected to increase with more light available to understory white spruce. Height growth increased with higher aspen site index (Fig. 2-3 and 2-4).

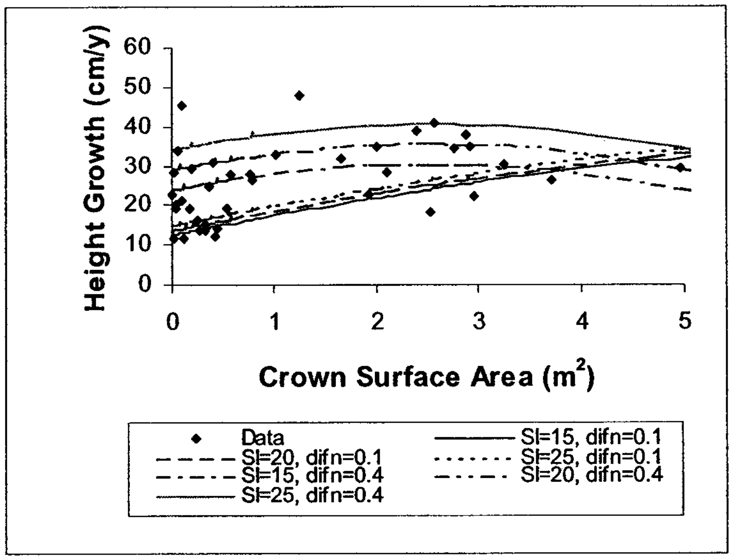

Figure 2-3: Scatter plot showing the relationships between crown surface area and height growth for site index (SI) values of 15, 20 and 25 and DIFN values of 0.1 and 0.4. The lines on the graph are explained by equation 1 Table 2-2.

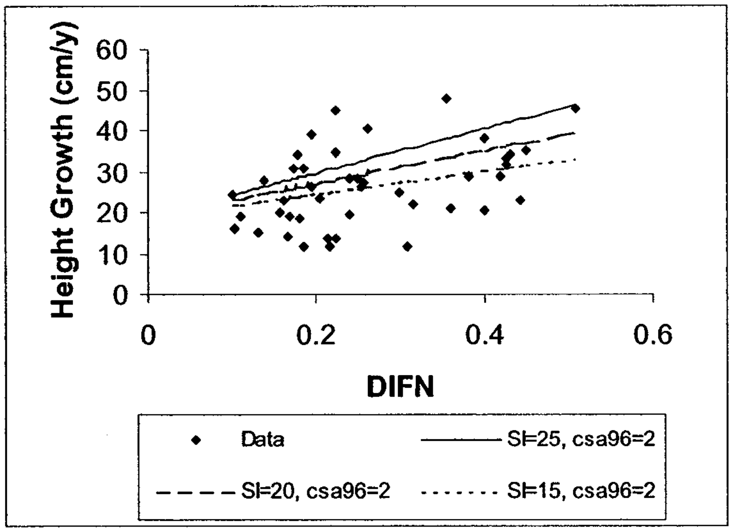

Figure 2-4: Scatter plot showing the relationships between light measured as diffuse non-interceptance and height growth for site index (SI) values of 15, 20 and 25 and crown surface area (CSA96) of $2m^2$. The lines on the graph are explained by equation 1 Table 2-2.

The Basal Area Increment Model

The best equation for predicting basal area increment (BA3Y) used initial spruce diameter, deciduous basal area (BADEC), aspen site index and the interaction between aspen site index and BADEC (equation 1 table 2-4). This equation had the greatest adjusted R^2 (0.90) and the lowest RMSE (0.37) (Appendix H). Equations that used initial spruce tree height, crown surface area, crown volume and breast height age could also be used to predict BA3Y but in this study the equation that used initial diameter as the initial size variable had a lower RMSE and greater adjusted R^2 (Appendix H). The equation that used breast height age had the lowest adjusted R^2 and the greatest RMSE (Appendix H).

When aspen site index was totally excluded from equation 1 in Table 2-4, the parameter estimate for BADEC was not significant (p=0.15) and when BADEC was excluded from the equation, the parameter estimate for aspen site index was not significant (Table 2-4). When the interaction term was dropped from the equation, parameter estimates for both aspen site index and BADEC were not significant. These findings suggested that the interaction between BADEC and aspen site index was an important variable in the equation. Alone, initial diameter explained 87% of the variation in BA3Y while parameter estimates in the equations showing relationships between BA3Y and BADEC or aspen site index were not significant (Equation 7,8 Table 2-4). The correlation matrix shows the relationships between independent variables (Table 2-5).

Table 2-4: Equations for predicting basal area increment together with the estimated values, observed significance level of parameter values, the adjusted R^2 values and the root mean square error of the model

Equation	Para-meter	Parameter Estimate	Parameter p-value	R^2adj	RMSE
1 $Ln(BA3Y)=b_0+b_1*ATSI+b_2*BADEC+b_3*DBH96+b_4*(BADEC*ATSI)+b_5*DBH96^2$	b_0	-4.35	<0.0001	0.90	0.37
	b_1	0.118	0.0004		
	b_2	0.071	0.0035		
	b_3	0.699	<0.0001		
	b_4	-0.004	0.0012		
	b_5	-0.036	<0.0001		
2 $Ln(BA3Y)=b_0+b_1*BADEC+b_2*DBH96+b_3*DBH96^2$	b_0	-2.02	<0.00001	0.87	0.43
	b_1	-0.00768	0.1452		
	b_2	0.728	<0.0001		
	b_3	-0.0387	<0.0001		

Table 2-4 (continued): Equations for predicting basal area increment together with the estimated values, observed significance level of parameter values, the adjusted R^2 values and the root mean square error of the model

Equation	Para-meter	Parameter Estimate	Parameter p-value	R^2adj	RMSE
3 $Ln(BA3Y)= b_0+b_1*ATSI+b_2*DBH96+b_3*DBH96^2$	b_0	-2.71	<0.0001	0.87	0.42
	b_1	0.0254	0.1036		
	b_2	0.7164	<0.0001		
	b_3	-0.0376	<0.0001		
4 $Ln(BA3Y)=b_0+b_1*ATSI+b_2*BADEC+b_3*DBH96+b_4 * bh96^2$	b_0	-2.493	<0.0001	0.87	0.42
	b_1	0.02344	0.1299		
	b_2	-0.00693	0.1821		
	b_3	0.7173	<0.0001		
	b_4	-0.03785	<0.0001		
5 $Ln(BA3Y)=b_0+b_1*ATSI+b_2*BADEC+b_3*DBH96+b_4 *(ATSI*BADEC)$	b_0	-4.54	<0.0001	0.76	0.58
	b_1	0.1572	0.0016		
	b_2	0.0963	0.0094		
	b_3	0.30561	0.0001		
	b_4	-0.00524	0.0053		
6 $Ln(BA3Y)= b_0+b_1*DBH96+b_2*DBH96^2$	b_0	-2.21	<0.0001	0.86	0.43
	b_1	0.73	<0.0001		
	b_2	-0.039	<0.0001		
7 $BA3Y=b_0+b_1*BADEC$	b_0	1.56	0.0002	0.02	1.15
	b_1	-0.014	0.3304		
8 $Ln(BA3Y)=b_0+b_1*ATSI$	b_0	-1.25	0.1593	0.03	1.18
	b_1	0.0447	0.2944		
9 $Ln(BA3Y)=b_0+b_1*DBH96$	b_0	-1.5299	<0.0001	0.71	0.64
	b_1	0.2976	<0.0001		

Table 2-5: Correlation matrix for the independent variables and the dependent variable (BA3Y) for the basal area increment model. The upper number is the correlation coefficient, the number in parenthesis is the p-value. N=47

	BADEC	ATSI	DBH96	BADEC* ATSI	$DBH96^2$	BA3Y
BADEC	1	-0.2543 (0.998)	-0.10344 (0.5092)	0.9940 (<0.0001)	-0.1289 (0.4098)	-0.13564 (0.3858)
ATSI	-0.2543 (0.0998)	1	0.03648 (0.8163)	-0.20532 (0.1866)	0.00279 (0.9858)	0.09709 (0.5357)
DBH96	-0.1034 (0.5092)	0.3648 (0.8163)	1	-0.0964 (0.5386)	0.950057 (<0.0001)	0.86814 (<0.0001)
BADEC* ATSI	0.99399 (<0.0001)	-0.20532 (0.1866)	-0.0964 (0.5386)	1	-0.1257 (0.4218)	-0.1258 (0.4215)
$DBH96^2$	-0.1289 (0.4098)	0.00279 (0.9858)	0.95057 (<0.0001)	-0.12572 (0.4218)	1	0.76825 (<0.0001)
BA3Y	-0.1356 (0.3858)	0.09709 (0.5357)	0.86814 (<0.0001)	-0.1258 (0.4215)	0.76825 (0.0001)	1

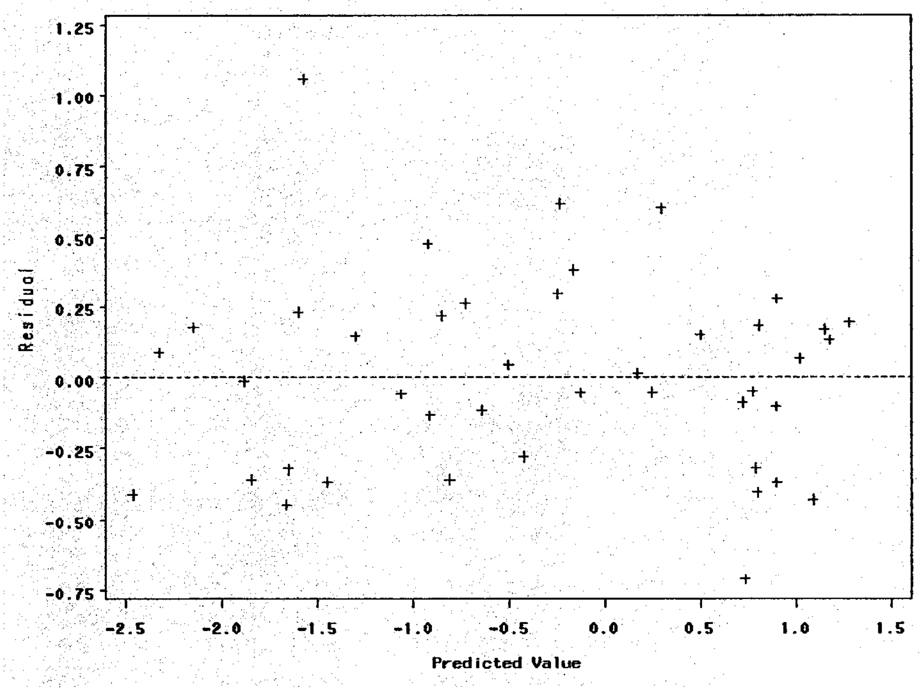

Figure 2-5: Plot of residuals versus predicted values for the basal area increment model

The residual plot for the basal area increment model showed that there were no specification errors because the residuals are a homogenous band centered around a mean error of zero (Fig. 2-5).

The relationship between BA3Y and initial tree diameter included growth increasing with larger diameter trees until initial diameter was 10 cm. When understory trees reached an initial diameter of 10 cm, BA3Y began to decrease and growth continued to decrease with size (Fig. 2-6).

The BA3Y model was based on both site and competition effects occurring in the boreal mixedwood stands. As site quality increased to an aspen site index of 18, BA3Y increased with increasing BADEC (Fig. 2-7). When site quality was greater than 18, BA3Y was reduced with higher BADEC (Fig. 2-7). When BADEC was less than 30 m^2, BA3Y increased with aspen site index (Fig 2-8). BA3Y decreased with increasing aspen site index when BADEC was greater than 30 m^2 (Fig. 2-8).

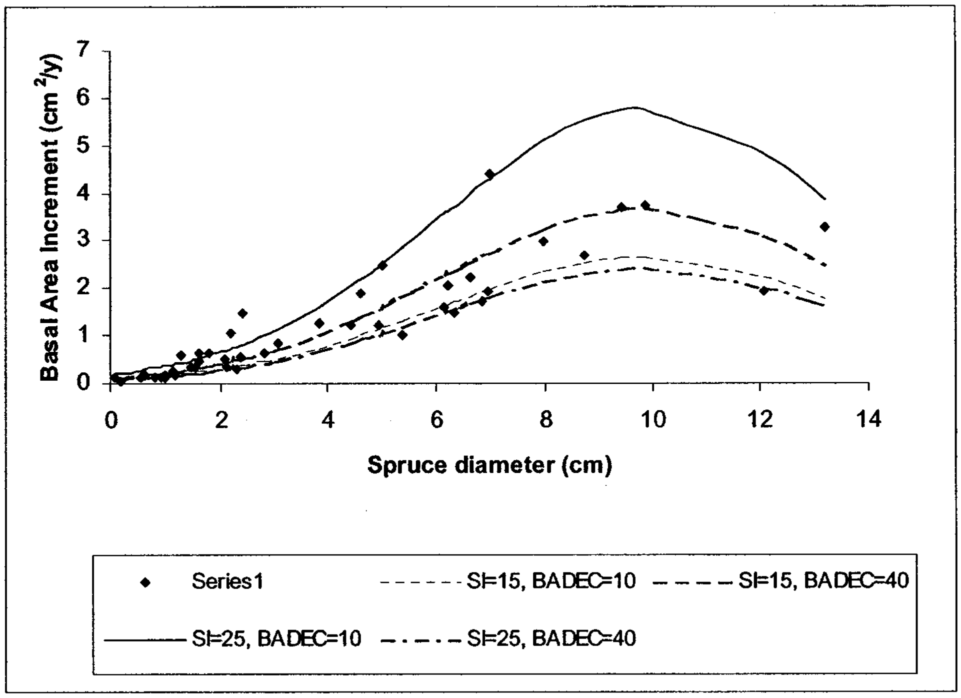

Figure 2-6: Scatter plot showing relationships between initial spruce diameter and basal area increment for aspen site index (SI) values of 15, 20 and 25 and deciduous basal area (BADEC) of 10 and 40 m^2/ha. The lines on the chart are explained by equation 1, Table 2-4.

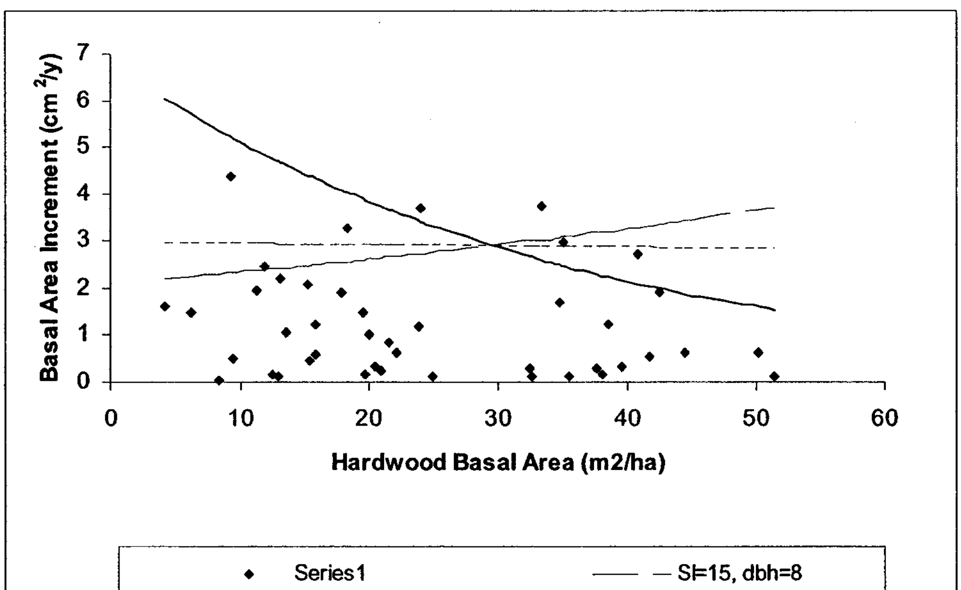

Figure 2-7: Scatter plot showing relationships between hardwood basal area and basal area increment prediction for aspen site index (SI) values of 15, 18 and 25 and an initial spruce diameter (dbh) of 8cm. The lines on the graph are explained by equation 1, Table 2-4.

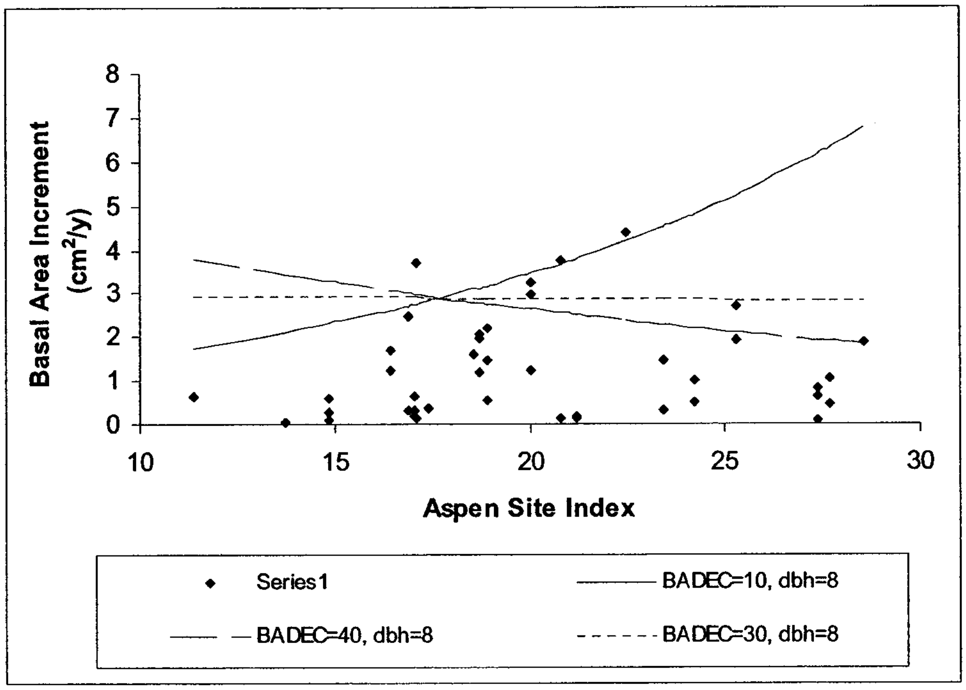

Figure 2-8: Scatter plot showing relationships between aspen sit index and basal area increment for deciduous basal area (BADEC) values of 10, 30 and 40 and an initial spruce diameter (dbh) of 8 cm. The lines on the graph are explained by equation 1, Table 2-4.

Discussion

Alone, initial diameter was a strong predictor of basal area increment (R^2=0.87). Although both site quality and DIFN were significant variables for explaining basal area increment, the inclusion of the two variables only increased basal area increment predictions by three percent. When absolute tree size was used as a predictor, the correlation between a growth variable and tree size tends to be strong. One method for diminishing the influence of tree size on growth is to express growth relative to the size of a plant. Although relative growth rates have been used extensively for growth predictions in annual plants, the use of relative growth rates become problematic when applied to perennials (Brand 1986). The continuous accumulation of nonproductive tissue by trees causes an artificial decline in relative growth rates over time (Brand 1986). Consequently, relative growth rates were not favored in this study as a means for predicting growth of the understory white spruce.

With initial diameter having a large contribution to the overall prediction of basal area increment, it would be possible to predict basal area increment from initial diameter as a single variable. However, tree growth is also dependent on interactions between site quality and competition (Reed et al, 1983) and this study showed that the two variables had a significant contribution in explaining variation in basal area increment. Without including site quality and competition in growth prediction equations, models would miss meaningful species interactions for resources. The acquisition of resources between species are displayed in positive and negative interactions for light, soil moisture and nutrients.

Using initial tree size, competition and site quality as independent variables, the basal area increment model suggested that there were both facultative and competitive interactions occurring simultaneously and influencing the growth of the understory white spruce in boreal mixedwood stands. Competitive effects were important in predicting basal area increment of the understory white spruce when aspen site index was greater than 18 and deciduous basal area was greater than 30 m^2/ha (Fig. 2-7, 2-8). Facultative interactions between white spruce and trembling aspen influenced understory white spruce basal area increment when aspen site index was less than 18 and deciduous basal area was less than 30 m^2/ha (Fig. 2-7, 2-8). Others have suggested facultative interactions are more important than competition when resource availability is limited and competition effects are more important than facilitation when resource availability is plentiful (Bertness and Callaway 1994; Holmgren et al. 1997).

There is strong evidence that species growing in mixture express interplay between facultative and competitive interactions (Chapin et al. 1994; Callaway and Walker 1997). Specifically with trembling aspen growing together with white spruce in boreal mixedwood ecosystem, improved litter decomposition and nutrient cycling rates, amelioration of environmental extremes and control of invasive herbaceous competitors have been identified as facultative interactions (Man and Lieffers 1999). These patterns of stand dynamics produced by the overstory canopy of the trembling aspen, provide favorable conditions for white spruce to grow in the understory. The basal area increment model developed in this study accounts for facultative and competitive interactions in boreal mixedwood stands. Facultative interactions between aspen and white spruce tend to be more important at sites with lower site quality and in addition, at sites supporting lower overstory competition. At the more productive side of the spectrum, including sites with greater site quality and greater overstory competition, competition between trembling aspen and white spruce tends to be the most important interaction for resources when predicting growth of understory white spruce.

Model Limitations

With the range of data (Table 2-1), the height growth model was most useful for trees that have a crown surface area smaller than 5 m^2, growing with DIFN from 0.1 to 0.5 and in stands with an aspen site index ranging between 11.4 and 28. A limitation of the height growth model includes the negative coefficient on the quadratic term. The model should not be used for trees with a crown surface area larger than 5 m^2 because relationships between the variables for trees with larger crown surface areas are not biologically reasonable; the small number of data points above 4m^2 and the negative sign on the quadratic term in the equation caused the estimate of height growth to decrease with increasing crown surface area.

With the range of data (Table 2-1), the basal increment model is most useful for trees growing between 0.1 and 0.5 DIFN and within stands having an aspen site index between 11.4 and 28. The model should not be used for trees growing with a breast height diameter greater than 13 cm.

Conclusion

This study clearly shows that site quality, predicted by aspen site index, competition and tree size can be used to predict the growth of understory white spruce in boreal mixedwood stands. Inclusion of all three variables in a model is important for capturing the complexity of species interactions that influence growth. The height growth model used crown surface area and an interaction between crown surface area with diffuse non-interceptance and the interaction between aspen site index and diffuse non-interceptance for predicting growth. The adjusted R^2 of the height growth model was 0.52. The height growth model was most useful for trees that have a crown surface area smaller than 5 m^2, growing under 0.1 and 0.5 DIFN and in stands with an aspen site index ranging between 11.4 and 28.

The basal increment model used initial diameter, stDBA, aspen site index and the interaction between aspen site index and stDBA for predicting growth. The adjusted R^2 for the basal area increment model was 0.90. The basal increment model was most useful for trees with a breast height diameter one to 13 cm, growing between 0.1 to 0.5 DIFN and within a stand with an aspen site index ranging between 11.4 and 28.

Although absolute size of the initial diameter was an effective variable for explaining variation in basal area increment, the interaction between deciduous basal area and aspen site quality was also an important variable in the growth prediction equation. Together, site quality and competition assimilate the complex interactions for resources between species into the growth prediction equation. In the context of growth and yield application, this study suggests that growth functions should incorporate tree size, site quality and competition variables into the equation so species interactions are accounted for in growth prediction equations.

With practical usage of these models developed in this study, caution is advised for extrapolating with these models beyond the range of data. It should also be realized that the data used to develop the models in this study were collected from a small number of stands located in north-eastern British Columbia. It would be more appropriate to use these models after implementation of proper model validation procedures.

