Modelling Jack Pine (*Pinus banksiana* Lamb) and Black Spruce [*Picea mariana* (Mill.) BSP] growth and yield in Manitoba

by

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ABSTRACT

This study develops forestry growth and yield models for two economically important tree species in Manitoba, black spruce [*Picea mariana* (Mill.) BSP] and jack pine [*Pinus banksiana* Lamb]. The growth and yield models developed include regression-based individual tree height growth and site index, tree diameter (basal area) growth, tree bole taper, and individual tree mortality models. These regression-based models were developed empirically, using stem analysis, growth and mortality data from 80 permanent sample plots located within the commercially important boreal forests of Manitoba. Model development involved the exploration, comparison and testing of numerous potential regression models and predictor variables. Statistical issues commonly encountered in forest growth and yield modeling, particularly data autocorrelation and variable multicollinearity, were addressed using nonlinear least squares (NLS), generalized nonlinear least squares (GNLS), and nonlinear mixed-effects model regression (NLMM) approaches.

Height growth and site index of black spruce and jack pine was modelled using a three-parameter generalized logistic function. NLMM regression was used since the data were spatially autocorrelated. The inclusion of prior measures from individual trees produced more accurate predictions. In the tree diameter (basal area) growth models, tree size variables were significant predictors for black spruce and managed jack pine stands. Site index (a measure of site productivity) was positively correlated, and basal area of trees larger than the target tree (a relative measure of competition) negatively correlated, with diameter increment. Thiessen polygon area, a spatial measure of competition, was a significant predictor for natural jack pine and upland black spruce stands. Tree bole taper was modeled by NLMM approach using a five-parameter equation based on dimensional analysis, with breast height diameter, total height and relative height as predictor variables. The inclusion of a single prior measure from each tree improved model prediction. Black spruce and jack pine mortality was modeled using logistic regression. The black spruce models predicted high survivorship for larger, fast-growing trees in less crowded stands. In the jack pine model, highest survivorship was predicted for larger, less locally crowded trees.

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CHAPTER 1 GENERAL INTRODUCTION AND LITERATURE REVIEW

1.1 BOREAL FOREST BIOME

The boreal forest biome occurs across the northern regions of the North American and Eurasian continents. In North America, the boreal forest forms a continuous band of vegetation extending from the Atlantic coast of Newfoundland to west-central Alaska. Over 80% of the total forested land in Canada lies within the boreal forest (Larsen 1980).

A continental climate is characteristic of the boreal forest biome. The summer growing season is short and cool, and winters are long and cold. Annual precipitation declines from east to west, ranging from 90-100 cm in the Atlantic region to 50-60 cm in western Canada. Over half of the annual precipitation occurs as rain during the summer months (Bryson 1966).

The eastern and north-central boreal forests of North America occur on shallow to deep glacial clays, silts and sands overlying Precambrian granite bedrock (the “Canadian Shield”). The granite parent material of the Canadian Shield produces soils that are somewhat to strongly acidic, and often nutrient-deficient. The Canadian Shield extends from Labrador and Quebec into central Ontario, east-central and northern Manitoba, northern Saskatchewan, Nunavut and the eastern portion of the Northwest Territories. By contrast, the northwest boreal forests (west-central Manitoba, central Saskatchewan, Alberta, northern British Columbia, western Northwest Territories, Yukon and Alaska) occur on shallow to very deep calcareous glacial tills derived from sedimentary and metamorphic rocks. These soils are basic to slightly acidic, and are moderately nutrient-deficient. Localized areas of lacustrine clay deposits, coarse glacial outwash, and alluvial sands also occur throughout the boreal forest biome (Larsen 1980).

In Manitoba’s boreal forests, the dominant tree species of nutrient-poor, well to excessively drained sandy soils and granite and limestone rock outcrops are jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*). Glacial tills and silt-clay mineral soils typically support more diverse mixed-wood stands. Species of well-drained mineral soils include trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), jack pine, paper birch (*Betula papyrifera*) and black spruce, whereas on moister sites white spruce, balsam poplar (*Populus balsamifera*), balsam fir (*Abies balsamea*) and paper birch are more likely to be encountered. Nutrient-poor, deep organic peaty substrates (e.g. oligotrophic bogs) are dominated by black spruce; on more mesotrophic organic substrates, tamarack may also occur. Rich alluvial soils often support stands of eastern white cedar (*Thuja occidentalis*), black ash (*Fraxinus nigra*) or balsam poplar (Zoladeski *et al*. 1998).

Wildfire is the predominant natural disturbance of the boreal forest, and plays a critical role in determining the composition, structure, dynamics and diversity of forest stands (Heinselman 1973). The fire cycle of upland boreal forest stands ranges from 40 – 100 years in the drier southwest (Alberta and Saskatchewan) and central (Manitoba, Ontario) regions, to up to 250 years in some of the mesic forests of eastern Canada (Payette 1992). The “pioneer” tree species, which endure or evade fire (e.g. jack pine, black spruce, trembling aspen), tend to dominate in areas with comparatively short fire cycles (< 100 years). Conversely, “seed-banking” fire-intolerant species (e.g. white spruce, balsam fir) are more frequently encountered in areas with somewhat longer fire cycles. Most boreal tree species have evolved adaptations to recurrent catastrophic forest fires (Bergeron 2000). Boreal pines (jack pine, lodgepole pine, and red pine) and black spruce produce fully or semi-serotinous cones that release their seed during a fire, thus re-establishing the species. Trembling aspen, paper birch, balsam poplar and many tall shrubs are capable of vegetative (clonal) growth from underground root or rhizome buds that normally survive stand-destroying fires. Even species less well adapted to fire, such as white spruce and balsam fir, produce prodigious amounts of seed that germinate and establish best on fire-exposed mineral substrates (Payette 1992). In most boreal forest stands, catastrophic fires are sufficiently recurrent that long-term succession processes are interrupted. In this way, diverse assemblages of both “pioneer” and “seed-banking” tree species are perpetuated on the landscape (Bergeron and Dubuc 1989; Zoladeski and Maycock 1990).

1.2 THE FOREST INDUSTRY IN MANITOBA

Jack pine (*Pinus banksiana* Lamb) and black spruce (*Picea mariana* (Mill.) BSP) are the most widespread and economically important tree species in Manitoba. The province of Manitoba contains an estimated 196 million cubic meters of merchantable volume of black spruce and 140.5 million cubic meters of jack pine. Together these two species represent about half (29% and 21% respectively) of the total merchantable volume (softwood and hardwood) in the province. Most of the jack pine and black spruce harvested in Manitoba is used by the pulp and paper industry. Other important timber species in Manitoba include trembling aspen and white spruce, which account for 30% and 7% of total merchantable volume respectively. Both trembling aspen and white spruce are used in the wood-fabricated materials and pulp-paper industries. The remaining merchantable volume in Manitoba includes balsam poplar (5%), and miscellaneous other hardwood and softwood species (5% and 3% respectively; Manitoba Conservation 2006).

Between 750,000 and 2,000,000 m^3 of timber volume is harvested annually in Manitoba (Manitoba Conservation 2006). The primary forest industries in the province are lumber, oriented strand board, and pulpwood-paper. Secondary industries include converted wood products (kitchen cabinets, windows and doors, millwork and so forth) and furniture. Manitoba forest product exports were valued at about $732 million in 2005, most of which is exported to the United States. The forest industry employed about 8,700 Manitobans in 2005, making it the fifth largest industry in the province (Manitoba Conservation 2006).

The modelling and prediction of forest growth and yield is essential to developing forest management plans, producing timber supply reviews and analyses, determining allowable annual cut (AAC), and developing strategies for sustainable forest management (Weiskittel *et al*. 2011). Growth and yield models are based on data from permanent sample plots (PSP). In these plots, repeated measurements of tree growth (height, bole diameter and/or total volume increments) are obtained from permanently marked trees in naturally regenerated stands. A large database of tree growth information has been compiled from PSP plots established in natural stands of jack pine and black spruce throughout southern and central Manitoba. However, reliable and accurate growth and yield models specific to Manitoba have not been developed for these two commercially important species. The modeling of growth and yield is mathematically challenging, and requires the development of systems of compatible, interdependent, and analytically related predictive equations (Clutter 1963; Borders and Bailey 1986; Huang and Titus 1999).

1.3 BIOLOGY AND ECOLOGY OF JACK PINE

Jack pine (*Pinus banksiana Lamb.*) is a coniferous species indigenous to the boreal forests of North America (Larsen 1980). It is the most widely distributed species of pine in Canada, ranging from Nova Scotia in the east to central Alberta in the west. In Alberta the distribution of jack pine overlaps with that of the closely related lodgepole pine (*P. contorta*), and the two may hybridize (Pollack and Dancik 1985). Jack pine occurs as far north as the tree line in the Northwest Territories, and as far south as the northern Great Lakes region of the United States. The species is particularly common in the drier continental boreal regions of the continent – Saskatchewan, Manitoba, and northwestern Ontario – where large forest fires are frequent and regular (Carleton and Maycock 1978). Jack pine occurs throughout much of Manitoba, although it is absent from the tundra regions along the Hudson Bay coast and from the grasslands in the southwest. The species is particularly common in the Boreal Plain and Boreal Shield forest ecozones of central Manitoba, which were historically subject to regular, frequent catastrophic fires (Zoladeski *et al*. 1998).

Jack pine often forms even-aged pure stands in Manitoba, particularly in areas prone to regular and repeated catastrophic fire. The species also occurs in mixed stands, usually in association with black spruce, trembling aspen, white birch and/or balsam poplar. Jack pine is considered a “pioneer” tree species, since it readily colonizes areas disturbed by fire but does not persist in older, undisturbed stands (Bergeron 2000).

1.3.1 Climate

Jack pine occurs in the boreal continental climatic region, which is characterized by short, warm to cool summers, very cold winters, and relatively low precipitation. Temperatures, precipitation and the frost-free period all increase from the northwest to the southeast portions of the species’ range (Cayford and McRae 1983). Over the main portion of the jack pine range, monthly mean temperature typically varies from 15 to 20°C in July and –15 to –20°C in January, with a mean annual temperature range of –5 to +5°C (Larsen 1980). Frost may occur during any month (though rarely in July and August) over much of the range, and in the northwest portion of its range jack pine may grow on permafrost soils (Bonan and Shugart 1989). Total annual precipitation ranges from 40 to 90 cm, about two-thirds of which occurs as rain over the summer months. Summer droughts are not uncommon, particularly in the south-central and western portions of the species’ range (Bryson 1966).

1.3.2 Edaphics

Jack pine is well adapted to growth on nutrient-poor, strongly acidic to slightly basic sandy soils and bedrocks (Carleton and Maycock 1978). The species is typically found on coarse to fine sandy soils, but it may also occur on loamy soils, granite rock outcrops, limestone flats, organic peat, and permafrost soils (Larsen 1980). In southeast New Brunswick, a short fire cycle has allowed jack pine to establish large persistent stands on clay soils (Cayford and McRae 1983).

Jack pine is encountered on level to gently rolling sandy plains over most of its range (Rudolph and Laidly 1990). Although the species grows best on well-drained sandy loams, it is more commonly found on drier, sandy or gravelly soils where productivity is lower (Zoladeski and Maycock 1990).

1.3.3 Forest Associates

A jack pine stand will reestablish itself from seed immediately following a catastrophic forest fire. Such fires burn away the soil organic (humus) layer, exposing the underlying mineral substrate that is an excellent seedbed for the species (Carleton and Maycock 1978; Brassard and Chen 2006). As a consequence, jack pine occurs in pure even-aged stands or as a major stand co-dominant over large regions of the Canadian boreal forest, including Manitoba (Zoladeski *et al*. 1990).

Jack pine may also occur in mixed forest stands, particularly in west-central Manitoba. In these mixed stands jack pine is most commonly associated with black spruce, trembling aspen, paper birch and white spruce; balsam poplar, tamarack and balsam fir are more occasional associates (Eyre 1980; Manitoba Conservation 2000; Arseneault and Sirois 2004).

1.3.4 Reproduction

Jack pine is a monoecious conifer species, producing ovulate (female) cones on primary and secondary branches of the upper crown, and staminate (male) cones on tertiary branches of the lower crown (Rudolph and Laidly 1990). Cone production begins at an earlier age in jack pine than most other conifers (Jeffers and Nienstaedt 1972); male cones may be produced as early as four years of age. Ovulate and staminate cone primordia develop in late summer. The staminate cones elongate the following spring, and shed their pollen in late-May to mid-June. The timing of staminate cone anthesis is dependent on weather conditions (Curtis and Popham 1972). In Manitoba, jack pine pollen is shed in mid-June during periods of warm, dry weather (Lee *et al*. 1996). Seed fertilization occurs about one year after pollination, after ovulate cones reach full size (Rudolf and Laidly 1990).

The female (ovulate) cones are oblong to conical, asymmetrical, straight or (more commonly) curved inward (Hosie 1990). Once cone production begins, it increases annually until intraspecific crown competition becomes a factor (Godman and Mattson 1976). Each cone contains between 15 and 75 seeds; strongly curved cones generally produce fewer seeds than straight ones. The mean number of scales per cone is about 80, but only about one-third of the scales in the upper portion of cone bear seed (Rudolph and Yeatman 1982).

The mature ovulate cones of jack pine are serotinous, the seeds remaining within the resin-sealed cones until released by fire. Seed viability is significantly reduced after 5 to 10 years, however, so that only cones less than six years of age contain appreciable amounts of viable seed (Baker 1980). The cone-sealing resin melts during a stand-destroying fire, opening the cone scales and releasing the seed. Seed viability is not markedly affected by heating unless the cone ignites prior to seed release, in which case the seeds are killed. A few jack pine cones may open at temperatures > 27° C if the relative humidity is low, but most remain closed until they are exposed to fire. Cones may also open in extreme cold, when the temperature fall below -45°C (Rudolph and Laidly 1990).

A number of factors and agents reduce jack pine cone and seed crops. Rainy weather during pollen release, and cone and ovulate abortion caused by adverse climatic conditions, can reduce the seed crop in a given year. A number of insect and fungal species are known to attack maturing and mature ovulate cones (Rudolph and Laidly 1990). Red squirrels, chipmunks, red-backed voles and some granivorous birds are known to open the cones and eat the seeds. White-tailed deer, caribou and snowshoe hare will occasionally browse mature cones (Cecich and Rudolph 1982).

1.3.5 Germination and Early Development

The majority of fire-released jack pine seed germinates within 15 to 60 days, provided that environmental and seedbed conditions are favourable (Krugman and Jenkinson 1974; Rudolph and Yeatman 1982). Germination generally occurs at air temperatures ≥ 18°C, but germination is delayed if the seedbed is dry and under severe drought conditions (Cayford *et al.*1967). Light levels strongly influence germination. Under full light conditions excellent germination occurs over a temperature range of 16 to 27°C, but germination is appreciably reduced under low light conditions (Ackerman and Farrar 1965). In recently burned or cutover areas, the shade cast by slash and snags can substantially reduce seed germination (Rudolf and Laidly 1990). However, very light shading may be desirable on dry sites since it reduces soil temperatures and prevents excessive evapotranspiration.

Germination of jack pine seed is strongly affected by seedbed type (Cayford *et al.*1967). In northeastern Minnesota, mean germination was about 60% on exposed mineral soil, 49% on burned duff, 47% on scarified and shaded duff, and only 17% on undisturbed duff (Rudolf 1965). Reduced germination on litter and humus was attributed to poor moisture conditions. Mineral soil and burned seedbeds provide optimum conditions for jack pine seed germination and seedling establishment, since competition from other vegetation is limited (Cayford *et al.*1967) and more moisture is available (Rudolf 1965).

Competition from associated species reduces both seed germination and the growth and survivorship of jack pine seedlings. Shading effects, and perhaps allelopathy, are thought to be important (Brown 1967). Smothering by deciduous leaves may also contribute to early seedling mortality. In Manitoba and Saskatchewan, competition from regenerating trembling aspen, beaked hazelnut (*Corylus cornuta*) and grasses was found to be the main factor reducing seedling survivorship in recently burned stands (Cayford *et al.*1967).

Seedling mortality is often high during the first and second growing seasons (Rudolf 1965). Summer drought and hot weather can kill many seedlings, particularly those growing on well-drained soils. Seedling survival is often low when a residual organic layer remains following a fire. Young jack pine stands (< 10 years in age) are also very susceptible to early spring fires.

Above ground growth in jack pine is slow during the first three years, but increases rapidly in the fourth and fifth years once a strong, deep taproot is established. In naturally regenerating stands, seedlings achieve a height of about 5 cm in the first year, increasing to 15 cm in the second year and reaching 30 – 90 cm by the fourth year. Sapling height (> 1.4 m) is normally achieved within five or six years, depending on edaphic and environmental conditions. After 18 – 20 years trees attain a height of about 6 m (Kenkel *et al*. 1997), and by 35 years stands are merchantable (mean DBH > 13 cm; Cayford *et al*. 1967). Early growth in plantations is often much greater, and may reach 30 – 45 cm per year on mesic, mesotrophic substrates (Rudolf 1965).

1.3.6 Root System

Jack pine seedlings quickly develop a strong primary taproot and numerous lateral roots. During the first growing season the taproot may grow to a depth of 13 – 25 cm. In subsequent years, root growth resumes when the soil temperature (upper 15 cm of soil) reaches 4°C, and ceases in the fall when the soil temperature remains below 7°C for six or more consecutive days. In Manitoba, below ground growth is confined mainly to the taproot in the first three years; strong lateral root development does not occur until the fourth year (Cayford *et al.* 1967).

On deep well-drained soils, the taproot of a mature jack pine tree can penetrate to a depth 2.5 m or more. Despite the presence of a persistent taproot, most of the mature root system consists of lateral feeder roots. These are generally confined to the upper 50 cm of soil, with the bulk occurring in the upper 15 cm. In seven-year-old saplings, the total aboveground volume (bole and stems, branches, and foliage) is about 4,000 cm^3 compared to a belowground volume (total root system) of 1,200 cm^3 (Rudolf 1965). In 25-year-old jack pine stands in central Wisconsin, total root dry biomass in the top 1.5 m of soil ranges from 11,000 to 14,000 kg/ha (Rudolf 1965). For a 40-year-old jack pine stand in northern Minnesota, the total root dry biomass was 28,000 kg/ha (Schlaegel 1975).

1.3.7 Growth and Yield

Jack pine is not a long-lived species, surviving to about 120-150 years on average over most of its range (Larsen 1980; Chen *et al*. 2008). Closed-canopy jack pine stands usually begin “breaking apart” between 70- 90 years of age, depending on site conditions. Under exceptional growing conditions in northern Minnesota, some trees can remain vigorous at 185 years of age (Rudolf and Laidly 1990). The oldest known specimen, from Lake Nipigon in northwestern Ontario, was 230 years old (Rudolf 1965).

When growing in dense stands, jack pine develops into a short to medium-tall, slender tree (Rudolf 1965). A crown ratio (the ratio of crown height to total tree height) of 10 – 20% is typical of trees in such stands. By contrast, an open-grown jack pine develops a stocky stem of poor form and a wide, spreading crown with persistent branches that may reach the ground (Fowells 1965). Under optimal growing conditions trees attain a height of 14 - 24 m at maturity (Hosie 1990). A typical mature tree is 17 – 20 m tall with a breast height diameter (DBH) of 20 – 25 cm, but under ideal growing conditions individuals may attain a height of 30 m and a DBH of 64 cm (Rudolf 1965).

For relatively low-density (2,470 trees/ha) jack pine stands in Michigan and Minnesota, 20-year-old trees achieve heights of 5.5 – 9.8 m, breast height stem diameters (DBH) of 5.8 – 10.2 cm, and basal areas of 6.7 – 20.0 m^2/ha, with the highest values occurring on the best sites (Alban and Laidly 1982). In a moderately dense (11,560 trees/ha) stand in southeast Manitoba, 20-year-old trees averaged 5.4 cm in DBH (Kenkel *et al*. 1997).

Total aboveground biomass of natural stands of jack pine in New Brunswick was estimated at 50,000 kg/ha at age 30, and 70,000 kg/ha at age 50 (MacLean and Wein 1976). For 30-year-old natural stands in northern Ontario, total belowground (root) biomass was estimated at 10,000 – 16,000 kg/ha (Morrison 1974). These results suggest that by 30 years of age 75 – 80% of the total tree biomass occurs above ground.

Annual aboveground biomass production (stand productivity) in 43-year-old natural jack pine stands in Quebec ranged from 1,420 – 2,470 kg/ha (Foster 1974). In natural stands in northern Ontario and New Brunswick, annual above-ground productivity is highest between 20 – 40 years of age (about 5,000 kg/ha), but declined thereafter to about 1,000 kg/ha (Hegyi 1972; MacLean and Wein 1976). Beyond the age of 80, the productivity of jack pine stands is normally very low (Rudlolf and Laidly 1990).

For natural stands in central Manitoba, the mean annual volume increment (mean annual increase in volume) for jack pine reaches a maximum of 2.5 m^3/ha/yr at 50-70 years of age. The corresponding value for northern

Saskatchewan is 2.0 m^3/ha/yr at age 70 (Kabzems and Kirby 1956), while in Ontario the average is 2.7 m^3/ha at age 60 (Plonski 1974).

1.3.8 Competitive Interactions

Jack pine is considered a “pioneer” species, and one of the most shade-intolerant of the boreal tree species (Fowells 1965). It is less shade-tolerant than most other northern pines (e.g. white pine (*Pinus strobus*) and red pine (*Pinus resinosa*)), and equally or slightly more shade-tolerant than lodgepole pine, trembling aspen, balsam poplar, paper birch, and tamarack. It is considered to be much less shade-tolerant than white spruce, black spruce, balsam fir and eastern white cedar. Although jack pine is considered a poor competitor, it is persistent in regenerating stands by virtue of its comparatively fast growth rate and rapid post-fire establishment (Carleton and Maycock 1978; Bergeron 2000).

Intraspecific competition (self-thinning) is also important. Pure stands of jack pine often establish at very high initial densities; a 15-year-old stand with 10,000 – 12, 000 trees/ha is considered “moderately” dense (Chrosciewicz 1971), and much higher densities are not uncommon. As these dense stands develop, space eventually becomes limiting and self-thinning starts to occur (Kenkel 1988). To examine this further, a permanent plot was established in a 15-year-old pure jack pine stand in southeast Manitoba and monitored at five-year intervals until age 55 (Kenkel *et al*. 1997). Initial stand density was 11,560 trees/ha. By age 20, only 11 of the original 468 trees had died. However, by age 25 the annual mortality rate had increased eight-fold, with 69 trees dying. The stand entered the self-thinning stage from ages 25 – 45 years, and during this period annual mortality rates peaked and nearly 80% of the trees died. Over the course of the 20-year self-thinning period, mortality was largely restricted to the smallest size (DBH) classes (see also Chen *et al*. 2008). Over the 40-year study period (ages 15 to 55) stand density declined from 11,560 to 2,075 trees/ha, while mean tree DBH increased from 4.65 to 14.34 cm.

1.3.9 Biotic Damaging Agents

A large number of biotic factors may result in damage to or mortality of jack pine trees. Some of the more important are summarized below.

Insect Pests

The more important insect pests of jack pine are root borers such as the pales weevil (*Hylobius pales*), shoot and stem borers such as the northern pine weevil (*Pissodes approximatus*), leaf feeders such as the jack pine sawfly (*Neodiprion pratti banksianae*), needle miners such as the jack pine tube moth (*Argyrotaenia tabulana*), root feeders including primarily white grubs *(Phyllaophaga* spp.), and sucking insects such as the midges (*Cecidomyia reeksi* and *C. piniinopis*). The jack pine tip beetle (*Conophthorus banksianae*) can cause extensive shoot tip mortality. The lodgepole terminal weevil *(Pissodes terminalis)* has been known to damage new terminal buds of jack pine in Saskatchewan (Rudolf 1965).

Fungal Pathogens

A number of fungal pathogens are known to attack jack pine seedlings and saplings, reducing survival and growth. The western pine-aster rust (*Coleosporium asterum*), pine-oak gall rust (*Cronartium quercuum*), pine-to-pine gall rust (*Endocronartium harknessii*) and other rust fungi can defoliate and kill both seedlings and mature trees (Rudolph and Laidly 1990). Diplodia blight (*Diplodia pinea*) may result in severe shoot blight and mortality in both seedlings and mature trees. Scleroderris canker (*Gremmeniella abietina*) has been known to seriously damage nursery stock. The main root-rot fungi of jack pine are the shoestring fungus (*Armillaria mellea*) and the annosum root rot (*Heterobasidion annosum*). The main wood decay fungi of mature jack pine include red ring rot (*Phellinus pini*) that attacks the heartwood, the velvet-top fungus (*Phaeolus schweinitzii*) that causes butt rot, and the polypore fungus *Fomitopsis pinicola*

(Rudolph and Laidly 1990).

Herbivores

At high population densities, white-tailed deer and elk have been known to browse and kill jack pine saplings. Porcupine and meadow voles may damage or kill mature jack pine trees (Cayford *et al.* 1967).

1.3.10 Genetics and Hybridization

The current range of jack pine was completely covered in ice during the most recent Wisconsin glaciation, which reached its maximum extent about 18,000 years ago. During the major phase of glacial retreat (15,000 to 8,000 years ago), jack pine migrated over considerable distances and colonized vast areas in a relatively short time period (Rudolph and Yeatman 1982). Edaphic conditions and climate vary considerably over the large distributional range of jack pine, resulting in strong natural selection pressures and considerable population differentiation (Rudolph and Laidly 1990). As a result, jack pine shows a high degree of genetic variability, both within populations and throughout its present distributional range (Rudolf and Yeatman 1982). At the continental scale, genetic variation in jack pine occurs along environmental gradients associated with latitude, longitude, and growing season length (Rudolph and Yeatman 1982). The high level of mortality in naturally established jack pine stands during the self-thinning stage may also serve to maintain high genetic diversity within populations (Kenkel *et al*. 1989a).

In central and northern Alberta, jack pine and the closely related lodgepole pine (*P. contorta*) occur sympatrically and are known to hybridize (Moss 1949; Pollack and Dancik 1985).

1.4 BIOLOGY AND ECOLOGY OF BLACK SPRUCE

Black spruce (*Picea mariana* (Mill.) BSP) is a slow growing conifer indigenous to the northern half of North America. Its distributional range overlaps considerably with that of jack pine, although it is somewhat more widely distributed. Along the Atlantic coast black spruce occurs from Massachusetts to northern Labrador. The range extends westward across Canada and into Alaska. In Canada the species occurs throughout the Maritime Provinces, in most of Quebec, Ontario, and Manitoba, in northern Saskatchewan, Alberta and British Columbia, and in Nunavut, Northwest Territories and Yukon south of the tree line. It occurs at the northern tree line throughout its range (Viereck and Johnston 1990). In Manitoba, black spruce is particularly abundant in the Boreal Plain and Boreal Shield forest ecozones (Zoladeski *et al*. 1998). It is the most important pulpwood species in Canada and Manitoba.

1.4.1 Climate

Like jack pine, black spruce occurs primarily in the boreal continental climatic region of North America. The boreal region has short cool summers, long cold winters, and relatively low precipitation. Within the range of black spruce, the mean annual temperature varies from 7°C in the south to -11°C near tree line in west-central Canada and Alaska. Annual precipitation ranges from 40 cm in western Canada, to 90 cm or more in the eastern portion of its range (Viereck and Johnston 1990).

1.4.2 Edaphics

Black spruce is the characteristic tree species of poorly drained, acidic, and nutrient-deficient organic peat lowlands in boreal North America (Larsen 1980). As a result, local topography and drainage largely determine the distribution of black spruce stands on the landscape (Viereck and Johnston 1990). In northern regions the species also occurs in upland sites, including mineral soils (clays, loams, sands and coarse tills), boulder pavements, and shallow soil mantles over bedrock (Carleton and Maycock 1978; Viereck and Johnston 1990).

The most productive black spruce stands occur on dark brown to blackish organic peat (well-decayed organic material) with good water flow and relatively high nutrient levels. Stands occurring on thick deposits of partially or poorly decomposed acidic sphagnum peat with poor drainage and low nutrient levels are much less productive (Larsen 1980; Viereck and Johnston 1990). In northern areas the annual thaw depth in organic peatlands is often < 50 cm, due to the strong insulating properties of peat (Larsen 1980).

In central Canada, upland black spruce stands on mineral soil are generally more productive than those occurring on lowland peat. The most productive stands in west-central Canada occur on well-drained substrates such as sandy glacial deposits, river terraces, and outwash plains. On such sites, black spruce often grows in association with jack pine and hardwood species such as trembling aspen, balsam poplar and white birch (Zoladeski *et al*. 1998).

1.4.3 Forest Associates

Black spruce often occurs as pure stands in poorly drained, nutrient-poor organic peatlands. Tamarack is a common associate on richer organic substrates. On well-drained upland sites in central Canada, black spruce typically occurs in mixture with jack pine, trembling aspen and paper birch (Brassard and Chen 2006; Hart and Chen 2006). Secondary forest associates on upland sites include white spruce, balsam fir, balsam poplar and lodgepole pine. In the southeast portion of its range, black spruce may be found in association with eastern white cedar, black ash, American elm (*Ulmus americana*) and red maple (*Acer rubrum*) (Viereck and Johnston 1990).

In Manitoba, black spruce is the major component of three forest cover types: the lowland black spruce-tamarack type on organic substrates, and the upland black spruce-white spruce and black spruce-paper birch types on mineral substrates (Eyre 1980; Manitoba Conservation 2000).

1.4.4 Reproduction

Black spruce is a monoecious coniferous species that produces ovulate (female) cones in the upper crown, and staminate (male) cones on the outer branches of the crown below the ovulate cones. Black spruce may produce a few cones by 10 years of age (Armson 1975), but the main cone-bearing period is from 30 to 250 years. Most cones are produced between 100 and 200 years of age (Black and Bliss 1980).

Ovulate and staminate cone develop in late summer. Staminate cones continue their development the following spring and shed pollen in late-May to mid-June. In Manitoba, black spruce pollen is shed in early June during periods of warm, dry weather (Lee *et al*. 1996). Following fertilization, ovulate cones develop rapidly and mature by late summer. Mature black spruce ovulate cones are small, averaging 1-4 cm in length (Rudolf and Laidly 1990) and are densely packed at the top of the tree (Larsen 1980).

The ovulate cones of black spruce are semi-serotinous; they remain partially closed, but over several years some cones scales will open and disperse seed. Seeds within the cones may remain viable for up to 25 years, although viability generally declines sharply after about 10 years (Haavisto 1975). Seed may be dispersed throughout the year, but seed dispersal peaks in the spring and declines sharply in the fall and winter months (Haavisto 1978). Fires facilitate complete opening of the cones, greatly increasing seed dissemination and dispersal. Although black spruce seeds are light and have relatively large wings, they are not usually dispersed over great distances (Johnston and Smith 1983).

Black spruce is also capable of vegetative (asexual or clonal) reproduction, especially in trees growing in organic peatlands or on mineral substrates with a very thick organic layer (Stanek 1961). In such sites, the sweeping lower branches may be gradually “buried” by accumulating surface organic matter. Such buried branches will root readily, eventually forming new upright stems adjacent to the parent tree. The impression created is of a larger (parent) tree surrounded by a fringe of younger trees (clones). This phenomenon of branch rooting, known as layering, is very common in stands growing on poorly decomposed peat (Gates 1938; Stanek 1961). At the northern tree limit, black spruce stands are thought to be reproduce almost entirely by layering (Viereck and Johnston 1990).

1.4.5 Germination and Early Development

In upland stands, forest fires usually remove the surface organic layer to expose a mineral substrate that provides a suitable seedbed for black spruce. Moist mineral substrates are considered to be optimal seedbeds for black spruce, although low-lying areas may be too waterlogged or subject to frost heaving (Jeglum 1979). *Shagnum* moss offers a continuously moist seedbed, but seedling growth on such substrates is often slow due to severe nutrient limitation (Jeglum 1979).

Black spruce seed germinate best in the spring. Seeds generally germinate within 60 days of being shed, and seed viability is lost within a few months (Winston 1975). Black spruce seedlings are somewhat shade tolerant, and can survive and grow at only 10% of full light (Fowells 1965). However, seedlings growth is much higher under full sunlight, provided there is adequate moisture. Seedling survival is high on organic peat and mineral soil surfaces with adequate moisture, but poor on burned organic duff (Viereck and Johnston 1990). Seedling mortality increases considerably if more than half of the root system is damaged

(Dumais *et al.* 2002).

Black spruce is considered the slowest growing boreal tree species (Fowells 1965). Under optimal growing conditions three-year-old saplings can reach 1 m in height, but growth is often much slower (Fowells 1965).

1.4.6 Root System

The root system of mature black spruce trees is shallow and wide, with a poorly developed and short taproot. Most of the root biomass is found in the top 20 cm of the soil, although some roots may occur to a depth of 60 cm (Viereck and Johnston 1990). This shallow lateral root system allows black spruce to survive on sites with very shallow soils, in saturated peat lands, and over permafrost. However, the shallow root system also makes black spruce susceptible to wind-throw except in very dense stands (Bigras and Margolis 1996). New surface roots develop quickly in sites where *Sphagnum* or feather moss (*Pleurozium schreberi*, *Hylocomium splendens*) biomass accumulates over time (Armson 1975).

1.4.7 Growth and Yield

The mean longevity of black spruce is approximately 200 years (Viereck and Johnston 1990). However, 280-year-old trees have been found near the treeline in the Northwest Territories (Black and Bliss 1980).

Black spruce develops into a short to medium-statured, slender tree with a crown ratio of 10 – 25% when growing in dense stands (Fowells 1965). Open-grown trees retain their lower branches; the basal branches often reach the ground, and will readily layer given an appropriate organic substrate (*Sphagnum* or feathermoss). In closed-canopy stands on productive upland sites, black spruce can achieve heights of 12 – 20 m and stem diameters (DBH) of 20 – 25 cm. The largest specimens occur in the Clay Belt of north-central Ontario, where some trees can reach 27 m in height and 46 cm in DBH (Fowells 1965). On less productive upland sites and organic peatlands, heights of 8 – 12 m and DBH values of 10 – 15 cm are more common (Viereck and Johnston 1990). In the far north, and in poorly drained oligotrophic peatlands, trees may only reach 3 – 6 m in height and 3 – 5 cm DBH (Jeglum 1974; Black and Bliss 1980).

In Ontario, plantation-grown black spruce can achieve a mean height of 2.5 m (range 1.5 – 4.0 m) after 10 years (Mullin 1978). In 40-year-old Minnesota plantations (1.2 x 1.2 m spacing, 1820 trees/ha), trees averaged 13.3 m in height and 15.0 cm (range 8 – 26 cm) DBH, with a total stand basal area of 33.1 m^2/ha and an estimated stand volume of 183 m^3/ha (Schlaegel 1975). One hundred year old natural black spruce stands on productive peatland and upland sites in southern Canada typically have stand volumes of about 200 m^3/ha (Fowells 1965). Natural stands in central Manitoba are generally less productive, achieving a mean stand volume is about 80 m^3/ha at 110 years of age. In these stands, the mean annual volume increment (mean annual increase in volume) reaches a maximum of 0.93 m^3/ha/yr at about 60 years of age.

Strong regional differences in black spruce growth are related to both climatic and edaphic (soil moisture and nutrients) factors. Patterns of height growth in the species also differ on peatland and upland substrates, particularly for older stands in unproductive habitats (Payandeh 1978). In northern Ontario peatlands, moisture-aeration and nutrient regimes together account for most of the observed variation in black spruce growth (Jeglum 1974).

Fertilization (nitrogen and phosphorus) generally results in increased black spruce growth (Van Nostrand 1979), with the greatest benefits occurring in oligotrophic sites (Weetman *et al.* 1976; Morrison and Foster 1979; Foster *et al*. 1986). Improving site drainage also increases black spruce growth in peatlands, particularly when combined with fertilization (McLaren and Jeglum 1998).

1.4.8 Competitive Interactions

Once established, black spruce will continue to dominate fire-prone sites, since fire results in the immediate reestablishment of the species from seed (Heinselman 1973). On dry upland sites, black spruce often establishes contemporaneously with jack pine (or lodgepole pine in the west). Black spruce remains in the sub-canopy of maturing pine stands, since it grows much more slowly (Carleton 1982). In older stands (> 80-100 years in age), pine mortality results in the competitive release of and eventual dominance by black spruce (Fowells 1965; Carleton 1982). In nutrient-rich peat lands, black spruce is often overtopped by tamarack, black ash and/or red maple for many years before it becomes dominant (Viereck and Johnston 1990). In the absence of disturbance, black spruce may eventually be succeeded by balsam fir and northern white cedar in moist habitats (Hatcher 1963).

Dense upland black spruce stands undergo intraspecific competition (self-thinning). Like jack pine, black spruce often establishes at high initial densities; 15-year-old stands with 10,000+ trees/ha are not uncommon. Carleton and Wannamaker (1987) used stem analysis techniques to reconstruct temporal mortality trends in ten pure, even-aged black spruce stands in Ontario that ranged in age from 44 to 82 years. Mortality was very low during the first 30 years of stand development, followed by a self-thinning phase lasting 20 – 25 years. During this stage, the mortality rate was proportional to live stand density, i.e. the highest mortality occurred in the densest stands. Mortality rates declined appreciably after age 60. By age 80, most stands had densities of 2,500 – 4,000 trees/ha (Carleton and Wannamaker 1987).

1.4.9 Biotic Damaging Agents

A number of biotic factors can damage or result in mortality of black spruce trees. Some of the more important are summarized below.

Insect Pests

The spruce budworm *(Choristoneura fumiferana)* is the most damaging defoliating insect of black spruce. Spruce budworm seriously damages cones and foliage, and may result in moderate to high stand mortality if defoliation occurs over several years (Vincent 1965; Viereck and Johnston 1990). Other important insect pests of black spruce include various sawflies, such as the European spruce sawfly (*Diprion hercyniae*), the yellow-headed spruce sawfly (*Pikonema alaskensis*) and the green-headed spruce sawfly (*P. dimmockii*)). The spruce beetle (*Dendroctonus rufipennis*), the spruce bud midge (*Rhabdophaga swainei*), and the *Monochamus* wood borer can also damage mature black spruce trees (Vincent 1965; Cerezke 1972).

Fungal Pathogens

The major fungal pathogens of black spruce are the spruce cone rust *(Chrysomyxa pirolata*) that damages mature ovulate cones, needle cast fungi *(Lophodermium* spp.) that attack the needles, spruce broom rust *(Chrysomyxa arctostaphyli*) that deforms the branches and foliage, and the snow blight *(Lophophacidium hyperboreum*) that attacks foliage. The main wood decay fungus is tomentosus rot (*Inonotus tomentosus*), which damages the roots and stems of trees in upland sites (Basham 1973; Whitney 1976).

Parasitic Plants

The eastern dwarf mistletoe *(Arceuthobium pusillum)* is a destructive parasitic flowering plant of forest stands in the Lake States and eastern Canada, including Manitoba (Hawksworth and Wiens 1972). In Manitoba, eastern dwarf mistletoe is known to attack black spruce, white spruce and tamarack. Mistletoe infection reduces tree vigor and growth, deforms branches or whole trees, and may eventually kill trees (Baker and French 1981).

Herbivores

Although herbivores generally avoid black spruce (Bryant *et al*. 1983), snowshoe hares and red squirrels may damage or destroy cones, seedlings and saplings. Damage is greatest when population densities of these herbivores are high (Viereck and Johnston 1990).

1.4.10 Genetics and Hybrids

A number of researchers have reported that upland (mineral soil) and lowland (organic peat) substrates harbour distinct “ecotypes” of black spruce, but there is no genetic evidence in support of edaphic ecotypes (Morgenstern 1973, 1978). Introgressive hybridization between black spruce and red spruce (*Picea rubens*) has been reported in Nova Scotia, New Brunswick, and western Quebec (Morgenstern and Farrar 1964; Gordon 1976). A natural hybrid between black spruce and white spruce (*P. glauca*), known as Rosendahl spruce, was reported from northern Minnesota (Little and Pauley 1958). However, subsequent investigation indicated that Rosendahl spruce is a naturally occurring variant of white spruce, and not a hybrid (Parker and McLauchlan 1978).

CHAPTER 2 REVIEW OF FOREST GROWTH AND YIELD MODELLING

2.1 GROWTH AND YIELD MODELS IN FORESTRY

Foresters and forest managers require knowledge of how forests change over time: what will be the composition, structure, productivity and density of a forest stand at some time in the future, and how much harvestable timber volume (yield) can be expected? Forest growth and yield models are developed and used to help forest managers forecast the growth and dynamics of forest stands. The main forest processes of concern are the growth, yield and mortality of trees (Philip 1998; Husch *et al.* 1982).

Tree growth is highly variable within species, among species, and among stands. The observed growth rate of a given tree is dependent on numerous factors: these include biotic ones such as genetics, photosynthetic capability and physiological performance (Prasad 1997; Larcher 2003), as well as potentially limiting abiotic factors such as light, temperature, soil water and nutrients and so forth (Bonan and Shugart 1989; Prasad 1997; Larcher 2003). Because trees are long-lived, it is difficult and time-consuming (but thankfully often unnecessary) to measure instantaneous growth rates of individual trees or forest stands (e.g. yearly bole diameter increments over the entire lifespan of a tree). Instead, more easily measured variables such as the mean growth rate (e.g. mean annual growth increment in bole diameter or timber volume) are often used in forest management applications (Philip 1998; Husch *et al.* 2003; Weiskittel *et al*. 2011).

Forest growth refers to the change in tree or stand attributes (e.g. diameter at breast height (DBH), height, density, volume and biomass) over time, while yield refers to the amount of a tree or stand attribute (e.g. timber volume) that can be harvest at a given point of time. Yield is therefore the sum of annual changes in growth components (Weiskittel *et al*. 2011). For example, volume yield is the net volume of wood present in a stand at any given age, whereas growth refers to the increase in wood volume in a given year. The recent growth of a tree or stand reflects current physiological and environmental conditions, whereas yield reflects both past and current conditions (Oliver and Larson 1996).

Two major types of forest growth and yield models are recognized: empirical models, and structure-process models (Kimmins 1990; Peng 2000). Empirical models are based on the analysis of large amounts of data from permanent sample plots; these data are used to obtain regression functions of tree and stand level variables in order to model forest growth rates. The empirical approach has the advantage of using “real” data to determine the relationships among variables, using specified mathematical functions that achieve efficiency, parsimony and accuracy in the provision of quantitative information for forest inventory and management. In specific applications empirical models require relatively few and simple inputs, and are easily incorporated into different forest growth and yield, inventory and management analyses (Pretzsch 2009; Weiskittel *et al*. 2011).

By contrast, process models aim to describe key ecosystem process, or to simulate tree or stand growth, based on a number of interacting processes such as photosynthesis, respiration, decomposition, and nutrient cycling (Kimmins 1990). Such models provide a framework for testing and generating alternative hypotheses, and have the potential to help describe and understand how ecological processes interact under specific environmental scenarios (Landsberg and Sands 2010). Process models require detailed and accurate physiological and ecological data, such as measures of leaf photosynthetic and respiration rates, decomposition rates, and nutrient cycling processes. In applied forestry, empirical growth and yield models are preferred since they provide more accurate and applicable estimates of timber yield (Zeide 1993; Peng 2000).

Three types of empirical growth models are recognized: whole stand models, diameter class models, and individual tree models (Davis and Johnson 1987;

Peng 2000). Whole stand models predict growth based on forest stand characteristics such as total basal area, stand age and site index (Buckman 1962; Moser and Hall 1969; Sullivan and Clutter 1972; McRoberts 2000). Diameter class models predict stand growth by tree bole diameter classes (Bailey and Dell 1973; Adams and Ek 1974; Solomon *et al.* 1995). Individual tree models, as the name suggests, predict individual tree growth using a combination of forest stand and individual tree characteristics.

Whole stand models are typically quite simple, and utilize relatively few input variables to simulate stand growth and yield. While useful for general stand-level forecasts, such models provide little or no information on the growth of individual trees within a stand (Vanclay 1994). Stand models have been used in the past to produce forestry yield tables (e.g. Plonski 1974). Diameter class models provide some information on growth as a function of stand structure, and are used mainly to model the development of uneven-aged forest stands (e.g. the stand table projection method of Ek (1974)). Individual tree models simulate the development of each individual tree as a function of establishment, growth and mortality, and sum these individual tree estimates to obtain stand-level values of growth and yield. The individual tree models can be further categorized into distance-dependent models, which require tree locations on order to determine spatial competition (Ek and Monserud 1974; Daniels and Burkhart 1975; Daniels and Burkhart 1988), and distance-independent models in which tree locations are not required (Stage 1973; Amateis *et al.* 1989; Cao 2000).

The following literature review emphasises individual tree modelling, since this is the main focus of my research.

2.2 ABSOLUTE AND RELATIVE GROWTH RATES

The instantanous absolute growth rate is simply the net increase in biomass per unit time (Hunt 1978):

[2.1] $$G = \frac{dW}{dT}$$

where G is the absolute growth rate and W is the dry weight (biomass) at time T.

In practice, absolute growth is determined as the mean absolute growth rate ($\overline{G}_{1-2}$),the incremental growth over a specified period of time:

[2.2] $$\overline{G}_{1-2} = \frac{W_2 - W_1}{T_2 - T_1}$$

where W_1 is the dry weight at time T_1, and W_2 is the dry weight at time T_2.

The instantaneous relative growth rate is the increase in biomass per unit of biomass per unit time (Hunt 1978):

[2.3] $$R = \frac{1}{W} \cdot \frac{dW}{dT} = \frac{d[\ln W(t)]}{dt}$$

where R is relative growth rate (also known by the acronym RGR), and W is the dry weight (biomass) at time T.

The mean relative growth rate ($\overline{R}_{1-2}$), or relativized incremental growth over a specified period of time, is given by:

[2.4] $$\overline{R}_{1-2} = \frac{\ln W_2 - \ln W_1}{T_2 - T_1}$$

where W_1 is the biomass at time T_1 and W_2 is the biomass at time T_2.

The relative growth rate R is a more useful measure when comparing growth rates among two or more individuals differing in initial size (i.e. size W_1 at T_1).

2.3 ALLOMETRIC RELATIONSHIPS

The study of proportional change in measured components of a tree resulting from growth is known as allometry. Allometry is a fundamental concept of growth and yield modeling in forestry. Over a finite time interval, an allometric relationship exists between two components of a tree (e.g. Y = tree height and X = stem diameter) when the following general relationship holds (Hunt 1978):

[2.5] $$Y = aX^{k}$$

where *a* is the proportionality coefficient, and *k* is the scaling component or "allometric constant". Taking logarithms of both sides gives:

[2.6] $$\log Y = \log a + k \log X$$

Thus, equation [2.5] can be fitted as a linear model by log-transforming the variables *X* and *Y*. Allometric relationships in plants are ubiquitous; examples include the relationship between above (shoot) and below (root) ground biomass (Hunt 1978), and structural scaling relationships (Niklas 1994; West *et al.* 1999).

Foresters often use allometric-type height – diameter models to predict total tree height based on measured bole diameters (Stout and Shumway 1982). Over thirty height-diameter models have been described in the forestry literature (e.g. Curtis 1967; Loetsch, *et al*. 1973; Arabatzis and Burkhart 1992; Huang *et al*. 1992, 2000b; Moore *et al.* 1996; Zhang *et al*. 2002). For example, variants of the following basic three-parameter model are widely used to model tree height – diameter relationships (Huang *et al.* 1992, 2000b; Zhang *et al.* 2002; Xu 2004):

[2.7] $$H = 1.3 + a(1 - e^{-bD})^{c}$$

Here *H* is total tree height, *D* is stem diameter at breast height (DBH), *a, b, c* are the regression parameters to be estimated, and *e* = 2.718… is the base of the natural logarithm. The constant 1.3 is added to account for the fact that stem diameter is measured at “breast height”(1.3 m from the tree base).

The predictive power and statistical accuracy of a height-diameter equation can often be improved by incorporating additional tree and stand variables. These additional variables include stand density, total stand basal area, and various indices of competition and site productivity (Curtis 1967; Huang and Titus 1994; Xu 2004). Tree or stand age may also be used, but since accurate age data are difficult to obtain (or simply unavailable) these variables are not always incorporated into height – diameter models (Huang and Titus 1994).

2.4 POLYNOMIAL GROWTH MODELS

In polynomial regression functions, a single dependent variable is expressed as a function of one or more independent variables. There are first, second, and higher order polynomial models; a first-order polynomial model is termed linear regression. For example, the relationship between tree stump age (age at 30 cm above ground) and breast height age (age at 1.3 m above ground) can be modelled as a first-order polynomial:

[2. 8] $$A_S = a + bA_B$$

where A_S is the stump age, A_B is the breast height age, and *a* and *b* are estimated parameters.

Polynomials regression models were widely used in the past to model growth in plant biology and forestry (Hunt 1978; Causton and Venus 1981). An early example employed second order (quadratic or parabolic) polynomials to model changes in the biomass *W* (dry weight) and leaf area L_A of maize (*Zea mays*) over time (Vernon and Allison 1963):

[2. 9] $$W = a + bT + cT^2$$

[2.10] $$L_A = a' + b'T + c'T^2$$

where T is time, and *a, b, c, a', b'* and *c'* are fitted parameters. Equation [2. 9] is differentiated to obtain the absolute growth rate:

[2.11] $$\frac{dW}{dT} = b + 2cT$$

Instantaneous values for unit leaf efficiency rate (E) were then determined as:

[2.12] $$E = \frac{1}{L_A} \cdot \frac{dW}{dT} = \frac{b + 2cT}{a' + b'T + c'T^2}$$

Vernon and Allison (1963) plotted E as a continuous function of T by solving this equation for successive values of T. This approach is straightforward, but suffers from a serious statistical drawback: a tendency for the variance of W and L_A (as opposed to ln W and ln L_A) to increase over time. In statistical terminology, the data are heteroscedastic (Zar 2009): the variance of each successive biomass harvest increases over time (Hunt 1978).

To overcome the problem of heteroscedasticity in plant growth modelling, biomass values are log-transformed prior to fitting polynomial functions. An early example (Hughes and Freeman 1967) modelled the growth of *Callistephus chinensis* (China aster) using the following third-order polynomials:

[2.13] $$\ln W = a + bT + cT^2 + dT^3$$

[2.14] $$\ln L_A = a' + b'T + c'T^2 + dT^3$$

Logarithmic transformation alleviates the heteroscedasticity problem, allowing for the statistical modeling of complex trends in plant growth (Hunt 1978). Hughes and Freeman (1967) used these polynomial growth models to derive equations for relative growth rate (R) and unit leaf efficiency rate (E).

In theory, more complex plant growth relationships can be fitted using higher order polynomials:

[2.15] $W = a + b_1T + b_2T^2 + b_3T^3 + ... + b_nT^n \quad (n > 3)$

However, in practice higher-order polynomials are cumbersome and often statistically unstable (Causton and Venus 1981). Furthermore, the fitted models are often highly sensitive to data anomalies, and they are biologically unrealistic (Hunt 1978). Asymptotic models are now used to overcome these and other deficiencies, as explained below.

Statistical polynomials are simple and flexible mathematical functions, and were widely used in the past to model plant growth (Causton and Venus 1981), and to model forest growth and yield (e.g. Ker 1980; Standish *et al*. 1985). However, polynomial-based equations are “devoid of any biological interpretation” (Zeide 1993), and are used only to obtain an empirical fit to data (Hunt 1978; Causton and Venus 1981).

2.5 ASYMPTOTIC GROWTH MODELS

A characteristic feature of asymptotic models is that the value of the dependent variable approaches a plateau (maximum organism size) known as the upper asymptote (Hunt 1978). Most asymptotic models are sigmoidal in form; i.e. they have both a lower and upper asymptote. Such models are biologically meaningful for most animal species, since animals undergo determinate growth (i.e. a growth pattern with a definite and prolonged maximum size). By contrast, most plant species have an indeterminate pattern of growth. However, it is also true that “even indeterminate growth will cease at some stage” (Causton and Venus 1981). For example, Zeide (1993) describes tree growth in terms of two opposing forces: a biological potential for exponential growth, counteracted by constaints imposed by both external (e.g. competition, stress) and internal (e.g. aging) variables that limit growth. As a result, over time the growth of a tree slows (and eventually ceases) as the individual approaches its maximum size or age

(Pretzsch 2009). Asymptotic functions are therefore broadly applicable for modeling growth of both animals and plants. The asymptotic family of growth models includes the Chapman-Richards group of functions, the Weibull function, and a number of non-linear empirical functions (Weiskittel *et al*. 2011).

Unlike polynomial functions, asymptotic functions are statistically nonlinear: parameters can be divided, multiplied or raised exponentially relative to one other, rather than simply being additively combined in a linear sequence. Since a closed-form solution does not usually exist for nonlinear equations, iterative non-linear procedures are required to fit asymptotic models by least squares. Three non-linear iterative procedures are widely used (e.g. SAS 2004): Gauss-Newton, Marquardt, and the method of steepest decent (Seber and Wild 2003). The Marquardt (1963) method is a compromise between the Gauss-Newton and steepest decent approaches, and it is most useful approach when the estimated parameters are highly correlated (Causton and Venus 1981).

A large number of asymptotic functions have been proposed to model plant growth (Causton and Venus 1981; Zeide 1993). This review focuses on the better-known functions, with an emphasis on those most commonly used in forest growth and yield modeling.

2.5.1 Monomolecular

The three-parameter monomolecular function, developed by physical chemists and often used in biological growth modelling (Causton and Venus 1981), is given by:

[2.16] $$W = a[1 - be^{-kT}]$$

where *W* is biomass (dry weight) at time *T*, *a* is the upper asymptote, *b* is the initial biomass, and *k* is the rate constant (Richards 1959; Avery and Burkhart

1994). Unlike in polynomial models, these parameters are biologically meaningful and relevant.

In this model, the relative growth rate declines linearly with time as a function of the reciprocal of size *W*. The monomolecular function is not sigmoidal; it has no point of inflection. For this reason, Zeide (1993) concluded that the monomolecular model "presents a rather unrealistic picture of growth". The rate of decline in absolute growth is specified by the rate constant *k*, which reflects the inherent capacity of a tree to increase its biomass (Causton and Venus 1981). The monomolecular function is also known as the "law of diminishing returns" in the fields of agriculture and economics (Zeide 1993), and the Brody-Bertalanffy equation (see below) in the aquatic sciences (Ricker 1975; Ebert 1980).

2.5.2 Bertalanffy

Bertalanffy (1957) developed a series of equations, based on proposed metabolic theories of anabolism and catabolism in animals, in an attempt to produce a "general theory of growth". His primary "metabolic type" assumes that anabolism is proportional to the surface area of an organism, whereas catabolism is proportional to organism mass (Zeide 1993). These assumptions produce the equation:

[2.17] $$W = a[1 - be^{-kT}]^3$$

Two other metabolic types were also described by Bertallanffy (1957), one of which produces the monomolecular function (Richards 1959). The Bertalanffy growth function has been used widely in organismal and fisheries biology (Bertalanffy 1957; Chen *et al*. 1992), although Ricker (1979) notes that Bertalanffy's metabolic theories are nothing more than "fanciful speculations". Bertalanffy-type functions have also been used to model allometric relationships in trees and forest stands (Chapman 1961; Pienaar and Turnbull 1973; Huang *et al.* 2000b; Zhang *et al.* 2002).

2.5.3 Autocatalytic (Logistic)

The autocatalytic or logistic function is commonly used to model the growth of populations under limiting conditions (Otto and Day 2007). It has also been used to model plant growth (Hunt 1978), and tree height – diameter relationships in forestry applications (Huang *et al.* 2000b; Zhang *et al.* 2002). Zeide (1989) concluded that the logistic equation produces less accurate models of tree diameter growth compared to other sigmoidal asymptotic functions. The autocatalytic function has three parameters, and takes the following form:

[2.18] $$W = a[1 + be^{-kT}]^{-1}$$

where W is biomass (dry weight) at time T, a is the asymptote, b is a scaling parameter, and k is a rate constant.

In this model, the relative growth rate declines with time T as a linear function of size W. The logistic function is sigmoidal and symmetric, with an inflection point at $W = a/2$ at time b/k. It follows that b and k are not biologically independent (Causton and Venus 1981).

In population growth modeling, the logistic function is usually written as:

[2.19] $$Y = a/[1 + be^{-kT}]$$

where Y is the population size, a is the population carrying capacity, b is a scaling parameter proportional to initial population size, and k is the population intrinsic rate of increase (Otto and Day 2007).

2.5.4 Gompertz

The theory underlying this function was developed initially to describe age distributions in human populations (Gompertz 1825). The Gompertz function was first suggested as a growth model by Winsor (1932). It is widely used in biology, and both empirical and theoretical considerations recommend its use in modeling growth (Medawar 1940; Causton and Venus 1981; Zeide 1993). The Gompertz function has been used in forestry to model tree growth, and in developing stand yield curves (Yang *et al*. 1978). It has three parameters, and contains a double exponent:

[2.20] $$W = ae^{-be^{-kT}}$$

In this model, the relative growth rate declines as a linear function of the logarithm of size W. The Gompertz function is sigmoidal but asymmetric; the inflection point occur at $W = a/e$ (versus $a/2$ for the logistic function) at time b/k. As a result, the asymptote is approached more gradually compared to the logistic model.

2.5.5 Weibull

The Weibull function describes a continuous probability distribution (Weibull 1951), but it has also proved useful as an empirical growth model (Zeide 1993). This function has four parameters, and it is the only sigmoidal growth function in which size W is a power function of time T:

[2.21] $$W = a[1 - e^{(b-kT)^c}]$$

In this equation, a is the upper asymptote and b, c and k are scaling parameters. In forestry, the Weibull function has been successfully applied in growth and yield modelling (Yang *et al.* 1978; Zeide 1989, 1993).

2.5.6 Richards (Generalised Logistic)

This function (also known as the Chapman-Richards function) was developed as a generalized form of the monomolecular, logistic, Bertalanffy and other asymptotic models (Richards 1959; Chapman 1961; Causton and Venus 1981). The Richards function was derived as a generalized extension of Bertalanffy's equations, and was expressed by Richards (1959) as:

[2.22] $$W^{1-m} = a^{1-m}[1 \pm be^{-kT}]$$

The negative form is used when $m < 1$, and the positive form when $m > 1$ (Richards 1959). This function is more conveniently expressed as:

[2.23] $$W = a[1 \pm be^{-kT}]^{1/(1-m)}$$

Note that the exponent m introduces the "generalizing" parameter, which allows many of the functions discussed above to be expressed as specific cases of the generalised Richards function:

m	Function
2	*Logistic (Autocatalytic)*
0	*Monomolecular*
2/3	*Bertalanffy*
-> 1	*Gompertz*

The inflection point for the Richards function occurs at $W/a = m^{1/(1-m)}$; as $m \to 1$, this reduces to $1/e$ (Richards 1959). Zeide (1993) notes that the Richards function "is used more than any other function in studies of tree and stand growth". This is undoubtedly attributable to the flexibility of the model; the “generalizing” parameter m allows for highly flexible empirical modeling over a continuum of asymptotic functions (Pienaar and Turnbull 1973).

Nelder (1961, 1962) proposed:

$$W = a/[1 + e^{-(b+kT)/d}]^{d} \tag{2.24}$$

as a generalization of the logistic function. This and other Nelder equations are “essentially reparameterizations of the Richards function” (Causton and Venus 1981).

2.6 TREE HEIGHT GROWTH AND SITE INDEX MODELS

In forestry, site index is defined as the mean height of dominant and co-dominant trees in a stand at 50 years of age, where age is measured at 1.3 m breast height (DBH: Carmean 1975; Goelz and Burk 1992; Huang *et al.* 1994b; Philip 1998; Manitoba Conservation 2000). The site index provides a standard for comparing the productivity potential of sites over a broad range of stand conditions. Dominant trees are the tallest in the stand, while co-dominants are trees whose crowns form the major crown cover level, i.e. trees that receive full light from above but comparatively little from the sides (Manitoba Conservation 2000). Direct estimation of site index in established forest stands is the most commonly used method for determining and comparing site quality in North America (Carmean 1975; Goelz and Burk 1992; Huang *et al.* 1997).

Site index is commonly used to measure forest productivity (Carmean 1975; Monserud 1984; Huang *et al.* 1994b; Wang and Huang 2000), and is a core variable in many growth and yield models for even-aged stands (Clutter *et al.* 1983; Davis and Johnson 1987). Note that the true stand age (e.g. post-fire age) is not used in determining site index. Instead, stand age is estimated at 1.3 m breast height (and termed the “breast height age”), since this is much more easily measured and because early height growth is often erratic and may not reflect actual site productivity (Clutter *et al.* 1983).

As the site index proceeds from low (relativedly unproductive stands) to high (productive stands), both the magnitude and shape of the sigmoidal height – age relationships change. Trees with lower site index values typically display a flatter, more linear relationship, whereas trees with a high site index approach the asymptote more rapidly. As a result, site index curves tend to be divergent at the younger age classes, but eventually become parallel or convergent at older age classes.

In Manitoba, site index is a critically important parameter for forest growth and yield analysis, site productivity estimation, site classification and forest inventory projections, and provincial wood supply analysis. The application of site index models developed in one region may not be generally applicable to other regions, due to differences in climatic and edaphic conditions that strongly affect forest tree growth and stand development (Peng *et al.* 2001). For example, the misapplication of regional models can produce highly biased results, over-estimating tree height by up to 29.1%, or under-estimating as much as 21.9% (Huang *et al.* 2000b).

2.7 TREE DIAMETER (BASAL AREA) INCREMENT MODELS

In forestry, diameter increment refers to the incremental growth in stem (tree bole) diameter at 1.3 m height (diameter at breast height, DBH) over a specified time interval. Tree bole diameter is the most commonly used allometric variable for determining tree biomass and timber volume, since it can be measured easily and accurately (Pretzsch 2009; Weiskittel *et al*. 2011). Incremental increases in bole diameter can be obtained by repeatedly measuring trees in permanent sample plots, or by coring trees and measuring distances between adjacent growth rings (Oliver and Larson 1996). Diameter growth data are used to estimate stand productivity (e.g. harvestable volume increases per unit time), or the type of product (e.g. pulpwood vs. timber) that can be obtained from individual trees or forest stands (Hann and Larsen 1991). Traditionally, foresters have used tree diameter (or basal area) models to predict the growth and yield of both managed and natural forest stands. In the past decades, a large number of individual tree diameter (basal area) growth and yield models have been developed for various forest regions, forest stand types, and tree species (e.g. Wykoff 1990; Quicke *et al*. 1994; Huang and Titus 1995; Monserud and Sterba 1996; Murphy and Shelton 1996; Cao 2000; Lessard *et al*. 2001).

Given the simple mathematical relationship between tree diameter and basal area, models based on diameter or basal area increment equations are equally precise (Vanclay 1994; West 1980); the decision of which variable to use is therefore based on convenience or personal preference (Vanclay 1994; Zhang *et al*. 2004). Most researchers prefer to use basal area, since it is more linearly related to tree biomass and volume growth than is diameter (Wykoff 1990; Monserud and Sterba 1996; Hokka and Groot 1999).

Over the past few decades there has been a trend toward the development of increasingly sophisticated and accurate individual tree growth and yield models for use in forestry practice, forest inventory, timber supply analysis and sustainable forest management. An early example was the development of growth models for eleven conifers species in the Northern Rocky Mountains, using incremental increases in squared diameter (log-transformed) as the dependent variable (Wykoff 1990). The independent variables included current tree diameter, current diameter squared, site factor variables, crown ratio, and two measures of crown competition. Monserud and Sterba (1996) developed a similar model based on five-year bole diameter increments (log-transformed) for individual tree growth. More recently, Zhao *et al.* (2004) developed an individual tree diameter growth model for bottomland mixed-species hardwood stands in the lower Mississippi, using the natural logarithm of five-year changes in (squared) diameter as the dependent variable. The independent variables included current stem diameter at breast height, current diameter squared, the reciprocal of current stem diameter, mean stand stem diameter, stand basal area, the ratio of current tree basal area to mean stand basal area, and a site effect variable.

Individual tree basal area growth can be modeled using either “growth potential independent” or “growth potential dependent” approaches. In the former approach, tree basal area increment is expressed directly as a function of measurable tree and stand level variables such as tree size, age and vigour, crown ratio, local competition, site index, stand density and various site characteristics (e.g. Wykoff 1990; Vanclay 1994; Monserud and Sterba 1996; Hokka and Groot 1999). Conversely, in the growth potential dependent approach the predicted growth is estimated as:

Predicted Growth = [Maximum Growth Potential x Modifier Function]

where the “maximum growth potential” is the theoretical potential (competition-free) growth of a tree, and the “modifier function” measures the deviation from the maximum potential growth attributable to competitive interactions with neighbouring trees. The modifier function is obtained by considering factors such as tree size, crown ratio and local competition (i.e. indices based on the size and proximity of neighbouring trees; Quicke *et al*. 1994). The growth potential approach poses several challenges, perhaps the greatest of which is the need to find and select trees that best represent maximum growth potential (Vanclay 1994). Some researchers utilize open-grown trees (e.g. Amateis *et al*. 1989), while others use the largest (or fastest-growing) tree or trees present in the data set (e.g. Schroder *et al*. 2002).

Comparative studies have shown that the growth potential dependent and independent models perform equally well over the range of conditions tested (e.g. Wykoff and Monserud 1988; Wykoff 1990). In my research the direct modelling (growth potential independent) approach is used, as it avoids the many problems associated with developing a “maximum potential growth” construct.

2.8 TREE BOLE TAPER MODELS

Tree taper quantifies the rate of diameter narrowing along a tree stem (Avery and Burkhart 1994). The taper profile of a tree is determined by taking successive diameter measurements along the entire length of the stem. The measurement and modeling of bole taper profile is critical to the development of reliable and accurate estimates of the volume of merchantable timber in forest stands; trees with low taper have greater volume than ones with high taper (Cao *et al.* 1980). Bole taper varies widely across tree species (Garber and Maguire 2003), as well as within species. For a given tree species, trees of comparable height and diameter can achieve timber volume differences as high as 20%, depending on taper (Heger 1965). Variation in bole taper among trees results from differences in diameter and height growth of the tree stem over time. Factors affecting the bole taper of a tree include biotic variables such as stand density, tree age, crown size and canopy position (Larson 1963, 1965), and abiotic variables such as edaphic and climatic conditions (Muhairwe 1994, Sharma and Parton 2009). Some studies have demonstated variation in bole taper among different crown ratio classes (e.g. Dell *et al.* 1979; Baldwin and Polmer 1981). Bole taper may be greater in trees with higher crown ratios (Valenti and Cao 1986), although Burkhart and Walton (1985) concluded that the relationship was not strong enough to warrant including crown ratio as an independent variable in bole taper models.

Tree taper models are developed to provide reliable and accurate diameter estimates (inside or outside the bark) at any point along the tree bole (Kozak 1988; Huang 1994b; Sharma and Zhang 2004). In Canada and other countries, taper models are used to provide accurate estimates of timber resources in forest inventory, timber supply analysis and sustainable forest management applications (Kozak 1988; Flewelling and Raynes 1993; Gal and Bella 1994; Huang 1994b; Huang *et al.* 1999; Sharma and Parton 2009). They are also used in applied forestry to estimate individual tree merchantable length, and to determine gross total or mechantable timber volume under different utilization standards (Kozak 1988; Trincado and Burkhart 2006). The main advantage of bole taper over volume equations is that total (or sectional) bole volume can be estimated using scaling rules, resulting in more accurate estimates (Williams and Reich 1997; Muhairwe 1999). As a result, bole taper equations are widely used to model and accurately estimate the timber volume of individual trees and forest stands in forest inventory, timber supply analysis and sustainable forest management applications (Huang 1994b; Newnham 1988b).

The earliest parametric bole taper models used the segmented taper functions approach. In this approach, the tree bole is divided into three segments each with a distinct geometric shape: a neiloid frustum at the tree base, a paraboloid frustum in the mid-section, and a cone frustum at the top (Husch *et al.* 1982). Different equations are used to obtain statistical fits for each segment, and these are subsequently joined mathematically to generate an overall bole taper function (Max and Burkhart 1976; Trincado and Burkhart 2006). The segmented functions approach is challenging, as it requires proper identification of inflection or other joining points and the development of empirical smooth functions to fit the adjoining segments together (Max and Burkhart 1976).

More recently developed parametric bole taper models employ the variable exponent taper functions approach (Kozak 1988; Newnham 1992; Huang *et al.* 2000a; Sharma and Zhang 2004). These models, which assume that form changes continuously along the tree bole, utilize functions in which the exponent changes with relative tree height. This results in a single equation that fully describes the neiloid, paraboloid, and conic bole segments, thus eliminating the need to specify different equations for each segment (Kozak 1988). The variable-exponent model has less local bias, and greater precision in taper prediction, compared to the segmented functions approach (Newnham 1988b; 1992; Kozak 1988; Perez *et al.* 1990; Kozak and Smith 1993; Muhairwe 1999); it is also much easier to fit (Kozak 2004). The variable-exponent taper equation proposed by Kozak (1988) is:

[2.25] $$d_i = a_0 D^{a_1} a_2^{D} X_i^{b_1 z_i^2 + b_2 \ln(z_i + 0.001) + b_3 \sqrt{z_i} + b_4 e^{z_i} + b_5 (D/H)} + \varepsilon_i$$

where $z_i = \frac{h_i}{H}$ and $X_i = \frac{1 - \sqrt{h_i / H}}{1 - \sqrt{p}}$

Numerous studies have demonstrated that Kozak’s (1988) taper equation provides accurate diameter and volume predictions for major tree species in British Columbia, Alberta and Saskatchewan (Kozak 1988, 2004; Gal and Bella 1994; Huang 1994b; Huang *et al.* 1999). For example, Gal and Bella (1994) compared three taper equations – developed by Demaerschalk and Kozak (1977), Kozak (1988), and Hilt (1980) – for modeling bole taper of twelve timber species in Saskatchewan. Kozak’s (1988) variable-exponent taper model achieved overall superior performance in all cases.

Kozak’s (1988) bole taper equation has been expanded and modified to include forest stand (independent) variables such as site class, crown class, stand age, crown ratio and the quadratic mean stem diameter. However, improvements in model performance are often minimal, and therefore statistically and economically unjustifiable (Muhairwe *et al.* 1994). It has been suggested that adding variables to the function itself (as opposed to the exponent) might improve model performance (Muhairwe *et al*. 1994), and that including silvicultural treatment and stand density variables may improve model precision (Tasissa *et al.* 1997; Sharma and Parton 2009).

2.9 TREE MORTALITY MODELS

Long-term forest stand dynamics and tree mortality are complicated processes, as they are affected by a great many biological and ecological factors. Dynamic change in forest stands is usually gradual, but under some circumstances (e.g. pest or pathogen outbreaks) tree mortality may be very abrupt (Waring 1987). The accurate prediction of mortality (or survivorhsip) is an essential feature of most forest stand growth models (Monserud 1976; Yang *et al.* 2003; Zhao *et al.* 2004). Spatial and temporal patterns of tree mortality are poorly understood (Lee 1971; Hamilton 1986) and often unpredictable and stochastically episodic (e.g. catastrophic fires, large scale insect pest and pathogen outbreaks), making prediction difficult. Predictions can be simplified by modelling general trends in expected survivorship (as in survival tables), ignoring the specific mechanisms causing regular or episodic mortality (Yang *et al.* 2003).

Tree mortality varies considerably over time and is affected by a number of factors, some of which are density-dependent (e.g. spatial competition and self-thinning) and others density-independent (e.g. drought, pests and pathogens). Changes in forest composition and structure attributable to stand dynamics are a critically important part of this process (Oliver and Larson 1996). However, the complexity of the mortality process, and uncertainty in the timing of tree death, makes mortality one of the least understood components of growth and yield estimation. It is nevertheless important to model tree mortality, particularly in boreal forest ecosystems where it is often a key process driving stand dynamics (Carleton and Wannamaker 1987; Kenkel *et al*. 1997). Indeed, reliable predictions of mortality rates are essential to the accurate prediction of stand dynamics. Although patterns and causes of tree death are complex, and mortality predictions complicated (Franklin *et al.* 1987), some generalities can be derived and tree mortality can often be modelled successfully using parameters such as relative tree size, stand density, spatial competition and individual tree growth rates (Hamilton 1986).

Early tree mortality models used linear and polynomial regression functions (Lee 1971; Hawkes 2000), which are incompatible with the known behavior of tree mortality (e.g. in such models, predicted mortality probability is not guaranteed to range from 0 – 1; see Hamilton 1974). Nonlinear models that are implicitly defined to range between 0 and 1, and their cumulative probability distributions (including the negative binomial, Weibull and gamma distributions), have been more successfullu used to model mortality (Buford and Hafley 1985). More recently, logistic regression has been advocated as a superior method for modelling individual tree mortality, and has been widely applied (Hamilton 1986; Vanclay 1995; Monserud and Sterba 1999; Yao *et al.* 2001; Yang *et al.* 2003; Zhao *et al.* 2004). For example, Vanclay (1995) found that the logistic function fitted to individual tree data produced the best model of tree mortality in Australian forests.

