

**Estimates of genetic parameters for growth traits and of effects of
climatic transfer and edaphic conditions for select families of New
Brunswick black spruce**

by

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A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of

Master of Science in Forestry

in the Graduate Academic Unit of Forestry and Environmental Management

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This thesis is accepted by the
Dean of Graduate Studies

THE UNIVERSITY OF NEW BRUNSWICK

January, 2017

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ABSTRACT

The knowledge of genetic parameters estimate for black spruce in New Brunswick (NB) is limited. In this thesis, the estimates of genetic parameters for growth traits (bole volume, height, and diameter at breast height) and for stem forking (SF) in black spruce 35-year old family tests in NB are presented. These include heritability estimates (individual heritability and family mean heritability), type-B genetic correlation, age-age genetic correlation, and trait-trait genetic correlation. The growth of bole volume (V), tree height (HT) and diameter at breast height (DBH) are highly genetically controlled while SF is not. Type-B genetic correlations are moderately high for the growth traits, implying the weak environment \times genetic interactions within the geographic region. Age-age genetic correlations are strong for the growth traits but weak for SF. Trait-trait genetic correlations for V and HT, as well as V and DBH are strong and positive, but are weak for V and SF.

The potential effects of climatic transfer and of edaphic conditions on height growth of black spruce families are explored. Both the mean annual temperature and accumulated growing degree-days are important for height growth of black spruce in NB. Height growth is better on planting sites cooler than seed-source locations. Higher air temperatures resulting from changing climate will likely reduce black spruce height growth. Transfer difference in precipitation has little critical effect on height growth of black spruce from local NB sources planted in the province. In practice, temperature variable seems the most important climatic variable compared with other variables when deploying black spruce families. Transferring seed sources to relatively cooler sites will optimize height growth of black spruce in the province. Medium-rich soils of moderate moisture are the best for height growth of local black spruce in NB.

ACKNOWLEDGEMENTS

I express my gratitude to my supervisor, Dr. Krasowski for choosing me as his student and giving me a chance to study in Canada, for the continuous support of my graduate study, for teaching me stronger critical thinking. It was through his support, understanding, and kindness that I completed my master's degree. I could not imagine having a better supervisor for my graduate study.

I thank the other members of my Advisory Committee, my co-supervisor Dr. Yuhui Weng, for teaching me quantitative genetic analysis and providing me with direction, and technical support for the thesis; Dr. Guohua Yan, for opening the world of mathematical and statistical modeling to me; Michele Fullarton, for organizing and assisting with the field work.

I thank my family for giving birth to me and supporting me through my entire life. In particular, I must acknowledge my husband, whose love and encouragement made this thesis possible.

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Chapter 1: General Introduction

1.1 Introduction of black spruce

Black spruce (*Picea mariana* Mill. B.S.P.) is a wide-ranging, abundant conifer that grows across the northern parts of North America (Burns & Honkala, 1990). It is found in all 10 provinces and 3 Arctic territories of Canada, and extends into northern parts of the United States (Farrar, 1995; Larsen, 1980). Black spruce is widely distributed in New Brunswick (NB) (Burns & Honkala, 1990; NBDNR, 2007), where summers are short and cool, winters are long and cold, and humidity and precipitation tend to be high (Environment Canada, 2008). Black spruce can tolerate poorly drained, very acidic, and nutrient-deficient sites (Farrar, 1995). The range of soil moisture conditions it can tolerate is from very dry to very wet, and nutrient regimes vary from very poor to rich. The most productive sites for black spruce have well-decayed organic material, soils are moist but well-drained and have relatively high nutrient levels (Burns & Honkala, 1990).

Black spruce is monoecious. It occasionally reproduces asexually by a process called “layering”, especially on poor soil (Gates, 1938). The root system of black spruce is wide spreading but shallow, with most roots in the upper 20 cm of the soil (Burns & Honkala, 1990). The average longevity of black spruce is approximately 200 years, but ages up to 280 years have been reported in the Northwest Territories (Black & Bliss, 1980; Burns & Honkala, 1990). Rotation age of black spruce ranges from 90 to 130 years, based on the site condition, and mature black spruce averages 12 - 20 m in height and 20- 25 cm in DBH on good sites but only 8 - 12 m in height and 10 - 15 cm in DBH on poor quality sites (Burns & Honkala, 1990).

1.2 The importance of black spruce to forest industry in NB.

New Brunswick has approximately 6.1 million hectares of forests with 39 native tree species covering 85% of the landscape, providing wildlife habitat, recreational opportunities, and high-quality water and air (Martin, 2003; NBDNR, 2007). Forestry is NB's largest industry. Historically, forestry has been the cornerstone of NB's society and economy. The livelihood of many New Brunswickers' has depended on forestry, which directly employs over 22,000 people, contributes over \$1.45 billion to the NB economy annually, sustains about 40 mills throughout rural areas and provides opportunities for more than 1,500 forestry-supporting businesses (Martin, 2003; New Brunswick Department of Natural Resources, 2010).

Black spruce is ecologically and economically one of the most important tree species in NB (Martin, 2003). Due to its long wood fibers, the major commercial use of black spruce is the production of high quality pulp (Burns & Honkala, 1990). The strong, relatively light-weight, yellow-white wood makes black spruce ideal for lumber production and manufacturing of other wood products.

1.3 Black spruce family tests in New Brunswick

As one of the most important commercial tree species in New Brunswick, black spruce has been widely planted across the province (Martin, 2003). New Brunswick Tree Improvement Council (NBTIC) has been working on black spruce since the late 1970s with the goal of selecting, testing, and breeding fast growing families for use in reforestation (Fullarton, 2014).

In 1977, the NBTIC members started the selection of phenotypically desirable trees of black spruce (the "plus-trees") in natural stands. Trees displaying rapid growth, good crown form, and straight boles were selected as the plus trees (NBTIC, 1979, 1980). In

total, around 400 plus trees were selected by NBTIC members. Cones were collected from these trees and seeds were extracted, cleaned and sown at Kingsclear forest nursery. These provided greenhouse-grown black spruce seedlings materials for the following family tests (NBTIC, 1979, 1980).

Seven and eight black spruce first-generation family test sites were established in the 1979 series and 1980 series, respectively. Some of these test sites were subsequently abandoned for various reasons, leaving six test sites in each series. Some families were also abandoned due to inadequate quantities of seeds or seedlings, leaving 157 and 128 families for the 1979 and 1980 series, respectively.

1.4 Genetic parameter estimates for select NB black spruce

Despite the extensive work on black spruce in NB, the understanding of genetic control of its growth is still limited. Estimates of genetic parameters are required to guide the NBTIC breeding programs. These include the heritability (individual heritability, and family mean heritability), type-B genetic correlations, age-age and trait-trait genetic correlations among selected traits. Individual heritability and family mean heritability are the two common measures of the relative amount of genetic control for a given trait (White et al., 2007). Individual heritability is the ratio of additive genetic variance to total phenotypic variance, and family mean heritability is the ratio of the entire genetic variance to the total phenotypic variance (White et al., 2007). Type-B genetic correlation is estimated for a certain trait between each pair of environment. It is commonly used to quantify the family \times environment interaction in tree breeding program.

Several studies have reported genetic parameter estimates for black spruce. Lu and Charrette (2008) estimated genetic parameters of growth traits (height, DBH and stem volume) for black spruce in northwestern Ontario. Heritability estimates for DBH and stem volume (V) were lower than those for height, suggesting that height would be a

better target for selection in black spruce than the other examined traits. Type-B genetic correlations were relatively high for all traits, implying a limited importance of genetic \times environment interaction in practice. High estimates of age-age genetic correlations (>0.88) were reported in that study for tree height at 6, 11, and 19 years after planting. But contradicting results on height growth in black spruce were reported from central Nova Scotia by Mullin & Park (1994), being individual heritability was only 0.076 at age 5 and 0.052 at age 10 for height, while family mean heritability was 0.114 and 0.135 for the same periods, respectively. Age-age genetic correlations for height growth were strong, indicating that better trees selection can be done based on their young growth performance. Genetic \times environment interactions were statistically strong. Genetic parameter estimates for other conifer species have been reported from worldwide locations (e.g. Adams et al., 1994; Dieters et al., 1995; Dieters, 1996; Hodge & Dvorak, 2001; Lambeth, 1980; Mullin et al., 1995; 1992). But these studies were either based on relatively small samples or short trial durations. Large datasets and many years of growth are required for accurate genetic parameter estimation for long-living trees. Hence, more dependable estimates of genetic parameter estimates for black spruce families in NB are required.

While the primary objective of the black spruce selection and breeding program has been on increased growth, obtained benefits may be offset by reduced bole quality. Stem forking (SF), is a serious bole quality problem affecting many conifer species (Dvorak et al., 2007; Ladrach & Lambeth, 1991; Schermann et al., 1997; Xiong et al., 2014), and it is common in black spruce plantations (Krause & Plourde, 2008). Stem forking results in separation of the trunk into two or more trunks, often of similar sizes (Xiong et al. 2014). This decreases height and volume growth and wood quality, compromising its mechanical strength and reducing timber uniformity (Krause & Plourde, 2008; Xiong et al., 2010). Genetic studies on stem forking in coniferous species have rarely been reported and the few published studies have presented mixed results (Doede & Adams,

1998; Savill et al., 1999; Vargas-Hernandez et al., 2003; Weng et al., 2014). Xiong et al. (2010, 2014) showed that stem forking on loblolly pine (*Pinus taeda* L.) in South Carolina was partially under genetic control at family level but it was determined by environmental factors at the individual tree level. In contrast, stem forking in *Pinus patula* Schl. Et Cham. in Colombia was reported to be under moderate genetic control at individual tree level (Ladrach & Lambeth, 1991). No studies on genetic control of stem forking have been reported for black spruce in eastern Canada. If stem forking is under strong enough genetic control in black spruce, breeders may incorporate selection against this trait into the current black spruce breeding program. Otherwise, it would make more sense to focus on eliminating environmental causes of stem forking in black spruce.

This thesis estimates genetic parameters for growth traits (height, DBH and bole volume) and stem forking based on the first-generation black spruce family tests using approximately 280 open-pollinated families and more than 57,000 individual trees growing on 12 family testing sites in NB. Temporal variations in the genetic parameters are evaluated by comparing data gathered at different times from trial establishment.

1.5 Climatic transfer effects on height growth of select NB black spruce

Phenotypic expression is determined by the genotype and environmental conditions under which individuals live (Falconer & Mackay, 1996; Griffiths, Wessler, & Carroll, 2000). The maximum growth can be achieved through distributing the fastest growing families to planting sites that allow full expression of their genetic potential. So far, this matching has not been practiced in NB. One may assume that trees grow best at their original seed-source locations where conditions fit their needs very well. It is unknown if transfer to other conditions compromises or further improves the performance of the selected families. Which of these environmental conditions (i.e. temperature, precipitation, heat conditions) are most important to the expression of a target trait is another question.

Finally, the extent of dependence of a heritable trait on environmental factors would either offer possibilities for increasing genetic gains or for sparing time and effort if expected gains are too small.

Previous research on black spruce in NB showed that genetic gain can reach as high as 22.6% in 5-year height growth (Mullin et al., 1992). Relevant research has been reported for other conifer species worldwide (Andersson et al., 2003; Dhakal et al., 1996; Weng et al., 2010). For instance, research in New Zealand showed that the potential for volume growth in radiata pine (*Pinus radiata* D. Don) was 11% higher in improved than unimproved materials (Johnson et al., 1992). Even larger genetic gains were obtained in Aleppo pine (*Pinus halepensis* Mill.) in the area of Amphiloichia, Greece. Realized genetic gains of 21.25% in 10 years volume was achieved using the improved materials (Matziris, 2000). Similar result was reported in Australia that volume production in improved radiata pine at 10-12 years old was 22% greater than that of unimproved planting materials (Eldridge, 1982).

It is hypothesized that trees are best suited to environmental conditions where they originally established and display excellent growth (Smith, 1997; Tappeiner et al., 2007). If so, deploying their offspring to similar sites should provide most suitable conditions for expressing genetic potential for growth. However, it has not been necessarily the case. For instance, Schmidting (1994) showed that loblolly pine moved a modest distance to a cooler area than the seed source out-performed local trees in height growth but this reversed on sites much colder or warmer than the original seed source locations. A study in Slovakia showed that Norway spruce (*Picea abies* (L.) Karst.) grew better at planting sites with mean annual temperature approximately 1°C higher and growing season 12 days longer than their seed-source origins (Krajmerová et al., 2009). Research on Norway spruce and jack pine (*Pinus banksiana* L.) indicated that an increase in temperature affected growth positively within limits of species tolerance, but temperature changes

exceeding such limits were deleterious to growth (Matyas, 1994).

Currently, climate is changing rapidly. Between 2010 and 2099, the mean air temperature may increase by approximately 4°C in NB (Swansburg et al., 2004). Forest trees, including black spruce, are facing challenges in adapting to the changing climate. Locally adapted species may experience extreme climate conditions that they may not tolerate (Farjat et al., 2015; Gray et al., 2016; Ledig & Kitzmiller, 1992). We need to know the anticipated effects of climate change on survival and growth of local tree species.

In this study, the relationship between height growth of black spruce and climatic transfer difference will be examined with the goal of identifying the most important climatic variables affecting height growth. Evaluating the extent of their effects would determine how worthwhile it may be to seek the most suitable conditions for height growth of black spruce originating from different local sources in NB.