References

Alberta Forest Service. 1985. Alberta phase 3 forest inventory: yield tables for unmanaged stands. ENR. Rep. No. Dep. 60a.

Baskerville, G.L. 1972. Use of logarithmic regression in the estimation of plant biomass. Can. J. For. Res. 2: 49-53.

Bazzaz, F.A., R.W. Carlson. 1982. Photosynthetic acclimation to variability in the light environment of early and late successional plants. Oecologia 54: 313-316.

Bell, F.W., M.T. Ter-Mikaelian., R.G. Wagner. 2000. Relative competitiveness of nine early-successional boreal forest species associated with planted jack pine and black spruce seedlings. Can. J. For. Res. 30: 790-800.

Bertness,k M.D., R.M. Callaway. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9: 191-193.

Brand, D.G. 1986. A competition index for predicting the vigor of planted Douglas-fir in southwestern British Columbia. Can. J. For. Res. 16: 23-29.

Burton, P.J. 1993. Some limitations inherent to static indices of plants. Can. J. For. Res. 23: 2141-2152.

Callaway, R.M., L.R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78(7): 1958-1965.

Canham, C.D. 1988. An index for understory light levels in and around canopy gaps. Ecology 69(5): 1634-1638.

Chapin, F.S., III., L.R. Walker., C.L. Fastie., L.C. Sharman. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. Ecological Monographs 64: 149-175.

Chen, H.Y.H. 1997. Interspecific responses of planted seedlings to light availability in interior British Columbia: survival, growth, allometric patterns, and specific leaf area. Can. J. For. Res. 27: 1383-1393.

Claveau, Y. C. Messier., P.G. Comeau., K.D. Coates. 2002. Growth and crown morphological responses of boreal conifer seedlings and saplings with contrasting shade tolerance to a gradient of light and height. Can. J. For. Res. 32: 458-468.

Coates, K.D., Burton, P.J. 1999. Growth of planted tree seedlings in response to ambient light levels in northwestern interior cedar-hemlock forests in British Columbia. Can. J. For. Res. 29: 1374-1382.

Comeau, P. 2003. Estimating and managing understory light using aspen density and diameter in central and north-eastern B.C. Centre for Enhanced Forest Management. Advances in Forestry research., Department of Renewable Resources. EFM Research Note. Edmonton, Alberta.

Comeau, P.G. 2001. Relationships between stand parameters and understory light in boreal aspen stands. B.C. Journal of Ecosystem Management. 1(2): 1-8.

Comeau, P.G. 2000. Measuring light in the forests. B.C. Min. For., Research Branch, Victoria, B.C., Extension Note 42, 7pp.

Comeau, P.G. 1996. Why Mixedwoods? *In* Silviculture of boreal and temperate broadleaved-conifer mixtures. P.G. Comeau and K. Thomas (editors) B.C. Ministry of Forests, Victoria, B.C., Land Management Handbook No. 36, pp.1-7.

Comeau, P.G., J.R. Wang., T. Letchford. 2003. Influences of paper birch competition on growth of understory white spruce and subalpine fir following spacing. Can. J. For. Res. 33: 1962-1973.

Comeau, P.G., F. Gendron., T. Letchford. 1998. A comparison of several methods for estimating light under a paper birch mixedwood stands. Can. J. For. Res. 28: 1843-1850.

Daniels, R.F., H.E. Burkhart., T.R. Clason. 1986. A comparison of competition measures for predicting growth of loblolly pine trees. Can. J. For. Res. 16:1230-1237.

Delong, C., A. MacKimmon., L. Jang. 1990. A field guide for identification and interpretation of ecosystems of the Northeast portion of the Prince George Forest Region. B.C. Ministry of Forests, Res. Br., Victoria, British Columbia. Land Management Handb. 22.

Drew, A.P., W.K. Ferrell. 1977. Morphological acclimation to light intensity in Douglas-fir seedlings. Can. J. Bot. 55: 2033-2042.

Drever, C.R., K.P. Lertzman. 2001. Light-growth responses of coastal Douglas-fir and western redcedar saplings under different regimes of soil moisture and nutrients. Can. J. For. Res. 31: 2124-2133.

Golser, M., H. Hasenauer. 1997. Predicting juvenile tree height growth in uneven-aged mixed species stands in Austria. For. Ecol. Manage. 97: 133-146.

Greis, I., and S. Kellomaki. 1981. Crown structure and stem growth of Norway spruce undergrowth under varying shading. Silv. Fenn. 15: 306-322.

Haeussler, S. D. Coates. 1986. Autecological characteristics of selected species that compete with conifers in British Columbia: A literature review. Information Services Branch, Ministry of Forests, Victoria, British Columbia. Land Management Report No. 33. 180 pp.

Holmgren, M., M. Scheffer., M.A. Huston. 1997. The interplay of facilitation and competition in plant communities. Ecology 78(7): 1966-1973.

Huang, S., S.J. Titus. 1994. An age-independent individual tree height prediction model for boreal spruce-aspen stands in Alberta. Can. J. For. Res. 24: 1295-1301.

Hix, D.M., C.G.Lorimer. 1990. Growth-competition relationships in young hardwood stands on two contrasting sites in south-western Wisconsin. For. Sci. 36: 1032-1049.

Holmes, M.J. and D.D. Reed. 1991. Competition indices for mixed species northern hardwoods. For. Sci. 37(5): 1338-1349.

Jobidon, R. 2000. Density-dependent effects of northern hardwood competition on selected environmental resources and young white spruce (*Picea glauca*) plantation growth, mineral nutrition and stand structure development-15-year study. For. Ecol. Manage. 130: 77-97.

Keyes, M.R., C.C. Grier. 1981. Above-and below-ground net production in 40-year old Douglas-fir stands on low and high productivity sites. Can. J. For. Res. 11: 599-605.

Lanner, R.M. 1985. On insentivity of height growth to spacing. For. Ecol. Manage. 13: 143-148.

Lautenschlager, R.A. 1995. Competition between forest brush and planted white spruce in north-central Maine. NJAF 12(4): 163-167.

LI-COR. 1992. LAI-2000 plant canopy analyzer. Instruction manual. LI-COR, Inc., Lincoln, Nebr.

Lieffers, V.J., B.D. Pinno., K.J. Stadt. 2002. Light dynamics and free-to-grow standards in aspen-dominated mixedwood forests. For. Chron. 137-145.

Lieffers, V.J., C. Messier, K.J. Stadt, F. Gendron, P.G. Comeau. 1999. Predicting and managing light in the understory of boreal forests. Can. J. For. Res. 29: 796-811.

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

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

Logan, K.T. 1969. Growth of tree seedlings as affected by light intensity IV. Black spruce, white spruce, balsam fir and eastern white cedar. Dept. of Fisheries and Forestry, Canadian Forest Service. Publication 1256.

Lorimer, C.G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. For. Ecol. Manage. 6:343-360.

Mallows, C.P. 1973. Some comments on C(p). Technometrics. 15: 661-665.

Man, R., V.J. Lieffers. 1999. Are mixtures of aspen and white spruce more productive than single species stands? For. Chron. 75(3): 505-513.

MacDonald, B., D.M. Morris., P.L. Marshall. 1990. Assessing components of competition indices for young boreal plantations. Can. J. For. Res. 20: 1060-1068.

Meidinger, D., J. Pojar. 1991. Ecosystems of British Columbia. B.C. Ministry of Forests, Res. Br. Victoria, B.C. Special Report Series 6.

Messier, C., R. Doucet., J.C. Ruel., Y. Claveau., C. Kelly., M.J. Lechowicz. 1999a. Functional ecology of advance regeneration in relation to light in boreal forests. Can. J. For. Res. 29: 812-823.

Messier, C., S. Parent., M. Chengaou., J. Beaulieu. 1999b. Juvenile growth and crown morphological plasticity of eastern white pine (*Pinus strobus* L.) planted along a natural light gradient: results after 6 years. For. Chron. 75: 275-279.

Montgomery, D.C., E.A. Peck., G.G. Vining. 2001. Introduction to linear regression analysis., 3rd edition. John Wiley & Sons, Inc. Toronto.

Nigh, G.D. 1997. Early height growth and site index of lodgepole pine under wet and dry soil moisture regimes in British Columbia. WJAF. 12(1):5-8.

Oliver, C.D., B.C. Larson. 1990. Forest stand dynamics. McGraw-Hill. Inc., New York, 673 pp.

Pinno, B.D. 2000. Crown characteristics and understory light in young trembling aspen stands (*Populus tremuloides*). MSc. thesis. University of Alberta, Edmonton,Alberta. 85 pp.

Reed, K.L., J.S. Shumway., R.B. Walker., C.S. Bledsoe. 1983. Evaluation of interaction of two environmental factors affecting Douglas-fir seedling growth: light and nitrogen. For. Sci. 29(1): 193-203.

SAS Institute Inc. 1999. SAS/ETS user's guide. Version 8. Cary. NC.

Shirley, H.L. 1945. Reproduction of upland conifers in the lake states as affected by root competition and light. Am. Mid. Nat. 33(3): 537-552.

Smith, D.M., B.C. Larson., M.J. Kelty., P.M.S. Ashton. 1997. The practice of silviculture applied forest ecology. ninth edition. John Wiley & Sons, Inc. 1-525pp.

Wagner, R.G., S.W. Rodesevich. 1991. Interspecific competition and other factors influencing the performance of Douglas-fir saplings in the Oregon Coast Range. Can. J. For. Res. 21: 829-835.

Wright, E.F., K.D. Coates., C.D. Canham., P. Bartemucci. 1998. Species variability in growth response to light across climatic regions in northwestern British Columbia. Can. J. For. Res. 28: 871-886.

Chapter 3: Influences of Site Series and Overstory Age on the Growth of Understory White Spruce in Boreal Mixedwood Stands

Introduction

In British Columbia, the province's biogeoclimatic classification system is widely used by forest managers to make decisions about harvesting activities and silviculture treatments (DeLong et al. 1990; Meidinger and Pojar 1991; British Columbia, Ministry of Forests 2002). The system of classification uses climatic conditions, soil properties and indicator vegetation to classify sites into zones, subzones and site series (Pojar et al. 1987). Zone and subzone are indicative of regional climate factors such as elevation, accumulation of precipitation, soil temperature and atmospheric temperature. Site series is the smallest unit of classification and is determined on a more local scale by soil moisture regime and soil nutrient status. Soil moisture regime (SMR) is defined as the amount of soil water available for evapotranspiration by vascular plants and should approximate a yearly average taken over several years. Soil nutrient regime (SNR) is defined as the amount of essential nutrients available to vascular plants and is also based on a yearly average taken over several years. Together, the SMR and SNR are placed onto an edatopic grid and the position on the grid corresponds to the site series. The horizontal axis refers to the soil nutrient regime and is defined A-E, where A=very poor, B=poor, C=medium, D=rich, E=very rich. The vertical axis refers to the soil moisture regime and is defined 1-7 where 1=xeric, 2=subxeric, 3=submesic, 4=mesic, 5=subhygric, 6=hygric and 7=subhydric.

Site series has been used as a measurement of site quality and has been related to height growth of trees (Green et al. 1989; Wang 1995; Kayahara et al. 1998) and in most cases the relationships have mainly focused on coniferous species growing in pure species stands. For example in the sub-boreal spruce (SBS) subzone located in the interior of British Columbia, height growth of white spruce growing in pure stands increased with more nutrient availability (Wang 1997). In the past, few studies have focused on relationships between site quality and growth of conifers while in mixture with deciduous species such as trembling aspen. One of the reasons for this is that growth of the understory is dependent on multiple factors with the main one being overstory competition (Canham 1988; Coates and Burton 1999). With methods for measuring light in the understory of forests there is an opportunity for management. Light can be measured as diffuse non-interceptance (DIFN) which is the diffuse portion of incident light and under a forest canopy it is the portion of the sky not blocked by foliage (Li-Cor 1992).

An appreciable number of studies have focused on light dynamics in boreal mixedwood stands (Lieffers and Stadt 1994; Lieffers et al. 1999; Messier et al. 1999; Comeau 2001). Although light dynamics in mixedwood stands tend to be variable, it can be generalised that white spruce growing in the understory of aspen experience a bottleneck effect when in competition with aspen for light (Lieffers et al. 2002) and possibly other resources (Shirley 1945). As aspen become established during the first 10-15 years after a disturbance, understory white spruce recruitment tends to be gradual, and understory growing conditions are adequate for growth. At 15-25 years after stand establishment, aspen stands reach maximum leaf area and light availability for understory white spruce tends to be lowest (Lieffers et al. 2002). After 25 years and until the spruce become the dominant species, light levels increase while deciduous stems are lost through self-thinning. These findings suggest that development of mixedwood stands follows a succession pathway and that stand age might also be an important variable in modelling understory growth.

The main objectives to this study were: 1) to determine if site series and age class were important variables for explaining growth of understory white spruce in mixedwood stands, 2) to determine what initial tree size variables were the most useful for building relationships with diffuse non-interceptance light (DIFN) for explaining growth of understory white spruce.

Methods

Data for this study were collected during July and August of 2000 and 2001 from 27 stands comprised of 80% trembling aspen in the overstory, up to 20% conifer in the overstory and white spruce in the understory. The stands were located in the moist warm Boreal White and Black Spruce subzone (BWBSmw1) (DeLong et al. 1990) near Dawson Creek and Fort St. John, British Columbia. Stands were selected to cover a wide range of site qualities and age classes. Based on either historical records or actual age of the aspen, each stand was classified into one of three age classes: stands 10 to 20 years, stands 21 to 40 years and stands older than 40 years of age. Site characteristics (Table 3-1, Appendix B) and stand attributes (Table 3-2) were collected from each site and used to classify the stands into site series (DeLong et al. 1990).

In each stand, up to nine understory white spruce were selected as measurement trees. Selected trees were healthy, showed no signs of insect damage or pathogen problems and were not overtopped by shrubs or herbaceous vegetation. Each understory sample tree was selected as the tallest white spruce within a 5.64-meter distance from one of nine established reference points (Fig. 3-1). Depending on the size of the mixedwood stand, the first reference point was placed 80-125 meters at a random bearing from the stand edge or access trail. From the first reference point, three more reference points were positioned at a bearing of 150 degrees and a distance of 10 meters between the points. The next three reference points were placed 10 meters apart at a bearing at 270 degrees from the fourth reference point. The last two points were placed 10 meters apart at 30 degrees from the seventh established point forming an approximate triangle. If an understory white spruce was not within 5.64 meters of the reference point, a tree was not selected.

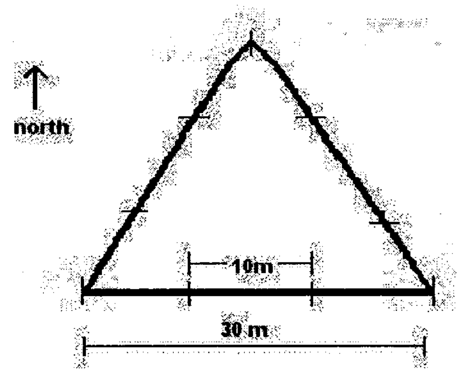

Figure 3-1: Schematic diagram of the plot layout. White spruce measurements were taken at 10 meter intervals around the perimeter of the triangle. Each stand with a plot cluster was classified into an age class and site series.

Understory White Spruce Measurements

Measurements of the understory white spruce included total height, height increments from the previous 5 years, height to the base of the live crown, crown radius measured in the cardinal directions, lateral branch increments from the previous 5 years measured in the cardinal directions, diameter outside the bark, age, and diameter increments from the previous five years. For larger understory spruce, diameters were measured 130 cm above ground level and diameter increments and age were determined from one core at the same position above ground level. For smaller understory spruce, diameter was measured at ground level and diameter increments and age were measured from sections or cores taken 30 cm above ground level. Growth rings were counted with a dissecting scope and increment widths were measured using a mechanical Parker micrometer mounted on a dissecting scope. Radial increments for the sections were based on measurements from four perpendicular axes with the first axis being the position on the main stem with the longest diameter. Four axes were used for measurements because most of the understory trees had highly variable ring widths with tension and compression wood being present.

Table 3-1: A Summary of site characteristics for the 27 sampled stands (see Appendix B for a description of the variables)

Site	Disturbance Type	Year of Disturb.	Regen. Type	Latitude	Longitude	Slope (%)	Aspect	Soil texture	% Coarse fragments	Drainage	SMR	SNR	Site Series	Age Class	# obs. small trees	# obs. large trees
Utah2	Clearcut	1979	Natural	56°55'	122°20'	14	S	SiL	5	MW	5	C	06	2	0	2
DR1	Cleared	1970	Natural	56°02'	121°30'	6	SW	SCL	5	W	3	C	01	2	0	0
BP	Clearcut	1960	Natural	56°05'	122°10'	2	S	SL	0	W	4	C	01	3	5	0
GW	Burned	1938	Natural	56°16'	120°06'	2	S	SL	5	W	4	C	01	3	0	0
WV	Clearcut	1985	Natural	55°52'	121°20'	2	SW	SL	0	W	4	C	01	1	0	0
IN	Burned	1955	Natural	56°37'	121°40'	4	NE	SCL	5	MW	4	C	01	3	0	0
U1	Clearcut	1979	Planted	56°55'	122°20'	12	W	SiL	0	MW	5	C	06	2	6	1
IO40	Burned	1935	Natural	55°20'	120°15'	15	SW	LS/SL	20	W	4	C	01	3	7	3
IA	Clearcut	1978	Planted	55°45'	121°30'	3	E	SCL	0	I	5	C	06	1	1	2
SEP	Burned	1950	Natural	55°55'	121°10'	15	NW	SL	20	R	3	C	03	3	4	7
MUS	Clearcut	1985	Planted	55°23'	122°46'	12	N	SL	0	W	4	C	01	1	6	3
OIY	Clearcut	1988	Planted	55°20'	120°17'	6	NE	LS/SL	0	W	4	C	01	1	4	0
SUN	Burned	1952	Natural	55°40'	121°20'	4	NE	LS/SL	40	W	4	C	01	3	1	5

Table 3-1 (continued): A Summary of site characteristics for the 27 sampled stands (see Appendix B for a description of the variables)

Site	Disturbance Type	Year of Disturb.	Regen. Type	Latitude	Longitude	Slope (%)	Aspect	Soil texture	% Coarse fragments	Drainage	SMR	SNR	Site Series	Age Class	# obs. small trees	# obs. large trees
TP	Burned	1948	Natural	55°18'	120°48'	2	NE	LS/SL	0	W	3	B	03	3	3	2
DR2	Cleared	1970	Natural	56°02'	121°30'	4	NE	L/CL	2	MW	4	B	01	2	3	1
HS3001	Clearcut	1974	Planted	56°45'	121°15'	3	NE	SiL	0	MW	5	C	06	2	7	3
MSR01	Clearcut	1974	Natural	55°46'	122°10'	6	SW	SiCL	5	MW	4	C	01	2	2	1
SC1501	Clearcut	1985	Planted	56°10'	120°28'	4	SE	SiL/CL	0	W	4	C	01	1	6	6
SM4501	Burned	1939	Natural	55°45'	122°15'	6	SW	SL/LS	10	W	4	D	01	3	4	3
SM5001	Clearcut	1979	Natural	55°50'	122°15'	4	SW	SiCL	5	W	5	D	06	2	1	1
BE2501	Clearcut	1979	Natural	56°35'	121°11'	4	SW	L	0	I	4	C	01	2	7	4
BE3001	Clearcut	1979	Natural	56°37'	121°11'	4	NE	SiL	0	MW	4	C	01	2	9	6
BE4001	Burned	1934	Natural	56°52'	121°30'	2	NW	CL	0	W	3	C	03	3	7	7
FS1501	Clearcut	1985	Planted	56°16'	120°02'	16	SW	SiL	0	MW	4	C	01	1	7	8
GL3001	Clearcut	1988	Planted	56°16'	120°02'	2	SW	L	0	W	4	C	01	1	6	5
GL4001	Burned	1949	Natural	56°17'	120°02'	3	NE	SiL	0	I	4	C	01	3	4	6
GL4501	Burned	1955	Natural	56°17'	120°04'	4	NE	SiL	2	W	3	C	03	3	8	6

Table 3-2: Stand attributes consisting of aspen age, aspen total density, mean aspen diameter, mean total height of aspen, aspen basal area per hectare, aspen site index, white spruce total density and white spruce basal area per hectare for the 27 stands sampled

Site	Aspen Age (y)	Aspen density (tph)	Aspen mean dbh (cm)	Aspen height (m)	Aspen ba/ha (m^2/ha)	Aspen SI (m)	Spruce density (tph)	Spruce ba/ha (m^2/ha)
1A	23	3533	9.0	9.5	6.83	28.5	367	0.19
BE2501	22	4733	8.0	9.7	16.33	21.2	2367	1.02
BE3001	22	3600	9.9	11.8	14.98	28.6	1133	1.76
BE4001	67	1300	21.7	21.8	41.93	17.07	700	0.31
BP	41	633	21.0	18.2	11.51	18.56	333	8.45
DR1	31	5770	7.5	9.5	16.72	18.69	633	4.77
DR2	31	6567	6.0	8.9	15.93	17.07	267	1.23
FS1501	16	4733	6.7	6.8	14.80	21.16	867	2.00
GL3001	13	17666	4.7	6.1	16.53	14.84	1200	0.42
GL4001	52	2533	18.0	18.6	40.03	20.77	233	0.53
GL4501	46	3100	13.9	12.5	22.27	18.89	1933	2.87
GW	62	3333	4.3	15.5	30.59	20	233	1.97
HS3001	27	2400	11.0	13.8	17.93	22.47	2000	2.98
IN	45	3367	12.4	14.8	28.40	16.86	900	2.28
MSR01	27	7167	8.5	11.1	35.63	19.61	100	0.01
MUS	16	4433	7.1	7.2	16.10	27.01	1667	1.14
OI40	66	1600	18.5	18.3	30.74	17.38	1067	1.83
OIY	13	13833	3.8	5.0	8.34	24.66	900	0.06
SC1501	16	2933	8.4	7.8	8.85	23.44	400	1.15
SEP	51	767	22.1	15.0	24.4	16.43	333	3.85
SM4501	62	1100	21.7	21.9	32.18	18.89	433	1.70
SM5001	22	3750	10.2	10.8	30.38	26.27	6450	4.38
SUN	49	867	17.9	20.8	30.06	25.32	400	1.49
TP	53	1300	19.5	15.5	14.33	13.74	100	2.96
UTAH1	21	5100	7.7	9.5	10.07	24.24	1100	0.17
UTAH2	21	4300	8.8	12.3	23.22	27.39	3467	1.12
WV	15	8767	6.6	7.6	13.46	27.77	433	0.10

Crown width was measured as the horizontal distance from the bole of the tree to the drip line with the branches projected downwards. Branch increments were measured in cardinal directions on the longest branch. If the longest branch was 2.5 meters or more above ground level, it was removed from the tree for measurements. When the longest branch could not be reached with the 6-meter pruning pole, a shorter branch was measured for growth. For measuring total height and height growth, a tree between one and four meters was measured with a tape measure, a height pole was used to measure trees heights between four and 12 meters and a clinometer and tape measure were used to measure trees taller than 12 meters. For a few of the tallest understory trees, an estimate of height growth was made rather than a measurement because the top of the tree was obscured by the aspen canopy. An estimate of height growth occurred less than three percent of the time.