A number of complex mortality models have been developed in recent years, for various tree species and stand types. For example, an individual tree mortality model for boreal mixed wood stands in Alberta, based on logistic regression, predicted annual survival probability using tree and stand level attributes (and their combinations) that included tree stem diameter and diameter increment, stand basal area, site productivity index and species composition (Yang *et al*. 2003). A similar model was developed to model individual tree mortality in bottomland mixed-species hardwood stands of the lower Mississippi region (Zhao *et al.* 2004).

Logistic regression assumes a particular functional form of survival probability as a function of one or more explanatory variables. Unlike ordinary least squares regression, logistic regression uses maximum likelihood estimation to derive parameter estimates. Overall goodness-of-fit of a binary logistic regression model is assessed using the Hosmer and Lemeshow (2000) test, which is considered more robust than the traditional chi-square test (Yang *et al.* 2003; Zhao *et al.* 2004).

2.10 THEORETICAL AND STATISTICAL ISSUES IN GROWTH MODELLING

A major assumption of regression analysis is that the error terms are independent, identically distributed, normal random variables. Repeated data measurements on the same tree (e.g. bole diameters at regular intervals along a single tree trunk), or over time (e.g. incremental increase in diameter at five-year intervals), are commonly utilized in forestry modelling. Such data are spatially or temporally autocorrelated, and therefore violate the assumption of independence of error terms. The application of regression analysis to autocorrelated data has a number of deleterious consequences. While the estimated regression coefficients remain unbiased and consistent, they no longer have the minimum variance property. In addition, both the mean squared error of the variance and the standard errors of the coefficients may be underestimated. Finally, statistical tests and associated confidence intervals are no longer reliable (Neter *et al.* 1990; Kmenta 1986; Kozak 1997).

Multicollinearity is a second problem when using regression analysis in empirical forest modeling. Multicollinearity is a common phenomenon in overcomplicated models with several polynomial terms (Kozak 1997), especially when there are high inter-correlations among the independent variables. It is a common problem in many bole taper models used in forestry (Kozak 1997; Huang *et al.* 1997; Huang 1997). The presence of multicollinearity is assessed using the variance inflation factor (*VIF*), which is calculated as the condition number of the correlation matrix of the partial derivates with respect to each of the model parameters. At high levels of multicollinearity, minor changes in the data can result in large differences in parameter estimates, and high standard errors of the estimates. In addition, parameter estimates may attain unreasonable magnitudes (Kleinbaum *et al.* 1988; Myers 1986; Fox 1991).

Until relatively recently, forest growth and yield modellers failed to address the serious issues of autocorrelation and multicollinearity in forestry data, since few statistical tools were available to deal with these problems. Generalized least squares regression techniques were used to address some of these issues (Monserud 1984; Goelz and Burk 1992; Huang 1992), but with modest success. More recently, nonlinear mixed-effects models (NLMM) have been introduced to address the autocorrelation problem (Fang and Bailey 2001; Leites and Robinson 2004; Trincado and Burkhart 2006; Huang *et al.* 2009; Sharma and Parton 2009). This technique estimates the covariance matrix of correlated data, and contains both fixed- and random-effects parameters in the model to deal with spatial or temporal autocorrelation (Schabenberger and Pierce 2001; Trincado and Burkhart 2006). Some recent studies have shown that use of the nonlinear mixed-effect technique improves model performance in forestry applications (e.g., Sharma and Parton 2009).

2.11 STUDY OBJECTIVES

Jack pine and black spruce are among the most widespread and economically important tree species in Manitoba. Reliable and accurate individual tree growth models for these two species are needed in order to develop forest management plans, to produce appropriate timber supply reviews and analyses, to determine values of annual allowable cut, to determine optimal stand rotation ages, and to develop strategies for the sustainable management of our provincial forests. However, to date little effort has been made to develop comprehensive tree growth and yield models for these species in Manitoba. The development of such models requires large amounts of reliable, long-term growth data, as well as an understanding of the complex and sophisticated approaches to statistical modelling used in modern applied forestry.

The overall objective of this study is to develop statistically robust and accurate individual tree growth models for jack pine and black spruce in eastern and central Manitoba. This objective requires the development of separate models for height growth and site index, incremental growth in diameter (basal area), bole taper, and individual tree mortality. Together, these models are central to the accurate estimation of forest growth and yield.

The development of robust growth and yield models requires considerable time and effort. In this study, consideration was given to a number of factors thought to affect model efficiency, accuracy and robustness. These include:

(1) Examination and selection of relevant predictor variables (including both individual tree and stand level variables) needed to obtain reliable and accurate model estimates of height growth and site index, incremental diameter growth, stem taper and individual tree mortality of jack pine and black spruce.

(2) Exploration and application of various statistical approaches to growth and yield modelling, including nonlinear least square (NLS), generalized nonlinear least square (GNLS) and nonlinear mixed-effects modeling (NLMM) methods.

(3) Examination and resolution of statistical problems associated with spatial autocorrelation, heteroscadacity and multicollinearity in forest growth and yield modeling.

(4) Validation of the developed growth and yield models, using independent data.

(5) Exploration of the role of tree spatial pattern (intraspecific competition) in predicting the diameter growth and mortality of individual trees in jack pine and black spruce stands.

(6) Evaluation of the role of tree crown ratio in determining bole taper in jack pine and black spruce.

CHAPTER 3 MODELLING HEIGHT GROWTH AND SITE INDEX OF BLACK SPRUCE AND JACK PINE

3.1 INTRODUCTION

Tree height growth and site index are commonly used to measure stand productivity and site quality in North American forestry practice (Carmean 1975; Goelz and Burk 1992; Huang *et al.* 1997). Site index, defined as the mean height of dominant and co-dominant trees in a stand 50 years after they have reached breast height (1.3 m), is widely used as a measure of site productivity in forest inventory studies (Carmean 1975; Goelz and Burk 1992; Huang, *et al.* 1994b; Philip 1998; Manitoba Conservation 2000). For example, a jack pine stand containing trees that are taller at breast height age 50 than other similar-aged stands of the same species is more productive, and will have a higher site index. Breast height age (i.e. tree age at 1.3 m height) rather than actual tree age is used since early height growth is erratic and does not necessarily reflect site productivity (Clutter *et al.* 1983). Dominant trees are defined as the tallest trees in the stand, while co-dominant trees are those whose crowns form the predominant stand crown height and receive full light from above, but comparatively little from the sides (Manitoba Conservation 2000).

The site index is a core variable in many forest growth and yield models (Clutter *et al.* 1983; Davis and Johnson 1987), as it provides a standardized comparison of productivity potential among sites over a broad range of stand conditions. Stands with a high site index yield greater merchantable timber volume, and are therefore more productive, than stands with the lower site index.

As a standardized measure of the rate of growth in tree height, the site index provides a comprehensive numeric measure of site productivity. Site productivity is an important baseline variable for forest-level planning and in the development of silviculture strategies. Estimates of site index are therefore used to describe site quality, to project timber volume growth and yield, and to formulate silviculture prescriptions and treatments in order to optimize forest stand yield (Husch *et al*. 2003). Site index is also used in forest growth and yield modelling, and in applied forest inventory projections to determine timber supply and sustainable annual allowable cuts.

The rate of growth in tree height is determined by a number of factors, including climate (e.g. temperature, precipitation and light), edaphics (e.g. soil moisture, nutrients, and aeration), and stand conditions (e.g. intra and inter-specific competition). In sites with optimal conditions, trees grow well and the site index is therefore high. Growing conditions are compromised when one or more site factors are limiting (or in excess), with the result that trees grow less well and the site index is lower.

The site index of a given species is known to vary across biogeoclimatic units (Klinka and Carter 1990), but the precise relationship is not always simple or clear. Indeed, the site index of a given forest stand most likely reflects the complex interaction of numerous influential environmental and edaphic factors (Klinka and Carter 1990; Wang *et al.* 1994; Wang and Klinka 1995; Wang and Klinka 1996). Due to strong differences in climatic and edaphic factors among ecoregions, the uncritical application of a model developed for one region often results in biased predictions of tree height growth when applied to other regions (Huang *et al.* 2000b; Peng *et al.* 2001). For example, the uncritical application of height-diameter models from one region resulted in tree height overestimations of up to 29.1%, and underestimations of up to 21.9%, in other regions (Huang *et al.* 2000b).

There are a number of theoretical and statistical challenges in height growth and site index modeling, the most important of which is variable autocorrelation. The fundamental assumption of error independence (i.e. lack of autocorrelation) in regression analysis is often violated in height and site index modelling, since stem analysis data are measured along different sections of the same tree bole and are therefore spatially autocorrelated (Kozak 1997). The lack of error independence attributable to autocorrelation has a number of consequences related to statistical inference, including: (a) estimated regression coefficients are unbiased and consistent, but no longer have the minimum variance property; (b) both the mean squared error of the variance and the standard errors of the coefficients may be underestimated; (c) statistical tests, and associated confidence interval estimates, are no longer reliable or strictly valid (Neter *et al.* 1990; Kmenta 1986; Kozak 1997).

Although tree height growth data are inherently spatially autocorrelated, until recently most height growth and site index models failed to fully address issues of autocorrelation due to the lack of appropriate statistical tools and approaches. Generalized least squares techniques were used to address some of the issues and problems related to autocorrelation (e.g. Monserud 1984; Goelz and Burk 1992; Huang 1992), but with limited success. More recently, nonlinear mixed-effects model (NLMM) techniques have been employed to more effectively address problems of spatial autocorrelation in forest tree height growth modelling (Fang and Bailey 2001; Leites and Robinson 2004; Trincado and Burkhart 2006; Huang *et al.* 2009; Sharma and Parton 2009). In the NLMM approach, the covariance matrix of autocorrelated data is estimated and random-effects parameters are incorporated into the model to account for the autocorrelation structure (Schabenberger and Pierce 2001; Trincado and Burkhart 2006). In forestry tree growth applications, the NLMM technique has been shown to improve model performance (e.g. Sharma and Parton 2009).

Jack pine and black spruce are among the most widespread and economically important tree species in Manitoba. Reliable height and site index models for these two species are needed in order to develop forest management plans, timber supply reviews and analyses, annual allowable cut determination and sustainable forest management. In an effort to find the most appropriate approaches and models that suit local conditions, the Forestry Branch of Manitoba Conservation has sectioned hundreds of jack pine and black spruce trees across the province.

The objective of this study is to develop biologically reasonable, parsimony, compatible and independently validated height growth and site index models for black spruce and jack pine in Manitoba. The developed models can be used to predict site index given tree height and age data, or to predict height given site index and tree age data.

3.2 STUDY AREA

The stem analysis data used in this study were collected in the Boreal Shield and Boreal Plain ecozones of Manitoba, which contain the commercially important forests of Manitoba (**Figure3.1**). A continental climate of long cold winters, and short warm summers, is characteristic of the region. The mean annual temperature ranges from -3.3^{o}C in the northwest (Lynn Lake, MB), to 2.5^{o}C in the southeast (Sprague, MB); mean July and January temperature ranges are 16.0 to 18.7^{o}C, and -25.0 to $-17.4\ ^{o}$C, respectively. The mean annual precipitation ranges from 48 cm (Lynn Lake, MB) to 61 cm (Sprague, MB), approximately two-thirds of which falls (mostly as rain) between the months of May and September (Environment Canada 2008).

The Boreal Shield ecozone is underlain by acidic Precambrian granite bedrock. The major surficial deposits in the southern portion of this ecozone include granite rock outcrops, organic peat deposits, and glacial till. In the northern regions of the Boreal Shield, deep basin glaciolacustrine deposits of clay, silt and sand predominate; deposits of glacial till occur in regions adjacent to the Saskatchewan border. The major soil types in the southern regions are organic peatlands, chernozems, and luvisols. Granite rock outcrops and organic peatlands predominate in the region east of Lake Winnipeg. In the northern section of this ecozone, the major edaphic types are luvisols, organic peatlands, and granite rock outcrops, with brunisolic soils occurring in areas adjacent to the Saskatchewan border (Weir 1983).

The southeastern portion of the Manitoba Boreal Shield is dominated by mixed wood stands of trembling aspen and white spruce, with extensive stands of jack pine on sandy soils and black spruce on organic peatlands. The forests further north are dominated by conifers: white spruce and jack pine on luvisolic soils and rock outcrops, and black spruce on organic peatlands. The major softwood species in this ecozone (in order of declining abundance) are black spruce, jack pine, white spruce, tamarack and balsam fir. The major hardwoods are trembling aspen, balsam poplar and white birch (Zoladeski *et al.* 1995).

The Boreal Plains ecozone is underlain with basic, calcareous sedimentary and metamorphic limestones. Surficial deposits of the Manitoba Escarpment (Riding Mountain, Duck Mountain and Porcupine Hills) are dominated by moderately calcareous glacial till derived from Mesozoic shales. This region contains large areas of stagnation moraine (rolling topographic with a relief of 8 m) and glacial till plains. In the northern regions of the Boreal Plains, the surficial deposits are mostly highly calcareous glacial tills derived from Paleozoic carbonate rock. Luvisolic soils are characteristic of the Manitoba Escarpment. The Interlake and northern regions are more edaphically variable, and include chernozemic soils in the south, brunisols north of Lake Winnipegosis, and peatland organic soils along the western shores of Lake Winnipeg and Lake Winnipegosis (Weir 1983).

Much of the Boreal Plains ecozone is dominated by mixed-wood stands of trembling aspen and white spruce. Extensive stands of jack pine occur on sandy soils, and black spruce dominates on organic peatlands. The major softwood species are white spruce, black spruce, jack pine, balsam fir and tamarack. The major hardwood species are trembling aspen, balsam poplar and white birch (Zoladeski *et al.* 1995).

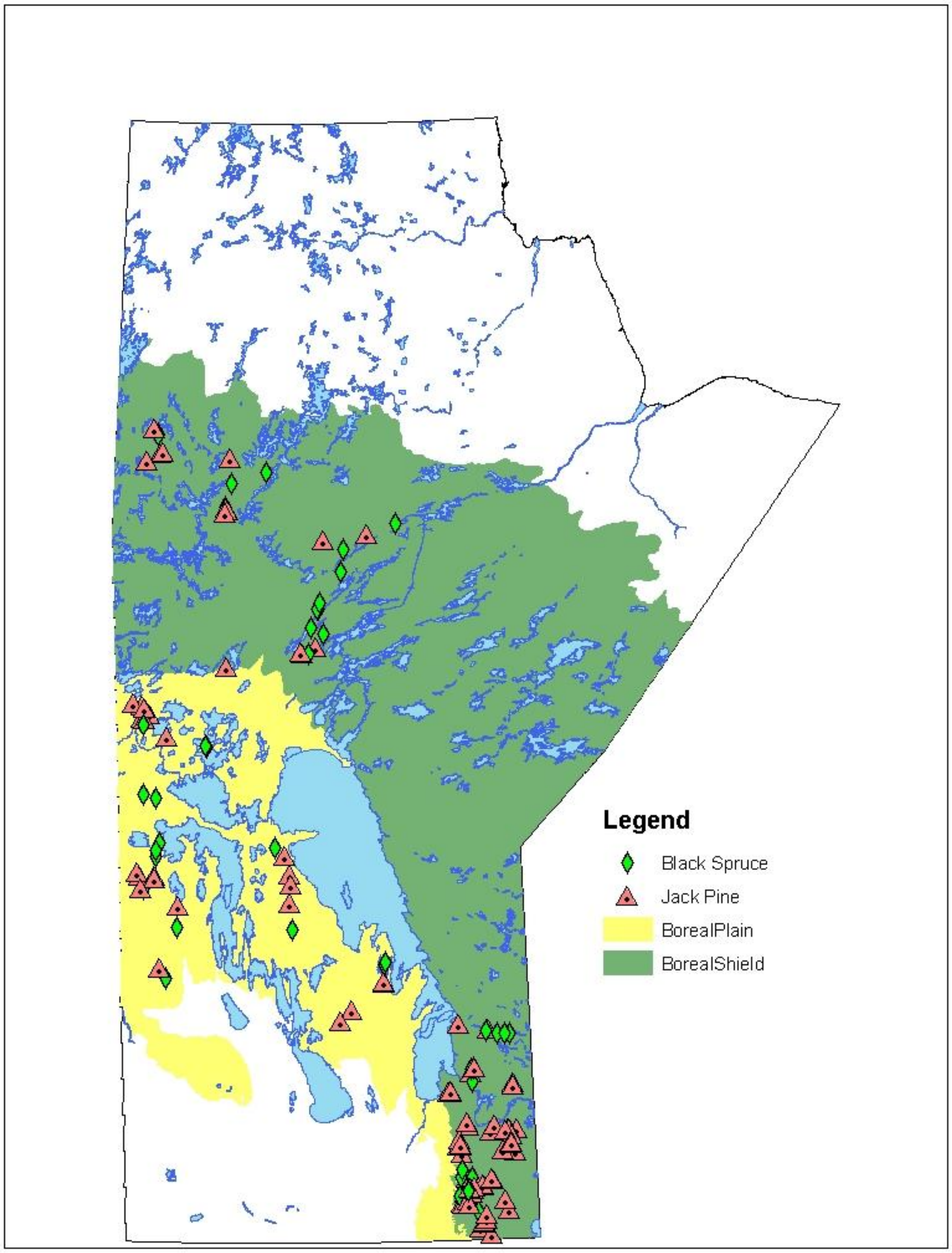


Figure 3.1. Locations of the black spruce (*n* = 28) and jack pine (*n* = 52) permanent sample plots (PSP) within the Boreal Plain and Boreal Shield ecozones of Manitoba.

3.3 STEM ANALYSIS DATA

Stem (or bole) analysis or sectioning is a commonly used in forest mensuration to quantify height and diameter growth, and changes in overall form, of a tree (Husch *et al.* 2003). Specifically, the temporal development of tree height, diameter, form and volume can be accurately reconstructed by counting tree rings and measuring the diameter of each cut surface from a felled and sectioned tree (Spurr 1952). In this study, stands were selected for stem analysis according to the following criteria; (a) species composition of the stands is > 80% basal area of jack pine or black spruce; (b) stands are fully stocked, mature, and even-aged; (c) stands are undisturbed by humans since initiation.

Standardized sampling procedures were used to select the trees used in stem analysis. A 300 m^2 circular (radius = 9.77 m) plot was randomly located and established within each selected forest stand, at least 100 m from the stand boundary and roads. Within each plot, all trees (DBH ≥ 7 cm) were tallied. For the development of site index models, three dominant and co-dominant trees (usually two dominant trees and one co-dominant tree) were selected, excluding trees with visible breakages, large forks, or other features that might interrupt normal height growth. Prior to felling, each selected tree was marked on its north side at heights of 0.33, 0.67, 1.0 and 1.3 m. Tree stem diameter was recorded at these four heights and at ground level, and crown width was determined.

After felling each selected tree, the height to live crown and total tree height were recorded. Stem cross-sections (so-called “cookies”) were then taken at bole heights of 0.33, 0.67, 1.0 and 1.3 m, and at 1.3 m height intervals above breast height (1.3 m) until the bole reached a diameter (outside bark) of 7 cm. Thereafter stem cross-sections were taken at 20 cm intervals until the bole reached a diameter of 4 cm. The north direction was recorded on each stem cross-section. All stem cross-sections were aged twice, by counting the number of rings in the north and east directions. Rings were counted in the laboratory under magnification, marking every 10th ring to facilitate recounting. In both jack pine and black spruce, a single growth ring is produced each year making the conversion to age very straightforward (Carmean 1972; Newberry 1991). In order to obtain the breast-height age, the number of years to reach breast height was subtracted from the total tree age. The horizontal cuts for stem analysis usually occur between the pith nodes, resulting in a small bias that affects the breast height age determination by a half-year on average (Carmean 1972; Dyer and Bailey 1987; Newberry 1991; Nigh 1995; Salas and García 2006). This bias is very small in practical applications (Nigh 1995), especially for relatively slow growing species such as black spruce and jack pine.

For each tree, height was plotted against breast-height age to examine the data for logical errors and atypical height-age patterns. Fourteen trees showing atypical growth patterns that were attributed to suppression, physical damage, or errors in data collection or collation were removed from the dataset. To minimize the problem of unequal length intervals in the stem cross-sections, every sixth data measurement was used for data collected at heights above 7 cm bole diameter. As a result, the measurement for the lower portion of the tree (stem diameter > 7 cm) was 1.3 m, and for the upper portion of the trees (stem diameter < 7cm) was 1.2 m.

Two approaches to site index model development have been described in the literature. The first is the stand interpolation approach, in which the height and age data of trees within a plot are interpolated to obtain plot-averaged height and age data that is used to determine the site index for model fitting (Nigh *et al*. 2002). The second method is the single tree approach, in which the cross-sectional data for each tree is used directly in model fitting (Carmean 1972; Huang *et al.* 1994b; Huang 1997). It has been shown that the interpolation approach may introduce additional errors and distort the shape of height-age curves (e.g. Huang 1997; Salas and García 2006). The single tree approach was therefore used in this study.

A total of 333 trees (201 black spruce and 132 jack pine) with breast height ages > 50 years were used for site index model development and validation (**Table 3.1**). The distribution of the 201 black spruce and 132 jack pine trees by site index and age class are summarized in **Tables 3.2** and **3.3**. Site index values for black spruce trees are quite low (< 11 m for over half the trees), and the range of breast height ages (50-200 years) is quite wide. There are relatively few black spruce stands with higher site index values, and this is particularly true for older stands. Most black spruce stands in Manitoba are relatively unproductive (Zoladeski et al. 1998), and many of the more productive stands were likely harvested in the past. By contrast, the site index values for jack pine tree are somewhat higher (mostly 11-19 m), with tree breast height ages ranging from 50 to 120 years.

Approximately 80%, or 265, of the trees (160 black spruce trees and 105 jack pine) were randomly selected and used for model fitting, while the remaining 68 trees (41 black spruce and 27 jack pine) were reserved for later model validation.

3.4 MODEL SELECTION AND ANALYSIS

3.4.1 Candidate Height Growth and Site Index Models

Based on a comprehensive review of the literature on tree height growth and site index modeling, the following candidate models were selected for consideration in this study. These models are commonly used to model height growth of boreal trees species in various regions of Canada (BC MOF 1981; Clutter *et al.* 1983; Newnham 1988a; Ker and Bowling 1991; Huang 1997; Nigh *et al.* 2002, 2009):

[3.1]

$$H = 1.3 + (SI - 1.3) \cdot \{\frac{1 + b_0 (SI - 1.3) + \exp[b_1 + b_2 \ln(50 + b_3) - \ln(SI - 1.3)]}{1 + b_0 (SI - 1.3) + \exp[b_1 + b_2 \ln(Bhage + b_3) - \ln(SI - 1.3)]}\}$$

(Huang 1997)

[3.2]

$$H = 1.3 + (SI - 1.3) \cdot \{\frac{1 + \exp[b_1 + b_2 \ln(50 + b_3) - \ln(SI - 1.3)]}{1 + \exp[b_1 + b_2 \ln(Bhage + b_3) - \ln(SI - 1.3)]}\}$$

(Huang 1997)

[3.3]

$$H = 1.3 + (SI - 1.3) \cdot \{\frac{1 + \exp[b_1 + b_2 \ln(50 + b_3) - b_4 \ln(SI - 1.3)]}{1 + \exp[b_1 + b_2 \ln(Bhage + b_3) - b_4 \ln(SI - 1.3)]}\}$$

(Huang 1997)

[3.4]

$$H = 1.3 + (SI - 1.3) \cdot \{\frac{1 + \exp[b_0 + b_1 \ln(49.5) + b_2 \ln(SI - 1.3)]}{1 + \exp[b_0 + b_1 \ln(Bhage - 0.5) + b_2 \ln(SI - 1.3)]}\}$$

(Nigh *et al.* 2002, 2009)

[3.5]

$$H_2 = 1.3 + (H_1 - 1.3) \cdot \left(\frac{1 - \exp(-bT_2)}{1 - \exp(-bT_1)} \right)^c$$

where $b = b_0 (H_1 - 1.3)^{b_1} b_2^{(H_1 - 1.3)}$

$$c = b_3 (H_1 - 1.3)^{b_4} T_1^{b_5}$$

(Clutter *et al.* 1983; Huang 1997)

[3.6]

$$H_2 = 1.3 + (H_1 - 1.3) \cdot \left(\frac{1 - \exp(-bT_2)}{1 - \exp(-bT_1)} \right)^c$$

where $b = b_0 (H_1 - 1.3)^{b_1} b_2^{(H_1 - 1.3)/T_1}$

$$c = b_3 (H_1 - 1.3)^{b_4} T_1^{b_5}$$

(Clutter *et al.*1983; Huang 1997)

Table 3.1. Statistical summary, by ecozone, of the trees used for stem analysis and site index model development of black spruce and jack pine.

ECOZONE	**SPP***	**Mean**	**Min**	**Max**	**SD**	**Variables**
Boreal Plains	BS	102	74	182	22.4	Breast height age (years)
	(*n*=51)	16.1	9	25.8	3.05	DBH (cm)
		16.4	11.6	23.7	2.71	Total height (m)
	JP	85	52	122	20	Breast height age (years)
	(*n* = 50)	19.7	13.3	31.2	4.1	DBH (cm)
		16.6	10.1	22.3	2.53	Total height (m)
Boreal Shield	BS	95	53	190	22.8	Breast height age (years)
	(*n* = 150)	17.8	9.3	35.2	3.71	DBH (cm)
		16.5	10	25	2.43	Total height (m)
	JP	77	53	111	17.1	Breast height age (years)
	(*n* = 82)	22.1	13.2	38	4.12	DBH (cm)
		17.6	11.5	23.5	2.64	Total height (m)

* BS = Black Spruce; JP = Jack Pine.

Table 3.2. Summary of the 201 black spruce trees used for site index model development, cross-classified by breast height age (yrs) and site index (m).

Breast height age class (years)	**SITE INDEX (m)**					
	≤ 9	9-10.9	11-12.9	13-14.9	15-16.9	Total
50-59		1		3	1	**5**
60-69		1	4	9	7	**21**
70-79		3	6	6	3	**18**
80-89	6	5	7	4	1	**23**
90-99	10	19	15	11	2	**57**
100-109	10	10	4	1		**25**
110-119	18	5	4			**27**
120-129	6	1	2	1		**10**
130-139	3					**3**
140-149	5	2				**7**
150-159	2	1				**3**
180-189	1					**1**
190-199	1					**1**
Total	**62**	**48**	**42**	**35**	**14**	**201**

Table 3.3. Summary of the 132 jack pine trees used for site index model development, cross-classified by breast height age (yrs) and site index (m).

Breast height age class (years)	**SITE INDEX (m)**							
	≤ 9	9-10.9	11-12.9	13-14.9	15-16.9	17-18.9	19-20.9	TOTAL
50-59		1	3	7	7	6	1	**25**
60-69		1	1	5	3	3	1	**14**
70-79	1	3	8	10	18	2	2	**44**
80-89			1	2	3		1	**7**
90-99			4	4	1	1		**10**
100-109	4	3	7	6	7			**27**
110-119		1			1			**2**
120-129				2	1			**3**
Total	**5**	**9**	**24**	**36**	**41**	**12**	**5**	**132**

[3.7] $$H = 1.3 + b_1(SI - 1.3)^{b_2}\left(1 - K^{\frac{Bhage - 0.5}{49.5}}\right)^{b_3(SI - 1.3)^{b_4}}$$

where $$K = 1 - \left\{\frac{SI - 1.3}{b_1(SI - 1.3)^{b_2}}\right\}^{\frac{1}{b_3(SI - 1.3)^{b_4}}}$$ (Newnham 1988a)

[3.8] $$H = 1.3 + (b_0 + b_1 SI)(1 - \exp(-b_2(Bhage - 0.5)))^{\left(b_3 SI^{b_4}\right)}$$

(Ker and Bowling 1991)

[3.9] $$H = 1.3 + b_1 SI(1 - \exp(\ b_2(Bhage - 0.5)))^{b_3}$$

(BC MOF 1981)

[3.10] $$H = 1.3 + (b_0 SI^{b_1})(1 - \exp(-b_2(Bhage - 0.5)))^{\left(b_3 SI^{b_4}\right)}$$

(modified from Ker and Bowling 1991)

In these regression models *H* = height (m), *SI* = site index (m), *Bhage* = breast height age (years), H_1 = tree height (m) at time one, H_2 = tree height (m) at time two, T_1 = breast height age (years) at time one, and T_2 = breast height age (years) at time two. Note that $H_2 > H_1$, and $T_2 > T_1$.The parameters to be estimated are given by $b_{0,}$ - b_5. The constant 1.3 is used in all models to account for the fact that site index is expressed in terms of age above breast height (1.3 m).

Models [3.1] to [3.4] are similar in structure, and are derived from the generalized logistic expression $y = f_1/[1+\exp(f_2)]$, by constraining parameter f_1 and defining various linear combinations of the logarithms of age and site index in parameter f_2 (Monserud 1984). For example, for the derivations of model [3.4] one defines:

$$f_2 = b_0 + b_1 \ln(Bhage - 0.5 + b_2 \ln(SI - 1.3)$$

$$y = H - 1.3$$

Substitution into the generalized logistic equation yields:

[3.4a] $$H - 1.3 = f_1 /(1 + \exp(b_0 + b_1 \ln(Bhage - 0.5) + b_2 \ln(SI - 1.3)$$

Note that when *Bhage* = 50 years, *H* becomes *SI* (based on the definition of site index) and [3.4a] is expressed as

[3.4b] $$SI - 1.3 = f_1 /(1 + \exp(b_0 + b_1 \ln(50 - 0.5) + b_2 \ln(SI - 1.3)$$

Substituting f_1 in [3.4a] with that in [3.4b] yields:

[3.4c] $$(H - 1.3) /(SI - 1.3) = \{ \frac{1 + \exp[b_0 + b_1 \ln(49.5) + b_2 \ln(SI - 1.3)]}{1 + \exp[b_0 + b_1 \ln(Bhage - 0.5) - b_2 \ln(SI - 1.3)]} \}$$

Simple re-arrangement of [3.4c] produces model [3.4].

Models [3.1] and [3.3] have four parameters ($b_0 - b_3$), whereas the simpler models [3.2] and [3.4] have three parameters ($b_0 - b_2$). Models [3.5] and [3.6] are Chapman-Richards non-reciprocal difference equation models and have six parameters (Huang 1997). Model [3.7] is a conditioned four-parameter Chapman-Richards function (Newnham 1988a).

Models [3.4] and [3.9] are used to predict the site index of black spruce in British Columbia (Nigh *et al.* 2002, 2009; BC MOF 1981), while model [3.8] is the site index model used for black spruce and jack pine in New Brunswick (Ker and Bowling 1991). Model [3.10] is a modified version of [3.8], in which the term $b_0+b_1(SI)$ is changed to $b_0(SI^{b1})$.

Horizontal cut points in stem analysis usually occur between the pith node, producing an average bias in the determination of breast height age of one-half a year (Carmean 1972; Newberry 1991; Nigh 1995). To be consistent with previous site index model applications (e.g. Nigh 1995; Nigh *et al*. 2002), a 0.5-year adjustment of breast height age (i.e. *Bhage* - 0.5) was used for all models in this study.

3.4.2 Data Structure

When fitting models, site index (SI) is required as an independent variable in models [3.1] – [3.4] and [3.7] – [3.10]. The site index of each tree was determined by direct tree ring count at 50 years breast height age, or when necessary by interpolation of the two sections above and below the 50 years breast-height age point.

The difference equation models [3.5] and [3.6] can be expressed as the general form $H_2 = f(H_1, T_1, T_2)$. Two strategies are available for fitting difference equation models: all possible intervals, versus non-descending intervals only. Both approaches yield similar results (e.g. Borders et al 1988; Cao 1993; Huang 1997). In this study, only non-descending growth intervals (i.e. growth intervals where $H_2 > H_1$ and $T_2 > T_1$) were used.

3.4.3 Model Fitting and Analysis

The Gauss-Newton method of the SAS non-linear least squares procedures and Proc Model procedures (SAS/STAT, SAS Institute 2004) were used for the model fitting. To ensure that the non-linear regressions were global and not merely local least-squares solutions, different starting values of the model parameters were used to ensure consistency in parameter estimates. The fitted models were assessed using various statistical evaluation metrics, including the mean bias ($\bar{e}$), mean absolute error (*MAE*), percent bias (*Bias%*), root mean square error (*RMSE*), and the coefficient of determination (R^2):

[3.11]
$$\bar{e} = \frac{\sum_{i=1}^{n} (Y_i - \hat{Y}_i)}{n}$$

[3.12] $$MAE = \frac{\sum_{i=1}^{n} \left| Y_i - \hat{Y}_i \right|}{n}$$

[3.13] $$Bias\ \% = (\bar{e} / \bar{Y}) \times 100 = \frac{\bar{e}}{\sum Y_i / n} \times 100$$

[3.14] $$RMSE = \sqrt{\bar{e}^2 + SD^2}$$

[3.15] $$R^2 = 1 - \frac{\sum_{i=1}^{n} (Y_i - \hat{Y}_i)^2}{\sum_{i=1}^{n} (Y_i - \bar{Y})^2}$$

In these equations Y_i is the measured height of the *i*th tree, $\hat{Y}_i$ is its model estimated height, $\bar{Y}$ is the mean of the measured tree heights, *SD* is the standard deviation of the prediction errors, and *n* is the number of trees. The statistic *RMSE*, which combines the mean bias and the variation of the biases, gives an overall measure of model accuracy and was used in this study as a primary criterion for model evaluation (Cochran 1977; Yang *et al.* 2009).

The statistical significance of the fitted model parameters was determined using standard methods (SAS Institute 2004), and residual plots were examined to detect outliers, to determine overall goodness-of-fit, and to ensure variance equality. In addition, height growth and site index curves for black spruce and jack pine were produced from the model results. These fitted model curves were empirically evaluated to ensure that the results were biological reasonable.

3.4.4 Model Validation

Model validation, a critical component of model development, is performed to obtain sufficient confidence with respect to model robustness, credibility and realism (Otto and Day 2007). In this study, the randomly selected stem analysis data (68 trees and 688 sections, including 41 black spruce trees (407 sections) and 27 jack pine trees (281 sections)) that were not used to develop the models were used in model validation. In this approach, the fitted models are tested using an independent data set (the validation data).

Commonly used prediction statistics, such as the R-squared values (R_p^2), root mean squared error ($RMSE_p$), mean bias ($\bar{e}$), percent bias (Bias%), mean absolute error (MAE), and the standard deviation of the prediction errors (s_e), were used to evaluate the fitted models using the validation data set. The mean and percent bias statistics are both measures of the average of differences between observed and predicted tree heights, the former in absolute terms and the latter in relative terms.

3.4.5 Comparison of Models Between Ecozones

The nonlinear extra sum of squares method (Bates and Watts 1988; Judge *et al.* 1988; Huang *et al.* 2000b) was used to test for differences in the height growth and site index models between the Manitoba Boreal Plains and Boreal Shield ecozones. This method has been used to compare differences among regionalized single tree volume equations (Pillsbury *et al.* 1995) as well as height-diameter equations (Huang *et al.* 2000b; Zhang *et al.* 2002).

The nonlinear extra sum of squares method requires the fitting of both full and reduced models. The full model incorporates different sets of parameters for the two ecozones, whereas in the reduced model the same set of parameters are used for both ecozones. Using the indicator (dummy) variables approach (Bates and Watts 1988; Huang *et al.* 2000b; Zhang *et al.* 2002), the full model [3.4] for the two ecozones is written as:

[3.16] $$H = 1.3 + (SI - 1.3) \cdot \left\{ \frac{1 + \exp[b_0 + b_{01}x + (b_1 + b_{11}x)\ln(49.5) + b_2 + (b_{21}x)\ln(SI - 1.3)]}{1 + \exp[b_0 + b_{01}x + (b_1 + b_{11}x)\ln(Bhage - 0.5) + (b_2 + b_{21}x)\ln(SI - 1.3)]} \right\}$$

A single indicator variable x is used in this equation to classify the two ecozones:

$x = 0$ for the Boreal Plains ecozone.
$x = 1$ for the Boreal Shield ecozone.

Note that the full model has six parameters. The error sum of squares for the full model, denoted as SSE(F), has $df_F = (n - 6)$ degrees of freedom; n is the total number of observations from both ecozones. The reduced model, in which the same set of parameters is used for both ecozones, takes the form of equation [3.4]. The corresponding error sum of squares term SSE(R) has $df_R = (n - 3)$ degrees of freedom since model [3.4] has three parameters.

The equality of models [3.4] and [3.16] is tested by considering the following hypotheses:

$$H_0 : b_{01} = b_{11} = b_{21} = 0$$

H_a: At least one of the equalities in H_0 is not true.

The appropriate test statistic (Bates and Watts 1988) is given by:

$$F = \frac{SSE(R) - SSE(F)}{df_R - df_F} \div \frac{SSE(F)}{df_F} \qquad [3.17]$$

If $F > F_{critical}(1 - \alpha ; df_R - df_F , df_F)$, then H_0 is rejected and it is concluded that separate models are required for the two ecozones. Conversely, if the F-statistic is not statistically significant (H_0 accepted) the combined or full model is adequate and appropriate; separate models for the two ecozones are not required.

3.4.6 Testing for the Effects of Autocorrelation

The site index models were developed using stem section analysis data, in which measurements are taken at different sections (heights) along a tree bole. The measurements and error terms resulting from stem analysis are therefore spatially auto-correlated. This presents problems in the application of regression analysis, which assumes that error terms are independent, identically distributed, normal random variables. When error terms are autocorrelated (i.e. non-independent), the estimated regression coefficients are unbiased and consistent, but they no longer have the minimum variance property. In addition, both the mean squared error of the variance and the standard errors of the coefficients may be underestimated, and statistical tests (and associated confidence interval estimates) are no longer reliable (Neter *et al.* 1990; Kmenta 1986; Kozak 1997).

Three approaches for dealing with and testing for the effects of spatial autocorrelation on tree height growth and site index predictive modeling were considered in this study. Generalized least squares techniques have been widely used to account for autocorrelation in forest growth modeling (Monserud 1984; Goelz and Burk 1992; Huang 1992). An alternative approach is to utilize a single randomly chosen measure for each tree (Kozak 1997). While this approach meets the independent error terms assumption, much of the measurement data collected on the trees is not utilized. A more recent approach uses nonlinear mixed-effects model (NLMM) techniques to address the problem of autocorrelation in forest growth modeling (Huang *et al.* 2009; Nigh *et al.* 2009; Sharma and Parton 2009). Each of these three approaches is discussed in greater detail below.

Generalized Nonlinear Least Squares Model (GNLS)

In this approach, the *i*th measurement in the height growth (site index) model with first-order autoregressive errors AR(1) is written as:

[3.18] $H_i = f(x_i, \theta) + \varepsilon_i$ where $\varepsilon_i = \rho\varepsilon_{i-1} + \mu_i$

Here tree height H_i (i = 1 to n) is expressed as a nonlinear function of the independent variable matrix x_i, θ is the parameter matrix, ε_i are random errors that follow an AR(1) process, ρ is the autoregressive parameter, and μ_i are the independent and identically distributed random errors (with mean zero and constant variance σ_μ^2).

The (i-1)th observation is similarly expressed as:

[3.19] $H_{i-1} = f(x_{i-1}, \theta) + \varepsilon_{i-1}$

Multiplying both sides of Eq. [3.19] by ρ and subtracting the results from Eq. [3.18] results in the following nonlinear equation with uncorrelated errors:

[3.20] $H_i = \rho H_{i-1} + f(x_i, \theta) - \rho f(x_{i-1}, \theta) + \varepsilon_i$

The non-linear least square (NLS) estimates for the parameters of [3.20] were obtained using the SAS/ETS software (SAS/STAT, SAS Institute 2004).

Random Selection of One Observation per Tree

As mentioned previously, autocorrelation in stem analysis data results from the utilization of several non-independent measurements from a given tree. Therefore, a straightforward method for avoiding autocorrelation is to randomly select and utilize a single measurement for each tree. While this approach ensures the independence of error terms, it has the drawback of not utilizing most of the collected measurement data. The method is nevertheless useful in forestry applications when testing for autocorrelation bias during model development (e.g. Kozak 1997).

Nonlinear Mixed-Effects Models (NLMM)

The nonlinear mixed-effects model approach has been used recently to address the autocorrelation problem in forestry modelling (Fang and Bailey 2001; Leites and Robinson 2004; Trincado and Burkhart 2006; Huang *et al.* 2009; Sharma and Parton 2009). This technique estimates the covariance matrix of correlated data, and considers both fixed and random-effects in the model through the incorporation of specified random-effects parameters (Schabenberger and Pierce 2001; Trincado and Burkhart 2006).

In mixed-effects models, the fixed-effects parameters are the mean responses (i.e. those common to all trees), whereas the random-effects parameters are localized responses (i.e. those specific to each tree). An important but challenging aspect of fitting mixed-effects models is the requirement to specify which parameter(s) in the model should be treated as fixed-effects, and which parameter(s) should be modeled as mixed-effects (i.e. fixed plus random).

In this study, different combinations of all parameter types were evaluated in the mixed-effects model approach. For example, the following seven models ([3.21] to [3.27]) were derived from model [3.4] by adding one ([3.21] to [3.23]), two ([3.24] to [3.26]) or three [3.24] random parameters in different locations within model [3.4]. All seven models were fitted and evaluated for both black spruce and jack pine.

[3.21]

$$H = 1.3 + (SI - 1.3) \cdot \{\frac{1 + \exp[b_0 + u_1 + b_1 \ln(49.5) + b_2 \ln(SI - 1.3)]}{1 + \exp[b_0 + u_1 + b_1 \ln(Bhage - 0.5) + b_2 \ln(SI - 1.3)]}\}$$

[3.22]

$$H = 1.3 + (SI - 1.3) \cdot \{\frac{1 + \exp[b_0 + (b_1 + u_1) \ln(49.5) + b_2 \ln(SI - 1.3)]}{1 + \exp[b_0 + (b_1 + u_1) \ln(Bhage - 0.5) + b_2 \ln(SI - 1.3)]}\}$$

[3.23]

$$H = 1.3 + (SI - 1.3) \cdot \{\frac{1 + \exp[b_0 + b_1 \ln(49.5) + (b_2 + u_1) \ln(SI - 1.3)]}{1 + \exp[b_0 + b_1 \ln(Bhage - 0.5) + (b_2 + u_1) \ln(SI - 1.3)]}\}$$

[3.24] $$H = 1.3 + (SI - 1.3)\cdot\{\frac{1+\exp[b_0 + u_1 + (b_1 + u_2)\ln(49.5) + b_2 \ln(SI - 1.3)]}{1+\exp[b_0 + u_1 + (b_1 + u_2)\ln(Bhage - 0.5) + b_2 \ln(SI - 1.3)]}\}$$

[3.25] $$H = 1.3 + (SI - 1.3)\cdot\{\frac{1+\exp[b_0 + u_1 + b_1 \ln(49.5) + (b_2 + u_2)\ln(SI - 1.3)]}{1+\exp[b_0 + u_1 + b_1 \ln(Bhage - 0.5) + (b_2 + u_2)\ln(SI - 1.3)]}\}$$

[3.26] $$H = 1.3 + (SI - 1.3)\cdot\{\frac{1+\exp[b_0 + (b_1 + u_1)\ln(49.5) + (b_2 + u_2)\ln(SI - 1.3)]}{1+\exp[b_0 + (b_1 + u_1)\ln(Bhage - 0.5) + (b_2 + u_2)\ln(SI - 1.3)]}\}$$

[3.27] $$H = 1.3 + (SI - 1.3)\cdot\{\frac{1+\exp[b_0 + u_1 + (b_1 + u_2)\ln(49.5) + (b_2 + u_3)\ln(SI - 1.3)]}{1+\exp[b_0 + u_1 + (b_1 + u_2)\ln(Bhage - 0.5) + (b_2 + u_3)\ln(SI - 1.3)]}\}$$

The parameters were estimated using maximum likelihood (ML) estimation, implemented through the SAS macro %NLINMIX with zero expansion (Littell *et al.*, 2006).

In addition to general mixed-effects model, the first-order autoregressive AR(1) approach was also introduced into the mixed-effects model. The best specified mixed-effects model was then determined using the two goodness-of-fit criteria, Akaike’s information criterion (*AIC*, Akaike, 1973) and Schwarz’s Bayesian information criterion (*BIC*, Schwarz, 1978):

[3.28] $$AIC = -2\ln(L) + 2k$$

[3.29] $$BIC = -2\ln(L) + k\ln(m)$$

In these equations *L* is the maximum likelihood (ML) value, *k* is the number of parameters of the model (i.e. the sum of the number of fixed-effects parameters and the effective number of estimated variance and covariance parameters), and *m* is the number of trees (for mixed-effects models) or the total number of observations (for fixed-effects models). The model with the smallest values for the goodness-of-fit criteria (*AIC* and *BIC* statistics) was selected over the others.

In order to make subject-specific predictions, the random parameters **u**$_i$ were predicted first using one or more prior measurements from each tree. This calculation was achieved by using the approximate Bayes estimator **u**$_i$ (Vonesh and Chinchilli 1997; Trincado and Burkhart 2006):

[3.30]
$$\hat{u}_i = \hat{D}Z_i^T (Z_i\hat{D}Z_i^T + \hat{R}_i)^{-1}\hat{e}_i$$

where $\hat{e}_i = H_i - f(x_i, \hat{\beta}, 0)$

In this equation $\hat{D}$ is the estimated variance–covariance matrix for random parameters **u**$_i$, $\hat{R}_i$ is the estimated variance–covariance matrix for the error term, and ***Z**$_i$* is the partial derivatives matrix of ***H**$_i$* with respect to random parameters:

[3.31]
$$Z_i = \partial f(x_i, \beta, 0) / \partial u_i \,|_{\hat{\beta},0} \,.$$

After the random parameters were predicted, tree-specific height predictions were obtained using (Vonesh and Chinchilli 1997; Huang *et al.* 2009):

[3.32]
$$\overset{\frown}{H}_i = f(x_i, \hat{\beta}, 0) + Z_i\hat{u}_i$$

Note that the predictions of random parameters depend on the number of prior measurements available (Calama and Montero 2004).

For testing purpose, three scenarios were considered based on the validation data:

(a) All the height measurements of each tree at different stem sections were used.
(b) A single measurement per tree (at height of 2.6 m) was used.
(c) Two measurements per tree (at heights of 2.6 and 5.2 m) were used.

For each scenario, the predicted root mean squared error (*RMSEp*) was used to compare model performance, since it considers both bias and variations in model predictions (Cochran 1977; Yang *et al.* 2009).

3.5 RESULTS

3.5.1 Fitting Height Growth and Site Index Models

The fitted nonlinear least squares parameter estimates, and associated goodness-of-fit statistics (coefficient of determination (R^2) and root mean squared error (*RMSE*)) for models [3.1] to [3.10] for black spruce and jack pine are presented in **Table 3.4**. All the models successfully converged, and most of the regression parameters were statistically significant ($P < 0.05$). The only non-significant parameters were b_2 for black spruce models [3.7] and [3.9], b_2 for jack pine model [3.7], and b_0 for jack pine model [3.1].

3.5.2 Model Comparisons: Goodness-of-fit Statistics

Black spruce models [3.1] to [3.4], [3.8] and [3.10] performed quite well compared to the other models (**Table 3.4**). The R^2 values for these models are very high (> 0.94, explaining over 94% of variation in height), and the *RMSE*s values are low (< 1.00 m). Model [3.3] has the smallest $RMSE = 0.929$. The difference equation models [3.5] and [3.6] produced the poorest fits ($R^2 < 0.92$, $RMSE = 1.29$).

Similar results were obtained for jack pine, with models [3.2] to [3.4], and [3.8] to [3.10], showing the best performance. The R^2 values for these models are very high (> 0.96, explaining over 96% of variation in height), and the RMSEs values are low (< 0.90 m). As with black spruce, the difference equation jack pine models [3.5] and [3.6] produced the poorest fits ($R^2 < 0.94$, $RMSE = 1.18$).

Table 3.4. Estimated regression parameters (b_0 – b_5) and goodness-of-fit statistics for model [3.1] to [3.10], for black spruce and jack pine.

Spp.	Model	*b0*	*b1*	*b2*	*b3*	*b4*	*b5*	R^2	*RMSE*	*n*
BS	[3.1]	0.3405	12.5285	-2.0152	15.4910			0.9537	0.933	1666
	[3.2]		15.1707	-2.8481	34.4994			0.9507	0.963	1666
	[3.3]		12.9441	-2.0981	17.2428	1.6610		0.9541	0.929	1666
	[3.4]	11.030	-1.1816	-2.3934				0.9486	0.982	1666
	[3.5]	0.0161	-0.5171	1.0074	0.6542	-0.4417	0.3653	0.9172	1.293	16442
	[3.6]	0.0180	-0.5317	0.7696	0.6494	-0.4608	0.3773	0.9174	1.292	16442
	[3.7]		31.2523	0.0319*	3.3442	-0.5174		0.9520	0.949	1666
	[3.8]	15.722	1.2556	0.0086	3.6155	-0.5169		0.9537	0.933	1666
	[3.9]		5.1465	-0.0293*	-0.0037	0.9931		0.9419	1.045	1666
	[3.10]	10.164	0.4381	0.0090	3.8520	-0.5417		0.9520	0.95	1666
JP	[3.1]	0.0665*	7.5819	-1.0231	1.1804			0.9640	0.859	1174
	[3.2]		6.9827	-1.0664	1.5328			0.9637	0.863	1174
	[3.3]		8.1884	-1.0241	1.1867	1.4798		0.9640	0.859	1174
	[3.4]	8.6425	-0.9032	-1.7148				0.9641	0.857	1174
	[3.5]	0.0300	-0.4966	1.0505	0.8026	-0.5000	0.3749	0.9357	1.176	12356
	[3.6]	0.0237	-0.1351	0.9078	0.7683	-0.4609	0.3667	0.9347	1.184	12356
	[3.7]		307.7456	-0.9610*	0.8760	-0.1910		0.8120	1.964	1174
	[3.8]	3.8609	1.3564	0.0152	2.5012	-0.3884		0.9642	0.857	1174
	[3.9]		1.6718	-0.0588	-0.0164	0.9174		0.9628	0.873	1174
	[3.10]	2.5182	0.8385	0.0149	2.4031	-0.3774		0.9639	0.861	1174

Note: BS = black spruce; JP = jack pine; R^2 - prediction coefficient of determination; RMSE - root mean square error of prediction; *n* = total number of observations (height-Bhage pairs) from sectioned trees.

* indicates that the fitting parameter was not statistical significant.

In general, all ten models produced similar fits for both black spruce and jack pine. Those models with four or five parameters (i.e. models [3.1], [3.3] and [3.5] to [3.10]) typically performed no better than (and sometimes less well than) models [3.2] and [3.4], which have only three parameters. This indicates that the more parsimonious (i.e. fewer parameters) models [3.2] and [3.4] are superior to the other, over-parameterized, models.

3.5.3 Model Comparisons: Residuals and Height-Age Curves

Residual plots (i.e. residuals plotted against predicted height) of models [3.1] to [3.10] for black spruce and jack pine are shown in **Figures 3.2** and **3.3** respectively. The residual plots for black spruce models [3.7] and [3.9], and those for jack pine models [3.1] and [3.7], are not presented since one parameter in each of these four models was not statistically significant.

For both the black spruce and jack pine, the residual plots for models [3.1] to [3.4], and models [3.8] to [3.10], display an approximately horizontal band of data points centered on zero, mostly within the ± 2 m range. The residual plots for models [3.5] and [3.6] indicate much higher residual values, confirming the comparatively poor fit of these two models. Note that stem analysis data are measured at specific heights on each tree, which produces the parallel line patterns seen in the residual plots.

The residual plots also indicate that the regression residuals are quite large (mostly within ± 2 m, with some as large as ± 4 m or more). This is not surprising, however, given that the stem analysis data were obtained over a very wide range of site and stand conditions.

Site index curves generated from models [3.1] to [3.10], overlain with the observed tree stem sectioning data for black spruce and jack pine, are shown in

Figures 3.4 and **3.5** respectively. Site index values (i.e. predicted tree heights at 50 years breast height age) for the range *SI* = 5 – 25 m, in 5 m increments, are displayed. The shape of the fitted site index curves changes as *SI* increases. The lower site index curves (e.g. *SI* = 5) are flatter and almost linear, whereas the higher site index curves (e.g. *SI* = 25) have a higher initial slope and approach the asymptote (maximum tree height) more quickly. These models are biologically reasonable, since it is known that trees grow rapidly in height at younger ages but slow their rate of height growth at later ages as they approach a biologically constrained maximum height (Husch et al. 2003). The site index curves for black spruce models [3.5], [3.6] and [3.8], and jack pine model [3.9], display non-asymptotic trends over time, particularly for larger *SI* values. Such results are biologically unrealistic, and it is concluded that models [3.1] to [3.4] and [3.10] for black spruce, and models [3.2] to [3.6], [3.8] and [3.10] for jack pine, produce more biologically reasonable model results.

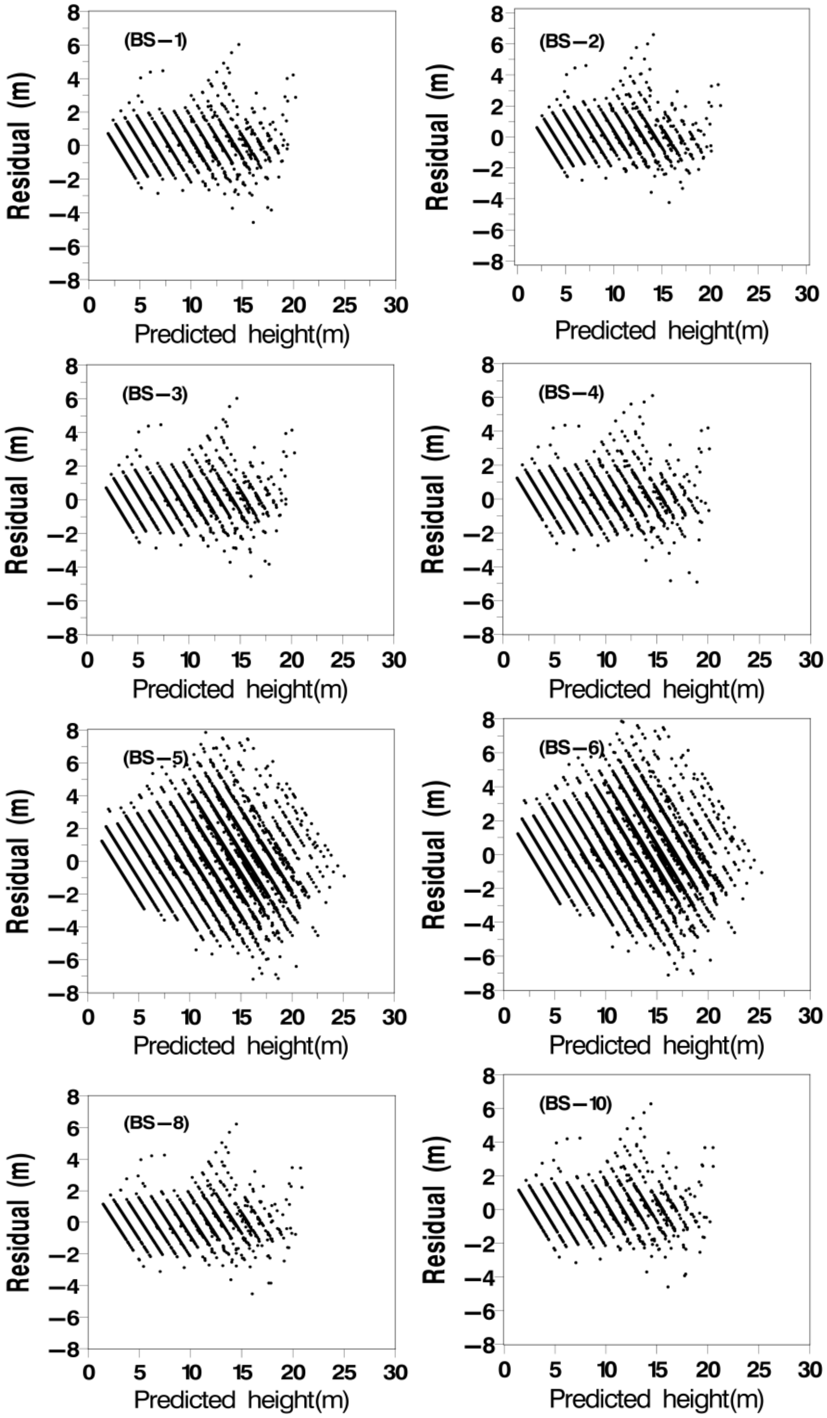


Figure 3.2. Residuals plotted against predicted height of black spruce from model [3.1] to [3.10]. Plot for models [3.7] and [3.9] were not shown, since the parameters of b_2 were not statistically significant.

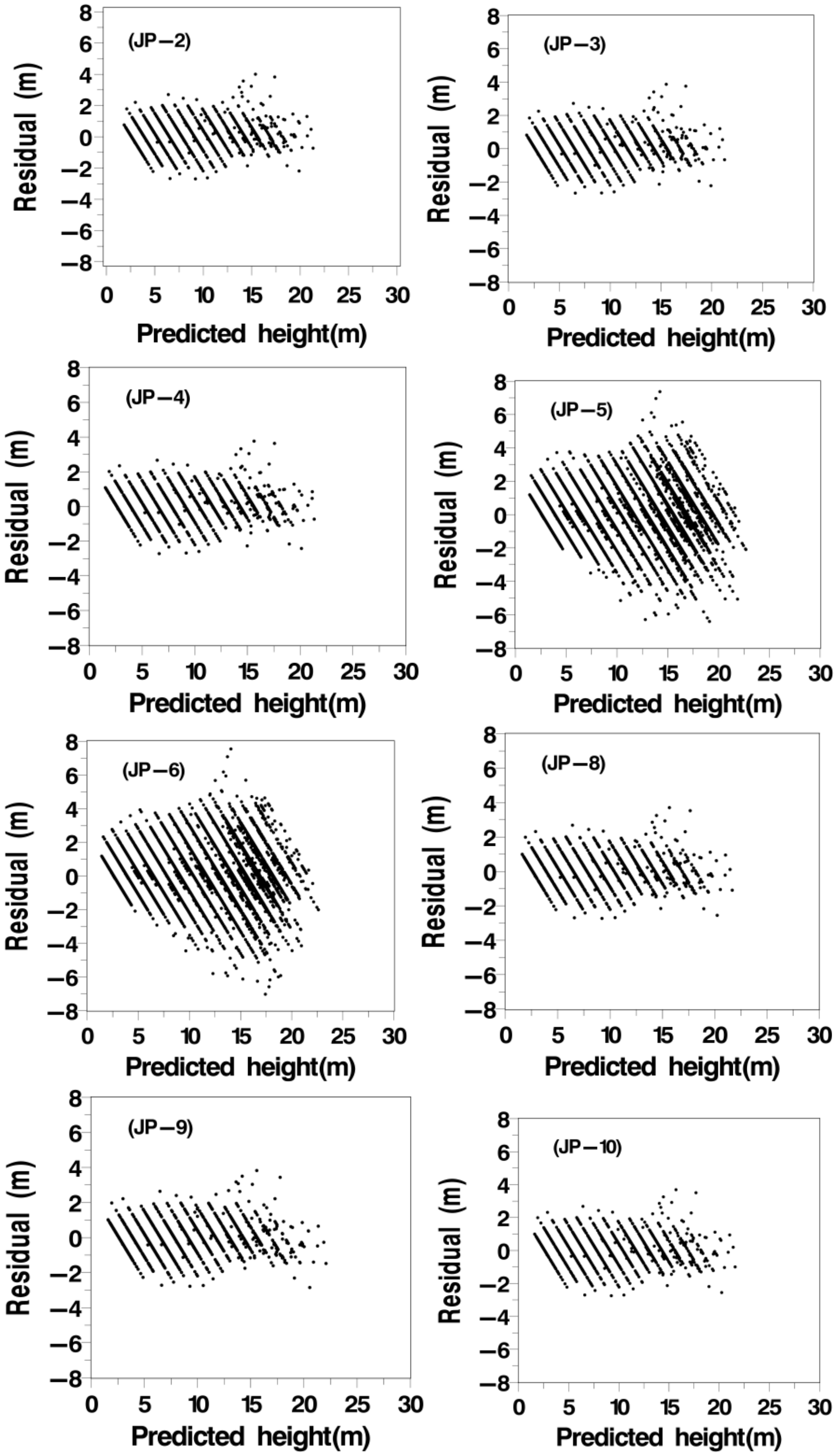


Figure 3.3. Residuals plotted against predicted height of jack pine from model [3.1] to [3.10]. Plots for models [3.1] and [3.7] are not shown, since the parameters of b_0 in [3.1] and b_2 in [3.7] were not statistically significant.

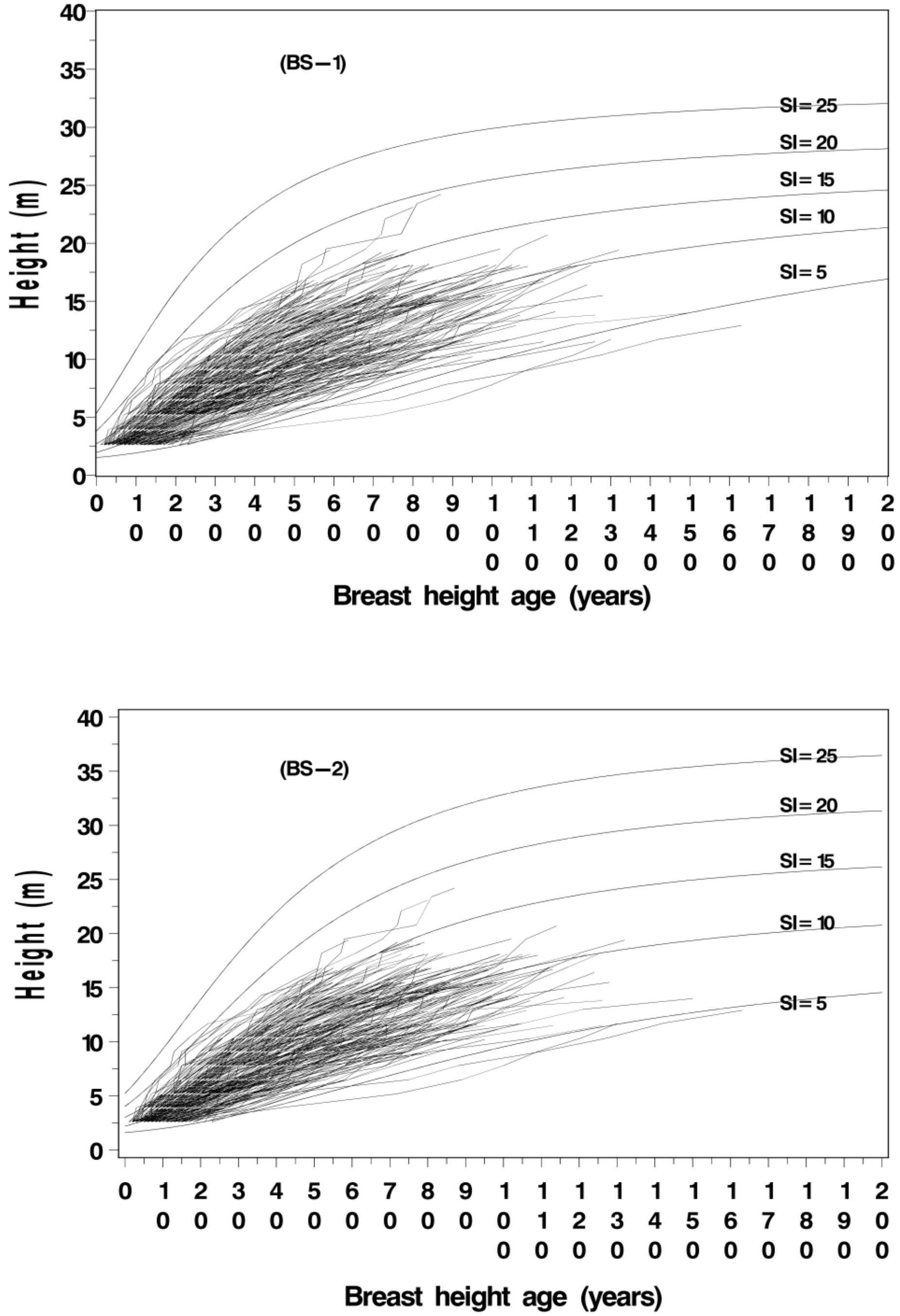
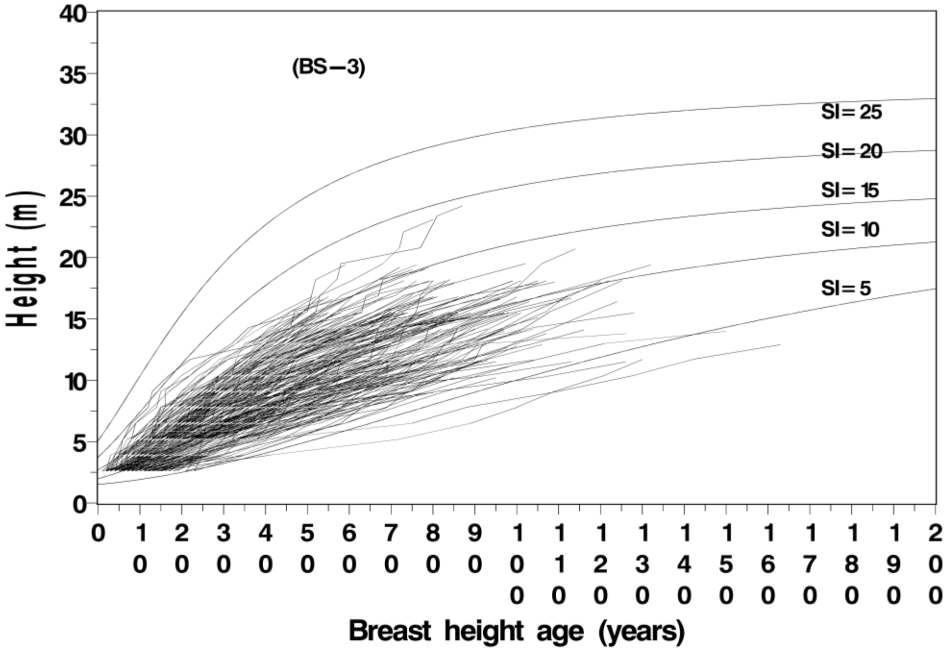
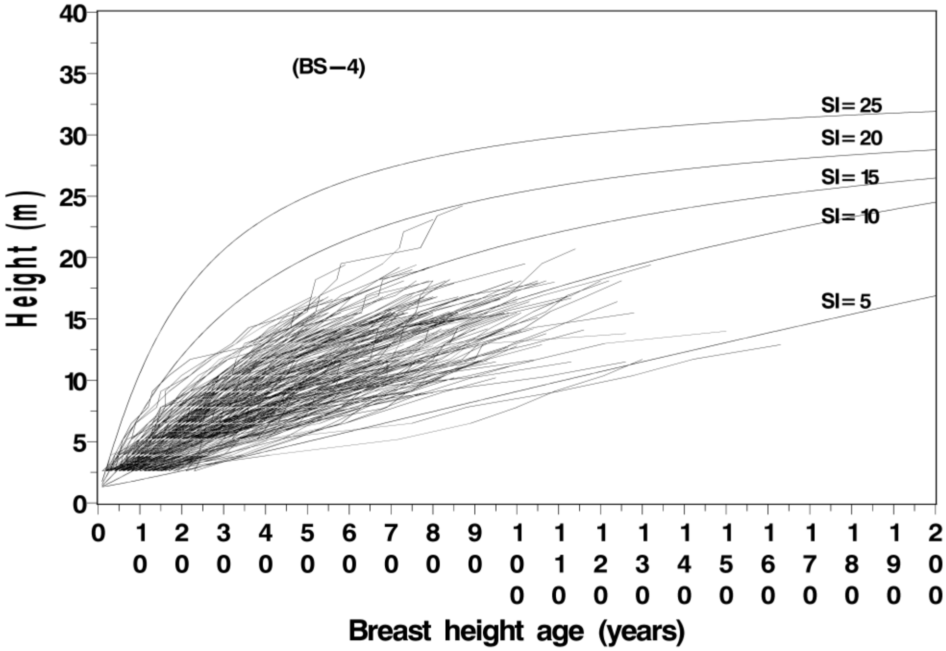


Figure 3.4. Height growth and site index curves for black spruce, generated using models [3.1] to [3.10] (labeled as BS-1 to BS-10). The observed tree sectioning data are overlain. Site index values at 50 years are given for each site index curve (SI = 5 to 25). The curves for models [3.7] and [3.9] are not shown, since the parameters of b_2 were not statistically significant.





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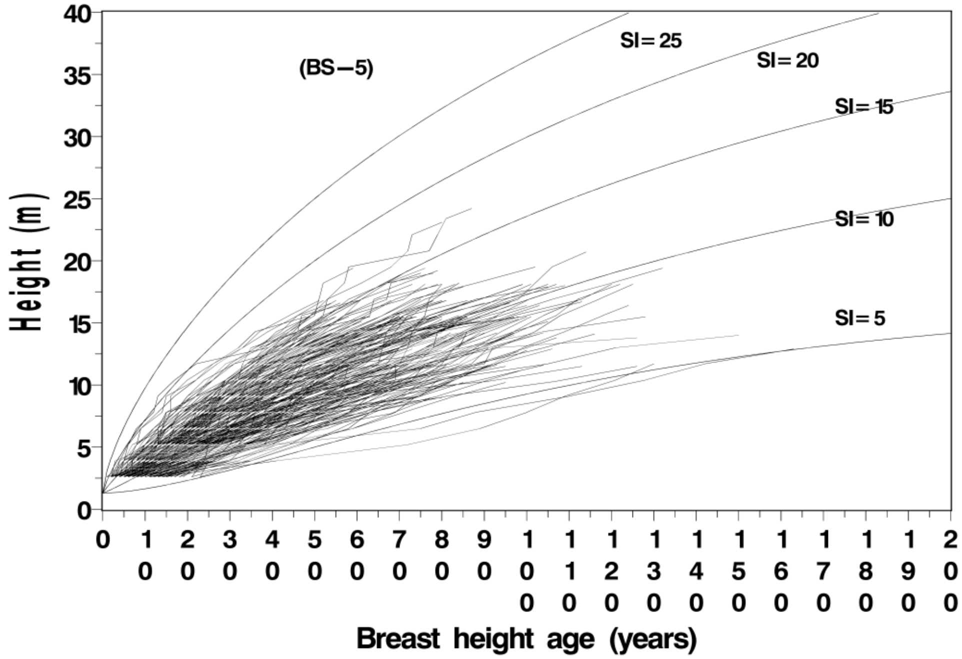

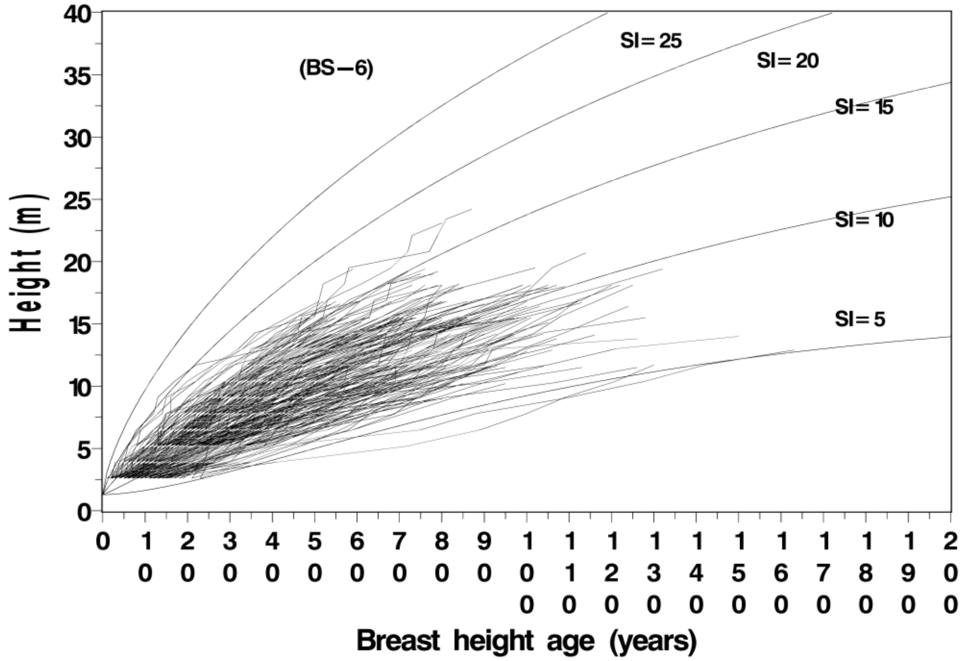

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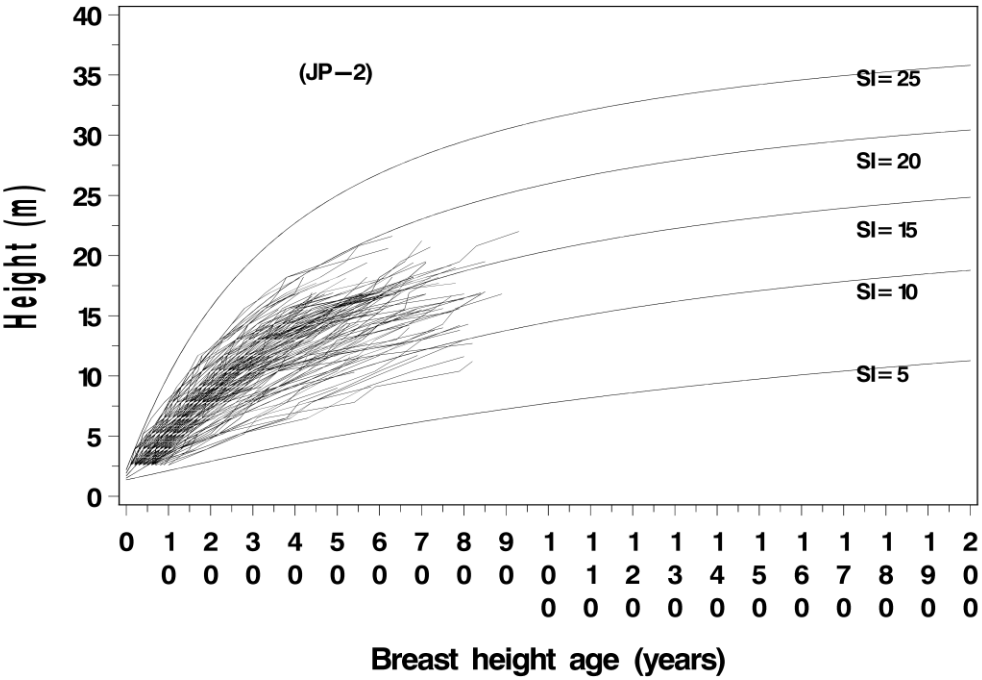
Figure 3.4 (continued).