1.6 Edaphic effects on height growth of select NB black spruce

Soil moisture and nutrient conditions at the forest site significantly impact height growth of black spruce (Burns & Honkala, 1990). For instance, on dry sites, tree growth may decrease because of the lack of moisture, but excessive moisture can lead to low oxygen levels in the soil, slow nutrient cycling, slow decomposition and accumulation of organic matter, all resulting in poor height growth (Burns & Honkala, 1990). In my thesis, the relationship between height growth of black spruce and edaphic conditions of the planting sites will be examined with the goal of providing a guide for deploying black spruce to sites with most suitable edaphic conditions.

1.7 Objectives and contributions of the thesis

After 40 years of tree improvement for black spruce in New Brunswick, many elite black spruce families have been identified and used in reforestation. Currently, black spruce

families are deployed across the province without attempting to match them with most appropriate planting sites for maximizing growth. Thus the current practice may not maximize the growth potential.

The overall objective of this thesis is to provide information for guiding black spruce seedlots deployment. Specific goals are: 1) to estimate genetic parameters for the first-generation black spruce family tests in NB and explore their temporal patterns; 2) to identify how and to what extent climatic and edaphic conditions influence height growth of black spruce, so this knowledge would allow to choose sites optimizing height growth of black spruce families from different geographic locations.

This thesis will refine the estimates of genetic parameters of black spruce and identify important environmental factors that may be worth considering in developing most productive deployment strategies for the superior black spruce families in the province.

Chapter 2: Genetic parameters of growth and stem forking for black spruce in first-generation family tests in New Brunswick

Abstract:

Genetic parameters for growth traits and stem forking were estimated in black spruce [*Picea mariana* (Mill.) B.S.P.] (bS) first-generation family tests in New Brunswick (NB) including 285 open-pollinated families and more than 57,000 individual trees within two test series (1979 series and 1980 series). Height (HT), diameter at breast height (DBH), and stem forking (SF) were periodically measured between ages 5 to 35. The bole volume (V), HT and DBH were highly genetically controlled, with individual narrow-sense heritability (h_i^2) estimates of 0.29, 0.30 and 0.26, and family mean heritability (h_f^2) estimates of 0.80, 0.82 and 0.80, respectively. However, SF had low heritability, with mean of h_i^2 and h_f^2 of 0.03 and 0.11, respectively, indicating SF would be an ineffective selection target in black spruce. The moderately high type-B genetic correlation (r_B) estimates for all the traits (V, HT, DBH, and SF) implied negligible genotype \times environment interactions. Temporal trends of heritability and r_B had been shown in this study. Strong age-age genetic correlation (r_{age}) estimates were found for V, HT, and DBH, suggesting genetic selection can be made based on early tree growth. Estimates of genetic correlation between V and HT were positive and strong, as well as for V and DBH, indicating that improved volume growth can be achieved through selecting for either HT or DBH, whichever is least costly to measure and has higher heritability. Based on negligible negative genetic correlations between V and SF, as well as the weak age-age genetic correlations for SF, tree breeders may ignore SF as a selection target.

2.1 Introduction

Black spruce [*Picea mariana* (Mill.) B.S.P.] is one of the most important commercial tree

species in New Brunswick (Martin, 2003) and it has traditionally been used for lumber, pulp and paper, and other wood products. Due to its economic importance, New Brunswick Tree Improvement Council (NBTIC) has been working on black spruce since the late 1970s with the goal of selecting and breeding for fast growth families (Fullarton, 2014). The program started with plus-trees selection from natural stands and field testing of families derived from these selected trees.

Despite the extensive breeding work on black spruce in NB, understanding of inheritance patterns for growth traits such as volume, height, and DBH is still limited. Mullin and his colleagues (1992; 1994) have shown that black spruce growth traits are under moderately strong genetic control, but their work were either based on a relatively small sample size or on limited growth time period. It is well known that large datasets are required for accurate estimates of genetic parameters and that genetic parameters vary with tree ages.

While the primary objective of the black spruce breeding program is growth improvement, achieving this goal may be offset by compromised bole quality. SF (stem forking) is the separation of the trunk into two or more stems of similar size (Xiong et al. 2014). Stem forking can result in decrement in growth and wood quality such as the strength, timber harvest and wood uniformity, accordingly decrease the economic value of the wood (Xiong et al. 2010). Studies on stem forking in coniferous species have rarely been done. There were few reported studies attributed forking to environment conditions (Kerr & Boswell, 2001; Kerr, 1995; Savill et al., 1999). They had assumed that forking is mainly caused by environmental sources, i.e. late-season frosts, leader breakage or dieback, silvicultural practices. While others concluded it was partially under genetic control (Ladrach & Lambeth 1991; Xiong et al. 2010), i.e., assessment conducted in common ash (*Fraxinus excelsior* L) showed that genetic control of stem forking exists among common ash families (Savill et al., 1999). There have been few studies of the genetic control of forking in black spruce. If stem forking is under genetic control in

black spruce, breeders may incorporate its prevention into the current black spruce breeding program.

In this chapter, we estimate genetic parameters for growth traits (V, HT, DBH) and stem forking for the black spruce, including estimates of individual heritability (h_i^2) and family mean heritability (h_f^2), age-age genetic correlation (r_{age}), trait-trait genetic correlation (r_{trait}), and type-B genetic correlation (r_B). Approximately 280 open-pollinated families were planted on 12 test sites in NB. We also investigated temporal trends of these estimated genetic parameters.

2.2 Materials and methods

2.2.1 Family tests, trait measurements, and calculations

The NBTIC selected nearly 400 phenotypic plus-trees from black spruce natural stands in NB in the late 1970s. Plus-trees displayed desirable characters, such as rapid growth, straight boles, and good crown form. Seeds were collected from these plus-trees and seedlings were subsequently grown to establish the family tests. Two series of such tests were established, one in 1979 and another in 1980, with 157 and 128 families respectively, with six test sites in each series. A randomized complete block design was used for all test sites with 10 blocks per site and 4-trees per plot. Trees were planted at 2 × 2 m spacing. Individual tree HT, DBH, and SF were periodically measured/assessed at varying trial ages post-establishment (Table 1). Stem forking was recorded as binary variable (e.g. 1 for forking and 0 for no forking). Total bole volume was calculated using the equation provided by Honer (1983).

In the 35-year measurement, the NBTIC members and I randomly chosen 10 trees per block per site to measure height, since it was time consuming to measure all trees in a dense and tall plantation. Height at age of 35 years (HT_{35}) was predicted using the

following equation:

$$[1] \quad HT_{ijk} = \mu + S_i + B(S)_{j(i)} + DBH35_{ijk} + \varepsilon_{ijk}$$

where HT_{ijk} is the predicted HT_{35} of k th tree on j th block nested within i th site, μ is the overall mean, S_i is the effect of i th site, $B(S)_{j(i)}$ is the effect of j th block nested within i th site, $DBH35_{ijk}$ is the effect of DBH measurement at 35 years post-establishment for k th tree on j th block nested within i th site, ε_{ijk} is the error term. The regression coefficient of determination (r^2) was 0.81, indicating that HT at 35 years could be well predicted using equation [1].

V, HT and DBH were analyzed as continuous variables, whereas SF was analyzed as a categorical variable. In this paper, V, HT, DBH, and SF were recorded as V_n , HT_n , DBH_n , and SF_n , with n representing the trial ages post-establishment.

2.2.2 Statistical models and analysis

The validity of data was inspected using the SAS PROC UNIVARIATE procedure; outliers (outside of the three-interquartile range) were checked and excluded from further analysis (SAS Institute Inc, 2009). The cleaned data for V, HT and DBH were approximately normally distributed in all periodic measurements within each test series. Data were analyzed separately for each series because there were no common families between them. Preliminary data analysis showed that spatial heterogeneity was not substantial.

In each series, analyses of variance for V, HT and DBH were performed using the following model:

$$[2] \quad \mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}$$

where \mathbf{y} is the vector of observation on V_n , HT_n , or DBH_n ; \mathbf{X} is the design matrix of the fixed effect (e.g. the effects of site and block nested within site); \mathbf{b} is the vector of fixed factors; \mathbf{Z} is the design matrix of the random effects (e.g. family, family-site interaction, family-block interaction); \mathbf{u} is the vector of random factors; and \mathbf{e} is the vector of residuals. Variance components were estimated using the SAS Mixed procedure with the restricted maximum likelihood (REML).

The analysis for SF was performed using the following model:

$$[3] \quad \text{logit}(\mathbf{y}) = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u}$$

where \mathbf{y} is the vector of observation on SF_n ; \mathbf{X} , \mathbf{b} , \mathbf{Z} , \mathbf{u} are the same for Model[2]; Stem forking was recorded as binary (forked or unforked) and analyzed on the 1/0 score using a generalized linear mixed model with a logit link function of the SAS PROC GLIMMIX procedure. Over-dispersion was not a problem, the function fitted the SF_n data well, as indicated by the “fit statistics”.

The open-pollinated families were treated as true half-sib families, the genetic variance among them accounted for 1/4 of the total additive genetic variance (White & Hodge, 1989). The additive genetic coefficient of variation (GCV(%)), individual narrow-sense heritability (h_i^2), family mean heritability (h_f^2), and type-B genetic correlation (r_B) were calculated as follows:

$$[4] \quad \text{GCV} = 2\sigma_f / \bar{x} \times 100$$

$$[5] \quad h_i^2 = 4\sigma_f^2 / (\sigma_f^2 + \sigma_{sf}^2 + \sigma_{bf}^2 + \sigma_e^2)$$

$$[6] \quad h_f^2 = \sigma_f^2 / (\sigma_f^2 + \sigma_{sf}^2 / n_s + \sigma_{bf}^2 / (n_b \times n_s) + \sigma_e^2 / (n_b \times n_s \times n_r))$$

$$[7] \quad r_B = \sigma_f^2 / (\sigma_f^2 + \sigma_{sf}^2)$$

where σ_f^2 is the estimate of family variance; σ_{sf}^2 is the variance component of the family \times site interaction; σ_{bf}^2 is the variance component of the block \times family interaction; and σ_e^2 is the estimate of residual variance. For SF_n, σ_e^2 is fixed to be $\pi^2/3=3.29$ (Gilmour et al. 1985). Next, \bar{x} is the mean of a trait for specific age within a test series, while n_s , n_b , n_r were the actual numbers of sites, blocks per site, and trees per plot formulating the expected mean squares, owing to the nature of unbalanced data. Standard errors of variance and heritability were calculated using the Delta method. The estimate of heritability was considered to be low when it was below 0.15, moderate when between 0.15 and 0.40, and high at higher values (Weng et al. 2014).

Estimated type-B genetic correlation (r_B) was a quantitative criterion to test the site \times family interaction between sites within two test series (Lu & Charrette 2008). Site \times family interaction was considered negligible when the estimate of r_B was greater than 0.6 (Dieters, 1996).

Age-age genetic correlation (r_{age}) and trait-trait genetic correlation (r_{trait}) were calculated with the following formula:

$$[8] \quad r = \sigma_{y_1y_2} / (\sigma_{y_1}\sigma_{y_2})$$

where $\sigma_{y_1y_2}$ represents the genetic covariance of traits y_1 and y_2 measured at the same age on the same individual or between ages y_1 and y_2 measured of the same trait; σ_{y_1} , σ_{y_2} are the square roots of the genetic variance components of y_1 and y_2 , respectively.

2.3 Results and discussion

2.3.1 Growth performance

The two test series provided a large dataset for family performance evaluation. Table 2 shows family performance for V, HT, DBH and SF at varying ages across the two series.

Tree growth traits (V, HT, and DBH) varied significantly with test sites within each series ($Pr < 0.01$). Field test sites in colder and drier northwestern regions produced larger trees than sites in other regions of NB. A likely explanation was that tree phenotypic growth was influenced by climate and site productivity. Despite the significant differences among sites, mean V was similar for the same ages in the two test series (Table 2), with the same pattern for HT and DBH. The effect of site on SF was also significant ($Pr < 0.01$). There was a rough trend that test sites with faster tree growth had lower frequency of SF. Trees had a higher probability of being forked at younger than at older ages in both series. The frequency of SF was higher in the 1979 series than in the 1980 for the same ages, except for 10 years post-establishment (Table 2).

2.3.2 Estimates of genetic parameters

Estimates of h_i^2 , h_f^2 , GCV, and r_B were presented for the two test series at different ages (Table 3). On average, estimates of σ_f^2 accounted for 7.2% for V, 7.4% for HT, 8.3% for DBH, and 1.27% for SF, of the respective total phenotypic variance. The contribution of σ_f^2 to phenotypic variance for V, HT and DBH, increased with trial ages and then decreased, with the highest values occurring at trial ages of 15 to 20 years. It remained relatively stable over all ages for SF in both series. The estimates of σ_e^2 accounted for more than 70% of the total phenotypic variance (range: 70.82% - 97.11%) for all traits in both series and with different ages.