Competition Measurements

Diffuse non-interceptance (DIFN) was measured in the cardinal directions around each understory sample tree using a LAI-2000 (Li-Cor Inc. 1992) during July and August of 2001 for all sites with the exception of three sites which were measured during 2000. Sampling points with the LAI-2000 instrument corresponded directly to the crown radius measurements by marking the precise location with flagging tape. DIFN is the diffuse portion of incident light. Under a canopy it is the portion of sky not blocked by foliage (Li-Cor Inc. 1992). To avoid direct beam light interfering with the readings, the north and west sides of the tree were measured in the morning and the south and east sides of the tree in the late afternoon. LAI measurements were taken at mid canopy with the height determined by the understory subject tree. Since the LAI-2000 has a 10-meter radius field of view, a 180-degree view restrictor cap was placed over the lens to avoid inclusion of the subject tree in the measurements. Two LAI-2000 instruments were calibrated together and used for sampling. One instrument was placed in a nearby opening and used for open sky readings and the second instrument was used for measurements under the canopy. The open sky instrument was programmed to take readings every 30-seconds for the length of time required to complete the measurements under the canopy.

For each LAI measurement, DIFN was calculated with C2000 software (Li-Cor Inc. 1992). The LAI-2000 sensor head contains five detectors arranged in concentric rings that measure how quickly diffuse sky radiation is attenuated as it passes through a vegetation canopy. The detectors are arranged at five zenith angles with the first ring measuring 0 to 13 degrees and the fifth ring measuring 61 to 74 degrees. In this study, the fifth ring was turned off because other studies have suggested that computation of DIFN is more reliable with exclusion of the fifth ring. DIFN can be interpreted as an indicator of canopy structure and an indicator of canopy light absorption, particularly absorption of diffuse, short wave (<490 nm) radiation (Li-Cor Inc. 1992). C2000 software was used to calculate DIFN from the LAI 2000 readings. One DIFN value for each tree was calculated by averaging measurements taken in the cardinal directions around each understory tree.

Data Preparation and Calculations

The data collected in this study were used to calculate the dependent variables height growth, basal area increment, stem volume increment and height to diameter ratio for the 1997, 1998 and 1999 growing seasons.

Height growth was calculated as:

$$HTG3Y=SHTI_i/3$$

where HTG3Y was measured in cm/y and HTI_i was the height increment of the subject tree measured in cm during the ith year (1997, 1998, 1999).

Basal area increment for the larger trees (diameter and age measured at 1.3 m above ground level) was calculated using the following equations. DBH variables were substituted with diameter at stump height (DSH) for the smaller trees (diameter and age measured at 30 cm above ground level). The DBH and DSH substitution applies to BA3Y, SVG3Y and HDR.

$$BA3Y=p(DBH99/2)^2-p\ (DBH96/2)^2\ /3$$

where BA3Y was three-year periodic annual basal area increment measured in cm^2/y

DBH99 was calculated as:

$$DBH99=DBH_m-SDIAINC_i$$

where DBH99 was diameter 130 cm above ground level at the end of the growing season in 1999 measured in cm, DBH_m was diameter at the time of the field work, measured in cm outside the bark at 1.3 m above ground level, $DIAINC_i$ was diameter increment measured in micrometers and converted to centimeters for the growth seasons i (2001, 2000).

DBH96 was calculated as:

$$DBH96 = DBH_m - SDIAINC_i$$

where DBH96 was diameter 130 cm above ground level at the end of the growing season in 1996 measured in cm, DBH_m was diameter at the time of the field work, measured in cm outside the bark at 1.3 m above ground level, $DIAINC_i$ was diameter increment measured in micrometers and converted to centimeters for the growth seasons i (2001, 2000, 1999, 1998, 1997).

Stem volume increment assumed a cylindrical form and was calculated as:

$$SVG3Y == p(DBH99/2)^2 * TH99 - p\ (DBH96/2)^2 * TH96$$

where SVG3Y was periodic stem volume increment calculated in cm^3/y, DBH99 and DBH96 were diameters at the end of the growing seasons 1999 and 1996 as defined above.

TH99 was calculated as:

$$TH99 = TH_m - SHTI_i$$

where TH99 was total tree height at the end of the growing season in 1999 and was measured in cm, TH_m was tree height at the time of field measurements measured in cm, HTI_i was height increment of the subject tree measured in cm during the ith year (2001, 2000).

TH96 was calculated as:

$$TH96 = TH_m - SHTI_i$$

where TH96 was total tree height at the end of the growing season in 1996 and was measured in cm, TH_m was tree height at the time of field measurements measured in cm, HTI_i was height increment of the subject tree measured in cm during the ith year (2001, 2000, 1999, 1998, 1997).

Height to diameter ratio was calculated as:

$$HDR=TH_m/DBH01$$

where HDR was height to diameter ratio, TH_m was defined above, DBH01 was diameter 130 cm above ground level, outside the bark in 2001, measured in cm.

Initial Tree Size Variables

To avoid spurious correlations between the explanatory and response variables, size variables were based on measurements determined at the beginning of the growth period. The initial tree size variables were age, diameter, tree height, crown volume and crown surface area. Depending on the size of the understory white spruce, age was either determined at 130 cm (BHAGE) or 30 cm (SHAGE) above ground level. Age was determined by observation and did not require computation.

Initial tree height was calculated as:

$$TH96=TH_m-SHTI_i$$

where TH96 was tree height measured in cm at the beginning of the growth period, TH_m was tree height at the time of measurement in cm, HTI_i were height increments measured during the growth seasons of i (2001, 2000, 1999, 1998 and 1997).

Initial tree diameter was calculated as:

$$DBH96=DBH_m-SDIAINC_i$$

where DBH96 was diameter measured in cm at the beginning of the growth period for the larger trees. The location of the diameter measurements was 130 cm above ground level. DBH variables were substituted with DSH for the smaller trees (diameter and age measured at 30 cm above ground level). The same measurements taken for the larger and smaller trees but the reference height changes from130 cm above ground level to 30cm. DBH_m was diameter at the time of the field work, measured in cm outside of the bark at 1.3 m above ground level, $DIAINC_i$ was diameter increment measured in micrometers and converted to cm for the growth season i (2001, 2000, 1999, 1998 and 1997).

Crown surface area and crown volume were calculated based on the assumption that tree crowns were conical in form. Initial crown surface area was calculated as:

$$CSA96 = (p*CR96*CSAL96) /10000$$

where CSA96 was crown surface area measured in m^2 at the beginning of the growth period.

CR96 was calculated as:

$$CR96 = SCR_d/ 4$$

where CR96 was crown radius measured in cm at the beginning of the growth period.

CR_d was calculated as:

$$CR_d=CW_d-SCRINC_{di}$$

where CW_d was crown radius measured in cm at the time of measurements in d defined as one of the cardinal directions (N,S,E or W), and $CRINC_{di}$ was the length of the branch increment measured in cm in d (one cardinal direction) for the ith year (2001, 2000, 1999, 1998, 1997).

CSAL96 was used to calculate CSA96 and is equivalent to the hypotenuse of a 90 degree angled triangle. CSAL96 was calculated as:

$$CSAL96=(CR96^2+CL96^2)^{1/2}$$

where CR96 is defined above and CL96 is defined below.

Initial crown volume was calculated as:

$$CVOL96 = (p*CR96^2 *CL96)/3 * 1000000$$

where CVOL96 was crown volume measured in m^3 for the beginning of the growth period, CR96 was defined above.

CL96 was crown length measured in cm and calculated as:

$$CL96 = TH_m - (SHTI_i + HTLC)$$

where CL96 is crown length at the beginning of the growth period, HTLC is the height to the base of the live crown at the time of field measurement, in cm, TH_m was tree height at the time of measurement measured in cm, HTI_i were height increments measured in cm during the growth seasons of i (2001, 2000, 1999, 1998 and 1997). HTLC was assumed as not rising throughout the growth period.

Data Analysis

Regression analysis was used to determine a relationship between growth, a tree size variable and DIFN for two groups of understory trees: 1) larger trees with diameter increment measurements and age taken 130 cm above ground level and 2) smaller trees with diameter increment measurements and age taken 30 cm above ground. Linear, allometric and various exponential models were tested to determine which function provided the best fit to the data. The allometric function was considered to provide the best results and was defined as:

$$Y=aX^{b1}$$

where Y is growth, x is an independent variable and a and b_1 are estimated parameters. The parameter "a" controls the rate of increase or decrease of the curve and the parameter "b_1" controls the shape of the curve. Using the allometric function, five initial tree size variables were tested with DIFN to determine which combination of variables showed the best relationship with the response variable (Appendix I-L). One equation was selected for each dependent variable and the selection process was based on significant (a=0.05) parameter estimates, the lowest MSE, greatest adjusted R^2 and a homogenous band of residuals that were centered around zero when plotted against the predicted values.

To determine if site series and age class were important variables for explaining variation in the response variables, the non-linear extra sums of squares principal was applied to the equations by using site series and age class as indicator variables. Huang (1999) used this procedure for developing ecoregion-based individual tree height-diameter models for lodgepole pine located in Alberta.

For the analysis, there were two models:

A simpler model:

$Y= a_0 DBH96^{b_0} DIFN^{c_0}$

And a more complex model:

$Y=a_0 DBH96^{(b_0+b_1x_1+b_2x_2)} DIFN^{(c_0+c_1x_1+c_2x_2)}$

where, Y was a growth variable, DBH96 was the initial tree size variable, DIFN was diffuse non-interceptance, a_0, b_0, b_1, b_2, c_0, c_1 and c_2 were estimated parameters. The above model applies to the larger trees. DBH96 was substituted with DSH96 for the smaller trees.

Site series was treated as a dummy variable, with site series 01 used as the reference. Hence:

$x_1=1$ if site series was 03 otherwise $x_1=0$

$x_2=1$ if site series was 06 otherwise $x_2=0$

We tested the hypothesis that each coefficient t was zero (the a,b and c) using the following f-test (Montgomery et al. 2001 p. 271-272).:

$F=(SSE_s-SSE_c/df_s-df_c)/(SSE_c/df_c)$

SSE_s was sums of squares error for the simpler model, df_s was the degrees freedom for the simpler model, SSE_c was sums of squares error for the complex model, df_c was the degrees freedom for the complex model.

if $b_1=0$ then site series 03 was not different from site series 01

if $b_2=0$ then site series 06 was not different from site series 01

if $b_1=b_2=0$ then site series had no effect

The same procedure was used to evaluate the influence of overstory age on the growth of the understory white spruce. Overstory age class was treated as a dummy variable, with age class 2 used as the reference. Hence:

$x_1=1$ if overstory age class was 1 otherwise $x_1=0$

$x_2=1$ if overstory age class was 3 otherwise $x_2=0$

if $b_1=0$ then overstory age class1 was not different from age class 2

if $b_2=0$ then overstory age class 3 was not different from age class 2

if $b_1=b_2=0$ then overstory age class had no effect

Results

For all dependent variables, and for both the larger and smaller trees, diameter was the best initial tree size variable because while in combination with DIFN, it produced equations with the highest R^2 and lowest MSE (Appendix I-L). Crown surface area, crown volume and tree height could also be used as initial tree size variables but in this study diameter was favored as the initial tree size variable. In most cases, age of the understory white spruce was a significant variable for explaining growth but it generally did not perform as well as the other size variables. Descriptive statistics for the independent variables were given in Appendix I.

When the non-linear extra sums of squares method was applied to the data, to test if site series influenced the growth of understory white spruce, the results suggested that the models with different coefficients for site series were significantly better than the models that had one coefficient for all site series (Table 3-3 and 3-4). An exception to this was height to diameter ratio, where the simple model fit as well as the complex model (Table 3-3). Descriptive statistics for the larger and smaller trees within each site series are given in Tables 3-5 and 3-6.

The models with different coefficients for each overstory age class were significantly better than the models that had only one coefficient for all age classes (Table 3-3 and 3-4). Descriptive statistics for the larger and smaller trees within each overstory age class were given in Tables 3-7 and 3-8.

Table 3-3: F-tests for the influence of site series and overstory age on growth of larger understory trees

Dependent Variable	Simple Models			Complex Models (Site Series)				Complex Models (Age Class)			
	$SSE_{(r)}$	$Df_{(r)}$	$MSE_{(r)}$	$SSE_{(f)}$	$df_{(f)}$	$MSE_{(f)}$	F-val.	$SSE_{(f)}$	$Df_{(f)}$	$MSE_{(f)}$	F-val.
HTG3Y	8901.4	84	105.97	6521.1	80	81.51	7.3*	5865.8	80	73.32	10.4*
BA3Y	46.3504	84	0.55175	38.64	80	0.4830	4.0*	25.377	80	0.3172	16.5*
SVG3Y	39849398	84	474445.44	28202444	80	593.7	8.3*	28256752	80	353209	8.2*
HDR	27569.4	84	324.3	26110.8	80	326.4	0.1	20282.4	80	253.5	7.2*

* denotes significant F values

Table 3-4: F-tests for the influence of site series and overstory age on growth of smaller understory trees

Dependent Variable	Simple Models			Complex Models (Site Series)				Complex Models (Age Class)			
	$SSE_{(r)}$	$Df_{(r)}$	$MSE_{(r)}$	$SSE_{(f)}$	$df_{(f)}$	$MSE_{(f)}$	F-val.	$SSE_{(f)}$	$df_{(f)}$	$MSE_{(f)}$	F-val.
HTG3Y	8817.3	107	82.65	6203.3	103	60.226	10.9*	6651.6	103	64.57	8.4*
BA3Y	56.56	107	0.529	46.36	103	0.4501	5.7*	33.51	103	0.3254	17.7*
SVG3Y	46467768	107	434278	17492133	103	169827	42.6*	18825057	103	182768	37.8*
HDR	26173.8	107	244.6	21877.7	103	212.4	5.1*	24148.1	103	234.4	2.47*

* denotes significant F values

Throughout the study, the independent variables explained the greatest amount of variation in stem volume increment, followed by basal area increment, periodic annual height growth and height to diameter ratio. For height growth, the adjusted R-square ranged between 0.41 and 0.58, for basal area increment between 0.73 and 0.87, stem volume increment ranged from 0.93 to 0.95 and the adjusted R-square for the height to diameter ratio equations ranged between 0.16 to 0.73 (Tables 3-9 & 3-10). The amount of variation in height to diameter ratio explained was generally lower for the smaller trees.

For height growth, the b1 and b2 coefficient showed the relationships with initial diameter and DIFN were less than 1 and this produced a concave down and increasing curve. The b1 coefficient for basal area increment and stem volume increment was greater than 1 and this produced a concave up and increasing curve (Fig. 3-2 to 3-5). Excluding height growth, the relationships between growth and DIFN were generally not the same across site series and overstory age classes. This was most pronounced in the relationship between stem volume increment and DIFN.

Height growth, basal area increment and stem volume increment were greatest for site series 06, followed by 01 and then 03 and greater for trees with larger diameters. Height to diameter ratio generally decreased with larger diameter trees.

Table 3-5: Descriptive statistics for trees with measurements taken at 130 cm above ground level as classified by site series

		Site Series 01					Site Series 03					Site Series 06				
Variable	Units	N	Mean	SD	Min.	Max.	N	Mean	SD	Min.	Max.	N	Mean	SD	Min.	Max.
CVOL96	m^2	56	2.17	3.53	0.0007	17.75	23	7.53	16.10	0.035	67.75	8	1.10	0.79	0.001	2.00
CSA96	m^3	56	1.70	1.91	0.0140	8.37	23	3.76	5.76	0.118	24.32	8	1.16	0.72	0.014	2.00
DBH96	cm	56	4.13	2.70	0.2713	11.45	23	5.74	5.70	0.976	23.21	8	3.96	1.49	1.44	5.37
TH96	cm	56	303	188	72.9	847	23	418	292	130.1	1143	8	304	132.6	62.2	473
BHAGE	y	56	13.8	9.30	5.00	48.00	23	20.0	10.78	7.00	41.0	8	10.13	1.81	7.00	12.0
DIFN	-	56	0.324	0.173	0.117	0.90	23	0.248	0.0974	0.0893	0.442	8	0.188	0.108	0.091	0.427

Table 3-6: Descriptive statistics for trees with measurements taken at ground level and 30 cm above ground level as classified by site series

		Site Series 01					Site Series 03					Site Series 06				
Variable	Units	N	Mean	SD	Min.	Max.	N	Mean	SD	Min.	Max.	N	Mean	SD	Min.	Max.
CVOL96	m^2	66	0.57	1.09	0.0002	4.21	23	1.71	3.10	0.0002	13.88	21	0.91	1.34	0.00003	4.83
CSA96	m^3	66	0.68	0.96	0.0051	3.85	23	1.56	1.78	0.0063	7.067	21	0.87	0.97	0.00216	3.22
GLD96	cm	66	4.28	2.30	1.44	10.80	23	5.091	2.26	1.23	12.21	21	3.99	2.30	1.28	8.75
TH96	cm	66	187	114	53.2	467	23	287	180	73.0	744	21	251	145	83.0	661
SHAGE	y	66	15.70	7.26	5.00	40.00	23	26.96	9.25	10.0	44.0	21	14.71	4.09	6.00	24.00
DIFN	-	66	0.305	0.155	0.117	0.900	23	0.26	0.11	0.090	0.48	21	0.184	0.080	0.104	0.427

Table 3-7: Descriptive statistics for trees with measurements taken at 130 cm above ground level as classified by age class

		Age Class 1 (10-20 years)					Age Class 2 (21-40 years)					Age Class 3 (+40 years)				
Variable	Units	N	Mean	SD	Min.	Max.	N	Mean	SD	Min.	Max.	N	Mean	SD	Min.	Max.
CVOL96	m^2	24	0.477	0.735	0.0011	2.96	19	1.09	1.29	0.003	4.05	44	6.17	12.03	0.0007	67.75
CSA96	m^3	24	0.590	0.691	0.0147	2.95	19	1.17	0.97	0.027	3.18	44	3.51	4.39	0.14	24.32
DBH96	cm	24	3.16	1.82	0.271	7.81	19	3.38	1.95	0.94	7.39	44	5.80	4.55	0.54	23.21
TH96	cm	24	207	114	62.2	473	19	267	111	130.1	443	44	431	254	114	1143
BHAGE	y	24	8.17	2.71	5.00	13.00	19	10.53	4.56	5.00	22.00	44	20.80	10.41	5.00	48.00
DIFN	-	24	0.404	0.213	0.091	0.900	19	0.28	0.12	0.10	0.53	44	0.233	0.091	0.089	0.442

Table 3-8: Descriptive statistics for trees with measurements taken at ground level and 30 cm above ground level as classified by age class

		Age Class 1 (10-20 years)					Age Class 2 (21-40 years)					Age Class 3 (+40 years)				
Variable	Units	N	Mean	SD	Min.	Max.	N	Mean	SD	Min.	Max.	N	Mean	SD	Min.	Max.
CVOL96	m^2	30	0.30	0.61	0.0002	2.96	42	0.80	1.30	0.0003	4.83	38	1.40	2.58	0.0002	13.88
CSA96	m^3	30	0.43	0.59	0.0051	2.95	42	0.81	0.98	0.0022	3.21	38	1.37	1.61	0.0063	7.07
GLD96	cm	30	4.17	1.84	1.51	9.00	42	4.02	2.43	1.28	10.28	38	4.99	2.42	1.23	12.21
TH96	cm	30	170.6	98.6	53.2	408	42	220	137	60.7	661	38	259	163	55.9	744
SHAGE	y	30	12.17	3.10	5.00	21.0	42	14.62	4.48	6.00	24.00	38	25.95	0.09	10.00	44.00
DIFN	-	30	0.36	0.18	0.13	0.90	42	0.25	0.12	0.10	0.61	38	0.23	0.10	0.089	0.48

Table 3-9: Equations for predicting height growth, basal area increment, stem volume increment and height to diameter ratio for the larger understory trees with estimated values, adjusted R^2 and root mean square error of the model

	Model	Parameter	Estimate	N	Adjusted R^2	RMSE
Site Series	$HTG3Y=aDBH96^{b1}DIFN^{b2}$ (site series 01)	a	33.85	87	0.41	9.0
	$HTG3Y=aDBH96^{b1a}DIFN^{b2a}$ (site series 03)	b1	0.2595			
	$HTG3Y=aDBH96^{b1b}DIFN^{b2b}$ (site series 06)	b1a	-0.0423			
		b1b	0.4718			
		b2	0.3995			
		b2a	0.3013			
		b2b	0.4091			
	$BA3Y=aDBH96^{b1}DIFN^{b2}$ (site series 01)	a	0.4136	87	0.83	0.70
	$BA3Y=aDBH96^{b1a}DIFN^{b2a}$ (site series 03)	b1	1.245			
	$BA3Y=aDBH96^{b1b}DIFN^{b2b}$ (site series 06)	b1a	1.069			
		b1b	2.171			
		b2	0.4317			
		b2a	0.2783			
		b2b	1.020			
	$SVG3Y=aDBH96^{b1}DIFN^{b2}$ (site series 01)	a	113.7	87	0.95	594
	$SVG3Y=aDBH96^{b1a}DIFN^{b2a}$ (site series 03)	b1	1.900			
	$SVG3Y=aDBH96^{b1b}DIFN^{b2b}$ (site series 06)	b1a	1.574			
		b1b	2.636			
		b2	0.3189			
		b2a	-0.0141			
		b2b	0.8377			
	$HDR=aDBH96^{b1}DIFN^{b2}$ (site series 01)	a	140.4	87	0.66	18.1
	$HDR=aDBH96^{b1a}DIFN^{b2a}$ (site series 03)	b1	-0.348			
	$HDR=aDBH96^{b1b}DIFN^{b2b}$ (site series 06)	b1a	-0.231			
		b1b	-0.274			
		b2	-0.0290			
		b2a	0.0531			
		b2b	0.0394			
Age Class	$HTG3Y=aDBH96^{b1}DIFN^{b2}$ (age class 2)	a	25.97	87	0.47	8.6
	$HTG3Y=aDBH96^{b1a}DIFN^{b2a}$ (age class 1)	b1	0.4960			
	$HTG3Y=aDBH96^{b1b}DIFN^{b2b}$ (age class 3)	b1a	0.3880			
		b1b	0.0730			
		b2	0.2670			
		b2a	0.2710			
		b2b	0.1480			
	$BA3Y=aDBH96^{b1}DIFN^{b2}$ (age class 2)	a	0.2450	87	0.89	0.56
	$BA3Y=aDBH96^{b1a}DIFN^{b2a}$ (age class 1)	b1	1.138			
	$BA3Y=aDBH96^{b1b}DIFN^{b2b}$ (age class 3)	b1a	1.660			
		b1b	1.140			
		b2	-0.1520			
		b2a	0.2600			
		b2b	0.0014			
	$SVG3Y=aDBH96^{b1}DIFN^{b2}$ (age class 2)	a	117.9	87	0.95	594
	$SVG3Y=aDBH96^{b1a}DIFN^{b2a}$ (age class 1)	b1	1.870			
	$SVG3Y=aDBH96^{b1b}DIFN^{b2b}$ (age class 3)	b1a	1.940			
		b1b	1.530			
		b2	0.2170			
		b2a	0.3050			
		b2b	-0.0966			
	$HDR=aDBH96^{b1}DIFN^{b2}$ (age class 2)	a	144.6	87	0.74	15.9
	$HDR=aDBH96^{b1a}DIFN^{b2a}$ (age class 1)	b1	-0.2750			
	$HDR=aDBH96^{b1b}DIFN^{b2b}$ (age class 3)	b1a	-0.4570			
		b1b	-0.2480			
		b2	0.0314			
		b2a	-0.0204			
		b2b	0.0482			

Table 3-10: Equations for predicting height growth, basal area increment, stem volume increment and height to diameter ratio for the smaller understory trees with estimated values, adjusted R^2 and root mean square error of the model