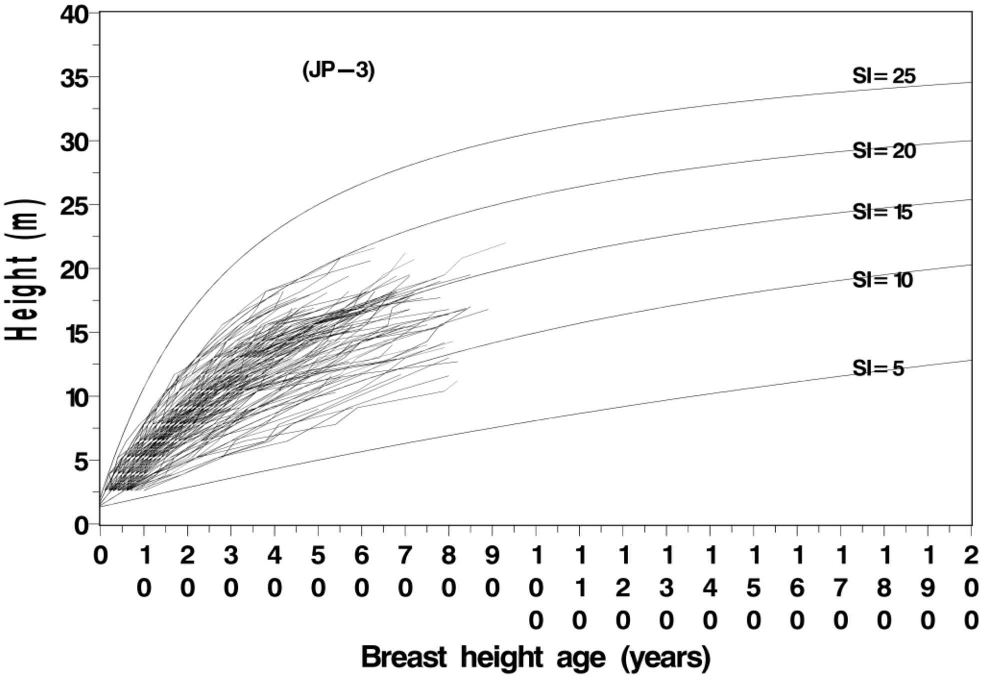


Figure 3.5. Height growth and site index curves for jack pine, generated using models [3.1] to [3.10] (labeled as JP-1 to JP-10). The observed tree sectioning data are overlain. Site index values at 50 years are given for each site index curve (SI = 5 to 25). The curves for models [3.1] and [3.7] are not shown, since parameters b_0 in [3.1] and b_2 in [3.7] were not statistically significant.

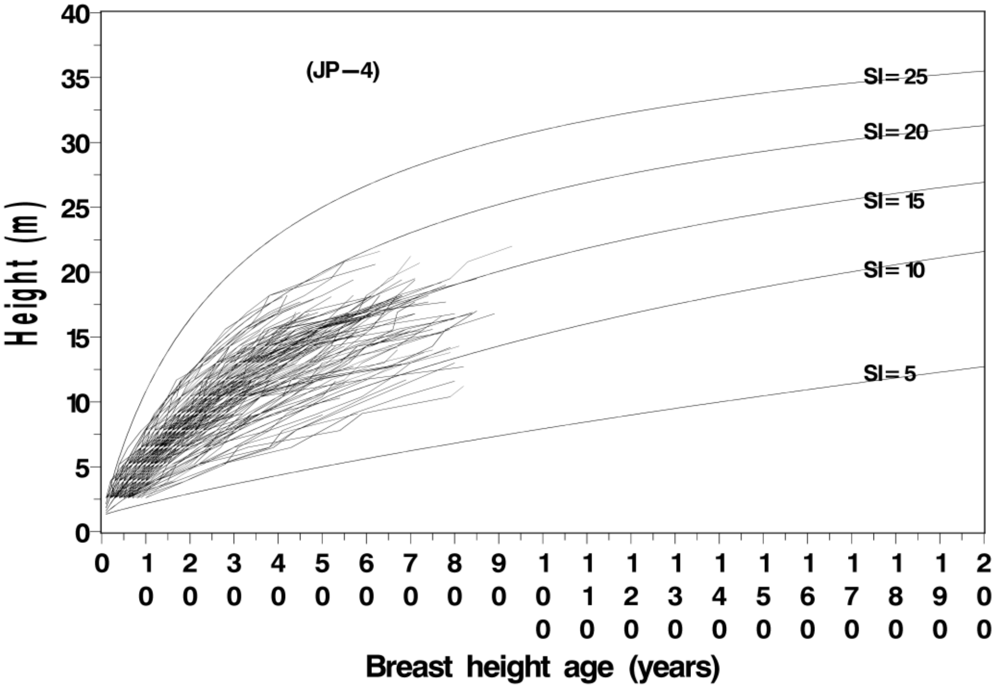


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Figure 3.5 (continued).

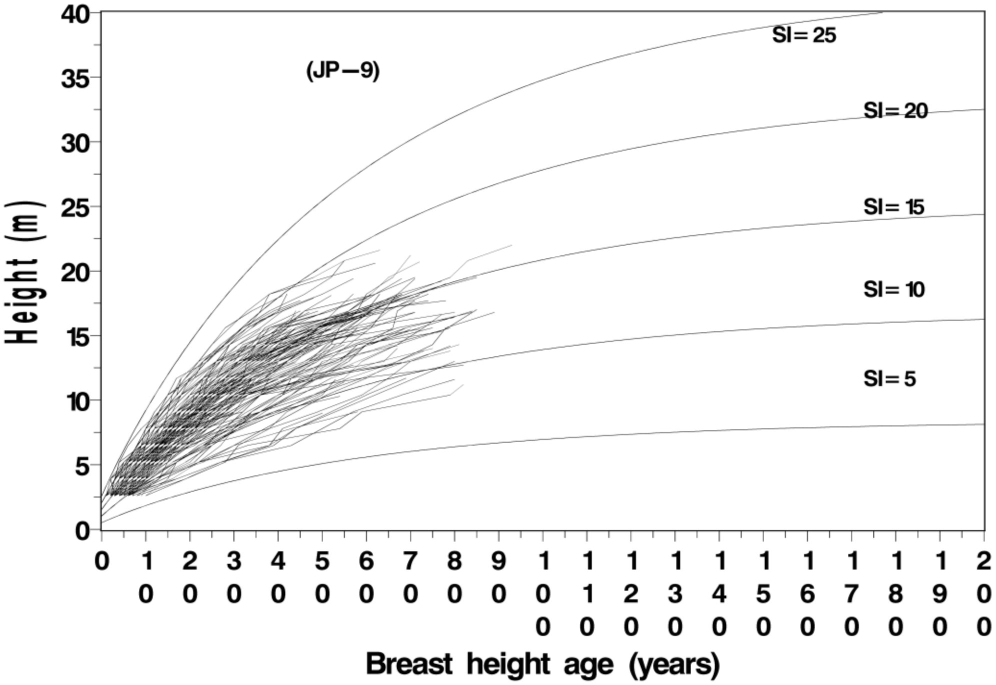


Figure 3.5 (continued).

3.5.4 Model Comparison: Validation Statistics

Height prediction statistics for models [3.1] to [3.10], based on the validation data for black spruce and jack pine, are presented in **Table 3.5**. Black spruce models [3.7] and [3.9], and jack pine models [3.1] and [3.7], are not included since one model parameter was not statistically significant in each of these four models.

For black spruce, all models except [3.5] to [3.6] performed quite well based on the validation data. The values of the prediction coefficient of determination (R_p^2) are high (> 0.93), and $RMSE_p$ values are low (< 1.1 m). Model [3.4] had the lowest $\mathrm{RMSE_p} = 0.935$. The paired t-tests indicated that models [3.8] and [3.10] produced prediction errors that differed significantly from zero, indicating poor model fits. Models [3.1] to [3.4] produced consistently good predictions based on the validation data results.

As with black spruce, all models except [3.5] and [3.6] performed quite well based on the jack pine validation data. Values for the prediction coefficient of determination ($\mathrm{R_p^2}$) for these models are high (> 0.96), and RMSE values are low (< 0.9 m). Model [3.4] had the lowest $\mathrm{RMSE_p} = 0.831$. Models [3.2] – [3.4] produced the lowest values for mean bias (0.02 – 0.06) and percent bias (0.16 – 0.44%), with model [3.4] having the lowest values. The paired t-tests indicated that model [3.6] produced prediction errors that differed significantly from zero, indicating poor model fit. Models [3.8] – [3.10] also showed evidence of prediction error bias (mean bias = 0.07 – 0.08), although this was not statistically significant ($t = 1.4 – 1.7$, $P > 0.05$). Overall, the jack pine validation data results indicate that model [3.4] produced the statistically most accurate and unbiased results. It is also the most parsimonious model, having fewer parameters than model [3.3].

The above comprehensive analyses compared the ten candidate height growth-site index models using model-fitting statistics, graphical examinations, and validation statistics. Based on the results of these comparisons, and taking into considerations issues of model parsimony (i.e. minimal number of model parameters) and application convenience, the three-parameter model [3.4] was selected as the "base" model for further analysis of height growth (site index) in Manitoba black spruce and jack pine.

3.5.5 Height Growth and Site Index Models by Ecozone

For both black spruce and jack pine, there were statistically significant differences in height growth (site index) models between the Boreal Plains and Boreal Shield ecozones (**Table 3.6).** This indicates that height growth patterns of jack pine and black spruce differ between these two ecozones.

Height growth – site index curves (based on model [3.4]) of the Boreal Plains and Boreal Shield ecozones for black spruce and jack pine are presented in **Figure 3.6**. For black spruce, there were nearly no differences in growth rates at breast height ages < 110 years. Growth curves for the two ecozones diverge somewhat beyond age 110: height growth is lower for the Boreal Shield ecozone at SI = 5 – 10, but slightly higher at SI = 15. For jack pine, there were few differences in growth rates between ecozones at breast height ages < 70 years. Beyond age 70, the growth curves begin to diverge, being lower for the Boreal Shield ecozone at SI = 5 – 15, and higher at SI = 20.

The divergence in height growth rates between the two ecozones is greater in jack pine than black spruce, but in general the differences between the two ecozones, while statistically significant, are relatively small. Even in the oldest stands, total predicted heights between the two ecozones differ by < 1 m for both black spruce and jack pine.

Table 3.5. Height prediction statistics of model [3.1] to [3.10] based on the validation data set for black spruce and jack pine.

Spp.	**Model**	R_p^2	$RMSE_p$	$\bar{e}$	***MAE***	***bias%***	***SE***	***t***	***n***
BS	[3.1]	0.9398	1.010	-0.031	0.680	-0.357	1.006	-0.620	407
	[3.2]	0.9475	0.942	-0.017	0.690	-0.197	0.94	-0.365	407
	[3.3]	0.9399	1.010	-0.031	0.682	-0.357	1.005	-0.620	407
	[3.4]	0.9483	0.935	0.037	0.644	0.428	0.932	0.802	407
	[3.5]	0.8990	1.339	-0.011	0.948	-0.124	1.338	-0.509	3796
	[3.6]	0.8990	1.339	-0.013	0.949	-0.147	1.338	-0.603	3796
	[3.8]	0.9462	0.956	-0.114	0.666	-1.318	0.945	-2.435	407
	[3.10]	0.9475	0.944	-0.110	0.670	-1.266	0.933	-2.368	407
JP	[3.2]	0.9645	0.838	0.040	0.629	0.441	0.834	0.802	281
	[3.3]	0.9646	0.838	0.052	0.628	0.570	0.832	1.038	281
	[3.4]	0.9651	0.831	0.015	0.623	0.161	0.828	0.296	281
	[3.5]	0.9306	1.211	-0.008	0.871	-0.088	1.210	-0.360	2794
	[3.6]	0.9292	1.222	0.052	0.871	0.550	1.220	2.239	2794
	[3.8]	0.9650	0.835	-0.076	0.631	-0.842	0.826	-1.546	281
	[3.9]	0.9641	0.845	-0.085	0.646	-0.939	0.836	-1.703	281
	[3.10]	0.9653	0.832	-0.068	0.629	-0.755	0.823	-1.391	281

Note: BS = black spruce; JP = jack pine; R_p^2 = prediction coefficient of determination; $RMSE_p$ = root mean square error of prediction; $\bar{e}$ = mean bias; MAE = mean absolute error; *t* = paired t-test value; *n* = total number of observations (or height-Bhage pairs) from sectioned trees.

Models [3.7] and [3.9] for black spruce, and models [3.1] and [3.7] for jack pine, are not shown since one model parameter was not statistically significant.

Table 3.6. F-test results for the height growth and site index model between the Boreal Plains and Boreal Shield ecozones.

	FULL MODEL		REDUCED MODEL				
Spp.	**SSE(F)**	**d.f. (F)**	**SSE(R)**	**d.f. (R)**	***n***	**F**	***P***
BS	1927.2	2067	1936.1	2070	2073	3.19	< 0.05
JP	1033.6	1449	1052.4	1452	1455	8.74	< 0.05

Note: F-value was calculated as {[SSE(R)-SSE(F)]/[*df*(R)-*df*(F)]}/ [SSE(F)/*df*(F)], where SSE(R) and SSE(F) are sum-of-squares of residual for reduced and full models, and *df*(R) and *df*(F) are degree-of-freedoms of residual for reduced and full models.

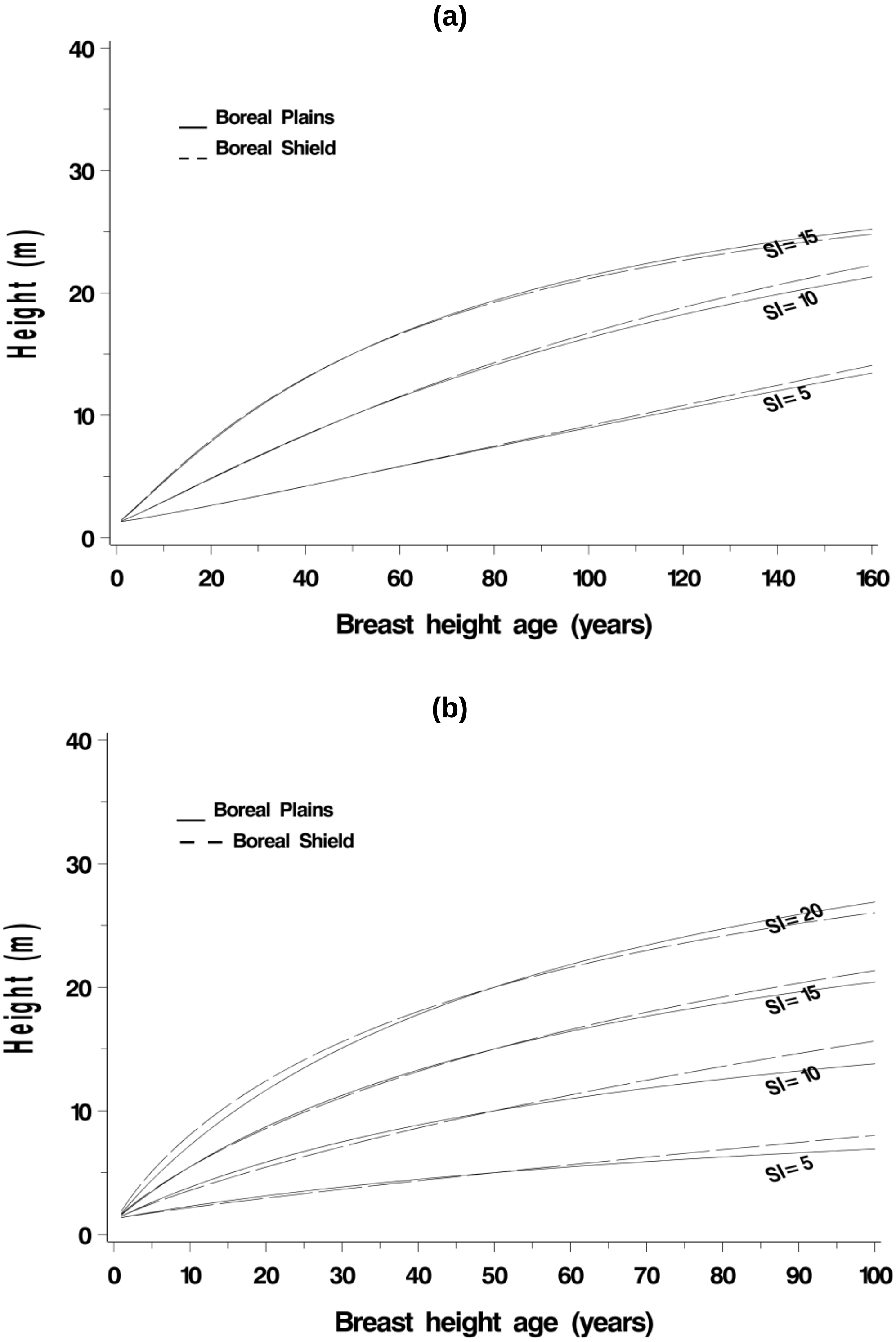


Figure 3.6. Overlain height growth and site index curves for the Boreal Plains and Boreal Shield zones for (a) black spruce and (b) jack pine, based on model [3.4].

3.5.6 Testing for Autocorrelation Effects

Three approaches – generalized nonlinear least square (GNLS) approach, random selection of a single observation from each tree, and the nonlinear mixed-effects model (NLMM) approach – were compared. The results are presented in the following sections.

Generalized Nonlinear Least Squares (GNLS) Model

The resulting fit statistics for the black spruce and jack pine height growth models are summarized in **Tables 3.7**. The Durbin-Watson statistics (*DW* = 1.890 and 1.902) for both black spruce and jack pine are greater than their respective upper bounds (critical value *DW* = 1.760; *P* = 0.05), indicating that autocorrelation of the adjusted error terms is not statistically significant, and that the AR(1) process specification is appropriate for the error terms.

Height growth – site index curves of black spruce and jack pine (model [3.4]) and the autocorrelation corrected curves (AR(1) process) are shown in **Figure 3.7**. For black spruce at *SI* = 5, the two growth curves are very similar. At *SI* = 10 and 15, the two sets of growth curves are similar up to a breast height age of 70 years. For older trees, the curves begin to diverge, with incorporation of the AR(1) process resulting in somewhat lower height predictions (about 2 m less by age 150). For jack pine at *SI* = 5, the two growth curves are virtually identical. At *SI* = 10 – 20, growth curves are similar up to breast height age 60, but begin to diverge thereafter. Incorporation of the AR(1) process results in somewhat lower height predictions (about 1 m less by 100 years of age). Overall, these results indicate that accounting for autocorrelation using the AR(1) process results in marginally lower predictions of black spruce and jack pine tree heights, particularly for older trees in more productive (higher *SI*) sites.

Table 3.7. Fit statistics and parameters of model [3.4] fitted by NLS, and NLS with AR(1), for black spruce and jack pine.

Spp.	Model	Parameter	Estimate	SE	*t**	RMSE	R^2	D-W
BS	**NLS**	b_0	11.0346	0.2459	44.87	0.9822	0.9486	0.5367
		b_1	-1.1813	0.0209	-56.44			
		b_2	-2.3953	0.1075	-22.28			
	NLS with AR(1)	b_0	10.4746	0.1993	52.56	0.6618	0.9766	1.8895
		b_1	-1.2906	0.0284	-45.41			
		b_2	-2.1283	0.0972	-21.89			
		AR1	0.7487	0.0166	45.21			
JP	**NLS**	b_0	8.6417	0.5142	16.80	0.8575	0.9641	0.5525
		b_1	-0.9029	0.0209	-43.28			
		b_2	-1.7145	0.1890	-9.07			
	NLS with AR(1)	b_0	7.7686	0.4345	17.88	0.5843	0.9833	1.9019
		b_1	-1.0586	0.0276	-38.42			
		b_2	-1.3610	0.1667	-8.16			
		AR1	0.7458	0.0198	37.60			

Note: NLS = Nonlinear least squares; R^2 = prediction coefficient of determination; RMSE = root mean square error of prediction; SE = standard error of the parameter; DW = Durbin-Watson statistic; AR1 = first-order autoregressive AR(1) parameter.

* $P < 0.001$ for all t-values.

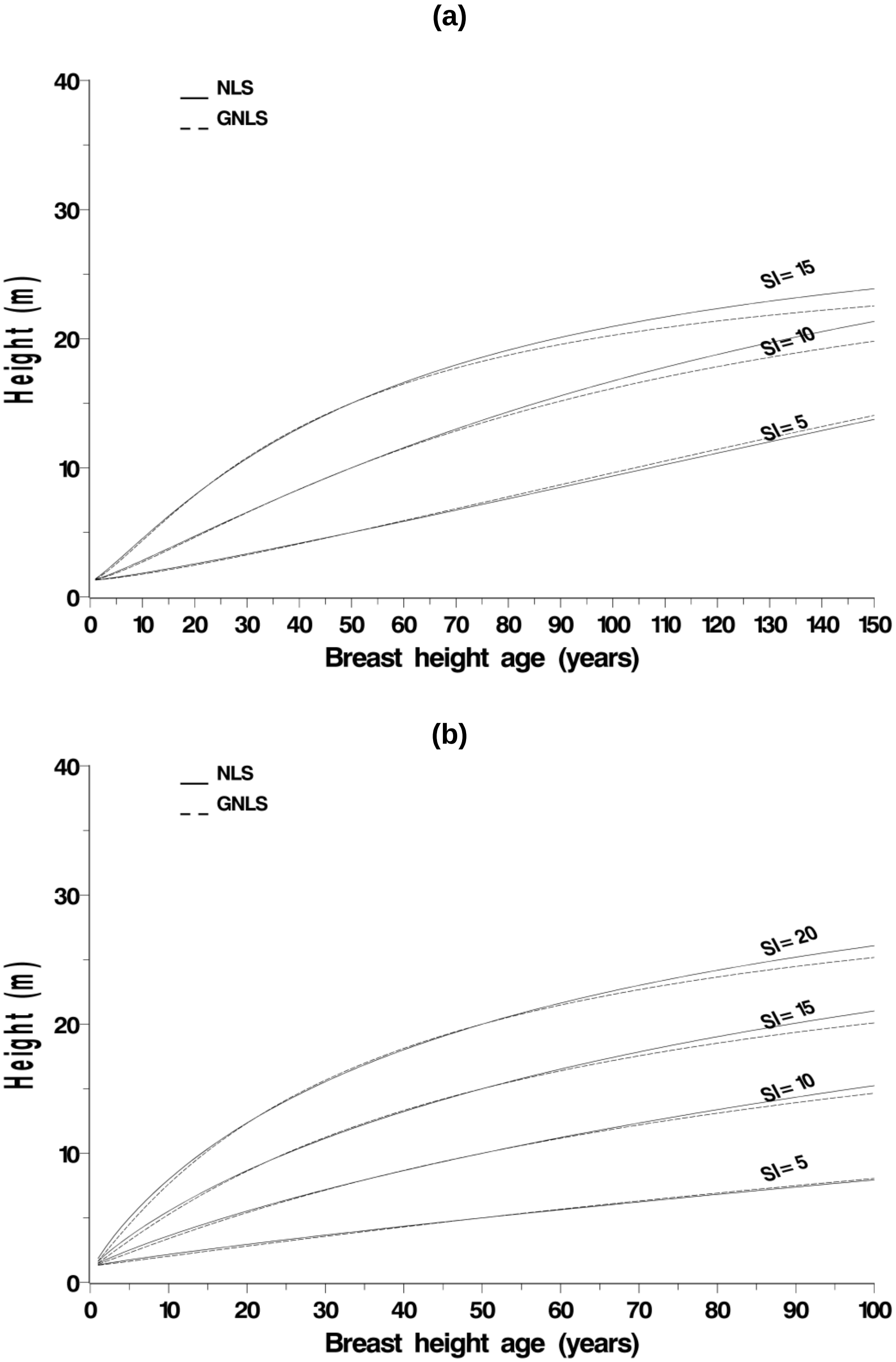


Figure 3.7. Height growth and site index curves overlay of model [3.4] by using NLS approach and NLS with AR(1) approach (*GNLS*) for (a) black spruce and (b) jack pine.

Random Selection of One Observation per Tree

For both black spruce and jack pine, comparisons were between models that utilized all measurements (model [3.4]; see **Figure 3.4**) and models that utilized a reduced data set in which a single measurement was randomly selected for each tree. The fitting parameters and statistics for these four models are presented in **Table 3.8**. All model fittings converged, and all parameters were statistically significant. When all measurements were included, the Durbin-Watson statistics for black spruce and jack pine (*DW* = 0.565 and 0.552 respectively) were both less than their respective lower bounds (*DW* =1.610; *P* = 0.05), indicating significant spatial autocorrelation in the data. Reducing the data by randomly selecting a single measurement per tree resulted in Durbin-Watson statistics for black spruce and jack pine (*DW* = 1.882 and 1.834 respectively) that were greater than their respective upper bounds (*DW* = 1.740; *P* = 0.05). This indicates that, as expected, reducing the data by randomly selecting a single measurement per tree effectively removed spatial autocorrelation from the data.

Height growth – site index curves for black spruce and jack pine (model [3.4]) based on all measurements (autocorrelated errors) versus a single randomly selected measurement from each tree (no error autocorrelation) are shown in **Figure 3.8**. For black spruce at *SI* = 5 and 10, the two sets of height growth curves are nearly identical. At *SI* = 15, the two sets of growth curves are very similar to age 100, after which they diverge slightly. The reduced data (autocorrelation removed) predicted slightly lower tree heights (< 0.5 m difference at age 150). The results for jack pine are similar. At *SI* = 5 and 10, the two sets of growth curves are almost identical. At *SI* = 15 and 20, predicted heights are slightly smaller (< 1 m at age 100) for the reduced data.

Table 3.8. Fit statistics and parameters of model [3.4] fitted by all observations and randomly selected one observation per tree for black spruce and jack pine.

Spp.	Data	Parameter	Estimate	SE	*t**	RMSE	R^2	D-W
BS	**All**	b_0	10.5573	0.240	43.97	0.9671	0.9491	0.5651
		b_1	-1.1296	0.018	-61.27			
		b_2	-2.2340	0.104	-21.58			
	One	b_0	10.5816	0.746	14.19	0.9600	0.9519	1.8816
		b_1	-1.1323	0.056	-20.32			
		b_2	-2.2746	0.324	-7.02			
JP	**All**	b_0	8.46224	0.448	18.91	0.8513	0.9643	0.5521
		b_1	-0.9100	0.019	-48.32			
		b_2	-1.6440	0.165	-9.96			
	One	b_0	8.6906	1.157	7.51	0.6988	0.9741	1.8341
		b_1	-0.9415	0.058	-16.28			
		b_2	-1.7703	0.431	-4.10			

Note: All = all sectioned data used; One = one section randomly selected per tree; R^2 = prediction coefficient of determination; RMSE = root mean square error of prediction; SE = standard error of the parameter; D-W = Durbin-Watson statistic.

* $P < 0.001$ for all *t*-values.

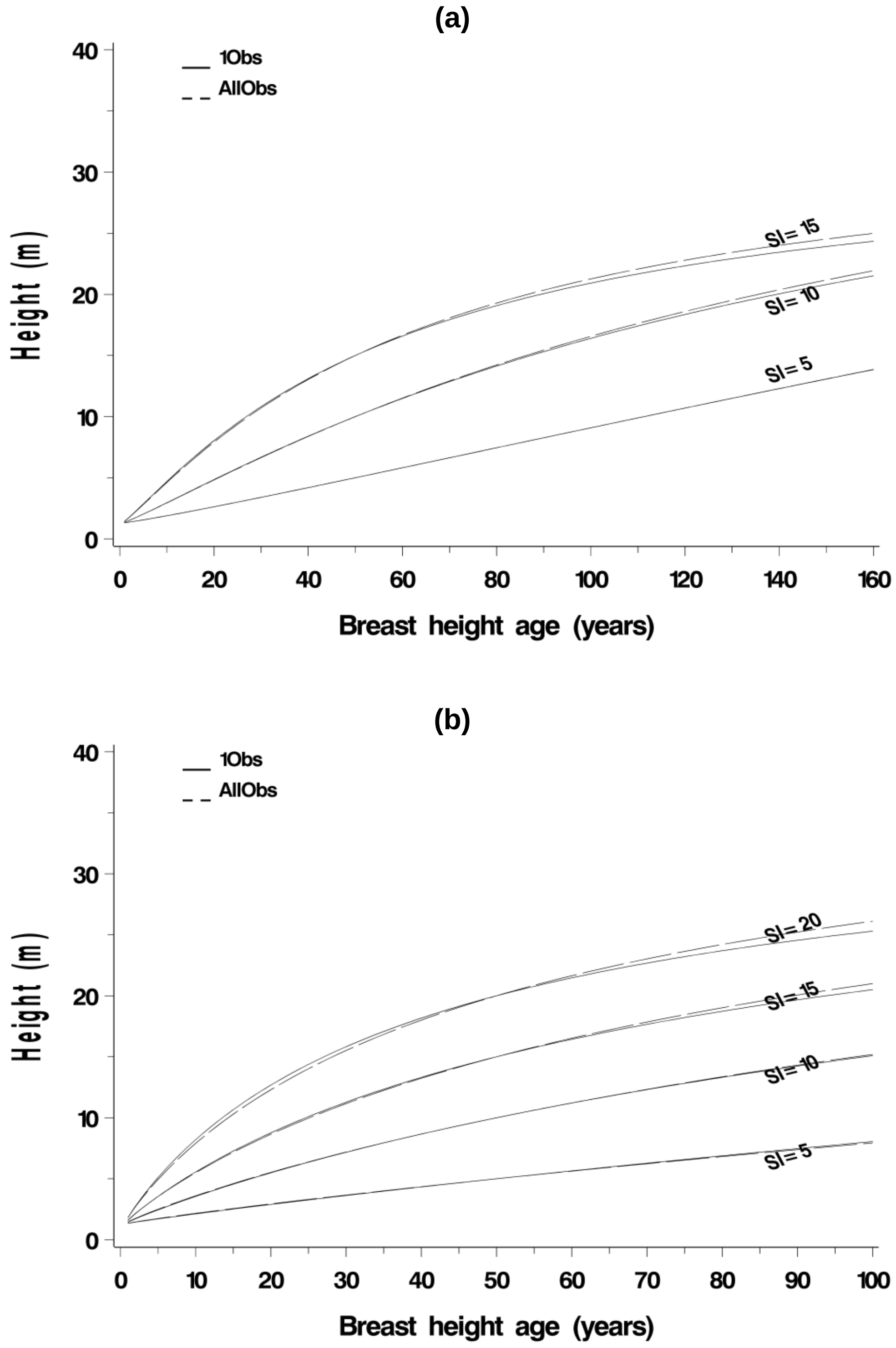


Figure 3.8. Overlain height growth and site index curves of model [3.4], using only one observation of each tree (solid line, *1 Obs*) and all the tree measurements (*dash line, All Obs*) for (a) black spruce and (b) jack pine.

Nonlinear Mixed-Effects Models (NLMM)

The *AIC* and *BIC* statistics for the base model [3.4], fitted with one (models [3.21] to [3.23]), two (models [3.24] to [3.26]) and three random-effects parameters (model [3.27]), are summarized in **Table 3.9**. Note that 9 of the 28 models failed to converge (indicated by NC = not convergent). For both black spruce and jack pine, *AIC* and *BIC* values declined as the number of random-effects parameters increased, in both the standard models and in the models incorporating first-order autoregressive functions (AR(1)). The inclusion of first-order autoregressive functions improved model performance (i.e. lower values for *AIC* and *BIC*) for both black spruce and jack pine.

Of the three one-parameter models ([3.21] – [3.23]), model [3.21] showed the best model performance for jack pine, while only model [3.22] converged for black spruce. Of the three two-parameter models ([3.24] – [3.26]), model [3.25] failed to converge and model [3.24] performed best, for both jack pine and black spruce. In both species, the inclusion of a second parameter improved model performance: for example, in jack pine (model without AR(1)), *AIC* = 2463.6 for the single-parameter (b_0+u_1) model [3.21] versus *AIC* = 2168.3 for the comparable two-parameter (b_0+u_1, b_1+u_2) model [3.24]. The three-parameter model [3.27] for jack pine failed to converge. For black spruce, there was little improvement in model performance by adding a third parameter (e.g. model without AR(1), *AIC* = 3027.8 for model [3.24] versus *AIC* = 2938.4 for model [3.27]). For application consistency and convenience, the two random parameters model [3.24] fitted with AR (1) was selected as the “best” mixed-effects model for further analysis.

Correlation coefficients between lagged normalized residuals for model [3.4], based on three regression fitting approaches (standard NLS; GNLS with AR(1); and NLMM with AR(1), model [3.24]) are shown in **Table 3.10**. The standard NLS regression fitting approach resulted in statistically significant positive residual autocorrelation ($P = 0.01$) over the first five lag periods for black spruce, and over the first seven lag periods for jack pine. Lag-correlations are particularly large for the first 3 – 4 lag periods. These positive correlations are likely attributable to between-tree variation in model parameters, which is not accommodated in the NLS model. Trends in spatial autocorrelation for NLS model [3.4] over the first three lag periods are displayed for black spruce and jack pine in **Figures 3.9** and **3.10** respectively.

For both black spruce and jack pine, the lag-correlations from the GNLS with AR(1) modelling approach are much smaller than those obtained using the NLS approach. Nevertheless, the first two lag-correlations coefficients are statistically significant ($P = 0.01$) for both species, and many of the higher lag-correlations are marginally significant for black spruce. These results indicate that the GNLS approach with AR(1) successfully accounted for much, but not all, of the autocorrelation, with the result that some positive residual autocorrelation remained unaccounted for.

Spatial autocorrelation was effectively eliminated for both the black spruce and jack pine data sets when using the NLMM with AR(1) regression approach (model [3.24], **Table 3.10**). None of the lag-correlation coefficients are statistically significant over the first ten lag periods, for both black spruce and jack pine. Spatial autocorrelation trends over the first three lag periods for black spruce and jack pine (**Figures 3.11** and **3.12** respectively) clearly demonstrate a lack of residual autocorrelation, confirming that the NLMM approach is very effective in addressing the autocorrelation issue.

NLMM approaches that account for both population mean and subject-specific (i.e. tree-specific) variation have the advantage of producing more accurate subject-specific (SS) predictions. The cost of this advantage is that at least one prior measurement for each subject tree is required, in order to increase the accuracy of population mean estimates and to calibrate localized information. In forestry practice, prior measurements are often not available due to difficulty and cost of aging live trees in the field. Therefore, in its operational form model [3.24] utilizes only fixed-effect parameters (typical mean, TM) to obtain a reasonable approximation of the true population mean response; random-parameter effects and AR(1) error structures are not normally applied in practice (Fang and Bailey 2001; Meng *et al.* 2008; Nigh *et al.* 2009; Yuqing Yang and Gord Nigh, *pers. comm.* 2010). As a result, model [3.24] in its operational form is usually the same as model [3.4].

Height growth and site index curves for black spruce and jack pine, obtained using the NLS approach versus the NLMM-TM approach, are compared in **Figure 3.13**. For black spruce, the curves are almost identical at breast height ages < 100 years. The curve diverge slightly thereafter, with the NLMM-TM model predicting lower heights at *SI* = 5 and marginally (< 1 m) greater heights at *SI* = 10 and 15. For jack pine, the two sets of curves are almost identical over all *SI* classes and breast height ages.

Table 3.9. Akaike's information criterion (AIC) and Schwarz's Bayesian information criterion (BIC) of model [3.4] fitted with one, two and three random effects for black spruce and jack pine.

			Black Spruce		Jack Pine	
Autocorrelation	**Model**	**Random effects**	***AIC***	***BIC***	***AIC***	***BIC***
No AR(1)	**[3.21]**	b_0+u_1	NC	NC	2463.6	2476.8
	[3.22]	b_1+u_1	3949.9	3965.3	2776.1	2789.4
	[3.23]	b_2+u_1	NC	NC	2472.1	2485.3
	[3.24]	b_0+u_1, b_1+u_2	3027.8	3049.4	2168.3	2186.9
	[3.25]	b_0+u_1, b_2+u_2	NC	NC	NC	NC
	[3.26]	b_1+u_1, b_2+u_2	3046.3	3067.8	2183	2201.6
	[3.27]	b_0+u_1, b_1+u_2, b_2+u_3	2938.4	2969.2	NC	NC
With AR(1)	**[3.21]**	b_0+u_1	NC	NC	1809.4	1825.4
	[3.22]	b_1+u_1	2711.3	2729.7	1838.2	1854.1
	[3.23]	b_2+u_1	NC	NC	1814.9	1830.9
	[3.24]	b_0+u_1, b_1+u_2	2537.9	2562.5	1799.5	1820.8
	[3.25]	b_0+u_1, b_2+u_2	2570.6	2595.2	NC	NC
	[3.26]	b_1+u_1, b_2+u_2	2544.6	2569.2	1805.7	1827
	[3.27]	b_0+u_1, b_1+u_2, b_2+u_3	2527.2	2561	NC	NC

Note: b_0, b_1 and b_2 are fixed parameters, u_1, u_2 and u_3 are random parameters.

NC = model fitting not convergent.

Table 3.10. Correlation coefficients of ten lagged normalized residuals for model [3.4] (fitted by the NLS and GNLS approaches) and model [3.24] (fitted by NLMM) for black spruce (BS) and jack pine (JP). Values in boldface indicate statistically significant autocorrelation ($P > 0.01$).

Spp.	lag	*n*	NLS	GNLS	NLMM	ρ
BS	1	1347	**0.815**	**0.181**	0.025	0.07
	2	1188	**0.638**	**0.152**	0.023	0.075
	3	1029	**0.455**	0.056	0.03	0.08
	4	870	**0.269**	-0.032	-0.019	0.087
	5	711	**0.13**	**-0.099**	0.023	0.097
	6	556	0.008	**-0.114**	0.026	0.109
	7	409	-0.082	**-0.152**	0.022	0.128
	8	278	-0.106	**-0.172**	0.146	0.155
	9	165	-0.128	-0.147	0.16	0.201
	10	85	-0.104	**-0.362**	0.015	0.28
JP	1	964	**0.809**	**0.183**	0.034	0.083
	2	859	**0.662**	**0.121**	0.052	0.088
	3	754	**0.517**	0.036	-0.04	0.094
	4	649	**0.416**	-0.011	-0.04	0.101
	5	544	**0.344**	-0.046	-0.012	0.111
	6	442	**0.268**	-0.013	0.019	0.123
	7	340	**0.159**	-0.065	-0.064	0.14
	8	243	0.097	-0.089	-0.042	0.166
	9	158	0.099	-0.114	0.036	0.205
	10	89	0.079	-0.09	-0.011	0.273

Note: ρ = Absolute critical value ($P = 0.01$) for confidence interval.
NLS = nonlinear least squares approach.
GNLS = generalized nonlinear least squares approach with AR(1).
NLMM = Nonlinear mixed-effects model approach with AR(1).

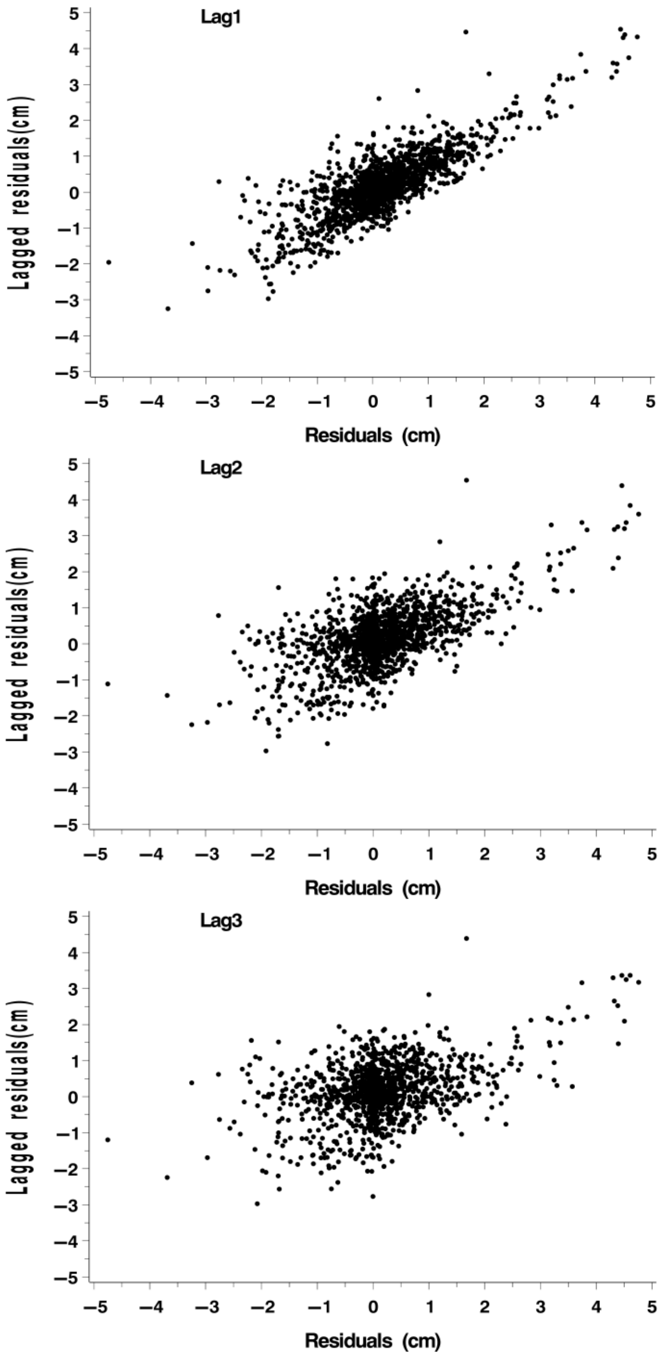


Figure 3.9. Lagged residuals (lag 1, lag 2 and lag 3, respectively from upper to bottom) for model [3.4] fitted by nonlinear least square (NLS) technique for black spruce.

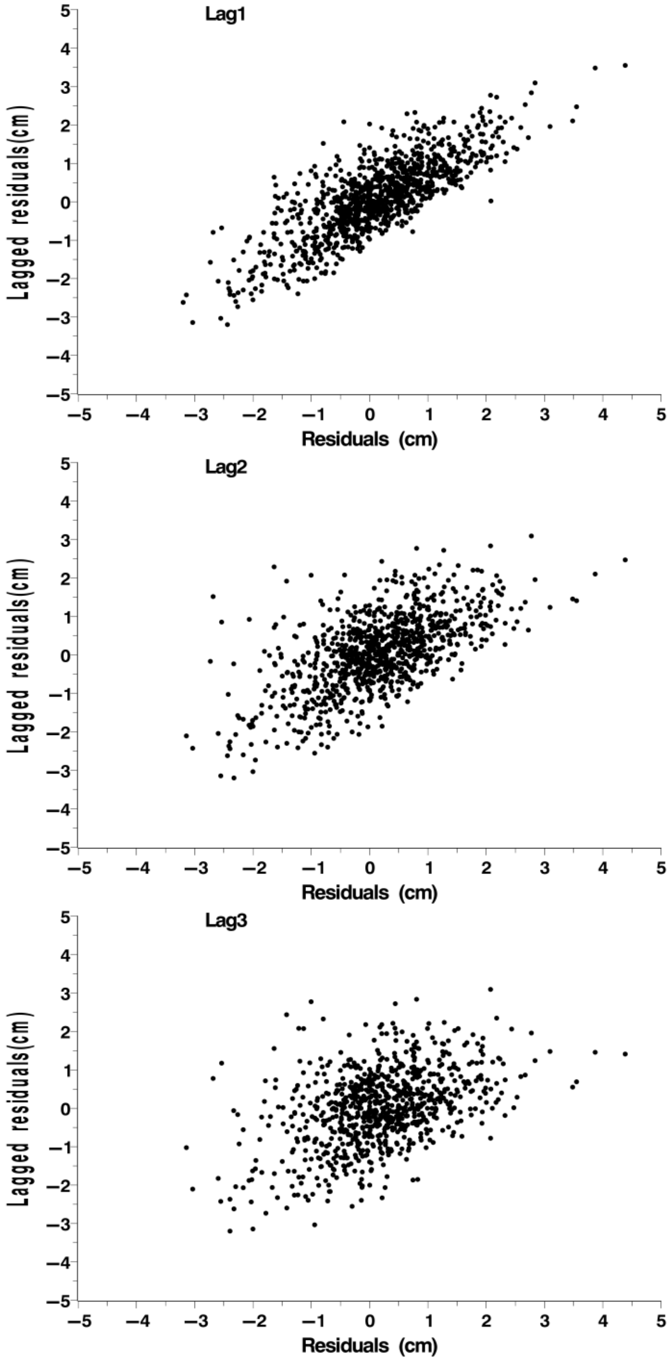


Figure 3.10. Lagged residuals (lag 1, lag 2 and lag 3, respectively from upper to bottom) for model [3.4] fitted by nonlinear least square (NLS) technique for jack pine.

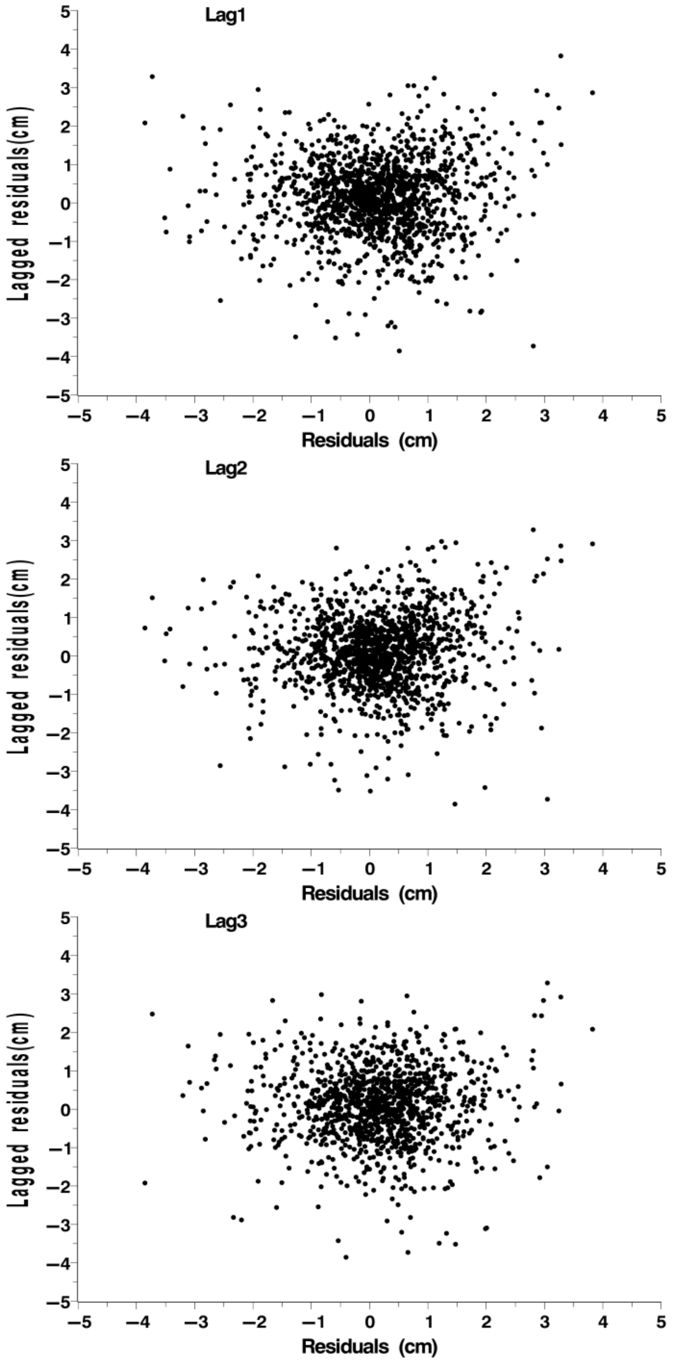


Figure 3.11. Lagged residuals (lag 1, lag 2 and lag 3, respectively from upper to bottom) for model [3.24] fitted by nonlinear mixed-effects model (NLMM) technique for black spruce.

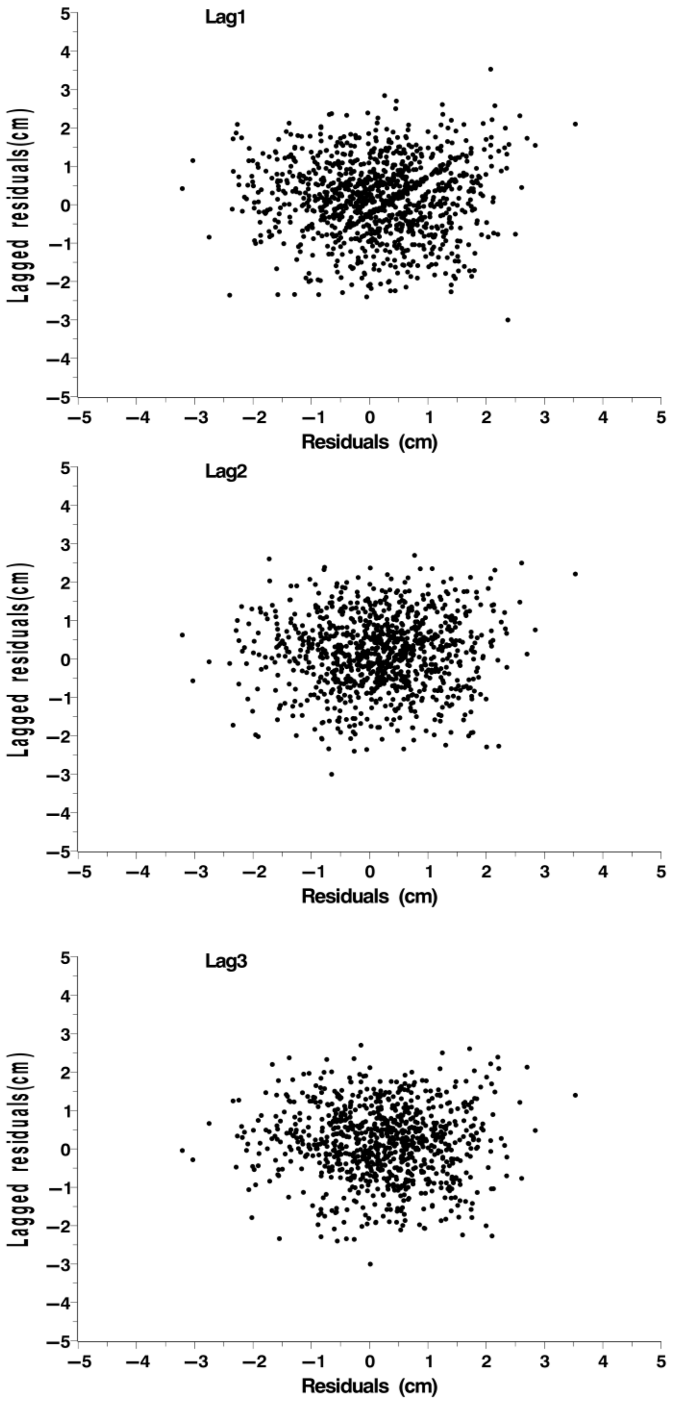
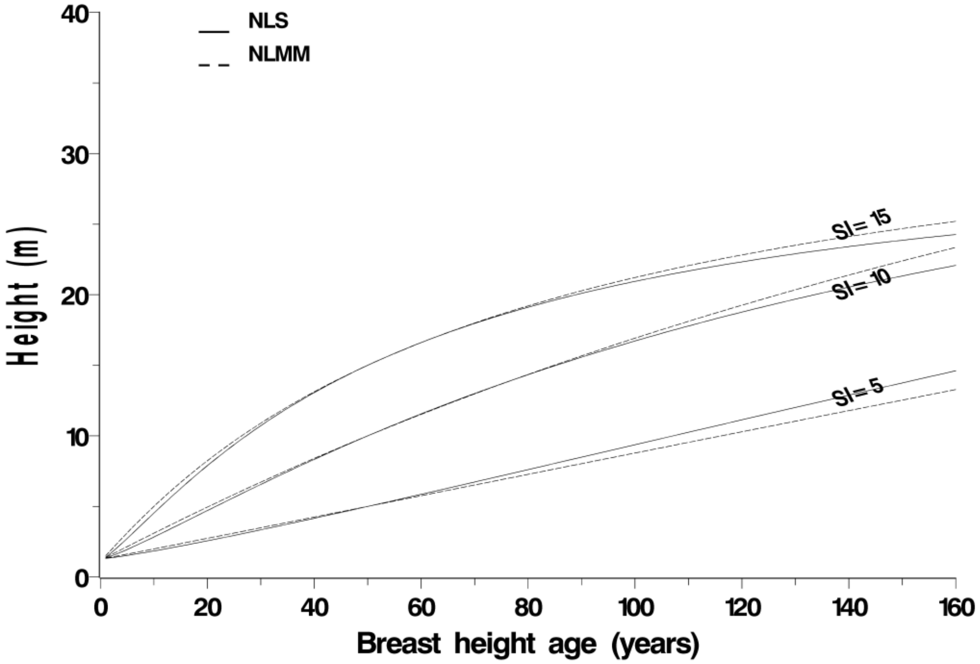


Figure 3.12. Lagged residuals (lag 1, lag 2 and lag 3, respectively from upper to bottom) for model [3.24] fitted by nonlinear mixed-effects model (NLMM) technique for jack pine.

(a) BLACK SPRUCE



(b) JACK PINE

Figure 3.13. Overlain height growth and site index curves of model [3.4] by NLS approach (*solid line*) and model [3.24] by NLMM mixed-model approach (*dash line*) for (a) black spruce and (b) jack pine.

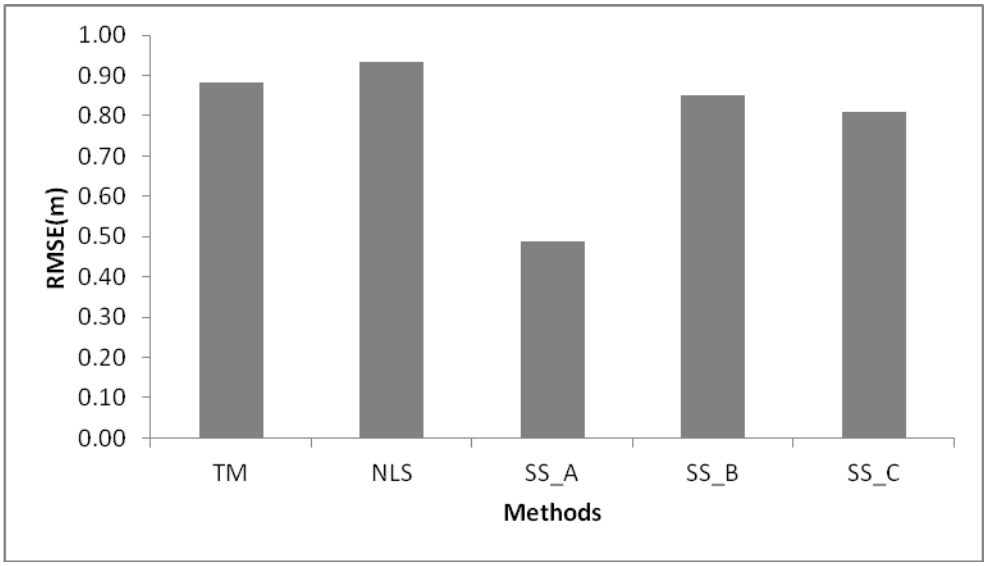
3.5.7 Comparison of Population-Averaged and Subject-Specific (SS) Approaches

To gain a sense of the importance of subject-specific information in model prediction, the NLS (model [3.4]) and NLMM-TM (model [3.24], fixed effects only) modeling results were compared with three subject-specific (SS) approaches. Comparisons were made, and model predictability assessed, using the predicted root mean squared errors (*RMSEp*) statistic. The three SS scenarios differed in the amount of prior information available to the model:

(A) All measurements from each tree.
(B) One measurement per tree, at 2.6 m height.
(C) Two measurements per tree, at 2.6. and 5.2 m height.

Predicted root mean squared errors (*RMSEp*) for the five models, for both black spruce and jack pine, are summarized in **Figure 3.14**. Values for the NLS and NLMM-TM were similar for both black spruce (*RMSEp* = 0.93 versus 0.88) and jack pine (*RMSEp* = 0.83 versus 0.82). Marginal reductions in *RMSEp* were obtained under subject-specific scenarios B and C (one or two measurements per tree). Subject-specific scenario A (all measurements used) resulted in a more substantial decrease in *RMSEp* values (0.49 for black spruce; 0.54 for jack pine). These results indicate that more accurate predictions are obtained when prior measurements are used, but that accuracy is only marginally improved when only one or two prior measurements per tree are available.

(a) BLACK SPRUCE



(b) JACK PINE

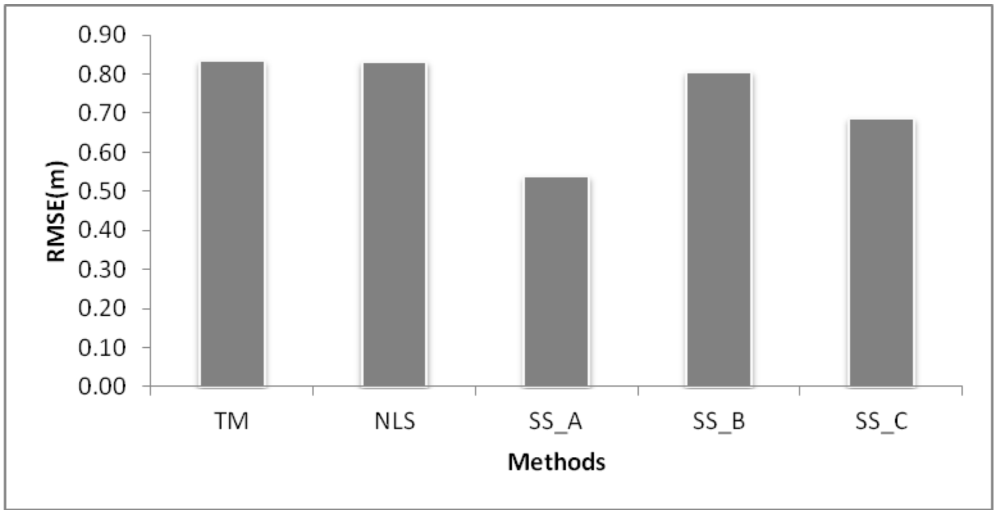


Figure 3.14. Predicted root mean squared errors (RMSEp) of the nonlinear mixed-effects model (TM), nonlinear least squares (NLS), and subject-specific (SS) scenarios A (SS-A), B (SS-B) and C (SS-C) responses for the validation data for (a) black spruce and (b) jack pine.

3.5.8 Comparison With Other Height Growth and Site Index Models

Height growth and site index models for black spruce and jack pine have been developed previously for other regions of Canada. Here, I compare model [3.4] for Manitoba black spruce and jack pine with the following models developed by other researchers: (a) jack pine and black spruce models developed for central and northern Alberta (Huang et al. 1994a); (b) jack pine model for northern Ontario (Carmean *et al.* 2001); (c) black spruce model for central British Columbia (Nigh *et al.* 2002, 2009); and (d) black spruce and jack pine models for New Brunswick (Ker and Bowling 1991). All these models were based on breast height age and a reference breast height age of 50 years, making them compatible and directly comparable with model [3.4]. Since the published models were developed using the NLS approach, comparisons are made with the NLS results of model [3.4] (Section 3.5.1).

For comparison purposes, the height growth models for the various provinces were plotted, with site index expressed as a function of breast height age (range = 0 to 150 years). Site index values of SI = 5, 10 and 15 m were graphed for black spruce (**Figure 3.15**), and SI = 5, 10, 15 and 20 m for jack pine (**Figure 3.16**).

For black spruce, the age-height growth curves for the four provinces at SI = 10 and 15 m are very similar at breast height age < 90 years (**Figure 3.15**). Beyond 90 years, the growth patterns are similar for Manitoba, New Brunswick and Alberta, but the British Columbia model predicts greater height growth in the older age classes (26 m by age 150 versus 21-22 m for the other three models). For the 5 m site index (low productivity black spruce stands), the age-height curves were similar except for the New Brunswick model, which predicts greater height growth beyond breast height age 60. These results indicate that Manitoba model [3.4] produces black spruce age-height growth curves that are similar to, and comparable with, those developed for other provinces.

For jack pine, the age-height growth curves for the four provinces are similar at *SI* = 10, 15 and 20 m when breast height age < 80 years (**Figure 3.16**). Some divergence in the four growth curves is seen for ages > 80 years, with the Alberta and Manitoba models predicting slightly greater height growth than the models for northern Ontario and New Brunswick. For low-productivity jack pine stands (*SI* = 5 m), the height growth curves are similar for all provinces. Again, these results indicate that Manitoba model [3.4] produces jack pine age-height growth curves that are similar to, and comparable with, those developed for other provinces.

3.5.9 Ecozone-Based Nonlinear Mixed-Effects Models

For practical forestry applications, the mixed-effects model [3.24] derived from model [3.4] was used to obtain individual for black spruce and jack pine height growth and site index models for both the Boreal Plains and Boreal Shield ecozones of Manitoba. In order to increase sample size and optimize model performance, the fitting and validation data were pooled to obtain the ecozone-specific models.

The estimated regression parameters and associated model fitting statistics for black spruce and jack pine models in each of the two ecozones are presented in **Table 3.11**. All model fittings converged, and all fitted parameters were statistically significant. To facilitate application in forestry research, the models were used to generate height growth and site index tables for black spruce and jack pine in the Boreal Plains and Boreal Shield ecozones of Manitoba. These tables are presented in **Appendices 1 – 4**.

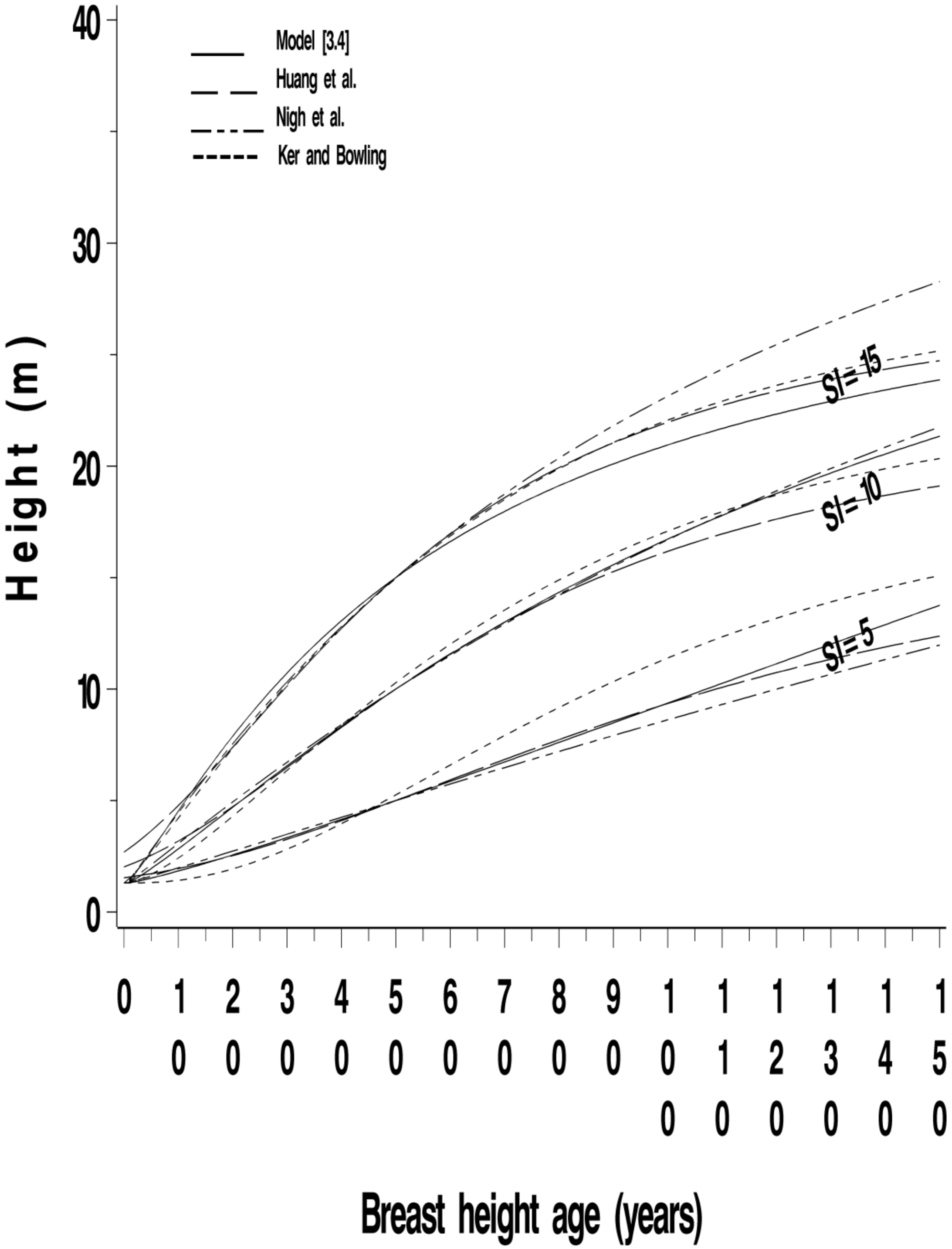


Figure 3.15. Height growth and site index curves plotted against breast height age for site indices 5, 10 and 15 m for model [3.4], Nigh *et al.* (2002), Huang *et al.* (1994) and Ker and Bowling (1991) for black spruce.

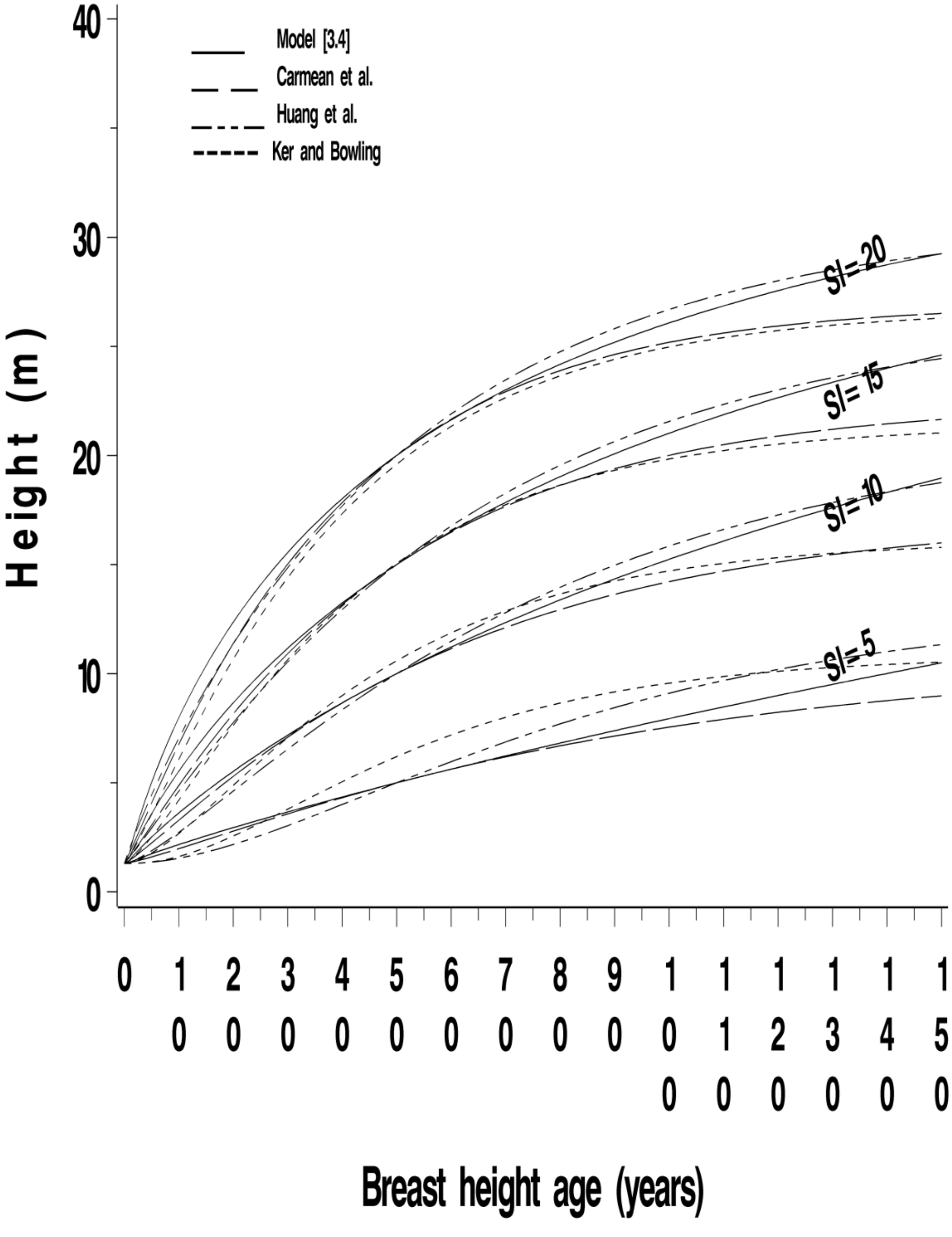


Figure 3.16. Height growth and site index curves plotted against breast height age for site indices 5, 10, 15 and 20 m for model [3.4], Huang *et al.* (1994), Ker and Bowling (1991) and Carmean (2001) for jack pine.

To obtain a general sense of the accuracy and precision of these ecozone-specific models, site index predictions were obtained for breast height age classes (10 year-intervals, expect for the youngest age class of 0 – 5 years). The observed and predicted site index values, absolute and percent bias, and RMSE values for the age classes of black spruce and jack pine are summarized in **Tables 3.12** and **3.13** respectively.

For black spruce, the overall site index prediction bias in Boreal Plains and Boreal Shield ecozones were -0.11 m and -0.23 m respectively, indicating that the models slightly over-estimated site index values. Associated root mean squared errors (*RMSE*) were 1.623 and 1.858, respectively (**Table 3.12**). On a relative (percentage) scale, the prediction biases were quite low: just -1.08% for the Boreal Plains, and -2.06% for the Boreal Shield.

For jack pine, the overall site index prediction biases were -0.34 m for the Boreal Plains and -0.30 m for the Boreal Shield ecozones, indicating slight over-estimation of site index values (**Table 3.13**). Associated root mean squared errors (*RMSE*) were 2.834 and 2.122, respectively. On a relative (percentage) scale, prediction biases were small: -2.36% for the Boreal Plains, and -2.00% for the Boreal Shield.

While overall site index prediction biases were very low in these models, the prediction biases for specific age classes were quite variable, and some biases (particularly in the youngest age classes) were quite large. In all four models, bias was generally highest in the youngest and oldest age classes, and lowest at middle age classes. This result confirms research indicating that site index models often provide unreliable site index estimates for young stands. The results also suggest that site index models should be used with caution in older stands.

Table 3.11. Estimated parameters and fitted statistics of model [3.24] for black spruce and jack pine by ecozone.