Genetic variations in growth traits were found (Table 3). On average, estimates of narrow-sense individual heritability (h_i^2) for HT were 0.22, 0.26, 0.36, 0.35, and 0.30 at ages 5, 10, 15, 20, and 35 years for two series, respectively (Figure 1). Mullin et al. (1994) reported mean h_i^2 estimates of 0.1 for tree height at ages of 10 – 15 years across six sites in the Maritimes planted with 45 open-pollinated black spruce families. Our heritability estimates were higher, with the mean of 0.39 and 0.23 for 1979 and 1980 series,

respectively, for tree height at ages of 10 – 15 years with more than 100 families in each series. The large dataset maybe contributed to the discrepancy. Family mean heritability (h_f^2) estimates for tree height remained relatively stable over time for both series (Figure 1). Heritability estimates were similar in both test series at the same ages and there was a trend for higher HT heritability estimates with increasing trial ages and then for a decrease at longest trial durations. The highest values were around 15 to 20 years after trial establishment (Figure 1). Similar temporal trends were also found for V and DBH (Table 3). The literature (Lu & Charrette 2008; Weng et al. 2007) documented analogous trends of heritability estimates for tree height up to approximately 20 years post trial establishment. Results from the present study detected this trend up to 35 years after establishment.

Individual heritability (h_i^2) estimates for V varied from 0.14 to 0.35 with the mean of 0.29, and family heritability (h_f^2) estimates varied from 0.72 to 0.86 with the mean of 0.80 across test series and trial ages (Table 3). Heritability estimates for DBH varied from 0.16 to 0.33 with the mean of 0.26 on individual-tree basis, and ranged from 0.74 to 0.86, with the mean of 0.80, when based on family means across the test series and trial ages (Table 3). Estimates of heritability for DBH were lower than those for height at ages lower than 20 years. The lower heritability estimates might have been caused by relatively small tree sizes likely increasing the magnitude of measurement errors. Some (Lu & Charrette 2008; Mullin et al. 1995) also documented lower heritability estimates for DBH than for height. These results indicated that HT is a better variable than DBH for selecting black spruce based on heritability, but our study showed that height and DBH were highly genotypically correlated in black spruce and that both HT and DBH were good for selecting black spruce for growth improvement.

Genetic coefficient of variation (GCV) was used to avoid the scale difference effects when comparing genetic variability among different ages and traits. The GCV remained

stable over all ages and in both series for each trait but it varied considerably while comparing different traits (Table 3). The V had the highest GCV with its mean of 27.12% over trial ages, followed by DBH (12.06%), HT (9.63%) and SF (1.3%) (Table 3).

For SF, the means of h_i^2 and h_f^2 were 0.03 and 0.11, respectively, across the test series and trial ages (Table 3). Estimates of h_i^2 and h_f^2 for SF were low and remained stable over all trial ages across the test series. Standard errors of heritability estimates were small. The low heritability and GCV estimates for SF might have been affected by its low frequency (Table 2). According to quantitative genetics, the estimates of heritability and GCV on binary traits (e.g. SF) were functions of their mean incidence frequencies (Falconer 1996). When the mean SF incident rate departed away from 50% (in this study, the mean incident rate for SF was about 30%), both phenotypic and genetic variances became smaller, resulting in relatively low h_i^2 , h_f^2 and GCV. The h_f^2 was relatively low when compared with others' results, where h_f^2 of SF ranged from 0.3~0.5 (Codesido & Fernández-López 2008; Weng et al. 2014; Xiong et al. 2010, 2014). This study confirmed that SF was under weak genetic control both on individual and family levels. It seemed more meaningful to focus on environmental than on genetic effects when considering stem forking in black spruce.

2.3.3 G × E interactions

The genotype × environment interactions were small for all traits through all ages and in both series as indicated by relatively large estimates of r_B (Table 3). From ages 5 to 35, the estimates of r_B for HT increased with time since planting in both series (Figure 2), and remained relatively high (range: 0.69~0.92, mean=0.81). Similar trends were found for V and DBH, indicating the weak genotype × environment interaction. Estimates of r_B for SF varied considerably between the two series and among measurement times, with the average of 0.69 (range: 0.40~1.00). There seemed to be little operational importance

of accounting for site \times family interaction in deployment of open-pollinated black spruce families in NB, according to the criteria for interpreting the site \times family interaction (Dieters, 1996). Insignificant site \times family interaction for black spruce and for some coniferous species were also reported across test sites in eastern Canada (Lu & Charrette 2008; Mullin et al. 1995; Mullin & Park 1994; Mullin et al. 1992; Weng et al. 2014).

2.3.4 Age-age genetic correlations

Estimates of r_{age} for V were positive and strong at different trial ages for both series (range: 0.85 ~ 0.99), as well as for HT and DBH (Table 4). The longer the interval between measurements, the lower the age-age genetic correlation estimates were (Table 4). Volume estimated at trial ages of 10 and 15 years showed strong and positive correlation with V estimated at ages 20 and 35 years in both series. Tree HT at early years (e.g. 5 or 10 years) also had a strong genetic correlation with those measured at later trial ages (15, 20, and 35 years) in both test series (r_{age} range: 0.76~0.95, mean=0.86). These strong age-age genetic correlations were also reported from other studies (Kang 1991; Lambeth 1980; Weng et al. 2007). For black spruce with rotation age of more than 60 years, this raises concerns about using age-age genetic correlations estimated at younger ages to predict the growth performance at maturity. Estimates of r_{age} for DBH from the two series were also high and positive with the mean of 0.94 over ages. DBH estimated at trial age of 10 or 15 years genetically correlated well with the DBH at the following trial ages.

Estimates of r_{age} for SF were lower than those for V, HT and DBH. Results of assessments at early ages were negatively genetically correlated to those in assessments at older ages. Low h_i^2 and h_f^2 for SF suggested that environmental effects could be the major cause for trees becoming forked, whereas genetic effects would be a minor cause. Late-season frosts, accidental damage such as bird attack, wind damage, or pathogenic

agents can also cause forking (Kerr & Boswell 2001). When SF occurred, one of the forks might have dominated the others (Drenou 2000). Trees will have lower probability of becoming forked as they grow older.

2.3.5 Trait-trait genetic correlations

Table 5 showed the genetic correlations among V, HT, DBH, and SF at varying trial ages. In both series, estimates of genetic correlation between V and HT were positive and strong at different trial ages (range: 0.81~0.99), as well as those for V and DBH (0.86~1.00). This was expected given the volume was calculated as a function of HT and DBH. Results also showed that genetic correlation between HT at different trial ages (HT₅, HT₁₀, HT₁₅, HT₂₀, HT₃₅) and DBH (DBH₁₀, DBH₁₅, DBH₂₀, DBH₃₅) were strong (mean= 0.87) and significantly different from zero, with small standard errors. These results were expected, given black spruce's well-coordinated growth in HT and DBH found in central and eastern Canada (Peng 1999). Because the main goal of black spruce tree improvement was to increase bole volume by rotation age, results indicated that maximum volume could be achieved through selecting for either HT or DBH, since the three traits (V, HT, and DBH) were strongly genetically correlated.

Negative and weak genetic correlations between V and SF were found, as well as for HT and SF in both series at various ages. They suggested that trees with faster height growth and larger bole volume may have a slightly lower probability of being forked than slower growing trees. Stem forking was, hence, of no concern when selecting black spruce families for fast growth.

2.4 Implications to black spruce tree improvement

Results of this study had implications for black spruce breeding programs going into advanced stages. Substantial genetic variations in V, HT, DBH and SF were found in the

family tests. Positive and strong genetic correlations between V and HT, as well as V and DBH, were found in this study, indicating that maximum volume growth can be achieved through selecting for either HT or DBH, whichever is less costly to measure. Strong genetic correlation between HT and DBH indicated that improving one trait would produce genetic gains in the other. The low heritability and weak genetic correlations with V eliminated SF as a selection target for black spruce.

Acknowledgements

The authors thank the dedicated NBTIC members, whose contribution and support made the success of this program possible. Support of the study by a grant from the Natural Sciences and Engineering Research Council of Canada to MJK is gratefully acknowledged.

Table 1. Information about black spruce family tests and trial assessment ages.

Test series	No. of sites	No. of families	Trial assessment (years from establishment)			
			V	HT	DBH	SF
1979	6	157	15,20,35	5,10,15,20,35*	15,20,35	5,10,15,20
1980	6	128	10,15,20,35	5,10,15,20,35*	10,15,20,35	5,10,15,20

Note: asterisk (*) indicates HT at 35 years predicted by regression model. V=volume, HT=height, DBH=diameter at breast height (1.3m), SF=stem forking, all are cumulative over time.

Table 2. Mean V (m³), HT (cm), DBH (cm), and incidence of SF, with standard deviation in parentheses for each trial series.

Series	V ₁₀	V ₁₅	V ₂₀	V ₃₅	
1979		0.011(0.009)	0.030(0.019)	0.109(0.061)	
1980	0.001(0.001)	0.011(0.006)	0.033(0.015)	0.105(0.043)	
	HT ₅	HT ₁₀	HT ₁₅	HT ₂₀	HT ₃₅
1979	80.3(30.2)	255.9(82.9)	489(103.7)	680.4(124.9)	1226(161)
1980	83.3(26.1)	265.3(70.6)	492.9(83.8)	684.2(103.7)	1240(97.3)
	DBH ₁₀	DBH ₁₅	DBH ₂₀	DBH ₃₅	
1979		6.9(2.4)	10.1(2.7)	14.9(3.8)	
1980	2.7(1.3)	7.0(1.8)	10.7(2.1)	15.0(2.9)	
	SF ₅	SF ₁₀	SF ₁₅	SF ₂₀	
1979	0.32	0.27	0.44	0.36	
1980	0.2	0.28	0.32	0.29	

Note: V=volume, HT=height, DBH=diameter at breast height, SF=stem forking

Table 3. Individual and family heritability (h_i^2 and h_f^2 , with standard errors in parentheses), genetic coefficients of variation (GCV), and type-B genetic correlations (r_B) for two series (1979 and 1980) of black spruce family trials in New Brunswick.

Trait	Series	Age	h_i^2 (SE)	h_f^2 (SE)	GCV(%)	r_B
V	1979	15	0.35(0.03)	0.84(0.11)	34.21	0.71
		20	0.32(0.05)	0.82(0.12)	27.09	0.76
		35	0.30(0.04)	0.77(0.11)	22.92	0.80
	1980	10	0.14(0.02)	0.72(0.10)	32.99	0.53
		15	0.26(0.04)	0.82(0.12)	25.28	0.91
		20	0.34(0.05)	0.86(0.12)	24.61	0.87
		35	0.31(0.05)	0.75(0.11)	22.76	0.92
HT	1979	5	0.24(0.03)	0.82(0.12)	15.36	0.70
		10	0.34(0.05)	0.86(0.12)	13.74	0.75
		15	0.44(0.06)	0.90(0.12)	10.99	0.89
		20	0.38(0.05)	0.85(0.11)	9.35	0.86
		35	0.30(0.04)	0.80(0.11)	4.81	0.92
	1980	5	0.19(0.03)	0.82(0.12)	12.09	0.72
		10	0.18(0.03)	0.79(0.12)	9.33	0.69
		15	0.27(0.04)	0.81(0.12)	7.75	0.89
		20	0.32(0.05)	0.84(0.12)	7.46	0.82
		35	0.30(0.05)	0.73(0.11)	5.37	0.89
DBH	1979	15	0.33(0.04)	0.86(0.16)	14.78	0.84
		20	0.28(0.04)	0.81(0.11)	11.20	0.84
		35	0.27(0.04)	0.79(0.11)	10.49	0.90
	1980	10	0.16(0.03)	0.78(0.12)	15.68	0.66
		15	0.23(0.04)	0.80(0.12)	11.65	0.92
		20	0.26(0.04)	0.84(0.12)	10.30	0.89
		35	0.31(0.05)	0.74(0.11)	10.33	0.90
SF	1979	5	0.01(0.00)	0.07(0.02)	0.87	0.51
		10	0.01(0.00)	0.10(0.02)	1.52	0.74
		15	0.01(0.00)	0.09(0.02)	0.92	0.70
		20	0.06(0.02)	0.10(0.02)	1.24	0.63
	1980	5	0.00(0.01)	0.11(0.09)	0.81	0.40
		10	0.01(0.00)	0.08(0.02)	1.23	0.53
		15	0.10(0.02)	0.13(0.02)	1.85	1.00
		20	0.09(0.02)	0.12(0.02)	1.96	1.00

Note: V=volume, HT=height, DBH=diameter at breast height, SF=stem forking

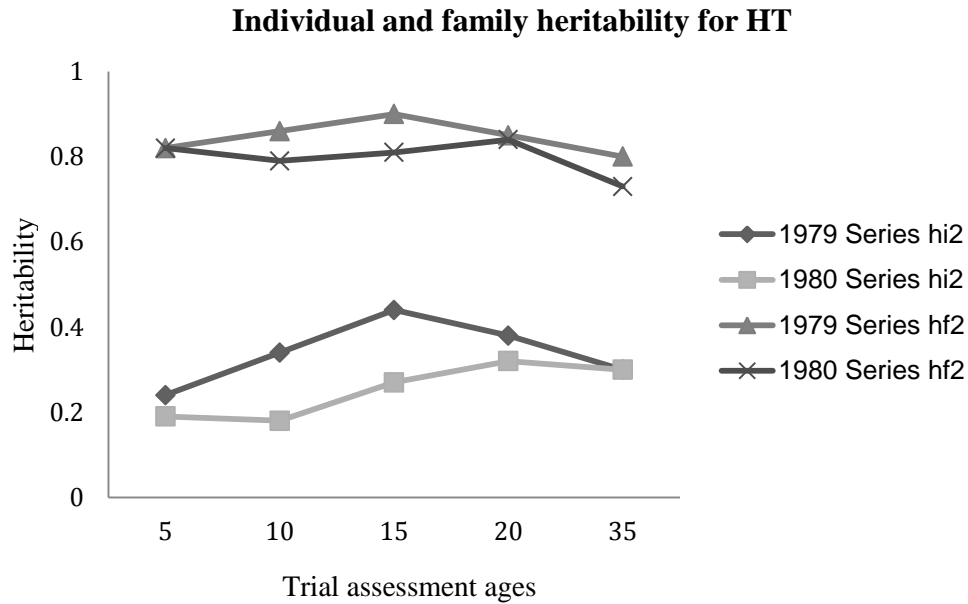


Figure 1. Temporal trends for individual and family heritability (h_i^2 and h_f^2) for height (HT) in 1979 and 1980 series of black spruce family trials in New Brunswick.