	Model	Parameter	Estimate	N	Adjusted R^2	RMSE
Site Series	HTG3Y=aDBH96^{b1}DIFN^{b2} (site series 01)	a	16.38	110	0.59	0.71
	HTG3Y=aDBH96^{b1a}DIFN^{b2a} (site series 03)	b1	0.6070			
	HTG3Y=aDBH96^{b1b}DIFN^{b2b} (site series 06)	b1a	0.1670			
		b1b	0.6120			
		b2	0.3380			
		b2a	0.0412			
		b2b	0.1982			
	BA3Y=aDBH96^{b1}DIFN^{b2} (site series 01)	a	0.2304	110	0.73	0.67
	BA3Y=aDBH96^{b1a}DIFN^{b2a} (site series 03)	b1	1.456			
	BA3Y=aDBH96^{b1b}DIFN^{b2b} (site series 06)	b1a	1.198			
		b1b	1.475			
		b2	0.3516			
		b2a	0.2409			
		b2b	0.2546			
	SVG3Y=aDBH96^{b1}DIFN^{b2} (site series 01)	a	25.94	110	0.93	412
	SVG3Y=aDBH96^{b1a}DIFN^{b2a} (site series 03)	b1	2.550			
	SVG3Y=aDBH96^{b1b}DIFN^{b2b} (site series 06)	b1a	2.044			
		b1b	2.605			
		b2	0.2933			
		b2a	-0.2070			
		b2b	0.2048			
	HDR=aDBH96^{b1}DIFN^{b2} (site series 01)	a	78.36	110	0.24	14.6
	HDR=aDBH96^{b1a}DIFN^{b2a} (site series 03)	b1	-0.1400			
	HDR=aDBH96^{b1b}DIFN^{b2b} (site series 06)	b1a	-0.1124			
		b1b	-0.1320			
		b2	0.0089			
		b2a	-0.0296			
		b2b	-0.1223			
Age Class	HTG3Y=aDBH96^{b1}DIFN^{b2} (age class 2)	a	13.54	110	0.56	8.0
	HTG3Y=aDBH96^{b1a}DIFN^{b2a} (age class 1)	b1	0.6770			
	HTG3Y=aDBH96^{b1b}DIFN^{b2b} (age class 3)	b1a	0.6208			
		b1b	0.3329			
		b2	0.1910			
		b2a	0.1503			
		b2b	0.0528			
	BA3Y=aDBH96^{b1}DIFN^{b2} (age class 2)	a	0.1050	110	0.80	0.57
	BA3Y=aDBH96^{b1a}DIFN^{b2a} (age class 1)	b1	1.528			
	BA3Y=aDBH96^{b1b}DIFN^{b2b} (age class 3)	b1a	2.006			
		b1b	1.480			
		b2	0.3670			
		b2a	0.5220			
		b2b	0.0200			
	SVG3Y=aDBH96^{b1}DIFN^{b2} (age class 2)	a	15.61	110	0.93	428
	SVG3Y=aDBH96^{b1a}DIFN^{b2a} (age class 1)	b1	2.670			
	SVG3Y=aDBH96^{b1b}DIFN^{b2b} (age class 3)	b1a	2.828			
		b1b	2.240			
		b2	-0.0142			
		b2a	0.2856			
		b2b	-0.3189			
	HDR=aDBH96^{b1}DIFN^{b2} (age class 2)	a	69.59	110	0.16	234
	HDR=aDBH96^{b1a}DIFN^{b2a} (age class 1)	b1	-0.0897			
	HDR=aDBH96^{b1b}DIFN^{b2b} (age class 3)	b1a	-0.1501			
		b1b	-0.0572			
		b2	-0.1238			
		b2a	-0.1140			
		b2b	-0.0096			

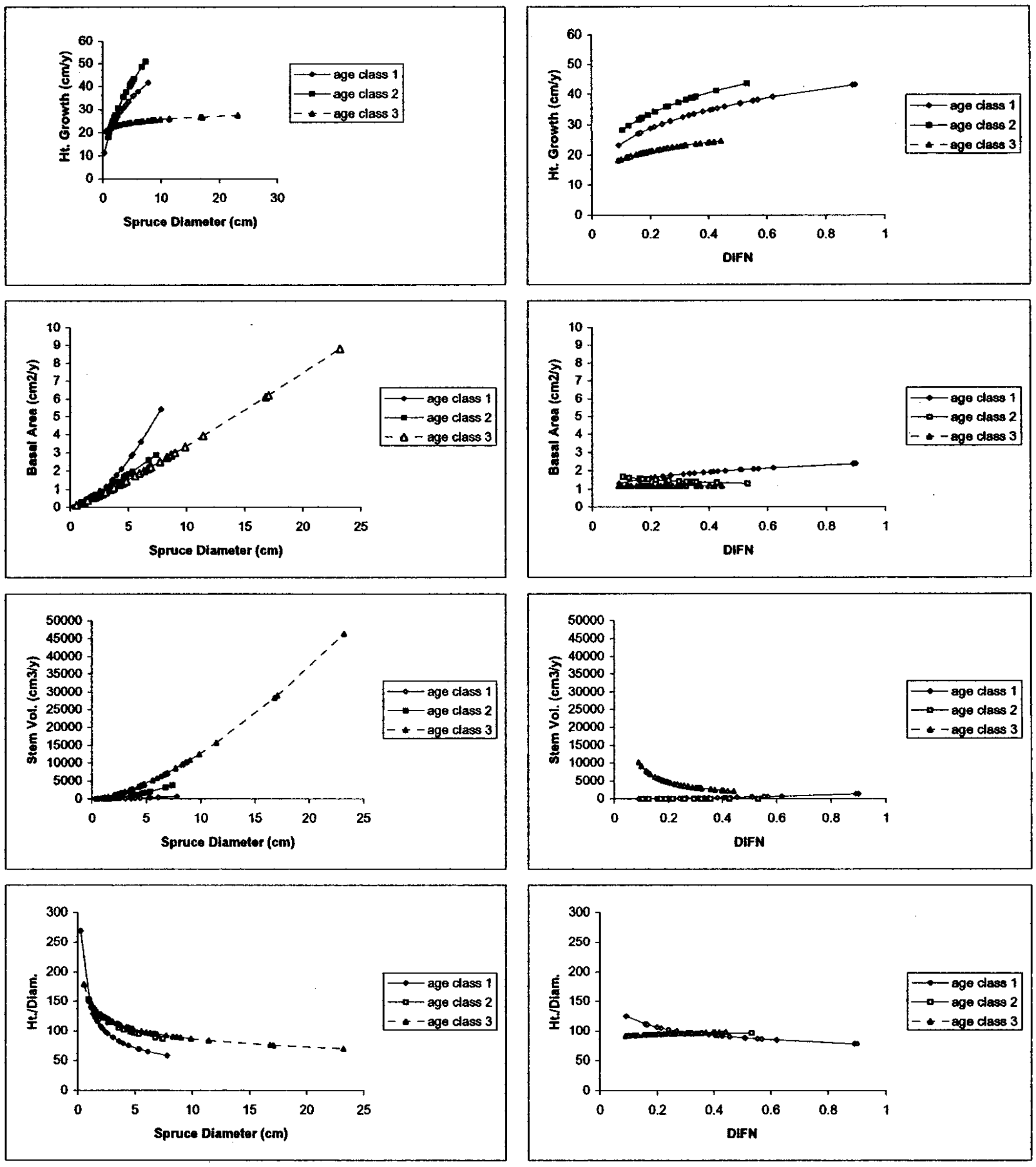

Figure 3-2: Fit regressions for predicting the large white spruce growth rates for the overstory age classes with initial diameter and DIFN. For the reference class (site series 01 and age class 2), shaded points mean the relationship was statistically significant, unshaded points mean the relationships was not statistically significant. For the other classes, shaded points mean the shift in the slope was significant whereas unshaded points mean the shift in the slope was not statistically significant.

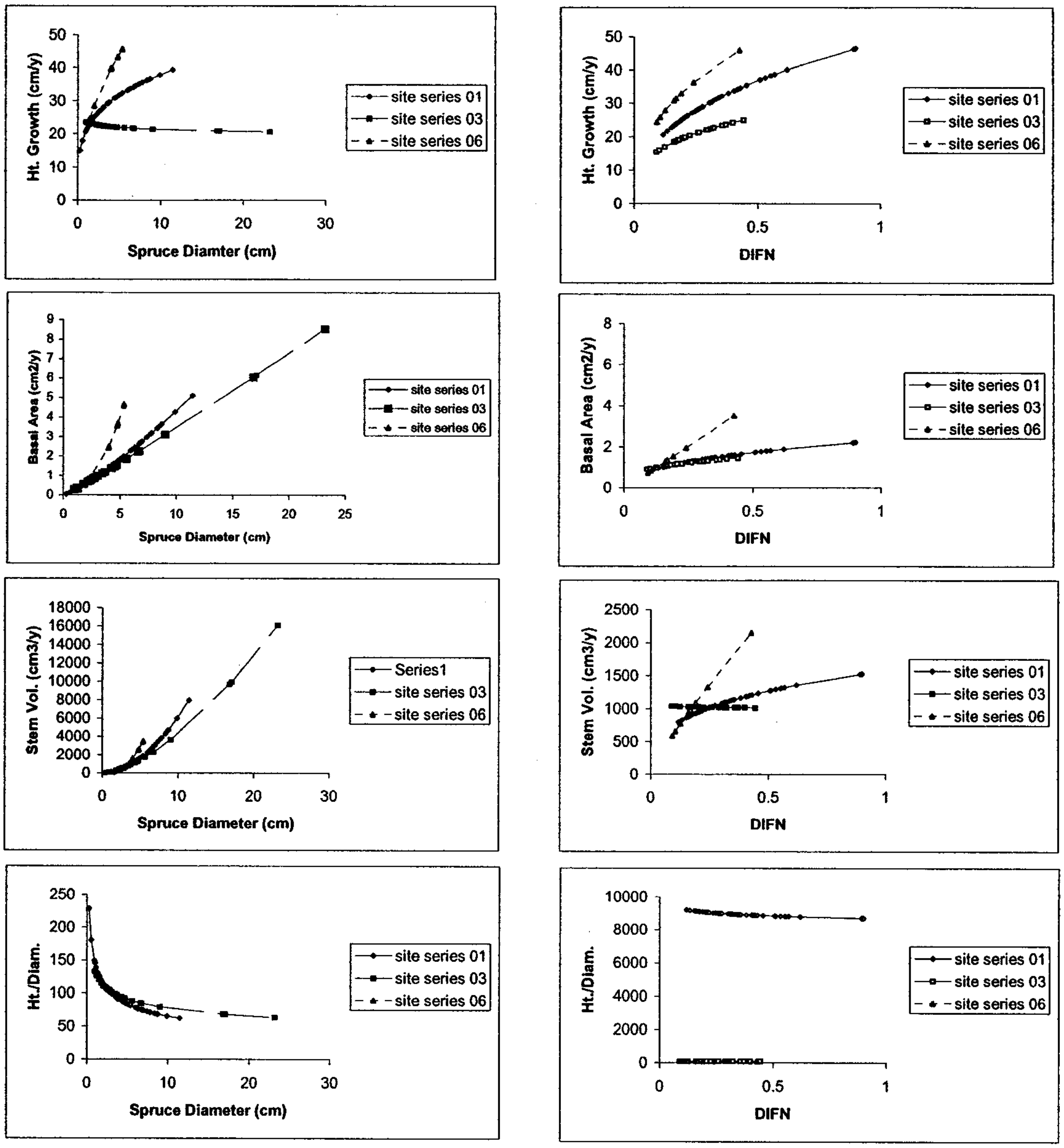

Figure 3-3: Fit regressions for predicting the large white spruce growth rates for site series with initial diameter and DIFN. For the reference class (site series 01 and age class 2), shaded points mean the relationship was statistically significant, unshaded points mean the relationships was not statistically significant. For the other classes, shaded points mean the shift in the slope was significant whereas unshaded points mean the shift in the slope was not statistically significant.

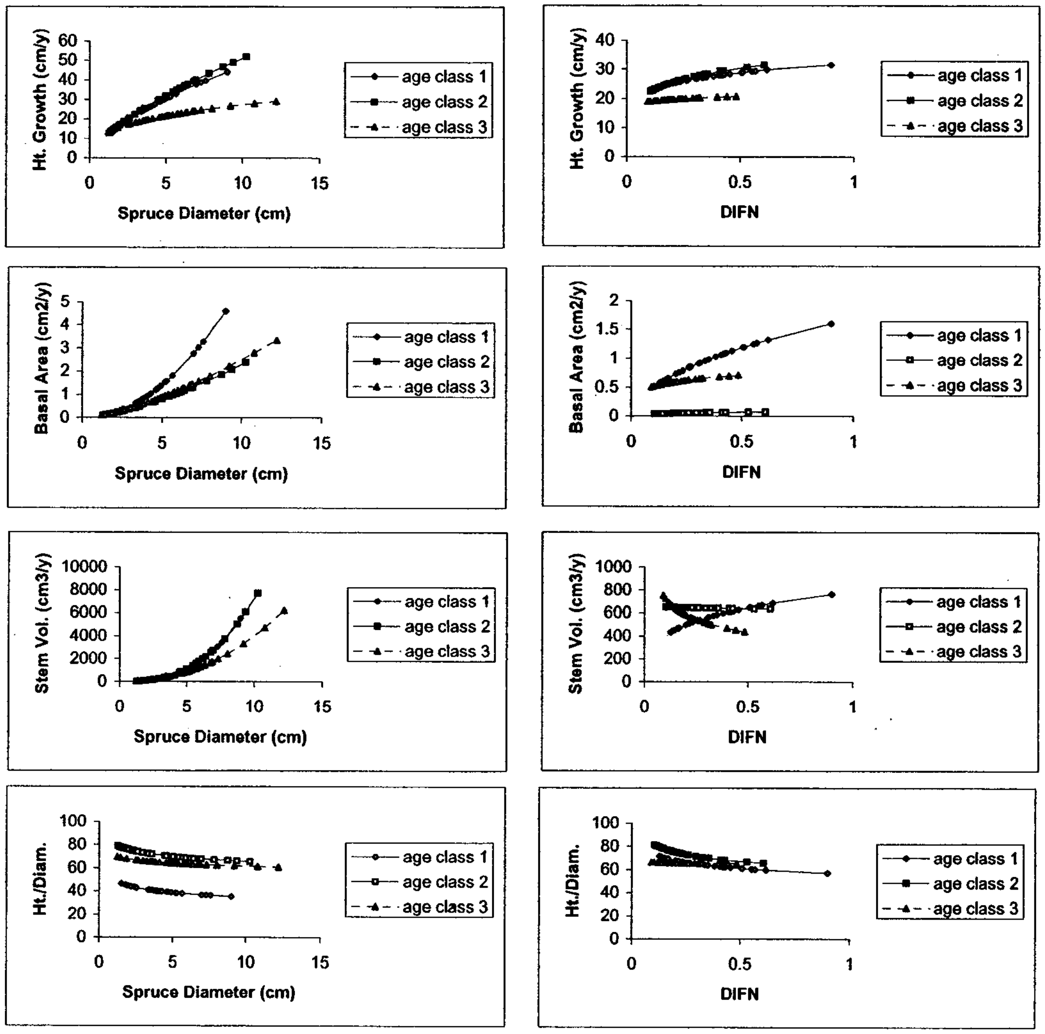

Figure 3-4: Fit regressions for predicting the small white spruce growth rates for the overstory age classes with initial diameter and DIFN. For the reference class (site series 01 and age class 2), shaded points mean the relationship was statistically significant, unshaded points mean the relationships was not statistically significant. For the other classes, shaded points mean the shift in the slope was significant whereas unshaded points mean the shift in the slope was not statistic

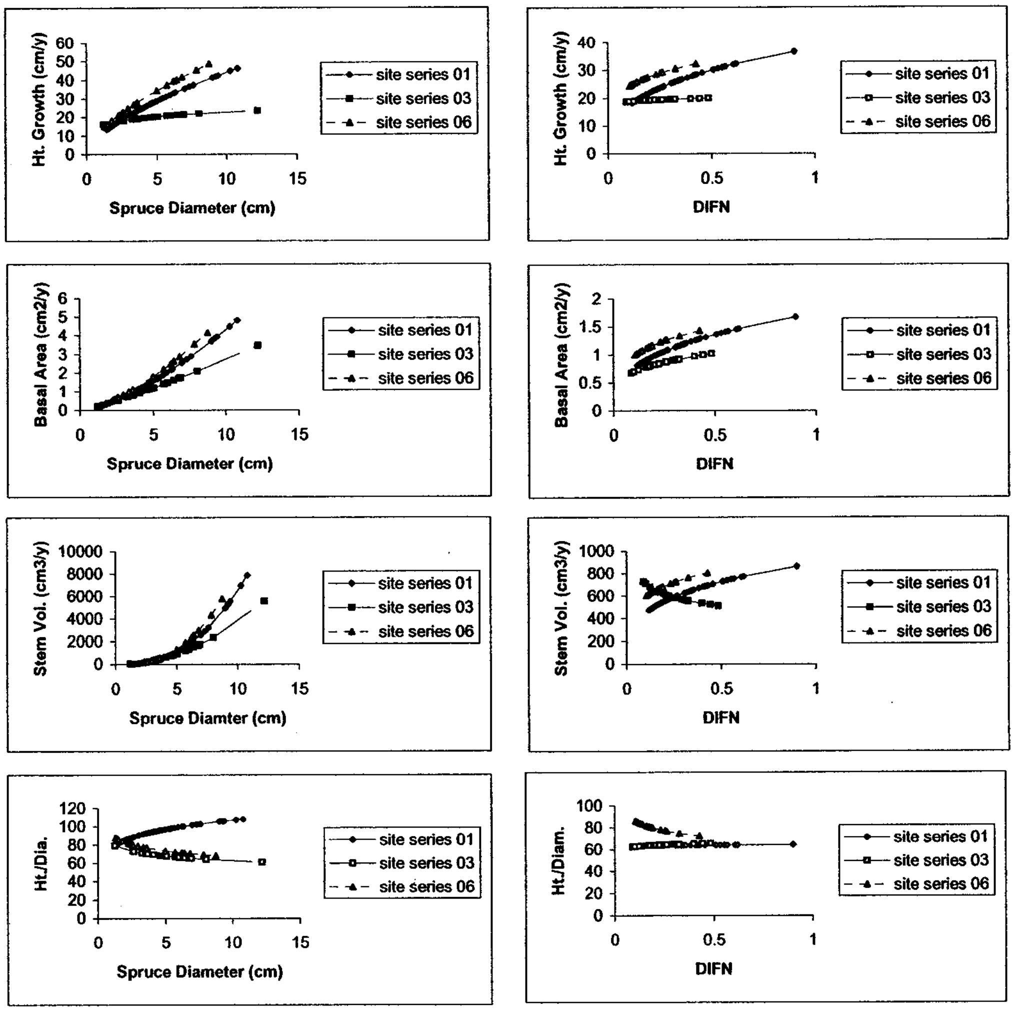

Figure 3-5: Fit regressions for predicting the small white spruce growth rates for site series with initial diameter and DIFN. For the reference class (site series 01 and age class 2), shaded points mean the relationship was statistically significant, unshaded points mean the relationships was not statistically significant. For the other classes, shaded points mean the shift in the slope was significant whereas unshaded points mean the shift in the slope was not statistically significant

Discussion

Site series was an important variable for predicting height growth, basal area increment and stem volume increment. The models predict height growth, basal area increment, and stem volume increment were greater for better site qualities (06>01>03). The difference between site series was based on the amount of moisture available in the soil for plants to carry out physiological processes required for growth and survival. The 06 site series was characterized by having more moisture availability for plant growth than the 03 and 01 site series. The 03 site series was characterized by having moderately dry soils throughout part of the growing season and moisture was limited more than for the 01 and 06 site series. The 01 site series was characterized by having intermediate characteristics, including a mesic soil moisture regime and a medium soil nutrient status. Lautenschlager (1995) also reported white spruce growth was dependent on soil drainage and it grew better on well-drained sites than on poorly drained sites. The models developed in this study suggest that highest growth rates were achievable on well-drained sites. Both 01 and 06 site series ranged between well drained to imperfectly drained drainage classes (Resource Inventor Branch, B.C. Ministry of Environment, Lands and Parks and Research Branch B.C. Ministry of Forests 1998). The range of data in this study did not include sites that were poorly drained and therefore it can not be tested if the model predicts lower growth rates for trees growing on poorly drained sites. However, the model does predict lower growth for trees at sites that have moderately dry soils during part of the growing season.

The relationships between growth and DIFN were highly variable across the range of site series indicating that the effects of understory light was not consistent across a range of site qualities. Others have found that competition effects vary across a range of site qualities (Cole and Newton 1987; Glover et al. 1989; White and Elliott 1992). Generally, with competing species that limit light availability, higher competition occurs at higher quality sites (Cole and Newton 1987; White and Elliott 1992). Although this study did not test if competition was more intense on higher quality sites, it does suggest that competition was not consistent across the gradient of site qualities. Site quality is an important variable and should be considered when modeling the growth of understory white spruce in boreal mixedwood stands.

With growth and DIFN relationships, height growth and basal area increment increase with more light availability to the understory for all site series and age classes. Stem volume increment increases with more light availability in the 01 and 06 site series however, in the 03 site series, stem volume increment decreases with increasing DIFN. This may be because site rather than competition has a stronger influence on stem volume increment for trees growing at sites in the 03 site series. Drever and Lertzman (2001) found that site quality was an important variable for predicting height of coastal Douglas-fir while growing in mixture with western red cedar when light levels were high at 40-60% of full sunlight. They also found that at low light levels, site influences on Douglas-fir growth were less than competition. The stem volume increment models predicts competition reduces stem volume increment at higher site qualities (site series 06 and 01) whereas, competition has minimal effects on stem volume increment at lower site qualities (03 site series).

Overstory age class was an important variable for explaining growth of understory white spruce in boreal mixedwood stands. Boreal mixedwood stands of different age classes differ in the amount of light transmitted into the understory. Light levels in developing young stands (10 to 20 years) tend to be suitable for tree establishment and growth but as the stand increases in age, the amount of light transmitted into the understory becomes lower. The second age class (21 to 40 years) includes the period when the overstory reaches maximum leaf area producing the lowest light levels available to the understory. The third age class in this study (+40 years) is when trees in the overstory were lost through self-thinning, resulting in increases of light availability to the understory with age. The models predict that age class 2 had the highest height growth rates for both the larger and smaller trees and it showed that understory white spruce in this age class developed a strategy of shade avoidance by increasing height growth. Other studies have suggested that white spruce develops a strategy of shade tolerance by increasing height growth at low levels of light (Gustafson 1943; Logan 1969). With some degree of shading, maximum height growth has been observed in Douglas-fir (Cole and Newton 1987) sycamore (Belanger and Pepper 1978) and loblolly pine (Strub et al. 1975).

When a system is limited by light, such as with trembling aspen growing with white spruce, competition results in progressively greater growth reductions with increasing density and age (Cole and Newton 1987). The influences of stand age on the growth of white spruce has been observed with increasing height growth with shading until the saplings were 8-10 years old (Posner and Jordan 2002). After which continual shading with age caused height growth to decrease. In this study, generally the oldest age class had significantly lower height growth than the two younger age classes. The lower height growth rates in age class 3 could result from trees putting more energy into diameter for stem strengthening, continual shading throughout the life span of the tree or perhaps leader whipping as the spruce trees reach the level of the aspen canopy.

Conclusions and Future Work

This study shows that overstory age and site series were important variables to consider when developing models for understory white spruce growing in aspen dominated stands in the BWBSmw1 sub-zone in British Columbia. When modeling, if these variables are not taken into consideration, there may be a tendency of the models to over or under estimate growth.