			BOREAL PLAINS					**BOREAL SHIELD**				
Spp		Parameter	**Estimate**	**SE**	***t***	***P***	**d.f.**	**Estimate**	**SE**	***t***	***P***	**d.f.**
BS	**Fixed effect**	b_0	12.216	2.4628	4.96	<.0001	419	11.9714	0.88670	13.5	<.0001	1253
		b_1	-0.9483	0.0476	-19.91	<.0001		-1.0600	0.02972	-35.66	<.0001	
		b_2	-3.0114	1.0421	-2.89	0.0047		-2.8624	0.37520	-7.63	<.0001	
	Variance	$\sigma_{u_1}^2$	0.9718	0.4726	2.06	0.0199		0.6340	0.13080	4.85	<.0001	
		$\sigma_{u_1u_2}$	0	n/a	n/a	n/a		-0.0949	0.02799	-3.39	0.0007	
		$\sigma_{u_2}^2$	0.054	0.0150	3.61	0.0002		0.0595	0.01303	4.56	<.0001	
		σ^2	0.3388	0.0452	7.50	<.0001		0.3779	0.03588	10.53	<.0001	
	Correlation	ρ	0.6014	0.0540	11.16	<.0001		0.6948	0.02984	23.28	<.0001	
	AIC	AIC	834.5					2313.0				
JP	**Fixed effect**	b_0	7.8761	1.38340	5.69	<.0001	432	9.6816	1.1489	8.43	<.0001	759
		b_1	-0.9807	0.05155	-19.03	<.0001		-0.9187	0.0333	-27.63	<.0001	
		b_2	-1.4617	0.54200	-2.70	0.0073		-2.1009	0.4366	-4.81	<.0001	
	Variance	$\sigma_{u_1}^2$	0.3656	0.10230	3.57	0.0002		0.3198	0.0882	3.63	<.0001	
		$\sigma_{u_1u_2}$	-0.0846	0.04005	-2.11	0.0346		0	n/a	n/a	n/a	
		$\sigma_{u_2}^2$	0.0921	0.02751	3.35	0.0004		0.0255	0.0141	1.81	0.0349	
		σ^2	0.2466	0.03589	6.87	<.0001		0.5319	0.0610	8.72	<.0001	
	Correlation	ρ	0.5490	0.06448	8.52	<.0001		0.7666	0.0267	28.73	<.0001	
	AIC	AIC	761.4					1421.8				

Note: b_0, b_1 and b_2 are fixed parameters; $\sigma_{u_1}^2, \sigma_{u_2}^2, \sigma_{u_1u_2}$ are variance-covariance components of random parameters u1 and u2; $\sigma^2$is residual variance of the model; ρ is the correlation parameter; AIC is the Akaike's information criterion; SE is standard errors for estimated parameters; df is degree of freedom; BS is black spruce; JP is jack pine.

Table 3.12. Site index prediction accuracy for black spruce from model [3.24] by ecozone.

Age Class		Boreal Plains						Boreal Shield					
		Obs	**Pred**	**Bias**	**Bias%**	**RMSE**	**n**	**Obs**	**Pred**	**Bias**	**Bias%**	**RMSE**	**n**
1	M	11.88	15.13	-3.26	-27.42	5.499	23	12.63	17.24	-4.61	-36.51	6.571	69
2	M	10.91	10.9	0	0.03	2.049	76	12.04	12.19	-0.15	-1.22	2.082	235
3	M	10.82	10.54	0.28	2.55	1.5	68	11.6	11.43	0.17	1.45	1.609	234
4	M	11.18	10.91	0.26	2.34	1.121	68	11.64	11.46	0.18	1.5	1.063	218
5	M	11.01	10.77	0.24	2.17	0.77	67	11.54	11.37	0.17	1.45	0.673	182
6	M	10.74	10.72	0.03	0.24	0.193	55	11.42	11.44	-0.02	-0.19	0.317	176
7	M	10.43	10.5	-0.07	-0.66	0.448	49	10.27	10.47	-0.2	-1.95	0.688	132
8	M	10.53	10.82	-0.29	-2.72	0.999	49	9.72	9.99	-0.27	-2.78	0.902	106
9	M	9.35	9.57	-0.21	-2.29	1.368	27	9.79	10.2	-0.41	-4.19	1.311	90
10	M	8.05	8.26	-0.21	-2.66	1.268	12	8.79	9	-0.21	-2.36	1.405	56
11	M	8.17	8.48	-0.31	-3.8	1.406	13	8.73	8.98	-0.25	-2.88	1.479	31
12	M	7.58	8.38	-0.8	-10.52	2.529	5	8.21	8.41	-0.21	-2.51	2.785	13
13	M	7.13	8.25	-1.12	-15.73	2.871	7	8.07	7.81	0.26	3.22		3
14	M	8.23	7.48	0.76	9.2		1	7.13	6.12	1	14.08	2.461	5
15	M							5.54	4.82	0.73	13.14		1
16	M	7.98	5.91	2.07	25.88		1	5.54	4.7	0.85	15.26		1
Overall	M	10.58	10.7	-0.11	-1.08	1.623	521	11.13	11.36	-0.23	-2.06	1.858	1552

Note: AgeC –Breast height age class; Obs –observed value; Pred –predicted value; Bias –prediction errors; Bias% -prediction error percent; RMSE - root mean square error; M –mean value; n – total number of observations.

Table 3.13. Site index prediction accuracy for jack pine from model [3.24] by ecozone.

Age Class		Boreal Plains						Boreal Shield					
		Obs	**Pred**	**Bias**	**Bias%**	**RMSE**	**n**	**Obs**	**Pred**	**Bias**	**Bias%**	**RMSE**	**n**
1	M	14.33	18.41	-4.08	-28.48	7.64	57	15.7	18.08	-2.38	-15.15	5.12	101
2	M	14.33	14.05	0.28	1.98	2.471	127	15.24	14.97	0.27	1.74	2.051	220
3	M	14.35	14.21	0.14	0.99	1.41	107	15.09	15.12	-0.03	-0.21	1.321	184
4	M	14.21	14.27	-0.06	-0.42	1.048	80	15.2	15.44	-0.24	-1.58	1.082	145
5	M	14.28	14.21	0.07	0.46	0.597	66	14.67	14.75	-0.08	-0.56	0.687	103
6	M	13.56	13.65	-0.09	-0.63	0.227	43	14.35	14.37	-0.02	-0.14	0.305	67
7	M	14.2	14.15	0.05	0.31	0.572	29	13.76	14	-0.25	-1.78	0.741	51
8	M	13.75	13.4	0.35	2.57	0.678	13	12.61	13.31	-0.7	-5.55	1.557	36
9	M	12.8	12.5	0.3	2.37	1.251	9	11.79	12	-0.21	-1.74	1.156	15
10	M	15.74	17.25	-1.51	-9.59		1	10.21	11.96	-1.75	-17.09		1
Overall	M	14.2	14.54	-0.34	-2.36	2.834	532	14.88	15.18	-0.3	-2	2.122	923

Note: AgeC –Breast height age class; Obs –observed value; Pred –predicted value; Bias –prediction errors; Bias% -prediction error percent; RMSE - root mean square error; M –mean value; n – total number of observations.

3.6 DISCUSSION

In this study, ten equations used to model tree height growth (site index) of various tree species in the boreal forests of Canada were selected for fitting to Manitoba black spruce and jack pine stem (bole) section data. A number of regression modeling approaches were also explored, including nonlinear least squares (NLS), generalized nonlinear least squares (GNLS), and nonlinear mixed-effects models (NLMM). These models and approaches were compared statistically and evaluated in order to select an unbiased, accurate and parsimonious height growth (site index) model for empirical use in predicting tree height and site index of black spruce and jack pine in Manitoba.

Considerations of model parsimony (i.e. minimizing the number of regression parameters), combined with a detailed examination of model statistical accuracy and goodness-of-fit, led to the selection of equation [3.4] (Nigh *et al*. 2002, 2009) as the “base” model for estimating tree height growth and site index of black spruce and jack pine in Manitoba’s Boreal Plains and Boreal Shield ecozones. This model, which is based on the generalized logistic function (Monserud 1984), was developed and successfully used to model height growth and site index of black spruce (Nigh *et al*. 2002) and paper birch (Nigh *et al*. 2009) in British Columbia.

Statistical goodness-of-fit, examination of residuals, and considerations of model accuracy and bias were used to evaluate the ten candidate height growth (site index) models. These investigations indicated that models [3.2] and [3.4], both of which are modified generalized logistic functions (Monserud 1984), produced results that were statistically accurate, parsimonious and unbiased. Models [3.2] and [3.4] both contain three parameters requiring estimation, and utilize SI (height at breast diameter age = 50) as an independent variable. Model [3.4] has been used to model height growth of black spruce in British Columbia (Nigh et al. 2002), while model [3.2] has been recommended for general use in modeling height growth of boreal tree species in Alberta (Huang 1997). Good results were also obtained from empirical model [3.8], which has been used to predict height growth of black spruce and jack pine in New Brunswick (Ker and Bowling 1991), and model [3.10] (a slightly modified version of [3.8]). However, models [3.8] and [3.10] both have five regression parameters requiring estimation, making them less parsimonious than models [3.2] and [3.4].

The model [3.8] described by Newnham (1988a) also performed well, but it produced non-asymptotic site index curves for black spruce. In addition, this model contains five parameters, two more than models [3.2] and [3.4] that performed equally well or better. The empirical model developed in 1981 by the British Columbia Ministry of Forests (model [3.9]) has only three parameters, but it performed less well (i.e. lower R^2, and larger root mean square error) than the other three-parameter models considered in this study.

The two difference equation models [3.5] and [3.6] differ from the other models in having the general form $H_2 = f\ (H_1, T_1, T_2)$. In addition, these models do not utilize *SI* as an independent variable (Clutter *et al.* 1983), which is advantageous when *SI* is undefined (e.g. younger trees < 50 years old at breast height). However, these models contain five parameters requiring estimation, and my analyses indicated that they performed poorly compared to models [3.2] and [3.4].

Model results indicated that site index predictions for younger black spruce and jack pine trees (< 20-30 years old) were unreliable and highly variable. The challenge of estimating the site index of young trees and forest stands is a common and well-known problem in forestry practice (Carmean 1978; Huang 1997), and is attributable to highly variable height growth rates in regenerating stands. It is generally recommended that site index should only be estimated for trees > 30 years old in order to minimize prediction errors (Curtis *et al.* 1974; Carmean 1978; Borders *et al.* 1984; Carmean and Lenthall 1989; Huang 1997).

There are also restrictions on the age range over which tree height growth (site index) models should be applied (Huang 1997; Carmean *et al*. 2001; Nigh *et al.* 2002). This is determined by the age range available to develop the model, as well as species longevity (maximum age) and stand rotation time (number of years between harvests). In this study, the models were presented over a range of 20 – 150 years (breast height age) for black spruce, and 20 – 100 years for jack pine. Beyond these ranges, model predictions are considered unreliable and potentially biased due to extrapolation beyond the age range of the fitted data (Otto and Day 2007).

The height growth and site index models developed for Manitoba black spruce and jack pine were compared with those used in other Canadian provinces, including Alberta black spruce and jack pine (Huang *et al.* 1994b), jack pine in northern Ontario (Carmean *et al.* 2001), black spruce in British Columbia (Nigh *et al.* 2002, 2009) and New Brunswick black spruce and jack pine (Ker and Bowling 1991). Plots of site index curves for these models indicated that patterns of tree height growth were quite similar, particularly within the 20 – 100 age range for black spruce and the 20 – 80 age range for jack pine. There was greater variation in predicted height for older trees, but the Manitoba site index model predictions remained well within the expected range predicted by the other, independently derived models.

The models developed for Manitoba black spruce and jack pine can be used to predict expected tree height for a given site index and breast height age values, or to determine site index for given tree height and breast height age values through iteration. For convenience and in practical applications, it would be ideal to obtain a single height growth model per species that could be used throughout the province of Manitoba. However, my investigations indicated minor differences in height growth of both black spruce and jack pine in the Boreal Plains and Boreal Shield ecozones. For accurate and reliable predictions of site index, the use of ecozone-specific models is recommended for Manitoba. This is a common practice in other provinces as well. For example, in British Columbia, species-specific site index models have been developed for each major biogeoclimatic zone (G. Nigh 2010; *pers. comm.*).

During model development, height growth (site index) equations are normally parameterized using stem (bole) section data consisting of several diameter measures taken at various locations along a tree bole. These spatially autocorrelated measures result in error terms that are statistically dependent, violating the important assumption of error independence in regression analysis (Neter *et al*. 1990). The use of standard nonlinear least square (NLS) regression to fit height growth models fails to adequately address the statistical problems associated with autocorrelation (Kozak 1997). In this study, three approaches were used to address autocorrelation in stem (bole) section data: random selection of a single measurement per tree, generalized nonlinear least square (GNLS) regression, and the nonlinear mixed-effects model (NLMM) regression approach. Random selection of a single measure per tree removed autocorrelation from the data, but this approach has the considerable disadvantage of not utilizing much of the information contained in field-collected data. Lagged residual analyses and correlation tests indicated that GNLS regression only partially resolved autocorrelation issues. The NLMM approach completely addressed the autocorrelation problems, and is the recommended regression method for the analysis of stem (bole) section data in applied forestry applications (Trincado and Burkhart 2006; Sharma and Parton 2009).

The nonlinear mixed-effects modeling (NLMM) approach addresses the problem of data autocorrelation by estimating the covariance matrix of inter-variable correlations, and by incorporating both fixed- and random-effects parameters into the model (Schabenberger and Pierce 2001; Trincado and Burkhart 2006). Such models are complex and analytically challenging, and their implementation requires careful decisions regarding whether each parameter should be modeled as a fixed or mixed (fixed plus random) effect (Trincado and Burkhart 2006). In this study, seven combinations of fixed and mixed parameters within model [3.4] were considered. Development and comparison of these seven potential NLMM models was very time-consuming, but the results clearly demonstrated that the selected model (equation [3.24]) successfully dealt with the autocorrelation present in the stem (bole) analysis data. Similar results have been obtained in other forest modeling studies (e.g. Trincado and Burkhart 2006).

A comparison of model fittings using different approaches (nonlinear least squares (NLS), generalized nonlinear least squares (GNLS) and nonlinear mixed-effects (NLMM) modeling) indicated that very similar height growth predictions were produced, for both black spruce and jack pine. This indicates that fitting height growth (site index) models using the nonlinear least squares (NLS) regression approach produces unbiased predictions of height growth: nonlinear least squares parameter estimates are asymptotically unbiased and consistent, even when autocorrelations are present (Gallant 1987; Judge *et al*. 1988). In practical forestry applications, parameter estimates obtained using nonlinear least squares techniques will therefore provide unbiased and reasonable predictions of tree height growth and site index values (Monserud 1984; Neter *et al.* 1990; Kmenta 1986; Huang 1992; Kozak 1997). Test statistics based on NLS should be interpreted with considerable caution, however, when data are known to be spatially autocorrelated (Neter *et al*. 1990). Instead, the analysis should focus on the practical examination of model validation results and residuals (Yang *et al*. 2003).

The NLMM regression approach, which accounts for both population mean and tree-specific variation, has the advantage of producing more accurate tree-specific predictions. This regression approach produced reliable height growth and site index models for both black spruce and jack pine, with root mean square errors (*RMSE*) that were consistently lower than those from the other modeling approaches. Furthermore, the inclusion of prior measurements from each tree resulted in more accurate predictions. The NLMM regression approach is therefore recommended when prior measurements are available. In practice, the high cost of collecting tree measurements from vast tracts of inaccessible forest precludes the use of NLMM models and prior measurements. Thus, fixed-effects models that account only for population variation are used to obtain a reasonable approximation of tree height growth and site index estimation (Fang and Bailey 2001; Meng *et al.* 2008; Nigh *et al.* 2009; Y. Yang and G. Nigh 2010, *pers. comm.*).

There are two major applications of height growth – site index models in applied forestry. The first application is in forest growth and yield forecasting, where site index models are used to predict the growth of dominant and co-dominant trees in order to forecast merchantable timber yield at some point in the future (e.g. a scheduled timber harvest). The second application is in forest stand productivity classification, the aim of which is to improve the accuracy and precision of forest inventory projections in order to ensure a reliable and sustainable forest management for future generations. The models developed in this study provide the tools necessary to obtain accurate and reliable forecasts of the growth of trees and stands of black spruce and jack pine in Manitoba.

CHAPTER 4 INDIVIDUAL TREE DIAMETER GROWTH MODELS FOR BLACK SPRUCE AND JACK PINE

4.1 INTRODUCTION

The quantitative analysis of tree diameter increment growth is undertaken to predict the rate of increase in tree size over time, and to summarize forest stand volume growth and yield. Accurate prediction of basal area growth is critically important to the development of more accurate and precise individual tree growth and yield models used in forest practice and inventory, timber supply analysis, and sustainable forest management (Stage 1973; Daniels and Burkhart 1975; Wykoff 1990).

Tree diameter at breast height (DBH = 1.3 m) is a widely used variable in forest growth modeling, since it is relatively easy to measure and has a well-established allometric relationship to tree volume. The diameter increment, which quantifies stem diameter growth at breast height (DBH), is obtained by measuring tree DBH at specified time intervals (e.g. five years in Manitoba forest inventory plots), or by measuring annual ring widths of tree cores (Oliver and Larson 1996). Growth models may be based on either diameter or basal area increments; either can be used, since there is a simple fixed relationship between stem diameter and basal area (Vanclay 1994; West 1980). In practice, many researchers base their models on tree basal area, since it is more linearly related to tree volume growth (Wykoff 1990; Monserud and Sterba 1996; Hokka and Groot 1999).

Tree diameter (or basal area) growth models have long been utilized in forest growth and yield prediction. Such models are used to directly predict tree and stand volumes (timber yield), or to obtain reliable estimates of how much of a specific forest product can be obtained from trees or forest stands (Hann and Larsen 1991). Tree diameter growth rates are highly variable, due to differences in tree species, site productivity, stand density and spacing, climatic conditions and numerous other factors. As a result, a great many individual tree diameter (or basal area) growth models have been developed for various tree species over a broad range of stand and environmental conditions (e.g. Wykoff 1990; Quicke *et al*. 1994; Huang and Titus 1995; Monserud and Sterba 1996; Murphy and Shelton 1996; Cao 2000; Lessard *et al*. 2001; Zhao *et al*. 2004).

Jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) are ecologically and economically important tree species in Manitoba (Manitoba Conservation 2001). Over the past 30 years, large amounts of data on the diameter growth of these two species have been obtained from permanent sample plots located within naturally regenerating and managed stands in the southeast and central regions of the province. Within these plots, individual tree locations were mapped (Manitoba Conservation 2000). These growth and spatial data have been collected with the goal of obtaining a long-term database on forest stand growth in the province. Such data are essential to the development of reliable, accurate and mathematically sophisticated individual tree growth models for Manitoba jack pine and black spruce. Diameter (basal area) growth models, which are used to develop meaningful and reliable sustainable forest management forecasts and strategies, are not currently available for these two economically important tree species in Manitoba.

The objective of this study is to develop reliable, accurate and statistically sophisticated diameter growth models for Manitoba black spruce and jack pine, utilizing available long-term permanent sample plot data. The development of such models requires the examination and consideration of effective model predictors, including both individual tree and stand level variables. The importance of the influence of tree spatial location (local competition) on the diameter growth of individual trees is also explored. Independent data, not used in developing the model, are used for model validation.

4.2 STUDY AREA

The study area is located in Boreal Shield and Boreal Plains ecozones of Manitoba. A summative description of these two ecozones is given in Section 3.2.

4.3 DATA

4.3.1 Permanent Sample Plots

The permanent sample plots used in this study were established within naturally regenerated and managed stands of jack pine and black spruce. These plots were located throughout the economically important forest regions of Manitoba in order to obtain representative examples of stands over a range of stand densities, ages and site productivity classes (Manitoba Conservation 2000). All plots were located at least 100 m from a forest stand boundary, and at least 50 m from roads or trails, in order to minimize human disturbance.

The permanent sample plots were circular, with a fixed radius of 12.62 m (area = 500 m^2 or 0.05 ha). At the time of plot establishment, an aluminum post was driven into the ground to mark the plot center. All living trees within a distance of 12.62 m from this post were marked with a numbered aluminum tag secured using an angled galvanized nail. The DBH of each tree was then measured, beginning at true north and proceeding in a clockwise direction around the plot. Physical damage (e.g. broken limbs), fungal pathogen infection and insect damage were also noted for each tree.

All trees within the plot were mapped, by measuring the distance and azimuth to the plot center; azimuth was measured using a compass, and distance using a vertex. Within each quadrant (1 – 90°, 91 – 180°, 181 – 270° and 271 – 360°) of the circular plot, two or three randomly selected dominant or co-dominant, healthy trees were cored to obtain estimates of stand age.

The permanent sample plots were re-measured on a five-year cycle. During each re-measurement period, the following information was recorded for each marked tree: status (live or dead); DBH (cm); height and canopy class (m); and notes on physical or insect damage, and pathogen diseases.

4.3.2 Classification of Plots

The growth patterns of black spruce on lowland (organic peatland) and upland (mineral soil) substrates are known to differ appreciably (Viereck and Johnston 1990). For modelling purposes, the black spruce permanent sample plots were therefore classed into two edaphic groups – lowland and upland stands – using the Manitoba vegetation type classification (Zoladeski *et al.* 1995). The following four vegetation types (V-types) were considered lowland black spruce stands:

V30 – Black Spruce/Labrador Tea/Feather Moss (Sphagnum): lowland black spruce stands on wet, organic, poorly drained soils.

V31 – Black Spruce/Herb Rich/Sphagnum (Feather moss): black spruce stands, with small amounts of white cedar or tamarack, on wet, poorly-drained organic soils with sphagnum and feather moss and herbs.

V32 – Black Spruce/Herb Poor/Sphagnum (Feather moss): lowland black spruce stands, with the occasional tamarack, on wet, poorly-drained organic soils with a carpet of sphagnum and feather moss and a sparse herb layer.

V33 – Black Spruce/Sphagnum: poorly stocked, stunted lowland black spruce stands on organic soil, with a carpet of sphagnum and feather moss.

All other vegetation types were considered upland black spruce stands (Zoladeski *et al*. 1995).

The jack pine stands were also classed into two groups: managed and natural stands. Stands that had undergone human activity or intervention (e.g. site preparation, planting, broadleaf herbicide application, thinning) were classed as “managed” stands, whereas naturally established stands with no human activity were classed as “natural” stands. Note that this distinction was not necessary for the black spruce plots, since all the black spruce permanent sample plots occurred in natural stands.

4.3.3 Plot Selection

A large number of permanent plots have been established and enumerated in Manitoba, but some were not suitable for use in this study. Diameter growth models are most reliably based on long-term data from pure, even-aged stands (Avery and Burkhart 1994). Therefore, the following criteria were used to select the permanent sample plot data used in this study:

1. Stands must be dominated by either jack pine or black spruce. In this study, stand dominance is defined as >70% total basal area of either jack pine or black spruce in the permanent sample plots (Manitoba Conservation, 2000). Mixed forest stands (< 70% total basal area of jack pine or black spruce) were not considered in this study.

2. The permanent sample plot data must include a minimum of two consecutive five-year growth intervals, i.e. the initial measurement at the time of plot establishment plus at least two re-measurements (spanning a 10-year period).

Using these selection criteria, a total of 80 permanent sample plots dominated by either black spruce or jack pine were used to develop and validate the diameter increment growth models. Of these 80 plots, 12 were lowland black spruce, 16 were upland black spruce, 30 were managed jack pine, and 22 were natural jack pine stands (**Table 4.1**). These stands were dominated by either black spruce or jack pine: over 95% of the trees in these 80 plots were either jack pine or black spruce. Most of the plots (56 of 80) were pure stands (> 95% basal area of jack pine or black spruce). The remaining 24 stands contained minor amounts (< 15% basal area) of trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), balsam fir (*Abies balsamea*)*,* white spruce (*Picea glauca*)*,* tamarack (*Larix laricina*) and/or balsam poplar (*P. balsamifera*).

4.3.4 Plot (Stand) Characterization

In order to minimize problems with temporal autocorrelation, only the most recent diameter growth interval measurement was used for each plot and tree. Thus, for plots measured three times, only the second to third measurements were used to determine incremental growth; for plots measured four times, only the third to fourth measurements were used; and for plots measured five times, only the fourth to fifth measurements were used. Only trees that were alive during both measurement times were included in the analysis, and trees with a zero diameter increment, or with missing data, were excluded. Trees subject to edge effects in the delineation of Thiessen polygon area (see Section 4.4.1.5) were also excluded.

A total of 7839 trees (4817 black spruce and 3022 jack pine) were used for model development and validation. Stand level attributes for the 80 permanent sample plots are summarized in **Table 4.2**. On average, the 28 black spruce stands were older than the 52 jack pine stands (75 versus 35 – 50 years old) and much denser (6800 – 8600 versus 2500 – 3000 trees/ha), but less productive (site index of 10 m versus 16 m). **Table 4.3** summarizes individual tree attributes. On average, black spruce trees are smaller than jack pine (6.0 – 6.5 cm versus 9.5 – 11.5 cm DBH), and less productive (diameter increments of 0.4 versus 0.9 cm). The mean Thiessen polygon areas of black spruce are much smaller than those of jack pine (1.1 – 1.4 m^2 versus 3.1 – 4.0 m^2), reflecting the much higher density of black spruce stands.

Cumulative DBH frequency distributions for the 28 black spruce plots are shown in **Figure 4.1a**; it is notable that the distributions are broadly sigmoidal in shape. **Figure 4.1b** summarizes changes in the cumulative frequency distribution of DBH over five measurements periods (1986 – 2006) for one of the 28 black spruce plots (plot 17, site index = 10). Note that the sigmoidal shape of the cumulative distribution is retained throughout 20-year sampling period. It is also apparent that the incremental growth of smaller trees (< 7 cm DBH in 1986) is low compared to larger trees.

Cumulative DBH frequency distributions for the 52 jack pine plots are illustrated in **Figure 4.2a**. The distributions are asymptotic, but not sigmoidal as in black spruce. **Figure 4.2b** summarizes changes in the cumulative frequency distribution of DBH over five measurements periods (1986 – 2006) for one of the 52 jack pine plots (plot 9, site index = 15). The upper-asymptotic shape of the cumulative distribution is retained throughout 20-year the sampling period. It is also apparent that the incremental growth of smaller trees is less than that of larger trees.

4.3.5 Model Development and Validation

Following model development, it is desirable – and indeed necessary – to validate the developed predictive model using independent data (Jeffers 1982). In this study, this was accomplished by randomly selecting 63 of the 80 permanent sample plots (about 80%) for model development, reserving the remaining 17 plots for model validation. **Tables 4.4** and **4.5** summarize stand and tree parameters for the 63 plots used in model development, while **Tables 4.6** and **4.7** summarize the same parameters for the 13 model validation plots.

4.4 METHODS

Selection of the “best” predictive empirical model is generally accomplished by identifying the equation that minimizes the residual error sum of squares. Simultaneously, the estimated parameters (associated with independent variables) are examined to ensure their statistical significance in the fitted equation. Consideration is also given to the biological and ecological relevance of the independent variables included in the model, and to the sign and scaling of regression coefficients.

The variables used to predict basal area growth in forestry include tree size (stem diameter at breast height and associated nonlinear terms, e.g. diameter squared, reciprocal of diameter), site productivity (e.g. site index), stand-level measures of overall competition (e.g. stand total basal area), and distance-independent (aspatial) individual competitive effects (e.g. relative diameter, basal area of trees larger than target tree); see Wykoff (1990); Yang *et al.* (2003); Zhao *et al. (*2004). In this study, I introduce a distance-dependent (spatial) measure of intraspecific competition, the Thiessen polygon area (TPA), as a potential predictor variable in the modeling of tree diameter growth.

4.4.1 Selection of Variables

A number of factors affect the physiological and ecological processes of individual tree growth and forest stand development. An understanding of the processes determining tree growth helps in formulating hypotheses, selecting potential predictor variables, and determining variable relationships when developing forest growth models. Such knowledge is also helpful in the structural evaluation and interpretation of forest growth models.

I provide here a brief literature summary of the variables considered important in predicting diameter (basal area) growth, and include an evaluation of their utility as potential predictor variables in this study (see also Wykoff 1990; Monserud and Sterba 1999; Yang *et al.* 2003; Zhao *et al.* 2004). My goal is to develop basal area growth models that explain the most variability, while using the smallest number of parameters to achieve a parsimonious model.

Tree Size: Stem Diameter

Diameter at Breast Height: D
Nonlinear Terms: Diameter Squared (D^2), Reciprocal of Diameter (D^{-1})

Diameter at breast height is the most widely used variable for modeling tree diameter (basal area) growth (Monserud and Sterba 1999; Yang *et al.* 2003; Zhao *et al.* 2004). Tree size (e.g. diameter) is generally used as a proxy for tree age in forest growth modelling (Yao *et al.* 2001), since individual tree age data often are not available and are costly to obtain. Diameter at breast height was used in this study as a size-age predictor variable, since accurate age values were not available for the jack pine and black spruce data.

The relationship between tree size (stem diameter) and diameter increment is unimodal and positively skewed: incremental growth increases to a maximum early in the life of a tree, and then slowly decreases over time as the tree matures (Wykoff 1990; Huang and Titus 1995). This nonlinear relationship can be modelled using diameter and diameter squared as predictor variables (Wykoff 1990; Monserud and Sterba 1999; Yang *et al.* 2003). Zhao *et al*. (2004) suggested including the hyperbolic transformation of diameter (i.e. reciprocal of diameter), to capture nonlinear effects related to the lower incremental growth of the smaller trees in a stand. Preliminary analyses indicated a non-linear relationship between tree size (diameter) and incremental growth in jack pine and black spruce (**Figure 4.3**). These nonlinear diameter terms were therefore considered in model development.

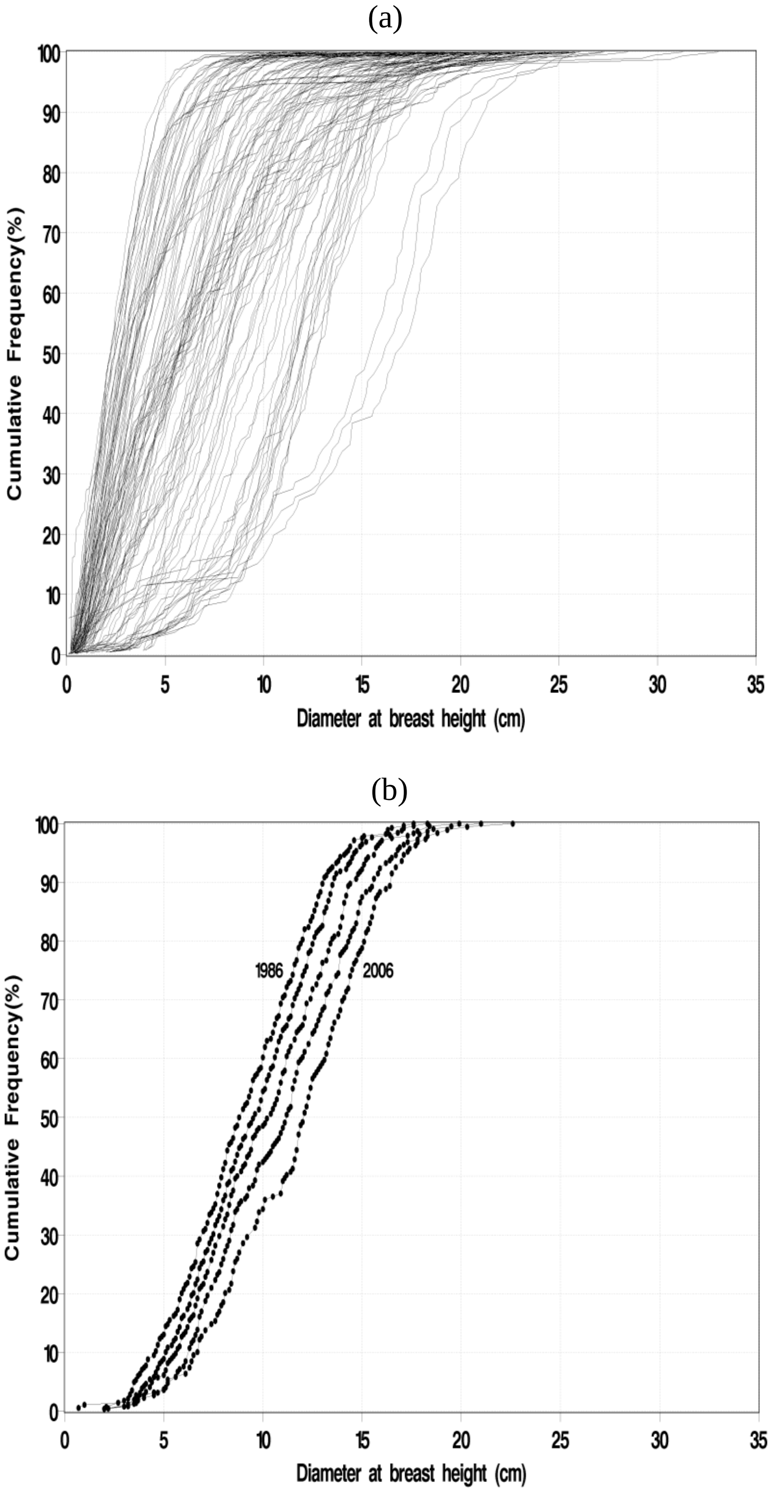


Figure 4.1. (a) Cumulative DBH distributions for the 28 black spruce permanent sample plots; (b) Cumulative DBH distributions for a tree from plot 17 (SI = 10) over five measurement periods, from 1986 to 2006 (five year intervals).

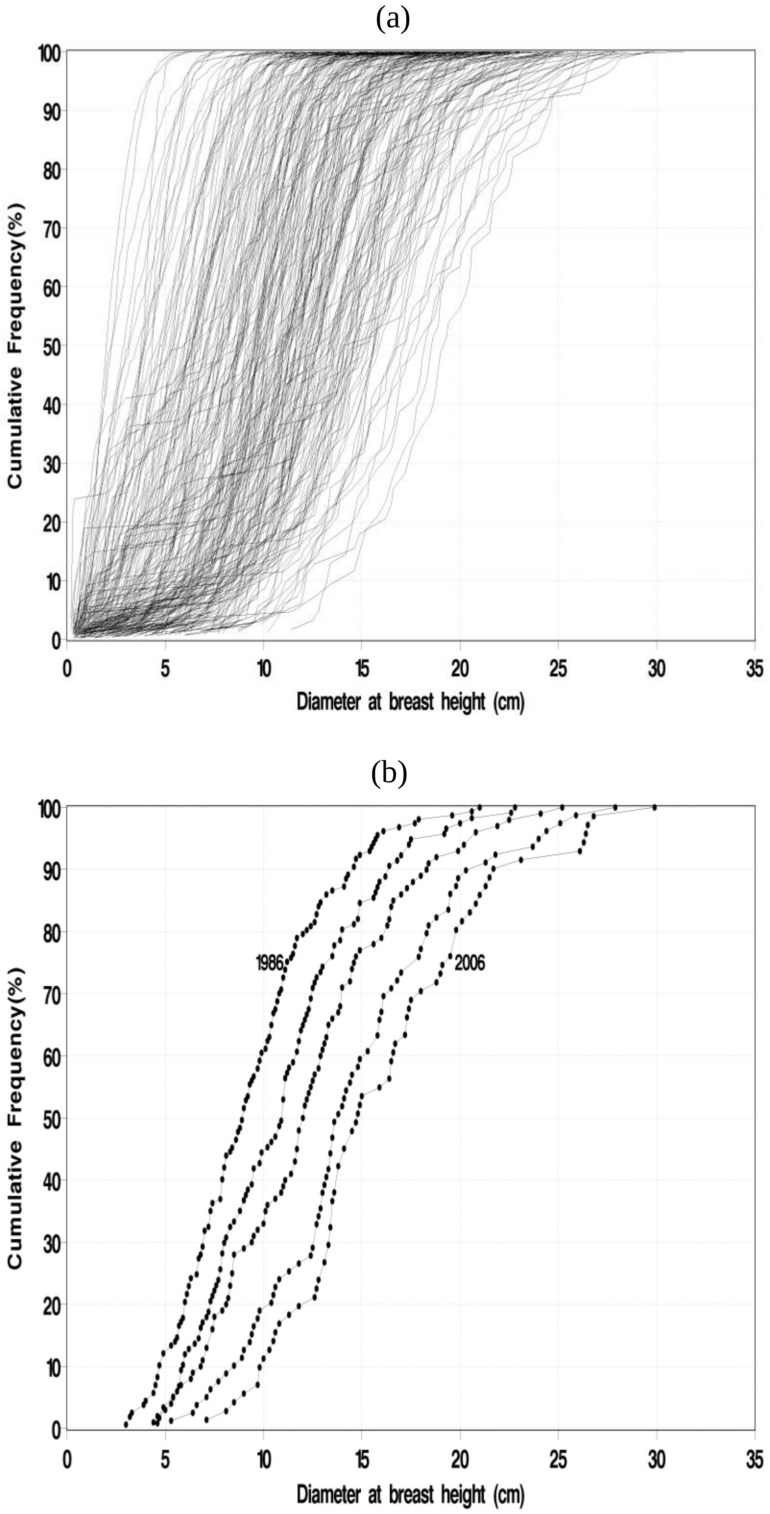


Figure 4.2. (a) Cumulative DBH distributions for the 52 jack pine permanent sample plots; (b) Cumulative DBH distributions for a tree from plot 9 (SI = 15) over five measurement periods, from 1986 to 2006 (five year intervals).

Table 4.1. Summary of the 80 permanent sample plots (PSP) used in this study. The plots are classified by species group (lowland black spruce, upland black spruce, managed jack pine, and natural jack pine stands), and by the number of repeated measurements on trees (five-year intervals). In this study, only the last measurement interval was used to determine incremental growth in diameter.

SPECIES GROUP	No. Measurements	No. Plots
Lowland Black Spruce	3	6
	4	4
	5	2
	Subtotal	**12**
Upland Black Spruce	3	4
	4	9
	5	3
	Subtotal	**16**
Managed Jack Pine	3	6
	4	8
	5	16
	Subtotal	**30**
Natural Jack Pine	3	3
	4	11
	5	8
	Subtotal	**22**
	TOTAL	**80**

Table 4.2. Summary of stand attributes for the 80 permanent sample plots, by species group, used in this study.

SPECIES GROUP	VARIABLE	MEAN	MIN	MAX	S.D.
Lowland BS*	Basal Area (m^2/ha)	29.31	18.74	46.78	8.73
(*n* = 12 plots)	Stand Age (yrs)	77.2	25	123	31.4
	Site Index (m)	10.07	4.07	15.2	3.18
	Density (trees/ha)	6790	1760	17620	5353
Upland BS*	Basal Area (m^2/ha)	30.19	16.34	43.79	9.36
(*n* = 16 plots)	Stand Age (yrs)	74.7	43	158	31
	Site Index (m)	9.57	4.52	16.77	3.55
	Density (trees/ha)	8614	3480	22480	5274
Managed JP*	Basal Area (m^2/ha)	23.97	11.38	33.75	5.33
(*n* = 30 plots)	Stand Age (yrs)	35.9	18	50	9.3
	Site Index (m)	16.27	11.15	19.65	2.15
	Density (trees/ha)	3017	860	9800	2203
Natural JP*	Basal Area (m^2/ha)	24.93	16.34	43.05	6.82
(*n* = 22 plots)	Stand Age (yrs)	48.3	29	91	16.8
	Site Index (m)	15.68	4.63	22.33	4.36
	Density (trees/ha)	2565	1140	5240	1243

* BS = Black Spruce, JP = Jack Pine.

Table 4.3. Summary of attributes of the 7839 trees (classified by species group) used in this study.

SPECIES GROUP	VARIABLE[†]	MEAN	MIN	MAX	S.D.
Lowland BS*	DBH (cm)	6.59	0.4	29.8	4.28
(*n* = 1837 trees)	DI (cm/5 yrs)	0.43	0.02	3.2	0.3
	Polygon Area (m^2)	1.42	0.01	13.03	1.5
Upland BS*	DBH (cm)	6.05	0.4	21.8	3.41
(*n* = 2980 trees)	DI (cm/5 yrs)	0.39	0.02	4.8	0.31
	Polygon Area (m^2)	1.13	0.02	10.06	1.14
Managed JP*	DBH (cm)	9.73	0.7	26.6	4.01
(*n* = 1941 trees)	DI (cm/5 yrs)	0.95	0.03	10.1	0.6
	Polygon Area (m^2)	3.06	0.04	19.19	2.31
Natural JP*	DBH (cm)	11.49	1.5	28.3	3.85
(*n* = 1081 trees)	DI (cm/5 yrs)	0.86	0.1	6.4	0.57
	Polygon Area (m^2)	3.96	0.16	22.6	2.94

* BS = Black Spruce, JP = Jack Pine.

[†] DBH = diameter at breast height (1.3 m); DI = diameter increment at 1.3 m; Polygon Area = area of Thiessen polygon associated with each tree (see text for details).

Table 4.4. Summary of stand attributes for the 63 permanent sample plots, by species group, used in model development.

SPECIES GROUP	VARIABLE	MEAN	MIN	MAX	S.D.
Lowland BS*	Basal Area (m^2/ha)	29.92	18.74	46.78	9.48
(*n* = 9)	Stand Age (yrs)	75.8	25	123	34.7
	Site Index (m)	9.76	4.07	15.2	3.39
	Density (trees/ha)	7893	2940	17620	5755
Upland BS*	Basal Area (m^2/ha)	28.19	16.34	43.79	9.24
(*n* = 13)	Stand Age (yrs)	66.3	43	103	21.0
	Site Index (m)	9.8	4.52	16.77	3.83
	Density (trees/ha)	9042	3480	22480	5521
Managed JP*	Basal Area (m^2/ha)	23.77	11.38	33.75	5.59
(*n* = 24)	Stand Age (yrs)	34.9	18	50	9.6
	Site Index (m)	16.34	11.15	19.3	2.10
	Density (trees/ha)	3116	860	9800	2332
Natural JP*	Basal Area (m^2/ha)	22.37	16.34	31.92	4.66
(*n* = 17)	Stand Age (yrs)	47.9	29	91	18.4
	Site Index (m)	15.03	4.63	22.33	4.56
	Density (trees/ha)	2642	1140	5240	1369

* BS = Black Spruce, JP = Jack Pine.

Table 4.5. Summary of attributes of the 6691 trees (classified by species group) used in model development.

SPECIES GROUP	VARIABLE[†]	MEAN	MIN	MAX	S.D.
Lowland BS*	DBH (cm)	6.26	0.4	29.8	4.01
(*n* = 1628 trees)	DI (cm/5 yrs)	0.42	0.02	2.9	0.29
	Polygon Area (m^2)	1.24	0.01	8.73	1.22
Upland BS*	DBH (cm)	5.56	0.4	21.8	3.17
(*n* = 2549 trees)	DI (cm/5 yrs)	0.39	0.02	3	0.3
	Polygon Area (m^2)	1.07	0.02	10.06	1.11
Managed JP*	DBH (cm)	9.42	0.7	26.6	4.05
(*n* = 1660 trees)	DI (cm/5 yrs)	0.95	0.1	10.1	0.6
	Polygon Area (m^2)	2.91	0.04	15.36	2.24
Natural JP*	DBH (cm)	10.76	1.5	22.5	3.6
(*n* = 854 trees)	DI (cm/5 yrs)	0.86	0.1	6.4	0.58
	Polygon Area (m^2)	3.77	0.16	22.6	2.97

* BS = Black Spruce, JP = Jack Pine.

[†] DBH = diameter at breast height (1.3 m); DI = diameter increment at 1.3 m; Polygon Area = area of Thiessen polygon associated with each tree (see text for details).

Table 4.6. Summary of stand attributes for the 17 permanent sample plots, by species group, used in model validation.

SPECIES GROUP	VARIABLE	MEAN	MIN	MAX	S.D.
Lowland BS*	Basal Area (m^2/ha)	27.50	19.81	34.36	7.31
(*n* = 3)	Stand Age (yrs)	81.3	56	105	24.5
	Site Index (m)	10.98	8.63	14.16	2.86
	Density (trees/ha)	3480	1760	5320	1783
Upland BS*	Basal Area (m^2/ha)	38.89	37.18	41.66	2.42
(*n* = 3)	Stand Age (yrs)	111.0	66	158	46
	Site Index (m)	8.58	6.49	10.87	2.2
	Density (trees/ha)	6760	3540	11780	4405
Managed JP*	Basal Area (m^2/ha)	24.77	19.18	30.77	4.49
(*n* = 6)	Stand Age (yrs)	40.0	33	50	6.6
	Site Index (m)	15.99	11.96	19.65	2.52
	Density (trees/ha)	2620	1480	6020	1700
Natural JP*	Basal Area (m^2/ha)	33.60	26.46	43.05	5.97
(*n* = 5)	Stand Age (yrs)	49.6	36	63	11
	Site Index (m)	17.90	14.05	20.31	2.92
	Density (trees/ha)	2304	1740	3400	706

* BS = Black Spruce, JP = Jack Pine.

Table 4.7. Summary of attributes of the 1148 trees (classified by species group) used in model validation.

SPECIES GROUP	VARIABLE[†]	MEAN	MIN	MAX	S.D.
Lowland BS*	DBH (cm)	9.21	0.9	24.8	5.31
(*n* = 209 trees)	DI (cm/5 yrs)	0.49	0.1	3.2	0.38
	Polygon Area (m^2)	2.80	0.19	13.03	2.44
Upland BS*	DBH (cm)	8.99	0.9	18.1	3.34
(*n* = 431 trees)	DI (cm/5 yrs)	0.43	0.1	4.8	0.39
	Polygon Area (m^2)	1.47	0.05	9.04	1.22
Managed JP*	DBH (cm)	11.58	5.1	22.4	3.20
(*n* = 281 trees)	DI (cm/5 yrs)	0.98	0.03	2.6	0.56
	Polygon Area (m^2)	3.98	0.25	19.19	2.53
Natural JP*	DBH (cm)	14.24	7.1	28.3	3.52
(*n* = 227 trees)	DI (cm/5 yrs)	0.90	0.1	3.2	0.50
	Polygon Area (m^2)	4.65	0.51	16.44	2.74

* BS = Black Spruce, JP = Jack Pine.

[†] DBH = diameter at breast height (1.3 m); DI = diameter increment at 1.3 m; Polygon Area = area of Thiessen polygon associated with each tree (see text for details).

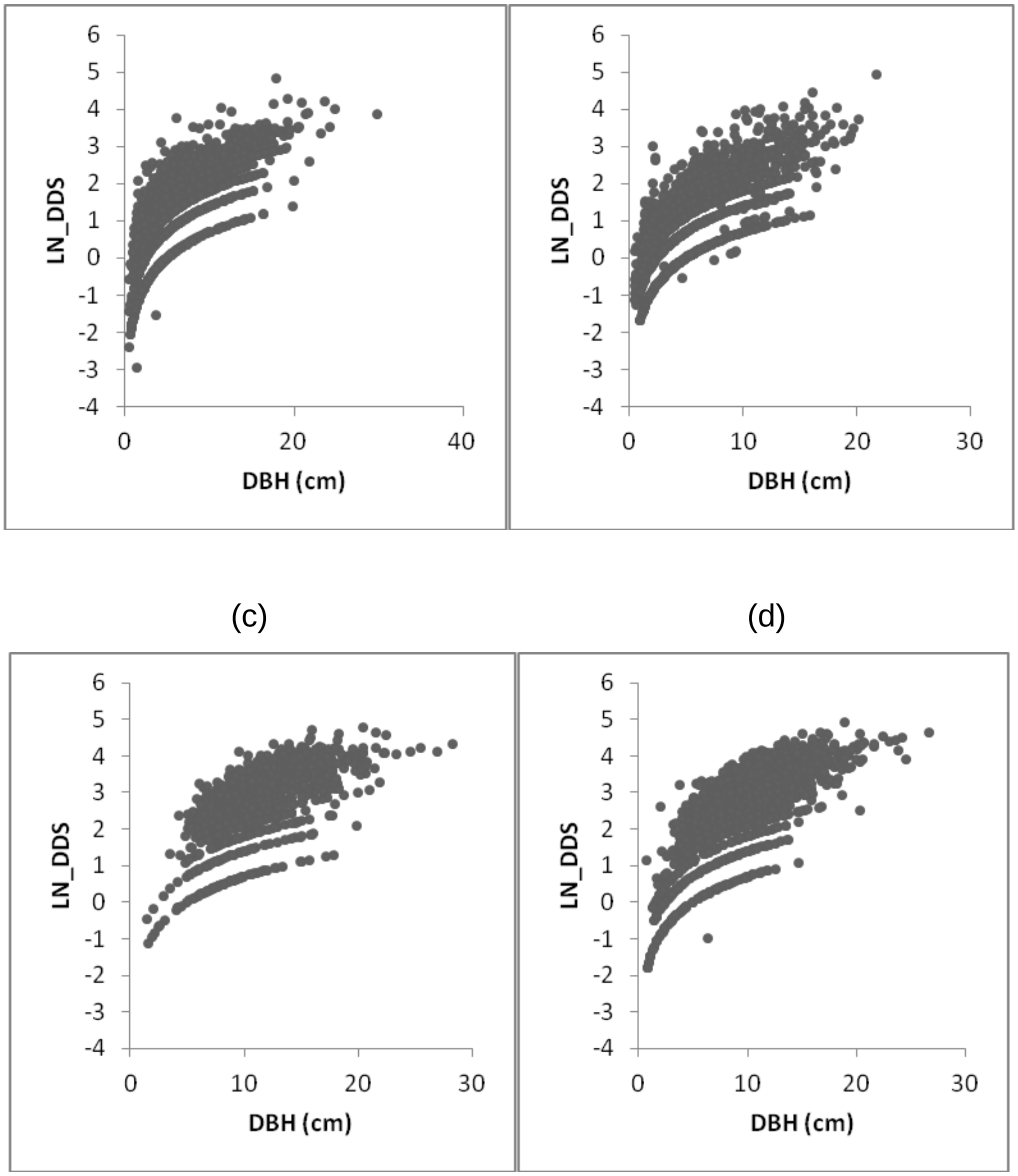

(a) (b) (c) (d)

Figure 4.3. Five-year incremental increase squared stem diameter (*ln* scale) as a function of stem DBH, for (a) lowland black spruce, (b) upland black spruce; (c) natural jack pine; (d) managed jack pine.

Site Effects: Site Index

SI = Site Index

Site index, the mean height of the dominant and co-dominant trees 50 years after they reached breast height (1.3 m), has long been used as a measure of overall site productivity (Carmean 1975; Monserud 1984; Huang *et al.* 1994b; Wang *et al.* 2000). It is therefore an important predictor variable in many growth and yield models (Clutter *et al.* 1983; Davis and Johnson 1987). Provided that stands are mono-dominant and even-aged, site index provides a convenient, standardized measure of productivity potential both among sites and over a broad range of stand conditions (Goelz and Burk 1992). Intuitively, a higher site index is expected to result in greater incremental growth.

Aspatial Competition: Relative Stem Diameter

Relative Diameter = D/MD, where MD = mean stem diameter of stand
Interaction term: D^2/MD

The relative diameter of an individual tree is the ratio of its stem diameter at breast height (D) to the mean stand diameter (MD). This is a simple overall measure of relative competition; the growth increment of a comparatively small tree in a given stand is more negatively affected by relative size than that of a comparatively large tree in another stand, even when their stem diameters are the same (Wykoff 1986). The interaction term D^2/MD is often used to account for non-linear interactions (Wykoff 1990; Zhao *et al*. 2004). Since the plots used in this study cover a broad range of tree sizes (stand ages), relative diameter and the interaction term were examined as potential predictor variables.

Aspatial Competition: Stand Basal Area

BAL = Basal area of larger trees in the stand

Stand total basal area, which incorporates both tree size and stand density, is a useful relative measure of overall stand “crowding”. At a given stand development stage, trees in stands of high total basal area will tend to experience more intense competition than those in stands with lower total basal area (Yang *et al.* 2003). Basal area of larger trees (*BAL*) is simply the summation of the basal areas of all trees that have a stem diameter greater than that of the target tree. This measure is commonly used to quantify individual-level competitive effects, particularly when spatial information (mapped tree positions) is lacking (Wykoff 1990; Yang *et al.* 2003). In this study, *BAL* is considered as a potential predictor variable to measure stand and individual-level competition.

Spatial Competition: Thiessen Polygon

TPA = Thiessen polygon area (m^2)

Individual trees in forest stands experience physical space limitations are they grow, resulting in competition for resources (e.g. light, water and soil nutrients) with their immediate neighbours (Kenkel 1988). The degree of competition experienced by a given tree depends on overall stand density, but more importantly on the spatial proximity and relative sizes and its immediate neighbours. As the amount of competition increases, the growth rate of a given tree declines (Dobbertin and Biging 1998). Variables describing spatial competition are therefore important in the modelling of diameter (basal area) growth.

Thiessen polygons (also known as Voronoi tessellations, Dirichlet regions, or Wigner–Seitz cells) define the “area of influence” associated with a point, or tree (Okabe *et al.* 2000). The boundaries of the Thiessen polygon associated with a given tree delineate an area that is closer to that tree than to any other (Mithen *et al.* 1984). Mathematically, this polygon is obtained by finding the perpendicular bisectors of triangulation lines that connect first-order neighbours (Kenkel *et al*. 1989b). Thiessen polygons have been widely used to model point pattern data, including structured media (such as liquids, poly-crystals and proteins) and fragmentation of the universe (Chirila *et al.* 2008). They have also been used in forestry and plant ecology to determine the “area potentially available” to a plant when studying the relationship between local competition and plant growth (Mithen *et al.* 1984; Daniels *et al*. 1986). For example, a significant positive correlation between diameter growth and Thiessen polygon area was found in a long-term study of jack pine stand dynamics in Manitoba (Kenkel *et al.* 1997). However, to my knowledge Thiessen polygon area has not been used previously as a predictor variable in diameter (basal area) growth models of boreal forest trees.

Thiessen polygon areas (TPA) for individual trees in each of the 80 permanent sample plots were generated using ArcInfo Software. Edge effects problems in the delineation of area polygons were addressed using the algorithm of Kenkel *et al.* (1989b). In edge effect correction, four distances are required: polygon center (tree location) to plot center (site center), Delaunay triangulation vertex to plot (site) center, vertex to polygon center, and vertex to edge. If none of the vertex to edge distances is greater than the distance to the polygon center, then the polygon is included in the analysis; otherwise it is eliminated to avoid edge effects (Kenkel *et al.* 1989b). Examples of Thiessen polygon area delineations, and edge effect exclusion, are illustrated for example plots of black spruce and jack pine in **Figure 4.4** and **Figure 4.5**.

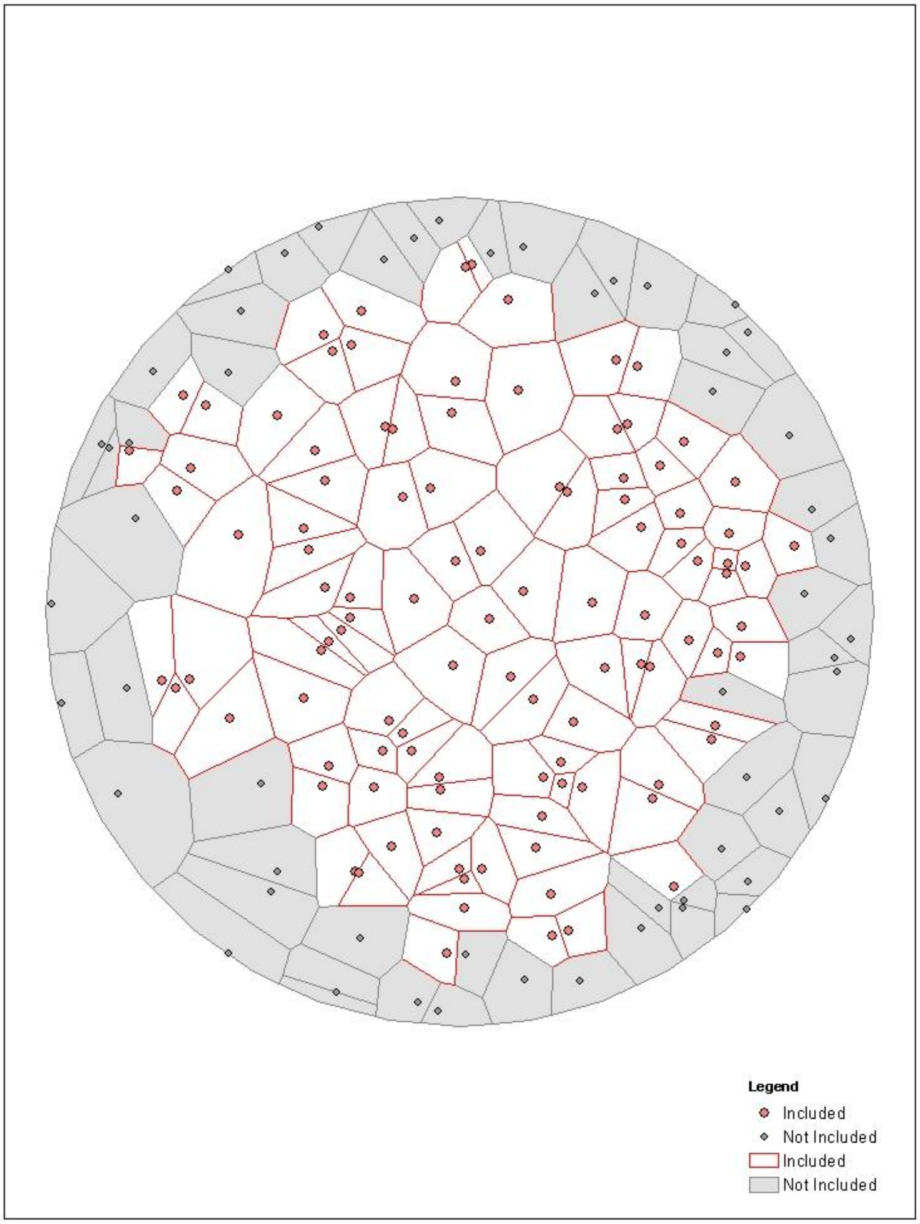


Figure 4.4. Black spruce tree mappings within a permanent sample plot (plot number 46 at year 2004; stand age = 116 years, SI = 8.4 m, upland stand). Tree polygons that are excluded due to edge effects are shaded grey.

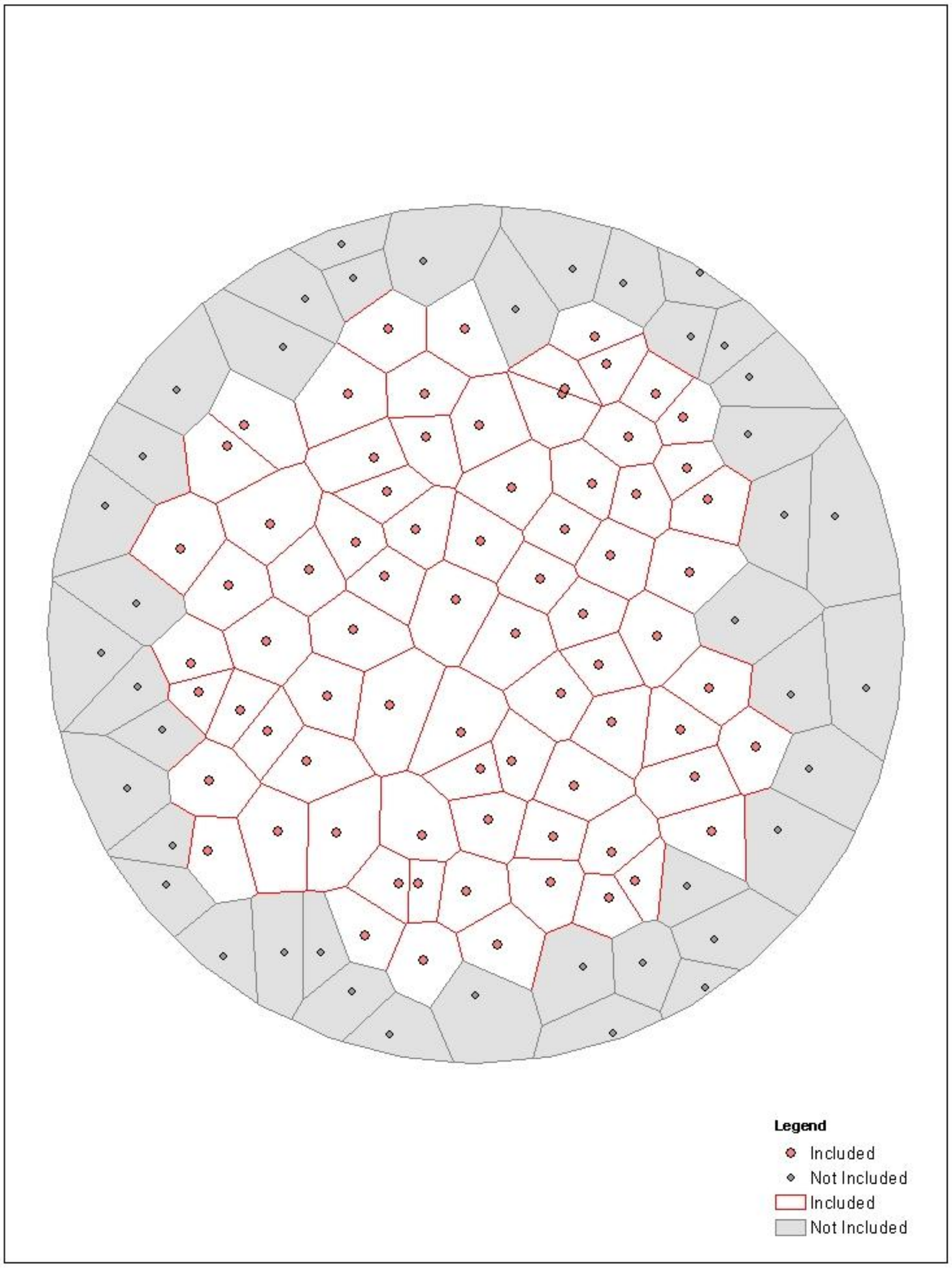


Figure 4.5. Jack pine tree mappings within a permanent sample plot (plot number 48 at year 2004; stand age = 36 years, SI = 15.7 m, managed jack pine). Tree polygons that are excluded due to edge effects are shaded grey.

4.4.2 Model Fitting

Choice of Dependent Variable

The selection of an appropriate dependent variable is important to the development of robust and reliable diameter (basal area) growth models (Wykoff 1990; Zhao *et al.* 2004). During my preliminary analyses, the following incremental growth measures, and their natural logarithms, were considered:

1. Five-year diameter increment: $DI = D_2 – D_1$.
2. Five-year squared diameter increment: $DDS = D_2^2 – D_1^2$
3. Five-year diameter growth rate: $DIR = (D_2 – D_1)/D_1$.

Based on examinations of model fit statistics and residual plots during preliminary analyses, the natural logarithm of *DDS* (*ln[DDS]*) was chosen as the dependent variable in this study (see also Wykoff (1990); Zhao *et al*. (2004). Squared diameter increment has the further advantage of being linearly proportional to basal area increment, making the transformation from diameter to basal area increment prediction very simple (Stage 1973; Vanclay 1994; Zhao *et al.* 2004).

Selection of Independent Variables and Models

For each of the four data sets, the stepwise regression selection approach (SAS Proc Reg procedures, SAS Institute 2004) was used to examine various combinations of the independent variables as predictors of incremental diameter growth (*ln [DSS]*). These preliminary analyses indicated that the following independent variables (in descending order of statistical importance) were the best predictors:

Lowland Black Spruce: D, D^{-1}, BAL, D^2, TPA and SI.

Upland Black Spruce: D, D^2, BAL, TPA, D^2/MD and D^{-1}.

Managed Jack Pine: D^{-1}, BAL, D, D^2, SI and TPA.

Natural Jack Pine: D^2/MD, D^{-1}, TPA, BAL, SI, D and D^2.

Subsequent analyses therefore focused on these variables and their combinations. A large number of fitted regression models were developed, and compared using standard fitting statistics (Section 4.4.2), residual plot examination, and validation predictions. Consideration was also given to the biological relevance of selected predictor variables, and to the consistency of independent variable selection across the four data sets. Only those variable achieving statistical significance (at 95% confidence) were considered; non-significant variables were removed during the modeling fitting process.

Considerable time and effort was devoted to the development and analysis of alternative models. Together, these analyses indicated that the following three models were statistically significant and biologically realistic predictors of diameter increment growth (*ln DSS*):

[4.1] $$ln[DDS] = a_0 + a_1D + a_2/D + a_3D^2 + a_4TPA + a_5D/MD + a_6BAL + a_7SI$$

[4.2] $$ln[DDS] = a_0 + a_1D + a_2/D + a_3D^2 + a_4TPA + a_5D^2/MD + a_6BAL + a_7SI$$

[4.3] $$ln[DDS] = a_0 + a_2/D + a_4TPA + a_5D^2/MD + a_6BAL + a_7SI$$

Here *ln[DSS]* = natural logarithm of five-year increase in squared diameter; *D* = diameter at breast height; *MD* = stand mean diameter; *TPA* = Thiessen polygon area; *BAL* = total basal area of trees larger than target tree; and *SI* = stand site index. Note that values for the predictor (independent) variables are taken at the beginning of the five-year diameter growth period.

Additional analyses found that the intercept of model [4.1] was not statistically significant, for both upland black spruce and natural jack pine. Further analysis therefore focused on models [4.2] and [4.3] in the prediction of tree diameter growth of both jack pine and black spruce.

Model Assessment

Since models [4.2] and [4.3] have different numbers of parameters (independent variables), Akaike's information criterion (*AIC*) and Schwarz's Bayesian information criterion (*BIC*) were used to compare and select models. *AIC* and *BIC* are log-likelihood function that "penalizes" regression models with a higher number of parameters (Weiss 2005). They are calculated as:

[4.4] $$AIC = n[\ln(MSE)] + 2k$$

[4.5] $$BIC = n[\ln(MSE)] + k[\ln(n)]$$

where *MSE* is the mean square error, *n* is the number of trees, and *k* is the number of model parameters.

Following ordinary least squares (OLS) model fitting to obtain parameter estimates, the statistical significance of parameters were determined and residual (and studentized residual) plots examined for lack of fit, unequal variance, and the presence of outliers. Model fitting statistics, including the coefficient of determination (R^2) and root mean squared error (RMSE), were also computed:

[4.6]

$$R^2 = 1 - \frac{\sum_{i=1}^{n} (Y_i - \hat{Y}_i)^2}{\sum_{i=1}^{n} (Y_i - \overline{Y})^2}$$

[4.7]

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n} (y_i - \hat{y}_i)^2}{n - m}}$$

where y_i is the measured value, $\hat{y}_i$ is the estimated value, and $\bar{y}$ is the mean of the measured value, n is the number of observations, m is the number of parameters in the model.

4.4.3 Model Validation

Model validation is a critically important step in model development and testing (Jeffers 1982). Validation involves comparing model results with those obtained from an independent data set, in order to examine and confirm model credibility, robustness and utility (Otto and Day 2007).

The performance of the predictive models, based on the validation data sets, were assessed used standard prediction statistics (coefficient of determination (R^2), root mean squared error (*RMSE*)) together with the following error assessment statistics: mean prediction bias ($\bar{e}$), mean absolute error (*MAE*) and percent bias (*bias%*). These are computed as:

[4.8]

$$\overline{e} = \frac{\sum_{i=1}^{n} (Y_i - \hat{Y}_i)}{n}$$

[4.9]

$$MAE = \frac{\sum_{i=1}^{n} \left| Y_i - \hat{Y}_i \right|}{n}$$

[4.10]

$$bias\,\% = 100\,(\overline{e} / \overline{y})$$

The mean prediction bias is the averaged difference between predicted and observed values. The mean absolute error is the mean prediction bias expressed in absolute terms, i.e. accounting for the trade-off between positive and negative prediction errors. Percent bias expresses the mean bias on a relative scale, for easier interpretation and for comparative purposes. The RMSE, which incorporates both bias and variation, is considered a useful measure of overall model performance.

4.5 RESULTS

4.5.1 Model Fitting

The fitting statistics and regression parameter estimates of models [4.2] and [4.3] for black spruce and jack pine are presented in **Table 4.8**. All model fittings successfully converged, and all variables included in the table are statistically significant. Note that the variable D^2/MD of model [4.2] for lowland black spruce and managed jack pine, and the variable *SI* of [4.2] for upland black spruce, were not statistically significant and were therefore not included in the final models shown in **Table 4.8**. Fit statistics (*t*-values) for the statistically significant estimated parameters for each model are summarized in **Table 4.9**.

The values of R^2 ranged from 0.6103 to 0.7525 for model [4.2], and from 0.6025 to 0.7231 for model [4.3], for the four data sets (lowland black spruce, upland black spruce, managed jack pine and natural jack pine). Comparing the fitting statistics, model [4.2] had higher coefficients of determination (R^2), and lower values for the Akaike Information Criterion (AIC), Schwarz’s Bayesian Criterion (BIC) and the root mean squared error (RMSE) compared to model [4.3] for all four data sets (**Table 4.8**). The fitting statistics therefore indicate that model [4.2] resulted in a better fit than model [4.3].

The positive coefficients for site index (*SI*) indicate that trees occurring on more productive sites (higher *SI*) have higher growth rates. The negative coefficients for the basal area of larger trees (*BAL*) variable indicates that smaller trees within a forest stand have a lower growth rate; this is particularly notable in jack pine stands. These results are consistent with many other studies (e.g., Wykoff 1990; Hann and Larsen 1991; Zhao *et al.* 2004).

In both models [4.2] and [4.3] the coefficients of the Thiessen polygon area (TPA) variable were positive for all the four data sets, indicating that trees undergoing less intraspecific spatial competition (larger *TPA*) have higher growth rates. This relationship was weakest for managed jack pine stands, which likely reflected the more regular spatial pattern of trees in managed (planted or thinned) stands.

The residual plots of model [4.2] for black spruce (lowland and upland) and jack pine (managed and natural) are presented in **Figures 4.6** and **4.7**, respectively. There are no apparent nonlinear or divergent trends in the residual plots, indicating that the model is an appropriate fit and that variance heterogeneity was successfully removed by log-transformation of the dependent variable. Similar residual plots were found for model [4.3] and are not shown here.

Table 4.8. Estimated parameters and fit statistics of models [4.2] and [4.3], for lowland black spruce, upland black spruce, managed jack pine, and natural jack pine stands. Standard errors are shown in parentheses.

Model	Variable*		**BLACK SPRUCE**		**JACK PINE**	
			Lowland	**Upland**	**Managed**	**Natural**
[4.2]	*Intercept*	a_0	0.5697 (0.1359)	-0.2536 (0.1016)	0.9449 (0.1655)	1.3421 (0.4810)
	D	a_1	0.2650 (0.0204)	0.3091 (0.0216)	0.3503 (0.0225)	0.1569 (0.0566)
	D^{-1}	a_2	-0.9593 (0.1221)	-0.5841 (0.0945)	-2.2077 (0.2200)	-5.0244 (1.0432)
	D^2	a_3	-0.0074 (0.0010)	-0.0120 (0.0011)	-0.0113 (0.0009)	-0.0077 (0.0021)
	TPA	a_4	0.0670 (0.0173)	0.1410 (0.0127)	0.0211 (0.0099)	0.0751 (0.0093)
	D^2/MD	a_5		0.0398 (0.0062)		0.0444 (0.0120)
	BAL	a_6	-0.0366 (0.0023)	-0.0104 (0.0021)	-0.0623 (0.0027)	-0.0537 (0.0069)
	SI	a_7	0.0224 (0.0062)		0.0371 (0.0090)	0.0632 (0.0070)
Fit statistics						
	R^2		0.6544	0.6515	0.7525	0.6103
	AIC		-1282.7	-2073.3	-1589.2	-644.8
	BIC		-1245	-2032.4	-1551.3	-606.8
	RMSE		0.6715	0.6640	0.6170	0.6792
	n		1628	2549	1660	854
[4.3]	*Intercept*	a_0	1.6271 (0.1042)	0.7875 (0.0633)	2.0327 (0.1481)	2.7825 (0.1885)
	D^{-1}	a_2	-2.1582 (0.0886)	-1.5621 (0.0669)	-4.3429 (0.1666)	-7.2434 (0.6030)
	TPA	a_4	0.1642 (0.0165)	0.1473 (0.0127)	0.0389 (0.0091)	0.0655 (0.0085)
	D^2/MD	a_5	0.0335 (0.0029)	0.0763 (0.0030)	0.0449 (0.0052)	0.0165 (0.0073)
	BAL	a_6	-0.0287 (0.0028)	-0.0071 (0.0021)	-0.0492 (0.0039)	-0.0627 (0.0066)
	SI	a_7	0.0190 (0.0066)	0.0119 (0.0048)	0.0754 (0.0089)	0.0643 (0.0068)
Fit statistics						
	R^2		0.6037	0.6242	0.7231	0.6025
	AIC		-1062.9	-1883.8	-1405.4	-633.8
	BIC		-1030.6	-1848.8	-1372.9	-605.3
	RMSE		0.7188	0.6894	0.6525	0.6852
	n		1628	2549	1660	854

* D = diameter at breast height; D^{-1} = inverse of diameter at breast height; D^2 = squared diameter at breast height; D/MD = relative diameter; *TPA* = Thiessen polygon area; *BAL* = basal area of trees larger than target tree; *SI* = site index; R^2 = coefficient of determination; RMSE = root mean squared error; AIC = Akaike Information Criterion; BIC = Schwarz's Bayesian Criterion. Higher $R^{2,}$ and lower AIC, BIC, RMSE, indicate a better model fit.