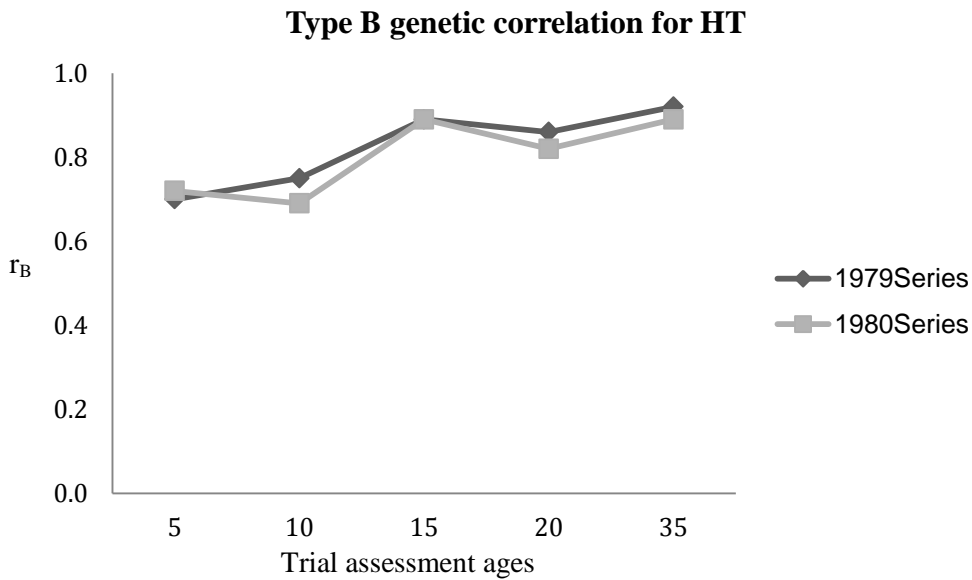


Figure 2. Temporal trends for type-B genetic correlation (r_B) for height (HT) in 1979 and 1980 series of black spruce family trials in New Brunswick.

Table 4. Estimates of age-age genetic correlations (r_{age}) for volume (V), height (HT), DBH (diameter at breast height) and SF (stem forking), with standard errors in the parentheses.

Series	Trait	V ₁₅	V ₂₀	V ₃₅		
1979	V ₁₅		0.99(0.00)	0.91(0.02)		
	V ₂₀			0.99(0.00)		
1980	V ₁₀	0.97(0.01)	0.90(0.02)	0.85(0.03)		
	V ₁₅		0.94(0.01)	0.85(0.03)		
	V ₂₀			0.97(0.01)		
		HT ₁₀	HT ₁₅	HT ₂₀	HT ₃₅	
1979	HT ₅	0.95(0.01)	0.91(0.02)	0.89(0.02)	0.83(0.03)	
	HT ₁₀		0.98(0.00)	0.97(0.01)	0.88(0.02)	
	HT ₁₅			1.00(0.00)	0.91(0.02)	
	HT ₂₀				0.87(0.02)	
1980	HT ₅	0.89(0.02)	0.85(0.03)	0.77(0.05)	0.76(0.05)	
	HT ₁₀		0.95(0.01)	0.88(0.02)	0.88(0.03)	
	HT ₁₅			0.98(0.00)	0.80(0.05)	
	HT ₂₀				0.96(0.01)	
		DBH ₁₅	DBH ₂₀	DBH ₃₅		
1979	DBH ₁₅		0.99(0.00)	0.90(0.02)		
	DBH ₂₀			0.99(0.00)		
1980	DBH ₁₀	0.96(0.01)	0.91(0.02)	0.85(0.03)		
	DBH ₁₅		0.98(0.00)	0.88(0.03)		
	DBH ₂₀			0.96(0.01)		
		SF ₁₀	SF ₁₅	SF ₂₀		
1979	SF ₅	-0.37(0.15)	-0.57(0.12)	-0.38(0.15)		
	SF ₁₀		-0.54(0.11)	-0.59(0.09)		
	SF ₁₅			-0.48(0.11)		
1980	SF ₅	-0.65(0.19)	-0.58(0.17)	-0.04(0.26)		
	SF ₁₀		-0.53(0.1)	-0.58(0.1)		
	SF ₁₅			-0.44(0.09)		

Note: V_n, HT_n, DBH_n, and SF_n, represent V, HT, DBH, and SF, respectively, with n representing the trial ages post-establishment.

Table 5. Estimates of trait-trait genetic correlations (r_{trait}), with standard error in parentheses for V (volume), HT (height), DBH (diameter at breast height), and SF (stem forking).

Series	Trait	H ₅	H ₁₀	H ₁₅	H ₂₀	H ₃₅	DBH ₁₀	DBH ₁₅	DBH ₂₀	DBH ₃₅	SF ₅	SF ₁₀	SF ₁₅	SF ₂₀
1979	V ₁₅	0.90(0.02)	0.98(0.00)	0.96(0.01)	0.86(0.02)	0.91(0.01)		0.97(0.01)	0.96(0.01)	0.94(0.05)	-0.09(0.14)	-0.21(0.11)	-0.25(0.11)	-0.33(0.10)
	V ₂₀	0.86(0.03)	0.91(0.01)	0.94(0.01)	0.92(0.01)	0.88(0.01)		0.97(0.01)	0.99(0.01)	0.98(0.01)	-0.13(0.14)	-0.26(0.11)	-0.26(0.12)	-0.30(0.11)
	V ₃₅	0.81(0.03)	0.86(0.03)	0.89(0.02)	0.85(0.03)	0.99(0.00)		0.94(0.01)	0.98(0.00)	0.99(0.00)	0.54(0.10)	-0.24(0.11)	-0.32(0.11)	-0.09(0.04)
	H ₅							0.89(0.00)	0.85(0.00)	0.84(0.00)	-0.52(0.11)	-0.45(0.1)	-0.47(0.1)	-0.42(0.10)
	H ₁₀							0.92(0.00)	0.87(0.02)	0.88(0.02)	-0.01(0.14)	-0.06(0.12)	-0.07(0.12)	-0.08(0.12)
	H ₁₅							0.90(0.02)	0.89(0.02)	0.90(0.02)	-0.00(0.14)	-0.06(0.12)	-0.05(0.12)	-0.08(0.12)
	H ₂₀							0.87(0.02)	0.86(0.03)	0.85(0.03)	-0.00(0.14)	-0.06(0.11)	-0.03(0.12)	-0.06(0.11)
	H ₃₅							0.90(0.02)	0.98(0.00)	1.00(0.00)	0.11(0.14)	-0.16(0.11)	-0.08(0.12)	-0.03(0.12)
1980	V ₁₀	0.99(0.01)	0.99(0.00)	0.90(0.02)	0.88(0.02)	0.87(0.03)	0.98(0.00)	0.93(0.01)	0.90(0.03)	0.88(0.02)	-0.16(0.23)	0.43(0.11)	-0.01(0.10)	-0.11(0.11)
	V ₁₅	0.91(0.02)	0.92(0.02)	0.94(0.01)	0.89(0.02)	0.76(0.05)	0.93(0.01)	0.97(0.00)	0.93(0.01)	0.90(0.02)	-0.25(0.23)	0.55(0.10)	-0.06(0.11)	-0.11(0.11)
	V ₂₀	0.75(0.04)	0.87(0.03)	0.85(0.03)	0.89(0.02)	0.89(0.04)	0.85(0.03)	0.95(0.01)	0.98(0.00)	0.97(0.00)	-0.11(0.24)	0.44(0.11)	-0.11(0.10)	-0.03(0.11)
	V ₃₅	0.64(0.06)	0.79(0.04)	0.80(0.03)	0.88(0.02)	0.99(0.00)	0.75(0.05)	0.86(0.03)	0.95(0.01)	1.00(0.00)	-0.04(0.24)	0.33(0.12)	-0.11(0.10)	-0.10(0.11)
	H ₅						0.89(0.03)	0.82(0.04)	0.77(0.05)	0.76(0.05)	-0.03(0.25)	0.12(0.13)	-0.03(0.11)	-0.01(0.11)
	H ₁₀						0.96(0.01)	0.88(0.03)	0.84(0.03)	0.85(0.03)	-0.05(0.25)	0.09(0.14)	-0.03(0.11)	-0.01(0.11)
	H ₁₅						0.88(0.03)	0.84(0.03)	0.81(0.04)	0.79(0.04)	-0.03(0.25)	0.08(0.14)	-0.03(0.11)	-0.01(0.11)
	H ₂₀						0.81(0.04)	0.80(0.04)	0.79(0.04)	0.90(0.02)	-0.02(0.24)	0.07(0.13)	-0.02(0.11)	-0.01(0.11)
H ₃₅						0.87(0.03)	0.87(0.03)	0.95(0.01)	1.00(0.00)	-0.06(0.25)	0.06(0.13)	0.00(0.11)	-0.01(0.11)	

Note: V_n, HT_n, DBH_n, and SF_n, represent V, HT, DBH, and SF, respectively, with n representing the trial ages post-establishment.

Chapter 3: Modeling climatic transfer and edaphic effects on height growth of select black spruce families in New Brunswick

Abstract:

Two separate statistical models were used to predict (i) the seed transfer response and (ii) edaphic effects of testing sites on the height growth of select black spruce (*Picea mariana* Mill. B.S.P.) families in New Brunswick (NB), Canada.

The transfer differences between seed-source locations and planting sites in mean annual temperature (D_MAT) and the number of growing degree days (D_GDD) were important to height. These variables and their squares (D_MAT, D_MAT², D_GDD, D_GDD²) jointly explained, on average, 24.2% and 20.3% variation in height growth at 20 years (HT₂₀) in the 1979 and 1980 series, respectively. Typically, families transferred to cooler planting sites than those of seed origin had better height growth than that at seed-source locations. Black spruce height growth at 20 years is predicted to increase by about 20.2% when moving seeds to planting sites with mean annual temperature 2°C lower than seed origin. The ongoing climate change with increased temperature may be detrimental to height growth of black spruce in NB. Transfer differences in mean annual precipitation were not critical for height growth of black spruce planted in NB. Best height growth in the trials was on nutritionally better sites of medium soil richness and moderate moisture.

3.1 Introduction

Black spruce (*Picea mariana* Mill. B.S.P.) is a transcontinental coniferous tree important in much of boreal Canada and in Alaska (Burns & Honkala, 1990; Farrar, 1995). In New Brunswick (NB), black spruce (bS) is widely used for lumber, pulp, paper, and other wood products (NBDNR, 2007). To enhance productivity of black spruce plantations, the New Brunswick Tree Improvement Council (NBTIC) initiated a black spruce tree improvement program in the late 1970s, and since then many genetic trials have been established. The main goal of the early trials was to select phenotypically desirable trees to derive families for testing and selecting these with best genetic predisposition for fast growth (Fullarton, 2014). Genotypes of the species may have significant influence on the productivity of plantations (Falconer & Mackay, 1996; Griffiths et al., 2000). Research on Scots pine (*Pinus sylvestris* L.) in Northern Sweden exemplifies benefits of genetic selection and improvement resulting in 10% greater growth in height than that of unimproved trees (Andersson et al. 2003). Even greater gains from genetic selection were obtained in the southern USA. Volume production in improved loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) was 10% to 30% greater than that of unimproved planting material (McKeand et al. 2003). Research on black spruce in NB showed that genetic gains for 5-year height growth of 22.6% might be achieved using the best 1% of the tested families (Mullin et al., 1992).

Studies of environmental effects on phenotypic growth of coniferous species have been reported. Salminen & Jalkanen (2005) found that the mean July temperature was the main environmental controller of height growth in Scots pine (*Pinus sylvestris* L.) in northern Finland. Subedi & Sharma (2013) developed tree-diameter growth models for black spruce and jack pine (*Pinus banksiana* Lamb.) in Ontario using a nonlinear mixed-effects approach. Their results showed that more precipitation during growing season increased diameter growth in these species but excessively wet growing seasons reduced diameter growth. Higher air temperatures during the growing season favored diameter growth in jack pine but decreased it in black spruce. Unfortunately, Subedi & Sharma (2013) sampled too few trees in too few growing seasons to provide a reliable estimate of the relationship between tree diameter growth and these climatic variables. Research in British Columbia showed that trembling aspen (*Populus tremuloides* Michx) and black spruce site indices increased significantly with increasing growing degree-days

(GDD) of a geographic locale (Messaoud & Chen, 2011). In New Zealand, mean growth of clover was strongly positively correlated with GDD (Hutchinson et al., 2000). These findings showed that GDD could be related to plant growth performance in different ecosystems.