Understory white spruce diameter was the most useful initial size variable for predicting most of the dependent variables examined in this study. Other variables that could be used as initial tree size variables are crown volume, crown surface area, tree height and breast height age but in this study, diameter showed to be the most useful initial size variable. From a forest management perspective, these results should be encouraging to foresters since they are collecting diameters as part of re-measurement projects. In an operational setting, diameters are a desirable measurement because they are more easily obtainable than tree heights, crown variables and breast height age.

Further analysis in this study would have included multiple comparisons to determine if fewer age classes or site series would be adequate for predicting growth. The power of this study was not strong enough to complete multiple comparisons because the data set in this study was too small, and the number of observations in each age class and site series were greatly unbalanced. Future work should include using a larger data set to determine the number of age classes and site series required to accurately predict understory white spruce growth. It would also be desirable to build a model that focuses on the possible interaction between site series and age class.

References

Belanger, R.P., W.D. Pepper. 1978. Seedling density influences the early growth of planted sycamore. For. Sci. 24: 493-496.

British Columbia, Ministry of Forests. 2002. Stocking and free growing survey procedures manual. B.C. Min. For., Forest Practices Br. Victoria, B.C.

Canham, C.D. 1988. An index for understory light levels in and around canopy gaps. Ecology 69(5): 1634-1638.

Coates, K.D., P.J. Burton. 1999. Growth of planted tree seedlings in response to ambient light levels in northwestern interior cedar-hemlock forests in British Columbia. Can. J. For. Res. 29: 1374-1382.

Cole, E.C., M. Newton. 1987. Fifth-year response of Douglas-fir to crowding and nonconiferous competition. Can. J. For. Res. 17: 181-186.

Comeau, P.G. 2001. Relationships between stand parameters and understory light in boreal aspen stands. B.C. J. Ecosystems and Management. 1(2): 1-8.

Delong, C., A. MacKimmon., L. Jang. 1990. A field guide for identification and interpretation of ecosystems of the Northeast portion of the Prince George Forest Region. B.C. Ministry of Forests, Res. Br., Victoria, British Columbia. Land management Handb. 22.

Drew, A.P., W.K. Ferrell. 1977. Morphological acclimation to light intensity in Douglas-fir seedlings. Can. J. Bot. 55: 2033-2042.

Drever, C.R., K.P. Lertzman. 2001. Light-growth responses of coastal Douglas-fir and western redcedar saplings under different regimes of soil moisture and nutrients. Can. J. For. Res. 31: 2124-2133.

Glover, G.R., J.L. Creighton., D.H. Gjerstad. 1989. Herbaceous weed control increases loblolly pine growth. J. For. 87: 47-50.

Gustafson, F.G. 1943. Influences of light upon tree growth. J. For. 41: 212-213.

Green, R.N., P.L. Marshall, K. Klinka. 1989. Estimating site index of Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) from ecological variables in southwestern British Columbia. For. Sci. 35: 50-63.

Huang, S. 1999. Ecoregion-based individual tree height-diameter models for lodgepole pine in Alberta. WJAF. 14(4): 186-193.

Kayahara, G.J., K. Klinka., P.L. Marshall. 1998. Testing site index-site factor relationships for predicting Pinus contorta and Picea engelmannii x P. glauca productivity in central British Columbia, Canada. For. Ecol. Manage 110: 141-150.

Lanner, R.M. 1985. On the insensitivity of height-growth to spacing. For. Ecol. Manage. 13: 143-148.

Lautenschlager, R.A. 1995. Competition between forest brush and planted white spruce in north-central Maine. NJAF 12(4): 163-167.

LI-COR. 1992. LAI-2000 plant canopy analyzer. Instruction manual. LI-COR, Inc., Lincoln, Nebr.

Lieffers, V.J., B.D. Pinno, K.J. Stadt. 2002. Light dynamics and free-to-grow standards in aspen-dominated mixedwood forests. For. Chron. 78(1): 137-144.

Lieffers, V.J., C. Messier, K.J. Stadt, F. Gendron, P.G. Comeau. 1999. Predicting and managing light in the understory of boreal forests. Can. J. For. Res. 29: 796-811.

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

Logan, K.T. 1969. Growth of tree seedlings as affected by light intensity IV. Black spruce, white spruce, balsam fir and eastern white cedar. Dept. of Fisheries and Forestry, Canadian Forest Service. Publication 1256.

Meidinger, D., J. Pojar. 1991. Ecosystems of British Columbia. B.C. Ministry of Forests, Res. Br. Victoria, B.C. Special Report Series 6.

Messier, C., R. Doucet, J.C. Ruel Y. Claveau., C. Kelly., M.J. Lechowicz. 1999. Functional ecology of advance regeneration in relation to light in boreal forests. Can. J. For. Res. 29: 812-823.

Montgomery, D.C., E.A. Peck., G.G. Vining. 2001. Introduction to linear regression analysis. 3rd edition. John Wiley & Sons, Inc. Toronto.

Pojar, J., K.Klinka, D.V. Meidinger. 1987. Biogeoclimatic Ecosystem Classification in British Columbia. For. Ecol. Manage. 22: 119-154.

Posner, S.D., P.A. Jordan. 2002. Competitive effects on plantation white spruce saplings from shrubs that are important browse for moose. For. Sci. 48(2): 283-288.

Resource Inventory Branch, B.C. Ministry of Environment, Lands and Parks., Research Branch, B.C. Ministry of Forests. 1998. Field manual for describing terrestrial ecosystems. B.C. Ministry of Environment, Lands, and Parks., and B.C. Ministry of Forests. Victoria, B.C. Land Management Handbook 25.

Shirley, H.L. 1945. Reproduction of upland conifers in the lake states as affected by root competition and light: Establishment and growth of conifers as influenced by shade and root competition of aspen. Am. Mid. Nat. 33(3): 553-572.

Strub, M.R., R.B. Vasey., H.E. Burkhart. 1975. Comparision of diameter growth and crown competition factors in loblolly pine plantations. For. Sci. 21: 427-431.

Wang, G.G. 1997. Soil nutrient regime classification for white spruce stands in the sub-boreal spruce zone of British Columbia. Can. J. For. Res. 27: 679-685.

Wang, G.G. 1995. White spruce site index in relation to soil, understory vegetation, and foliar nutrients. Can. J. For. Res. 25: 29-38.

White, A.S., K.J. Elliott. 1992. Predicting the effects of hardwood competition on red pine seedling growth. Can. J. For. Res. 22: 1510-1515.

Chapter 4 – Estimating White Spruce Site Index in Boreal Mixedwood Stands

Introduction

Boreal mixedwood forests are a common component of western Canadian forests and they are particularly important for timber production, recreational activities and cultural events. Generally, site productivity includes the sum of all the possible uses of a geographical area and in the context of forestry, site productivity is the amount of timber a site can produce within a certain time. With difficulties with actually measuring site productivity, foresters estimate site productivity using site quality. Site index is the most common method for estimating site quality and is defined as the top height of dominant and co-dominant trees at a specified reference age. Site index is important in forestry because it is used as an input variable in most growth and yield models (Huang et al. 2001). It is also essential for making decisions about opportunities and the magnitude of silviculture treatments.

When dominant and co-dominant trees are absent in a stand or trees are suppressed due to competition, disease or insect problems, alternative methods are required for estimating site quality. In the Boreal White and Black Spruce zone (BWBS) of British Columbia, mixtures of trembling aspen and white spruce are common and widespread. Due to its rapid initial growth rates, trembling aspen commonly overtops the slower growing white spruce for the first 40-60 years after stand establishment. Consequently, overstory white spruce site trees (i.e. trees that have grown almost free of the effects of competition over their lifetime) are rarely available for site index determination and therefore, the boreal mixedwood stand structure requires alternative methods for estimating the productivity potential of white spruce.

Other than site index, there are at least three methods for estimating site quality including: 1) the use of vegetation, environmental indicators and physiographic land features, 2) conversion equations, 3) the use of periodic height growth (growth intercept methods). Ecological variables such as site quality factors (soil moisture and nutrient availability), environmental conditions (climate, precipitation, seasonal temperatures, duration of the growing season), physiographic land classifications (topography, aspect, slope gradient, elevation) and understory vegetation have been used singly or in multiple factor analyses for estimating site index (Barnes et al. 1998 pp.306-328).

Climate, topography, edatope and soil properties have been used to predict aspen site index in the BWBSwm sub-zone in British Columbia (Chen et al. 1998a). In the sub-boreal spruce (SBS) zone, Wang (1995) found soil properties, foliar nutrients and understory vegetation composition accounted for a substantial amount of variation in white spruce site index. It has been determined that site quality potentials for both aspen and white spruce are responsive to edatope where values increase from dry nutrient poor sites to moist nutrient rich sites (Wang 1993; Wang 1995; Chen et al. 1998a; Chen et al. 1998b).

When suitable site trees are absent in a stand, site index for one species may be predicted from that of a second species by the use of conversion equations. One-way or two-way prediction equations may be developed from stands when both species are present using linear regression or geometric mean regression (Nigh 1995a). Linear regression techniques were used to develop one-way prediction models that suggested yellow poplar (*Liriodendron tulipifera*) located at superior sites in Indiana, Ohio and West Virginia, had consistantly higher site index than oak (*Quercus velutina, Q. alba, Q. coccinea, Q. prinus and Q. rubra*) (Carmean and Hahn 1983). In northern Alberta forests, Hostin and Titus (1996) used linear regression to predict white spruce index from trembling aspen site index, with and without other ecological variables. Alone, site index of trembling aspen was a poor predictor (r^2=0.087), however, combined with aspen diameter, density, elevation and soil nutrient regime, the amount of variation explained in spruce site index increased to 79.4 percent. Two-way conversion equations have been developed for lodgepole pine and white spruce (Nigh 1995b; Wang 1998) and Douglas-fir and western hemlock (Nigh 1995b) with r^2 values between 0.82-0.94.

Periodic height growth has been used to predict site index in young plantations (Wakeley and Marrero 1958; Ferree et al. 1958; Day et al. 1960; Gunter 1968; Beck 1971; Brown and Stires 1981; Nigh 1999; Huang et al. 2001 p.31-32). This method is known as the growth intercept method and it is designed specifically for estimating site quality in juvenile stands (Warrack and Fraser 1955; Wakeley and Marrero 1958; Ferree et al. 1958). A number of methods have been used to determine growth intercepts (Huang 1996). For example, the fixed growth intercept method uses an average of a certain number of annual height growth intervals (3,4,5 and 10) above a fixed base height (0.3, 0.5, 0.75, 1.0, 1.3 and 2.0 m above ground level) to determine site index. In red pine plantations, site index was predicted from 5-year height growth increments above breast height (Wakeley and Marrero 1958; Ferree et al. 1958; Day et al. 1960). Gunter (1968) predicted site index with 5-year height growth 1 growing season after red pine was released from suppression. Beck (1971) predicted white pine site index from 3 and 5 years height growth above breast height level. Brown and Stires (1981) predicted white pine site index from 5 years growth increment from 2 years above breast height. Alban (1972) suggested the accuracy of prediction of red pine site index was doubled when 5-year height increments were taken from the first node above 8 feet rather than from breast height. Although many growth intercept models have been developed for many species, there is no standard for the number of height growth increments to include in the equation, and contrary to Husch (1956), who suggested that the base height should be at breast height, there are no standards followed for level of the base height.

A second method for determining growth intercepts is the variable growth intercept procedure. In British Columbia, Nigh (1995, 1996a, 1996b, 1996c, 1997) has used this procedure to predict site index for most commercial species and it is particularly useful for species that do not produce distinct annual whorls. This method predicts site index from measurements of tree height and breast height age. A total of 30 sub-models for breast height ages 1 to 30 were developed using the following equation:

$$SI_A = 1.3 + b_0 x \ GI_A^{b1}$$

GI_A is defined as:

$$GI_A = 100*((H_A - 1.3)/(A - A_p))$$

where GI_A is the growth intercept at breast height age A (A=1,2...30), H_A is the total tree height in meters at breast height age A (A=1,2,...30), A_p=(1.3-H_0)/(H_1-H_0).
The A_p term is a correction factor because the first growth interval is incomplete because of the 1.3-meter base for the measurement (it is an estimate of the proportion of growing season between breast height ages zero and one in which trees were less than 1.3 m), H_0 is total height of the understory tree at bha 0, H_1 is total height of the understory tree at bha 1, b0 and b1 are estimated parameters. The GI_A equation is multiplied by 100 so that the growth intercept is converted to centimeters.

From the sub-model equations, Nigh (1995) developed a single equation that could be used to predict site index from the growth intercept and breast height age:

$$SI=b_1*exp^{b2*A}*GI_A^{b3*\,exp(b4*A)}$$

where, b1,b2,b3 and b4 are estimated parameters and GI_A is defined above. The variable growth intercept differs from the fixed growth intercept method by the number of growth intercepts used to determine site index. The variable growth intercept method averages all growth intervals above breast height. The variable growth intercept approach has advantages because it reduces the influence of abnormal growth years. It also avoids having to find annual height growth whorls that can be difficult to identify with certainty, in some cases.

Many studies have focused on the height growth of white spruce in response to shade and the results of numerous studies seem to fall into one of two categories: 1) white spruce develops a strategy of shade tolerance and 2) height growth is inhibited by all levels of shade. Some studies have suggested white spruce develops a strategy of shade tolerance by increasing height growth at low levels of shade (Gustafson 1943; Shirley 1945; Logan 1969). For example, white spruce have been found to increase height growth with shading until the saplings were 8-10 years old, after which continual shading caused height growth increments to decrease slightly (Posner and Jordan 2002). On the other hand, white spruce did not develop a strategy for shade avoidance by increasing height growth in shade. Jobidon (2000) found height growth was inhibited by all levels of overtopping by competing vegetation. Although observations on white spruce height growth in response to shading are somewhat difficult to understand, there appears to be some interaction between height growth and shading.

The main objective of this study was to evaluate the relationship between understory white spruce growth and site index for the Boreal White and Black Spruce (BWBS) zone in British Columbia. A second objective was to determine if the amount of light transmitted to the understory is a useful variable in the site index prediction equation.

Methods

Data for this study were collected during July and August of 2000 and 2001 from nine aspen dominated mixedwood stands located in the moist warm Boreal White and Black Spruce (BWBSmw1) sub-zone (DeLong et al. 1990) near Dawson Creek and Fort St. John, British Columbia. Stands were selected to cover a wide range of age classes and site qualities. Based on historical records or age of the aspen, each stand was classified into one of three age classes: stands 10 to 20 years, stands 21 to 40 years and stands older than 40 years. Site characteristics and stand attributes were collected from each site.

In each stand, up to nine understory white spruce were selected as measurement trees. Selected trees were healthy, showed no signs of insect damage or pathogen problems and were not overtopped by shrubs and herbaceous vegetation. Each understory sample tree was selected as the tallest white spruce within a 5.64-meter distance from one of nine established reference points (Fig. 4-1). Depending on the size of the mixedwood stand, the first reference point was placed 80-125 meters at a random bearing from the stand edge or access trail. From the first reference point, three more reference points were positioned at 10-meter intervals at a bearing of 150 degrees. The next three reference points were positioned 10 meters apart at 270 degrees from the fourth reference point. The last two points were placed 10 meters apart at 30 degrees from the seventh established point forming an approximate triangle. If an understory white spruce was not within 5.64 meters of the reference point, a tree was not selected.

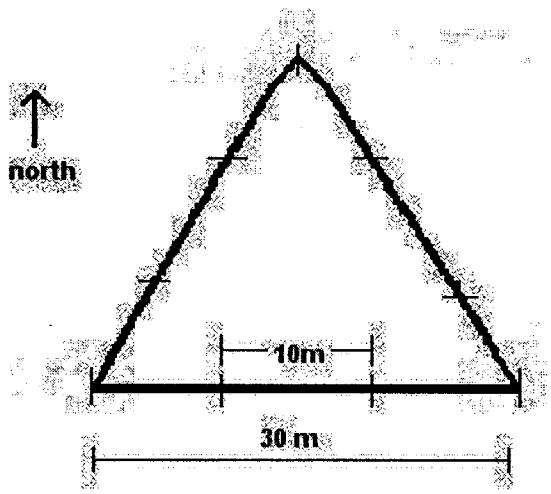

Figure 4-1: Schematic diagram of the plot layout. An understory white spruce tree was selected at 10 m intervals around the perimeter of the triangle. Growth and DIFN were measured for each understory white spruce. White spruce site index data were collected from the interior of the triangle.

Site Quality Measurements

Within the interior of the reference points (0.39 hectares) three dominant white spruce were measured for the determination of site index. These trees were healthy, showed no signs of stress such as insect damage, disease or major structural deformities. For each sample tree, total height was measured with a clinometer and measuring tape, and two cores were taken 1.3 meters above ground level. Ground level was determined as the highest point on the tree where the ground met the main stem. Cores were stored frozen until inspected in a laboratory. In the laboratory, age was determined and annual rings inspected for suppressed growth periods using a dissecting scope. If suppressed growth periods were identified, the core was discarded and the tree was eliminated as a measurement of site quality.

Understory White Spruce Measurements

Measurements of understory white spruce included age at 1.3 meters above ground level and total height. Trees with a diameter of 5 cm or more were cored once 1.3 m above ground level and trees with a smaller diameter were sectioned at the same height. Cores and sections were stored frozen until inspected in a laboratory. A dissecting scope was used to count annual rings from the cores and sections. Depending on the height of understory trees, total heights of trees shorter than four meters were measured with a tape measure, trees between four and 12 meters were measured with a height pole and trees taller than 12 meters were measured with a clinometer and tape measure.

Competition Measurements

Diffuse non-interceptance (DIFN) was measured in the cardinal directions around each of the understory sample trees using a LAI-2000 (Li-Cor 1992) during July and August of 2001. To avoid direct beam light interfering with the readings, the north and west sides of the trees were measured in the morning and the south and west sides in the late afternoon. LAI measurements were taken at mid canopy with the height determined by the height of the sample tree. Since the LAI has a 10-meter radius field of view, a 180-degree view restrictor cap was placed over the lens to avoid inclusion of the subject tree in the measurements. Two LAI-2000 instruments were calibrated together and used for sampling. One instrument was placed in a near-by opening and used for open sky readings and the second instrument was used for measurements under the canopy. The open sky instrument was programmed to take readings every 30-seconds for the length of time required to complete measurements under the canopy.

For each LAI measurement, DIFN was calculated with C2000 software (Li-Cor 1992). The fifth ring was turned off because other studies have suggested that computation of DIFN is more reliable with the exclusion of the fifth ring. One DIFN value for each tree was calculated by averaging the measurements taken in the cardinal directions around each understory tree.

Data Preparation and Calculations

From the site quality measurements, white spruce site index was calculated using two equations. For age class 1 and 2 (stand age less than 40 years) site index was calculated from a growth intercept equation (Nigh 1996a).

$$SI_A = 1.3 + b_0 x\ GI_A^{b1} \qquad (1)$$

where: SI_A is site index (m); b_0 and b_1 are age dependent estimated parameters given by Nigh (1996a); GI_A is calculated as:

$$GI_A = 100*((H_A-1.3)/A-A_p) \qquad (2)$$

where: GI_A is the growth intercept (cm/yr) at breast height age A (yr); A=1,2,3...30; $H_{i,A}$ is the total tree height(m) at breast height age A; and $A_p=(1.3-H_{i,0})/(H_{i,1}-H_{i,0})$. The A_p term is a correction factor for the first growth interval not beginning at exactly 1.3 meters above ground level. If this term was not included there would be a bias in the growth intercept predictions (i.e. the predictions of the growth intercept would be shifted approximately 0.5 years). The equation is multiplied by 100 so that the unit of the growth intercept is in cm.

For age class 3 (stand age older than 40 years), site index was calculated from curves (Goudie 1984).

Data Analysis

From equation 1, Nigh (1995b) derived a single equation model suitable for estimating site index from the growth intercept and age.

$$SI_A=b_1*\exp^{b2*A}*GI_A^{b3*\exp(b4*A)} \qquad (4)$$

where b_1, b_2, b_3 and b_4 were estimated parameters, A was breast height age and GI_A was calculated as:

$$GI_A=(H_A-130)/A \qquad (5)$$

where H_A was the total height of the tree during the year measurements were taken, A was breast height age.

Equation 4 was fit to the data where white spruce site index was based on 9 values (9 sites with the average of 3 tree site trees to determine one site index value for each stand) and GI_A was based on 48 understory spruce. Nonlinear regression was used to fit equation 4 using the NONLIN procedure in SAS (SAS Institute Inc. V8 1999). Model evaluation was based on a band of residuals showing homogenous variance, a low MSE and significant parameter estimates. An approximate R^2 value was calculated for the non-linear equations.

Results

Descriptive statistics for the independent and dependent variables are provided in Table 4-1.

Table 4-1: Descriptive statistics for the independent and dependent variables

Variable	Units	N	Mean	Std. Dev.	Minimum	Maximum
GI_A	cm/y	48	23.2	9.14	5.5	49.2
H_A	cm	48	483	239	163	1240
BHAGE	y	48	15.5	9.6	5.0	41.0
DIFN	-	48	0.30	0.13	0.09	0.62
SWSI	m	48	24	4.0	18.5	31.3

Stand attributes of the stands sampled are given in Table 4-2.

Table 4-2: Stand attributes (aspen age, total aspen density, mean aspen diameter, mean total aspen height, aspen basal area per hectare, total white spruce density, white spruce basal area per hectare, spruce site index and site series)

Site	Aspen Age (y)	Aspen density (tph)	Aspen mean dbh (cm)	Aspen height (m)	Aspen ba/ha (m^2/ha)	Spruce density (tph)	Spruce baha (m^2/ha)	Spruce site index (m)	Site series
BE2501	22	4733	8.0	9.7	16.33	2367	1.02	22.6	01
BE3001	22	3600	9.9	11.8	14.98	1133	1.76	19.2	01
BE4001	67	1300	21.7	21.8	41.93	700	0.31	18.5	03
BP	41	633	21.0	18.2	11.51	333	8.45	24.3	01
FS1501	16	4733	6.7	6.8	14.80	867	2.00	26.2	01
GL3001	13	17666	4.7	6.1	16.53	1200	0.42	31.3	01
MUS	16	4433	7.1	7.2	16.10	1667	1.14	22.1	01
SEP	51	767	22.1	15.0	24.4	333	3.85	26.1	03
SUN	49	867	17.9	20.8	30.06	400	1.49	27.2	01

Using the 4-parameter model (Equation 4), results of the fitted model showed that some of the parameter estimates were not significant. The model was modified to the following:

$$SI_A=b_1*\exp(b_2*A)*GI_{i,A}^{(b3*A)} \qquad (6)$$

$$SI_A=b_1*\exp(b_2*A)*GI_{i,A}^{(b3*A)}*DIFN^{b4} \qquad (7)$$

The revised model was fit both with DIFN (7) and without DIFN (6) using the NONLIN procedure in SAS (SAS Institute Inc. V8 1999).

When Equation 6 (without DIFN) was fit, results showed that parameter estimates were not significant and therefore the model was evaluated as having low precision for its prediction capabilities. When DIFN was placed into the equation (7), there were great improvements in the fit statistics (Table 4-3). The residuals were a band showing homogenous variance centered around a mean error of zero, the MSE was lower than the MSE from Equation 6 and all parameter estimates were significant. These statistics suggest that the model was an improved fit and that DIFN was a necessary variable to include while predicting white spruce site index.