Table 4.9. Fit statistics (*t*-values) for estimated parameters (Table 4.8) of models [4.2] and [4.3], for lowland black spruce, upland black spruce, managed jack pine, and natural jack pine stands. Probabilities (*P*-values) associated with each *t*-value are given in parentheses.

Model	Variable*		**BLACK SPRUCE**		**JACK PINE**	
			Lowland	**Upland**	**Managed**	**Natural**
[4.2]	*Intercept*	a_0	4.19 (<0.0001)	-2.50 (0.0126)	5.71 (<0.0001)	2.79 (0.0054)
	D	a_1	12.97 (<0.0001)	14.34 (<0.0001)	15.55 (<0.0001)	2.77 (0.0057)
	D^{-1}	a_2	-7.85 (<0.0001)	-6.18 (<0.0001)	-10.04 (<0.0001)	-4.82 (<0.0001)
	D^2	a_3	-7.48 (<0.0001)	-10.75 (<0.0001)	-12.45 (<0.0001)	-3.73 (0.0002)
	TPA	a_4	3.87 (0.0001)	11.13 (<0.0001)	2.14 (0.0326)	8.12 (<0.0001)
	D^2/MD	a_5		6.43 (<0.0001)		3.69 (0.0002)
	BAL	a_6	-15.74 (<0.0001)	-5.07 (<0.0001)	-22.96 (<0.0001)	-7.73 (<0.0001)
	SI	a_7	3.64 (0.0003)		4.12 (<0.0001)	9.07 (<0.0001)
[4.3]	*Intercept*	a_0	15.61 (<0.0001)	12.45 (<0.0001)	13.73 (<0.0001)	14.76 (<0.0001)
	D^{-1}	a_2	-24.35 (<0.0001)	-23.36 (<0.0001)	-26.07 (<0.0001)	-12.01 (<0.0001)
	TPA	a_4	9.98 (<0.0001)	11.57 (<0.0001)	4.27 (<0.0001)	7.75 (<0.0001)
	D^2/MD	a_5	11.40 (<0.0001)	25.67 (<0.0001)	8.56 (<0.0001)	2.27 (0.0234)
	BAL	a_6	-10.35 (<0.0001)	-3.36 (0.0008)	-12.69 (<0.0001)	-9.52 (<0.0001)
	SI	a_7	2.90 (0.0038)	2.46 (0.0138)	8.44 (<0.0001)	9.40 (<0.0001)

* D = diameter at breast height; D^{-1} = inverse of diameter at breast height; D^2 = squared diameter at breast height; D/MD = relative diameter; TPA = Thiessen polygon area; BAL = basal area of trees larger than target tree; SI = site index.

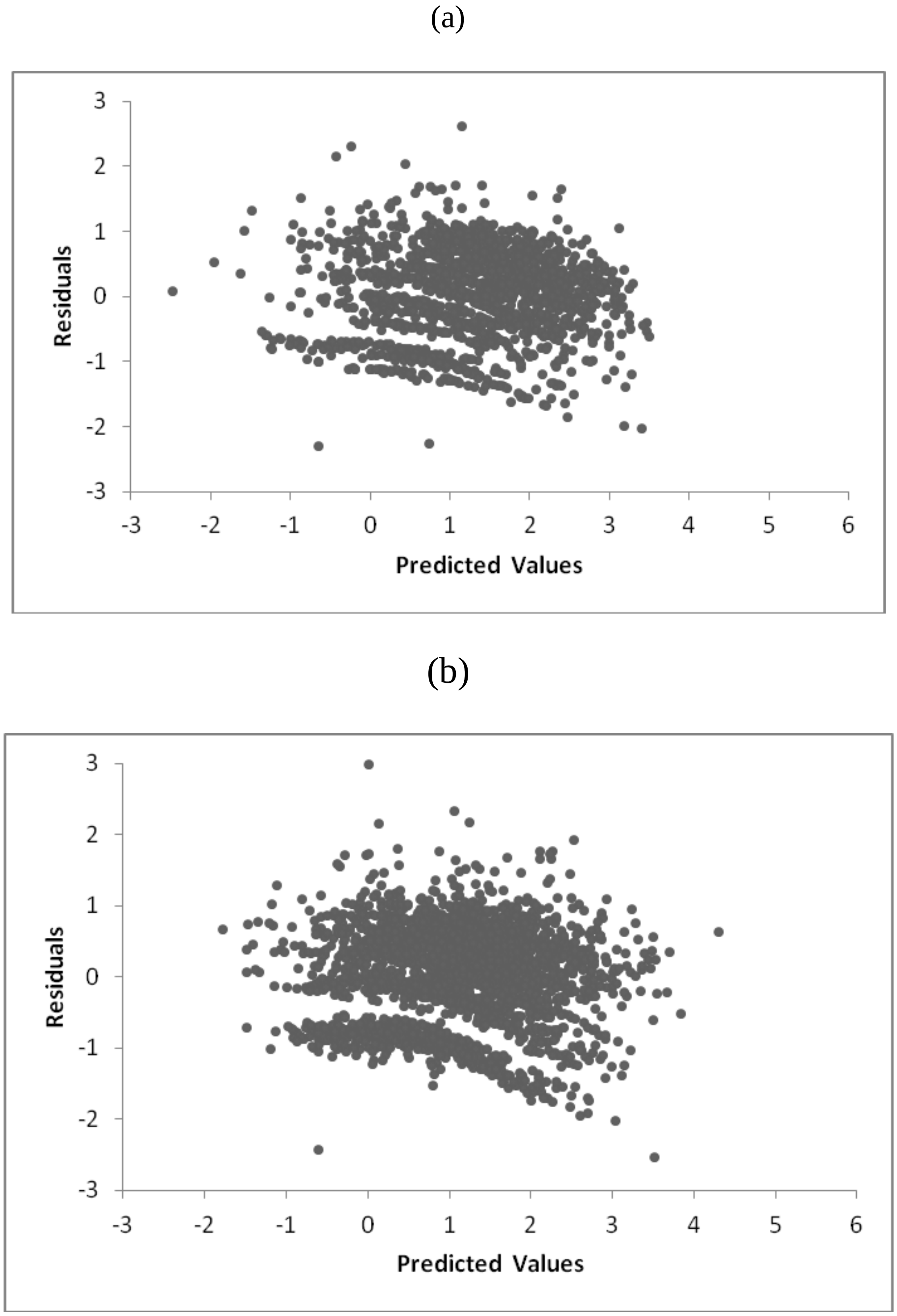
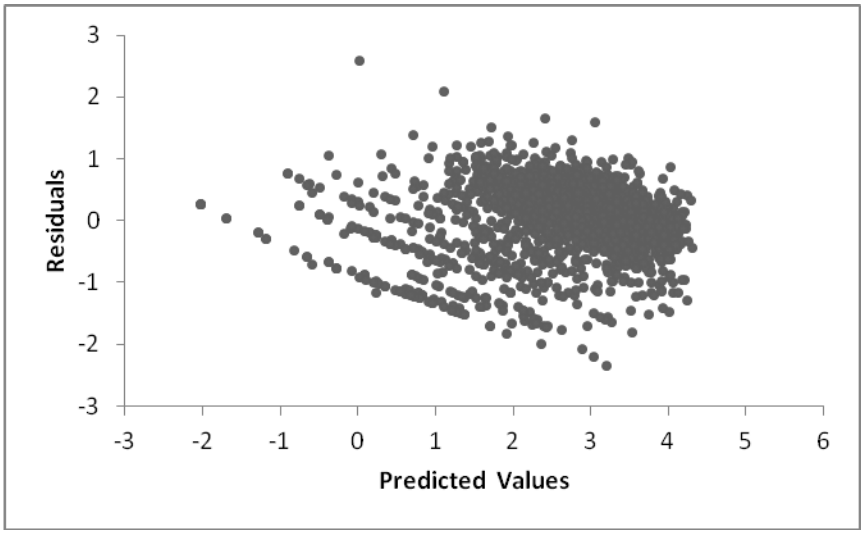


Figure 4.6. Residuals plotted as a function of predicted values of *ln*[*DSS*] for black spruce, model [4.2]: (a) lowland stands, n = 1628; (b) upland stands, n = 2549.

(a)



(b)

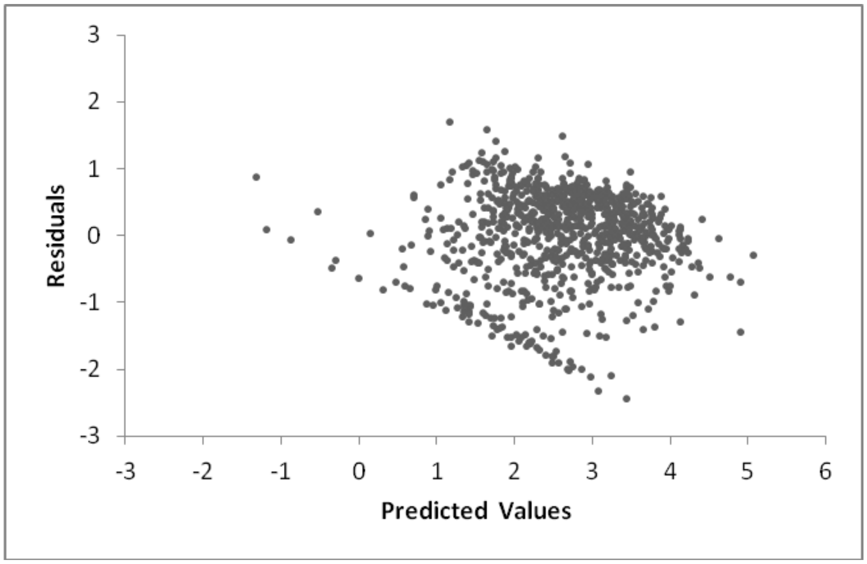


Figure 4.7. Residuals plotted as a function of predicted values of *ln*[*DSS*] for jack pine, model [4.2]: (a) managed stands, *n* = 1660; (b) natural stands, *n* = 854.

4.5.2 Importance of Thiessen Polygon Area (TPA)

During the model development process, it was found that Thiessen polygon area was a significant predictor variable, and that model [4.2] offered overall superior model performance in the modelling of diameter (basal area) growth. In order to determine the relative importance of Thiessen polygon area (*TPA*) as a predictor variable, model [4.2] was modified by removing variable *TPA*:

[4.11] $$ln[DDS] = a_0 + a_1 D + a_2 / D + a_3 D^2 + a_5 D^2 / MD + a_6 BAL + a_7 SI$$

Model [4.11] was then used to predict diameter growth, and its performance compared with that of model [4.2] (**Table 4.8**).

The fitting statistics and parameter estimates of the model [4.11] for black spruce and jack pine are shown in **Table 4.10**. The model fittings for black spruce and jack pine were convergent, and all the parameters included in the models are statistically significant. Note that the variable D^2/MD for managed jack pine, and variables D^{-1} and D^2 for natural jack pine, were not statistically significant and were therefore not included in the model.

The comparison of model fitting statistics (**Table 4.8** and **Table 4.10**) indicates that inclusion of Thiessen polygon area increased model prediction. However, considerable differences in the relative importance of Thiessen polygon area as a predictor variable were apparent among the four data sets. Polygon area is an important predictor of tree growth in natural jack pine stands; inclusion of Thiessen polygon area reduced the RMSE from 0.7086 to 0.6792 (4.33%). Inclusion of Thiessen polygon area reduced the RMSE for upland black spruce stands somewhat, from 0.6794 to 0.6640 (2.32%). Conversely, Thiessen polygon area was relatively unimportant in lowland black spruce (RMSE from 0.6731 to 0.6715, or 0.24%) and managed jack pine stands (RMSE from 0.6177 to 0.6170, or 0.11%). Similar trends were observed for other model fitting statistics (R^2, AIC and BIC). These results are consistent with expectations. In natural jack pine stands, local competitive effects (as measured by Thiessen polygon area) are known to influence tree growth and mortality in this highly shade-intolerant species (e.g. Kenkel *et al*. 1997). However, this effect is unimportant in managed jack pine stands; trees are more evenly spaced in managed stands, and this greatly reduces the variability (and therefore importance) in local competitive effects. Black spruce is a much more shade tolerant species, and this may explain the reduced importance of local competitive effects on tree growth and mortality in the species (Carleton and Wanamaker 1987). The relative unimportance of local competitive effects (Thiessen polygon area) in lowland black spruce likely reflects the lower density of these stands (6790 trees/ha, versus 8614 trees/ha for upland stands), since lower density reduces intraspecific competitive interactions.

4.5.3 Model Validation

Model validation statistics for individual tree diameter increment growth model [4.2] predictions, utilizing the black spruce and jack pine validation data sets, are presented in **Table 4.11**. Percent error prediction bias was generally low (< 5%), with the exception of natural jack pine stands (7.42%). Coefficient of determination (R^2) and RMSE values for the validation data sets were generally similar to those obtained from model development data sets (compare **Table 4.8** and **Table 4.11**). Values were somewhat lower for the black spruce upland, managed jack pine, and natural jack pine validation data sets, however. Overall, these results indicate the robustness of the models in predicting diameter increment growth in black spruce and jack pine.

Table 4.10. Estimated parameters and fit statistics of model [4.11], for lowland black spruce, upland black spruce, managed jack pine, and natural jack pine stands. Standard errors are shown in parentheses.

Variable*		**BLACK SPRUCE**		**JACK PINE**	
		Lowland	**Upland**	**Managed**	**Natural**
Intercept	a_0	0.6998 (0.1439)	-0.1744 (0.0602)	0.9093 (0.1648)	2.7366 (0.1949)
D	a_1	0.2774 (0.0205)	0.3162 (0.0222)	0.3550 (0.0224)	
1/D	a_2	-0.9628 (0.1226)	-0.5415 (0.0966)	-2.1748 (0.2197)	-7.3570 (0.6234)
D^2	a_3	-0.0062 (0.0010)	-0.0103 (0.0011)	-0.0111 (0.0009)	
D^2/MD	a_5	-0.0126 (0.0047)	0.0278 (0.0062)		0.0310 (0.0073)
BAL	a_6	-0.0386 (0.0028)	-0.0131 (0.0022)	-0.0612 (0.0027)	-0.0522 (0.0067)
SI	a_7	0.0176 (0.0062)	0.0106 (0.0048)	0.0377 (0.0090)	0.0629 (0.0071)
Fit Stats	R^2	0.6527	0.6352	0.7518	0.5743
	AIC	-1274.8	-1956.9	-1587.6	-578.4
	BIC	-1237.1	-1916	-1555.1	-554.7
	RMSE	0.6731	0.6794	0.6177	0.7086
	n	1628	2549	1660	854

* *D* = diameter at breast height; D^{-1} = inverse of diameter at breast height; D^2 = squared diameter at breast height; *D/MD* = relative diameter; *BAL* = basal area of trees larger than target tree; *SI* = site index; R^2 = coefficient of determination; RMSE = root mean squared error; AIC = Akaike Information Criterion; BIC = Schwarz's Bayesian Criterion. Higher $R^{2,}$ and lower AIC, BIC, RMSE, indicate a better model fit.

Table 4.11. Model validation statistics of individual-tree diameter increment growth model [4.2] for lowland black spruce, upland black spruce, managed jack pine, and natural jack pine stands.

Statistic*	**BLACK SPRUCE**		**JACK PINE**	
	Lowland	**Upland**	**Managed**	**Natural**
R^2	0.7580	0.5962	0.5952	0.4570
RMSE	0.6483	0.6704	0.6382	0.6436
$\bar{e}$	0.057	-0.054	-0.120	0.225
MAE	0.517	0.539	0.471	0.521
Bias%	3.23	-3.17	-4.14	7.42
n	209	431	281	227

*R^2 = coefficient of determination; RMSE = root mean squared error; $\bar{e}$, mean prediction error; MAE = mean absolute error of prediction; Bias% = prediction bias percent; *n* = number of trees.

Table 4.12. Model validation statistics of individual-tree diameter increment growth model [4.11] for lowland black spruce, upland black spruce, managed jack pine, and natural jack pine stands.

Statistic*	**BLACK SPRUCE**		**JACK PINE**	
	Lowland	**Upland**	**Managed**	**Natural**
R^2	0.7489	0.5934	0.5926	0.3935
RMSE	0.6604	0.6726	0.6392	0.6756
$\bar{e}$	0.105	-0.043	-0.110	0.133
MAE	0.530	0.532	0.475	0.531
Bias%	5.94	-2.55	-3.80	4.39
n	209	431	281	227

*R^2 = coefficient of determination; RMSE = root mean squared error; $\bar{e}$, mean prediction error; MAE = mean absolute error of prediction; Bias% = prediction bias percent; *n* = number of trees.

Model validation statistics for reduced model [4.11], i.e. excluding Thiessen polygon area, are presented in **Table 4.12**. The results suggest differences among the four data sets in the relative importance of local competition (as measured by Thiessen polygon area) on tree diameter growth. As found previously (Section 4.5.2), the greatest improvement in model prediction resulting from inclusion of polygon area occurred for natural jack pine stands, while managed jack pine stands had the least improvement in model performance.

4.6 DISCUSSION

The individual tree diameter increment models for lowland and upland black spruce and managed and natural jack pine stands in Manitoba were successfully fitted using ordinary least squares regression analysis. The fitted models possess desirable statistical properties, and are biologically reasonable. Important predictor variables in the final models include tree size (diameter), site productivity (site index), and competitive effects (polygon area, basal area of larger trees, and relative diameter).

My main objective was to obtain diameter increment growth models for black spruce and jack pine as a general function of appropriate and readily available predictor variables, including tree size, site productivity and both aspatial and spatial competitive effects. This objective necessitated the pooling of large amounts of data from environmentally variable sites differing appreciably in stand density and development, in order to obtain a generalized diameter increment growth model applicable across a broad spectrum of stand and environmental conditions (Wyloff 1990). The developed empirical models are intended mainly for prediction purposes in applied forestry practice.

Individual tree diameter increment growth models developed over the past few decades have utilized multiple predictor variables (e.g. Wykoff 1990; Hann and Larsen 1991; Zhao *et al.* 2004). These growth models typically use three classes of predictor variables: tree size, site factors, and competition effects. Most models have found that tree size variables (e.g. diameter and diameter squared) are most the important predictors, with site factors and competitive effects playing a lesser role (e.g. Wykoff 1990; Lessard *et al*. 2001; Zhao *et al*. 2004).

In my study, tree size (diameter D, squared diameter D^2 and inverse diameter D^{-1}) proved to be a strong predictor of diameter increment for the black spruce and managed jack pine stands, but tree size variables were less important for the natural jack pine stands. The three diameter variables were statistically significant for all four of the species groups, confirming the nonlinear relationship between incremental diameter growth and size (diameter or basal area) found in previous studies (see Wykoff 1990). Parameter coefficients were positive for diameter, and negative for both nonlinear terms (squared diameter and inverse diameter). These results confirm that jack pine and black spruce adhere to the presumed relationship between incremental diameter growth and tree size (Zhao *et al*. 2004): diameter increment increases to a maximum in younger (smaller) trees, and then declines slowly (approaching zero) as tree mature (Wykoff 1990).

Previous studies have found that site factors are often relatively unimportant in predicting diameter increment growth (e.g. Wykoff 1990; Zhao *et al*. 2004). For white spruce in Alberta, site productivity was found to negatively affect diameter increment (Huang and Titus 1995), a counter-intuitive result that the authors attributed to problems with quantifying site productivity, the limited range of site conditions in their data, and the possibility of greater height growth relative to diameter growth in more productive stands. In my study site index (a measure of site productivity) was, as expected, positively affected diameter increment. Site index was a particularly important variable in natural jack pine stands, but was of lesser importance in managed jack pine and lowland jack pine stands and insignificant in upland black spruce stands. The relative importance of site index in jack pine compared to black spruce stands has two possible explanations: (a) jack pine stands occur over a broader range of site conditions (from very well-drained and nutrient-deficient sandy soils to productive loamy soils) than do black spruce stands; (b) growth of jack pine increases when site conditions are improved (e.g. nutrient addition; Weetman *et al*. 1995), but such a response is not seen in black spruce stands (Jeglum 1974).

A number of variables quantifying competitive effects in forest stands have been utilized in forest growth and yield modelling (Biging and Dobbertin 1995). Stand basal area is a widely used variable, since it is an easily determined and readily available variable in most forest inventory data sets (Lessard *et al*. 2001). It is used to quantify the overall degree of competition experienced at the stand level: for trees of a given size, those growing in stands of lower total basal area are expected to have higher incremental growth. A number of studies have demonstrated that total basal area has a significant negative effect on diameter increment growth (e.g. Wykoff 1990; Huang and Titus 1995; Lessard *et al*. 2001; Zhao *et al*. 2004). In my study, preliminary analyses indicated that total stand basal area was not an important predictor of incremental growth, and it was therefore not included in final model development. The unimportance of stand density likely reflects the biology and ecology of jack pine and black spruce. Both species establish even-aged, mono-dominant stands of very high initial density following stand-destroying fires. Such stands undergo considerable self-thinning as they age (e.g. Carleton and Wanamaker 1987; Kenkel *et al*. 1997), producing (for a given age and species) stands of similar density and total basal area. Since most jack pine and black spruce stands are at or near the upper biological limit of their density and basal area (as determined by the self-thinning line: Mohler *et al*. 1978; Zeide 1987), total stand basal area is largely invariant and therefore a poor predictor of tree incremental growth.

Distance-independent (or aspatial) competition measures for individual trees in forest stands provide a more precise measure of competitive effects. The basal area of all trees larger than the focus individual (*BAL*) is widely used, since this variable is simple to measure and readily available (Wykoff 1990; Lessard *et al*. 2001). This variable is expected to negatively affect diameter increment growth, since the smaller trees in a stand will have large *BAL* values. While some studies have demonstrated that *BAL* is an important predictor of incremental tree growth (Wykoff 1990; Hann and Larsen 1991; Lessard *et al*. 2001), others have found that it is only sometimes statistically significant (e.g. Zhao *et al*. 2004). In my study, *BAL* was an important predictor variable for all four species groups, particularly for lowland black spruce and for both managed and natural jack pine stands. The coefficient parameters were all negative, indicating that (as expected) the smaller trees in a given stand have reduced incremental growth. An alternative competition measure for individual trees in forest stands is relative diameter (*D/MD*) and its interaction term (D^2/MD). Zhao *et al*. (2004) found that these variables were only occasionally important predictors of incremental growth. In my study, preliminary analyses indicated that relative diameter was not an important predictor, and it was therefore not included in the final model. The interaction term D^2/MD was included, but it proved to be a statistically significant predictor variable only for upland black spruce and (to a lesser extent) natural jack pine stands. These results suggest that *BAL* may be a more useful measure of individual tree competition than relative diameter.

Distance-dependent (or spatial) competition measures have not been widely used in models of diameter increment growth, but only because spatial information (mapped tree locations) is rarely available from forest inventory data sets (Wykoff 1990). However, spatial competition effects are expected to be important in forest stands, since the growth of a given tree is known to be influenced by the proximity and size of its immediate neighbours (Daniels *et al*. 1986; Kenkel 1990). Some of the earliest spatial competition indices were developed for jack pine and other boreal trees (Bella 1971; Hegyi 1974), in recognition of the importance of local competition effects on the growth of individual trees in mono-dominant, even-aged boreal forest stands. Of the many competition indices described, the Thiessen polygon area (also known as the “area potentially available”) has proven to be an especially useful competition variable in growth prediction (Daniels *et al*. 1986; Kenkel *et al*. 1997). Trees with larger polygons (greater area available, or lesser local competition) have higher growth rates (and are less likely to die) than trees with smaller polygon areas (Daniels 1976). In this study, the coefficients associated with Thiessen polygon area were positive and statistically significant for all four species groups. Thiessen polygon area was an important predictor in natural jack pine and upland black spruce stands, but was less important in lowland black spruce and (especially) managed jack pine stands. In natural jack pine stands, local competitive effects have been shown to strongly influence tree growth and mortality (Kenkel *et al*. 1997). However, the much more even spacing of trees in managed jack pine stands greatly reduces the variability, and thus the importance, of local competitive effects. The higher shade tolerance of black spruce may explain the reduced importance of local competitive effects on tree growth and mortality in this species (Carleton and Wanamaker 1987). The reduced importance of local competitive effects (Thiessen polygon area) in lowland black spruce likely reflects the lower density of these stands (6790 trees/ha, versus 8614 trees/ha for upland stands), since lower density implies reduced intraspecific competition.

Among the four species groups examined, the diameter increment growth model for managed jack pine stands resulted in the best prediction ($R^2 = 0.7525$). The relatively regular spacing of trees in these stands reduces intraspecific competition for available sources (light, water and soil nutrients); as a result, diameter growth is more closely linked to tree size (diameter variables) and less affected by competitive effects, improving model prediction. The diameter increment growth model for natural jack pine stands resulted in the lowest predictive power ($R^2 = 0.6103$). The high shade intolerance of jack pine, combined with high variation in spacing within natural stands, makes accurate growth prediction more difficult. In addition, the relatively high mortality in natural jack pine stands (see Chapter 6) reduces the predictive power of models, since trees dying during the study period were not included in the model. As a result, tree size was relatively unimportant in predicting diameter increment growth in natural jack pine stands, whereas competitive effects were comparatively important. The diameter growth models for lowland and upland black spruce, a comparatively shade-tolerant and slow growing species, had relatively high levels of predictive power (R^2 = 0.6544 and 0.6515 respectively). In these models, both tree size (diameter variables) and competitive effects (Thiessen polygon area for upland stands, basal area of larger trees for lowland stands) were important predictor variables.

The predictive capabilities of my models (60-75% of variance accounted for) compared favourably with diameter increment growth models described previously in the literature: 56-65% for white spruce in Alberta (Huang and Titus 1995); 43-72% for hardwood stands in the southern United States (Zhao *et al*. 2004); 8-56% for boreal forest species in Minnesota (Lessard *et al*. 2001). Even so, 25-40% of the variation in incremental growth remains unexplained by these models, and this should be recognized when applying these models in forestry practice.

A major contribution of this study is the demonstration that spatial competition (Thiessen polygon area) is an important predictor of diameter growth, particularly in natural (unmanaged) jack pine and black spruce stands. However, it must be acknowledged that obtaining spatial data on the mapped locations of individual trees is both time-consuming and expensive. Currently, spatial information (mapped tree locations) is not available for most forest inventory data, precluding the use of distance-dependent basal area growth models. When spatial information is lacking, distance-independent growth models can be used instead. Current developments of forest inventory technology, especially the application of advanced GIS and remote sense technologies, may soon allow for the rapid and efficient collection of spatial information. Under this scenario, distance-dependent diameter (basal area) growth models will become increasingly important in forest growth and yield modelling, forest inventory analysis, and sustainable forest management.

CHAPTER 5 MODELLING INDIVIDUAL TREE TAPER AND VOLUME USING NONLINEAR MIXED EFFECTS MODELS

5.1 INTRODUCTION

Tree taper is defined as the rate of narrowing in diameter along a tree bole of a given form (Avery and Burkhart 1994). Taper is typically determined by taking successive diameter measures along the length of a tree bole. Taper models are regression equations that estimate diameter (inside, or outside the bark) at all points along the tree bole (Kozak 1988; Huang 1994b; Sharma and Zhang 2004; Trincado and Burkhart 2006). It is suggested that a minimum of 60 – 100 trees, each with 6 – 15 bole diameter measurements taken along the entire bole length, are required when fitting models (Kozak 1988). In forestry practice, taper models are used to estimate individual tree merchantable length, tree gross total volume, and gross merchantable volume under various utilization standards (Kozak 1988; Huang 1994b; Sharma and Zhang 2004; Trincado and Burkhart 2006). Taper models are used widely to provide more accurate information for forest inventory, timber supply analysis, and sustainable forest management in Canada and other countries (Kozak 1988; Flewelling and Raynes 1993; Gal and Bella 1994; Huang 1994b; Huang *et al*. 1999; Sharma and Parton 2009).

Differences in tree bole profile have considerable effects on merchantable timber volume (Cao *et al*. 1980). Tree boles with low taper provide greater merchantable volume than those having high taper. For trees of comparable height and diameter at breast height (DBH), these volume differences can be as high as 20% (Heger 1965). The advantage of taper over volume equations is that individual log (i.e. sectional) volumes can be estimated using scaling rules; in addition, taper models are more accurate (Williams and Reich 1997; Muhairwe 1999). Taper models are thus necessary and flexible tools for the accurate and unbiased estimation of tree volumes (Newnham 1988b; Muhairwe 1999).

A number of factors affect the bole taper of trees, including species, edaphic factors (site quality), environmental conditions, disturbance history, stand density, as well as the age, crown size and canopy position of a tree (Larson 1963 1965; Muhairwe 1994). Differences in bole taper among trees result from differences in diameter and height growth along the tree bole over time. As a result, factors that affect height and diameter growth in trees also affect taper (Muhairwe1994, 1999; Sharma and Parton 2009). Some studies have demonstrated that bole taper is related to tree crown ratio (CR), which is the ratio of crown length to total tree height (Dell *et al.* 1979; Feduccia *et al.* 1979; Baldwin and Polmer 1981). For example, Valenti and Cao (1986) found that trees with larger crown ratios have higher taper than those with lower crown ratios (see also Muhairwe *et al.* 1994). However, Burkhart and Walton (1985) found that crown ratio is a poor predictor of tree taper.

Two major groups of parametric taper model approaches are used in forestry practice: the segmented taper equation approach, and the variable exponent taper equation approach. The segmented taper equation approach assumes that the tree bole is divisible into three geometric shapes: a neiloid frustum at the base, a paraboloid frustum in the middle portion, and a cone frustum at the top (Husch *et al.* 1982). These three segments are fitted with different equations, and later mathematically joined to generate an overall taper function (Max and Burkhart 1976; Trincado and Burkhart 2006). This approach requires the proper specification of inflection and other joining points to ensure smooth connections of the segments. In practice, the parameters of these models are difficult to estimate, and the volume calculations are somewhat cumbersome (Max and Burkhart 1976).

Variable exponent taper functions assume that tree form varies continuously along the bole. In these equations, the regression exponent varies with relative tree height, producing a single equation that describes the neiloid, paraboloid, and conic forms and thus eliminates the need to specify different equations for different sections of the bole. Variable exponent taper functions are much easier to fit, and result in lower local bias and more precise predictions of bole taper (Newnham 1988b; 1992; Kozak1988; Perez *et al*. 1990; Kozak and Smith 1993; Muhairwe 1999; Huang *et al.* 2000a; Kozak 2004). Variable exponent taper equations are widely used in applied forestry in Canada (Kozak 1988; Newnham 1992; Huang *et al.* 2000a; Sharma and Zhang 2004).

The tree bole profile of most conifers is often separated into three segments (Gray 1956; Assmann 1970; Husch *et al*.1982; Newnham 1992). In the basal segment (stump or butt), the taper rate declines with increasing height above ground. In the middle segment, (above the stump but below the tree crown), taper rate increases with increasing height above ground. In the top segment (from tree crown base to bole tip), the taper rate increases slightly or remains constant with increasing height above ground (Valentine and Gregoire 2001). For a given tree species, overall tree bole shape remains constant at all size classes (Demaerschalk and Kozak 1977).

Kozak’s (1988) variable-exponent taper equation has been shown to provide accurate diameter and volume predictions for major tree species in British Columbia, Alberta and Saskatchewan (Kozak 1988; 2004; Gal and Bella 1994; Huang 1994). Gal and Bella (1994) tested three equations (developed by Demaerschalk and Kozak (1977), Kozak (1988) and Hilt (1980)) in twelve tree species in Saskatchewan, and found that Kozak’s (1988) taper model achieved overall superior performance.

The variable-exponent equations developed by Kozak (1988), and later modified versions (Kozak 1997, 2004), are subject to the statistical problem of high multicollinearity. Multicollinearity is characteristic of over-complicated regression models having several polynomial terms (Kozak 1997), particularly when there is a high degree of inter-correlation amongst independent variables. The latter is a characteristic feature of tree taper models (Kozak 1997; Huang *et* *al.* 1997; Huang 1997). Multicollinearity presents a number of challenges in applied regression analysis. When multicollinearity is present, comparatively minor changes to the raw data can significantly affect and alter parameter estimates, and greatly increase the standard errors of such estimates. In addition, the estimated parameters may exhibit unreasonable magnitude (Kleinbaum *et al.* 1988; Myers 1986; Fox 1991). The presence of multicollinearity is quantified using the variance inflation factor (*VIF*), calculated as the condition number of a correlation matrix of partial derivates with respect to each of the regression parameters. In response to the multicollinearity problem, Kozak (1997) developed a set of variable-exponent taper equations that is less prone to multicollinearity. In practice, tree taper models that are less affected by multicollinearity issues should be used whenever possible (Kozak 1997).

Stem (bole) section analysis data, obtained by taking diameter measurements at regular intervals along the length of a tree bole, are generally used to develop and validate tree taper models. Such measurements, and their associated error terms, are necessarily spatially auto-correlated. This results in a violation of a major assumption of regression analysis: that the error terms are independent, identically distributed, normal random variables. When error terms are auto-correlated, the consequences for statistical inferences in regression analysis include: (a) estimated regression coefficients are unbiased and consistent, but they no longer have the minimum variance property; (b) the mean squared error of the variance, and the standard errors of the coefficients, may be underestimated; (c) statistical testing (e.g. *t* and *F* tests, and their confidence intervals) are no longer reliable (Neter *et al.* 1990; Kmenta 1986; Kozak 1997).

Until quite recently, tree taper models used in forestry research were developed using the nonlinear least squares (NLS) regression approach. Most researchers did not address the complicated statistical issues of autocorrelation and multicollinearity, in part due to the lack of appropriate statistical tools and methods. In the past few years, forest modellers have begun to use regression-based nonlinear mixed-effects models (NLMM) to deal with these issues (Huang *et al.* 2009; Sharma and Parton 2009; Yang *et al.* 2009).

Precise and accurate statistically based tree taper models are required to obtain reliable and useful estimates of individual tree volumes and timber yields. Tree taper equations provide diameter estimates along the entire length of the tree bole, allowing for the calculation of individual tree volume. In turn, individual tree volume values can be “scaled up” to estimate timber yield at forest stand and landscape levels. Such estimates are critically important, as they are the basis for decisions in sustainable forest management, timber supply analysis, annual allowable cut determination, forest biomass inventory, and forest carbon budget calculations (Husch *et al*. 2003).

The objective of this study is to develop statistically sound and biologically reasonable variable-exponent taper equations for black spruce and jack pine trees in the boreal forest of Manitoba, using nonlinear least square (NLS) and nonlinear mixed-effects modeling (NLMM) regression approaches. This objective is achieved by: (a) selecting the “best” baseline model from several candidate variable-exponent taper models; (b) examining the random parameters and error covariance structures, and addressing autocorrelation issues, using the nonlinear mixed-effects modeling (NLMM) approach; (c) evaluating the effects of inclusion of crown ratio as a variable in taper models; (d) evaluating the predictive ability of the fitted model on population-level and tree-specific calibrations of stem diameter and total tree and section volumes, using validation data.

5.2 STUDY AREA

The study area is located in Boreal Shield Ecozone and Boreal Plains ecozones of Manitoba. A summary description of these eozones is given in Section 3.2.

5.3 DATA

The stem (bole) analysis or sectioning data collection procedures are described in Chapter 3. The only difference is that all the tree section data were used to develop the tree taper models, whereas only data from dominant and co-dominant trees were used to develop the height growth and site index models (Chapter 3).

A total 719 tree boles were measured, including 378 black spruce trees and 341 jack pine trees. Representative tree bole profiles (diameter inside bark (DIB) plotted as a function of relative tree height) for black spruce and jack pine are shown in **Figure 5.1**. For model validation purpose, approximately 80% of the data (572 trees: 301 black spruce and 271 jack pine) were randomly selected and used for model fitting (**Table 5.1**). The remaining data (147 trees: 77 black spruce and 70 jack pine) were reserved for model validation (**Table 5.2**).

Table 5.1. Summary statistics of the black spruce and jack pine trees used to develop bole taper models.

Species	Mean	Min	Max	SD	Variable
BS	0.48	0.13	0.98	0.17	Crown ratio
(*n* = 301)	15.8	1.0	35.2	4.42	DBH (cm)
	7.86	0.2	15.1	3.16	Height to live crown (m)
	14.86	1.68	25	3.64	Total height (m)
JP	0.48	0.08	0.96	0.16	Crown ratio
(*n* = 271)	17.81	1.7	38	6.05	DBH (cm)
	8.02	0.2	18.4	3.59	Height to live crown (m)
	14.78	2.4	24.6	4.43	Total height (m)

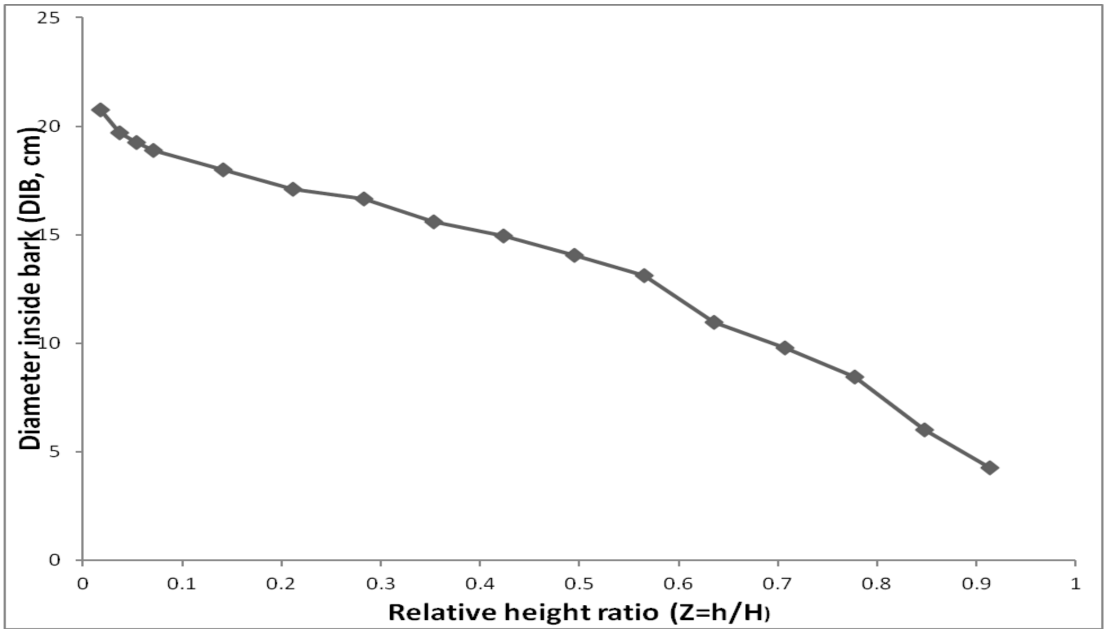
Note: BS = black spruce; JP = jack pine; Min = Minimum; Max = maximum; SD = standard deviation; n = number of trees.

Table 5.2. Summary statistics of the black spruce and jack pine trees used to validate the bole taper models.

Species	Mean	Min	Max	SD	VARIABLE
BS	0.48	0.11	0.83	0.17	Crown ratio
(*n* = 77)	15.75	7.3	25.2	4.17	DBH (cm)
	7.66	1.5	13.3	2.84	Height to live crown (m)
	14.88	6.65	22.7	3.38	Total height (m)
JP	0.44	0.1	0.78	0.14	Crown ratio
(*n* = 70)	18.36	7.5	30.6	4.53	DBH (cm)
	8.48	2.5	16.8	3.17	Height to live crown (m)
	14.98	7.35	22.1	3.4	Total height (m)

Note: BS = black spruce; JP = jack pine; Min = Minimum; Max = maximum; SD = standard deviation; n = number of trees.

(a) BLACK SPRUCE



(b) JACK PINE

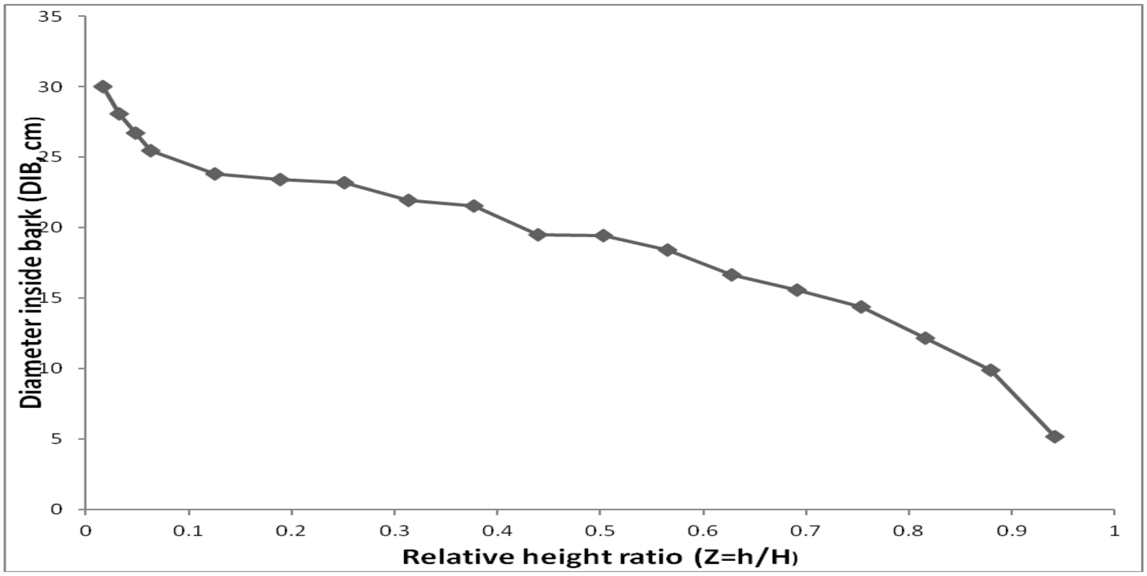


Figure 5.1. Two examples of tree profiles, plotting diameter (inside bark) as a function of tree relative height ratio (z=h/H, h = height above ground, H = total tree height), for (a) black spruce and (b) jack pine.

5.4 METHODS

5.4.1 Model Development

A number of existing individual tree volume taper equations were selected, fitted and compared. First, the following variable-exponent taper equations of Kozak (1988, 1997) were fit and compared using the NLS regression approach:

[5.1]

$$d_i = a_0 D^{a_1} a_2^{D} X_i^{b_1 z_i^2 + b_2 \ln(z_i + 0.001) + b_3 \sqrt{z_i} + b_4 e^{z_i} + b_5 (D/H)} + \varepsilon_i$$

where $z_i = \frac{h_i}{H}$ $X_i = \frac{1 - \sqrt{h_i / H}}{1 - \sqrt{p}}$

(Kozak 1988)

[5.2]

$$d_i = a_0 D^{a_1} a_2 D X_i^{b_0 + b_1 z_i^{1/4} + b_2 z_i^{1/3} + b_3 z_i^{1/2} + b_4 ArcSin(1 - z_i^{1/2}) + b_5 (D/H + z) + b_6 H} + \varepsilon_i$$

where $z_i = \frac{h_i}{H}$ $X_i = \frac{1 - \sqrt{h_i / H}}{1 - \sqrt{p}}$

(Kozak 1997)

[5.3]

$$d_i = a_0 D^{a_1} H^{a_2} X_i^{b_1 X_i^{1/10} + b_2 z_i^4 + b_3 ArcSin(1 - z_i^{1/2}) + b_4 / e^{D/H} + b_5 D^{X_i}} + \varepsilon_i$$

where $p = \frac{1.3}{H}$ $z_i = \frac{h_i}{H}$ $X_i = \frac{1 - z_i^{1/3}}{1 - p^{1/3}}$

(Kozak 1997)

In these equations, d_i is the diameter inside bark (cm) at h_i, h_i is the height (m) above ground ($0 \le h_i \le H$), H is the total tree height (m), D is the breast height diameter outside bark (cm), z_i is the ratio h_i/H, p is the inflection point, e is the base of the natural logarithm, $a_0 - a_2$ and $b_1 - b_5$ are regression model parameters, and ε_i is a random error term.

The inflection point *p* is the height at which the base of a tree bole changes from a neiloid to a paraboloid form (Demaerschalk and Kozak 1977; Newnham 1992). Values of *p* range from 0.15 and 0.35, depending on the species (Demaerschalk and Kozak 1977; Perez *et al*. 1990; Allen 1993). For a given tree species, the height of the inflection point *p* is often assumed to be constant, i.e. independent of tree size or age (Kozak 1988). A constant value of $p = 0.225$ was suggested by Kozak (1988), while Muhairwe (1999) suggested using a mean value of $p = 0.25$ based on measurements on various tree species. However, within a given species the relative height of the inflection point has often been found to vary with individual tree height (Bi 2000). While within-species variation in *p* has a limited impact on taper model predictions, the value of *p* should nonetheless be treated as a parameter rather than a constant (Perez *et al*. 1990). Kozak (1997) defined *p* as a function of tree total height (H); see equation [5.3]. In this study, the relative height of the inflection point *p* was treated as a parameter, the value of which is determined from the stem (bole) analysis data.

Preliminary analyses demonstrated that models [5.1] to [5.3] were strongly affected by variable multicollinearity and autocorrelations. In addition, some of the model parameters were not statistically significant (see Section 5.5). Various modifications of the Kozak variable-exponent taper equations were therefore developed in an attempt to reduce the effects of multicollinearity and to ensure that model parameters were statistically significant. These modifications were made based on an understanding of how the Kozak taper models were derived. Kozak's variable-exponent taper equations are allometric functions of the form:

[5.a1] $d = kX^c$

The dependent variable *d* is bole diameter (inside bark), *X* is an independent variable, *k* is a constant, and *c* is an exponent describing the changes in bole form along the length of the tree bole (Huang 1994b; Yang 2003). For the derivations, first linearize [5.a1] by taking the logarithm of both sides:

[5.a2] $$\ln(d) = \ln(k) + c\ln(X)$$

Next, define:

[5.a3] $$k = a_0 D^{a_1} a_2^{D}$$

[5.a4] $$c = b_1 Z^2 + b_2 \ln(Z + 0.001) + b_3\sqrt{Z} + b_4 e^{Z} + b_5 (D / H)$$

Substitution into [5.a2] gives:

[5.a5] $$\ln(d) = \ln(a_0) + a_1 \ln(D) + \ln(a_2)D + b_1 \ln(X)Z^2 + b_2 \ln(X)\ln(Z + 0.001) \\ + b_3 \ln(X)\sqrt{Z} + b_4 \ln(X)e^{Z} + b_5 \ln(X)(D / H).$$

Following re-arrangement and expression in allometric form, equation [5.a5] becomes:

[5.a6] $$d_i = a_0 D^{a_1} a_2^{D} X_i^{b_1 z_i^2 + b_2 \ln(z_i + 0.001) + b_3\sqrt{z_i} + b_4 e^{z_i} + b_5 (D / H)} + \varepsilon_i$$

where $$X_i = \frac{1 - \sqrt{h_i / H}}{1 - \sqrt{p}}$$

Note that model [5.a6] is the same as [5.1].

The above procedures were used to obtain the following modified versions of models [5.1] to [5.3], in an attempt to improve taper model performance:

[5.4] $$d_i = a_0 D^{a_1} X_i^{b_0 + b_1 z_i^2 + b_3\sqrt{z_i} + b_4 e^{z_i} + b_5 (D / H)} + \varepsilon_i$$

where $$z_i = \frac{h_i}{H} \qquad X_i = \frac{1 - \sqrt{h_i / H}}{1 - \sqrt{p}}$$

(Modified from Kozak 1988)

[5.5] $$d_i = a_0 D^{a_1} X_i^{\,b_0 + b_1 z_i^{1/4} + b_2 z_i^{1/3} + b_3 z_i^{1/2} + b_4 ArcSin\,(1 - z_i^{1/2}) + b_5 (D/H)} + \varepsilon_i$$

where $z_i = \frac{h_i}{H}$ $X_i = \frac{1 - \sqrt{h_i / H}}{1 - \sqrt{p}}$

(Modified from Kozak 1997)

[5.6] $$d_i = a_0 D^{a_1} X_i^{\,b_0 + b_1 \left(1 \big/ e^{\left(\frac{D}{H}\right)} \right) + b_2 (\ln D)^{X_i} + b_3 X_i^{D/H}} + \varepsilon_i$$

where $z_i = \frac{h_i}{H}$ $X_i = \frac{1 - z_i^{1/4}}{1 - p^{1/4}}$

(Modified from Kozak 1997)

[5.7] $$d_i = a_0 D^{a_1} H^{a_2} X_i^{\,b_0 + b_1 z_i^{4} + b_2 \left(1 \big/ e^{\left(\frac{D}{H}\right)} \right) + b_3 X_i^{0.1} + b_4 (1/D) + b_5 H^{Q} + b_6 X_i} + \varepsilon_i$$

where $p = \frac{1.3}{H}$ $z_i = \frac{h_i}{H}$ $X_i = \frac{1 - z_i^{1/3}}{1 - p^{1/3}}$

$$Q = 1 - z_i^{1/3}$$

(Modified from Kozak 1997)

[5.8] $$d_i = a_0 D^{a_1} a_2^{D} X_i^{\,b_0 + b_1 z_i^{4} + b_2 \left(1 \big/ e^{\left(\frac{D}{H}\right)} \right) + b_3 X_i^{0.1} + b_4 (1/D) + b_5 H^{Q} + b_6 X_i} + \varepsilon_i$$

where $p = \frac{1.3}{H}$ $z_i = \frac{h_i}{H}$ $X_i = \frac{1 - z_i^{1/3}}{1 - p^{1/3}}$

$$Q = 1 - z_i^{1/3}$$

(Modified from Kozak 1997)

The following model [5.9], recently developed by Sharma and Parton (2009) and based on dimensional analysis, was also considered:

[5.9]
$$d_i = b_0 D \left(\frac{H - h_i}{H - 1.3}\right)\left(\frac{h_i}{1.3}\right)^{b_1 + b_2 z + b_3 z^2} + \varepsilon_i$$

where $z_i = \frac{h_i}{H}$

(Sharma and Parton 2009)

Preliminary analyses using equation [5.9] found that this taper model easily converged, with limited multicollinearity attributable to low correlations among the four parameters $b_0 - b_3$. However, the parameter b_3 was not statistically significant in both black spruce and jack pine taper model fittings, and spatial autocorrelation remained a problem. Modifications to the base equation [5.9] were therefore made, focusing on the power term. Inclusion of logarithmic and reciprocal transformations of *z* produced model [5.10]:

[5.10]
$$d_i = b_0 D \left(\frac{H - h_i}{H - 1.3}\right)\left(\frac{h_i}{1.3}\right)^{b_1 + b_2 z + b_3 \ln z + b_5 / z} + \varepsilon_i$$

where $z_i = \frac{h_i}{H}$

(Modified from Sharma and Parton 2009)

Preliminary analysis indicated that model [5.10] performs well, and therefore it was included in the comparison with other models.

Tree crown ratio has been shown to be a useful and statistically significant predictor variable in tree taper models (Muhairwe *et al.* 1994), but other studies have found otherwise (e.g. Hann *et al.* 1987; Burkhart and Walton 1985). In this study, the importance of tree crown ratio (CR) as a predictor variable was examined by incorporating it into model [5.10], resulting in:

[5.11] $$d_i = b_0 D \left(\frac{H-h_i}{H-1.3}\right)\left(\frac{h_i}{1.3}\right)^{b_1 + b_2 z + b_3 \ln z + b_4 CR + b_5 / z} + \varepsilon_i$$

where $$z_i = \frac{h_i}{H}$$

(Modified from [5.10])

Two potentially problematic issues in bole taper modelling are predictor variable multicollinearity, and spatial autocorrelation of bole analysis data. Multicollinearity, which arises when the predictor variables of bole taper models are highly correlated, is especially problematic in complex models containing many variables (Kozak 2004). Multicollinearity results in unstable regression parameter estimates that have high standard errors (Kleinbaum *et al.* 1988; Myers 1986). The earliest developed variable-exponent taper equations (Kozak 1988, 1997) are particularly prone to multicollinearity issues (Kozak 2004).

As previously mentioned, bole section data are used to develop and fit individual tree taper models. Since diameter measurements are taken at various heights along a given tree bole, they are highly spatially auto-correlated. Autocorrelation violates basic regression analysis assumptions (Neter *et al.* 1990; Kmenta 1986; Kozak 1997), but recently statistical methods have been developed to alleviate the problem (Sharma and Parton 2009).

5.4.2 Nonlinear Least Square Modeling (NLS)

The Gauss-Newton method (SAS Proc NLIN procedures, and Proc Model procedures; SAS/STAT, SAS Institute 2004) was used to fit the nonlinear models. Different starting values of the model parameters were examined to ensure that the fitted non-linear regressions were global rather than local least square solutions. The various fitted models were statistically compared using the coefficient of determination (R^2) and the root mean squared error (*RMSE*). Autocorrelation and multicollinearity were examined using the Durbin-Watson and the variance inflation factor (VIF) statistic (Neter *et al*. 1990).

5.4.3 Nonlinear Mixed-Effects Modeling (NLMM)

The NLMM technique has been introduced recently in forest modelling research to address issues of autocorrelation (Fang and Bailey 2001; Leites and Robinson 2004; Trincado and Burkhart 2006; Huang *et al.* 2009; Sharma and Parton 2009). The technique involves the estimation of a covariance matrix of correlated data, and includes both fixed- and random-effects parameters in the model (Schabenberger and Pierce 2001; Trincado and Burkhart 2006).

Modelling Approaches

In mixed-effects models, the parameter estimates of individual trees will differ. The model parameters are broken down into fixed parameters (i.e. those common to all trees within the population) and random parameters (i.e. those specific to individual trees). Following the nonlinear mixed-model approach (Davidian and Giltinan 1995; Vonesh and Chinchilli 1997), the selected base model can be expressed in a general vector form as:

[5.12] $$d_i = f(x_i, \beta, \mu_i) + \varepsilon_i$$

In this equation ***d_i*** is an *n*-variable vector of bole diameter values for a given subject tree *i*; ***x_i*** is an (*n_i x p*) matrix of independent variables; □ is a *p*-variable vector of fixed parameters (i.e. common to all trees); ***u_i*** is a *q*-variable vector of random parameters unique to subject tree *i*, which are assumed to follow a multivariate normal distribution with mean zero and covariance matrix **D** (matrix **D** is modelled as unstructured); ε_i is an *n*-variable vector of the error term with $\varepsilon_i \sim N(0, R_i)$, and ***$R_i$*** is an (*$n_i$ x n_i*) positive-definite covariance matrix for the error term.

The fixed-effects parameters are the population mean responses common to all trees, while the random-effects parameters are localized responses specific to each tree. An important but challenging problem in mixed-effects modeling is determining which parameter (or parameters) should be modelled as fixed-effects and which should be modelled as mixed-effects (i.e. fixed plus random). Following the recommendations of Fang and Bailey (2001), a trial-and–error approach (using models [5.10] and [5.11]) that involved examining and evaluating various parameter combinations was used in this study to determine assignments of fixed versus mixed-effects. Regression parameters were estimated using maximum likelihood (ML) estimation implemented through the SAS macro %NLINMIX with zero expansion (Littell *et al.*, 2006).

Autocorrelation and Heteroscedasticity

Mixed-effects models have the flexibility and advantage of modelling within-tree autocorrelation and between-tree heteroscedasticity, through incorporation of random parameters and direct modelling of the within-unit covariance structure. Following Davidian and Giltinan (1995), the general form of the covariance matrix $\mathbf{R}_i$ is:

[5.13] $$R_i = \sigma^2 G_i^{1/2} \Gamma_i G_i^{1/2}$$

In this equation σ^2 is a scaling factor for the error dispersion, equivalent to the residual variance of the model; $\mathbf{G}_i$ is a (n_i x n_i) diagonal matrix describing the within- and between-tree error variance structures, which is required when heteroscedasticity is present; and Γ_i is a (n_i x n_i) correlation matrix of observations from tree *i*.

Preliminary analyses indicated that residual variances were approximately homogenous, and that heteroscedasticity was not a concern in this study. However, significant residual autocorrelations were present for the selected base model even after random parameters were included. The covariance matrix $\mathbf{R}_i$ was therefore modelled as:

[5.14] $$R_i = \sigma^2 \Gamma_i$$

Both time series and spatial covariance structures were evaluated as potential approaches to selecting the correlation matrix Γ_i in the mixed-effects modelling framework. Three approaches were considered: (a) first-order autoregressive AR(1); (b) Spatial Power (SP(POW)); (c) Toeplitz (4) (TOEP(4)) structures (Littell *et al.* 2006; Yang and Huang 2008). For these three approaches, the respective **R***i* within-tree autocorrelation matrices for a tree with four measurements are expressed as:

[5.15] AR(1)

$$R_i = \sigma^2 \begin{bmatrix} 1 & \rho & \rho^2 & \rho^3 \\ & 1 & \rho & \rho^2 \\ & & 1 & \rho \\ & & & 1 \end{bmatrix}$$

[5.16] SP(POW))

$$R_i = \sigma^2 \begin{bmatrix} 1 & \rho^{d_{12}} & \rho^{d_{13}} & \rho^{d_{14}} \\ & 1 & \rho^{d_{23}} & \rho^{d_{24}} \\ & & 1 & \rho^{d_{34}} \\ & & & 1 \end{bmatrix}$$

[5.17] TOEP(4)

$$R_i = \begin{bmatrix} \sigma^2 & T_2 & T_3 & T_4 \\ & \sigma^2 & T_2 & T_3 \\ & & \sigma^2 & T_2 \\ & & & \sigma^2 \end{bmatrix}$$

Here $\boldsymbol{\sigma}^2$ is the model overall residual variance; T_2, T_3, T_4 are the co-variances for the TOEP(4) structure, d_{xy} is the distance between two measurements x and y, ρ is the correlation parameter for AR(1) and SP(POW). AR(1) and TOEP(4) are generally used for equally spaced data, whereas SP(POW) is used when the data are unequally spaced (Littell *et al.* 2006).

Mixed-effects models are statistically evaluated using goodness-of-fit criteria, such as Akaike's information criterion (AIC; Akaike 1973) and Schwarz's Bayesian information criterion (BIC; Schwarz 1978); see equations [3.28] and [3.29]. Lower values of these goodness-of-fit statistics indicate a better model fit. The Proc IML procedure in SAS was applied to predict the random-effects parameters for each tree, based on prior information, for both black spruce and jack pine.

To test spatial lagged residual correlations (i.e. correlations of the residual values at adjacent heights along the bole), normalized residuals were calculated for both the NLS and nonlinear mixed-effects model approaches. For each fit, the normalized residuals (Pinheiro and Bates 2000) were derived:

[5.18]

$$r_i = (\hat{R}_i^{\,0.5})^T (d_i - \hat{d}_i)$$

Here d_i and $\hat{d}_i$ are the observed and predicted stem diameters (inside bark) for the *i*th tree, and $\hat{R}_i$ is the estimated covariance matrix of within-tree errors. Normalized residuals are an extension of Studentized residuals, the difference being that whereas Studentized residuals are weighted only by their respective variances, normalized residuals are weighted by both variances and covariances (Fortin *et al.* 2008; Yang *et al.* 2009).

Varying lags of paired normalized residuals were used to determine corresponding correlation coefficients. The calculated correlation coefficients were examined to determine whether they were statistically significant. Following Diggle *et al* (2002) and Yang *et al.* (2009), a general rule of thumb is that, under the null condition of no correlation and given *N* independent pairs of observations, a correlation coefficient has the standard error of roughly 1/*N*. The standard error can be used to calculate the confidence interval at a given level of significance. In this study, 99% confidence intervals were used to examine the significance of correlations between normalized residuals at different lag distances. Graphical examinations of the normalized residuals were also conducted and presented.

Diameter Predictions

In order to make tree-specific diameter predictions, random parameters $\mathbf{u}_i$ were predicted first using one or more prior diameter measurements from each tree. This calculation was performed using the approximate Bayes estimator (Vonesh and Chinchilli 1997; Trincado and Burkhart 2006):

[5.19] $$\hat{u}_i = \hat{D} Z_i^T (Z_i \hat{D} Z_i^T + \hat{R}_i)^{-1} \hat{e}_i$$

with $$\hat{e}_i = d_i - f(x_i, \hat{\beta}, 0)$$

Here $\hat{D}$ is the estimated variance–covariance matrix for random parameters $\mathbf{u}_i$, and $\hat{R}_i$ is the estimated covariance matrix for the error term. $\mathbf{Z}_i$ is the partial derivatives matrix of d_i with respect to the random parameters:

[5.20] $$Z_i = \partial f(x_i, \beta, 0) / \partial u_i \,|_{\hat{\beta}, 0} \,.$$

After the random parameters were predicted, tree-specific diameter predictions were derived using (Vonesh and Chinchilli 1997; Huang *et al.* 2009):

[5.21] $$\hat{d}_i = f(x_i, \hat{\beta}, 0) + Z_i \hat{u}_i$$

Prediction accuracy of random parameters is dependent on the number of prior diameter measures available (Calama and Montero 2004). In practice, it is impractical to use more than three diameter measurements per tree, since the collection of such field data are time-consuming and costly. Three scenarios were used to determine the minimum number of diameter values required to accurately predict the random parameters:

Scenario A: One bole diameter measure per tree.

Scenario B: Two bole diameter measures per tree, one above and one below diameter at breast height (DBH).

Scenario C: Three bole diameter measures per tree, two above and one below DBH.

Since some trees in the data set were < 9 m in height, the prior measurements used were restricted to the first nine heights at diameters were measured: 1 = 0.3 m, 2 = 0.67 m, 3 = 1.0 m, 4 = 1.3 m (DBH), 5 = 2.6 m, 6 = 3.9 m, 7 = 5.2 m, 8 = 6.5 m, and 9 = 7.8 m. Since the diameter value 4 = 1.3 m (DBH) was included as an independent variable in the model, it could not be used as a prior measure in mixed-effects model random parameter prediction. Thus scenario *A* resulted in eight sets of random parameters, i.e. one diameter measurement for each of the eight heights along the tree bole. or values 1 – 3 and 5 – 9 above. Scenario *B* resulted in 15 sets of random parameters predicted; i.e. the following pair-wise diameter combinations: (1, 5), (1, 6), (1, 7) ... (3, 7), (3, 8) and (3, 9). Scenario *C* resulted in 30 sets of random parameters predicted; i.e. the following diameter combination triplets: (1, 5, 6), (1, 5, 7) … (3, 7, 9), (3, 8, 9).

Using the validation data, the random parameters predicted using all combinations of the above three scenarios *A* – *C* were also combined with their fixed effects counterparts in [5.10] and [5.11] for further comparisons. After the diameters along the tree stem for each tree were estimated using the fixed-effects and random-effects parameters, the prediction errors (observed – predicted) were calculated.

To evaluate model performance over the entire length of the tree bole, each tree was divided into five relative height (*h/H*, where *h* = height and *H* = total tree height) classes: 0.0 – 0.2, 0.2 – 0.4, 0.4 – 0.6, 0.6 – 0.8, and 0.8 – 1.0. Under each scenario, four comparison criteria (root mean squared error (RMSE), mean bias ($\bar{e}$), mean bias percent ($\bar{e}$ %), and mean absolute error (MAE)) were used to compare and assess the model predictions. RMSE was considered as the main criteria for evaluating the overall model prediction accuracy, since it incorporates both bias and variation. These four criteria were also used to compare the results to models without any prior information (mean response or population level prediction).

Volume Predictions

A major application of taper models is for stem volume prediction. In this study, model-calibrated bole diameters were used to obtain volume predictions at both the tree and mean response (population) levels. For each tree section between two adjacent diameter measurements, volume was calculated using both observed and calibrated diameters; these are termed as the observed and predicted section volumes.

Volume of the top section of each tree was calculated using the diameter at the bottom of that section, assuming a cone shape. Volumes of all other sections were calculated using Smalian's formula (Clutter et al. 1983):

[5.22] $$VOL_{ik} = (A_{ik1} + A_{ik2})L_{ik} / 2$$

Here VOL_{ik} is the volume (m^3) for section k of tree i, A_{ik1} and A_{ik2} are the upper and lower end cross-sectional areas (m^2) for section k of tree I, and L_{ik} is the section length (m). If diameter inside bark (*dib*) values are used instead, [5.22] becomes:

[5.23] $$VOL_{ik} = 3.14159\ (dib_{ik1}{}^2 + dib_{ik2}{}^2) L_{ik} / 8$$

where dib_{ik1} and dib_{ik2} are the upper and lower end diameter inside barks (cm) for section k of tree i.

Total observed and predicted tree bole volumes were obtained by summing the corresponding section volumes.

Model Validation Comparison Criteria

The mean (population-level) and tree-specific calibrations of bole diameters were derived and compared to the observed values. Total tree and section volumes were also predicted and compared to observed values. The mean error ($\bar{e}$), mean error percent ($\bar{e}$ %), mean absolute error (MAE), and root mean square error (RMSE) (see equations [3.12] to [3.15], respectively) were used to assess the predictive ability of the final model. These criteria were applied to all observations, and as well as observations grouped using the five relative height classes discussed above.

5.5 RESULTS

5.5.1 Nonlinear Least Squares Modelling (NLS)

Using the NLS approach, models [5.1] to [5.11] were convergent for the both black spruce and jack pine data sets. However, for some models one or more of the fitted parameters were not statistically significant. For jack pine, the following parameters did not differ significantly from zero: b_4 in model [5.1], b_6 in model [5.2], a_2 in model [5.3], and b_3 in model [5.9]. The following parameter estimates were not statistically significant in the black spruce models: $b_0 - b_4$ in model [5.2], $b_1 - b_4$ in model [5.7], and b_0 in model [5.8]. Only those models that produced statistically significant parameters estimates for both black spruce and jack pine are discussed henceforth.

The parameter estimates and goodness-of-fit statistics for models [5.4], [5.5], [5.6], [5.10] and [5.11] are summarized in **Table 5.3**. For both black spruce and jack pine the values of the coefficient of determination were high ($R^2 > 0.97$) and root mean square error values were low ($RMSE < 1.1$), indicating good model fits. Among the models that did not include the crown ratio variable (model [5.11]), models [5.5] and [5.10] provide the best fits for black spruce and jack pine, respectively. Compared to model [5.10], inclusion of crown ratio (model [5.11]) slightly reduced the root means square error for both black spruce ($RMSE$ = 0.843 versus 0.856) and jack pine ($RMSE$ = 0.988 versus 0.990).

Spatial autocorrelation was detected in all models (**Table 5.4**); the Durbin-Watson (DW) statistic values ranged from $D\text{-}W = 0.48 – 0.76$, all well below the critical value ($D\text{-}W = 1.76$, $P = 0.05$) indicating statistically significant autocorrelation in both the black spruce and jack pine data. The lag-autocorrelation is illustrated for model [5.11] in **Figures 5.2** and **5.3**, which plot the first three lagged-residuals for black spruce and jack pine respectively, based on ordinary nonlinear least squares (NLS) regression. Given that spatially autocorrelated stem (bole) analysis data were used in fitting the models, this result is not unexpected. The autocorrelation issue is addressed and discussed below.

In regression analysis, values of $VIF > 10$ are often viewed as indicating that multicollinearity is a problem (Neter *et al.* 1989). However, $VIF < 50$ are generally tolerated when models contain polynomial and cross-product terms (Kozak 1997; Yang *et al.* 2009). The *VIF* values for models [5.1] – [5.11] varied markedly, with high values (*VIF* > 100) detected for models [5.1], [5.2], [5.4], [5.5], [5.7] and [5.8]; values were particularly high (*VIF* > 10,000) for models [5.2] and [5.5] (**Table 5.4**). Only models [5.9] – [5.11] consistently had *VIF* < 50. Generally, *VIF* values increased with the number of model parameters (**Table 5.4**). Kozak's variable-exponent taper models (Kozak 1988, 1997) and their modifications (i.e. models [5.1] – [5.8]), which have 7 – 11 regression parameters, had much higher *VIF* values than did models [5.9] – [5.11] (based on Sharma and Parton 2009), which have only 4 – 6 regression parameters.

Of the five models with statistically significant parameter estimates (**Table 5.3**), models [5.10] and [5.11] were selected for subsequent model development, based on model parsimony (5 – 6 versus 7 – 9 regression parameters), low multicollinearity (*VIF* < 50), and low root mean squared error (*RMSE* < 1.0).

Table 5.3. Estimated parameters and fitted statistics of model [5.4] to [5.6], [5.10] and [5.11] for black spruce and jack pine.

Species	Model	a_0	a_1	b_0	b_1	b_2	b_3	b_4	b_5	*P*	R^2	*RMSE*
BS	**[5.4]**	1.0886	0.9348	-4.8199	-6.1193		-3.3998	5.3881	0.2772	0.163	0.976	0.849
(*n* = 4098)	**[5.5]**	1.0912	0.9373	-12.1255	5.6749	1.2452	5.4654	8.8172	0.2746	0.148	0.975	0.847
	[5.6]	1.0994	0.9104	0.7474	-0.7831	0.0362	-0.2340			0.251	0.979	0.852
	[5.10]			0.9685	-0.1241	0.4301	-0.0617		-0.0032		0.974	0.856
	[5.11]			0.9682	-0.0938	0.4269	-0.0602	-0.0565	-0.0032		0.974	0.843
JP	**[5.4]**	0.9577	0.9328	-0.9106	-1.0530		-0.8757	1.2340	0.1270	0.379	0.98	0.992
(*n* = 3780)	**[5.5]**	0.9563	0.9322	46.2569	-84.7219	67.5193	-28.5329	-27.5633	0.1269	0.379	0.976	0.991
	[5.6]	0.9185	0.9210	0.7501	-0.9171	0.0025	-0.0615			0.439	0.974	1.048
	[5.10]			0.9677	-0.0875	0.4280	-0.0373		-0.0018		0.977	0.99
	[5.11]			0.9677	-0.0791	0.4304	-0.0385	-0.0234	-0.0019		0.977	0.988

Note: BS- black spruce; JP- jack pine; R^2 - prediction coefficient of determination; RMSE - root mean square error of prediction; n – total number of observations.

Table 5.4. The Durbin-Watson (D-W) statistics and maximum variance inflation factors (VIF) of the model [5.1] to [5.11] for black spruce and jack pine.

Model	# Parameters	*VIF*		*D-W*		
		BS	**JP**	**BS**	**JP**	Source
[5.1]	9	391.6	199.6	0.741	0.694	Kozak (1988)
[5.2]	11	51283	30833	0.728	0.683	Kozak (1997)
[5.3]	8	81.7	81.2	0.755	0.681	Kozak (1997)
[5.4]	8	1262	514.6	0.733	0.695	Modified Kozak (1988)
[5.5]	9	46641	26051	0.729	0.683	Modified Kozak (1997)
[5.6]	7	97.0	55.5	0.478	0.805	Modified Kozak (1997)
[5.7]	10	779.5	660.4	0.737	0.689	Modified Kozak 1997
[5.8]	10	788.4	665.6	0.747	0.691	Modified [5.5]
[5.9]	4	18.7	19.4	0.606	0.637	Sharma and Parton (2009)
[5.10]	5	39.8	38.8	0.576	0.619	Modified [5.9]
[5.11]	6	45.9	44.7	0.591	0.625	Modified [5.10], adding CR

Note: BS is black spruce; JP is jack pine.