It is hypothesized that trees are best suited to environmental conditions at sites where they originally established and display favorable phenotypic characteristics such as excellent growth (Carter, 1996; Farjat et al., 2015; Schmidting, 1994). If so, deploying their offspring to similar sites may provide very suitable growth conditions. However, it has been shown that this is not necessarily the case. Wells & Wakeley (1966) showed that, when moved the loblolly pine seed sources to the north a modest distance, the growth increased, but growth declined when seed sources moved too far north or south from original location. Another study in eastern North America showed that balsam fir (*Abies balsamea* L.) grows better at planting sites cooler than their seed origin in a certain range (Carter, 1996).

In this study, the relationships between height growth of black spruce and differences in temperature, precipitation, and GDD between seed-source locations and testing sites will be examined to determine if and to what extent they influence height growth of black spruce. Height was selected as the dependent variable because it is one of the most heritable growth traits in black spruce and is highly correlated with bole volume growth, according to the previous chapter of this thesis and as reported in another study (Mullin et al., 1992).

It is likely that edaphic conditions of planting sites significantly impact height growth of black spruce (Brady & Weil, 2007; Burns & Honkala, 1990; Farrar, 1995). To address this, another model examines how height growth of black spruce responds to edaphic variables of the planting sites. Overall, the study may provide results useful in guiding deployment of select black spruce families to most suitable sites with environmental conditions enhancing the genetic gain in growth by allowing the genetic potential to be fully realized.

3.2 Materials and Methods

3.2.1 Selection of families and their testing

During the late 1970s, approximately 400 black spruce plus-trees were selected from natural

forest stands in New Brunswick by New Brunswick Tree Improvement Council (NBTIC) members. The trees were selected for desired phenotypic characteristics, especially for vigorous height growth and good bole quality (Fullarton, 2014). Seeds from open-pollinated superior trees were collected and seedlings were subsequently grown for family tests. Two series of such tests were established, one in 1979 and another in 1980, with 157 and 128 families respectively. Each series used different families. Six testing sites were established in each series. The testing sites were widely distributed in the province (Fig. 3). A randomized complete block design was used for all the testing sites with 10 blocks per site and 4-trees per plot. Trees were planted at a spacing of 2×2 m. Tree height (HT) was periodically measured by the NBTIC members at 5, 10, 15, and 20 years after planting. In the 35-year measurement, only 10 trees per block per site were randomly chosen to measure height, so that height at 35-year were not included into the models.

3.2.2 Data

When the seed source locations and testing sites were located near the Environment Canada weather stations, climatic data for these sites were obtained directly from the nearest weather station. However, many seed sources were collected far from weather stations. In order to estimate climatic variables for such locations, multiple regressions were developed, using the geographic locations of weather stations across NB as independent variables and their climatic data as dependent variables. Latitudes and longitudes of all the Environment Canada weather stations in NB were accessed as well as their climatic data (1979-2000), including the mean annual temperature (MAT, °C), mean annual precipitation (MAP, mm/year), daily maximum (T_{\max} , °C) and minimum temperature (T_{\min} , °C) (see Environment Canada of New Brunswick website). The daily growing degree-days were calculated from T_{\max} and T_{\min} and the arbitrary base temperature of 5 °C as shown below:

$$\text{GDD} = \frac{T_{\max} + T_{\min}}{2} - T_{\text{base}}$$

$$\text{GDD} = 0 \text{ if } \frac{T_{\max} + T_{\min}}{2} < T_{\text{base}}.$$

The yearly average growing degree-days (GDD) for every Environment Canada weather station were calculated from the sums of GDD. Separate multiple regressions were built for MAT, MAP,

and GDD of the weather station, and the regression models fitted well (r^2 greater than 0.7). Geographic information (latitude and longitude) were available for every testing site and seed-source location, so the climatic variables were predicted for each of the location. The three climatic variables (MAT, MAP, yearly average growing degree-days GDD) were selected based on literature review and are likely the main controllers of black spruce height growth (Andalo et al., 2005; Burns & Honkala, 1990; Farjat et al., 2015; Gray et al., 2016; Matyas, 1994; Rehfeldt et al., 2003).

Information on ecosite classification was accessed from provincial records, for each testing site and seed source location (NBDNR 2007). Soil nutrient and moisture levels were adapted from ecosite descriptions and categorized for site richness as: poor, med, and rich; and for site moisture as dry, med, and wet (NBDNR 2007).

3.2.3 Statistical analysis

The validity of data in each test series was first inspected using the R (R Development Core Team, 2011), and outliers (located outside of three interquartile ranges) were removed. Less than 1% of the data were detected as outliers. Cleaned data on tree height were approximately normally distributed in all periodic measurements within each series.

3.2.3.1 Climatic transfer function for height growth of black spruce

Black spruce climatic transfer functions were built (Model [1]) considering height growth at 5, 10, 15, and 20 years from planting as a function of climatic transfer difference (climatic variable differences between the seed-source locations and testing sites). Data on height at 5, 10, 15, and 20 years after planting were first analyzed separately for each series and then for the two series combined. Height was treated as the dependent variable. Independent variables included the transfer differences between seed-source locations and testing sites in MAT, MAP, yearly average GDD, and their squares. These variables were expected to reflect the transfer effects on height growth of black spruce. Only climatic effects of seed transfer were considered in Model [1]:

$$\text{Model [1]} \quad \text{HT}_{ijk} = \beta_0 + \beta_1 X_1 + \beta_2 X_1^2 + \beta_3 X_2 + \beta_4 X_2^2 + \beta_5 X_3 + \beta_6 X_3^2 + \epsilon_{ijk}$$

Where HT_{ijk} is the mean height growth of family k with the seed source i at a testing site j , β_0 is the intercept and β_m for $m=1, \dots, 6$ are the regression coefficients, X_1 , X_2 , and X_3 are the transfer difference between seed-source location and testing site in mean annual temperature (D_MAT), mean annual precipitation (D_MAP), and yearly average growing degree-days (D_GDD), respectively, $\varepsilon_{ijk} \sim N(0, \sigma^2)$ is the random error with the mean of zero and constant variance of σ^2 . The model allows for quadratic term for each predictor as the relationship between height growth and climate is generally non-linear (Rehfeldt et al., 1999).

3.2.3.2 Edaphic response function for height growth of black spruce

Model [2] tests the dependence of height growth on soil properties at testing sites. Families in each series were divided into three ranking categories (“good”, “med”, and “low”) based on their average height-growth performance at 20 years across the testing sites. Each rank contained approximately 40 families from the top performance down, respectively. The dependence of height growth on soil properties of testing sites was explored using the following model:

$$\text{Model [2]} \quad HT_{ijk} = \text{Rank}_i \times \text{Nutrient}_{S_j} + \text{Rank}_i \times \text{Moist}_{S_k} + \varepsilon_{ijk}$$

Where HT_{ijk} is the height growth of the i th ranked family at the testing site with j th soil nutrient and k th moisture level, Rank_i is the effect of i th family rank, Nutrient_{S_j} and Moist_{S_k} are the effect of j th soil nutrient level and k th moisture level at each testing site. Soil nutrient is labeled as: poor, med, and rich, and as dry, med, and wet for soil moisture.

3.3 Results

Climatic-transfer variables in model [1] explained, on average, 33.0% and 22.0% of the total variation in height from all measurement times in the 1979 and 1980 series, respectively (Table 6). The climatic variables explained less phenotypic variation in height when data from both series were combined (Table 7) than when analyzed separately for each series (Table 6).

3.3.1 Climatic transfer effects on height growth: temperature

Differences in MAT resulting from seed transfer relate to height growth similarly in the two series. Coefficients of D_MAT have the same sign in both series at all measurement times (Table

6). The same is true for D_MAT^2 , except the first measurement at 5 years after planting (HT_5) (Table 6). D_MAT and D_MAT^2 coefficients varied more between the two series in earlier than in later height measurements. D_MAT and D_MAT^2 jointly explained, on average, 13.7% and 15.2% of the total variation in height (calculated according to the partial R^2 of D_MAT and D_MAT^2 in Table 6) over 20 years of growth in the 1979 and 1980 series, respectively (Table 6). The relationship of height with D_MAT was similar at all measurement times, so only HT_{20} will be shown. MAT at the seed origin was not found to be optimal for height growth, especially for families in the 1979 series (Fig. 4a). In that series, height growth was greater on colder planting sites than seed-source sites, and transfer seeds to sites warmer than seed-source location reduced height growth (Fig. 4a). However, in the 1980 series, height growth was unrelated to D_MAT (Fig. 4b). In the two series combined, better height growth was observed when black spruce families were transferred to sites with lower MAT than their sites of origin (Fig. 4c). Temperature variables (D_MAT and D_MAT^2) jointly can explain much larger variation in height growth than precipitation (D_MAP and D_MAP^2) can and heat variables (D_GDD and D_GDD^2) in Model [1] (Table 6).

3.3.2 Climatic transfer effect on height growth: heat accumulation (GDD)

With one exception, D_GDD effects were statistically significant for height at all measurement times and in both series. D_GDD and D_GDD^2 jointly explained, on average, 10.5% and 5.1% variation in height growth in the 1979 and 1980 series, respectively. With the exception of data from one early measurement, coefficients of D_GDD and D_GDD^2 had the same signs between the two series (Table 6). Coefficients differences in D_GDD between the two series were large in early measurements but diminished in later measurements, the same is true for D_GDD^2 (Table 6). Heat accumulation at the seed source locations was not optimal for height growth of the tested black spruce families (Fig. 5). In the 1979 series, height growth (HT_{20}) increased with positive D_GDD (when GDD of the testing sites less than that of seed-source locations) (Fig. 5a). In the 1980 series, and when both series were combined, this trend did not show (Fig. 5b-c).

3.3.3 Climatic transfer effects on height growth: precipitation

Even though D_MAP and D_MAP^2 showed statistically significant effects on height growth of

black spruce for most of the measurement times, on average, only 8.6% and 1.5% of height variation could be jointly explained by the two variables from all measurements times in the 1979 and 1980 series, respectively (Table 6). Further, the two series often differed in signs of D_MAP and D_MAP^2 coefficients (Table 6).

3.3.4 Edaphic effects on height growth

In Model [2], a large phenotypic variation in height could be explained by Rank×Nutrient and Rank×Moisture (Table 8). The model r^2 averaged across the height measurement times were 62% and 76% in the 1979 and 1980 series, respectively (Table 8). Family rankings (Low, Med, Good) were consistent for height growth performance at all nutrient and moisture levels (Fig. 7 - 8).

In the 1979 series, differences among family ranks were smaller in the Nutrient_Med level than at the other nutrient levels, and families in all ranks performed better on med or rich nutrient levels than on poor sites (Fig. 7a). Similar patterns showed when the two series were combined (Fig. 7c). In the 1980 series, only two nutrient levels were represented at testing sites, with med nutrient level missing (Fig. 7b).

Better height growth (HT_{20}) was found on med soil moisture levels while wet testing sites reduced height growth more than dry sites did, compared to med-moist sites, as shown for the 1980 series (Fig. 8b) and with the two series combined (Fig. 8c). In the 1979 series, only two moisture levels were represented at the testing sites, with the wet moisture level missing, and families of all ranks performing better on dry than wet sites (Fig. 8a). Differences among family ranks were smaller on dry sites than on other sites in the 1979, 1980 series and two series combined (Fig. 8).

3.4 Discussion

3.4.1 Climatic transfer affects height growth of select black spruce families.

Most independent variables (especially the temperature-transfer variables) in Model [1] significantly influenced height growth of black spruce but each explained only a modest portion of phenotypic variation. Reported transfer functions for loblolly pine and Norway spruce had r^2

ranging from 0.20 to 0.46 (Schmidtling, 1994), a range similar to those in our results. Transfer functions for loblolly pine and Norway spruce were developed mainly for differences in temperature between seed-source locations and testing sites. In our study, not only temperature but also precipitation and heat accumulation were included. This may provide a better base for evaluating transfer effects on height growth in black spruce. Differences in MAT and GDD between sites of origin and testing sites were more important to height growth than transfer differences in precipitation.

Our study did not support the assumption that “local seed is best for reforestation” when considering the temperature (Smith, 1997; Tappeiner et al., 2007). In our study, better height growth of black spruce was found on cooler planting sites but this only evaluated one tree characteristic. Our study had a relatively narrow range of D_MAT from -2.05°C to 1.80°C in the 1979 series, and from -2.99°C to 2.01°C in the 1980 series. Within that range, our study suggested that planting sites cooler in MAT by up to 2°C than the seed-source locations will increase height growth of black spruce families regardless of their performance ranks. This would increase gains from selection and deployment. Unfortunately, the ongoing climate change might increase average air temperatures by as much as 4 to 5°C by 2100 in NB (Swansburg et al., 2004). This may be detrimental to black spruce height growth, limiting gains from tree improvement. The relationship between height growth and D_MAT was different in the two series (Fig. 4), possibly reflecting a different assemblage of families in each series. Carter (1996) studied 10 North American tree species, finding most of them optimally adapted to temperature conditions at their original seed-source locations. However, balsam fir grew better at planting sites cooler than their seed-source origin. Black spruce and balsam fir are both boreal species adapted to cold sites throughout their ranges (Burns & Honkala, 1990) and this may explain their better growth at cooler sites. Another potential explanation of the difference between the two series in effects of D_MAT on height growth is the possible differences in site microclimates reflecting variation in site topographic positions, exposure, aspect, etc. These are influences that are not accounted for in data from meteorological stations. Perhaps NB does not have contrasting enough climates to outweigh this limitation.