Table 4-3: Equations for predicting white spruce site index with estimated values, observed significant level of the parameter values, approximate R^2 values and mean square error of the models

Equation	Parameter	Para.Estimate	Para. p-value	R^2	MSE
6 $SI_I=b_1*\exp(b_2*A)*GI_{I,A}^{(b3*A)}$	b_1	25.63	<0.0001	0.02	16.3
	b_2	-0.0384	0.1406		
	b_3	0.0055	0.1406		
7 $SI_I=b_1*\exp(b_2*A)*GI_{I,A}^{(b3*A)}*DIFN^{b4}$	b_1	22.24	<0.0001	0.19	13.7
	b_2	-0.0778	0.0148		
	b_3	0.0110	0.0148		
	b_4	-0.1646	0.0017		

Mean annual height growth of the understory, breast height age and DIFN explains 19% of the variation in white spruce site index (Table 4-3). The model predicts that white spruce site index increases with larger mean annual increment of understory white spruce. There are two ways by which mean annual increment could be increased. The first way is by reducing breast height age while holding total height constant (Fig. 4-2). The second way is by increasing total height while holding breast height age constant (Fig. 4-3). Equation 7 also predicts that spruce site index decreases with higher levels of DIFN in the understory (Figure 4-4).

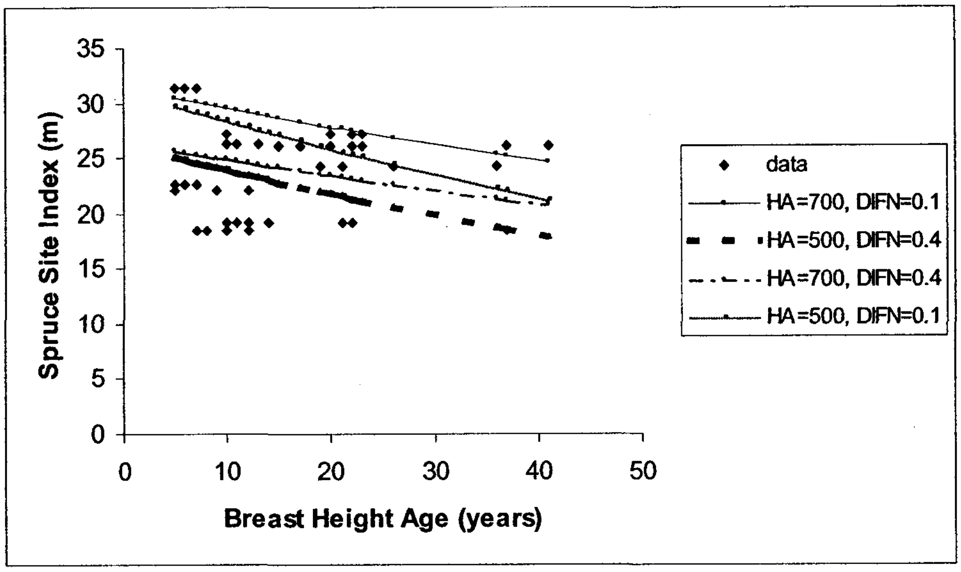

Figure 4-2: Scatter plot showing the relationship between breast height age (BHAGE) and white spruce site index for total tree height (H_A) values of 500 and 700 cm and DIFN values of 0.1 and 0.4. The lines on the graph are explained by Equation 7.

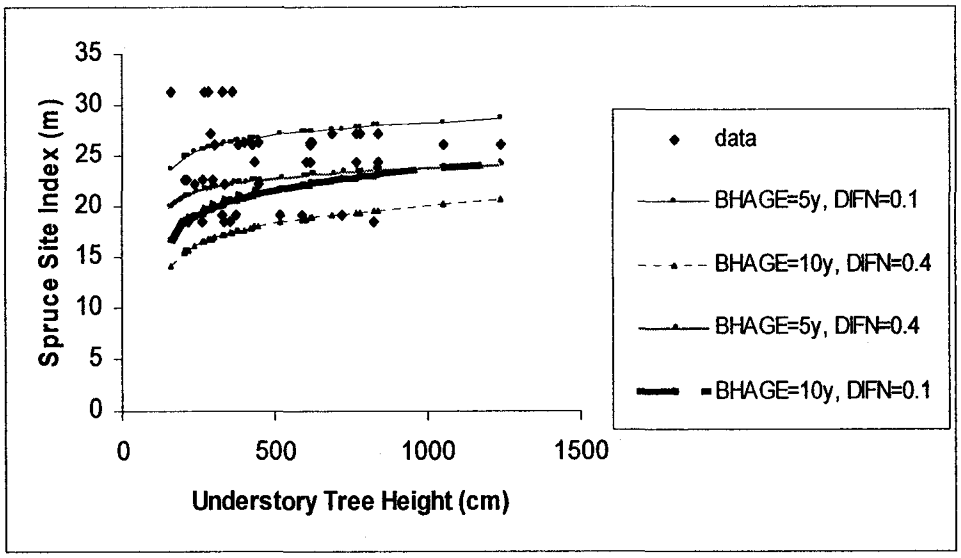

Figure 4-3: Scatter plot showing the relationship between total tree height and white spruce site index for breast height ages (BHAGE) of 5 and 10 years and DIFN values of 0.1 and 0.4. The line on the graphs are explained by Equation 7.

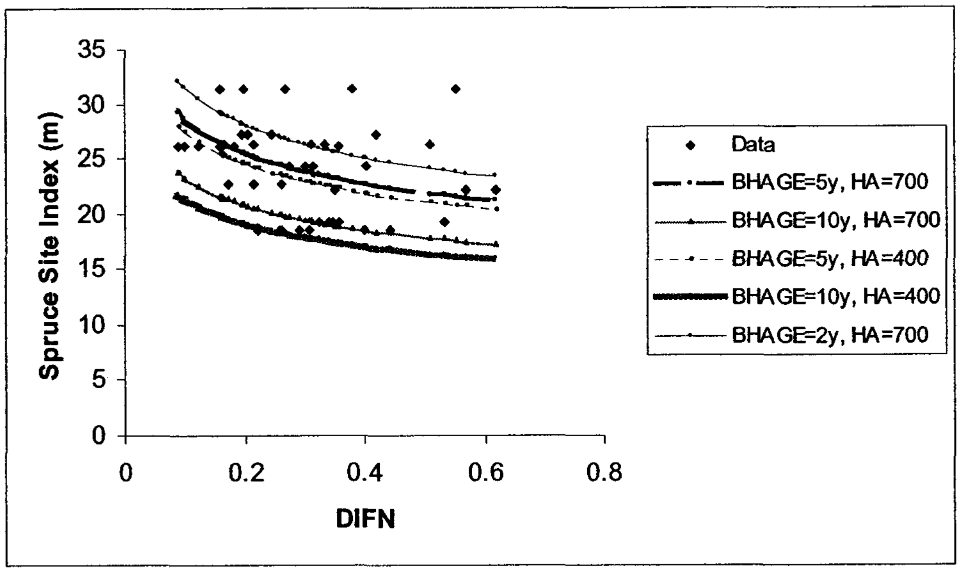

Figure 4-4: Scatter plot showing the relationship between DIFN and white spruce site index for total tree height (H_A) values 700 and 400 cm and breast height age (BHAGE) values 2, 5 and 10 years. The lines on the graph are explained by Equation 7.

Discussion

The results in this study clearly show that white spruce site index can be predicted from the understory mean annual height growth above breast height level, understory white spruce breast height age and DIFN. It was important to include DIFN in order to have a statistically significant equation. DIFN acts as a correction factor for the trees being in the understory rather than dominant in the canopy. The variable DIFN was likely important to include in the equation because this measurement captures density and size of the competition. The lens of the LAI-2000 instrument had a 10-meter field of view and provides a reasonable estimate of the amount of competition surrounding the understory tree. Although not tested in this study, it may be possible to substitute DIFN with any competition index that is representative of stand density and intensity of the competition.

The model in this study used mean annual height growth above breast height, breast height age and DIFN to explain approximately 19% of the variation in white spruce site index. The explanation of variation in spruce site index was much lower than for the models described by Nigh (1996a). This may be because the stands sampled in this study were of natural origin and consequently, there was a large amount of variation in the size of trees sampled. The breast height ages varied between 5 and 41 years and tree heights varied between 1.6 and 12.4 m. In contrast, the models developed by Nigh (1996a) were from stands of pure spruce. The model described in this study indicates that there is a large amount of variation unaccounted for in the model for explaining white spruce site index.

The low R^2 associated with the site index equation suggests that there are other variables that are unaccounted for in the model. Firstly, one DIFN value was generated for each understory tree by measuring one time throughout the rotation of the stand. Aspen stands, particularly when young are continually changing in structure by self-thinning. One measurement at one time may not be enough to provide an accurate measurement of competition. Chapter 2 of this thesis suggested overstory age was an important variable when modeling the growth of understory white spruce growing in boreal mixedwood stands. It may be possible that including overstory age as an additional variable in the site index equation may improve the fit of the model.
The low R^2 may also be a result of the model not accounting for seasonal variations in the amount of leaf area in the canopy or competition from understory herbaceous species.

The equation predicts when the mean annual height increment is the same for the understory trees, transmittance to the understory is higher on sites with lower site indices (Fig. 4-5). At better sites, growth is attained by lower light being compensated for by more soil moisture and soil nutrients available for plant growth. At lower quality sites more light is available in the understory because there is less leaf area in the canopy. Growth is attained at poor sites by there being more light available for growth. The lower soil moisture and nutrient levels at the poor sites are compensated for by greater light transmittance to the understory. The model also predicts that if DIFN is held constant, understory white spruce trees with a larger mean annual height increment are growing at sites with greater white spruce site index (Fig. 4-6). More soil moisture and nutrients available at the better sites allow for a greater mean annual height increment than at sites with lower white spruce site index.

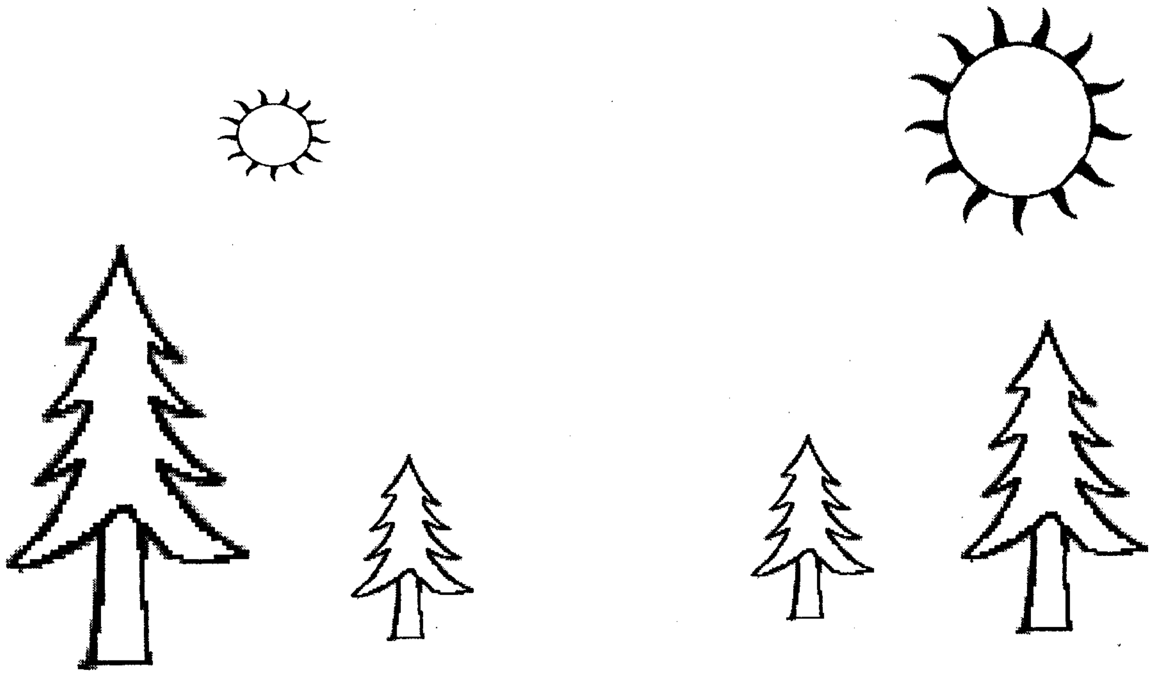

Figure 4-5: Schematic diagram showing predictions from Equation 7. When MAI is held constant (small trees) at different quality sites (large trees) growth of the understory is attained by there being more understory light (large sun) available at the poor sites. At the better site, there is less light available in the understory however, growth is attained by there being more soil moisture and nutrient available for understory tree growth.

Model Limitations

There is a slight concern with the relationship between white spruce site index and DIFN (Fig. 4-4). The negative coefficient associated with DIFN results in a negative relationship between spruce site index and DIFN. In this study, there were observations that had relatively high white spruce site indices with increasing DIFN values (Fig. 4-4). White spruce site index is predicted to increase if tree height increases while breast height age remains constant (Fig. 4-3) or if breast height age decreases while total tree height remains constant (Fig. 4-2). However in some instances, high predicted site index values arise from tree height and breast height age values that imply unrealistic mean annual height increments. In some cases, it may be possible that the model is under estimating white spruce site index at higher levels of DIFN.

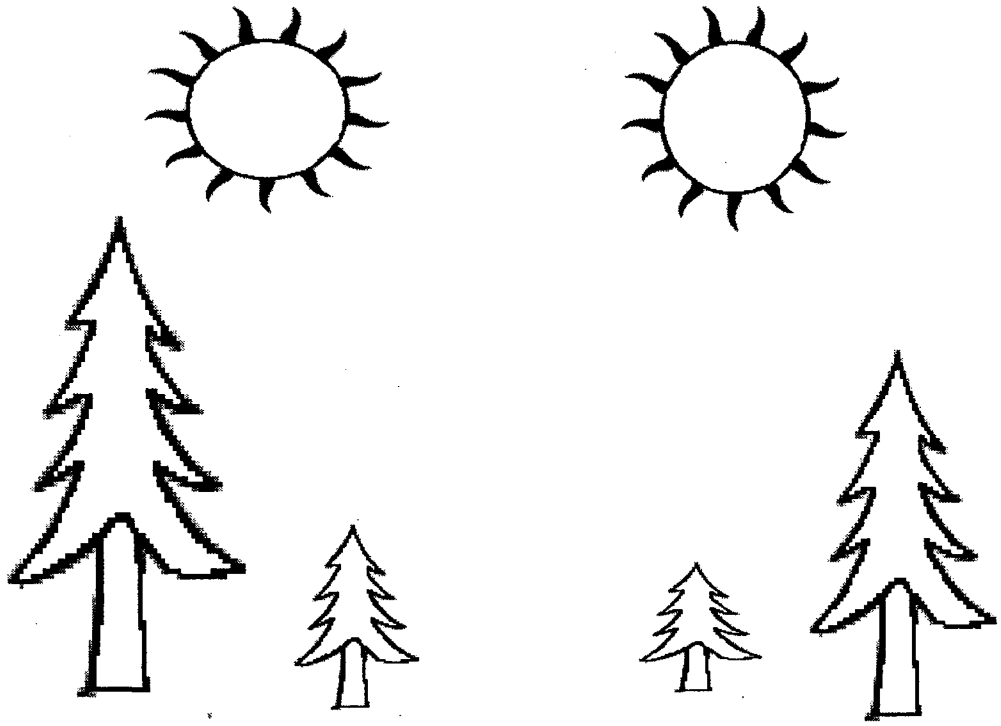

Figure 4-6: Schematic diagram showing predictions from equation 7. When DIFN (sun) is held constant, mean annual height increment (small trees) is larger for trees growing at sites with higher white spruce site index. Mean annual height increment is smaller for trees growing at sites with lower white spruce site index

Figure 4-2 shows that the upper limit of data for this model would be for a tree that is 700 cm tall growing with a DIFN of 0.1 and the lower limit would be for a tree that is 500 cm tall growing with a DIFN of 0.4. If trees are shorter, there is a tendency for the predictions of older trees to become less accurate because the prediction falls outside of the range of data. Also, to stay within the range of the data, the upper limit is a 5 year dbh tree growing with 0.1 DIFN and the lower is a 10 year dbh tree growing with 0.4 DIFN (Fig. 4-3). This model is most useful for trees that have a 5-10 yr old breast height age, 400-700 centimeters height and growing under 0.1 to 0.4 DIFN.

Conclusion

This study shows that white spruce site index can be predicted from understory mean annual height increment, breast height age and DIFN. This study differs from other studies that have predicted site index in that: 1) the predictions were made from understory trees and 2) competition was shown to be a significant variable in the prediction of site index. DIFN acts as a correction factor for the understory white spruce not being dominant in the forest canopy. Although the amount of variation explained by this model is low, improvements in the model could be possible by including other variables such as overstory age in the equation. From a forest management perspective, this study shows that equations can be generated for estimating white spruce site index in mixedwood stands. This procedure utilized conventional growth intercept methods and a correction for stand density by the use of a competition index.

References

Alban, D.H. 1972. An improved growth intercept method for estimating site index of red pine. USDA For. Ser. Res. Pap. NC-80.

Barnes, B.V., D.R. Zak., S.R. Denton., S.H. Spurr. 1998. Forest ecology, 4th edition. John Wiley & Sons, Inc. New York. 774pp.

Beck, D.E. 1971. Growth intercept as an indicator of site index in natural stands of white pine in the Southern Appalachians. USDA For. Serv. Res. Note SE-154.

Brown, J.H., J.L. Stires. 1981. A modified growth intercept method for predicting site index in young white pine stands. For. Sci. 27(1): 162-166.

Carmean, W.H. J.H. Hahn. 1983. Site comparision for upland oaks and yellow popular in the central States. J. For. 81: 736-739.

Chen, H.Y.H., K. Klinka, R.D. Kabzems. 1998a. Site index, site quality, and foliar nutrients of trembling aspen: relationships and prediction. Can. J. For. Res. 28: 1743-1755.

Chen, H.Y.H., K. Klinka., R.D. Kabzems. 1998b. Height growth and site index models for trembling aspen *(Populus tremuloides* Michx.) in northern British Columbia. For. Ecol. Manage. 102: 157-165.

Day, M.W., C.F. Bey., V.J. Rudolph. 1960. Site index for planted red pine by the 5-year growth intercept method. J. For. 58: 198-202.

DeLong, C.A., A. MacKinnon, L. Jang. 1990. A field guide for identification and interpretation of ecosystems in the northeastern portion of the Prince George Forest Region. B.C. Min. For. Res. Br. Victoria, B.C. Land Manage. Handbook No. 22.

Ferree, T., D. Shearer., E.L. Stone, Jr. 1958. A method of evaluating site quality in young red pine plantations. J. For. 56: 328-332.

Goudie, J.W. 1984. Height growth and site index curves for lodgepole pine and white spruce and interm managed stand yield tables for lodgepole pine in British Columbia. B.C. Min.For. Res. Br. Unpubl. Rep. 75 p.

Gunter, J.E. 1968. Site index for released red pine plantations. J. For. 66: 862-863.

Gustafson, F.G. 1943. Influence of light upon tree growth. J. For. 41: 212-213.

Hostin, P.J. S.J. Titus. 1996. Indirect site index models for white spruce in Alberta's boreal mixedwood forest. For. Chron. 72: 73-79.

Huang, S., D. Morgan, G. Klapstein., J. Heidt., Y. Yang., G. Greidanus. 2001. Gypsy: A Growth and yield projection system for natural and regenerated stands within an ecologically based, enhanced forest management framework. Land and Forest Division, Alberta Sustainable Resource Development. Edmonton.

Huang, S. 1996. Growth intercept models for assessing the site potential of young lodgepole pine stands in Alberta. Alberta Land and Forest Service, Tech. Rep. Pub. No. T/339, Edmonton, Alberta. 97pp.

Husch. B. 1956. Use of age at D.B.H. as a variable in the site index concept. J. For. 54: 340.

Jobidon, R. 2000. Density-dependent effects of northern hardwood competition on selected environmental resources and young white spruce (*Picea glauca*) plantation growth, mineral nutrition and stand structure development-15-year study. For. Ecol. Manage. 130: 77-97.

LI-COR. 1992. LAI-2000 plant canopy analyzer. Instruction manual. LI-COR, Inc., Lincoln, Nebr.

Logan, K.T. 1969. Growth of tree seedlings as affected by light intensity IV. Black spruce, white spruce, balsam fir and eastern white cedar. Dept. of Fisheries and Forestry, Canadian Forest Service. Publication 1256.

Nigh, G.D. 1999. Revised growth intercept models for coastal western hemlock, Sitka spruce, and interior spruce. B.C. Min. For., Res. Br., Victoria, B.C. Exten. Note 37. 8 pp.

Nigh, G.D. 1998. A system for estimating height and site index of western hemlock in the interior of British Columbia. For. Chron. 74(4): 588-596.

Nigh, G.D. 1997. A growth intercept model for coastal Douglas-fir. B.C. Min. For., Res. Br. Victoria, B.C. Res. Rep. 10. 20pp.

Nigh, G.D. 1996a. A variable growth intercept model for spruce in the Sub-Boreal Spruce and Englemann Spruce-Subalpine Fir biogeoclimatic zones of British Columbia. B.C. Min. For., Res. Br., Victoria. B.C. Res. Rep. 05, 20pp.

Nigh, G.D. 1996b. A variable growth intercept model for Sitka spruce. B.C. Min. For., Res. Br., Victoria, B.C. Ext. Note 03. 7pp.

Nigh, G.D. 1996c. Growth intercept models for species without distinct annual branch whorls: western hemlock. Can. J. For. Res. 26: 1407-1415.

Nigh, G.D. 1995a. The geometric mean regression line: a method for developing site index conversion equations for species in mixed stands. For. Sci. 41: 84-98.

Nigh , G.D. 1995b. Variable growth intercept models for lodgepole pine in the sub-boreal spruce biogeoclimatic zone, British Columbia. B.C. Min. For., Res. Br., Victoria, B.C. Res. Rep. 02. 23 pp.

Posner, S.D., P.A. Jordan. 2002. Competitive effects on plantation white spruce saplings from shrubs that are important browse for moose. For. Sci. 48(2): 283-289.

SAS Institute Inc. 1999. SAS/ETS user's guide. Version 8. Cary. NC.

Shirley, H.L. 1945. Reproduction of upland conifers in the lake states as affected by root competition and light: Establishment and growth of conifers as influenced by shade and root competition of aspen. Am. Mid. Nat. 33(3): 553-572.

Wakeley, P.C., J. Marrero. 1958. Five-year intercept as site index in southern pine plantations. J. For. 56: 332-336.

Wang, G.G. 1998. An ecologically based model for site index conversion among species. Can. J. For. Res. 28: 234-238.

Wang, G.G. 1995. White spruce site index in relation to soil, understory vegetation, and foliar nutrients. Can. J. For. Res. 25: 29-38.

Wang, G.G. 1993. Ecological site quality, site index, and height growth of white spruce stands in the Sub-boreal Spruce Zone of British Columbia. Ph.D. thesis, University of British Columbia, Vancouver.

Warrack, G.C., A.R. Fraser. 1955. Estimation of site quality in juvenile Douglas-fir stands. B.C. For. Serv. Res. Note 28. 5pp.

Chapter 5 – Research Summary, Forest Management Implications and Future Work

The first chapter shows that height growth and basal area increment can be predicted from site quality, competition and an initial tree size. The height growth model used crown surface area, an interaction between aspen site index and diffuse non-interceptance (DIFN) and an interaction between crown surface area and DIFN to explain 51.7% of the variation in height growth. When site quality (aspen site index) was removed from the equation, the resulting R^2 was substantially lower (0.42). The basal area increment model used initial diameter, deciduous basal area, aspen site index and an interaction between aspen site index and deciduous basal area to explain 90.2% of the variation in growth. When site quality was removed from the equation the resulting R^2 was 0.87. These results show that site quality, tree size and competition are important factors and should be accounted for when modeling height growth and basal area increment of white spruce in boreal mixedwood stands.