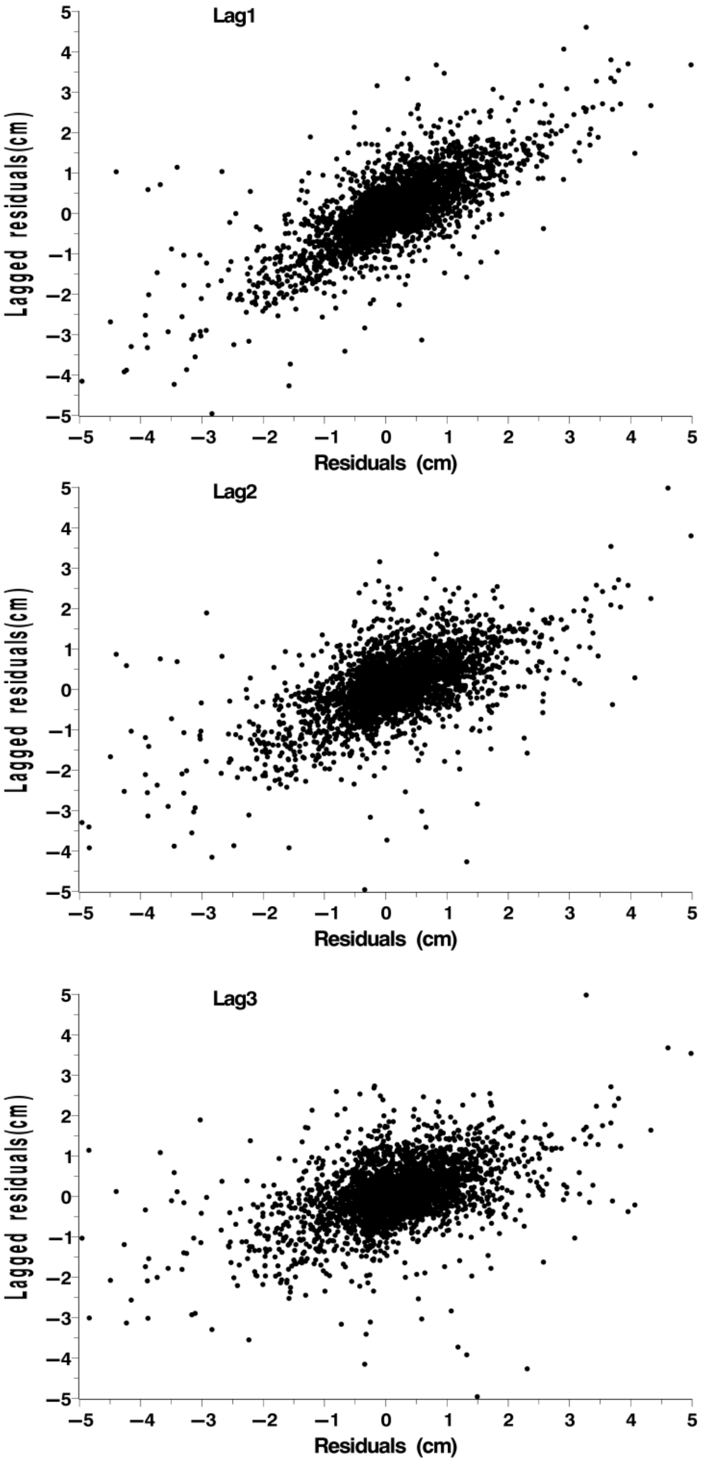


Figure 5.2. Lagged residuals (lag 1, lag 2 and lag 3, from top to bottom) for model [5.11] fitted by ordinary nonlinear least squares (NLS) method for black spruce. The correlation coefficients are 0.79, 0.655 and 0.557, respectively.

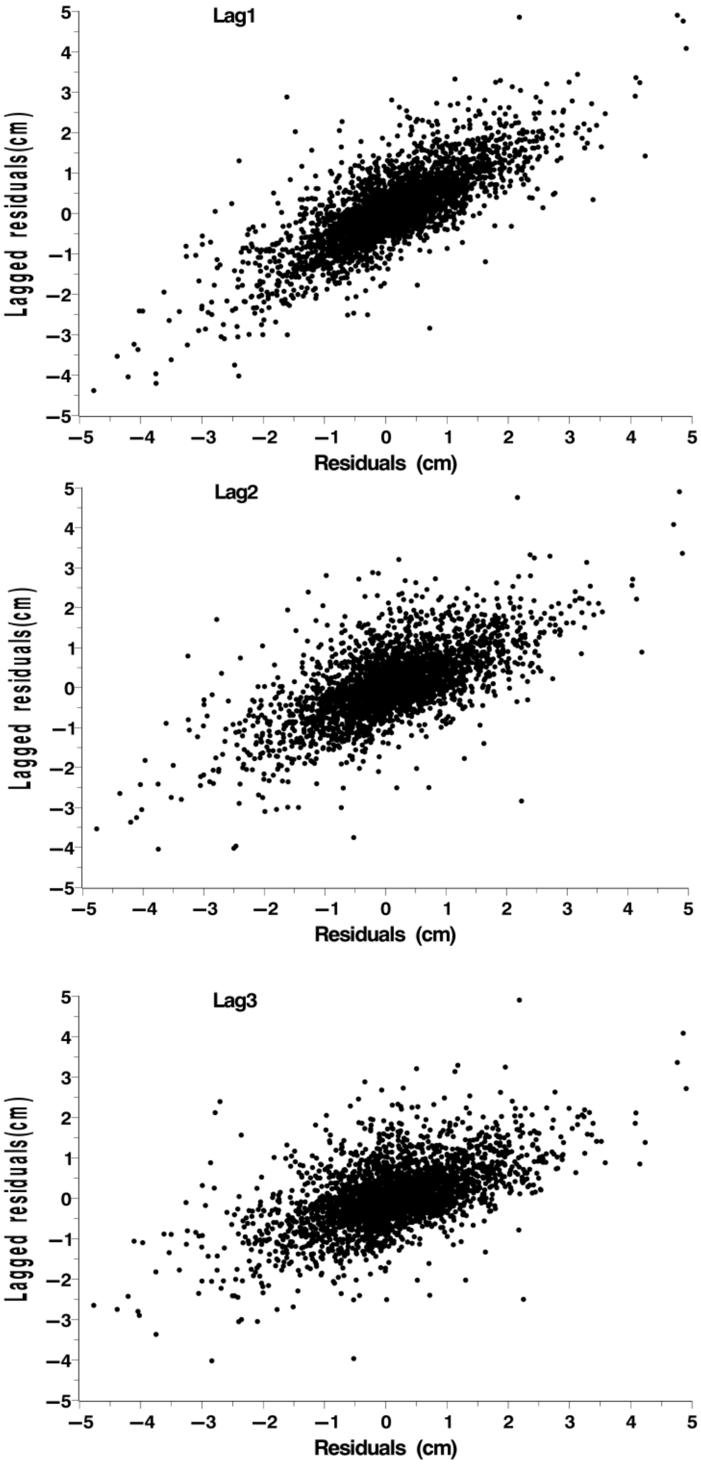


Figure 5.3. Lagged residuals (lag 1, lag 2 and lag 3, from top to bottom) for model [5.11] fitted by ordinary nonlinear least squares (NLS) method for jack pine. The correlation coefficients are 0.77, 0.67 and 0.583, respectively.

5.5.2 Nonlinear Mixed-Effects Modeling (NLMM)

Covariance Structure Selection

The statistical fit values of the AR(1), TOEP(4) and SP(POW) covariance structures for black spruce and jack pine (models [5.10] and [5.11]) are shown in **Table 5.5**. Note that smaller values of the statistics *-2ln(L)*, *AIC* and *BIC* indicate a better fit. For the two black spruce models, the statistical fits were very similar (differing by < 0.4%), with slightly smaller values for the AR(1) structure. For the two jack pine models, the fit statistics were consistently lower for the SP(POW) covariance structure. Given these results, the SP(POW) covariance structure was selected and used in all subsequent analyses and applications.

Random Parameter Selection

For all models, preliminary analyses revealed that increasing the number of random parameters from one to two to three improved model fit (i.e. resulted in lower *AIC* and *BIC* values). Models with four or five random parameters were also attempted, but most failed to converge. Attention therefore focussed on finding the three-parameter combination that produced the best statistical fit. For models [5.10] and [5.11], six three-parameter combinations were considered: $b_0b_1b_2$, $b_0b_1b_3$, $b_0b_1b_5$, $b_1b_2b_3$, $b_1b_2b_5$ and $b_2b_3b_5$. For the jack pine and black spruce models [5.10] and [5.11], three-parameter combination $b_1b_2b_3$ consistently resulted in the smallest values for the fit statistics *AIC* and *BIC*. Fit statistics for black spruce and jack pine models [5.10] and [5.11] with one (b_1), two (b_1+b_2) and three ($b_1+b_2+b_3$) random parameters, and a SP(POW) covariance structure, are summarized in **Table 5.6**. For all models, it is apparent that increasing the number of random parameters improved model fit. Subsequent analyses thus focus mixed-effects models with the three random parameters b_1, b_2 and b_3.

Table 5.5. Fit statistics comparisons by AR(1), TOEP(4) and SP(POW) covariance structures of model [5.10] and [5.11] for black spruce and jack pine.

		Model [5.10]			Model [5.11]		
Spp.	**STATISTIC**	**AR(1)**	**TOEP(4)**	**SP(POW)**	**AR(1)**	**TOEP(4)**	**SP(POW)**
BS	**-2ln(L)**	6093.3	6103.9	6113.6	6088.6	6099.0	6109.8
	AIC	6119.3	6133.9	6139.6	6116.6	6131.0	6137.8
	BIC	6167.5	6189.5	6187.8	6168.5	6190.3	6189.7
JP	**-2ln(L)**	7074.8	7076.8	6862.5	7063.3	7065.0	6848.6
	AIC	7100.8	7106.8	6888.5	7091.3	7097.0	6876.6
	BIC	7147.7	7160.8	6935.4	7141.7	7154.6	6927.0

Note: -2ln(L) is twice the negative log-likelihood; AIC is the Akaike's information criterion; BIC is Schwarz's Bayesian information criterion; BS is black spruce; JP is jack pine.

Table 5.6. Fit statistics comparison of model [5.10] and [5.11] fitted with the SP(POW) covariance structure by adding one, two and three random parameters for black spruce and jack pine.

Species	**Model**	**Random effects**	**Residual**	**-2ln(L)**	**AIC**	**BIC**
BS	**[5.10]**	b_1+u_1	0.801173	6455.9	6471.9	6501.5
		b_1+u_1, b_2+u_2	0.430055	6251.8	6271.8	6308.9
		b_1+u_1, b_2+u_2, b_3+u_3	0.407439	6113.6	6139.6	6187.8
	[5.11]	b_1+u_1	0.794768	6447.9	6465.9	6499.3
		b_1+u_1, b_2+u_2	0.430998	6242.8	6264.8	6305.5
		b_1+u_1, b_2+u_2, b_3+u_3	0.407232	6109.8	6137.8	6189.7
JP	**[5.10]**	b_1+u_1	1.17505	7272.7	7288.7	7317.6
		b_1+u_1, b_2+u_2	0.612638	7049.2	7069.2	7105.2
		b_1+u_1, b_2+u_2, b_3+u_3	0.528315	6862.5	6888.5	6935.4
	[5.11]	b_1+u_1	1.18303	7265.5	7283.5	7315.9
		b_1+u_1, b_2+u_2	0.608401	7044.8	7066.8	7106.4
		b_1+u_1, b_2+u_2, b_3+u_3	0.52711	6848.6	6876.6	6927

Note: b_1, b_2 and b_3 are fixed parameters; u_1, u_2 and u_3 are random parameters; BS is black spruce; JP is jack pine; -2ln(L) = log-likelihood; AIC = Akaike's information criterion; BIC = Schwarz's Bayesian information criterion.

Mixed-Effects Models with Three Random Parameters

Estimates and standard errors for the fixed-effects parameters and variance-covariance components of the random-effects parameters, and fitting statistics, are given in **Table 5.7** for black spruce models [5.10] and [5.11] with SP(POW) structures. All parameters were statistically significant ($P < 0.01$). The results indicate that inclusion of tree crown ratio as a predictor variable (model [5.11]) offered very little if any improvement to model prediction (e.g. $AIC = 6140$, versus 6138 for model [5.10]).

Table 5.8 presents estimates and standard errors for the fixed-effects parameters and the variance-covariance components of random-effects parameters, as well as fitting statistics, for jack pine models [5.10] and [5.11] with SP(POW) covariance structure. All parameter estimates were statistically significant ($P < 0.01$). As with black spruce, inclusion of tree crown ratio as a predictor variable failed to improve model prediction (**Table 5.8**).

In both the black spruce models [5.10], the variance-covariance components for random parameters were used to predict random parameters in order to obtain tree-specific calibrations of bole diameters and volumes.

Table 5.7. Parameter estimates for model [5.10] and [5.11] fitted with the SP(POW) covariance structure, based on 4098 observations from 301 trees for black spruce.

	Parameter	Model [5.10]		Model [5.11]	
		Estimate	S.E.	Estimate	S.E.
Fixed effect	b_0	0.9630	0.0021	0.9630	0.0021
	b_1	-0.0499	0.0099	-0.0416	0.0107
	b_2	0.3606	0.0137	0.3603	0.0138
	b_3	-0.0223	0.0042	-0.0224	0.0042
	b_4			-0.0177	0.0084
	b_5	-0.0016	0.0001	-0.0016	0.0001
Variance Components	σ_1^2	0.003092	0.000753	0.003144	0.000761
	σ_{21}	-0.005180	0.001264	-0.005264	0.001275
	σ_2^2	0.013261	0.002408	0.013261	0.002415
	σ_{31}	0.000970	0.000209	0.000974	0.000209
	σ_{32}	-0.001575	0.000346	-0.001569	0.000347
	σ_3^2	0.000332	0.000060	0.000330	0.000060
Correlation	ρ	0.655963	0.020996	0.655384	0.020960
	σ^2	0.407439	0.023641	0.407232	0.023542
Fit Statistics	*-2 ln (L)*	6113.6		6109.8	
	AIC	6139.6		6137.8	
	BIC	6187.8		6189.7	

Note: $\sigma_1^2, \sigma_2^2, \sigma_3^2$ are the variance for random parameter u_{1i}, u_{2i}, u_{3i}; σ^2 is the residual variance of the model; σ_{21}, σ_{31}, σ_{32} are the covariances between paired random parameters; ρ is the correlation for the SP(POW) structure. AIC is the Akaike's information criterion; BIC is Schwarz's Bayesian information criterion; -2 Ln(L) is twice the negative log-likelihood.

Table 5.8. Parameter estimates for model [5.10] and [5.11] fitted with the SP(POW) covariance structure, based on 3780 observations from 271 trees for jack pine.

	Parameter	Model [5.10] Estimate	Model [5.10] Se	Model [5.11] Estimate	Model [5.11] Se
Fixed effect	b_0	0.9625	0.0022	0.9626	0.0022
	b_1	-0.0432	0.0100	-0.0588	0.0106
	b_2	0.3940	0.0146	0.3937	0.0145
	b_3	-0.0153	0.0043	-0.0145	0.0043
	b_4			0.0366	0.0091
	b5	-0.0010	0.0001	-0.0010	0.0001
Variance components	σ_1^2	0.003611	0.000840	0.003500	0.000818
	σ_{21}	-0.006906	0.001546	-0.006733	0.001519
	σ_2^2	0.017958	0.003160	0.017952	0.003145
	σ_{31}	0.001176	0.000239	0.001173	0.000237
	σ_{32}	-0.002003	0.000430	-0.002017	0.000428
	σ_3^2	0.000412	0.000072	0.000416	0.000072
Correlation	ρ	0.622661	0.024969	0.622624	0.025033
	σ^2	0.528315	0.033567	0.527110	0.033573
Comparison criteria	-2 Ln(L)	6862.5		6848.6	
	AIC	6888.5		6876.6	
	BIC	6935.4		6927.0	

Note: $\sigma_1^2, \sigma_2^2, \sigma_3^2$ are the variance for random parameter u_{1i}, u_{2i}, u_{3i}; σ^2 is the residual variance of the model; σ_{21}, σ_{31}, σ_{32} are the covariances between paired random parameters; ρ is the correlation for the SP(POW) structure. AIC is the Akaike's information criterion; BIC is Schwarz's Bayesian information criterion; -2 Ln(L) is twice the negative log-likelihood.

Autocorrelation and Residuals

Normalized residuals (model [5.11]) plotted as a function of predicted bole diameter values (inside bark, DIB) for black spruce and jack pine are shown in **Figure 5.4**. The approximately horizontal bands of the data points indicate approximate homogeneity of residuals for both black spruce and jack pine.

Correlations between lagged normalized residuals for model [5.11], fitted using NLS and NLMM (mixed-effects) models with AR(1), SP(POW) and TOEP(4) structures, are presented in **Table 5.9**. For the NLS model fits, there was significant positive residual autocorrelation for the first 9-lag periods for black spruce, and for all 10-lag periods for jack pine. These autocorrelations are most likely attributable to inter-tree variation in model parameters, which are not accommodated in the NLS model (c.f. **Figures 5.2 – 5.3**). Similar results were also found for black spruce and jack pine models [5.10] (results not presented).

Autocorrelations were significantly reduced using the mixed-effects model approach (regardless of covariance structure) for black spruce and jack pine models [5.11] (**Table 5.9**). Only a few of the lag correlations were statistically significant ($P < 0.01$), and then only marginally so. Among the three covariance structures examined, SP(POW) had fewer statistically significant lag correlations compared to AR(1) and TOEP(4). Similar results were also found for black spruce and jack pine models [5.10] (results not presented).

The first three lag residual plots for black spruce and jack pine models [5.11], fit using the nonlinear mixed-effects model (NLMM) approach with SP(POW) covariance structure, are shown in **Figures 5.5** and **5.6** respectively. The results indicate that the NLMM substantially reduced residual autocorrelation in both black spruce (compare **Figures 5.2** and **5.5**) and jack pine (compare **Figures 5.3** and **5.6**). Similar results were observed for black spruce and jack pine models [5.10] (results not presented).

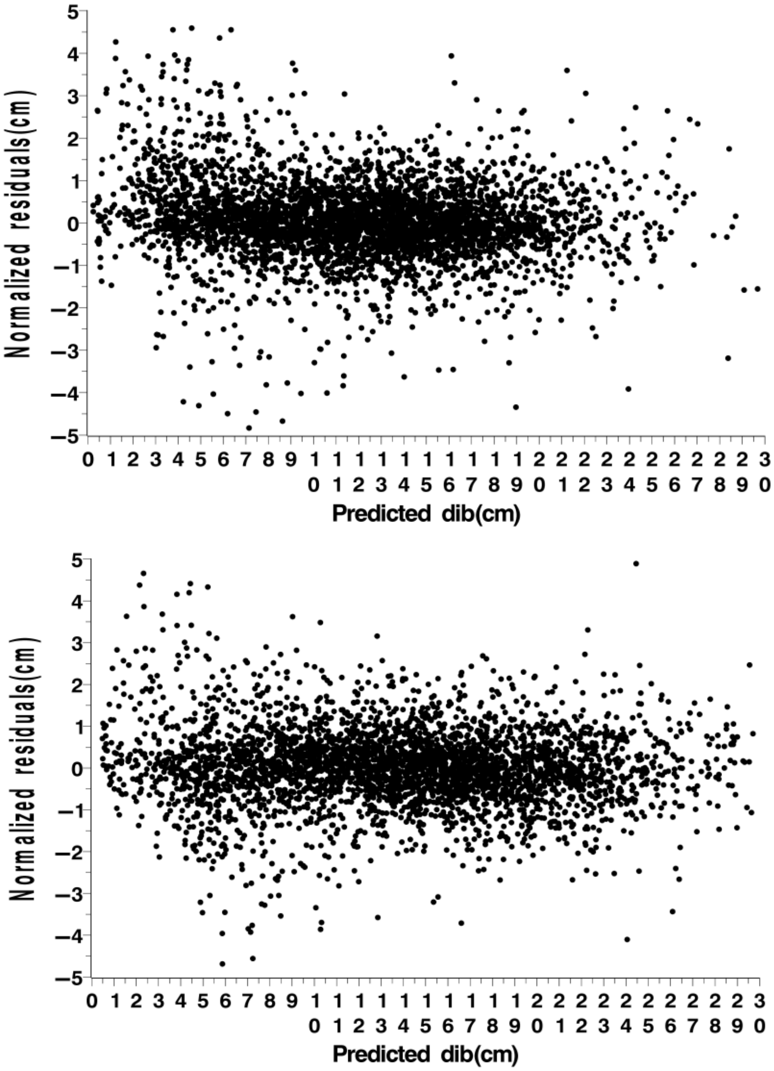


Figure 5.4. Normalized residuals vs predicted DIB for model [5.11] fitted by nonlinear mixed-effects modeling (NLMM) technique for black spruce (upper) and jack pine (lower).

Table 5.9. Correlation coefficients of 10 lagged normalized residuals for model [5.11] fitted by the NLS and NLMM with the AR(1), SP(POW) and TOEP(4) covariance structures for black spruce (BS) and jack pine (JP).

Species	Lag	***n***	**NLS**	**NLMM**			
				AR(1)	**SP(POW)**	**TOEP(4)**	ρ
BS	1	3496	**0.79**	**-0.05**	**-0.086**	-0.035	0.044
	2	3195	**0.655**	**0.053**	0.044	0.044	0.046
	3	2894	**0.557**	0.013	0.004	**0.079**	0.048
	4	2594	**0.478**	**0.06**	**0.068**	**0.089**	0.051
	5	2294	**0.405**	0.033	0.034	0.005	0.054
	6	1994	**0.329**	0.024	0.032	0.013	0.058
	7	1695	**0.255**	0.002	0.023	0.006	0.063
	8	1398	**0.173**	-0.036	-0.037	-0.037	0.069
	9	1109	**0.112**	-0.006	-0.013	-0.014	0.077
	10	833	0.068	-0.038	-0.048	-0.042	0.089
JP	1	3238	**0.77**	**-0.108**	-0.037	**-0.063**	0.045
	2	2967	**0.67**	**0.083**	0.033	**0.055**	0.047
	3	2696	**0.583**	**0.097**	**0.074**	**0.087**	0.05
	4	2425	**0.499**	0.038	0.042	**0.103**	0.052
	5	2156	**0.431**	0.034	0.042	0.011	0.056
	6	1887	**0.354**	0.005	-0.011	-0.011	0.059
	7	1619	**0.284**	0.01	0.012	0.01	0.064
	8	1356	**0.253**	0.036	0.023	0.044	0.07
	9	1097	**0.216**	0.061	0.045	0.062	0.078
	10	848	**0.193**	-0.039	-0.067	-0.033	0.089

Note: ρ - Absolute critical value for the 99% confidence interval for each sample size (n); NLS – nonlinear least squares approach; NLMM –Nonlinear mixed-effects model approach; values in boldface indicate significant correlation.

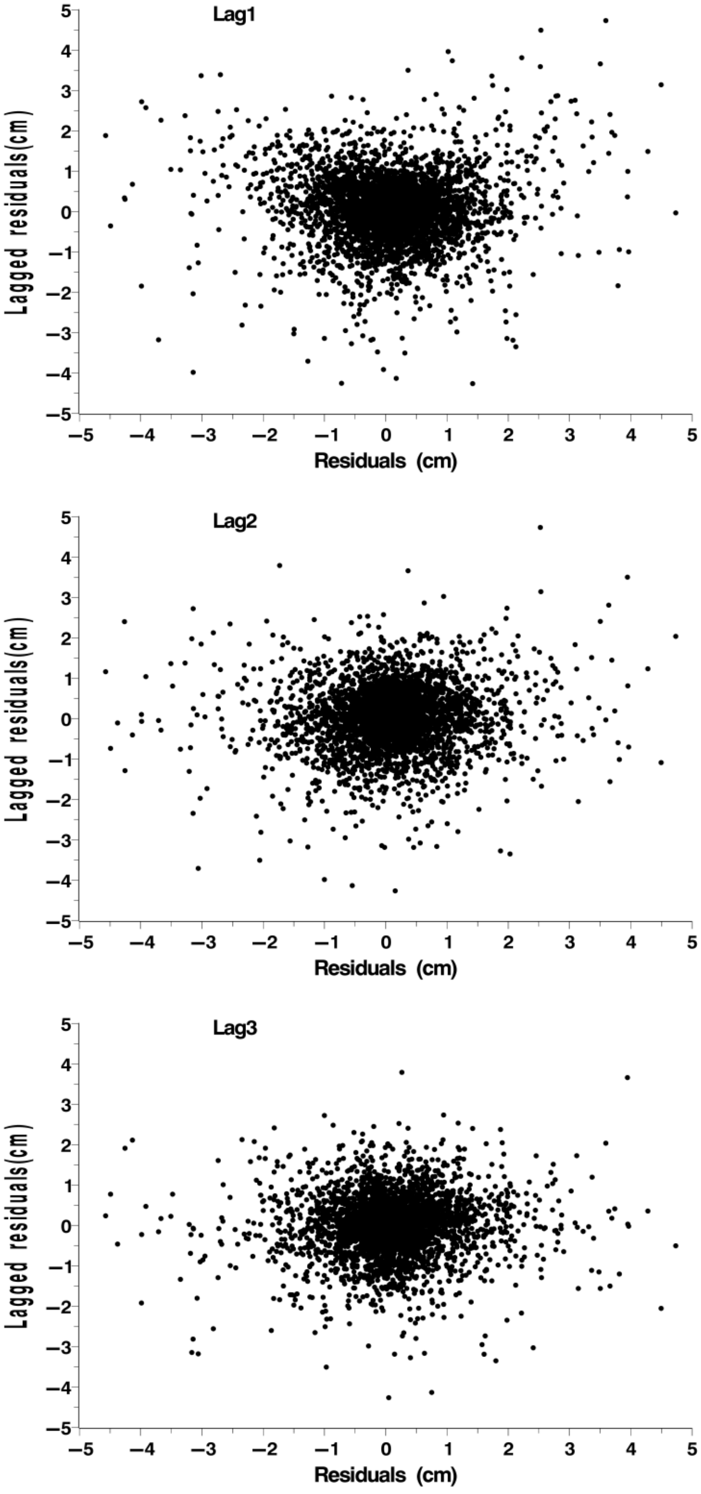


Figure 5.5. Lagged residuals (lag 1, lag 2 and lag 3, from top to bottom) for model [5.11] fitted by nonlinear mixed-effects modeling (NLMM) technique for black spruce. Correlation coefficients are -0.086, 0.044 and 0.004, respectively.

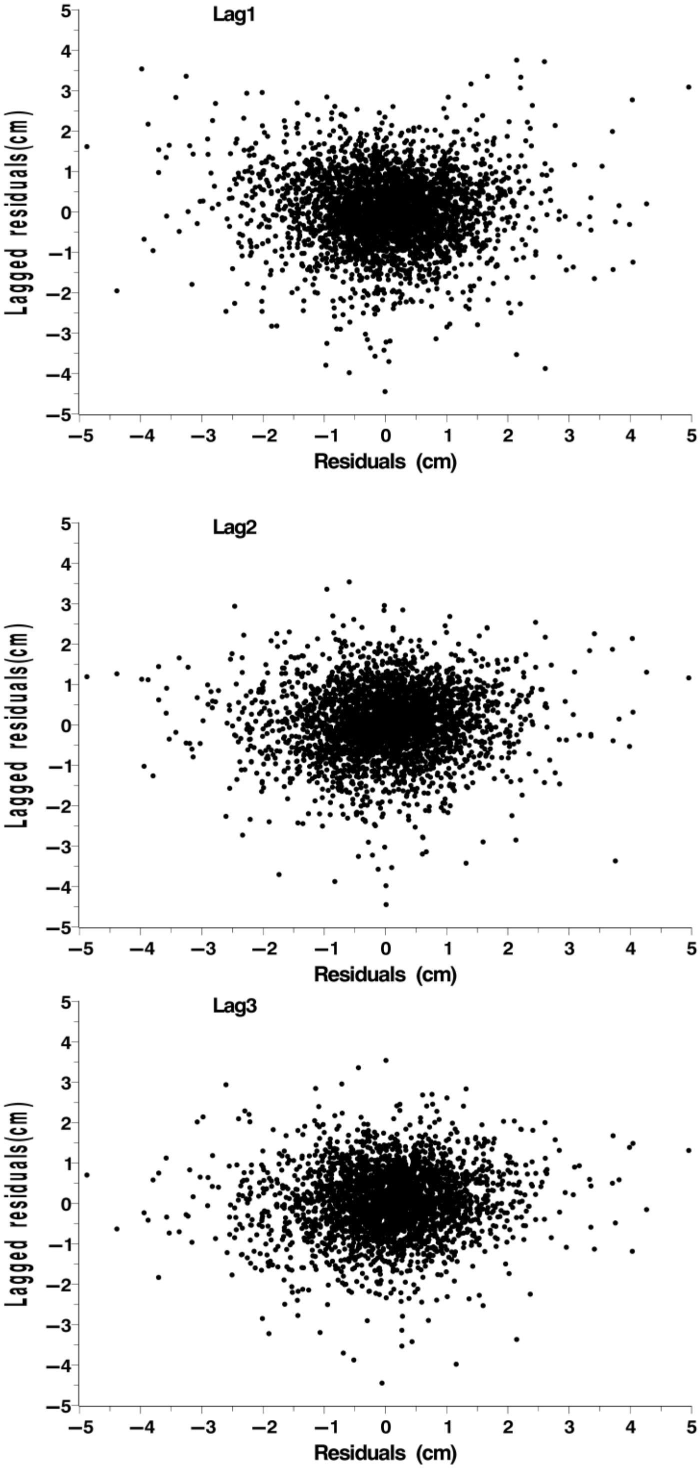


Figure 5.6. Lagged residuals (lag 1, lag 2 and lag 3, from top to bottom) for model [5.11] fitted by nonlinear mixed-effects modeling (NLMM) technique for jack pine. Correlation coefficients are -0.037, 0.033 and 0.074, respectively.

Individual Bole Diameter Predictions

The root mean square error (RMSE) and other fit statistics were used to select the best prior measurements under each of the three scenarios A, B and C. Under scenario A (i.e. a single prior diameter measure per tree), selection of the prior diameter measure at bole height = 6.5 m (section 8) resulted in the lowest RMSE values for both models [5.10] and [5.11], in both the black spruce and jack pine models. Under scenario B (i.e. two prior diameter measures per tree, one below and one above DBH height), selection of prior diameter measures at bole height of 0.3 m (section 1) and 6.5 m (section 8) resulted in the lowest RMSE values for both models and both species. Under scenario C (i.e three prior diameter measurements per tree, one below and two above DBH height), selection of prior diameter measures at bole heights of 0.3 m (section 1), 2.6 m (section 5) and 6.5 m (section 8) resulted in the lowest RMSE values for both models and both species.

Fit statistics for bole taper models [5.10] and [5.11], using each of the three selected scenarios (i.e. models with diameters at sections (8), (1,8), and (1,5,8) as prior measures), are summarized in **Table 5.10** for black spruce and **Table 5.11** for jack pine. For black spruce models [5.10] and [5.11], RMSE values were highest with no prior measurements, and declined as the number of prior measurements increased. However, the largest decline in RMSE occurred between models not including priors and those including a single prior measurement. For example, in model [5.10] for the whole tree data ("ALL" in **Table 5.10**), RMSE declined from 0.786 to 0.665 when a single prior measure (diameter at section 8 = 6.5 m) was included, but RMSE reductions were much smaller when two prior measures (RMSE = 0.608) or three prior measures (RMSE = 0.605) were used. These trends are illustrated graphically in **Figure 5.7a**. In general, values for mean error ($\bar{e}$) and mean percent error ($\bar{e}$%) were little affected by the inclusion of prior measures in the models (**Table 5.10**).

Similar results were obtained for jack pine. For model [5.10] whole tree data ("ALL" in **Table 5.11**), the RMSE declined from 0.777 to 0.664 when a single prior measure (diameter at 6.5 m) was included, but RMSE reductions were much smaller when two prior measures (RMSE = 0.608) or three prior measures (RMSE = 0.605) were used. These RMSE trends are illustrated graphically in **Figure 5.7b**. As with black spruce, values for mean error ($\bar{e}$) and mean percent error ($\bar{e}$%) were little affected by the inclusion of prior measures in the models (**Table 5.11**).

For both black spruce and jack pine, model prediction errors (RMSE values) are lowest at the tree base and increase with relative height along the bole (**Figure 5.7**). This is attributable to the fact that diameter at breast height (DBH = 1.3 m), a measure taken near the tree base, is used as a predictor variable in bole taper models. Mixed-effect model prediction errors were reduced when a single prior measure was included, but including additional prior measures had little effect on RMSE values in both the black spruce and jack pine bole taper models (**Figure 5.7**).

Table 5.10. Validation results in predicting diameter inside bark from [5.10] and [5.11] that used (8), (1,8) and (1,5,8) diameters as prior information along with the corresponding values from the models without any prior information for black spruce.

			Model [5.10]				Model [5.11]			
Stat	**Z**	***n***	**No prior**	**8**	**1,8**	**1,5,8**	**No prior**	**8**	**1,8**	**1,5,8**
MAE	0.0-0.2	365	0.386	0.384	0.296	0.294	0.387	0.384	0.298	0.295
	0.2-0.4	183	0.43	0.332	0.333	0.328	0.429	0.332	0.333	0.328
	0.4-0.6	186	0.592	0.37	0.363	0.361	0.588	0.372	0.365	0.363
	0.6-0.8	181	0.672	0.543	0.519	0.516	0.664	0.54	0.52	0.515
	0.8-1.0	122	0.964	0.914	0.914	0.917	0.96	0.914	0.913	0.918
	ALL	1037	0.549	0.462	0.426	0.424	0.546	0.462	0.427	0.425
RMSE	0.0-0.2	365	0.578	0.578	0.405	0.403	0.576	0.576	0.406	0.404
	0.2-0.4	183	0.601	0.446	0.446	0.44	0.594	0.445	0.446	0.44
	0.4-0.6	186	0.825	0.502	0.492	0.489	0.808	0.501	0.492	0.488
	0.6-0.8	181	0.911	0.717	0.685	0.679	0.894	0.714	0.686	0.678
	0.8-1.0	122	1.21	1.155	1.141	1.143	1.203	1.154	1.141	1.143
	ALL	1037	0.786	0.665	0.608	0.605	0.777	0.664	0.608	0.605
$\bar{e}$	0.0-0.2	365	0.089	0.087	0.051	0.058	0.087	0.085	0.051	0.058
	0.2-0.4	183	0.1	0.098	0.099	0.094	0.107	0.102	0.102	0.097
	0.4-0.6	186	-0.09	-0.069	-0.051	-0.047	-0.077	-0.064	-0.05	-0.044
	0.6-0.8	181	-0.127	-0.123	-0.084	-0.074	-0.115	-0.118	-0.085	-0.073
	0.8-1.0	122	0.298	0.318	0.357	0.367	0.309	0.321	0.354	0.367
	ALL	1037	0.046	0.051	0.053	0.059	0.052	0.054	0.054	0.06
$\bar{e}$ %	0.0-0.2	365	0.554	0.544	0.316	0.359	0.542	0.531	0.315	0.36
	0.2-0.4	183	0.745	0.729	0.738	0.701	0.797	0.756	0.758	0.72
	0.4-0.6	186	-0.821	-0.632	-0.469	-0.432	-0.704	-0.58	-0.453	-0.404
	0.6-0.8	181	-1.638	-1.591	-1.089	-0.96	-1.489	-1.526	-1.102	-0.941
	0.8-1.0	122	6.596	7.021	7.883	8.121	6.83	7.091	7.816	8.111
	ALL	1037	0.386	0.434	0.45	0.494	0.437	0.452	0.452	0.505

Note: RMSE - root mean square error of prediction; $\bar{e}$ - mean bias; MAE - mean absolute error; $\bar{e}$ %- mean bias %; *n* – total number of observations; Z is the relative height class.

Table 5.11. Validation results in predicting diameter inside bark from [5.10] and [5.11] that used (8), (1,8) and (1,5,8) diameters as prior information along with the corresponding values from the models without any prior information for jack pine.

Stat	**Z**	***n***	**Model [5.10]**				**Model [5.11]**			
			No prior	**8**	**1,8**	**1,5,8**	**No prior**	**8**	**1,8**	**1,5,8**
MAE	0.0-0.2	334	0.357	0.354	0.293	0.293	0.354	0.353	0.295	0.295
	0.2-0.4	176	0.57	0.456	0.457	0.458	0.561	0.443	0.444	0.446
	0.4-0.6	164	0.729	0.484	0.484	0.491	0.71	0.462	0.46	0.465
	0.6-0.8	169	1.032	0.866	0.868	0.861	1.024	0.869	0.877	0.869
	0.8-1.0	112	1.205	1.124	1.124	1.117	1.204	1.122	1.124	1.119
	ALL	955	0.679	0.576	0.555	0.554	0.672	0.57	0.551	0.55
RMSE	0.0-0.2	334	0.479	0.472	0.384	0.383	0.481	0.473	0.388	0.387
	0.2-0.4	176	0.761	0.596	0.598	0.599	0.745	0.58	0.58	0.584
	0.4-0.6	164	0.9	0.621	0.619	0.623	0.879	0.606	0.601	0.603
	0.6-0.8	169	1.329	1.1	1.101	1.091	1.319	1.103	1.11	1.101
	0.8-1.0	112	1.606	1.477	1.477	1.471	1.599	1.477	1.482	1.477
	ALL	955	0.967	0.822	0.806	0.803	0.958	0.819	0.805	0.803
$\bar{e}$	0.0-0.2	334	-0.04	-0.035	-0.034	-0.033	-0.046	-0.041	-0.036	-0.034
	0.2-0.4	176	-0.036	-0.009	-0.009	-0.009	-0.02	0.003	0.005	0.006
	0.4-0.6	164	-0.058	-0.01	-0.007	-0.009	-0.047	-0.004	-0.002	-0.002
	0.6-0.8	169	-0.035	0.052	0.056	0.053	-0.028	0.054	0.054	0.053
	0.8-1.0	112	0.184	0.186	0.187	0.184	0.186	0.185	0.181	0.179
	ALL	955	-0.015	0.015	0.017	0.016	-0.011	0.017	0.019	0.019
$\bar{e}$ %	0.0-0.2	334	-0.218	-0.19	-0.183	-0.177	-0.247	-0.221	-0.194	-0.186
	0.2-0.4	176	-0.229	-0.06	-0.057	-0.057	-0.128	0.017	0.035	0.037
	0.4-0.6	164	-0.446	-0.073	-0.057	-0.07	-0.36	-0.03	-0.016	-0.017
	0.6-0.8	169	-0.361	0.54	0.585	0.556	-0.292	0.563	0.565	0.557
	0.8-1.0	112	3.577	3.622	3.642	3.583	3.619	3.585	3.51	3.484
	ALL	955	-0.109	0.111	0.124	0.119	-0.078	0.121	0.137	0.138

Note: RMSE - root mean square error of prediction; $\bar{e}$ - mean bias; MAE - mean absolute error; $\bar{e}$ %- mean bias %; n – total number of observations; Z is the relative height class.

(a) Black Spruce

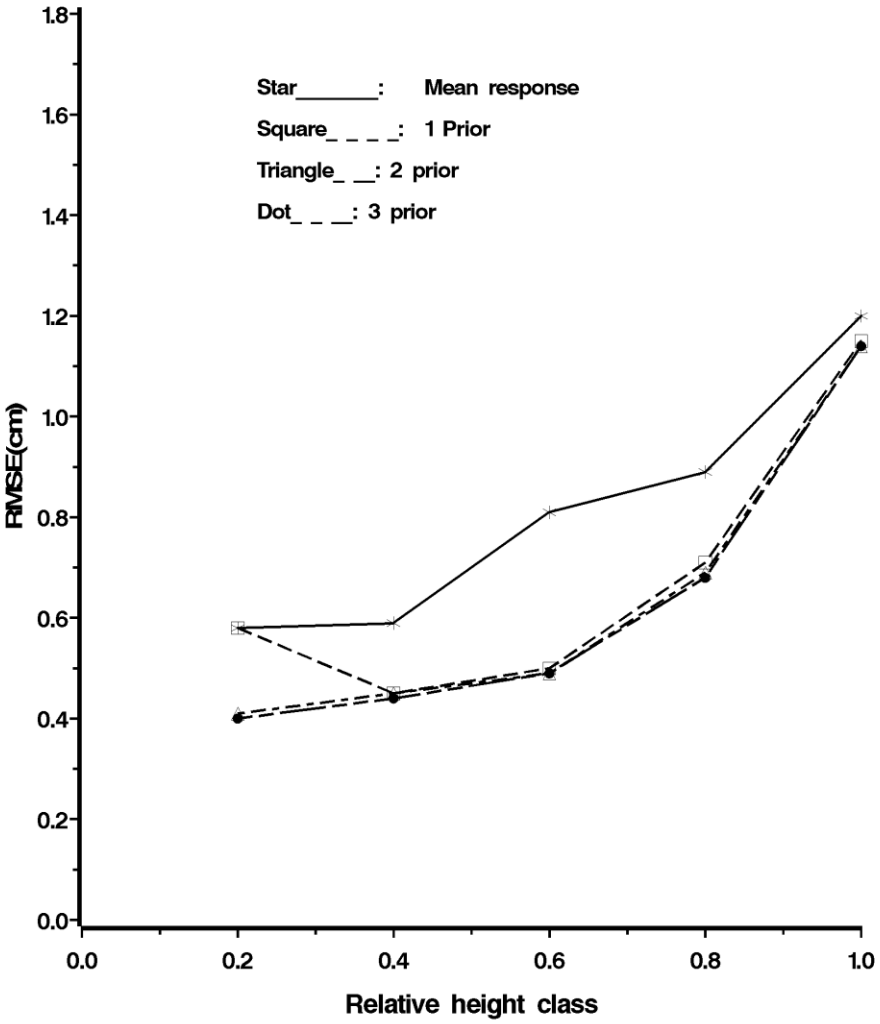


Figure 5.7 (a). Black Spruce: Root mean square error (RMSE) vs tree relative height classes on tree diameter predictions from [5.11] using nonlinear mixed-effects modeling (NLMM) technique with non prior (mean response), one, two and three prior diameter measurements.

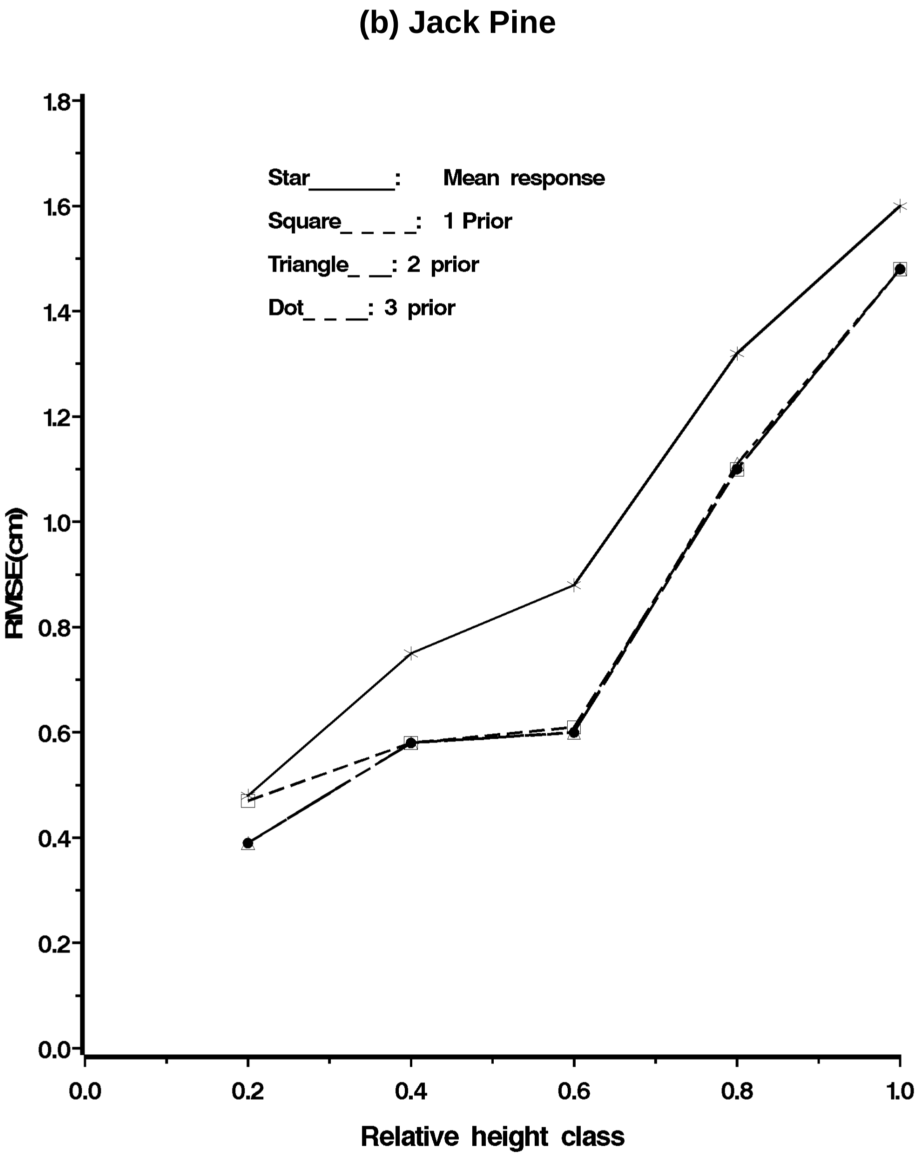


Figure 5.7 (b). Jack Pine: Root mean square error (RMSE) vs tree relative height classes on tree diameter predictions from [5.11] using nonlinear mixed-effects modeling (NLMM) technique with non prior (mean response), one, two and three prior diameter measurements.

Individual Bole Volume Predictions

Fit statistics for the prediction of tree bole volume using models [5.10] and [5.11], with and without the inclusion of prior measurements (scenarios A, B and C), are summarized in **Table 5.12** for black spruce and **Table 5.13** for jack pine. In general, results were similar to those obtained for bole diameter predictions (summarized above). For black spruce models [5.10] and [5.11], RMSE values were highest for the mixed-models with no prior measurements and declined as the number of prior measurements increased. However, the addition of more than one prior measurement did little to improve model prediction errors. For example, in model [5.10] for the entire bole ("ALL" in Table 5.12), RMSE declined from 0.152 to 0.104 by including a single prior measure, but RMSE reductions were much less when two prior measures (RMSE = 0.096) or three prior measures (RMSE = 0.095) were included (**Figure 5.8a**). Mean error ($\bar{e}$) and mean percent error ($\bar{e}$%) values tended to be slightly higher in models that included prior measures, but trends varied with height along the tree bole (**Table 5.12**).

Similar results were obtained for jack pine (**Table 5.13**). Inclusion of a single prior measurement reduced the value of RMSE from 0.194 to 0.149, but including additional prior measurements had little effect (RMSE = 0.147 and 0.146 for two or three prior measures respectively, **Figure 5.8b**). In general, the inclusion of prior measurements reduced the mean percent error ($\bar{e}$%), except for estimates at the top of the tree (relative height > 0.6).

For both black spruce and jack pine, bole volume predictions using model [5.11] without prior measures were most accurate at relative height classes 0.2 and 1.0, i.e. at the base and top of the bole (**Figure 5.8**). By including prior measures, the RMSE declined and resulted in comparatively more uniform predictions errors along the bole length (**Figure 5.8**).

For both black spruce and jack pine, the RMSE values for bole volume predictions were very similar for models [5.10] and [5.11] (**Tables 5.12** and **5.13**). This indicates that including the dependent variable crown ratio (added to model [5.10] to create model [5.11]) resulted in little improvement in taper model prediction. This demonstrates that crown ratio is not a necessary variable to include in Manitoba black spruce and jack pine bole taper models.

Individual Tree Profiles

The nonlinear least squares (NLS) and nonlinear mixed-effects (NLMM) models [5.11] were used to obtain bole taper predictions for two randomly chosen representative trees, one black spruce and one jack pine. Three NLMM models were compared, utilizing one (section 8), two (sections 1 and 8), and three (sections 1, 5 and 8) prior measures. The randomly selected black spruce tree had DBH = 20.7 cm, a total height H = 18.1 m, and a crown ratio of 0.54. The randomly selected jack pine tree had DBH = 16.2 cm, a total height H = 14.0 m, and a crown ratio of 0.64. The observed and fitted model values for the black spruce tree are shown in **Figure 5.9**, and for the jack pine tree in **Figure 5.10**.

In general, the models accurately predicted tree diameters in the lower portion of the bole. In both black spruce models diameter in the uppermost portion of the bole (relative height > 0.8) was underestimated. This discrepancy between observed and fitted data likely reflects the difficulty in accurately measuring bole diameter in the canopy portion of a tree.

For both black spruce and jack pine, the NLMM approach produced a better fit to the observed data than did the NLS modeling approach (**Figures 5.9** and **5.10**). Using a single prior measure (at height 6.5 m) to predict random effects parameters was sufficient to accurately model the bole taper profiles of black spruce (compare **Figures 5.9 a** – **c**) and jack pine (compare **Figures 5.10 a – c**).

Table 5.12. Validation results in predicting total tree volume by relative class from [5.10] and [5.11] that used (8), (1, 8) and (1, 5, 8) diameters as prior information along with the corresponding values from the models without any prior information for black spruce.

Stat	**Z**	***n***	**Model [5.10]**				**Model [5.11]**			
			No Prior	**8**	**1,8**	**1,5,8**	**No Prior**	**8**	**1,8**	**1,5,8**
MAE X10^4	0.0-0.2	365	4.701	4.643	3.346	3.318	4.703	4.638	3.362	3.336
	0.2-0.4	183	10.855	8.172	8.196	8.041	10.898	8.142	8.181	8.005
	0.4-0.6	186	13.751	7.999	7.841	7.753	13.512	7.995	7.882	7.774
	0.6-0.8	181	11.784	8.673	8.208	8.14	11.577	8.614	8.224	8.147
	0.8-1.0	122	8.873	7.587	7.54	7.567	8.789	7.589	7.526	7.557
	ALL	1037	9.138	6.917	6.35	6.289	9.057	6.9	6.362	6.292
RMSE X10^2	0.0-0.2	365	0.077	0.077	0.054	0.054	0.077	0.077	0.055	0.054
	0.2-0.4	183	0.182	0.123	0.123	0.12	0.178	0.122	0.123	0.119
	0.4-0.6	186	0.21	0.111	0.108	0.107	0.205	0.111	0.108	0.107
	0.6-0.8	181	0.178	0.126	0.116	0.115	0.174	0.125	0.116	0.115
	0.8-1.0	122	0.121	0.1	0.097	0.097	0.119	0.1	0.097	0.097
	ALL	1037	0.152	0.104	0.096	0.095	0.148	0.104	0.096	0.095
$\bar{e}$ X10^4	0.0-0.2	365	1.929	1.895	1.275	1.364	1.9	1.864	1.276	1.366
	0.2-0.4	183	2.621	2.997	3.076	2.865	2.882	3.133	3.187	2.964
	0.4-0.6	186	-2.627	-1.606	-1.166	-1.092	-2.247	-1.45	-1.114	-1.012
	0.6-0.8	181	-3.668	-3.21	-2.382	-2.185	-3.387	-3.1	-2.407	-2.161
	0.8-1.0	122	1.514	2.054	2.593	2.746	1.686	2.097	2.547	2.736
	ALL	1037	0.208	0.589	0.672	0.731	0.382	0.655	0.691	0.767
$\bar{e}$ %	0.0-0.2	365	1.77	1.739	1.171	1.252	1.744	1.711	1.171	1.253
	0.2-0.4	183	1.255	1.434	1.472	1.371	1.379	1.5	1.525	1.419
	0.4-0.6	186	-1.852	-1.132	-0.822	-0.77	-1.584	-1.022	-0.786	-0.713
	0.6-0.8	181	-4.753	-4.16	-3.087	-2.832	-4.389	-4.018	-3.12	-2.801
	0.8-1.0	122	4.83	6.553	8.273	8.761	5.381	6.693	8.128	8.73
	ALL	1037	0.177	0.5	0.57	0.621	0.324	0.556	0.587	0.651

Note: RMSE - root mean square error of prediction; ē - mean bias; MAE - mean absolute error; ē%- mean bias %; n – total number of observations; Z is the relative height class.

Table 5.13. Validation results in predicting total tree volume by relative class from [5.10] and [5.11] that used (8), (1, 8) and (1, 5, 8) diameters as prior information along with the corresponding values from the models without any prior information for jack pine.

Stat	**Z**	***n***	**[5.10]**				**[5.11]**			
			No Prior	**8**	**1,8**	**1,5,8**	**No Prior**	**8**	**1,8**	**1,5,8**
MAEX10^4	0.0-0.2	334	4.691	4.607	3.613	3.615	4.635	4.553	3.616	3.621
	0.2-0.4	176	16.215	13.091	13.049	13.014	16.070	12.966	12.960	13.044
	0.4-0.6	164	18.574	11.452	11.422	11.613	18.204	10.867	10.773	10.946
	0.6-0.8	169	18.618	14.676	14.588	14.443	18.525	14.638	14.545	14.434
	0.8-1.0	112	13.874	12.962	12.944	12.775	13.929	12.997	12.989	12.865
	All	955	12.740	10.108	9.729	9.711	12.620	9.963	9.601	9.613
RMSEX10^2	0.0-0.2	334	0.069	0.066	0.055	0.055	0.070	0.067	0.056	0.056
	0.2-0.4	176	0.233	0.183	0.183	0.183	0.231	0.180	0.180	0.181
	0.4-0.6	164	0.253	0.160	0.159	0.160	0.247	0.153	0.151	0.152
	0.6-0.8	169	0.243	0.191	0.190	0.187	0.242	0.191	0.191	0.189
	0.8-1.0	112	0.199	0.180	0.180	0.178	0.198	0.180	0.181	0.180
	All	955	0.194	0.149	0.147	0.146	0.192	0.148	0.145	0.145
$\bar{e}$ X10^4	0.0-0.2	334	-0.215	-0.089	-0.141	-0.143	-0.268	-0.151	-0.146	-0.142
	0.2-0.4	176	-2.708	-1.616	-1.662	-1.651	-2.157	-1.161	-1.144	-1.139
	0.4-0.6	164	-3.331	-1.247	-1.226	-1.326	-2.949	-1.000	-0.954	-1.007
	0.6-0.8	169	-1.175	1.201	1.294	1.162	-0.985	1.293	1.332	1.267
	0.8-1.0	112	2.777	3.036	3.044	2.954	2.815	3.026	2.974	2.925
	All	955	-1.029	0.026	0.020	-0.030	-0.842	0.145	0.159	0.135
$\bar{e}$ %	0.0-0.2	334	-0.151	-0.062	-0.099	-0.100	-0.188	-0.106	-0.102	-0.100
	0.2-0.4	176	-0.996	-0.594	-0.611	-0.607	-0.793	-0.427	-0.421	-0.419
	0.4-0.6	164	-1.686	-0.631	-0.621	-0.671	-1.492	-0.506	-0.483	-0.510
	0.6-0.8	169	-0.992	1.014	1.093	0.981	-0.832	1.092	1.124	1.070
	0.8-1.0	112	6.249	6.831	6.848	6.647	6.334	6.809	6.691	6.582
	All	955	-0.643	0.016	0.012	-0.019	-0.526	0.091	0.099	0.084

Note: RMSE - root mean square error of prediction; ē - mean bias; MAE - mean absolute error; ē%- mean bias %; n – total number of observations; Z is the relative height class.

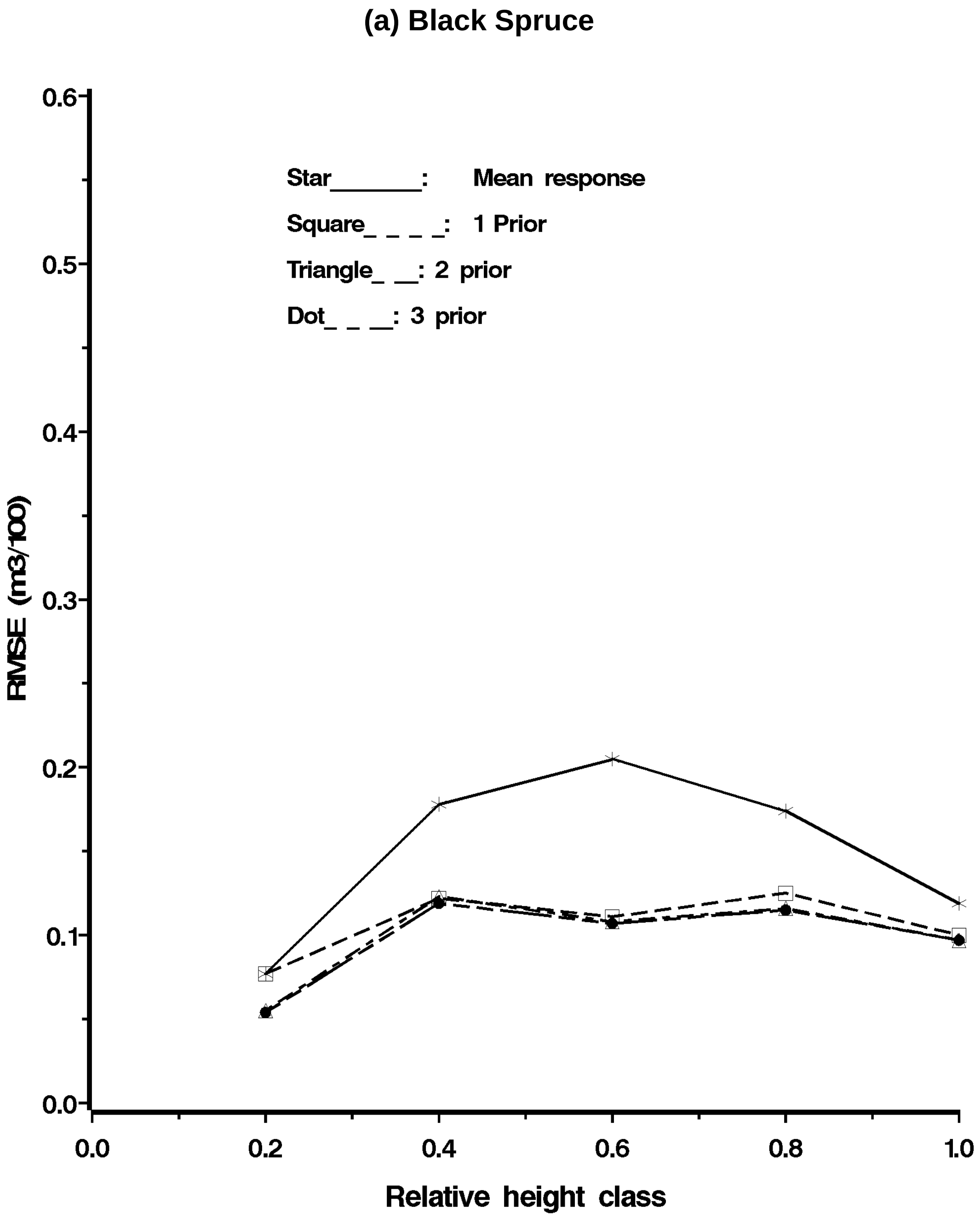


Figure 5.8. (a) Black Spruce: Root mean square error (RMSE) vs. tree relative height classes on tree volume predictions from [5.11] using nonlinear mixed-effects modeling (NLMM) technique with no prior (mean response), and one, two and three prior diameter measurements.

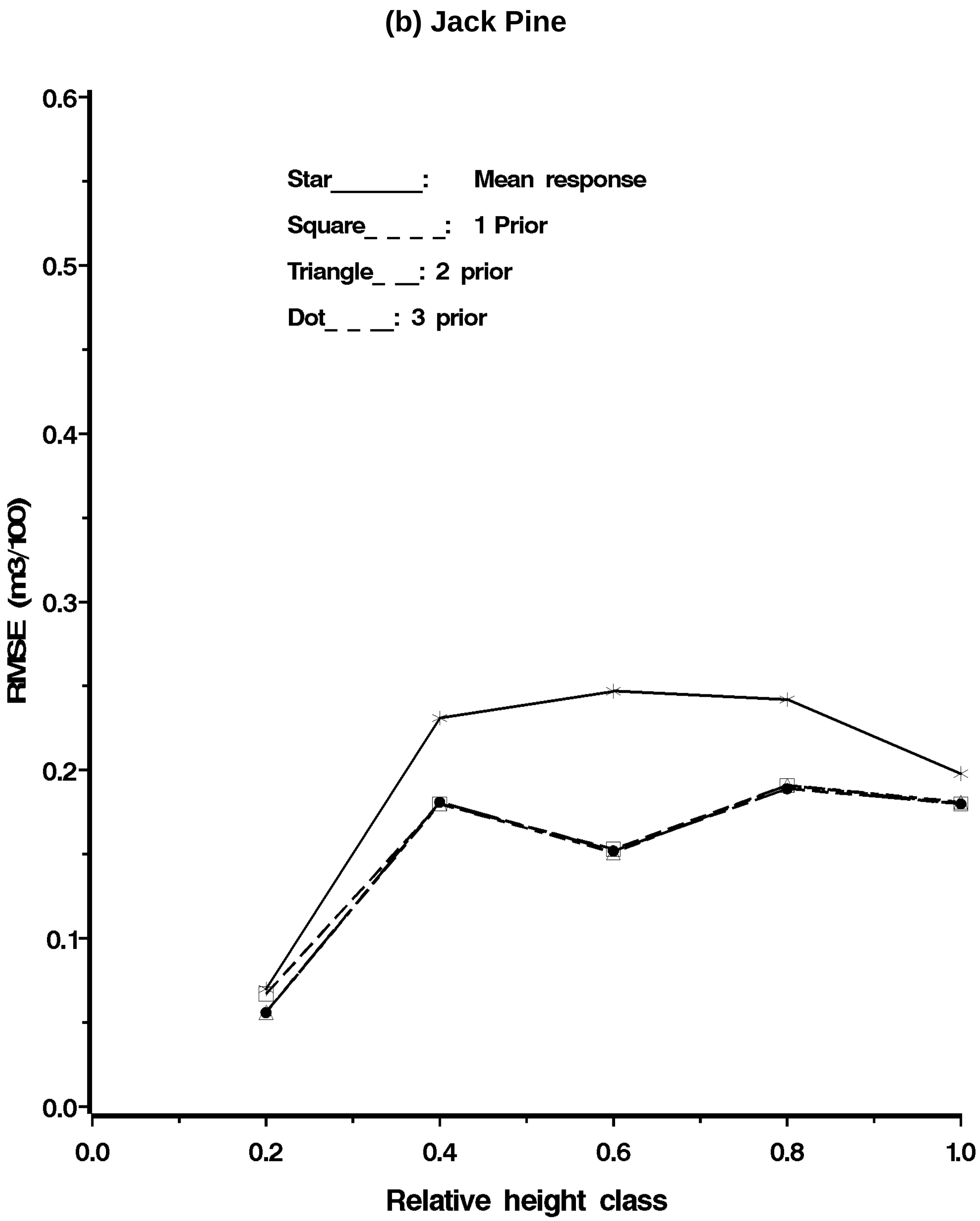


Figure 5.8 (b) Jack Pine: Root mean square error (RMSE) vs. tree relative height classes on tree volume predictions from [5.11] using nonlinear mixed-effects modeling (NLMM) technique with no prior (mean response), and one, two and three prior diameter measurements.

(a)

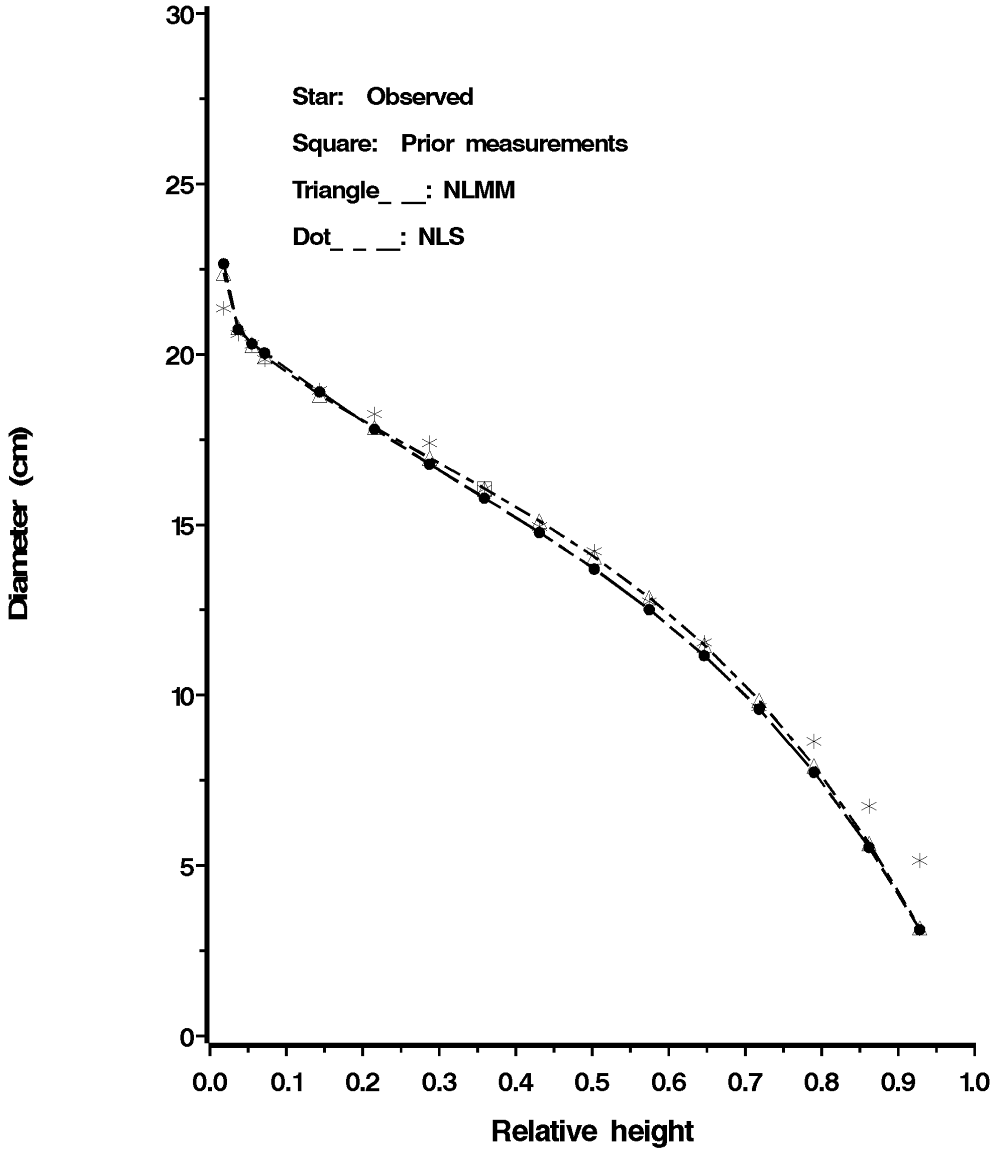


Figure 5.9. Tree profiles generated from [5.11] using a black spruce tree (DBH = 20.7 cm, total height =18.1 m and crown ratio = 0.54), fitted by nonlinear least squares (NLS) approach and nonlinear mixed-effects modeling (NLMM) technique with (a) one, (b) two, and (c) three prior diameter measurements.

(b)

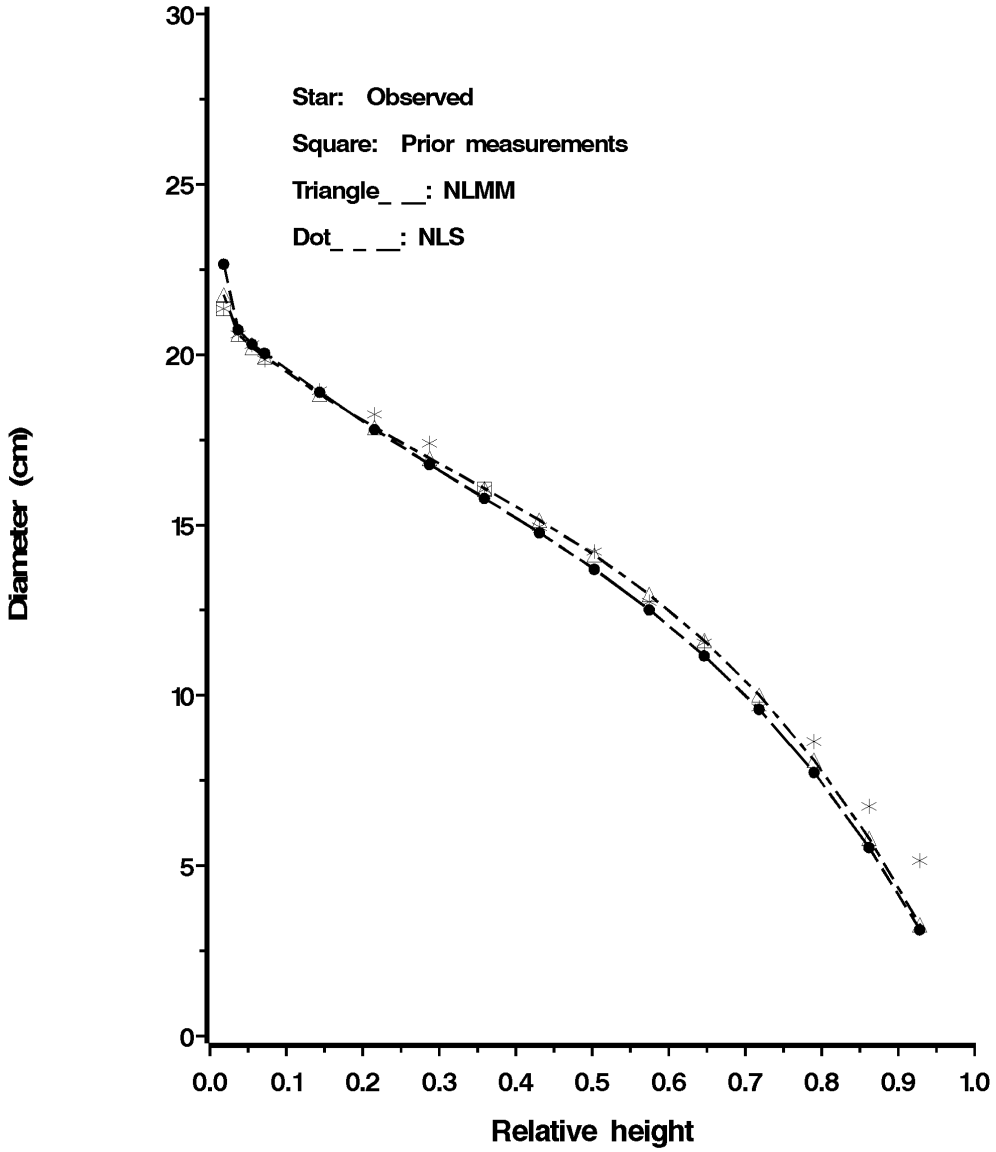


Figure 5.9 (continued).

(c)

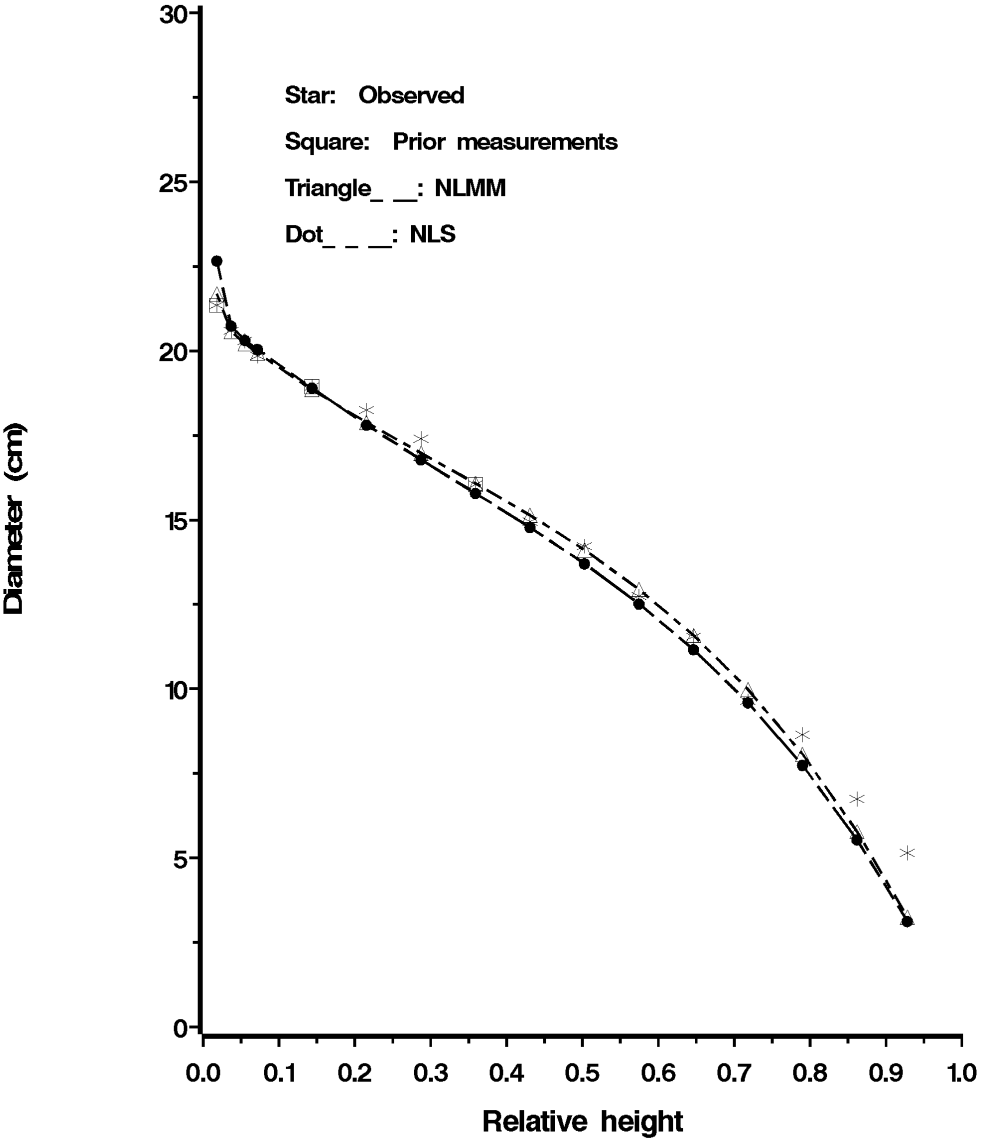


Figure 5.9 (continued).