Effects of differences in heat accumulation (D_GDD) between the sites of seed origin and testing sites were similar to the effects of D_MAT. Height growth of black spruce could be improved by

deploying black spruce families to testing sites with less GDD than their seed-source locations in the 1979 series and the two series combined. But this trend did not shown in the 1980 series. Differences between outcomes of analyses of the 1979 and 1980 series regarding D_GDD were puzzling and probably result of the different assemblages of families in each series or factors unaccounted for in this study.

Differences in mean annual precipitation between seed origin and planting sites do not seem to be greatly affecting height growth of black spruce in NB (Fig. 6). However, research in Quebec showed that transferring white spruce (*Picea glauca* (Moench) Voss) to drier sites with less precipitation will produce an increase in tree growth (height and DBH) (Andalo et al., 2005). Possibly, our study sites were all within precipitation range adequate for the growth of black spruce. Overall, the transfer differences in precipitation do not appear to be critical determinants of height growth for black spruce planted in NB from local sources. The ongoing changing climate will increase precipitation in NB (Swansburg et al., 2004), but may not dramatically affect the performance of black spruce unless the magnitude and frequency of floods result in infrastructure damage, soil erosion, or tree damage (Houghton et al., 2001).

3.4.2 Most suitable soil condition for black spruce

Results of Model [2] showed that height growth of black spruce families would be better on planting sites with medium nutrient and medium moisture. Medium soil richness and moisture were generally better for height growth of black spruce, and growth reductions were greater on wet than on dry sites, compared to the med-moisture sites. Excessive moisture can lead to low oxygen levels in the soil, slow nutrient cycling, slow decomposition and accumulation of organic matter, all resulting in poor height growth (Burns & Honkala, 1990).

3.4.3 Recommendation for black spruce family deployment

Our study shows that temperature is important for optimal height growth of black spruce in NB, both the MAT and accumulated GDD. Typically, cooler planting sites than those of seed origin had better height growth than that at the seed-source locations or on warmer than seed-source sites, shown in our study and others' research on black spruce and other boreal tree species (Farjat et al., 2015; Thomson et al., 2009). But opportunities for seed transfer to cooler sites in a

small province such as NB are limited (see Environmental Canada). The growth potential of black spruce families will likely be even more underutilized with increasing temperatures resulting from global warming. Height growth at 20 years (HT_{20}) is predicted to decrease by about 32.9% when future MAT is 2°C higher than present for the black spruce families in the 1979 series (Fig 4.a). However, for the families in the 1980 series, height growth is unrelated to the changing climate (Fig 4.b). This may probably result from the different assemblages of families in each series, or may result from the microclimate variation in the testing sites, as microclimate may be somewhat different even at very similar geographic coordinates. Using out-of province seed sources may be considered in long-term plans, although opportunities for that are also limited due to NB being in the southern, warmer portion of the species range (Burns & Honkala, 1990). Our results indicated that precipitation was less important for height growth than temperature. In all, temperature variables should be the major consideration when deploying black spruce families in NB. Transferring seed sources to relatively cooler sites will optimize height growth of black spruce. Both in and out-of province seed sources should be considered. Black spruce height performance at 20 years is predicted to increase by about 20.2% when moving seeds to planting sites with mean annual temperature is 2°C lower than seed origin. Really cold sites, with little heat accumulation should also be avoided.

Planting sites with medium nutritional quality and medium moisture are best for height growth of black spruce. Soil moisture is not dependent only on precipitation and such factors as drainage, slope, soil texture, and depth to water table influence the soil moisture (Brady & Weil, 2007; Kozłowski et al., 1991). Overall, it is better to plant black spruce on dry than on wet sites.

3.5 Limitations and uncertainties of the study

There are limitations and uncertainties in this study that need to be acknowledged. Firstly, only temperature, precipitation and growing degree-days were included in the climatic transfer function (Model[1]). Perhaps, statistically better models with higher r^2 could be obtained by accounting for effects of more environmental variables. But very complex models are rarely practical for the tree improvement program. Also, high correlations among environmental variables complicate separating their individual effects. These three variables used in our Model[1] are likely the most important climatic factors for height growth, based on the literature

review (Andalo et al., 2005; Farjat et al., 2015; Gray et al., 2016; Matyas, 1994; Rehfeldt et al., 2003).

Secondly, the climatic and edaphic variables were in separate models even though interactions between them could exist. Our main goal was to find the best deployment strategy to distribute black spruce families into their most suitable planting sites so that the maximum gain could be achieved. Incorporating climatic, edaphic and their interaction terms into a single model will make it very complicated and unlikely to be used in practice. Unlike the analysis of climatic factors, our evaluation of edaphic influences is limited to planting sites, without considering differences between the site of seed origin and the testing site. Thus, the dynamics of transferring seeds between sites of different qualities have not been explored.

Finally, our research area was restricted to only a portion of the entire natural range of black spruce and within a limited time during the ongoing climate change. The transfer functions built for black spruce in NB may not be useful in other portions of the species range. Nevertheless, our models summarize effects of key environmental variables relevant to the height growth of black spruce in NB. They can be used as guide for distributing black spruce families into suitable planting sites in the province.

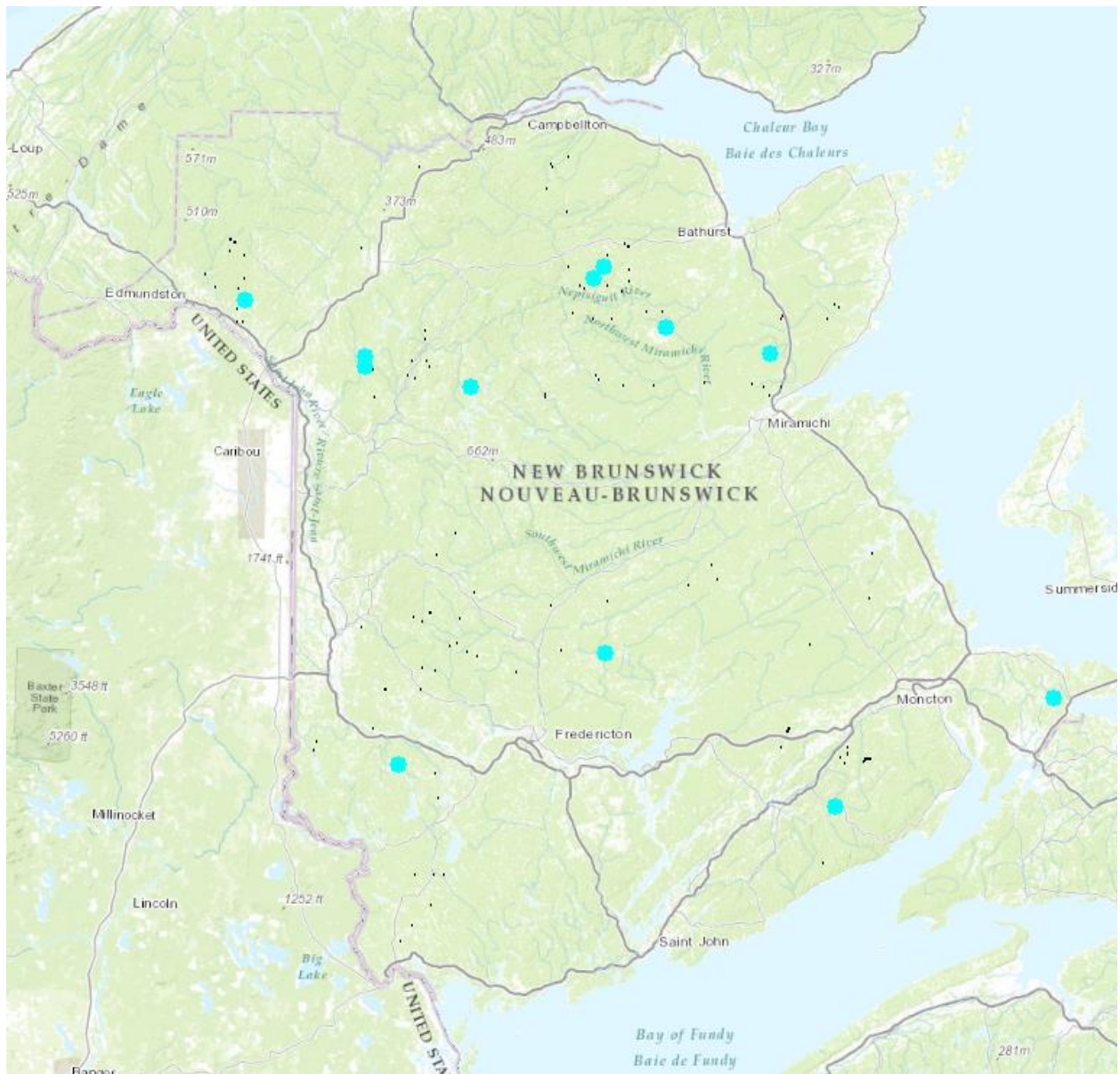


Figure 3. Map of the 1979 and 1980 series of black spruce family test sites.

Table 6. Parameter estimates with standard error (SE) and partial r^2 for Model [1] in the 1979 and 1980 series of black spruce family trials. Results for the 1980 series are shown in parentheses.

Climatic Variable	Coef	HT5			HT10			HT15			HT20		
		Estimate	SE	Partial r^2	Estimate	SE	Partial r^2	Estimate	SE	Partial r^2	Estimate	SE	Partial r^2
Intercept	β_0	82.1 (79)	1.1 (0.9)		261.9 (258.5)	3.4 (2.8)		489.2 (486.8)	4.2 (3.7)		684.3 (677.5)	5.0 (4.8)	
D_MAT	β_1	31.9 (1.8)	2.7 (1.0)	0.081 (0.016)	110.9 (16.8)	8.3 (3.2)	0.134 (0.028)	110.7 (23.2)	1.0 (4.2)	0.132 (0.034)	135.4 (34.8)	12.2 (5.4)	0.162 (0.037)
D_MAT ²	β_2	-1.4 (5.1)	1 (0.5)	0.008 (0.152)	1.5 (12.4)	3.0 (1.6)	0.009 (0.109)	7.2 (19.1)	3.6 (2.2)	0.01 (0.136)	11.4 (19.8)	4.3 (2.8)	0.012 (0.097)
D_MAP	β_3	-0.2 (0.01)	0.02 (5.3e-03)	0.09 (0.005)	-0.5 (0.03)	0.06 (0.02)	0.051 (0.009)	-0.5 (0.06)	0.07 (0.02)	0.036 (0.016)	-0.5 (0.06)	0.09 (0.03)	0.029 (0.016)
D_MAP ²	β_4	1.9e-04 (-5.2e-05)	7.6e-05 (3.8e-05)	0.049 (0.004)	9.4e-04 (6.8e-05)	2.4e-04 (1.2e-04)	0.043 (0.004)	7.7e-04 (-5.5e-05)	2.9e-04 (1.6e-04)	0.026 (0.004)	7.8e-04 (1.9e-04)	3.5e-04 (2.1e-04)	0.019 (0.004)
D_GDD	β_5	-0.09 (7.9e-03)	0.01 (5.7e-03)	0.037 (0.025)	-0.2 (-0.04)	0.04 (0.02)	0.055 (0.035)	-0.1 (-0.08)	0.05 (0.02)	0.067 (0.063)	-0.1 (-0.1)	0.06 (0.03)	0.079 (0.041)
D_GDD ²	β_6	-6.1e-05 (-3.2e-05)	2.2e-05 (1.3e-05)	0.02 (0.014)	-3.9e-04 (-5.2e-05)	7.0e-05 (4.3e-05)	0.041 (0.008)	-6.8e-04 (-1.3e-04)	8.6e-05 (5.7e-05)	0.058 (0.01)	-0.001 (-6.2e-05)	1e-04 (7.3e-05)	0.069 (0.007)
r^2			0.28 (0.22)			0.33 (0.19)			0.33 (0.26)			0.37 (0.20)	

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Abbreviations: D_MAT, D_MAP and D_GDD are the difference between seed-source locations and testing sites in mean annual temperature, precipitation, and yearly average growing degree-days, respectively. Their square terms (D_MAT², D_MAP², D_GDD²) have also been incorporated in this model. HT₅, HT₁₀, HT₁₅, HT₂₀ are height growth at 5, 10, 15, 20 years post-planting, respectively.

Table 7. Parameter estimates with standard errors (SE) and partial r^2 for Model [1] in combined data from the two series of black spruce family trials.