The third chapter in the thesis showed that site series and age class were important variables to consider when modeling height growth, basal area increment, stem volume increment and height to diameter ratio. Due to limitations in the data (i.e. the unequal representation of data in each site series and age class) a model could not be constructed that included both age class and site series. Future work should focus on producing one model that includes both of these variables. Also, multiple comparisons should be completed to determine if fewer site series and age classes could be used for predicting growth.

The fourth chapter in the thesis showed that white spruce site index can be predicted from understory white spruce mean annual height growth, breast height age and DIFN. Presently, there are no formal methods for predicting white spruce site index in boreal mixedwood stands because white spruce site index trees are rarely available for site index determination. The results in this chapter show that white spruce site index can be predicted using conventional growth intercept equations with an adjustment made for overstory competition. Although the r-square for the equation was relatively low, it should be recognized that the sampling was completed in stands where the understory trees ranged greatly in size and age. Future work in this area should focus on using stem analysis to determine the correct ages of sample trees and the selection of sites may include more uniform sizes for the sample understory spruce trees.

Appendix A

Development of a crown-based competition index

A competition index was developed to determine if the length of the aspen crowns above the height of the understory subject tree could be used as an assessment of competition for predicting growth. The index was calculated as the sum of aspen crown lengths above the height of the subject tree within a 5.64-meter radius plot. Tree heights and crown lengths are exceptionally time consuming to measure and therefore it is common for monitoring and inventory projects to measure a sub-sample of the population but provide estimated heights and estimated crown lengths for all the members of the population. Regression analysis can then be applied to predict tree heights or crown lengths from estimated values. In this study this procedure was used to develop the crown-based index. Three trees per plot (one tree in each crown class) had total height and height to the base of the live crown measurements. Two regression models were developed and used to determine the length of the aspen crowns. The following steps were used to develop the index:

1. The percent of live crown was determined for the aspen with measured total height and measured height to the base of the live crown.
2. A linear regression equation was developed for predicting measured percent live crown from the estimated percent live crown and then used to determine the percent of live crown for the aspen without measurements.
3. A second regression equation was developed to predict measured heights from estimated heights and then used to determine tree heights for trees without measured heights.
4. The length of the live crown was determined for each aspen and then the competition index was calculated. For the transect method, the sum of the aspen crowns above the height of the subject tree were multiplied by 4.43. The performance of the equations did not improve when crown class was used as an indicator variable.

The regression equations and statistics used in developing the competition are shown below.

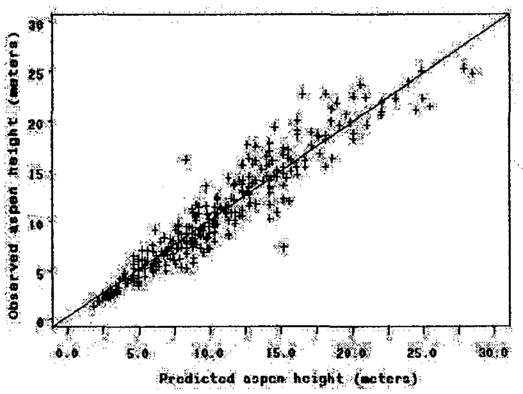

Figure 1: Estimating aspen heights

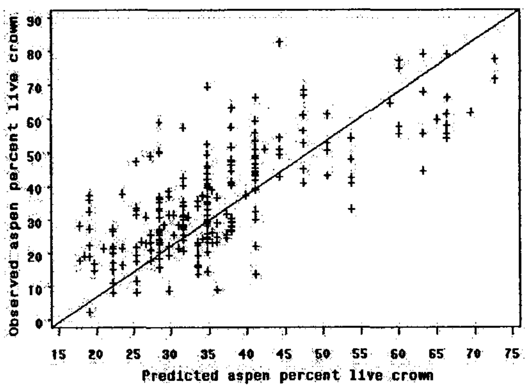

Figure 2: Estimating aspen % live crown

Table 1: Statistics for the equations used to predict aspen heights and percent live crowns

Equation	Parameter	Estimate	Para. p-Value	R^2	RMSE	N
Measured height=b_0+b_1*Estimated height	b_0	0.5418	0.0063	0.9092	1.70	309
	b_1	0.9771	<0.0001			
Measured % live crown= b_0+b_1*Estimated % live crown	b_0	15.86	<0.0001	0.5312	10.85	231
	b_1	0.6314	<0.0001			

Appendix B
A Description of Site Characteristic Coding

1. Soil Texture

Code	Code Definition	Code	Code Definition
L	loam	SiC	silty clay
SiL	silty loam	C	clay
Si	silt	HC	heavy clay
SCL	sandy clay loam	S	sand
CL	clay loam	SL	sandy loam
SiCL	silty clay loam	FSL	sine sandy loam
SC	sandy clay	LS	loamy sand

2. Soil Drainage

Code	Code Definition
R	rapidly drained
W	well-drained
MW	moderately well-drained
I	imperfectly drained
P	poorly drained
V	very poorly drained

3. Soil Moisture Regime

Code	Code Definition
1	Xeric
2	Subxeric
3	Submesic
4	Mesic
5	Subhygric
6	Hygric
7	Subhydric

4. Soil Nutrient Regime

Code	Code Definition
A	very poor
B	Poor
C	Medium
D	Rich
E	very rich

See the following for precise definitions of the code definitions.
B.C. Ministry of Environment, Lands, and Parks., B.C. Ministry of Forests. 1998. Field Manual for describing terrestrial ecosystems. Res. Bran. Ministry of Forests., Victoria, B.C.

Appendix C
Predicting height growth with one independent variable

Equation	Pa ra.	Parameter Estimate	Parameter p-value	r^2	RMSE
1 HTG3Y=b_0+b_1*CSA96+b_2*CSA96^2	b_0	21.36	<0.0001	0.2041	8.68
	b_1	5.68	0.0034		
	b_2	-0.70	0.0126		
2 HTG3Y=b_0+b_1*cvol96+b_2*cvol96^2	b_0	23.64	<0.0001	0.1252	9.10
	b_1	2.26	0.0226		
	b_2	-0.136	0.0529		
3 HTG3Y=b_0+b_1*th96+b_2*th96^2	b_0	14.98	<0.0001	0.2357	8.51
	b_1	0.06	0.0020		
	b_2	-0.000052	0.0081		
4 HTG3Y=b_0+b_1*DBH96+b_2*DBH96^2	b_0	16.83	<0.0001	0.2804	8.25
	b_1	4.70	0.0004		
	b_2	-0.349	0.0018		
5 HTG3Y=b_0+b_1*bhage+b_2*bhage^2	b_0	13.66	0.0214	0.1147	9.16
	b_1	1.98	0.0314		
	b_2	-0.06	0.0450		
6 HTG3Y= b_0+b_1*DIFN	b_0	16.69	<0.0001	0.1795	8.71
	b_1	36.43	0.0046		
7 HTG3Y= b_0+b_1*BADEC	b_0	32.04	<0.0001	0.1014	9.11
	b_1	-0.24	0.0046		
	b_1	-3.23	0.0200		
8 HTG3Y= b_0+b_1*ATSI	b_0	13.68	0.0512	0.0795	9.22
	b_1	0.62	0.0670		
9 HTG3Y= b_0+b_1*ln(CI1)	b_0	39.53	0.0001	0.1241	8.99
	b_1	-3.04	0.0205		
10 HTG3Y= b_0+b_1*ln(CI2)	b_0	26.38	0.0028	0.0000	9.611
	b_1	-0.033	0.9849		

Appendix D
Predicting basal area increment with one independent variable

Equation	Parameter	Parameter Estimate	Parameter p-value	r^2	RMSE
1	b_0	-1.40	<0.0001		
$\ln(BA3Y)=b_0+b_1*CSA96+b_2*CSA96^2$	b_1	0.98	<0.0001	0.6383	0.726
	b_2	-0.09	<0.0001		
2	b_0	-1.05	<0.0001		
$\ln(BA3Y)=b_0+b_1*cvol96+b_2*cvol96^2$	b_1	0.51	<0.0001	0.5668	0.7942
	b_2	-0.02	0.0005		
3	b_0	-2.42	<0.0001		
$\ln(BA3Y)=b_0+b_1*th96+b_2*th96^2$	b_1	0.0094	<0.0001	0.7313	0.626
	b_2	-0.0000057	0.0001		
4	b_0	-2.21	<0.0001		
$\ln(BA3Y)=b_0+b_1*DBH96+b_2*DBH96^2$	b_1	0.73	<0.0001	0.8714	0.4328
	b_2	-0.0.039	<0.0001		
5	b_0	-2.94	<0.0001		
$\ln(BA3Y)=b_0+b_1*bhage+b_2*bhage^2$	b_1	0.359	0.0004	0.3732	0.9554
	b_2	-0.00944	0.0035		
6	b_0	0.818	0.0796	0.0227	1.15
$BA3Y= b_0+b_1*DIFN$	b_1	1.56	0.3349		
7	b_0	1.56	0.0002	0.0231	1.15
$BA3Y= b_0+b_1*BADEC$	b_1	-0.014	0.3304		
8	b_0	3.64	0.0001	0.7220	0.628
$\ln(BA3Y)= b_0+b_1*\ln(CI1)$	b_1	-0.911	0.0001		
9	b_0	2.479	0.0105	0.1899	1.0728
$\ln(BA3Y)= b_0+b_1*\ln(CI2)$	b_1	-0.6054	0.0035		
10	b_0	-1.25	0.1593	0.0268	1.176
$\ln(BA3Y)= b_0+b_1*ATSI$	b_1	0.0447	0.2944		

Appendix E
Predicting height growth with competition and initial tree size

Equation	Para	Para. Est.	Para. P-value	R^2_a	RMSE
1 HTG3Y=b_0+b_1*DIFN+b_2*CSA96+b_3*$CSA96^2$*DIFN	b_0	7.71	0.0342	0.4149	7.26
	b_1	53.02	0.0001		
	b_2	5.53	0.0001		
	b_3	-2.69	0.0004		
2 HTG3Y=b_0+b_1*DIFN+b_2*cvol96+b_3*$cvol96^2$*DIFN	b_0	12.46	0.0010	0.2798	8.06
	b_1	41.83	0.0007		
	b_2	2.67	0.0056		
	b_3	-0.745	0.0179		
3 HTG3Y=b_0+b_1*(th96*DIFN)+b_2*$th96^2$-b_3*($th96^2$*DIFN)	b_0	12.36	0.0005	0.3484	7.67
	b_1	0.320	0.0002		
	b_2	0.000047	0.0311		
	b_3	-0.00051	0.0039		
4 HTG3Y=b_0+b_1*DIFN+b_2*DBH96-b_3*$DBH96^2$	b_0	7.75	0.0349	0.4078	7.31
	b_1	34.49	0.0013		
	b_2	4.67	0.0001		
	b_3	-0.352	0.0005		
5 HTG3Y=b_0+b_1*bhage+b_2*(bhage*DIFN)-b_3*($bhage^2$*DIFN)	b_0	10.42	0.0453	0.2220	8.38
	b_1	0.613	0.1100		
	b_2	7.81	0.0009		
	b_3	-0.332	0.0041		
6 HTG3Y=b_0+b_1*BADEC+b_2*(CSA96*BADEC)-b_3*($CSA96^2$*BADEC)	b_0	31.45	0.0001	0.2844	8.03
	b_1	-0.405	0.0005		
	b_2	0.214	0.0017		
	b_3	-0.0245	0.0103		
7 HTG3Y=b_0+b_1*BADEC+b_2*(cvol96*BADEC)-b_3*$cvol96^2$	b_0	32.75	0.0001	0.2080	8.45
	b_1	-0.355	0.0025		
	b_2	0.0802	0.0069		
	b_3	-0.149	0.0288		
8 HTG3Y=b_0+b_1*BADEC+b_2*(th96*BADEC)-b_3*($th96^2$*BADEC)	b_0	32.17	0.0001	0.3325	7.76
	b_1	-0.729	0.0001		
	b_2	-0.00275	0.0006		
	b_3	-0.0000025	0.0033		
9 HTG3Y=b_0+b_1*BADEC+b_2*(DBH96*BADEC)-b_3*$DBH96^2$	b_0	31.95	0.0001	0.3311	7.94
	b_1	-0.570	0.0001		
	b_2	0.1767	0.0012		
	b_3	-0.01368	0.0006		

10 HTG3Y=b_0+b_1*BADEC+b_2*(bhage*BADEC)-b_3*bhage96^2	b_0	31.88	0.0001	0.2121	8.43
	b_1	-0.7866	0.0006		
	b_2	0.0821	0.0066		
	b_3	-0.0023	0.0130		
11 HTG3Y=b_0+b_1*ln(CI1)	b_0	39.53	0.0001	0.1241	8.99
	b_1	-3.04	0.0205		
12 hti3y=b_0+ b_1*(CSA96*ln(ci2))+ b_2*CSA96^2	b_0	20.80	0.0001	0.2388	8.29
	b_1	1.49	0.0005		
	b_2	-0.801	0.0025		
13 hti3y=b_0+ b_1*(cvol96*ln(ci2))+ b_2*cvol96^2	b_0	23.12	0.0001	0.1473	8.77
	b_1	0.667	0.0043		
	b_2	-0.172	0.0134		
14 hti3y=b_0+ b_1*(th96*ln(ci2))+ b_2*th96^2	b_0	15.98	0.0001	0.2310	8.33
	b_1	0.0106	0.0008		
	b_2	-0.000028	0.0158		
15 hti3y=b_0+ b_1*(DBH96*ln(ci2))+ b_2*(DBH96^2*ln(ci2))	b_0	15.17	0.0001	0.2997	7.95
	b_1	1.22	0.0001		
	b_2	-0.0888	0.0005		
16 hti3y=b_0+ b_1*(bhage*ln(ci2))+ b_2*(bhage^2*ln(ci2))	b_0	11.46	0.0541	0.1052	8.98
	b_1	0.476	0.0149		
	b_2	-0.0134	0.0283		

Appendix F
Predicting basal area increment with competition and initial tree size

Equation	Para	Para. Est.	Para. P-value	R^2_a	RMSE
1 $\ln(BA3Y)=b_0+b_1*DIFN+b_2\ln(CSA96)$	b_0	-0.606	0.0360	0.6430	0.704
	b_1	2.02	0.0470		
	b_2	0.522	0.0001		
2 $\ln(BA3Y)=b_0+b_1*DIFN+b_2\ln(cvol96)$	b_0	-0.428	0.1131	0.6827	0.663
	b_1	2.10	0.0296		
	b_2	0.342	0.0001		
3 $\ln(BA3Y)=b_0+b_1*th96+b_2*(DIFN*th96)-b_3*(th96^2*DIFN)$	b_0	-2.68	0.0001	0.7667	0.569
	b_1	0.00629	0.0001		
	b_2	0.0195	0.0001		
	b_3	0.00003272	0.0001		
4 $\ln(BA3Y)=b_0+b_1*DBH96+b_2*DIFN-b_3*(DBH96^2*DIFN)$	b_0	-2.51	0.0001	0.7901	0.540
	b_1	0.494	0.0001		
	b_2	2.58	0.0050		
	b_3	-0.066	0.0002		
5 $\ln(BA3Y)=b_0+b_1*bhage+b_2*DIFN+b_3*(bhage*DIFN)+b_4*bhage^2+b_5*bhage^2*DIFN$	b_0	-5.78	0.0003	0.3890	0.921
	b_1	0.821	0.0007		
	b_2	12.76	0.0247		
	b_3	-2.17	0.0233		
	B4	-0.0244	0.0014		
	B_5	0.0734	0.0242		
6 $\ln(BA3Y)=b_0+b_1*\ln(CSA96)+b_2*\ln(BADEC)$	b_0	1.21	0.0391	0.6524	0.6943
	b_1	0.525	0.0001		
	b_2	-0.420	0.0254		
7 $\ln(BA3Y)=b_0+b_1\ln(cvol96)+b_2*BADEC$	b_0	0.550	0.0216	0.6804	0.666
	b_1	-0.0176	0.0346		
	b_2	0.340	0.0001		
8 $\ln(BA3Y)=b_0+b_1*BADEC+b_2*(th96*BADEC)-b_3*(th96^2*BADEC)$	b_0	-2.32	<0.0001	0.7076	0.6368
	b_1	0.0088	<0.0001		
	b_2	-0.0394	0.4564		
	b_3	-00000536	0.0008		
9 $\ln(BA3Y)=b_0+b_1*\ln(DBH96)+b_2*\ln(BADEC)$	b_0	-7.50	0.0001	0.7229	0.573
	b_1	1.48	0.0001		
	b_2	-0.321	0.0369		
10 $\ln(BA3Y)=b_0+b_1*BADEC+b_2*bhage-b_3*bhage96^2$	b_0	-2.61	0.0003	0.3462	0.952
	b_1	-0.0129	0.2682		
	b_2	0.356	0.0004		
	b_3	-0.00933	0.0038		

19 $\ln(BA3Y)=b_0+b_1*\ln(CI2)$	b_0	-1.02	0.0001	0.7220	0.628
	b_1	3.64	0.0001		
20 $\ln(BA3Y)=b_0+ b_1*\ln(ci2)+ b_2*CSA96$	b_0	0.310	0.0707	0.5070	0.827
	b_1	-0.275	0.0982		
	b_2	0.373	0.0001		
21 $\ln(BA3Y)=b_0+ b_1*\ln(ci2)+ b_2*cvol96^2+b_3*\ln(ci2)*cvol96$	B_0	5.98	0.4285	0.5504	0.790
	b_1	-0.332	0.0335		
	b_2	-0.099	0.0022		
	B_3	0.106	0.0001		
22 $\ln(BA3Y)=b_0+ b_1*th96+b_2*\ln(ci2)*th96\ b_3*\ln(ci2)*th96^2$	b_0	-2.72	0.0001	0.7136	0.6303
	b_1	0.007	0.0005		
	b_2	0.00097	0.0119		
	B_3	-0.00000189	0.0004		
23 $\ln(BA3Y)=b_0+ b_1*(DBH96*\ln(ci2))+ b_2*DBH96+b_3*DBH96^2+\ln(ci2)*DBH96^2$	b_0	-3.82	0.0001	0.8809	0.406
	b_1	0.289	0.0136		
	B_2	0.849	0.0001		
	B_3	-0.0249	0.0068		
	B_4	-0.00529	0.0322		
24 $\ln(BA3Y)=b_0+ b_1*\ln(ci2)+ b_2*bhage+bhage^2$	b_0	-1.66	0.2532	0.3411	0.956
	B_1	-0.208	0.3357		
	B_2	0.323	0.0025		
	B_3	-0.0087	0.0086		

Appendix G
Predicting height growth with initial tree size, competition and site quality

Equation	Para.	Para. Est.	Para. p-value	r^2_a	RMSE
1 hti3y=b_0+b_1*CSA96+b_2*(ATSI*DIFN)+b_3*(CSA96^2*DIFN)	b_0	8.57	0.0036	0.5170	6.60
	b_1	5.18	0.0001		
	b_2	2.56	0.0001		
	b_3	-2.57	0.0002		
2 hti3y=b_0+b_1*cvol96+b_2*(ATSI*DIFN)+b_3*(cvol96^2*DIFN)	b_0	12.04	0.0001	0.3958	7.38
	b_1	2.61	0.0032		
	b_2	2.20	0.0001		
	b_3	-0.754	0.0092		
3 hti3y=b_0+b_1*th96+b_2*(ATSI*DIFN)+b_3*(th96^2*ATSI)	b_0	5.78	0.1153	0.4478	7.06
	b_1	0.0516	0.0012		
	b_2	2.02	0.0001		
	b_3	-0.000002	0.0072		
4 hti3y=b_0+b_1*DBH96+b_2*(ATSI*DIFN)+b_3*(DBH96^2*DIFN)	b_0	7.86	0.0218	0.4751	7.14
	b_1	2.45	0.0008		
	b_2	2.45	0.0001		
	b_3	-0.589	0.0044		
5 hti3y=b_0+b_1*(bhage*ATSI)+b_2*(ATSI*DIFN)+b_3*(bhage^2*ATSI)	b_0	8.08	0.0570	0.3877	7.71
	b_1	1.65	0.0019		
	b_2	0.07	0.0251		
	b_3	-0.002	0.0452		
6 hti3y=b_0+b_1*BADEC+b_2*(CSA96*BADEC)+b_3*(CSA96^2*BADEC)	b_0	31.45	0.0001	0.2844	8.03
	b_1	-0.405	0.0005		
	b_2	0.214	0.0017		
	b_3	-0.0245	0.0103		
7 hti3y=b_0+b_1*BADEC+b_2*(cvol96*BADEC)+b_3*(cvol96^2*BADEC)	b_0	31.85	0.0001	0.2554	8.50
	b_1	-0.328	0.0044		
	b_2	0.0815	0.0099		
	b_3	-0.00453	0.0381		
8 hti3y=b_0+b_1*(BADEC*ATSI)+b_2*(th96*ATSI)+b_3*(th96^2*ATSI)	b_0	19.99	0.0001	0.3479	7.67
	b_1	-0.123	0.0109		
	b_2	0.00324	0.0001		
	b_3	-0.00000279	0.0006		
9 hti3y=b_0+b_1*BADEC+b_2*(DBH96*ATSI)+b_3*(bDBH96^2*ATSI)	b_0	22.57	0.0001	0.3607	7.59
	b_1	-0.212	0.0263		
	b_2	0.221	0.0001		
	b_3	-0.0167	0.0006		

10 $hti3y=b_0+b_1*(BADEC*ATSI)+b_2*(bhage*ATSI)+b_3*(bhage^2*ATSI)$	b_0	16.19	0.0007	0.2557	8.19
	b_1	-0.0115	0.0259		
	b_2	0.119	0.0006		
	b_3	-0.00352	0.0018		
	b_1	0.771	0.0254		
	b_2	-0.00386	0.0822		

Equation	Para.	Para. Est.	Para. p-value	r^2_a	RMSE
11 $hti3y=b_0+ b_1*ATSI+ b_2*\ln(CI1))$	b_0	26.99	0.0024	0.1635	8.68
	b_1	0.619	0.0530		
	b_2	-3.04	0.0169		
12 $hti3y=b_0+ b_1*(CSA96*\ln(ci2))+ b_2*CSA96^2$	b_0	20.80	0.0001	0.2388	8.29
	b_1	1.49	0.0005		
	b_2	-0.801	0.0025		
13 $hti3y=b_0+ b_1*(cvol96*\ln(ci2))+ b_2*cvol96^2$	b_0	23.12	0.0001	0.1473	8.77
	b_1	0.667	0.0043		
	b_2	-0.172	0.0134		
14 $hti3y=b_0+ b_1*(th96*\ln(ci2))+ b_2*th96^2$	b_0	15.98	0.0001	0.2310	8.33
	b_1	0.0106	0.0008		
	b_2	-0.000028	0.0158		
15 $hti3y=b_0+ b_1*(DBH96*\ln(ci2))+ b_2*(DBH96^2*\ln(ci2))$	b_0	15.17	0.0001	0.2997	7.95
	b_1	1.22	0.0001		
	b_2	-0.0888	0.0005		
16 $hti3y=b_0+ b_1*ATSI+ b_2*\ln(ci2) +b_3*bhage\ b_4*(\ln(ci2)*ATSI)+ b_5*(bhage^2*ATSI)$	b_0	-143.97	0.0043	0.2748	8.09
	b_1	7.21	0.0035		
	b_2	24.75	0.0052		
	b_3	2.91	0.0005		
	b_4	-1.17	0.0110		
	b_5	-0.0042	0.0011		

Appendix H
Predicting Basal Area Increment with initial tree size, competition and site quality