(a)

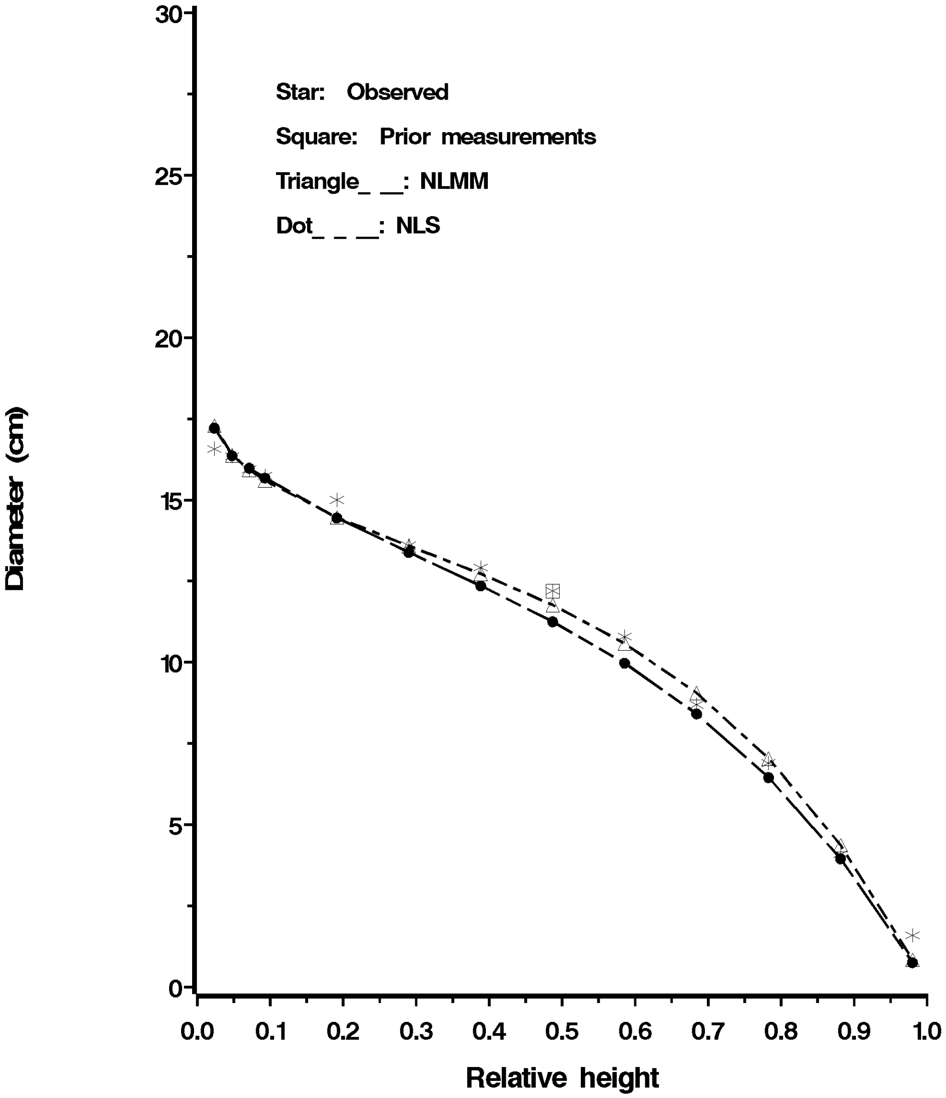


Figure 5.10. Tree profiles generated from [5.11] using a jack pine tree (DBH = 16.2 cm, total height=14.0 m, crown ratio=0.64), fitted by nonlinear least squares (NLS) approach and nonlinear mixed-effects modeling (NLMM) technique with (a) one, (b) two, and (c) three prior diameter measurements.

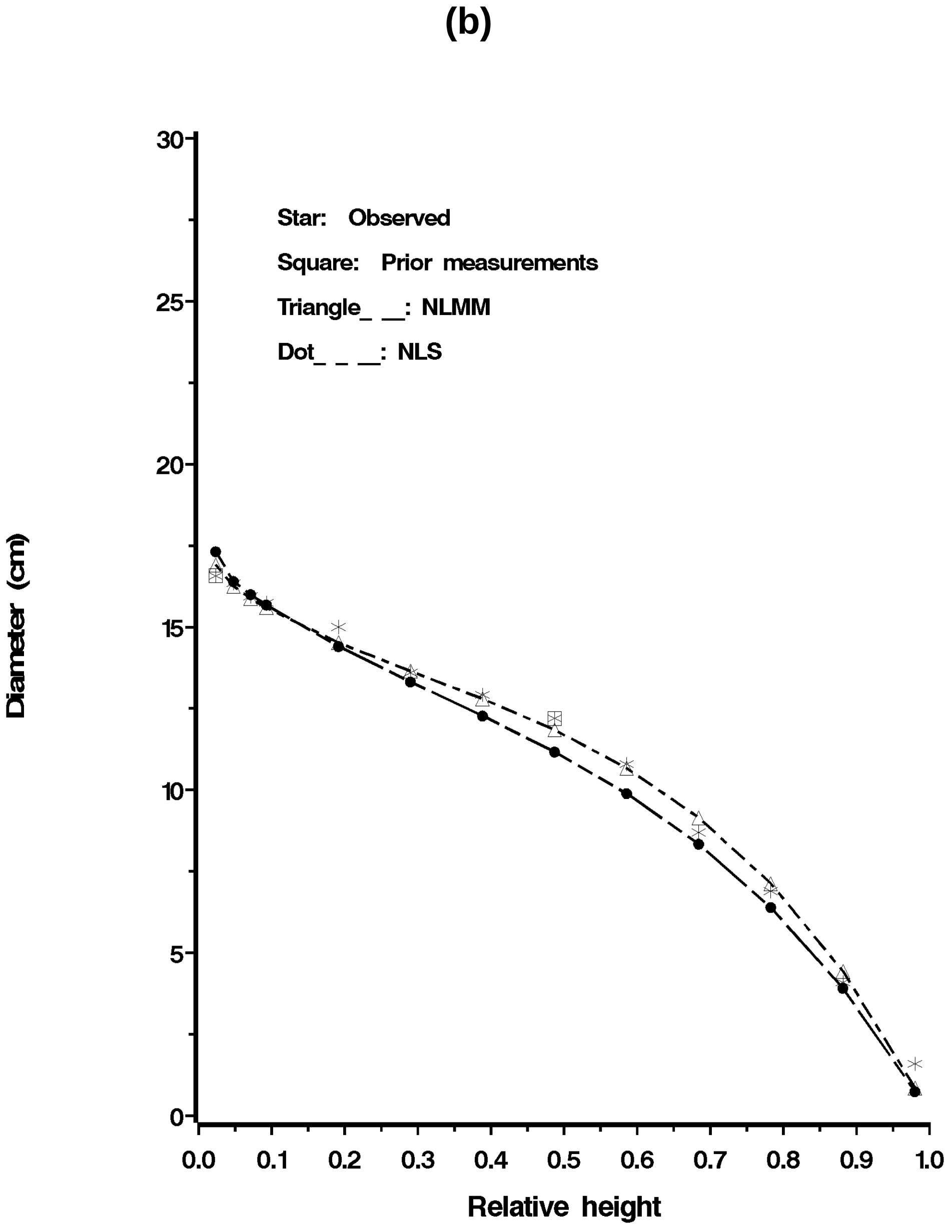


Figure 5.10 (continued).

(c)

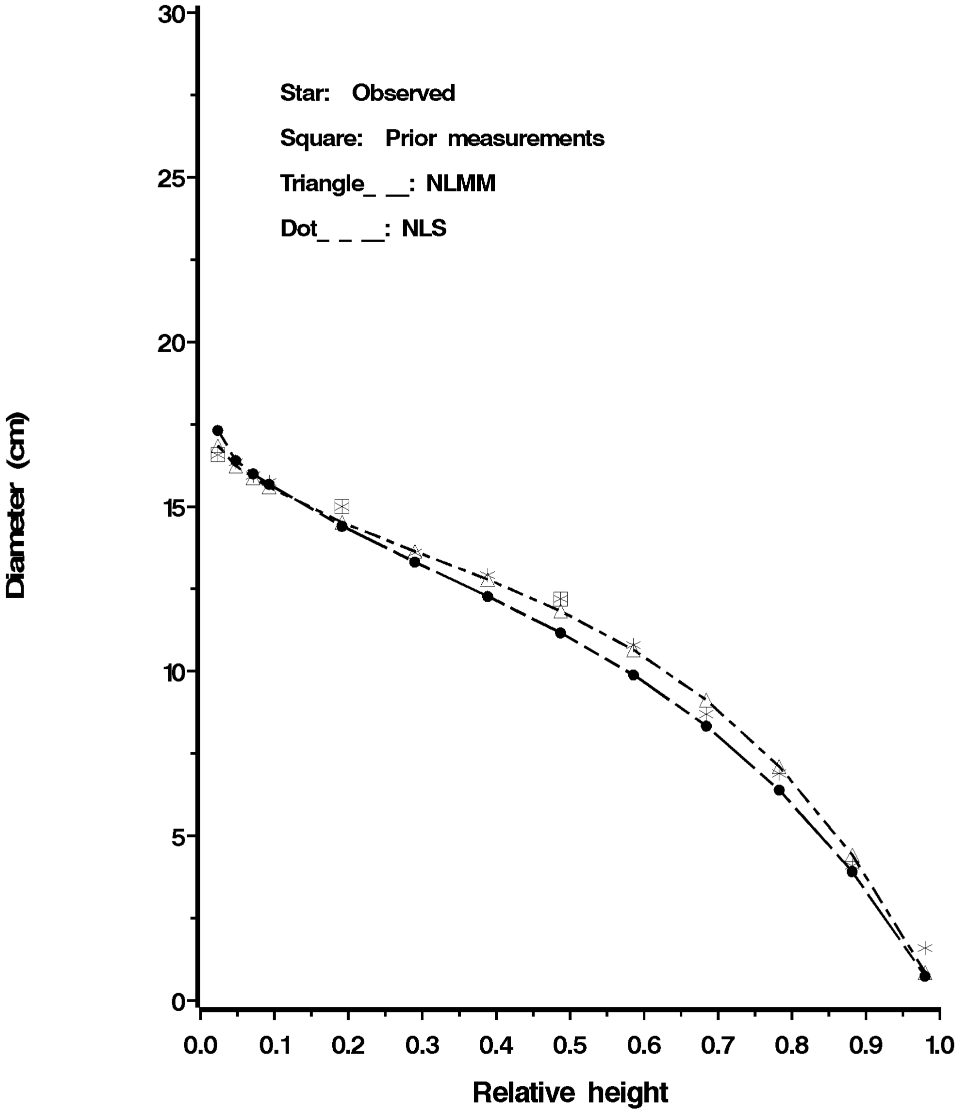


Figure 5.10 (continued).

Having demonstrated little improvement in NLMM model fitting using two or three prior measurements in the taper models for black spruce (**Figures 5.9**) and jack pine (**Figure 5.10**), additional examples of empirical model fitting using NLS and NLMM with a single prior measure were undertaken to confirm model robustness. Three additional trees of each species were randomly selected for comparison with model fits:

Black Spruce (a): DBH = 22.0 cm; H = 19.9 m; CR = 0.51
Black Spruce (b): DBH = 18.0 cm; H = 16.2 m; CR = 0.58
Black Spruce (c): DBH = 14.6 cm; H = 13.8 m; CR = 0.60

Jack Pine (a): DBH = 23.3 cm; H = 17.9 m; CR = 0.54
Jack Pine (b): DBH = 20.4 cm; H = 14.2 cm; CR = 0.52
Jack Pine (c): DBH = 15.5 cm; H = 13.7 m; CR = 0.35.

The observed and model-fitted values are shown in **Figures 5.11** and **5.12** for black spruce and jack pine respectively. The results again confirm the greater accuracy of NLMM over NLS in bole taper model fitting. For all six trees, the NLMM model closely approximated the empirical data, confirming overall model utility and robustness.

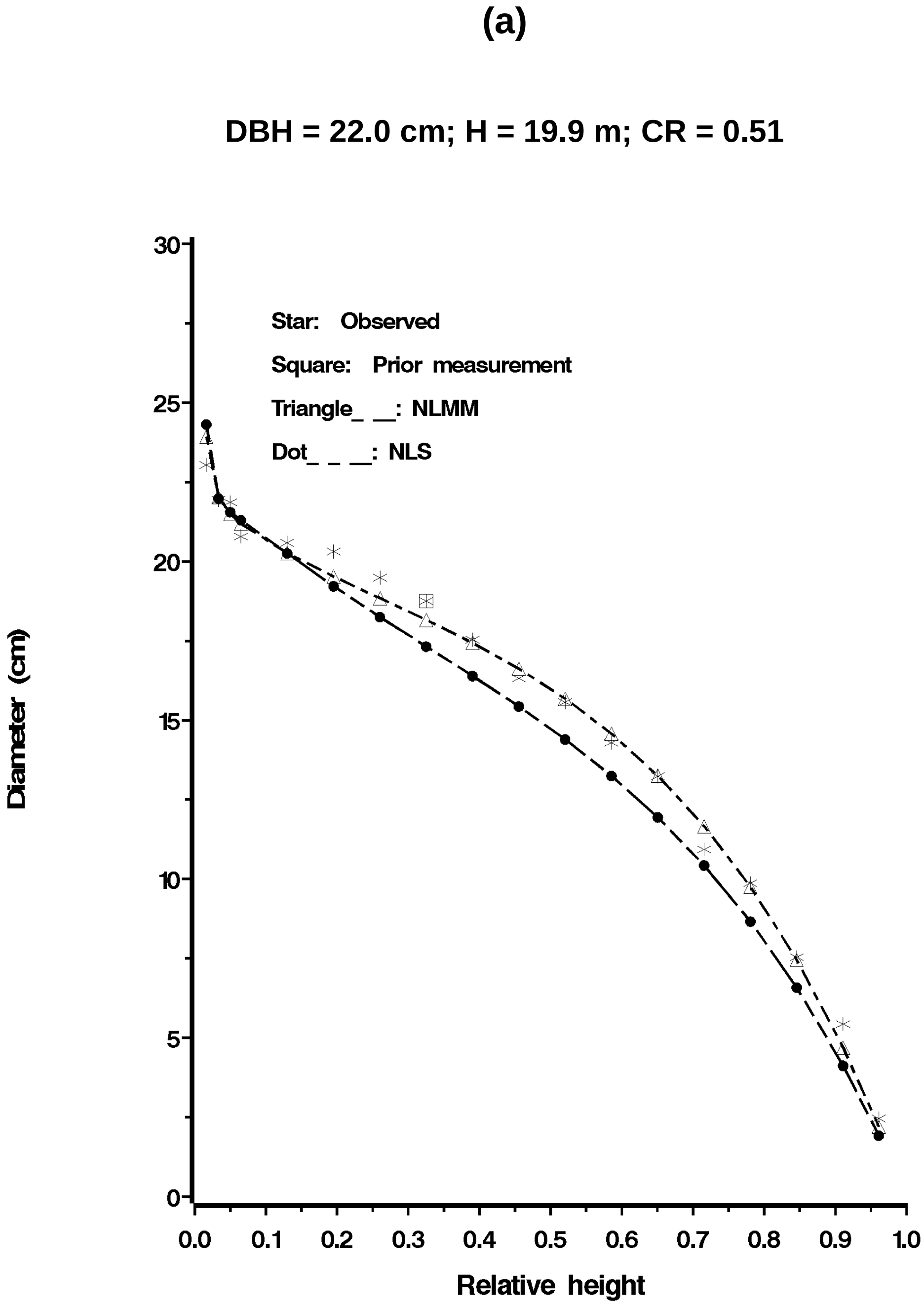


Figure 5.11. Black spruce tree profiles generated from [5.11] for three randomly selected trees (see text), fitted by NLS and nonlinear mixed-effects modeling (NLMM) techniques with one prior diameter measurement.

(b)

DBH = 18.0 cm; H = 16.2 m; CR = 0.58

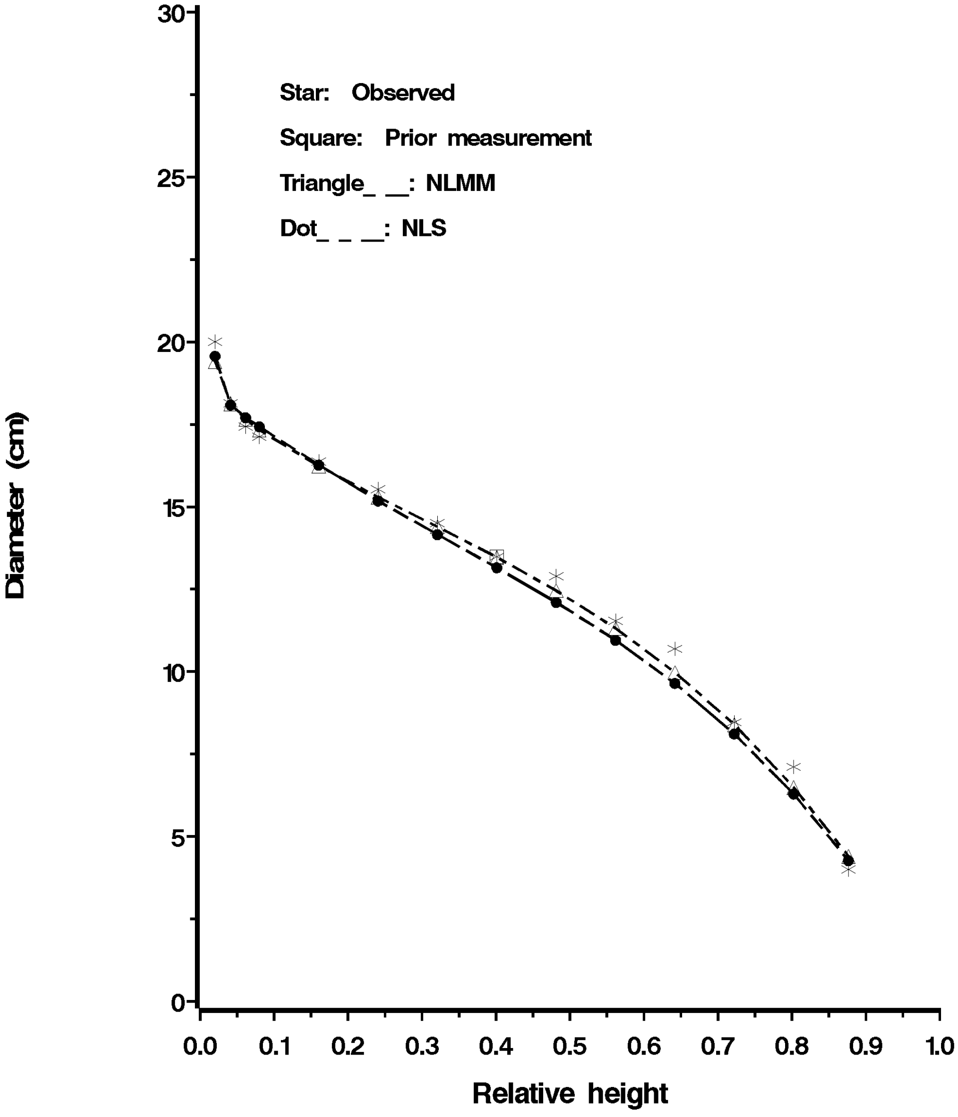


Figure 5.11 (continued).

(c)

DBH = 14.6 cm; H = 13.8 m; CR = 0.60

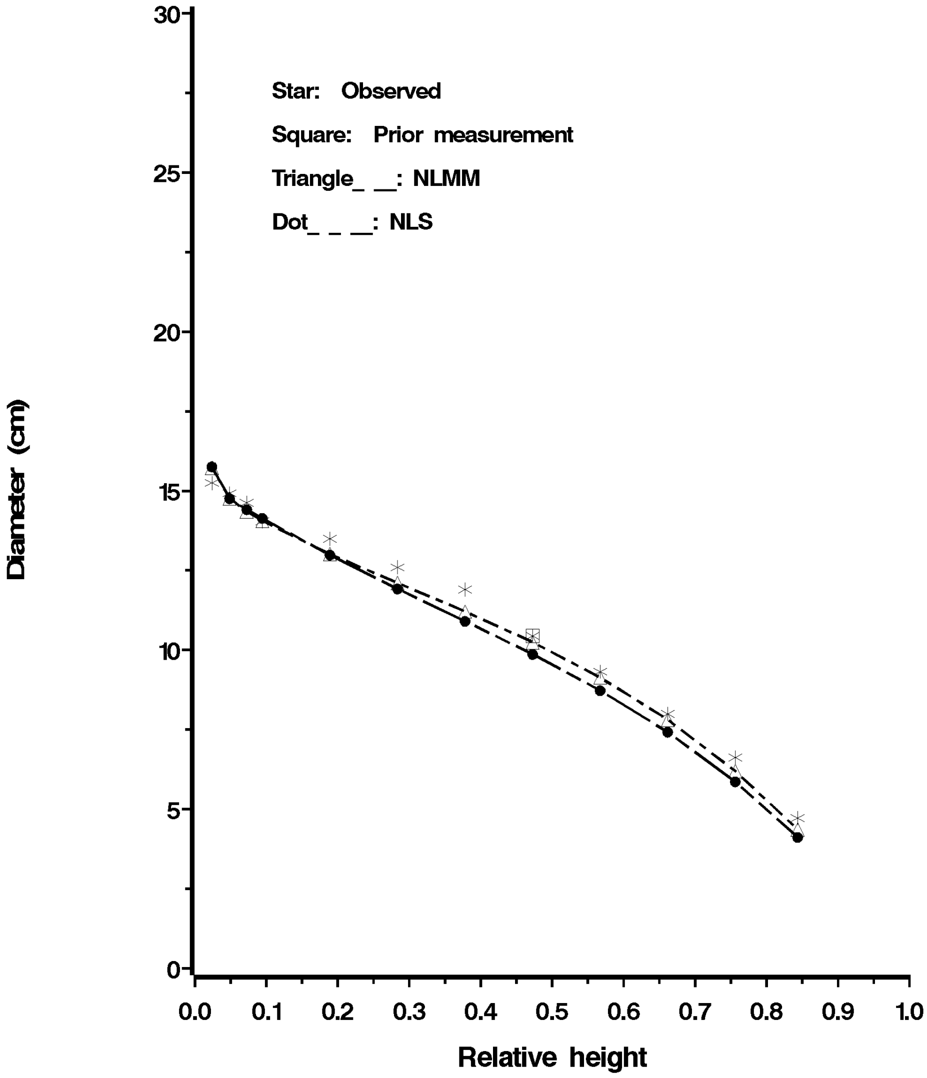


Figure 5.11 (continued).

(a)

DBH = 23.3 cm; H = 17.9 m; CR = 0.54

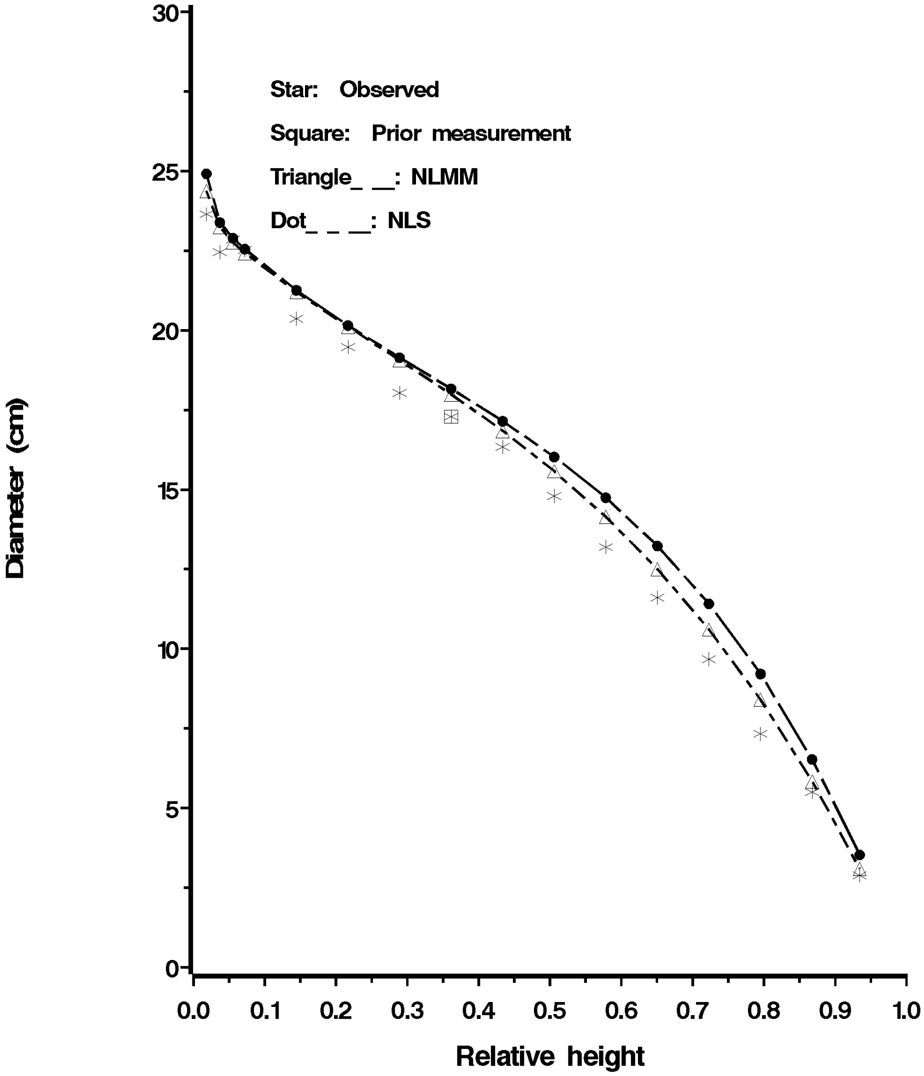


Figure 5.12. Jack pine tree profiles generated from [5.11] for three randomly selected trees (see text), fitted by NLS and nonlinear mixed-effects modeling (NLMM) techniques with one prior diameter measurement.

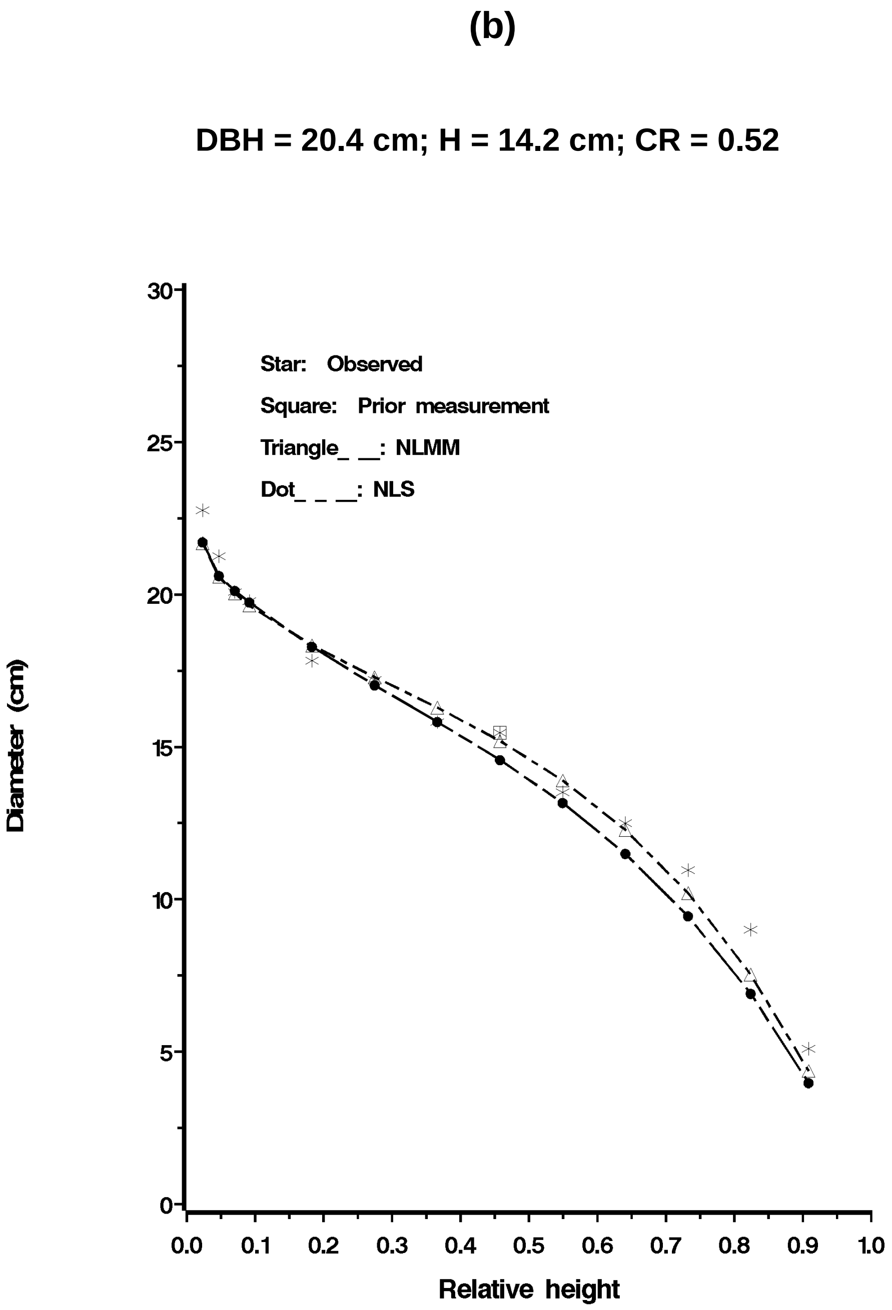
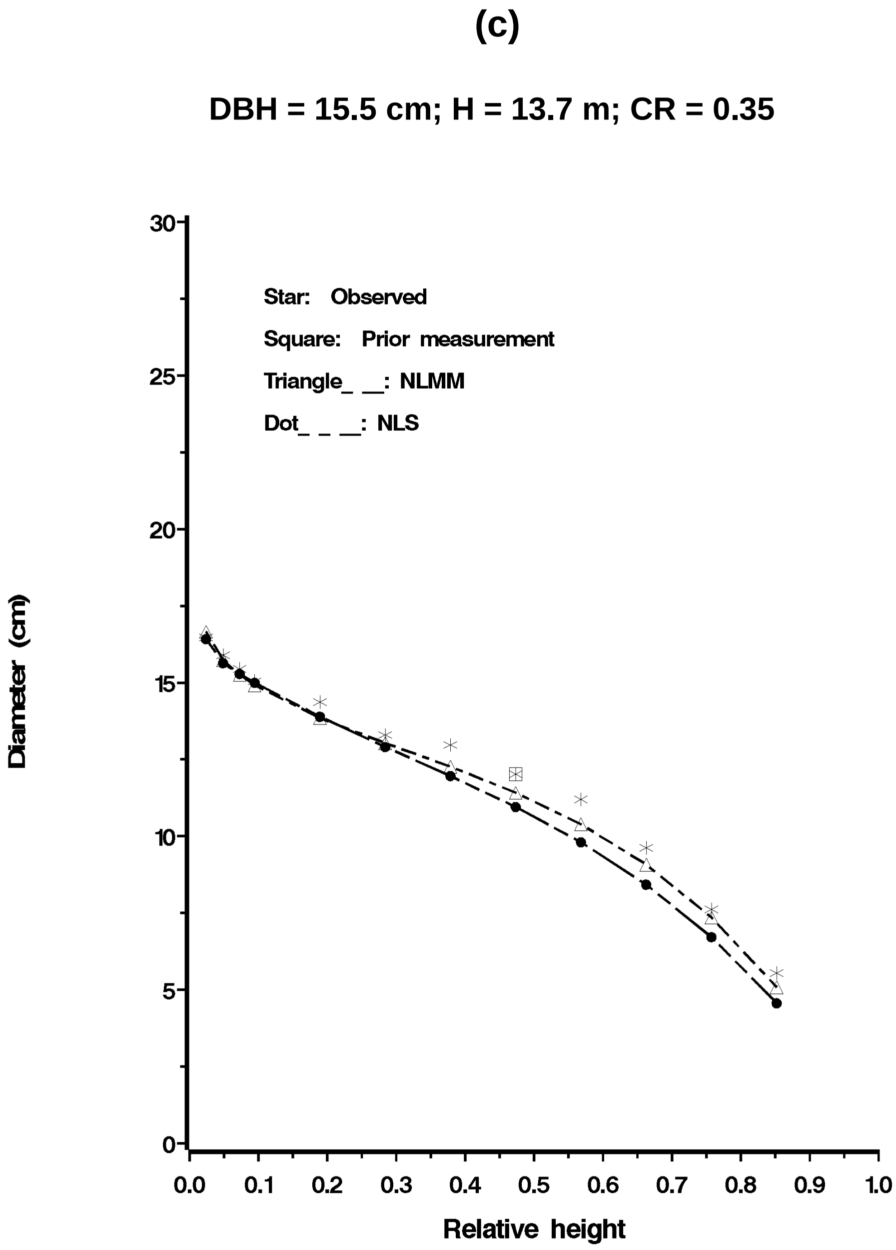


Figure 5.12. (continued).



(c)

DBH = 15.5 cm; H = 13.7 m; CR = 0.35

Figure 5.12. (continued).

5.6 DISCUSSION

This study compared the nonlinear least squares (NLS) and nonlinear mixed-effects model (NLMM) regression approaches to modeling tree bole taper in black spruce and jack pine. The taper models were developed using an extensive set of stem (bole) analysis data collected from black spruce and jack pine trees from the boreal forests of Manitoba. Using these two regression approaches, the variable exponent taper equations developed by Kozak (1988, 1997) were compared to more recently developed taper equations based on dimensional analysis (e.g. Sharma and Parton 2009).

A total of eleven models, eight based on Kozak's variable exponent approach (Kozak 1988, 1997) and three based on dimensional analysis (Sharma and Parton 2009), were compared using nonlinear least squares (NLS) regression analysis. Most of these models performed well, having high coefficients of determination and low root mean square error values. However, all of the variable exponent taper models displayed severe multicollinearity (as measured by the variance inflation factor, *VIF*). This high multicollinearity was attributable to the large number of parameters in these models (ranging from 7 to 11), resulting in high positive correlations among the dependent variables (Kozak 2004). By contrast, multicollinearity was much lower (*VIF* < 50) in the equations based on dimensional analysis, which contained only 4 – 6 parameters. Given that multicollinearity can result in highly unstable regression parameter estimates (Neter *et al*. 1989), models based on dimensional analysis (models [5.10] and [5.11], modified from Sharma and Parton 2009) were selected over those based on the variable exponent approach to develop taper models for Manitoba black spruce and jack pine.

In forestry, stem (bole) analysis data typically include several measurements taken at various locations on the same tree bole. Such data are highly spatially autocorrelated, which violated the important assumption of error independence in

NLS regression. Non-independence of error terms has a number of statistical consequences, including regression coefficients that no longer have the minimum variance property, underestimation of the mean square error and standard error of coefficients, and unreliability of statistical tests (Neter *et al.* 1990; Kmenta 1986; Kozak 1997).

Analysis of lagged normalized residuals indicated that nonlinear least square (NLS) regression was strongly affected by positive spatial autocorrelation in the data. This problem was addressed by analyzing the data using nonlinear mixed-effects model (NLMM) regression analysis. The NLMM approach has been used recently in forestry to successfully deal with autocorrelation issues when analyzing stem analysis data (Huang *et al*. 2009; Sharma and Parton 2009; Yang *et al*. 2009). In nonlinear mixed-effects modeling, the autocorrelation problem is addressed by defining an appropriate covariance structure for the model parameters, and by incorporating random parameters into the model. In mixed-effects modelling, parameters are partitioned into a fixed component (a population mean response that is common to all trees) and a random component (responses that are specific to each tree). By accounting for variation unique to each tree, such models offer considerable flexibility and advantages in addressing data autocorrelation issues.

The specification of random parameters is an important but challenging aspect of NLMM model development (Fang and Bailey 2001). A trial-and–error approach is generally used to determine which parameters should be modelled as fixed-effects, and which as mixed-effects (i.e. fixed plus random). Tree taper models have numerous parameters (five in model [5.10]), resulting in the need to examine numerous combinations of parameters in order to select the optimal model. In this study, various combinations of one, two and three potential random parameters were investigated. For each of these model fits, a detailed analysis of model convergence, parameter significance, and goodness-of-fit was required; it proved to be a complicated and time-consuming process. In general, increasing the number of random parameters resulted in improved model fits, and a model containing three random parameters was selected for further investigation.

The NLMM approach also requires selection of an appropriate covariance structure for the model parameters. In this study, the spatial power (SP(POW)) covariance structure resulted in improved model performance compared to models based on first-order autoregressive AR(1) and TOEP (4) covariance structures. In contrast, Yang *et al.* (2009) found the TOEP(4) covariance structure to be superior to SP(POW) when modelling white spruce bole taper. AR(1) and TOEP(4) structures are generally used when data measures are equally spaced (as in this study), whereas SP(POW) is recommended when measures are unequally spaced (Littell *et al.* 2006). My results suggest that SP(POW) covariance structures also offers superior model performance when data measures are approximately equally spaced.

In this study, the NLMM approach using three mixed-effects parameters and a SP(POW) covariance structure proved very effective in dealing with the spatial autocorrelation present in the black spruce and jack pine stem (bole) analysis data. NLMM regression is therefore recommended as a method for developing tree taper models based on autocorrelated stem (bole) analysis data (Sharma and Parton 2009).

Prior measures are often used to increase the prediction accuracy of mixed-effects models (Calama and Montero 2004). In forestry applications, prior measures are generally tree diameter values (other than DBH) measured under field conditions. Such field measurements are costly to obtain, but are often used to obtain more accurate and precise estimates of timber volume in applied forestry. In this study, three prior measure scenarios were investigated: one prior measure per tree (bole diameter at 6.5 m height); two prior measures per tree (bole diameter at 0.3 and 6.5 m heights); and three prior measures per tree (bole diameter at 0.3, 2.6 and 6.5 m heights). The results indicated that model predictions of tree height and volume were greatly improved by including a single prior measure, but little additional benefit was incurred by including two or more prior measures. It is therefore recommended that, when available, a single prior measure (bole diameter at 5.6 m height) should be used to increase the prediction accuracy of taper models of black spruce and jack pine in Manitoba.

The taper equation developed here is a variant of the dimensional analysis model proposed by Sharma and Parton (2009); model [5.9]. A modification of the basic equation (i.e. model [5.9]) was required, since my investigations found that one of the parameters (b_3, relative height squared in the quadratic exponent) was not statistically significant in Manitoba black spruce taper models. It was found that substitution of the squared term with two terms, the reciprocal and log (base e) of relative height, resulted in a five-parameter model [5.10] in which all parameters were statistically significant. A further modification to model [5.10], in which crown ratio (*CR*) was included as an additional potential independent variable, did not improve model performance. It was therefore concluded that inclusion of crown ratio is not necessary or desirable when modelling bole taper of black spruce and jack pine in Manitoba. While some studies have found that crown ratio is useful predictor of bole taper (e.g. Valenti and Cao 1986; Muhairwe *et al*. 1994), other studies are in agreement with my finding that crown ratio is unimportant (e.g. Burkhart and Walton 1985).

In applied forestry applications, bole taper models are used to estimate individual tree bole volume. These individual tree volume values are then “scaled up” to obtain estimates of the timber volume (merchantable yield) of forest stands, management units or regional landscapes (Husch *et al*. 2003). Current or projected estimates of timber volume are used widely in timber supply analysis, forest inventory, biomass and carbon budget analyses, and in sustainable forest management. The taper models developed in this study will provide accurate and reliable estimates of timber volume of black spruce and jack pine in the boreal forest regions of Manitoba.

CHAPTER 6 INDIVIDUAL TREE MORTALITY MODELS FOR BLACK SPRUCE AND JACK PINE

6.1 INTRODUCTION

Mortality of boreal forest tree species is a function of numerous biological and ecological factors (Lee 1971; Hamilton 1986; Carleton and Wannamaker 1987; Chen *et al.* 2008). The factors affecting mortality interact in complex ways, and may result in either gradual tree decline (“mortality spiral”, Franklin *et al*. 1987) or abrupt death (Waring 1987). Large-scale disturbances such as catastrophic wildfire and spruce budworm outbreaks are largely unpredictable events that result in abrupt mortality across large areas of the landscape. In the regenerating stands that develop following such disturbances, individual trees experience above and below ground competition with neighbouring trees for limited space and resources such as light, water and nutrients (Antonovics and Levin 1980). The degree of competition experienced by a given tree is a function of stand density, as well as the size and proximity of neighbouring trees. The intensity of competition greatly influences an individual’s growth rate (Dobbertin and Biging 1998), and prolonged intense competition may result in density-dependent mortality (Kenkel 1988). Density-independent factors such as pathogenic diseases, insect pests and wind-throw may also result in tree mortality, but such factors are much more difficult to predict or model (Yang *et al.* 2003; Chen *et al.* 2008).

Over the past few decades, a number of individual tree mortality (or survival) models have been developed for forestry applications (e.g. Lee 1971; Buford and Hafley 1985; Hamilton 1986; Hawkes 2000; Yang *et al.* 2003; Zhao *et al.* 2004; Lacerte *et al.* 2006; Chen *et al.* 2008). The earliest mortality algorithms were empirical-based linear and polynomial functions (e.g. Lee 1971) or nonlinear models (e.g. Buford and Hafley 1985). More recently, logistic regression has been the preferred approach for modelling individual tree mortality (e.g. Hamilton

1986; Monserud and Sterba 1999; Yao *et al.* 2001; Yang *et al.* 2003; Zhao *et al.* 2004; Lacerte *et al.* 2006; Chen *et al.* 2008). The logistic function provides an estimated probability (range [0,1]) of mortality or survivorship (Vanclay 1995). Individual tree mortality is a discrete event: 0 = dead, for trees that die at some point during a specified measurement interval (generally > 1 year); and 1 = live, for trees that remain alive over the measurement interval.

In logistic tree mortality models, the dependent or response variable is a discrete binary measure of individual survivorship (1 = alive, 0 = dead), and the independent or predictor variables are normally continuous (though they may be discrete as well). Common predictor variables include absolute or relative tree size (or age), relative growth rate or vigour, stand density, and various measures of local and stand-level competition (Hamilton 1986; Monserud and Sterba 1999; Yang *et al.* 2003; Zhao *et al.* 2004; Lacerte *et al.* 2006; Chen *et al.* 2008).

Logistic regression mortality models have invariably used non-spatial variables to quantify the degree of competition experienced by a given tree (e.g. Lacerte *et al.* 2006; Chen *et al.* 2008). These “competition variables” are based on tree size (e.g. the size of an individual relative to other trees in the stand) and stand basal area (e.g. the total basal area of all trees larger than the individual). This is an indirect approach to measuring competitive effects, since it fails to consider the spatial component of interactions among sedentary individuals, in particular the size and proximity of neighbors. Spatial measures have been shown to provide a more complete description and ecologically meaningful competitive interactions in trees and other plants (Bella 1971; Kenkel 1988; Little 2002).

Jack pine and black spruce are among the most widespread and economically important tree species in Manitoba. Reliable individual tree mortality models for these two species in Manitoba are required in practice for sustainable forest management. The objective of this study is to develop logistic regression mortality models appropriate for black spruce and jack pine in Manitoba. Potential predictor variables include tree size (bole diameter), diameter growth increment, and two aspatial competition measures: relative stem diameter, and the total basal area of all trees larger than the target tree. A spatial measure of local competition, the Thiessen polygon area (area potentially available), was also included since the data used for the model included mapped tree locations. The models were verified and validated using independent data sets.

6.2 STUDY AREA AND DATA

Data from the Manitoba permanent sample plots (Manitoba Conservation 2000) were used to develop the individual tree mortality models for jack pine and black spruce. Summary descriptions of the study area, species groups, data collection procedures, and other technical details are presented in Chapter 4 (Sections 4.2 and 4.3).

The criteria used to select appropriate permanent sample plots used here are summarized in Chapter 4. Briefly, the stands selected were dominated by either black spruce or jack pine (i.e. > 70% basal area of black spruce or jack pine). As well, the selected plots included a minimum of two consecutive five-year measurement intervals. A total of 50 permanent plots were included in this study: 12 lowland black spruce, 16 upland black spruce, and 22 natural jack pine stands. The managed jack pine stands were subjected to various human interventions, including site preparation, planting, application of herbicides and thinning (see Chapter 4). Since natural mortality processes were strongly affected by such interventions, the managed jack pine stands were not considered in this study.

To minimize the autocorrelation problems inherent in repeated measurement data, only the final five-year measurement interval was used to assess tree mortality in the permanent sample plots. In this study, all living trees at the start of the last five-year interval were included in the analysis. Those still alive after five years were designated as “live” trees, while those that died during the five-year interval were designated as “dead”. Data from previous (next to final) growth period were used only to calculate stem diameter increments.

A total of 8349 trees (6911 black spruce and 1438 natural jack pine) were used for the development and validation of the black spruce and jack pine mortality models. Summary variables for these trees are presented in **Table 6.1**. A summary of five-year survivorship for these black spruce and jack pine trees is given in **Table 6.2**. Black spruce mortality was 5.38% (4.28% for lowland stands, 6.04% for upland stands), whereas mortality in natural jack pine was much higher at 15.16%.

Among the 50 plots, 39 plots were randomly selected (about 80% of the total plots) for model development and the remaining 11 plots for model validation (Wetherill *et al*. 1986; Yang *et al*. 2003). The 39 plots randomly selected for model development covered a range of stand conditions, for both black spruce (9 lowland black spruce plots, *n* = 2286 trees; and 13 upland black spruce plots, *n* = 3724 trees) and jack pine (17 natural jack pine plots, *n* = 1146 trees). Summary variables for the trees used in model development are given in **Table 6.3**. The 11 plots selected for model validations included 3 lowland black spruce plots (*n* = 285 trees), 3 upland black spruce plots (*n* = 616 trees), and 5 jack pine plots (*n* = 292 trees). Summary variables for the trees used in model validation are presented in **Table 6.4**.

Table 6.1. Summary of attributes for the *n* = 8349 trees (classified by species group) used in this study.

SPECIES GROUP	VARIABLE[†]	MEAN	MIN	MAX	S.D.
Lowland BS*	DBH (cm)	5.89	0.4	29.8	4.1
(*n* = 2571 trees)	DI (cm/5 yrs)	0.57	0.00	4.10	0.39
	Polygon Area (m^2)	1.27	0.01	13.06	1.4
Upland BS*	DBH (cm)	5.34	0.4	21.8	3.38
(*n* = 4340 trees)	DI (cm/5 ys)	0.38	0	3.6	0.29
	Polygon Area (m^2)	1.02	0.01	10.06	1.07
Natural JP*	DBH (cm)	10.6	0.7	28.3	4.04
(*n*= 1438 trees)	DI (cm/5 yrs	0.92	0	3.8	0.66
	Polygon Area (m^2)	3.64	0.15	22.6	2.78

* BS = Black Spruce, JP = Jack Pine.

[†] DBH = diameter at breast height (1.3 m); DI = diameter increment at 1.3 m; Polygon Area = area of Thiessen polygon associated with each tree.

Table 6.2. Total numbers of live trees at the start of the study, the number of trees dying during the 5-year study period, and the percent mortality over the 5-year period for each species group.

SPECIES GROUP	LIVE TREES	DEAD TREES	MORTALITY (%, 5 years)
LOWLAND BS*	2571	110	4.28
UPLAND BS*	4340	262	6.04
COMBINED BS*[†]	6911	372	5.38
NATURAL JP*	1438	218	15.16

* BS = Black spruce; JP = Jack pine.

[†] Combined = lowland BS + upland BS.

Table 6.3. Summary of attributes for the n = 7156 trees (classified by species group) used in model development (39 permanent sample plots).

SPECIES GROUP	VARIABLE[†]	MEAN	MIN	MAX	S.D.
Lowland BS[*]	DBH (cm)	5.62	0.40	29.80	3.85
(n = 2286)	DI (cm/5 yrs)	0.58	0.00	4.10	0.4
	Polygon Area (m^2)	1.12	0.01	13.06	1.16
Upland BS[*]	DBH (cm)	4.92	0.40	21.80	3.11
(n = 3724)	DI (cm/5 yrs)	0.39	0.00	3.60	0.29
	Polygon Area (m^2)	0.96	0.01	10.06	1.04
Natural JP[*]	DBH (cm)	9.86	0.7	22.50	3.77
(n = 1146)	DI (cm/5 yrs)	0.93	0.00	3.80	0.7
	Polygon Area (m^2)	3.45	0.15	22.60	2.76

* BS = Black Spruce, JP = Jack Pine.

[†] DBH = diameter at breast height (1.3 m); DI = diameter increment at 1.3 m; Polygon Area = area of Thiessen polygon associated with each tree.

Table 6.4. Summary of attributes for the n = 1193 trees (classified by species group) used in model validation (11 permanent sample plots).

SPECIES GROUP	VARIABLE[†]	MEAN	MIN	MAX	S.D.
Lowland BS[*]	DBH (cm)	8.08	0.80	24.80	5.23
(n = 285)	DI (cm/5 yrs)	0.51	0.00	2.50	0.33
	Polygon Area (m^2)	2.42	0.16	13.03	2.29
Upland BS[*]	DBH (cm)	7.89	0.70	18.10	3.81
(n = 616)	DI (cm/5 yrs)	0.36	0.00	2.60	0.29
	Polygon Area (m^2)	1.45	0.05	9.13	1.31
Natural JP[*]	DBH (cm)	13.49	3.30	28.30	3.77
(n = 292)	DI (cm/5 yrs)	0.85	0.00	2.40	0.51
	Polygon Area (m^2)	4.93	0.51	17.55	3.24

* BS = Black Spruce, JP = Jack Pine.

[†] DBH = diameter at breast height (1.3 m); DI = diameter increment at 1.3 m; Polygon Area = area of Thiessen polygon associated with each tree.

6.3 METHODS

Factors contributing to tree mortality fall into three broad categories: relative tree size or age (e.g. stem diameter, height), relative growth rate or vigour (e.g. diameter increment, crown ratio), and local and stand-level competition with member of the same and/or different species (Buchman *et al*. 1983). Within a given stand, so-called “suppressed” individuals (i.e. trees that are smaller than average, those growing slowly, and/or those experiencing strong intraspecifc or interspecific competition) enter into a “mortality spiral”, a positive feedback in which the tree becomes increasingly predisposed to mortality (Franklin *et al*. 1987; Manion 1990).

A number of studies have examined the factors contributing to tree morality in forest stands (Wykoff *et al.* 1982; Monserud and Sterba 1999; Yang *et al.* 2003; Zhao *et al.* 2004; Lacerte *et al.* 2006; Chen *et al.* 2008). These and other studies were consulted in order to select an appropriate and meaningful set of predictor variables in the development of mortality models for black spruce and jack pine in Manitoba.

6.3.1 Selection of Variables

In developing the mortality models, the following variables were selected as potential predictors of individual tree mortality in jack pine and black spruce.

Size: Stem Diameter

D = Diameter at Breast Height (cm)
Nonlinear Terms: Diameter Squared (D^2), Reciprocal of Diameter (D^{-1})

In the absence of reliable information on tree ages, size (typically, stem diameter at breast height) is commonly used as a predictor variable when modelling tree mortality (e.g. Monserud and Sterba 1999; Yang *et al.* 2003; Zhao *et al.* 2004; Lacerte *et al.* 2006; Chen *et al.* 2008). In general, the larger trees in a stand are better able to compete for limiting resources (e.g. light, nutrients) than are smaller trees (Cannell *et al*. 1984). As a result, the smaller trees in a stand have lower survivorship (i.e. higher likelihood of mortality). However, as trees get older (larger) they become “senescent”, increasing the likelihood of mortality (Harcombe 1987). A further complication is the mortality probability may be disproportionately high for the smallest trees (Monserud and Sterba 1999). These potential nonlinear effects in the relationship between tree size and mortality probability can be modelling by including the terms D^2 and D^{-1} (i.e. hyperbolic transformation) as variables in the logistic regression (Buchman *et al*. 1983; Lorimer and Frelich 1984; Monserud and Sterba 1999; Yang et al. 2003). Individual tree diameter (D), diameter squared (D^2), and the reciprocal of diameter (D^{-1}) were therefore considered as potential predictor variables in this study.

Growth: Diameter Increment

DI = Diameter Increment (cm / 5 years)

Tree growth or vigour, which is often quantified as the increase in stem diameter per unit time (i.e. diameter increment or *DI*, Buchman *et al*. 1983), has been widely used as a predictor variable in the modelling of individual tree mortality (Monserud 1976; Hamilton 1990; Yang *et al.* 2003). More vigorous (i.e. faster-growing) trees are “healthier” and therefore have higher survivorship than slow-growing trees (Cannell *et al*. 1984).

The relationship between growth (diameter increment) and survivorship for black spruce in upland stands is shown in **Figure 6.1**. Across all size (diameter at breast height, DBH) classes, trees dying over a five-year interval have (on average) lower incremental diameter growth than surviving trees. Diameter increment was therefore considered as a potential predictor of stem mortality in this study.

Aspatial Competition: Relative Stem Diameter

D/MD = Relative Diameter (where MD = Mean Stem Diameter of Stand)
D^2/MD = Non-linear Term

The relative diameter (ratio of the stem diameter at breast height (D) to the mean stem diameter (MD) of the stand) measures the relative competition or “canopy status” of a tree. Within a given stand, relatively larger trees ($D/MD > 1$) will be at the competitive advantage in the acquisition of limiting resources (e.g. light, nutrients) compared to smaller ($D/MD < 1$) trees (Wykoff 1986). It is therefore expected that trees with higher D/MD values will show greater survivorship. The non-linear term D^2/MD is often included to account for the possibility that the relationship between stem relative diameter and survivorship is not linear (Wykoff 1990; Zhao *et al*. 2004). Relative diameter and the non-linear interaction term were therefore considered as potential predictors of individual stem mortality in this study.

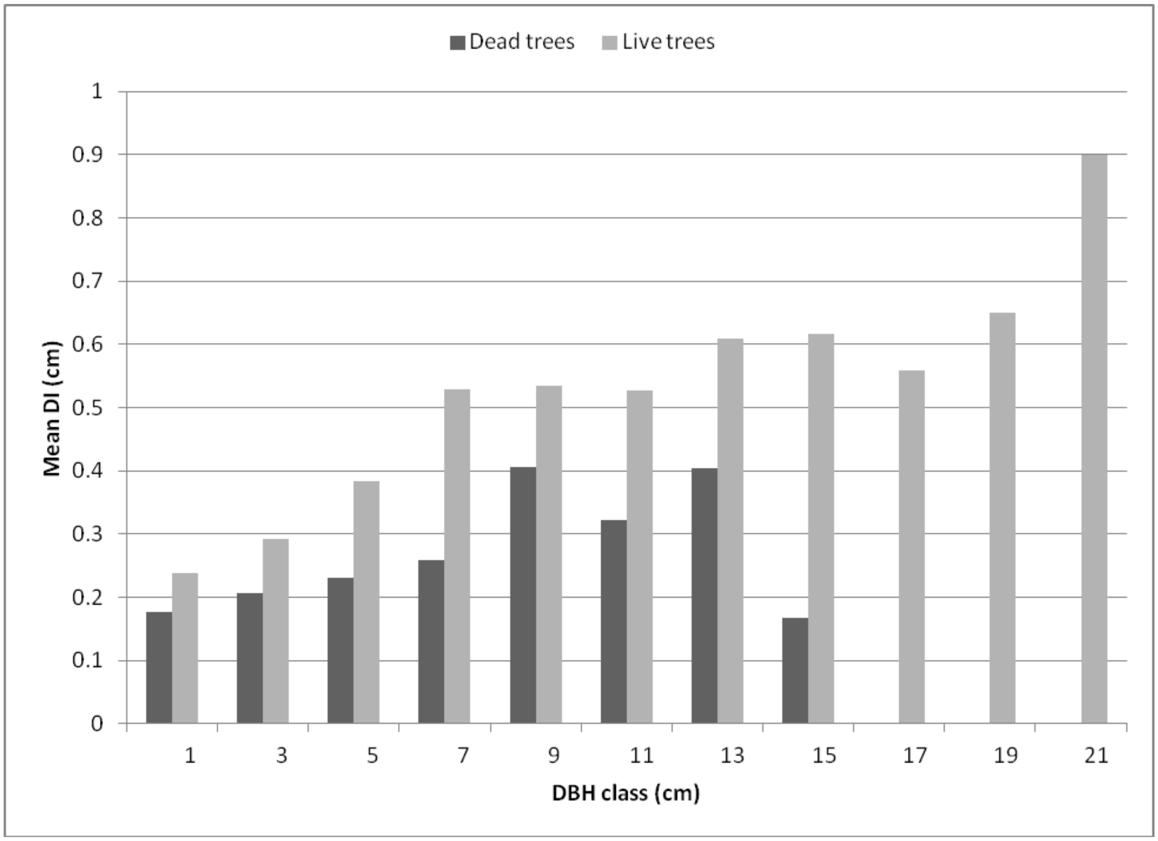


Figure 6.1. Mean diameter increment (DI) of trees that lived and those that died at the end of growth intervals for upland black spruce. DBH classes are midpoint values.

Aspatial Competition: Stand Basal Area

BAL = Basal Area of Larger Trees in the Stand

The basal area of larger trees (BAL), which is the sum of the basal areas of all trees larger in diameter than the subject tree, is an alternative measure of the relative competition or “canopy status” of a tree (Wykoff *et al.* 1982; Wykoff 1990). For a given stand BAL = 0 for the largest tree, while for the smallest tree BAL is equal to the stand basal area minus that tree’s basal area. A tree with a large BAL value is therefore comparatively small (“suppressed”), and is expected to have a lower probability of survival (Yang *et al.* 2003). Basal area of larger trees (BAL) was therefore considered as a potential predictor variable in modelling individual tree mortality in this study.

Spatial Competition: Thiessen Polygon

TPA = Thiessen Polygon Area

In Chapter 4, it was shown that Thiessen polygon area (TPA) is a useful predictor of individual tree diameter growth. Thiessen polygon area has also been shown to be an important predictor of mortality in jack pine (Kenkel *et al.* 1997). Within a given stand, trees with smaller polygons have comparatively less space for resource acquisition (“area potentially available”; Mithen *et al*. 1984) and therefore have a lower survival probability (Kenkel *et al.* 1997). Representative examples of Thiessen polygon tessellations for stands of jack pine and black spruce are shown in **Figures 6.2** and **6.3**.

The relationship between Thiessen polygon area (TPA) and survivorship for the natural jack pine stands is shown in **Figure 6.4**. For most of the size (DBH) classes, those trees dying over a five-year interval have (on average) lower polygon areas than do the surviving trees. Thiessen polygon area, a spatial measure of local competition, was therefore considered as a potential predictor of tree mortality in this study.

6.3.2 Model Fitting

In this study, the survival probability of individual trees was modeled using logistic regression. Mortality can be modeled either annually (*n* = 1), or more commonly over an interval of *n* > 1 years (Monserud and Sterba 1999; Zhao *et al.* 2004). The data used in this study had equal measurement intervals over *n* = 5 years. The logistic model for five-year survival probability of individual trees is given by:

$$p_s = [1 + \exp(-X\beta)]^{-1} \tag{6.1}$$

In this model, p_S is the five-year survival probability, $\boldsymbol{X}$ is the matrix of predictor variables, and $\boldsymbol{\beta}$ is a vector of logistic regression coefficients (Legendre and Legendre 1998).

The maximum likelihood method was used to estimate logistic regression coefficients (Hosmer and Lemeshow 2000; Menard 2000). Maximum likelihood is the standard method for estimating the parameters of a logistic function, and is available in all major statistical software packages. In this study, the SAS Logistic Procedure with stepwise variable selection was used for model fitting and parameter estimation (SAS Institute 2004).

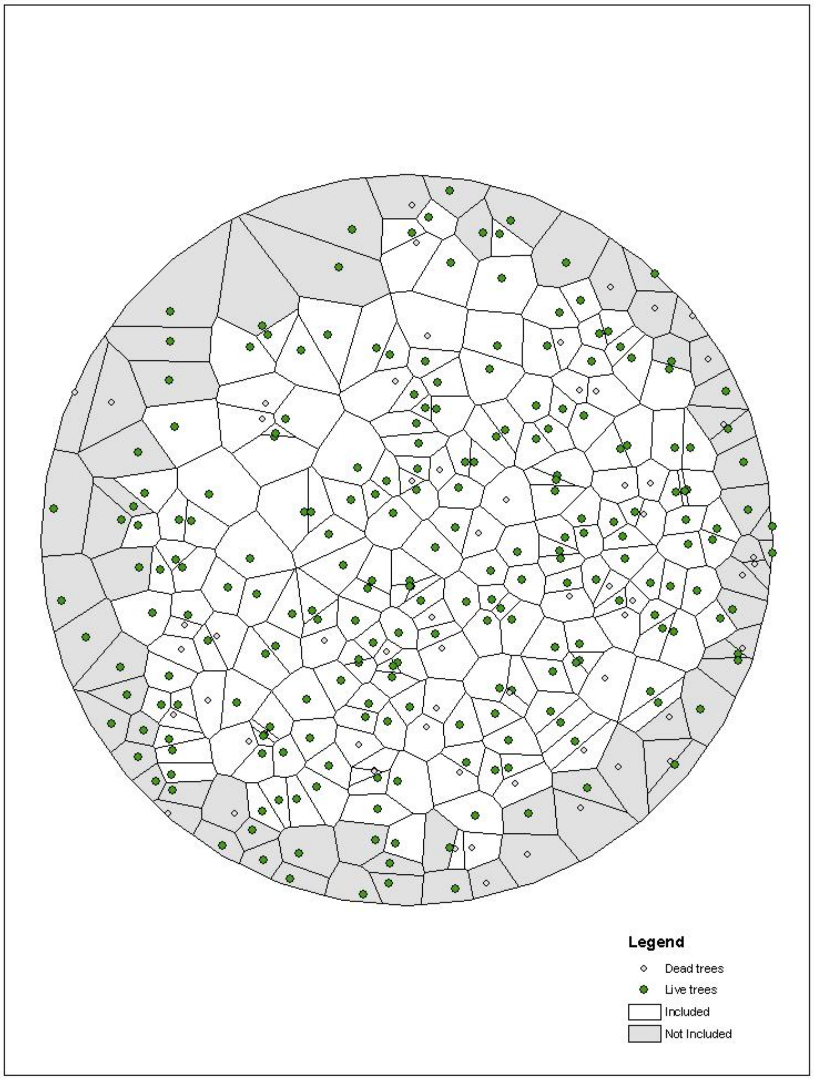


Figure 6.2. Black spruce tree mapping within a permanent sample plot (plot number 52 at year 2003, plot diameter is 12.62 m and plot area is 500 m^2, 163 years old, SI is 6.5 m): Thiessen polygon area of each live and dead trees within the plot and edge effect (grey).

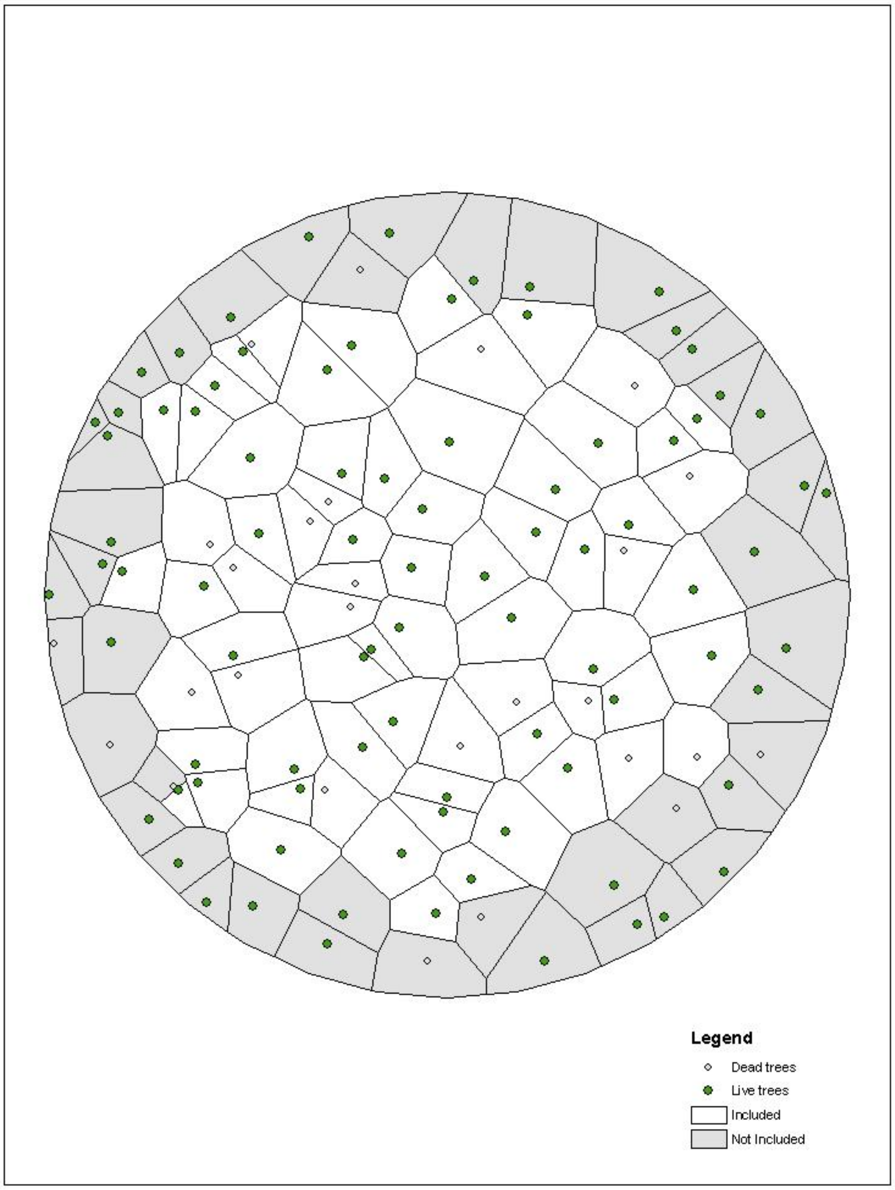


Figure 6.3. Jack pine tree mapping within a permanent sample plot (plot number 29 at year 2001, plot diameter is 12.62 m and plot area is 500 m^2, 68 years old, SI is 20.3 m): Thiessen polygon area of each live and dead trees within the plot and edge effect (grey).

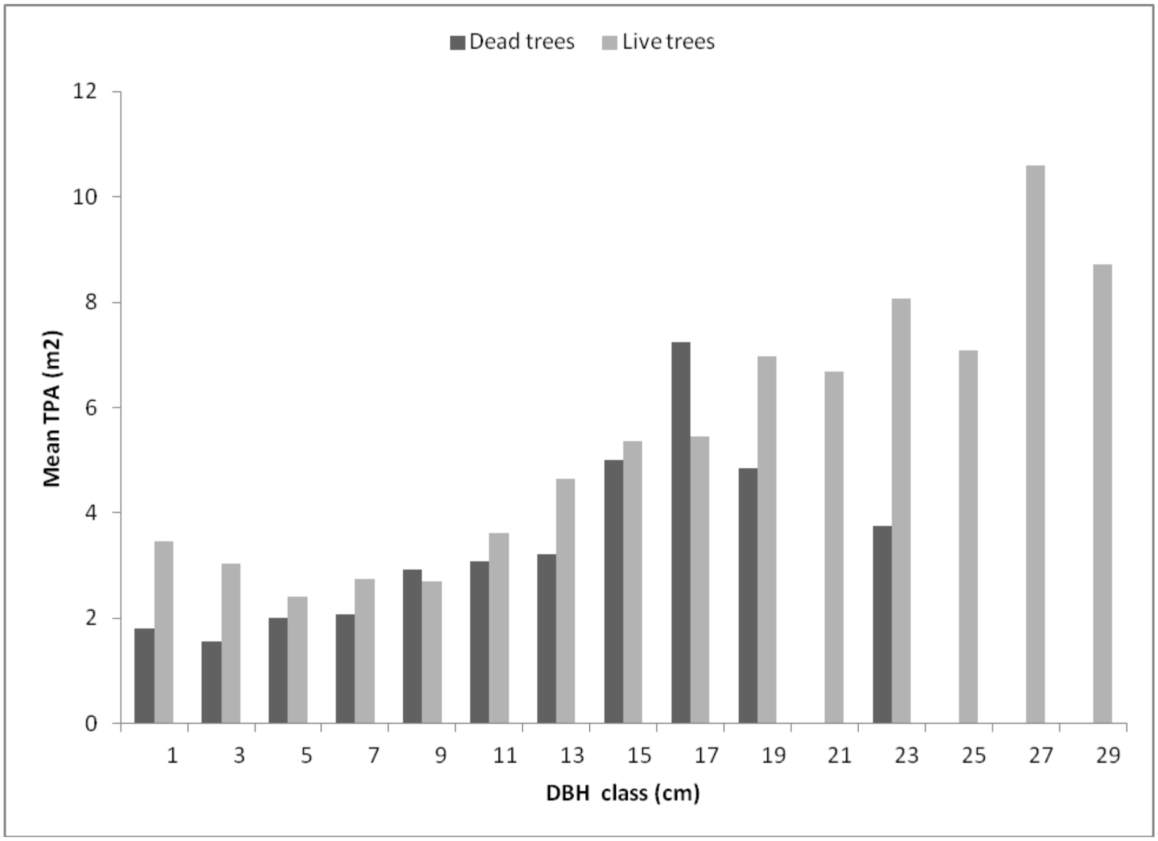


Figure 6.4. Thiessen polygon area (TPA) of trees that lived and those that died at the end of growth intervals for jack pine. DBH classes are midpoint values.

As part of the model development process, all potential variables (D, D^2, D^{-1}, DI, BAL, D/MD, D^2/MD and TPA) were initially included in the logistic model to obtain some sense of their relative importance as model predictors. The variable selection process used the standard stepwise approach (Hosmer and Lemeshow 2000) to determine variable parameter significance. Model prediction errors (Menard 2000), as well as considerations of model realism and meaningfulness from biological and ecological perspectives (Jeffers 1982), were also considered in developing the final models.

6.3.3 Goodness-of-Fit Tests for Logistic Regression

For continuous response variables, the coefficient of determination (R^2) is widely used to assess the relative goodness-of-fit of alternative regression models (Legendre and Legendre 1998). However, in logistic regression the standard coefficient of determination is of limited use in logistic regression since the response variable is binary (Menard 2000). A measure of the coefficient of determination suitable for multiple logistic regression analysis is the log-likelihood ratio (Menard 2000):

[6.2] $$R_L^2 = [\mathit{ln}\ (L_O) - \mathit{ln}\ (L_M)] \, / \, \mathit{ln}\ (L_O)$$

where L_O is the likelihood function for the logistic model containing only the intercept, and L_M is the likelihood function for the logistic model containing all predictor variables.

An alternative approach is to evaluate the goodness-of-fit of logistic mortality models using the chi-square contingency approach (Hamilton and Edwards 1976; Hamilton 1986; Loftsgaarden and Andrews 1992; Yang *et al.* 2003; Zhao *et al.* 2004). In this approach, the data are first grouped into several classes based on the independent variables. The chi-square statistic is then computed for the observed and expected (i.e. model predicted) numbers of survivors and dead trees in each class, and compared to the critical value at the appropriate degrees of freedom (Hamilton 1986).

Two grouping methods have been proposed for logistic models with two or more independent variables (Hosmer and Lemeshow 2000). Both methods are based on probabilities predicted from the fitted logistic model; the first utilizes fixed values of the predicted probabilities, while the second utilizes percentiles of the predicted probabilities. The first method often results in unbalanced groups, with some groups having a large number of observations and others having few or no observations. The second method produces more balanced groups, and is therefore more suited to testing using the χ^2 distribution (Hosmer *et al.* 1988).

In this study, the second grouping method was used to create ten groups, which is the recommended number for most applications (Hosmer and Lemeshow 2000). For each fitted model, the Hosmer–Lemeshow (*HL*) goodness-of-fit statistic was calculated and compared to the critical chi-square value at a 95% confidence level (i.e. $P = 0.05$). If a model fits the data well, the computed *HL* statistic has probability $P > 0.05$, indicating that there is no significant difference between the fitted model and the data (i.e. that the model provides a good fit, see Hosmer and Lemeshow 2000; Yang *et al*. 2003).