Climatic Variable	Coef	HT5			HT10			HT15			HT20		
		Estimate	SE	Partial r^2	Estimate	SE	Partial r^2	Estimate	SE	Partial r^2	Estimate	SE	Partial r^2
Intercept	β_0	77.1	0.7		250.8	2.2		478.8	2.8		671.3	3.5	
D_MAT	β_1	5.2	1.0	0.011	29.2	3.2	0.034	33.9	4.2	0.035	45.8	5.2	0.052
D_MAT ²	β_2	4.5	0.5	0.061	14.9	1.6	0.058	23.4	2.0	0.076	26.9	2.5	0.059
D_MAP	β_3	-0.02	5e-03	0.012	-0.05	0.02	0.004	-0.03	0.0	0.003	-9.9e-03	0.03	0.006
D_MAP ²	β_4	1.5e-04	3.3e-05	0.025	5.4e-04	1.0e-04	0.018	2.9e-04	1.3e-04	0.006	3.0e-04	1.6e-04	0.004
D_GDD	β_5	3.2e-03	5.8e-03	0.006	-0.03	0.02	0.010	-6.3e-03	0.02	0.011	-9.0e-03	0.03	0.013
D_GDD ²	β_6	-5.781e-05	1.3e-05	0.008	-2e-04	4.1e-05	0.011	-3.3e-04	5.3e-05	0.014	-3.7e-04	6.5e-05	0.012
r^2		0.12			0.13			0.14			0.15		

Abbreviations: D_MAT, D_MAP and D_GDD are the difference between seed source locations and testing sites in mean annual temperature, precipitation, and yearly average growing degree-days, respectively. Their square terms (D_MAT², D_MAP², D_GDD²) have also been incorporated in this model. HT₅, HT₁₀, HT₁₅, HT₂₀ are height growth at 5, 10, 15, 20 years post-planting, respectively.

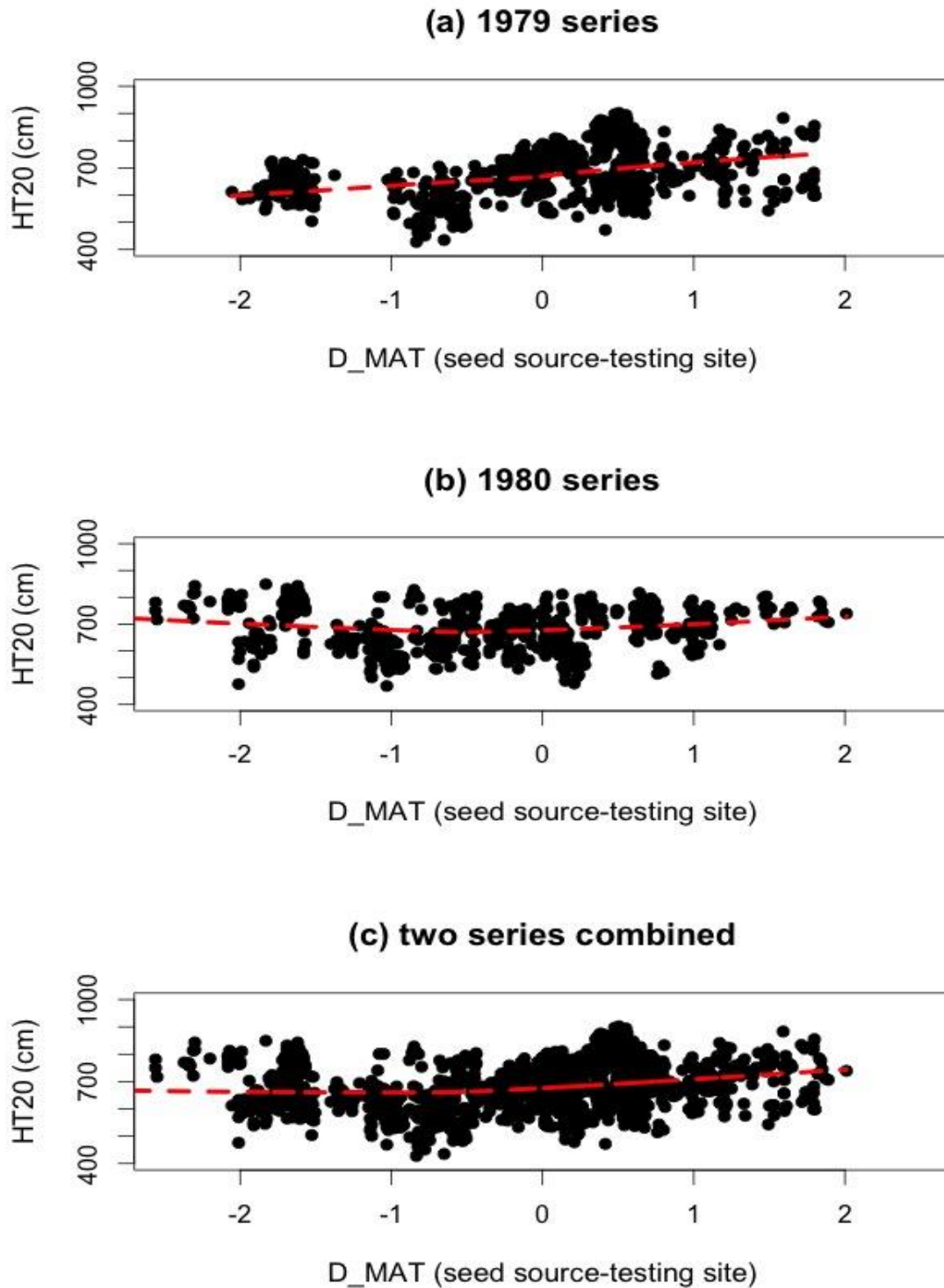


Figure 4. Plots of HT20 (20-year height) versus D_MAT (mean annual temperature differences between seed source and testing site), for 1979 series (a), 1980 series (b), and for combined data from these two series (c)

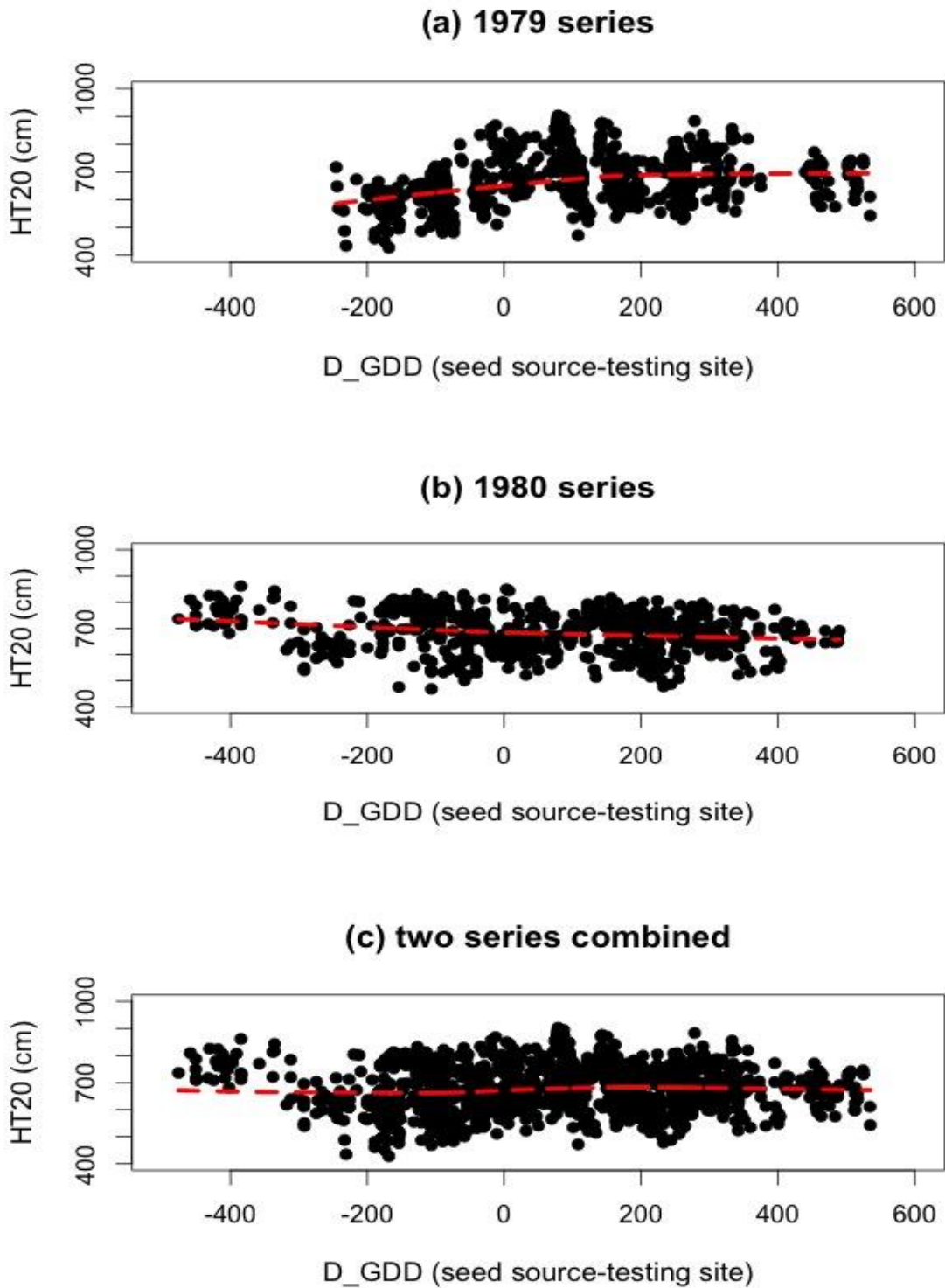


Figure 5. Plots of HT20 (20-year height) versus D_GDD (yearly average growing degree-days difference between seed source and testing site), for 1979 series (a), 1980 series (b), and for combined data from these two series (c)

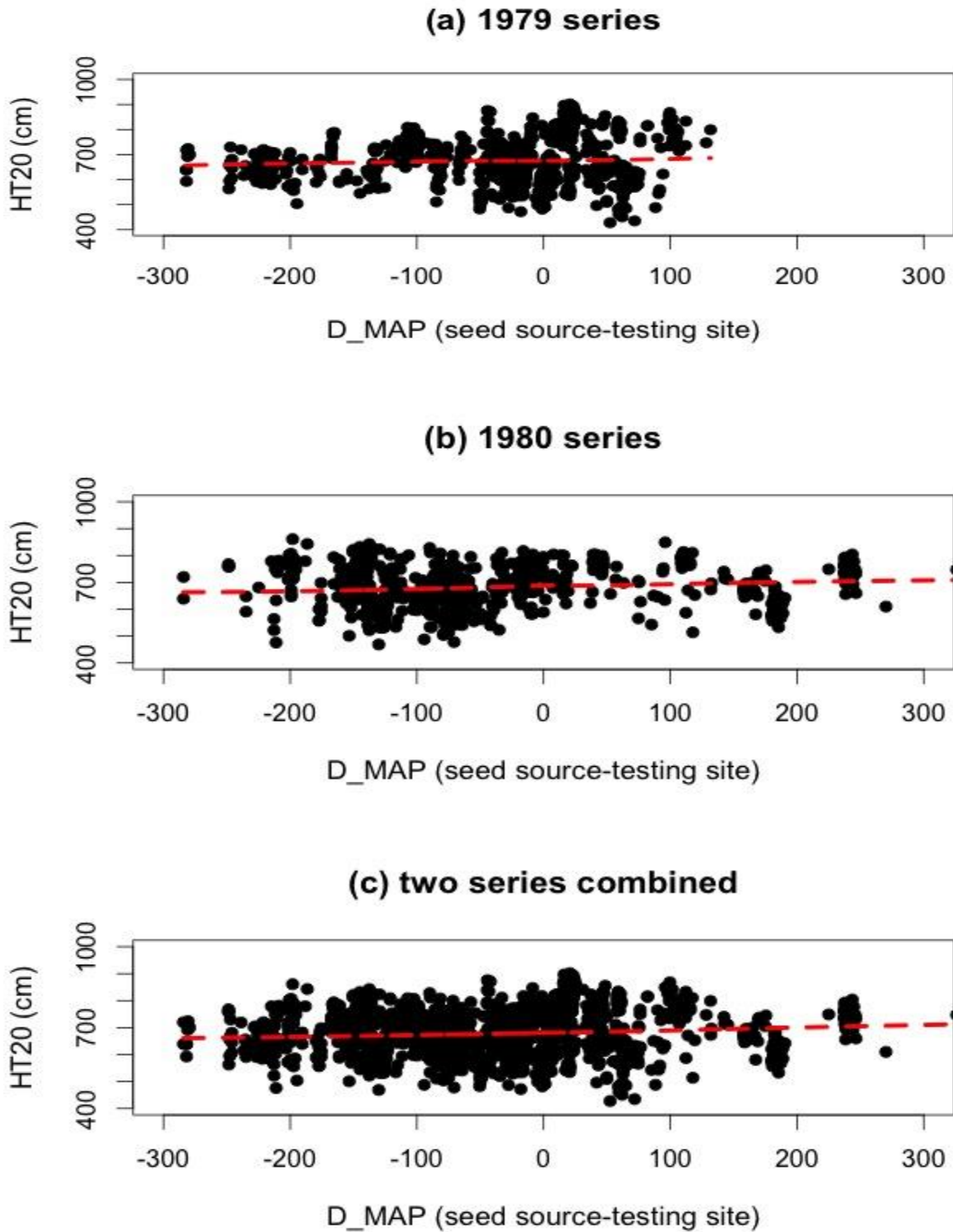


Figure 6. Plots of HT20 (20-year height) versus D_MAP (mean annual precipitation difference between seed source and testing site), for 1979 series (a), 1980 series (b), and for combined data from these two series (c)