Equation	Para.	Para. Est.	Para. p-value	r^2_a	RMSE
1 $ln(BA3Y)=b_0+b_1*CSA96+b_2*(ATSI*DIFN)+b_3*(CSA96^2*DIFN)$	b_0	-1.429	0.0001	0.6531	0.6936
	b_1	0.5219	0.0001		
	b_2	2.02	0.0005		
	b_3	-0.395	0.0001		
2 $ln(BA3Y)=b_0+b_1*cvol96+b_2*(ATSI*DIFN)+b_3*(cvol96^2*DIFN)$	b_0	-1.704	0.0001	0.5893	0.7547
	b_1	0.538	0.0001		
	b_2	0.1268	0.0093		
	b_3	-0.115	0.0002		
3 $ln(BA3Y)=b_0+b_1*th96+b_2*(DIFN*th96)+b_3*(th96^2*DIFN)$	b_0	-2.68	0.0001	0.7667	0.5687
	b_1	0.00629	0.0001		
	b_2	0.0195	0.0001		
	b_3	0.00003272	0.0001		
4 $ln(BA3Y)=b_0+b_1*DBH96+b_2*(ATSI*DIFN)+b_3*(DBH96^2*DIFN)+b_4*(DBH96^2*ATSI)$	b_0	-2.72	0.0001	0.8831	0.4027
	b_1	0.714	0.0001		
	b_2	0.105	0.0003		
	b_3	-0.00136	0.0001		
	b_4	-0.039	0.0020		
5 $ln(BA3Y)=b_0+b_1*bhage+b_2*(ATSI*DIFN)+b_3*(bhage^2*DIFN)+ b_4*bhage^2+ b_5*(bhage^2*DIFN)$	b_0	-4.09	0.0001	0.4264	0.8919
	b_1	0.567	0.0001		
	b_2	0.280	0.0067		
	b_3	-1.056	0.0216		
	b_4	-0.0169	0.0005		
	b_5	0.03909	0.0377		
6 $ln(BA3Y)=b_0+b_1*ATSI+b_2*BADEC+b_3*CSA96 +b_4*(BADEC*ATSI) +b_5*(ATSI*CSA96)+b_6*CSA96^2+ b_7*(CSA96^2*ATSI)$	b_0	-6.39	0.0001	0.7822	0.5496
	b_1	0.269	0.0001		
	b_2	0.160	0.0001		
	b_3	3.38	0.0015		
	b_4	-0.00905	0.0001		
	b_5	-0.115	0.0226		
	b_6	-0.676	0.0016		
	b_7	0.0288	0.0052		

7 $\ln(BA3Y)=b_0+b_1*ATSI+b_2*BADEC+b_3*cvol96^2+b_4*(BADEC*ATSI)+b_5*cvol96^2$	b_0	-4.859	0.0001	0.6773	0.6690
	b_1	0.210	0.0005		
	b_2	0.141	0.0018		
	b_3	0.566	0.0001		
	b_4	-0.00811	0.0005		
	b_5	-0.0243	0.0001		
8 $\ln(BA3Y)=b_0+b_1*ATSI+b_2*BADEC+b_3*th96+b_4*(BADEC*ATSI)-b_5*th96^2$	b_0	-4.797	0.0001	0.7869	0.5437
	b_1	0.135	0.0039		
	b_2	0.096	0.0067		
	b_3	0.00959	0.0001		
	b_4	-0.00565	0.0018		
	b_5	-0.0000057	0.0001		
9 $\ln(BA3Y)=b_0+b_1*ATSI+b_2*BADEC+b_3*DBH96+b_4*(BADEC*ATSI)-b_5*DBH96^2$	b_0	-4.35	0.0001	0.9023	0.3681
	b_1	0.118	0.0004		
	b_2	0.071	0.0035		
	b_3	0.699	0.0001		
	b_4	-0.00400	0.0012		
	b_5	-0.0355	0.0001		
10 $\ln(BA3Y)=b_0+b_1*BADEC+b_2*(BADEC*ATSI)+b_3*(bhage^2*ATSI)-b_4*bhage^2*ATSI)$	b_0	-2.94	0.0001	0.4526	0.8679
	b_1	0.720	0.0219		
	b_2	-0.0045	0.0047		
	b_3	0.206	0.0001		
	b_4	-0.000531	0.0002		
11 $\ln(BA3Y)= b_0+b_1*ATSI+ b_2*\ln(CI1))$	b_0	2.74	0.0001	0.7358	0.605
	b_1	0.0444	0.0470		
	b_2	-0.910	0.0001		
22 $Ln(BA3Y)=b_0+b_1*\ln(ci2)+b_2*CSA96+b_3*ATSI+b_4 CSA96^2+b_5*(\ln(ci2)*CSA96^2)+b_6*(\ln(ci2)*ATSI)+b_7*(CSA96*ATSI)+b_8*(CSA96^2*ATSI)$	b_0	-18.87	0.0001	0.7872	0.5433
	B_1	2.93	0.0001		
	B_2	4.24	0.0002		
	B_3	1.03	0.0001		
	B_4	-0.76	0.0025		
	B_5	0.048	0.0441		
	B_6	-0.177	0.0001		
	B_7	-0.172	0.0014		
	B_8	0.024	0.0198		

13 Ln(BA3Y)=b_0+b_1*ln(ci2)+b_2*ATSI+b_3*(ln(ci2)*cvol96)+b_4 *(ln(ci2)*CSA96^2)+b_5*(ln(ci2)*ATSI)+b_6*(cvol96*ATSI)	b_0	-15.77	0.0002	0.6838	0.662
	B_1	2.66	0.0008		
	B_2	0.970	0.0001		
	B_3	0.243	0.0001		
	B_4	-0.0033	0.0114		
	B_5	-0.180	0.0002		
	B_6	-0.0346	0.0025		
14 Ln(BA3Y)=b_0+b_1*ln(ci2)+b_2*th96+b_3*ATSI+b_4 *(ln(ci2)*th96)+b_5*(ln(ci2)*th96^2)+b_6*ln(ci2)*ATSI+b_7(th96*ATSI)	b_0	-16.50	0.0001	0.7878	0.5424
	B_1	2.30	0.0006		
	B_2	0.011	0.0125		
	B_3	0.974	0.0002		
	B_4	0.0016	0.0016		
	B_5	-0.000001	0.0137		
	B_6	-0.149	0.0002		
	B_7	-0.00049	0.0043		
15 Ln(BA3Y)=b_0+b_1*ln(ci2)+b_2*DBH96+b_3*ATSI+b_4 *(ln(ci2)*DBH96)+b_5*(ln(ci2)*DBH96^2)+b_6*ln(ci2)*ATSI+b_7(DBH96*ATSI)	b_0	-11.30	0.0001	0.9100	0.3532
	B_1	1.44	0.0021		
	B_2	0.866	0.0001		
	B_3	0.486	0.0021		
	B_4	0.0829	0.0006		
	B_5	-0.0099	0.0001		
	B_6	-0.790	0.0046		
	B_7	-0.0235	0.0032		
16 Ln(BA3Y)=b_0+b_1*ln(ci2)+b_2*bhage+b_3*ATSI+b_4 *(ln(ci2)*ATSI)+b_5*(bhage^2*ATSI)	b_0	-26.67	0.0001	0.6518	0.483
	B_1	4.08	0.0001		
	B_2	0.41	0.0001		
	B_3	1.29	0.0001		
	B_4	-0.230	0.0001		
	B_5	-0.000579	0.0001		

Appendix I: Predicting height growth with DIFN and an initial tree size variable

Descriptive statistics for trees with measurements taken at 130 cm above ground level

	Units	N	Mean	SD	Min.	Max.
Cvol96	m^2	87	3.49	8.96	0.0007	67.75
CSA96	m^3	87	2.19	3.43	0.0140	24.32
DBH96	cm	87	4.54	3.70	0.2712	23.21
Th96	cm	87	333	220	62.2	1143
Bhage	y	87	15.07	9.76	5.00	48.00
DIFN	-	87	0.29	0.16	0.089	0.90

Height Growth Models for trees with measurements taken at 130 cm above ground level

Model	Para.	Para. Est.	Para. P-value	R^2_a	MSE
$HTG3Y=a*CSA96^{b1}*DIFN^{b2}$	a	45.12	0.0001	0.1962	110.6
	b1	0.0493	0.0445		
	b2	0.3910	0.0001		
$HTG3Y=a*cvol96^{b1}*DIFN^{b2}$	a	45.79	0.0001	0.2057	109.3
	b1	0.0365	0.0266		
	b2	0.3892	0.0001		
$HTG3Y=a*th96^{b1}*DIFN^{b2}$	a	24.08	0.0040	0.1969	110.5
	b1	0.1133	0.0410		
	b2	0.4005	0.0001		
$HTG3Y=a*DBH96^{b1}*DIFN^{b2}$	a	36.92	0.0001	0.2297	106.0
	b1	0.1346	0.0074		
	b2	0.3706	0.0001		
$HTG3Y=a*bhage^{b1}*DIFN^{b2}$	a	41.32	0.0001	0.1657	114.8
	b1	0.0361	0.3081		
	b2	0.3962	0.0001		
$HTG3Y=a*CSA96^{b1}$	a	27.06	0.0001	0.0218	134.6
	b1	0.0499	0.0600		
$HTG3Y=a*cvol96^{b1}$	a	27.53	0.0001	0.334	133.0
	b1	0.0378	0.03536		
$HTG3Y=a*th96^{b1}$	a	14.944	0.00976	0.0145	135.6
	b1	0.105	0.07817		
$HTG3Y=a*DBH96^{b1}$	a	22.40	0.0001	0.0625	129.0
	b1	0.1455	0.00652		
$HTG3Y=a*bhage^{b1}$	a	27.59	0.0001	0.0116	139.2
	b1	-0.0090	0.4561		
$HTG3Y=a*DIFN^{b1}$	a	44.72	0.0001	0.1788	113.8
	b1	0.3872	0.0001		

Descriptive statistics for trees with measurements taken at ground and 30 cm above ground level

	Units	N	mean	SD	Min.	Max.
Cvol96	m^2	110	0.873	1.78	0.00004	13.89
CSA96	m^3	110	0.902	1.21	0.0022	7.067
Gld96	cm	110	4.39	2.30	1.23	12.21
Th96	cm	110	220	141	53.2	744
Shage	y	110	17.86	8.60	5.00	44.0
DIFN	-	110	0.272	0.142	0.0892	0.900

Height Growth Models for trees with measurements taken at ground and 30 cm above ground level

Model	Para.	Para. Est.	Para. P-value	R^2_a	MSE
$HTG3Y=a*CSA96^{b1}*DIFN^{b2}$	a	46.59	<0.0001	0.3076	100.6
	b1	1.252	<0.0001		
	b2	0.385	<0.0001		
$HTG3Y=a*cvol96^{b1}*DIFN^{b2}$	a	48.1065	<0.0001	0.3428	95.50
	b1	0.0890	<0.0001		
	b2	0.3683	<0.0007		
$HTG3Y=a*th96^{b1}*DIFN^{b2}$	a	6.1293	0.0039	0.3900	88.65
	b1	0.3644	<0.0001		
	b2	0.3877	0.2768		
$HTG3Y=a*gld96^{b1}*DIFN^{b2}$	a	17.26	<0.0001	0.4329	82.40
	b1	0.5060	<0.0001		
	b2	0.2694	0.0005		
$HTG3Y=a*shage^{b1}*DIFN^{b2}$	a	29.7445	0.0018	0.1748	119.9
	b1	0.1534	0.06083		
	b2	0.4554	<0.0001		
$HTG3Y=a*CSA96^{b1}$	a	27.5899	<0.0001	0.1631	121.6
	b1	0.1297	0.0001		
$HTG3Y=a*cvol96^{b1}$	a	29.1956	<0.0001	0.2065	115.2
	b1	0.0938	<0.0001		
$HTG3Y=a*th96^{b1}$	a	3.2341	0.00369	0.2368	110.9
	b1	0.3833	<0.0001		
$HTG3Y=a*gld96^{b1}$	a	10.89	<0.0001	0.3593	93.10
	b1	0.5674	<0.0001		
$HTG3Y=a*shage^{b1}$	a	20.6050	0.0047	0.0060	146.2
	b1	0.0610	0.27921		
$HTG3Y=a*DIFN^{b1}$	a	43.759	<0.0001	0.1624	121.7
	b1	0.4263	<0.0001		

Appendix J: Predicting Basal Area Increment with DIFN and an initial tree size variable

Basal area increment models for trees with measurements taken at 130 cm above ground level

Model	Para.	Para. Est.	Para. P-value	R^2_a	MSE
$BA3Y=a*CSA96^{b1}*DIFN^{b2}$	a	2.33	0.0001	0.6013	1.1152
	b1	0.536	0.0001		
	b2	0.448	0.0003		
$BA3Y=a*cvol96^{b1}*DIFN^{b2}$	a	2.488	0.0001	0.6629	0.9430
	b1	0.377	0.0001		
	b2	0.397	0.0005		
$BA3Y=a*th96^{b1}*DIFN^{b2}$	a	0.003	0.0566	0.6737	0.9126
	b1	1.181	0.0001		
	b2	0.479	0.0001		
$BA3Y=a*DBH96^{b1}*DIFN^{b2}$	a	0.588	0.0001	0.8027	0.5518
	b1	0.998	0.0001		
	b2	0.359	0.0001		
$BA3Y=a*bhage^{b1}*DIFN^{b2}$	a	0.362	0.0088	0.4036	1.6680
	b1	0.949	0.0001		
	b2	0.824	0.0001		
$BA3Y=a*CSA96^{b1}$	a	1.22	0.0001	0.5620	1.2252
	b1	0.577	0.0001		
$BA3Y=a*cvol96^{b1}$	a	1.400	0.0001	0.6331	1.0262
	b1	0.406	0.0001		
$BA3Y=a*th96^{b1}$	a	0.001	0.0811	0.6350	1.0209
	b1	1.296	0.0001		
$BA3Y=a*DBH96^{b1}$	a	0.340	0.0001	0.7673	0.6510
	b1	1.040	0.0001		
$BA3Y=a*bhage^{b1}$	a	0.169	0.0227	0.2678	2.0481
	b1	0.842	0.0001		
$BA3Y=a*DIFN^{b1}$	a	2.964	0.0001	0.0324	2.7064
	b1	0.473	0.0142		

Basal area increment models for trees with measurements taken at ground and 30 cm above ground level

Model	Para.	Para. Est.	Para. P-value	R^2_a	MSE
$BA3Y=a*CSA96^{b1}*DIFN^{b2}$	a	3.756	<0.0001	0.5242	0.7799
	b1	0.4076	<0.0001		
	b2	0.5936	<0.0001		
$BA3Y=a*cvol96^{b1}*DIFN^{b2}$	a	4.03	<0.0001	0.5590	0.7228
	b1	0.2718	<0.0001		
	b2	0.5465	<0.0001		
$BA3Y=a*th96^{b1}*DIFN^{b2}$	a	0.0324	0.04061	0.5328	0.7657
	b1	0.8529	<0.0001		
	b2	0.6345	<0.0001		
$BA3Y=a*DBH96^{b1}*DIFN^{b2}$	a	0.2650	0.0008	0.6774	0.5287
	b1	1.3306	<0.0001		
	b2	0.3133	0.0009		
$BA3Y=a*bhage^{b1}*DIFN^{b2}$	a	0.8029	0.02938	0.2201	1.2783
	b1	0.6319	0.0059		
	b2	1.0053	<0.0001		
$BA3Y=a*CSA96^{b1}$	a	1.660	<0.0001	0.4071	0.9717
	b1	0.4409	<0.0001		
$BA3Y=a*cvol96^{b1}$	a	1.9206	<0.0001	0.4597	0.8856
	b1	0.3041	<0.0001		

BA3Y=a*th96^{b1}	a	0.0073	0.08069	0.4161	0.9570
	b1	0.9630	<0.0001		
BA3Y=a*DBH96^{b1}	a	0.1428	0.0003	0.6413	0.5879
	b1	1.4454	<0.0001		
BA3Y=a*bhage^{b1}	a	0.4309	0.04694	0.0296	1.5905
	b1	0.3898	0.02627		
BA3Y=a*DIFN^{b1}	a	3.9553	<0.0001	0.1381	1.4127
	b1	0.8685	<0.0001		

Appendix K: Predicting stem volume increment with DIFN and an initial tree size variable

Stem volume increment models for trees with measurements taken at 130 cm

Model	Para.	Para. Est.	Para. P-value	R^2_a	MSE
$Svg3y=a*CSA96^{b1}*DIFN^{b2}$	a	1381.5	0.0001	0.7947	1399987
	b1	10.8531	0.0001		
	b2	0.2575	0.01524		
$Svg3y=a*cvol96^{b1}*DIFN^{b2}$	a	1420.8	0.0001	0.8604	951540
	b1	0.6135	0.0001		
	b2	0.1689	0.04245		
$Svg3y=a*th96^{b1}*DIFN^{b2}$	a	0.00999	0.9854	0.8612	946522
	b1	2.0388	0.0001		
	b2	0.1570	0.06484		
$Svg3y=a*DBH96^{b1}*DIFN^{b2}$	a	222.2	0.0001	0.9304	474397
	b1	1.4272	0.0001		
	b2	0.1563	0.00661		
$Svg3y=a*bhage^{b1}*DIFN^{b2}$	a	68.1684	0.07788	0.4764	3570124
	b1	1.5468	0.0001		
	b2	0.8496	0.0001		
$Svg3y=a*CSA96^{b1}$	a	917.1	0.0001	0.7869	1452978
	b1	0.8890	0.0001		
$Svg3y=a*cvol96^{b1}$	a	1084.7	0.1541	0.8579	968818
	b1	0.6322	0.0001		
$Svg3y=a*th96^{b1}$	a	0.00473	0.0857	0.8599	954981
	b1	2.1204	0.0001		
$Svg3y=a*DBH96^{b1}$	a	169.1	0.0001	0.9268	499077
	b1	1.4577	0.0001		
$Svg3y=a*bhage^{b1}$	a	37.6678	0.0982	0.3635	4340100
	b1	1.3745	0.0001		
$Svg3y=a*DIFN^{b1}$	a	2723.8	0.0087	0.0020	6804514
	b1	0.3629	0.1317		

Stem volume increment models for trees with measurements taken at ground and 30 cm above ground level

Model	Para.	Para. Est.	Para. P-value	R^2_a	MSE
$Svg3y=a*CSA96^{b1}*DIFN^{b2}$	a	3412.2	<0.0001	0.6395	934279
	b1	0.6666	<0.0001		
	b2	0.5801	<0.0001		
$Svg3y=a*cvol96^{b1}*DIFN^{b2}$	a	3797.6	<0.0001	0.6819	824383
	b1	0.4424	<0.0001		
	b2	0.5047	<0.0001		
$Svg3y=a*th96^{b1}*DIFN^{b2}$	a	2.7585	0.07779	0.6361	943157
	b1	1.2754	<0.0001		
	b2	0.5942	<0.0001		
$Svg3y=a*DBH96^{b1}*DIFN^{b2}$	a	54.5755	0.00012	0.8324	434278
	b1	2.0685	<0.0001		
	b2	0.1484	0.01082		
$Svg3y=a*bhage^{b1}*DIFN^{b2}$	a	218.5	0.08218	0.2276	2001671
	b1	1.1368	0.0001		
	b2	1.21184	<0.0001		
$Svg3y=a*CSA96^{b1}$	a	1475.3	<0.0001	0.5474	1173038
	b1	0.7277	<0.0001		
$Svg3y=a*cvol96^{b1}$	a	1838.0	<0.0001	0.6159	995470
	b1	0.5019	<0.0001		
$Svg3y=a*th96^{b1}$	a	0.4854	0.12470	0.5639	1130102
	b1	1/4330	<0.0001		
$Svg3y=a*DBH96^{b1}$	a	38.9172	0.0002	0.8264	449921

	b1	2.1422	<0.0001		
$Svg3y=a*bhage^{b1}$	a	131.1	0.11255	0.0795	2385610
	b1	0.7709	0.00200		
$Svg3y=a*DIFN^{b1}$	a	3551.8	0.00025	0.0680	2415353
	b1	0.8571	0.00040		

Appendix L: Predicting height to diameter ratio with DIFN and an initial tree size

Height to diameter ratio models for trees with measurements taken at 130 cm

Model	Para.	Para. Est.	Para. P-value	R^2_a	MSE
Hdr=a*CSA96^b1^*DIFN^b2^	a	96.64	<0.0001	0.1543	817.5
	b1	-0.079	<0.0001		
	b2	-0.00581	0.9240		
Hdr=a*cvol96^b1^*DIFN^b2^	a	94.35	<0.0001	0.1641	808.0
	b1	-0.0534	<0.0001		
	b2	-0.00467	0.9386		
Hdr=a*th96^b1^*DIFN^b2^	a	291.1	0.0005	0.1511	820.6
	b1	-0.2014	<0.0001		
	b2	-0.0320	0.6414		
Hdr=a*DBH96^b1^*DIFN^b2^	a	140.7	<0.0001	0.6612	372.5
	b1	-0.3305	<0.0001		
	b2	-0.0161	0.6892		
Hdr=a*bhage^b1^*DIFN^b2^	a	152.81	<0.0001	0.1242	846.6
	b1	-0.20846	0.0003		
	b2	-0.062	0.3349		
Hdr=a*CSA96^b1^	a	97.3955	<0.0001	0.1638	808.0
	b1	-0.0793	<0.0001		
Hdr=a*cvol96^b1^	a	94.9461	<0.0001	0.1739	798.6
	b1	-0.0535	<0.0001		
Hdr=a*th96^b1^	a	300.91	0.0003	0.1579	814.0
	b1	-0.19959	<0.0001		
Hdr=a*DBH96^b1^	a	143.804	<0.0001	0.6645	324.3
	b1	-0.33066	<0.0001		
Hdr=a*bhage^b1^	a	161.3	<0.0001	0.1237	847.1
	b1	-0.1964	0.0005		
Hdr=a*DIFN^b1^	a	96.965	<0.0001	-0.0112	977.4
	b1	-0.01456	0.8313		

Table 12: Height to diameter ratio models for trees with measurements taken at ground and 30 cm above ground level

Model	Para.	Para. Est.	Para. P-value	R^2_a	MSE
HDR=a*CSA96^b1^*DIFN^b2^	a	57.6278	0.0001	0.0444	266.5
	b1	-0.00032	0.9801		
	b2	-0.1252	0.0091		
HDR=a*cvol96^b1^*DIFN^b2^	a	58.1578	0.0001	0.0470	265.8
	b1	0.00461	0.5933		
	b2	-0.1261	0.0084		
HDR=a*th96^b1^*DIFN^b2^	a	39.8644	0.0001	0.0800	256.6
	b1	0.0724	0.0442		
	b2	-0.1191	0.0111		
HDR=a*gld96^b1^*DIFN^b2^	a	70.8291	0.0001	0.1230	244.6
	b1	-0.1280	0.0018		
	b2	-0.0993	0.0340		
HDR=a*bhage^b1^*DIFN^b2^	a	70.8291	0.0001	0.1230	244.6
	b1	-0.1280	0.1293		
	b2	-0.0993	0.0034		
HDR=a*CSA96^b1^	a	68.8894	0.0001	-0.0009	281.4
	b1	-0.00176	0.8989		
HDR=a*cvol96^b1^	a	69.5627	0.0001	0.0080	281.1
	b1	0.00353	0.6953		
HDR=a*th96^b1^	a	46.0201	0.0001	0.0308	270.3
	b1	0.0777	0.357		
HDR=a*gld96^b1^	a	83.7199	0.0001	0.0943	252.6
	B1	-0.1465	0.0004		
HDR=a*bhage^b1^	a	77.2715	0.0001	0.00326	279.8
	b1	-0.0407	0.4273		
HDR=a*DIFN^b1^	a	57.6456	0.0001	0.0618	264.0
	b1	-0.1252	0.0085		