6.3.4 Model Validation

The Hosmer–Lemeshow (HL) goodness-of-fit statistic and the log-likelihood ratio (R_L^2) were used to select statistically significant mortality models for black spruce and jack pine. However, in modelling a good statistical fit does not necessarily result in optimal model prediction (Wetherill *et al.* 1986). Model validation is a necessary and appropriate step to ensure that the model produces meaningful and accurate predictions (Otto and Day 2007).

The randomly selected validation data (see Section 6.2; **Table 6.4**) were used to evaluate the robustness of the developed mortality models. The mean deviation *E* and mean absolute deviation *MAE* statistics, which are widely employed in model validation (Burk 1986; Cao 2000; Yang *et al.* 2003), were used here to validate the developed black spruce and jack pine mortality models:

[6.3] $$E = \frac{\sum_{i=1}^{n} (Y_i - P_i)}{n}$$

[6.4] $$MAE = \frac{\sum_{i=1}^{n} \left|(Y_i - P_i)\right|}{n}$$

Here Y_i is the observed survival status of the *i*th tree (1 = alive, and 0 = dead), P_i is the predicted survival probability of the *i*th tree, and *n* is the number of trees.

In addition, for each 5-cm stem diameter class the observed number of live trees (from the validation data) was compared to the predicted number. Here, the predicted number of live trees is the summation of the predicted survival probabilities for all trees in a given diameter class. The *E* and *MAE* statistics were computed for each diameter class in order to reveal potential prediction deficiency at certain diameter classes.

6.4 RESULTS

6.4.1 Model Fitting

The estimated logistic regression coefficients and corresponding standard errors for all final models are presented in **Table 6.5**. In the model fitting processes, the non-significant variables were removed and therefore all the regression parameters listed are statistically significant ($P < 0.05$).

Lowland Black Spruce

For lowland black spruce, the stepwise logistic regression procedure indicated that the variables diameter increment (*DI*), basal area of larger trees (*BAL*), relative diameter (*D*/*MD*) and its interaction term (D^2/MD) make a statistically significant contribution to the prediction of individual tree survivorship. The logistic model for black spruce survivorship in lowland sites is therefore:

$$p_s = \{1 + \exp[-(b_0 + b_2 DI + b_3 BAL + b_5 D / MD + b_6 D^2 / MD)]\}^{-1} \quad \textbf{[6.5]}$$

A number of alternative models were also examined, in order to confirm the statistical robustness of model [6.5]. For example, adding the variable *TPA* did not improve model performance (i.e. *TPA* was not statistically significant). Removal of the variables *D*/*MD* or D^2/MD from [6.5] produced a model with higher prediction errors that was not statistically significant (Hosmer–Lemeshow goodness-of-fit statistic, $P < 0.05$).

Upland Black Spruce

For upland black spruce, the stepwise logistic regression procedure indicated that the variables of diameter increment (*DI*), basal area of larger trees (*BAL*), relative diameter (*D*/*MD*) and its interaction term (D^2/MD) make a statistically significant contribution to the prediction of individual tree survivorship. These are the same variables that were selected for the lowland black spruce data. Therefore, logistic equation [6.5] was also appropriate for modelling black spruce survivorship in upland sites.

Alternative models were also examined, in order to confirm that statistical robustness of model [6.5] for upland black spruce. For example, models that included size variables (D, D^2, D^{-1}) were not statistically significant, and adding the variable *TPA* did not improve model performance. Removal of *BAL*, D/MD or D^2/MD from model [6.5] resulted in mortality models that were not statistically significant (Hosmer-Lemeshow goodness-of-fit statistic, $P < 0.05$).

Combined (Lowland + Upland) Black Spruce

Since lowland and upland black spruce stands resulted in the same logistic mortality equation (model [6.5]), the lowland and upland groups were combined to obtain a single black spruce category. As anticipated, the stepwise logistic regression process applied to these combined black spruce data selected the variables diameter increment (*DI*), basal area of larger trees (*BAL*), and relative diameter (D/MD) plus its interaction term (D^2/MD), i.e. model [6.5].

Alternative models were examined to confirm the statistical robustness of model [6.5] for black spruce. Adding size (D, D^2, D^{-1}) and spatial competition (*TPA*) variables did not improve model performance, and removal of *BAL*, D/MD or D^2/MD variables from equation [6.5] resulted in mortality models that were not statistically significant (Hosmer-Lemeshow goodness-of-fit statistic, $P < 0.05$).

For all three black spruce mortality models the coefficients of variable *DI* are positive, indicating that survivorship increases as tree growth (stem diameter increment) or vigour increases. This result is intuitive and consistent with previous studies of tree mortality (Johnstone 1997; Dobbertin and Biging 1998).

In all models the coefficients for variable *BAL* (basal area of trees larger than a given tree) are negative, indicating that trees with a less favourable competitive status (i.e. high *BAL*) have lower survivorship. Again, this is expected and consistent with previous studies demonstrating that competitively "suppressed" trees are more prone to mortality (Franklin *et al*. 1987). Another measure of aspatial competition, D/MD (ratio of individual tree diameter to mean tree diameter of the stand) and the nonlinear term D^2/MD, are also significant variables in the black spruce mortality models. In all models the coefficients for D/MD are positive, while those of D^2/MD are negative. This indicates a nonlinear relationship between D/MD and survivorship, in which smaller-than-average trees ($D/MD < 1$) are particularly prone to mortality (Monserud and Sterba 1999).

Jack Pine

For jack pine, the stepwise logistic regression procedure indicated that the variables Thiessen polygon area (*TPA*), squared stem diameter (D^2), and relative diameter (D/MD) and its interaction term (D^2/MD) make a statistically significant contribution to the prediction of tree survivorship. The logistic model for jack pine is therefore:

[6.6]
$$p_s = \{1 + \exp[-(b_0 + b_1 TPA + b_4 D^2 + b_5 D / MD + b_6 D^2 / MD)]\}^{-1}$$

Alternative models were examined to confirm the statistical robustness of equation [6.6] in predicting jack pine survivorship. Removing the variable *TPA*, or the addition of variable *DI*, produced models that were not statistically significant (Hosmer–Lemeshow's goodness-of-fit statistic, $P < 0.05$). The addition of *D*, $D^{-1,}$ and *BAL* did not improve model prediction (i.e. variables were not statistically significant).

Spatial data (i.e. mapping of the coordinate positions of trees) is often lacking in forest inventory data. An alternative model was therefore developed in which the spatial competition variable *TPA* (Thiessen polygon area) was not included. The stepwise regression procedure indicated that the variables basal area of larger trees (*BAL*), squared stem diameter (D^2), and relative diameter (*D*/*MD*) and its interaction term (D^2/MD) were statistically significant contributors to the prediction of jack pine tree survivorship. The logistic model is therefore:

[6.7] $$p_s = \{1 + \exp[-(b_0 + b_3 BAL + b_4 D^2 + b_5 D / MD + b_6 D^2 / MD)]\}^{-1}$$

Note that this model is similar to model [6.6], differing only in the substitution of the aspatial competition variables *BAL* for the spatial competition variable *TPA*.

The logistic regression coefficient for *TPA* is positive, indicating that jack pine trees with larger polygon areas (i.e. less crowded individuals) have higher survivorship. This result is consistent with previous studies demonstrating that spatial competition is an important predictor of individual jack pine mortality (Kenkel 1986; Kenkel *et al*. 1997). The coefficient for tree size (D^2, or basal area) is also positive, indicating that larger trees show higher survivorship compared to smaller trees. This result is consistent with previous findings on tree mortality (Buchman *et al*. 1983; Yang *et al*. 2003). As in the black spruce models, both *D*/*MD* (the ratio of individual tree diameter to mean tree diameter of the stand) and the nonlinear term D^2/MD are important predictors of jack pine mortality. The coefficient for *D*/*MD* is positive, and that for D^2/MD is negative. This indicates a nonlinear relationship between D/MD and survivorship, in which smaller-than-average trees ($D/MD < 1$) are particularly prone to mortality (Kenkel *et al*. 1997; Monserud and Sterba 1999).

Exclusion of the spatial variable *TPA* resulted in a model in which *BAL* was substituted for *TPA*; otherwise the model was unchanged. As expected, the coefficient for *BAL* (basal area of trees larger than a given tree) is negative, indicating lower survivorship for trees with a less favourable competitive status (i.e. high *BAL*). This is consistent with previous studies indicating that competitively “suppressed” trees are likely to die (Franklin *et al*. 1987).

6.4.2 Goodness-of-Fit Tests

The Hosmer–Lemeshow (H-L) goodness-of-fit statistic indicated good fit for all models (**Table 6.5**). In all models $P > 0.05$, which indicates no significant difference between the observed data and the model predictions, i.e. a “good” model fit (Hosmer and Lemeshow 2000). Values for the log-likelihood ratio R_L^2 were also statistically significant ($P < 0.01$).

The relative importance of the predictor variables in the black spruce and jack pine mortality models is summarized in **Table 6.6**. Here, a larger chi-square value indicates higher importance. All four statistically significant variables are about equally important in the combined black spruce model. For the jack pine model with *TPA*, the most important variables are *TPA* and *D*/*MD*, whereas all four variables are about equally important in the jack pine model without *TPA* (**Table 6.6**).

Table 6.5. The estimated parameters and *P*-values of Hosmer–Lemeshow goodness-of-fit test of individual-tree mortality models for lowland black spruce, upland black spruce and natural jack pine (with and without TPA).

VARIABLE		**BLACK SPRUCE**			**JACK PINE**	
		Lowland [6.5]	**Upland [6.5]**	**Combined [6.5]**	**With TPA [6.6]**	**Without TPA [6.7]**
Intercept	b_0	**2.4048** (0.6228)	**2.2062** (0.3745)	**2.2904** (0.3214)	**-4.0278** (0.6279)	**1.8267** (0.7122)
TPA	b_1				**0.3112** (0.0600)	
DI	b_2	**1.7189** (0.4883)	**2.0427** (0.4324)	**1.9437** (0.3163)		
BAL	b_3	**-0.0371** (0.0161)	**-0.0423** (0.0096)	**-0.0409** (0.0082)		**-0.2120** (0.0226)
D^2	b_4				**0.0168** (0.0074)	**0.0473** (0.007)
D/MD	b_5	**1.6160** (0.4922)	**1.8851** (0.3362)	**1.6994** (0.2699)	**7.1355** (1.2397)	**7.3890** (1.0463)
D^2/MD	b_6	**-0.0941** (0.0252)	**-0.1301** (0.0231)	**-0.1059** (0.0163)	**-0.3835** (0.1329)	**-0.8289** (0.1159)
H-L statistic		14.728	9.275	6.895	9.503	14.155
P (H-L)		0.0646	0.3196	0.5840	0.3016	0.0778
R_L^2		0.0977	0.1001	0.1028	0.2096	0.2719

Note: Standard errors are given in parentheses; D is diameter at breast height (DBH, at 1.3 m height); BAL is the sum of basal area of larger trees than the object tree; MD is mean stand DBH; TPA is tree Thiessen polygon area; DI is tree diameter increment; n is total number of trees. H–L's statistic is Hosmer–Lemeshow's goodness-of-fit statistic; pHL is p-values of Hosmer–Lemeshow's goodness-of-fit test. *P* > 0.05 indicates a statistically significant model fit.

Table 6.6. Chi-square values for the parameter estimates for logistic regression mortality models for black spruce and jack pine (see Table 6.5). For all chi-square values indicated, $P < 0.05$.

SPECIES GROUP	**VARIABLE**[*]					
BLACK SPRUCE	*TPA*	D^2	*DI*	*BAL*	*D/MD*	D^2/MD
Lowland [6.5]			12.4	5.3	10.8	13.9
Upland [6.5]			22.3	19.6	31.4	31.6
Combined [6.5]			37.8	24.9	39.7	42.3
JACK PINE						
With TPA [6.6]	26.9	5.1			33.1	8.3
Without TPA [6.7]		45.6		87.6	49.9	51.2

Note: D is diameter at breast height (DBH, at 1.3 m height); BAL is the sum of basal area of larger trees than the object tree; MD is mean stand DBH; TPA is tree Thiessen polygon area; DI is tree diameter increment; n is total number of trees. Higher Chi-square means relatively more important within the model fitted.

6.4.3 Model Validation

Mean deviations, and mean absolute deviations (overall, and for each 5-cm diameter class), between observed and model-predicted survival probabilities are summarized in **Table 6.7**. Overall mean deviations for the lowland black spruce, upland black spruce and combined black spruce models are low (< 0.05), with the combined black spruce model producing the lowest mean deviation (0.0157). The overall mean deviation for the jack pine model that included *TPA* was also low (-0.0193), but mean deviation for the jack pine model without *TPA* was much higher (0.1032). The positive overall mean deviation for the latter model indicates a tendency toward underestimating tree survival rates.

For DBH classes < 15 cm for the lowland black spruce model, DBH classes < 10 cm and 20-25 cm for the jack pine with *TPA* model, and DBH class 20-25 cm for the jack pine without *TPA* model, mean deviations were slightly negative. This indicates a tendency to overestimate survival rates in these classes. The remaining DBH classes for these models show positive mean deviations, indicating a tendency to slightly underestimate survival rates. With the exception of model [6.7] (jack pine without *TPA*), the overall mean deviations are quite small.

Overall success in predicting survivorship was very high for all black spruce models: 97.3% for lowland black spruce, 95.7% for upland black spruce, and 98.3% for combined black spruce. For the jack pine model with *TPA* (model [6.6]) survival prediction was also high, at 97.8%. However, the survival prediction for the jack pine model without *TPA* (model [6.7]) was only 88.0%, indicating that model [6.6] provide superior prediction performance.

Table 6.7. Mean deviations and mean absolute deviations of the validation data for lowland black spruce, upland black spruce and natural jack pine.

DBH (cm)	LOWLAND BLACK SPRUCE			UPLAND BLACK SPRUCE			COMBINED BLACK SPRUCE			JACK PINE					
	[6.5]			[6.5]			[6.5]			[6.6]			[6.7]		
	E [*]	***MAE***	***n***	***E***	***MAE***	***n***	***E***	***MAE***	***n***	***E***	***MAE***	***n***	***E***	***MAE***	***n***
0-5	-0.0539	0.1865	91	0.0540	0.2545	166	0.0123	0.2279	257	-0.2899	0.5142	7	0.0984	0.3608	7
5-10	-0.0353	0.0996	113	0.0237	0.1183	262	0.0025	0.1097	375	-0.1629	0.4381	44	0.1919	0.4789	44
10-15	-0.0072	0.0783	46	0.0538	0.0751	171	0.0334	0.0686	217	0.0321	0.1602	153	0.1447	0.2186	153
15-20	0.0584	0.0584	27	0.0207	0.1211	17	0.0429	0.0838	44	0.0042	0.0882	69	0.0118	0.0881	69
20-25	0.0817	0.0817	8				0.1125	0.1125	8	-0.1036	0.1402	16	-0.1224	0.1275	16
25-30										0.0038	0.0038	3	0	0	3
Overall	-0.0245	0.1195	285	0.0401	0.1431	616	0.0157	0.1323	901	-0.0193	0.1908	292	0.1032	0.2232	292

***** ***E*** = mean deviation; ***MAE*** = mean absolute deviation; ***n*** = number of trees.

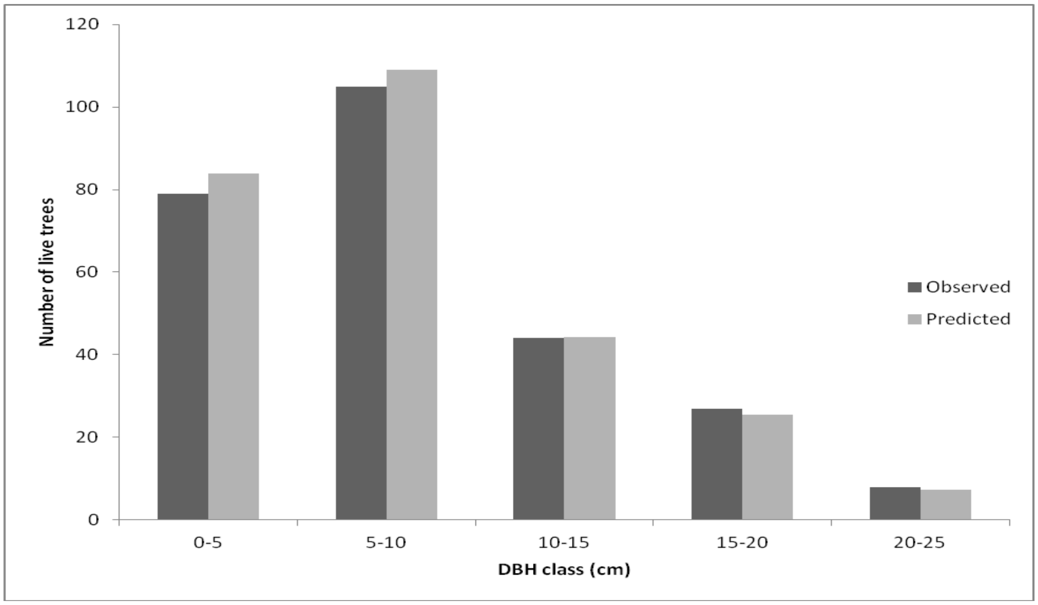


Figure 6.5. Observed and predicted numbers of live trees using survival model [6.5] for lowland black spruce validation prediction test.

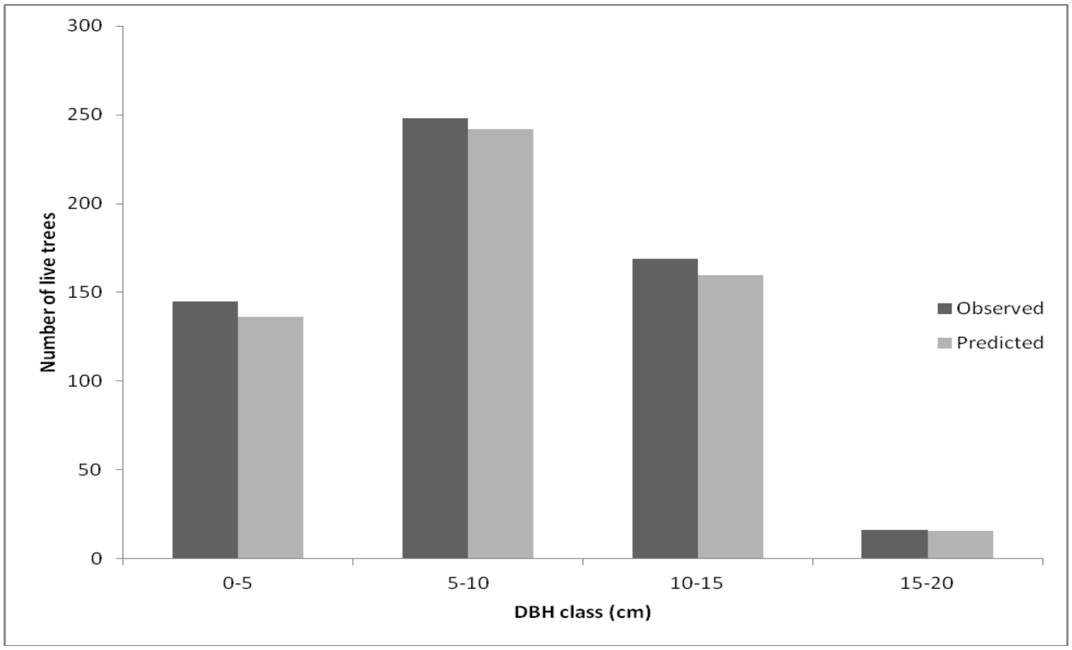


Figure 6.6. Observed and predicted numbers of live trees using survival model [6.5] for upland black spruce validation prediction test.

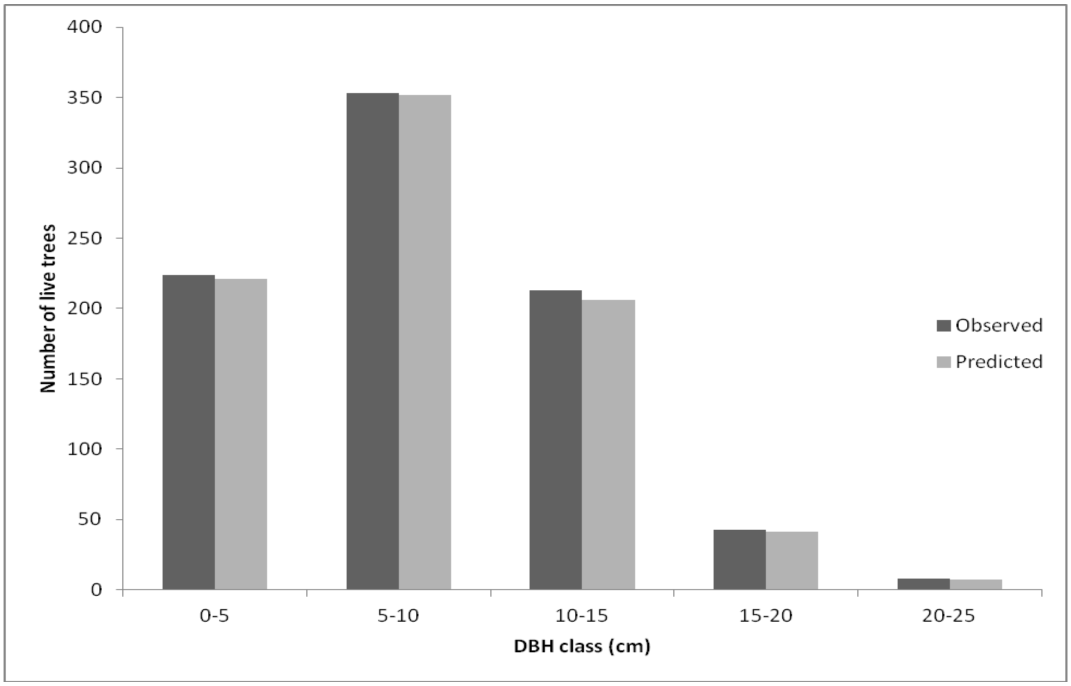


Figure 6.7. Observed and predicted numbers of live trees using survival model [6.5] for combined black spruce validation prediction test.

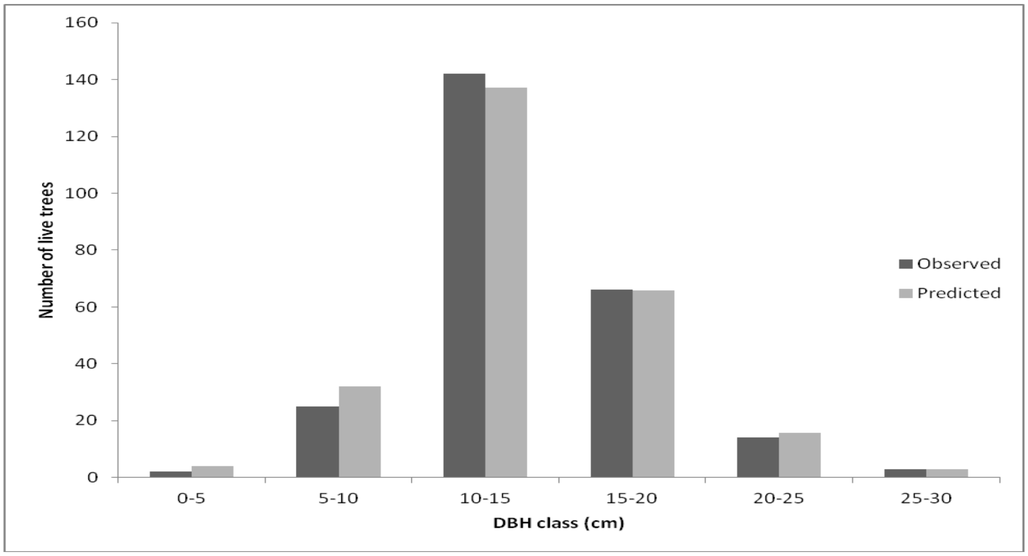


Figure 6.8. Observed and predicted numbers of live trees using survival model [6.6] that with TPA for natural jack pine validation prediction test.

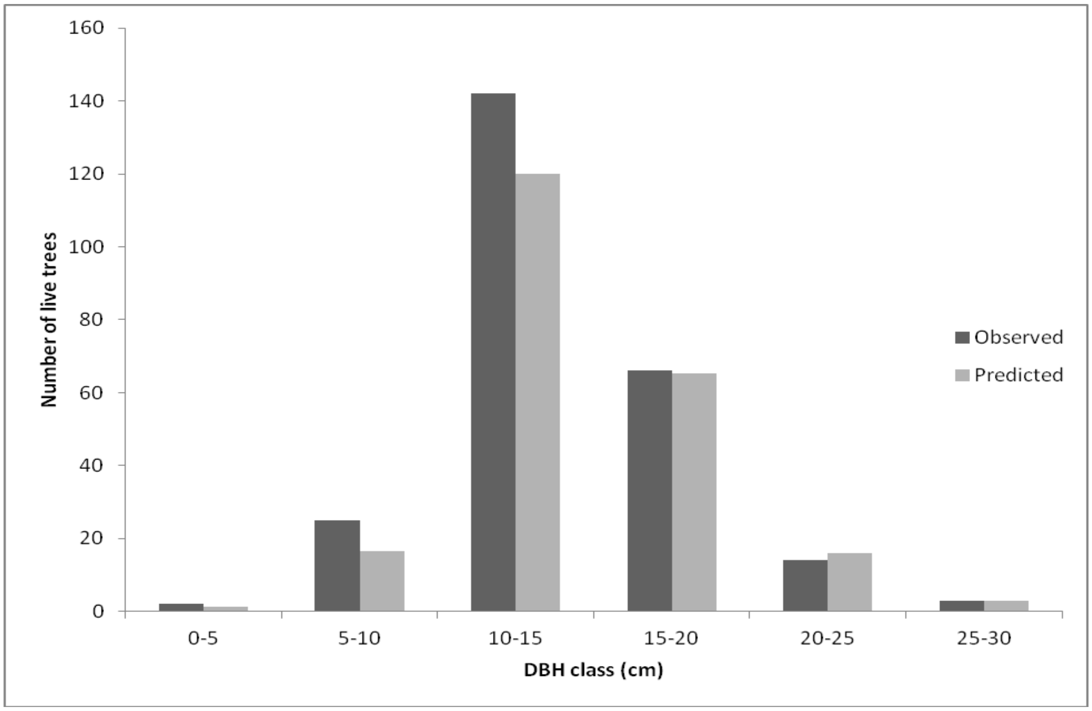


Figure 6.9. Observed and predicted numbers of live trees using survival model [6.7] that without TPA for natural jack pine validation prediction test.

The observed and predicted numbers of surviving trees by diameter classes for five models are summarized in **Figures 6.5 – 6.9**. Over all diameter classes, there is a high degree of correspondence between observed and predicted numbers of live trees for all three black spruce models (model [6.5]; **Figures 6.5 – 6.7**), and for the jack pine with TPA model (model [6.6]; **Figure 6.8**). By contrast, there were strong deviations between observed and predicted number of surviving trees for the jack pine without TPA model (model [6.7]; **Figure 6.9**), particularly within the smaller size classes (5-15 cm). This model clearly overestimates the survivorship of smaller trees.

In general, the model fitting statistics and validation results indicate that the individual-tree mortality models developed in this study are accurate and robust. For jack pine, the results indicate that the inclusion of spatial information (Thiessen polygon area) is necessary to increase model accuracy and prediction.

6.5 DISCUSSION

Changes in forest structure over time are largely driven by stand dynamics, with individual tree mortality playing a critically important role. Mortality is a major determinant of changes in forest stand composition, structure and productivity (Oliver and Larsson 1996). In applied forestry, tree mortality models are used to predict patterns of stand dynamics and mortality, and to improve forecasts of forest stand growth and future timber yields.

Individual tree mortality is determined by a number of factors, the effects of which are often synergistic (Franklin *et al*. 1987). The primary factors contributing to the mortality likelihood of a given tree are its relative size and growth rate, and the degree of competition it experiences (Buchman *et al*. 1983). Comparatively small, slower-growing trees (so-called “suppressed” individuals) in a forest stand experience strong competition from neighbouring trees, which further weakens them and makes them increasing susceptible to secondary factors such as insect pest and fungal pathogen attack (Franklin *et al*. 1987; Manion 1990).

In this study, spatial-dependent and spatial-independent individual tree mortality models were developed and validated for jack pine and black spruce in the boreal forests of Manitoba. Given that the factors contributing to individual tree mortality are numerous and synergistic in their effects (Franklin *et al*. 1987), multiple predictor variables were used to model tree mortality. Various combinations of potential predictor variables, including tree size (absolute and relative), growth rate and aspatial and spatial competition measures, were considered during the development of logistic regression mortality models. The predictor variables used in the final models were selected based on statistical significance, with consideration given to their ecological and biological relevance.

For both the upland and lowland black spruce mortality models, three predictor variables were statistically significant: bole diameter increment (*DI*), relative bole diameter (*D/MD*) and the total basal area of larger trees (*BAL*). Diameter increment (i.e. the absolute increase in bole diameter over five years), a measure of tree growth and vigour, was positively correlated with survivorship. Thus, less vigorous (i.e. slower-growing) trees are predicted to have a higher probability of mortality. This intuitive result is consistent with numerous other studies (e.g. Johnstone 1997; Dobbertin and Biging 1998; Yang *et al*. 2003). Relative bole diameter, a measure of canopy position of the tree in a stand, was also positively correlated with survivorship. The model therefore predicts that the smaller trees in a stand have a higher mortality risk (Ford 1975). The variable *BAL* (the total basal area within a plot of trees larger than the target tree) was negatively correlated with survivorship, indicating that mortality risk is greater for smaller trees in more “crowded” stands (i.e. stands with high total basal area). To summarize, the black spruce mortality models predict that survivorship is highest for larger, fast-growing trees in less crowded stands, and lowest for smaller, slow-growing trees in crowded stands (Carleton and Wannamaker 1987).

Three predictor variables proved statistically significant in the jack pine mortality model: Thiessen polygon area (*TPA*, an area-based measure of local crowding), tree size (D^2 or basal area) and relative bole diameter (*D/MD*). The polygon area ("area potentially available", Mithen *et al*. 1984) of a tree was positively correlated with survivorship; i.e. more locally crowded trees (i.e. small TPA) were more likely to die than less crowded ones. Previous studies in Ontario and Manitoba have also found that a higher intensity of local competition (smaller *TPA*) increases the probability of mortality in jack pine (Kenkel *et al*. 1989a, 1997). Tree size (squared diameter, or tree basal area) was negatively correlated with survivorship, indicating that smaller trees have higher mortality risk. As in black spruce, relative bole diameter was positively correlated with survivorship in jack pine. Thus, the model predicts that smaller-than-average trees within a given stand (i.e. suppressed individuals) are more likely die. This negative relationship between tree size and mortality likelihood is well documented for jack pine (e.g. Kenkel *et al*. 1997) and other tree species (e.g. Yang *et al*. 2003; Zhao *et al*. 2004; Chen *et al*. 2008).

Since spatial mapping information (required for *TPA* determination) is often not available in forest inventory data, a jack pine mortality model that excluded the variable *TPA* was also developed. In this second model, tree size (D^2 or basal area) and relative bole diameter (*D/MD*) were again statistically significant. The variable *BAL* (the total basal area within a plot of trees larger than the target tree) was also statistically significant, and was negatively correlated with survivorship. This indicates that mortality risk is higher for small trees in more "crowded" stands (i.e. stands with high total basal area). This substitution of the aspatial variable *BAL* for the spatial variable *TPA* in the model is perhaps not surprising, since *BAL* also measures the degree of crowding (though at the stand, rather than local, level). The aspatial model was found to provide less accurate predictions of tree mortality than the spatial model (i.e. the model containing variable *TPA*).

Both black spruce and jack pine establish very dense, mono-dominant and even-aged stands following a stand-destroying catastrophic forest fire (Larsen 1980). In jack pine, a highly shade-intolerant species, extensive self-thinning (density-dependent mortality) occurs as these post-fire stands develop (Yarranton and Yarranton 1975; Metsaranta *et al*. 2008). In a Manitoba jack pine permanent sample plot, for example, total stand mortality was > 80% between the ages of 15 and 55, and mortality was largely restricted to the smallest size (diameter) classes (Kenkel *et al.* 1997). Stands of black spruce, a shade-tolerant species, develop quite differently. Some self-thinning does occur, but not to the extent seen in jack pine. Indeed, very little mortality occurs in less dense stands, and even in very dense stands density-dependent mortality is limited (Carleton and Wannamaker 1987). As a result, established black spruce stands are often very dense and include smaller, somewhat suppressed trees; mortality is largely restricted to the most highly suppressed individuals in these stands (Carleton and Wannamaker 1987). My results provide evidence for these differences: the mean stand density of black spruce stands was almost four times higher than that of jack pine, but five-year jack pine mortality was much higher (15.2%, versus 5.4% for black spruce). In jack pine stands of a given age, extensive self-thinning results in stands of similar density. For example, 70 to 90 year-old stands (*n* = 10) in Saskatchewan and Manitoba averaged 1578 ± 362 trees/ha, ranging from 1200 – 2100 trees/ha (Metsaranta *et al*. 2008). By contrast, black spruce self-thinning is much less intensive, resulting in much more variable stand densities. For example, 60 to 80 year-old stands in northern Ontario (*n* = 8) averaged 5875 ± 2340 trees/ha, ranging from 2500 – 9000 trees/ha (Carleton and Wannamaker 1987).

In light of these differences, it is instructive to consider the similarities and differences between the black spruce and jack pine mortality models. In both models, relative diameter (i.e. tree diameter relative to the mean stand diameter) was a significant predictor of mortality for both black spruce and jack pine. Both models predict that smaller-than-average (“suppressed”) individuals have lower survivorship, an expected result when density-dependent mortality predominates (Ford 1975**)**. Total stand basal area of trees larger than the target tree (*BAL*) was a significant predictor of mortality in the black spruce model, and in the jack pine model that excluded the spatial variable (Thiessen polygon area). This indicates that mortality of small trees is highest in very dense stands, which has previously been described for black spruce stands (Carleton and Wannamaker 1987).

A major difference between models was the significance of local spatial competition (Thiessen polygon area) in the jack pine model, but not in the black spruce model. This suggests that the intensity of localized competitive interactions (i.e. among immediate neighbours, Kenkel *et al*. 1989a) is important in shade-intolerant species such as jack pine, but comparatively unimportant in shade-tolerant species such as black spruce.

A second difference between the models relates to the importance of tree growth versus size in predicting mortality. Tree growth (incremental increase in bole diameter) was a significant predictor of mortality in black spruce, but not in jack pine. Conversely, absolute tree size (bole diameter squared, or basal area) proved a significant predictor of mortality in jack pine, but not in black spruce. Again, these findings likely reflect differences in shade-tolerance between the two species. In black spruce, mortality is largely restricted to the smallest trees in the densest stands; such trees are expected to grow very slowly if at all, resulting in a significant positive relationship between low incremental growth and mortality likelihood (Carleton and Wannamaker 1987). By contrast, a slow-growing jack pine tree can survive provided it is not space-limited (i.e. by having a large Thiessen polygon area), as demonstrated in long-term studies of jack pine stand dynamics (Kenkel *et al*. 1989a, 1997). However, larger jack pine trees are more likely to survive than smaller ones, particularly during the self-thinning stage (Kenkel 1988). By contrast, self-thinning is less intense in black spruce stands and absolute tree size is therefore not an important predictor of mortality.

These findings have practical significant in forestry practices. The importance of local competitive interactions in jack pine implies that natural stand management should focus on thinning out smaller trees in order to obtain a more regular (over-dispersed) spatial pattern. Jack pine plantations should be established at relatively low densities, and tree should be planted in a regular grid in order to minimize mortality (and thus maximize timber yield). My results suggest that such practices would have limited benefit in black spruce stands, however, and would therefore be a waste of valuable time and resources.

Spatially dependent mortality models require mapped locations of all individual trees (Bella 1971; Hegyi 1974; Weiner 1982, 1984; Radtke *et al.* 2003), the collection of which is costly and time-consuming. As a result, mapped tree locations are often not available in large forest inventory data, limiting the application of spatial mortality models. However, recent developments of forest inventory technology – particularly in the areas of remote sensing and geographic information systems – will render the collection of mapped tree data easier and more cost-effective. This in turn will result in the wider application of spatially based mortality models in forest inventory and sustainable forest management.

Finally, a number of authors have noted that accurate modelling of individual tree mortality is challenging and difficult (Lee 1971; Hamilton 1986; Yang *et al.* 2003; Zhao *et al.* 2004). A great many factors contribute to tree mortality, and these are synergistic in their effects (Franklin *et al*. 1987). Furthermore, while the factors determining density-dependent mortality are quantifiable and reasonably well understood, density-independent factors (e.g. wind and ice storm damage, pathogenic disease, insect attack, bole girdling by large mammals) are very difficult if not impossible to predict. As a result, most mortality models (including the present study) focus on tree and stand-level attributes that are likely to predict density-dependent mortality.

CHAPTER 7 SUMMARY

Forests cover over 60% of the land surface of Manitoba. Two of the most economically important tree species in Manitoba, black spruce [*Picea mariana* (Mill.) BSP] and jack pine [*Pinus banksiana* Lamb], are found throughout these forests. There are over 330 million cubic meters of merchantable volume of black spruce and jack pine in Manitoba, or more than half the total merchantable volume (Manitoba Conservation 2006).

The objective of this study was to develop biologically reasonable and statistically robust growth and yield models for jack pine and black spruce in Manitoba. Such models are required in order to develop sound sustainable management policies for Manitoba's forest resources, and to provide reliable growth and yield estimates that are required for timber supply analysis. The growth and yield models developed for black spruce and jack pine included regression-based individual tree height growth and site index, tree diameter (basal area) growth, tree bole taper, and individual tree mortality models. The development of these models required the exploration, comparison and testing of a large number of potential regression equations and independent (factor) variables. In addition, statistical issues commonly encountered in forest growth and yield modeling, particularly problems of data autocorrelation and variable multicollinearity, were addressed using nonlinear least squares (NLS), generalized nonlinear least squares (GNLS), and nonlinear mixed-effects model (NLMM) regression approaches.

HEIGHT GROWTH AND SITE INDEX

Ten candidate height growth and site index regression equations, based on models used in other regions of Canada, were tested and compared for their utility in modeling height growth and site index of black spruce and jack pine in Manitoba.

Standard nonlinear least squares (NLS) regression analysis is sensitive to the spatial autocorrelation present in the bole (stem) analysis data used to develop height growth and site index models. Three approaches were therefore investigated to deal with the autocorrelation issue: generalized nonlinear least square (GNLS) regression, nonlinear mixed-effects model (NLMM) regression, and data reduction through random selection of a single value from each tree. Statistical tests and graphical examinations showed that these approaches produced similar results. The GNLS regression approach alleviated much, but not all, of the autocorrelation. The more statistically robust NLMM approach, which incorporates both fixed and random-effects parameters to estimate the covariance matrix of correlated data, successfully addressed the autocorrelation issue in the model fitting. As expected, the simple approach of data reduction (random selection of one value per tree) removed all spatial autocorrelation from the data.

Interestingly, the NLS models using one value per tree resulted in fitted model statistics, parameters and empirical height growth equations that were very similar to those obtained using all of the data (i.e. the autocorrelated data, with multiple values per tree). Indeed, a comparison of model predictions showed that all approaches (NLS, GNLS, NLMM) produced very similar height growth and site index results for both black spruce and jack pine. Thus, the presence of spatial autocorrelation in the bole analysis data did not appear to adversely affect model parameterization and prediction, suggesting that height growth and site index models fitted using NLS regression approach should not result in biased predictions in practical forestry applications.

The NLMM approach that accounts for both population mean and tree-specific variation was found to produce more accurate and reliable tree-specific prediction than the other modeling approaches. Prediction accuracy was further improved when one or more prior measurements were incorporated into the model. It was concluded that when prior measures are available, the NLMM approach should be used to increase prediction accuracy. In practical forestry applications, a fixed-effects model (which account only for variation in the population mean) will provide a reasonable working model.

As has been found in other studies, my results indicate that height growth and site index predictions are variable and somewhat unreliable for younger trees (< 20 years breast height age). In addition, limitations in the empirical data dictate that these height growth models should be restricted to predictions within an age range of 20 to 150 years (breast height age) for black spruce, and 20 to 100 years for jack pine.

Comparisons of the height growth and site index models developed for Manitoba black spruce and jack pine with those used in other Canadian provinces demonstrated that tree growth patterns were quite similar for all models over an age range of 20 to 100 years for black spruce, and 20 to 80 years for jack pine. The Manitoba models produced height growth predictions within the range of other Canadian models. The developed models can be used in Manitoba to predict tree height for a given site index and breast height age, or to iteratively determine site index using height and breast height age data. Height and site index tables for black spruce and jack pine in the Boreal Plain and Boreal Shield ecozones of Manitoba are given in the Appendix of this thesis.

DIAMETER (BASAL AREA)

Individual tree diameter increment models were developed for Manitoba lowland and upland black spruce stands, and managed and natural jack pine stands, using ordinary least squares regression analysis. A number of potential independent variables were considered during model fitting, particularly those related to tree size, site productivity, and both aspatial and spatial competitive effects.

Tree size variables were found to be good predictors of diameter (basal area) increment in black spruce and managed jack pine stands, but they were less important in natural jack pine stands. Parameter coefficients were positive for diameter but negative for both nonlinear terms (squared diameter and inverse diameter), indicating that diameter increment increases to a maximum in younger (smaller) trees, but then declines slowly (approaching zero) as trees mature. As expected, site index (a measure of site productivity) was also positively correlated with diameter increment. This variable was particularly important in natural jack pine stands, but was of lesser importance in managed jack pine and black spruce stands. Total stand basal area was not an important predictor of incremental growth, but the basal area of trees larger than the target tree (a relative measure of competition) was an important predictor variable, particularly for lowland black spruce and for both managed and natural jack pine stands. As expected, the model predicts that smaller trees in a given stand will have reduced incremental growth.

I also considered a distance-dependent (or spatial) competition measure, the Thiessen polygon area, as a potential variable to predict incremental growth of black spruce and jack pine. Thiessen polygon area proved to be an important predictor variable for natural jack pine and upland black spruce stands, but was less important in lowland black spruce and (especially) managed jack pine stands. This is expected, since local competitive effects are known to strongly influence growth in natural jack pine stands, but are much less important in managed stands due to the more even spacing of trees. The higher shade tolerance of black spruce likely explains the reduced importance of local competitive effects on the growth of this species.

BOLE TAPER

In this study, bole taper models were developed using stem (bole) analysis data from black spruce and jack pine in Manitoba. The variable exponent taper equations developed by Kozak (1988, 1994, 1995) were compared to more recently developed taper equations based on dimensional analysis (Sharma and Parton 2009). These models were initially compared using nonlinear least squares (NLS) regression analysis. Most of the models fit the data well, but the variable exponent taper equations showed severe multicollinearity. This was attributed to the large number of parameters (ranging from 7 to 11) in these models. Multicollinearity was much lower in the dimensional analysis models, which had only 4 – 6 parameters. Models based on dimensional analysis were therefore used to develop bole taper models for black spruce and jack pine in Manitoba.

Stem (bole) analysis data are spatially autocorrelated, since several measurements are taken from the same tree bole. Bole taper modelling based on nonlinear least square (NLS) regression was found to be strongly affected by data autocorrelation. To address the autocorrelation problem, the bole taper models were developed using nonlinear mixed-effects model (NLMM) regression analysis. This approach requires definition of an appropriate covariance structure for the model parameters, and the partitioning of parameters into a fixed component (a population mean response that is common to all trees) and a random component (responses that are specific to each tree). In addition, it is necessary to determine which parameters should be modelled as fixed-effects, and which as mixed-effects. The NLMM approach, using three random parameters and a SP(POW) covariance structure, proved very effective in dealing with the autocorrelation present in the black spruce and jack pine stem (bole) analysis data.

Prior measures are often used to increase the prediction accuracy of mixed-effects models. In this study, three prior measurement scenarios were investigated: one prior measure per tree (bole diameter at 6.5 m); two prior measures per tree (bole diameter at 0.3 and 6.5 m); and three prior measures per tree (bole diameter at 0.3, 2.6 and 6.5 m). Predictions of tree taper and volume were greatly improved by incorporating a single prior measure into the model, but the inclusion of additional prior measures provided little additional benefit. When available, the inclusion of a single prior measure (bole diameter at 6.5 m) is therefore recommended to increase the prediction accuracy of taper models of black spruce and jack pine in Manitoba.

The taper equations recommended for black spruce and jack pine in Manitoba are variants of the dimensional analysis model proposed by Sharma and Parton (2009). This equation required modification, however, since one of the parameters (relative height squared in the quadratic exponent) was not statistically significant for the Manitoba black spruce and jack pine bole data. Substituting the squared relative height term with two new terms – the reciprocal and log (base e) of relative height – improved model fit. A second modification – inclusion of crown ratio as a predictor variable – did not improve model performance, indicating that it is not necessary to include crown ratio in bole taper models for black spruce and jack pine in Manitoba.

MORTALITY

The major factors affecting survivorship of a given tree in a stand are its relative size, growth rate, and the degree of competition it experiences.

Comparatively small, slower-growing “suppressed” trees experience a disproportionate degree of competition from neighbouring trees, weakening them further and making them increasingly susceptible to secondary factors such as insect pest and fungal pathogen attack.

Both spatial-dependent and spatial-independent individual tree mortality models were developed and validated for jack pine and black spruce in Manitoba. Various combinations of potential predictor variables, including tree size (absolute and relative), growth rate, and both aspatial and spatial competition measures, were considered in developing the logistic regression mortality models. The predictor variables used in the final models were selected based on statistical significance, with consideration given to their ecological and biological relevance.

The predictive variables of bole diameter increment, relative bole diameter, and total basal area of trees larger than the target tree were statistically significant in the black spruce mortality models. Diameter increment, a measure of tree growth and vigour, was positively correlated with survivorship. Relative bole diameter, which measures the relative canopy position of a tree in a stand, was also positively correlated with survivorship. The total basal area of trees larger than the target tree was negatively correlated with survivorship, indicating that mortality risk is greater for smaller trees in more “crowded” stands. The black spruce mortality models therefore predict high survivorship for larger, fast-growing trees in less crowded stands, and lower survivorship for smaller, slow-growing trees in crowded stands.

In the jack pine mortality model, Thiessen polygon area (a measure of local crowding), tree size, and relative bole diameter were statistically significant predictor variables. Polygon area was positively correlated with survivorship, indicating that less crowded trees are more likely to survive than crowded ones. Tree size was negatively correlated with mortality likelihood, indicating that smaller trees have higher mortality risk. As in black spruce, relative bole diameter was positively correlated with survivorship, indicating that smaller-than-average trees within a given stand (i.e. suppressed individuals) are more likely die.

A jack pine mortality model that excluded Thiessen polygon area was also developed, since tree mappings are often not available in forest inventory data. In this second model, tree size and relative bole diameter were again statistically significant. The total basal area of trees larger than the target tree was also statistically significant, and as expected was negatively correlated with survivorship. This indicates that mortality probability is highest for small trees in crowded stands. This second model provided less accurate predictions of tree mortality than did the model that included Thiessen polygon area, however, indicating that the spatial location of a tree within a stand is an important predictor of mortality in natural jack pine stands.

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APPENDIX 1
Height and site index prediction table for black spruce (Boreal Plains Ecozone)

	SITE INDEX (m)																					
Age (years)	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**
5	1.6	1.7	1.8	1.9	2.0	2.2	2.3	2.5	2.6	2.8	3.1	3.3	3.6	4.0	4.4	4.8	5.3	5.8	6.4	7.0	7.7	8.4
10	1.9	2.1	2.3	2.5	2.8	3.0	3.3	3.6	4.0	4.3	4.8	5.2	5.8	6.4	7.0	7.7	8.5	9.3	10.2	11.1	12.1	13.1
15	2.1	2.5	2.8	3.1	3.5	3.9	4.3	4.7	5.2	5.7	6.3	6.9	7.6	8.4	9.2	10.0	11.0	11.9	13.0	14.0	15.1	16.2
20	2.4	2.8	3.3	3.7	4.2	4.7	5.2	5.7	6.3	7.0	7.7	8.4	9.2	10.1	11.0	12.0	13.0	14.0	15.1	16.2	17.4	18.5
25	2.7	3.2	3.7	4.3	4.8	5.4	6.0	6.7	7.4	8.1	8.9	9.8	10.6	11.6	12.6	13.6	14.6	15.7	16.8	17.9	19.1	20.2
30	3.0	3.6	4.2	4.8	5.5	6.2	6.9	7.6	8.4	9.2	10.1	11.0	11.9	12.9	13.9	15.0	16.0	17.1	18.2	19.3	20.5	21.6
35	3.2	3.9	4.7	5.4	6.1	6.9	7.7	8.5	9.4	10.3	11.2	12.1	13.1	14.1	15.1	16.2	17.2	18.3	19.4	20.5	21.6	22.7
40	3.5	4.3	5.1	5.9	6.8	7.6	8.5	9.4	10.3	11.2	12.2	13.2	14.1	15.2	16.2	17.2	18.3	19.3	20.4	21.5	22.5	23.6
45	3.7	4.6	5.6	6.5	7.4	8.3	9.3	10.2	11.2	12.1	13.1	14.1	15.1	16.1	17.1	18.2	19.2	20.2	21.3	22.3	23.3	24.3
50	4.0	5.0	6.0	7.0	8.0	9.0	10.0	11.0	12.0	13.0	14.0	15.0	16.0	17.0	18.0	19.0	20.0	21.0	22.0	23.0	24.0	25.0
55	4.3	5.3	6.4	7.5	8.6	9.7	10.7	11.8	12.8	13.8	14.8	15.8	16.8	17.8	18.8	19.7	20.7	21.7	22.7	23.6	24.6	25.6
60	4.5	5.7	6.9	8.0	9.2	10.3	11.4	12.5	13.6	14.6	15.6	16.6	17.6	18.5	19.5	20.4	21.4	22.3	23.2	24.2	25.1	26.1
65	4.8	6.0	7.3	8.6	9.8	11.0	12.1	13.2	14.3	15.3	16.3	17.3	18.3	19.2	20.1	21.0	21.9	22.9	23.8	24.7	25.6	26.5
70	5.0	6.4	7.7	9.1	10.3	11.6	12.8	13.9	15.0	16.1	17.0	18.0	18.9	19.8	20.7	21.6	22.5	23.3	24.2	25.1	26.0	26.9
75	5.3	6.7	8.2	9.6	10.9	12.2	13.4	14.6	15.7	16.7	17.7	18.6	19.5	20.4	21.3	22.1	23.0	23.8	24.6	25.5	26.3	27.2
80	5.5	7.1	8.6	10.1	11.5	12.8	14.1	15.3	16.4	17.4	18.3	19.2	20.1	21.0	21.8	22.6	23.4	24.2	25.0	25.8	26.7	27.5
85	5.8	7.4	9.0	10.5	12.0	13.4	14.7	15.9	17.0	18.0	18.9	19.8	20.6	21.5	22.2	23.0	23.8	24.6	25.4	26.2	27.0	27.8
90	6.0	7.7	9.4	11.0	12.6	14.0	15.3	16.5	17.6	18.6	19.5	20.3	21.2	21.9	22.7	23.4	24.2	24.9	25.7	26.5	27.3	28.1
95	6.3	8.1	9.8	11.5	13.1	14.6	15.9	17.1	18.2	19.2	20.0	20.9	21.6	22.4	23.1	23.8	24.5	25.2	26.0	26.7	27.5	28.3
100	6.5	8.4	10.2	12.0	13.6	15.1	16.5	17.7	18.7	19.7	20.6	21.3	22.1	22.8	23.5	24.2	24.8	25.5	26.3	27.0	27.7	28.5
105	6.8	8.7	10.6	12.5	14.1	15.7	17.0	18.2	19.3	20.2	21.0	21.8	22.5	23.2	23.8	24.5	25.1	25.8	26.5	27.2	27.9	28.7
110	7.0	9.1	11.1	12.9	14.7	16.2	17.6	18.8	19.8	20.7	21.5	22.2	22.9	23.5	24.2	24.8	25.4	26.1	26.7	27.4	28.1	28.9

115	7.3	9.4	11.5	13.4	15.2	16.7	18.1	19.3	20.3	21.2	22.0	22.7	23.3	23.9	24.5	25.1	25.7	26.3	27.0	27.6	28.3	29.0
120	7.5	9.7	11.9	13.8	15.7	17.3	18.7	19.8	20.8	21.7	22.4	23.0	23.6	24.2	24.8	25.3	25.9	26.5	27.2	27.8	28.5	29.2
125	7.7	10.0	12.3	14.3	16.2	17.8	19.2	20.4	21.3	22.1	22.8	23.4	24.0	24.5	25.1	25.6	26.2	26.7	27.3	28.0	28.7	29.3
130	8.0	10.4	12.6	14.8	16.7	18.3	19.7	20.8	21.8	22.6	23.2	23.8	24.3	24.8	25.3	25.8	26.4	26.9	27.5	28.1	28.8	29.5
135	8.2	10.7	13.0	15.2	17.1	18.8	20.2	21.3	22.2	23.0	23.6	24.1	24.6	25.1	25.6	26.1	26.6	27.1	27.7	28.3	28.9	29.6
140	8.5	11.0	13.4	15.7	17.6	19.3	20.7	21.8	22.7	23.4	24.0	24.5	24.9	25.4	25.8	26.3	26.8	27.3	27.9	28.4	29.1	29.7
145	8.7	11.3	13.8	16.1	18.1	19.8	21.2	22.3	23.1	23.8	24.3	24.8	25.2	25.6	26.0	26.5	27.0	27.5	28.0	28.6	29.2	29.8
150	8.9	11.7	14.2	16.5	18.6	20.3	21.6	22.7	23.5	24.2	24.7	25.1	25.5	25.9	26.3	26.7	27.1	27.6	28.1	28.7	29.3	29.9

Note: The age here means breast height age; site index in meters and values in the table are tree height (in meters).

APPENDIX 2
Height and site index prediction table for black spruce (Boreal Shield Ecozone)

	SITE INDEX (m)																					
Age (yrs)	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**
5	1.5	1.6	1.7	1.8	1.9	2.0	2.1	2.2	2.4	2.6	2.8	3.0	3.3	3.6	4.0	4.4	4.8	5.3	5.9	6.5	7.1	7.8
10	1.8	2.0	2.1	2.3	2.6	2.8	3.0	3.3	3.7	4.0	4.5	4.9	5.4	6	6.7	7.4	8.1	8.9	9.8	10.7	11.7	12.7
15	2.0	2.3	2.6	2.9	3.2	3.6	4.0	4.4	4.9	5.4	6.0	6.6	7.3	8.1	8.9	9.8	10.7	11.7	12.8	13.8	14.9	16.0
20	2.3	2.7	3.1	3.5	3.9	4.4	4.9	5.5	6.1	6.7	7.4	8.2	9	9.9	10.9	11.8	12.9	13.9	15.0	16.1	17.3	18.4
25	2.6	3.1	3.6	4.1	4.6	5.2	5.8	6.5	7.2	7.9	8.7	9.6	10.5	11.5	12.5	13.5	14.6	15.7	16.8	17.9	19.1	20.2
30	2.9	3.5	4.1	4.7	5.3	6.0	6.7	7.4	8.2	9.1	10.0	10.9	11.9	12.9	13.9	15.0	16.0	17.1	18.3	19.4	20.5	21.6
35	3.1	3.8	4.5	5.3	6.0	6.8	7.6	8.4	9.3	10.2	11.1	12.1	13.1	14.1	15.1	16.2	17.3	18.4	19.4	20.5	21.6	22.7
40	3.4	4.2	5.0	5.8	6.7	7.5	8.4	9.3	10.2	11.2	12.1	13.1	14.1	15.2	16.2	17.3	18.3	19.4	20.4	21.5	22.6	23.6
45	3.7	4.6	5.5	6.4	7.3	8.3	9.2	10.2	11.1	12.1	13.1	14.1	15.1	16.1	17.2	18.2	19.2	20.2	21.3	22.3	23.3	24.4
50	4.0	5.0	6.0	7.0	8.0	9.0	10.0	11.0	12.0	13.0	14.0	15.0	16.0	17.0	18.0	19.0	20.0	21.0	22.0	23.0	24.0	25.0
55	4.3	5.4	6.5	7.6	8.7	9.7	10.8	11.8	12.8	13.8	14.8	15.8	16.8	17.8	18.8	19.7	20.7	21.7	22.6	23.6	24.6	25.5
60	4.6	5.8	7.0	8.1	9.3	10.4	11.5	12.6	13.6	14.6	15.6	16.6	17.5	18.5	19.4	20.4	21.3	22.2	23.2	24.1	25.0	26.0
65	4.9	6.2	7.5	8.7	9.9	11.1	12.2	13.3	14.4	15.4	16.3	17.3	18.2	19.1	20	20.9	21.8	22.7	23.7	24.6	25.5	26.4
70	5.2	6.6	7.9	9.3	10.6	11.8	12.9	14.0	15.1	16.1	17.0	17.9	18.8	19.7	20.6	21.5	22.3	23.2	24.1	25.0	25.8	26.7
75	5.4	7.0	8.4	9.8	11.2	12.5	13.6	14.7	15.8	16.7	17.7	18.5	19.4	20.3	21.1	21.9	22.8	23.6	24.5	25.3	26.2	27.1
80	5.7	7.3	8.9	10.4	11.8	13.1	14.3	15.4	16.4	17.4	18.3	19.1	19.9	20.8	21.6	22.4	23.2	24.0	24.8	25.6	26.5	27.3
85	6.0	7.7	9.4	10.9	12.4	13.7	14.9	16.0	17.0	18.0	18.8	19.6	20.4	21.2	22.0	22.7	23.5	24.3	25.1	25.9	26.7	27.6
90	6.3	8.1	9.9	11.5	13.0	14.4	15.6	16.7	17.6	18.5	19.4	20.1	20.9	21.6	22.4	23.1	23.9	24.6	25.4	26.2	27.0	27.8
95	6.6	8.5	10.3	12.0	13.6	15.0	16.2	17.3	18.2	19.1	19.9	20.6	21.3	22.0	22.7	23.4	24.2	24.9	25.6	26.4	27.2	28.0
100	6.9	8.9	10.8	12.6	14.2	15.6	16.8	17.8	18.8	19.6	20.3	21.0	21.7	22.4	23.1	23.7	24.4	25.1	25.9	26.6	27.4	28.2
105	7.2	9.3	11.3	13.1	14.7	16.1	17.4	18.4	19.3	20.1	20.8	21.4	22.1	22.7	23.4	24	24.7	25.4	26.1	26.8	27.6	28.4

110	7.5	9.7	11.8	13.6	15.3	16.7	17.9	18.9	19.8	20.5	21.2	21.8	22.4	23.0	23.7	24.3	24.9	25.6	26.3	27.0	27.8	28.5
115	7.8	10.1	12.2	14.2	15.8	17.3	18.5	19.5	20.3	21.0	21.6	22.2	22.8	23.3	23.9	24.5	25.1	25.8	26.5	27.2	27.9	28.7
120	8.1	10.5	12.7	14.7	16.4	17.8	19.0	20.0	20.7	21.4	22.0	22.5	23.1	23.6	24.2	24.7	25.4	26.0	26.6	27.3	28.1	28.8
125	8.4	10.9	13.2	15.2	16.9	18.4	19.5	20.5	21.2	21.8	22.4	22.9	23.4	23.9	24.4	25.0	25.5	26.2	26.8	27.5	28.2	28.9
130	8.7	11.3	13.6	15.7	17.5	18.9	20.0	20.9	21.6	22.2	22.7	23.2	23.6	24.1	24.6	25.2	25.7	26.3	27.0	27.6	28.3	29.0
135	9.0	11.7	14.1	16.2	18	19.4	20.5	21.4	22.0	22.6	23.0	23.5	23.9	24.4	24.8	25.3	25.9	26.5	27.1	27.7	28.4	29.1
140	9.3	12.0	14.5	16.7	18.5	19.9	21.0	21.8	22.4	22.9	23.4	23.8	24.2	24.6	25.0	25.5	26.0	26.6	27.2	27.9	28.5	29.2
145	9.6	12.4	15.0	17.2	19.0	20.4	21.5	22.2	22.8	23.3	23.7	24.0	24.4	24.8	25.2	25.7	26.2	26.7	27.3	28.0	28.6	29.3
150	9.9	12.8	15.5	17.7	19.5	20.9	21.9	22.7	23.2	23.6	24.0	24.3	24.6	25.0	25.4	25.8	26.3	26.9	27.4	28.1	28.7	29.4

Note: The age here means breast height age; site index in meters and values in the table are tree height (in meters).

APPENDIX 3

Height and site index prediction table for jack pine (Boreal Plains Ecozone)

	SITE INDEX (m)																					
Age (years)	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**
5	1.6	1.7	1.8	1.9	2.1	2.3	2.4	2.6	2.8	3	3.2	3.5	3.7	4	4.3	4.6	4.9	5.2	5.6	5.9	6.3	6.7
10	1.9	2.1	2.4	2.6	2.9	3.2	3.6	3.9	4.3	4.7	5.1	5.5	6	6.5	6.9	7.5	8	8.6	9.1	9.7	10.3	11
15	2.2	2.5	2.9	3.3	3.7	4.1	4.6	5.1	5.6	6.1	6.7	7.3	7.9	8.5	9.1	9.8	10.5	11.2	11.9	12.7	13.4	14.2
20	2.4	2.9	3.4	3.9	4.4	4.9	5.5	6.1	6.8	7.4	8.1	8.8	9.5	10.2	11	11.8	12.6	13.4	14.2	15	15.9	16.7
25	2.7	3.3	3.8	4.4	5.1	5.7	6.4	7.1	7.8	8.6	9.3	10.1	10.9	11.7	12.6	13.4	14.3	15.2	16	16.9	17.9	18.8
30	3	3.6	4.3	5	5.7	6.5	7.2	8	8.8	9.6	10.5	11.3	12.2	13.1	14	14.9	15.8	16.7	17.6	18.6	19.5	20.4
35	3.2	4	4.7	5.5	6.3	7.2	8	8.8	9.7	10.6	11.5	12.4	13.3	14.2	15.2	16.1	17	18	19	19.9	20.9	21.9
40	3.5	4.3	5.2	6	6.9	7.8	8.7	9.6	10.5	11.5	12.4	13.3	14.3	15.3	16.2	17.2	18.2	19.1	20.1	21.1	22.1	23.1
45	3.7	4.7	5.6	6.5	7.5	8.4	9.4	10.3	11.3	12.3	13.2	14.2	15.2	16.2	17.2	18.1	19.1	20.1	21.1	22.1	23.1	24.1
50	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
55	4.2	5.3	6.4	7.5	8.5	9.6	10.6	11.6	12.7	13.7	14.7	15.7	16.7	17.7	18.8	19.8	20.8	21.8	22.8	23.8	24.8	25.8
60	4.5	5.6	6.8	7.9	9	10.1	11.2	12.2	13.3	14.3	15.4	16.4	17.4	18.4	19.4	20.5	21.5	22.5	23.5	24.5	25.5	26.5
65	4.7	6	7.1	8.3	9.5	10.6	11.7	12.8	13.8	14.9	16	17	18	19.1	20.1	21.1	22.1	23.1	24.1	25.1	26.1	27.1
70	5	6.3	7.5	8.7	9.9	11.1	12.2	13.3	14.4	15.5	16.5	17.6	18.6	19.6	20.6	21.7	22.7	23.7	24.7	25.7	26.7	27.7
75	5.2	6.6	7.9	9.1	10.3	11.5	12.7	13.8	14.9	16	17	18.1	19.1	20.2	21.2	22.2	23.2	24.2	25.2	26.2	27.2	28.2
80	5.4	6.8	8.2	9.5	10.7	11.9	13.1	14.2	15.4	16.4	17.5	18.6	19.6	20.6	21.7	22.7	23.7	24.7	25.7	26.7	27.7	28.7
85	5.7	7.1	8.5	9.9	11.1	12.4	13.5	14.7	15.8	16.9	18	19	20.1	21.1	22.1	23.1	24.1	25.1	26.1	27.1	28.1	29.1
90	5.9	7.4	8.8	10.2	11.5	12.8	13.9	15.1	16.2	17.3	18.4	19.4	20.5	21.5	22.5	23.5	24.5	25.5	26.5	27.5	28.5	29.5
95	6.1	7.7	9.2	10.6	11.9	13.1	14.3	15.5	16.6	17.7	18.8	19.8	20.9	21.9	22.9	23.9	24.9	25.9	26.9	27.9	28.8	29.8
100	6.3	7.9	9.5	10.9	12.2	13.5	14.7	15.9	17	18.1	19.2	20.2	21.2	22.3	23.3	24.3	25.3	26.2	27.2	28.2	29.2	30.1
105	6.5	8.2	9.8	11.2	12.6	13.8	15.1	16.2	17.4	18.4	19.5	20.6	21.6	22.6	23.6	24.6	25.6	26.6	27.5	28.5	29.5	30.4

110	6.7	8.5	10.1	11.5	12.9	14.2	15.4	16.6	17.7	18.8	19.8	20.9	21.9	22.9	23.9	24.9	25.9	26.9	27.8	28.8	29.8	30.7
115	6.9	8.7	10.3	11.8	13.2	14.5	15.7	16.9	18	19.1	20.2	21.2	22.2	23.2	24.2	25.2	26.2	27.1	28.1	29.1	30	31
120	7.2	9	10.6	12.1	13.5	14.8	16	17.2	18.3	19.4	20.5	21.5	22.5	23.5	24.5	25.5	26.4	27.4	28.4	29.3	30.3	31.2
125	7.4	9.2	10.9	12.4	13.8	15.1	16.3	17.5	18.6	19.7	20.7	21.8	22.8	23.8	24.7	25.7	26.7	27.6	28.6	29.6	30.5	31.5
130	7.6	9.5	11.2	12.7	14.1	15.4	16.6	17.8	18.9	20	21	22	23	24	25	26	26.9	27.9	28.8	29.8	30.7	31.7
135	7.8	9.7	11.4	13	14.4	15.7	16.9	18.1	19.2	20.2	21.3	22.3	23.3	24.3	25.2	26.2	27.1	28.1	29	30	30.9	31.9
140	7.9	9.9	11.7	13.2	14.6	16	17.2	18.3	19.4	20.5	21.5	22.5	23.5	24.5	25.4	26.4	27.4	28.3	29.2	30.2	31.1	32.1
145	8.1	10.1	11.9	13.5	14.9	16.2	17.4	18.6	19.7	20.7	21.8	22.8	23.7	24.7	25.7	26.6	27.6	28.5	29.4	30.4	31.3	32.2
150	8.3	10.4	12.2	13.7	15.2	16.5	17.7	18.8	19.9	21	22	23	23.9	24.9	25.9	26.8	27.7	28.7	29.6	30.5	31.5	32.4

Note: The age here means breast height age; site index in meters and values in the table are tree height (in meters).

APPENDIX 4
Height and site index prediction table for jack pine (Boreal Shield Ecozone)

	SITE INDEX (m)																					
Age (yrs)	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**
5	1.6	1.7	1.8	2	2.1	2.3	2.4	2.6	2.8	3	3.3	3.5	3.8	4.1	4.4	4.7	5.1	5.5	5.9	6.4	6.8	7.3
10	1.9	2.1	2.4	2.6	2.9	3.2	3.5	3.8	4.2	4.6	5	5.5	5.9	6.4	7	7.6	8.2	8.8	9.4	10.1	10.9	11.6
15	2.2	2.5	2.9	3.3	3.6	4.1	4.5	5	5.5	6	6.5	7.1	7.8	8.4	9.1	9.8	10.6	11.4	12.2	13	13.9	14.7
20	2.5	2.9	3.4	3.8	4.3	4.9	5.4	6	6.6	7.2	7.9	8.6	9.3	10.1	10.9	11.7	12.6	13.5	14.4	15.3	16.2	17.2
25	2.7	3.3	3.8	4.4	5	5.6	6.3	6.9	7.7	8.4	9.1	9.9	10.8	11.6	12.5	13.4	14.3	15.2	16.2	17.1	18.1	19.1
30	3	3.6	4.3	5	5.6	6.4	7.1	7.9	8.6	9.4	10.3	11.1	12	12.9	13.8	14.8	15.7	16.7	17.7	18.7	19.7	20.7
35	3.2	4	4.7	5.5	6.3	7.1	7.9	8.7	9.6	10.4	11.3	12.2	13.2	14.1	15.1	16	17	18	19	20	21	22
40	3.5	4.3	5.2	6	6.9	7.7	8.6	9.5	10.4	11.3	12.3	13.2	14.2	15.2	16.1	17.1	18.1	19.1	20.1	21.1	22.1	23.2
45	3.8	4.7	5.6	6.5	7.4	8.4	9.3	10.3	11.2	12.2	13.2	14.1	15.1	16.1	17.1	18.1	19.1	20.1	21.1	22.1	23.1	24.1
50	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
55	4.2	5.3	6.4	7.5	8.5	9.6	10.7	11.7	12.7	13.8	14.8	15.8	16.8	17.8	18.8	19.8	20.8	21.8	22.8	23.8	24.8	25.8
60	4.5	5.7	6.8	8	9.1	10.2	11.3	12.4	13.4	14.5	15.5	16.5	17.5	18.5	19.5	20.5	21.5	22.5	23.5	24.5	25.5	26.4
65	4.7	6	7.2	8.4	9.6	10.8	11.9	13	14.1	15.1	16.2	17.2	18.2	19.2	20.2	21.2	22.2	23.2	24.1	25.1	26.1	27
70	5	6.3	7.6	8.9	10.1	11.3	12.5	13.6	14.7	15.8	16.8	17.9	18.9	19.9	20.9	21.8	22.8	23.8	24.7	25.7	26.6	27.6
75	5.2	6.6	8	9.3	10.6	11.8	13	14.2	15.3	16.4	17.4	18.5	19.5	20.5	21.4	22.4	23.4	24.3	25.2	26.2	27.1	28.1
80	5.4	6.9	8.4	9.7	11.1	12.4	13.6	14.7	15.9	17	18	19	20	21	22	22.9	23.9	24.8	25.7	26.7	27.6	28.5
85	5.7	7.2	8.7	10.2	11.5	12.9	14.1	15.3	16.4	17.5	18.6	19.6	20.6	21.5	22.5	23.4	24.3	25.3	26.2	27.1	28	28.9
90	5.9	7.5	9.1	10.6	12	13.3	14.6	15.8	16.9	18	19.1	20.1	21.1	22	23	23.9	24.8	25.7	26.6	27.5	28.4	29.3
95	6.1	7.8	9.5	11	12.4	13.8	15.1	16.3	17.5	18.5	19.6	20.6	21.5	22.5	23.4	24.3	25.2	26.1	27	27.9	28.7	29.6
100	6.3	8.1	9.8	11.4	12.9	14.3	15.6	16.8	17.9	19	20	21	22	22.9	23.8	24.7	25.6	26.5	27.3	28.2	29.1	30
105	6.6	8.4	10.2	11.8	13.3	14.7	16	17.3	18.4	19.5	20.5	21.5	22.4	23.3	24.2	25.1	26	26.8	27.7	28.5	29.4	30.2

110	6.8	8.7	10.5	12.2	13.7	15.2	16.5	17.7	18.8	19.9	20.9	21.9	22.8	23.7	24.6	25.4	26.3	27.1	28	28.8	29.7	30.5
115	7	9	10.8	12.6	14.2	15.6	16.9	18.1	19.3	20.3	21.3	22.3	23.2	24.1	24.9	25.8	26.6	27.4	28.3	29.1	29.9	30.8
120	7.2	9.3	11.2	12.9	14.6	16	17.4	18.6	19.7	20.7	21.7	22.6	23.5	24.4	25.2	26.1	26.9	27.7	28.6	29.4	30.2	31
125	7.5	9.6	11.5	13.3	14.9	16.4	17.8	19	20.1	21.1	22.1	23	23.9	24.7	25.6	26.4	27.2	28	28.8	29.6	30.4	31.2
130	7.7	9.8	11.8	13.7	15.3	16.8	18.2	19.4	20.5	21.5	22.4	23.3	24.2	25	25.9	26.7	27.5	28.3	29.1	29.8	30.7	31.5
135	7.9	10.1	12.2	14	15.7	17.2	18.6	19.8	20.9	21.9	22.8	23.7	24.5	25.3	26.1	26.9	27.7	28.5	29.3	30.1	30.9	31.7
140	8.1	10.4	12.5	14.4	16.1	17.6	18.9	20.1	21.2	22.2	23.1	24	24.8	25.6	26.4	27.2	28	28.7	29.5	30.3	31.1	31.8
145	8.3	10.7	12.8	14.7	16.5	18	19.3	20.5	21.6	22.5	23.4	24.3	25.1	25.9	26.7	27.4	28.2	28.9	29.7	30.5	31.2	32
150	8.5	10.9	13.1	15.1	16.8	18.3	19.7	20.8	21.9	22.9	23.7	24.6	25.4	26.1	26.9	27.7	28.4	29.1	29.9	30.7	31.4	32.2

Note: The age here means breast height age; site index in meters and values in the table are tree height (in meters).