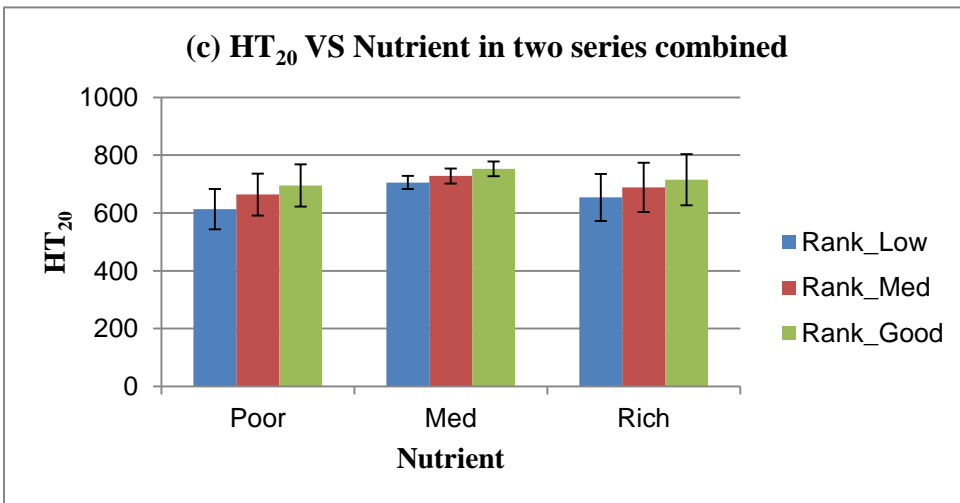
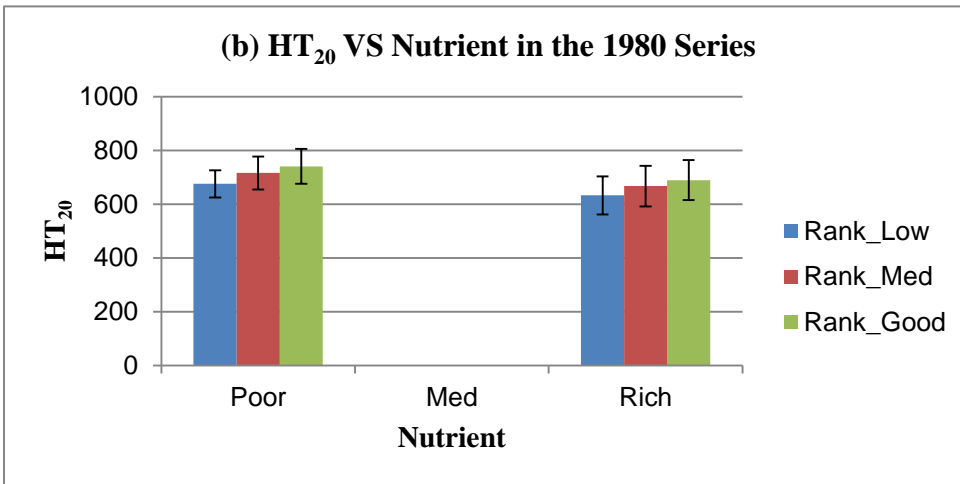
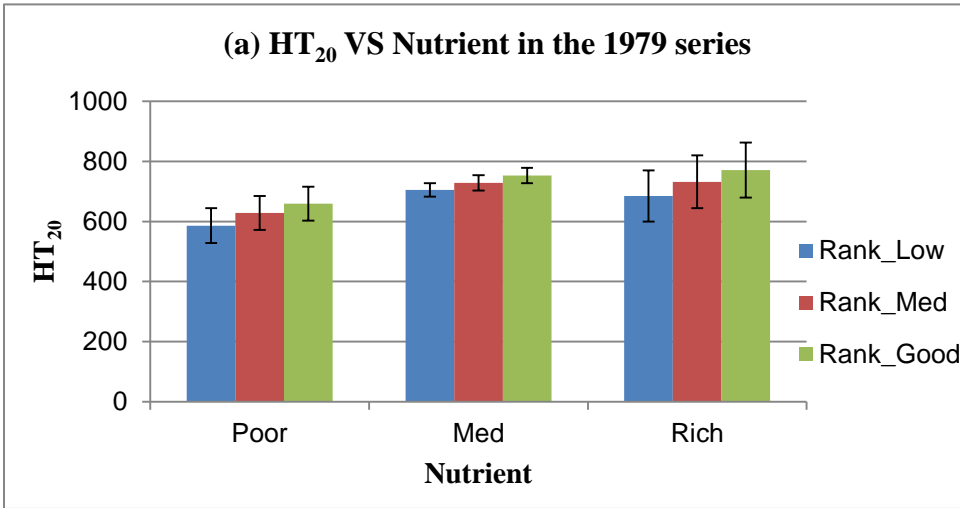


Figure 7. Mean HT₂₀ (height at 20 years) for each of three family ranks growing on testing sites of different soil richness (nutrient = poor, med, and rich) for 1979 series (a), 1980 series (b), and for combined data from these two series (c)

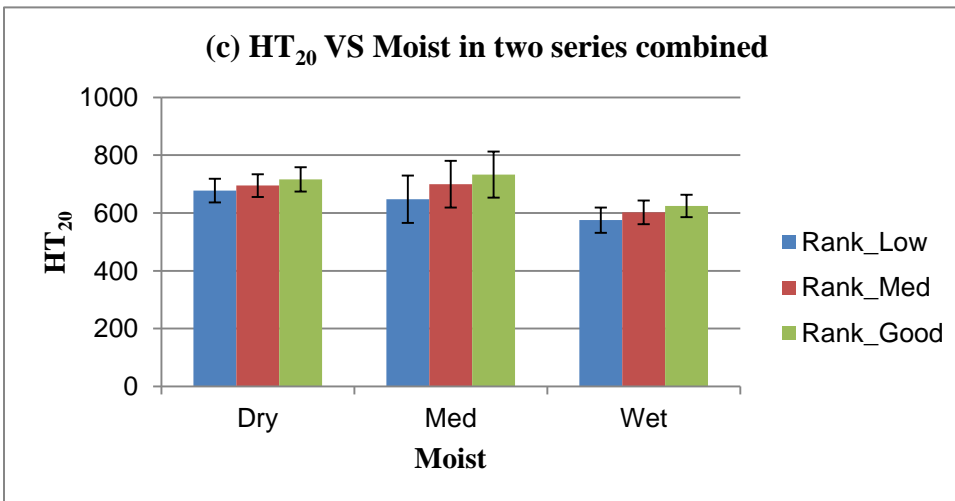
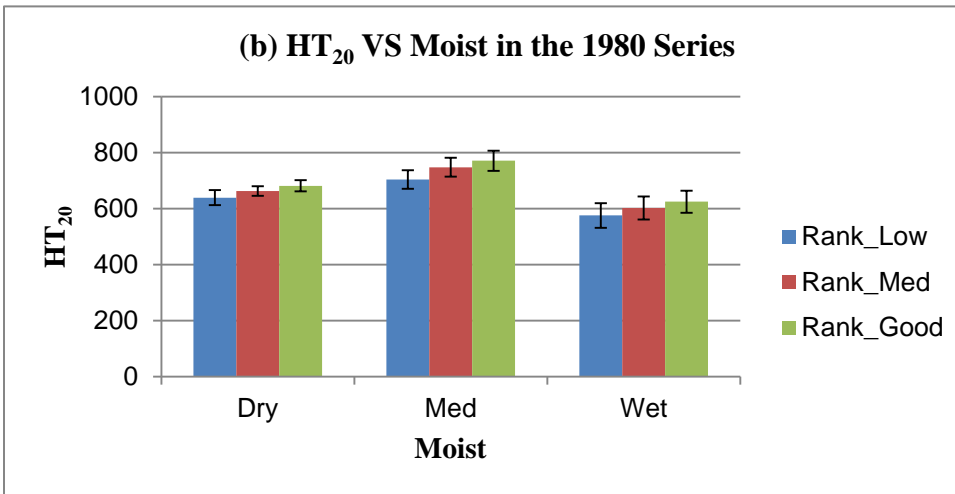
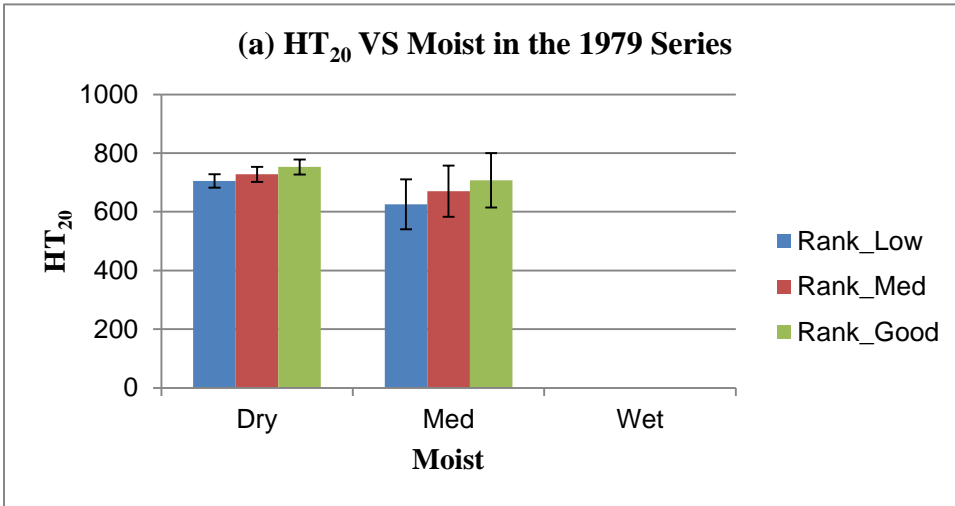


Figure 8. Mean HT₂₀ (height at 20 years) for each of three family ranks growing on testing sites of different soil moisture (Moist = dry, med, and wet) for 1979 (a), 1980 series (b), and for combined data from these two series (c).

Table 8. Parameter estimates, P-value (Pr) and model r^2 for Model [2] in the 1979 and 1980 series of black spruce family trials. Results for the 1980 series are shown in parentheses.

Variables	Coef	HT5		HT10		HT15		HT20	
		Estimate	Pr	Estimate	Pr	Estimate	Pr	Estimate	Pr
Intercept	β_0	60.1	<0.01	190.5	<0.01	407.5	<0.01	585.7	<0.01
		(81.5)	(<0.01)	(228.7)	(<0.01)	(453.5)	(<0.01)	(604.0)	(<0.01)
Rank_Good:Moi_Dry	β_1	44.4	<0.01	130.3	<0.01	152.4	<0.01	167.2	<0.01
		(1.6)	(<0.01)	(39.2)	(<0.01)	(12.7)	(<0.01)	(77.2)	(<0.01)
Rank_Med:Moi_Dry	β_2	41.6	<0.01	118.5	<0.01	136.5	<0.01	142.3	<0.01
		(-1.1)	(<0.01)	(28.8)	(<0.01)	(-0.2)	(<0.01)	(58.1)	(<0.01)
Rank_Low:Moi_Dry	β_3	31.5	<0.01	92.1	<0.01	100.7	<0.01	119.7	<0.01
		(-6.1)	(<0.01)	(17.2)	(<0.01)	(-17.8)	(<0.01)	(34.8)	(<0.01)
Rank_Good:Moi_Med	β_4	21.7	<0.01	73.9	<0.01	98.9	<0.01	121.7	<0.01
		(14.3)	(<0.01)	(79.5)	(<0.01)	(101.6)	(<0.01)	(166.3)	(<0.01)
Rank_Med:Moi_Med	β_5	17.6	<0.01	58.7	<0.01	71.6	<0.01	84.5	<0.01
		(11.6)	(<0.01)	(72.5)	(<0.01)	(87.0)	(<0.01)	(143.3)	(<0.01)
Rank_Low:Moi_Med	β_6	9.8	<0.01	33.9	<0.01	37.0	<0.01	39.9	<0.01
		(4.1)	(<0.01)	(52.8)	(<0.01)	(57.0)	(<0.01)	(99.2)	(<0.01)
Rank_Good:Moi_Wet	β_7	(-7.2)	(<0.01)	(-1.5)	(<0.01)	(6.1)	(<0.01)	(20.1)	(<0.01)
Rank_Med:Moi_Wet	β_8	(-10.0)	(<0.01)	(-11.5)	(<0.01)	(-14.9)	(<0.01)	(-2.1)	(<0.01)
Rank_Low:Moi_Wet	β_9	(-14.0)	(<0.01)	(-25.6)	(<0.01)	(-40.4)	(<0.01)	(-28.9)	(<0.01)
Rank_Good:Nutr_Poor	β_{10}	8.7	<0.01	29.6	<0.01	55.3	<0.01	72.9	<0.01
		(14.3)	(<0.01)	(71.1)	(<0.01)	(74.4)	(<0.01)	(136.5)	(<0.01)
Rank_Med:Nutr_Poor	β_{11}	6.6	<0.01	21.8	<0.01	34.7	<0.01	42.6	<0.01
		(10.9)	(<0.01)	(59.4)	(<0.01)	(58.5)	(<0.01)	(112.1)	(<0.01)
Rank_Low:Nutr_Poor	β_{12}	NA	NA	NA	NA	NA	NA	NA	NA
Rank_Good:Nutr_Med	β_{13}	(2.6)	(<0.01)	(40.3)	(<0.01)	(26.7)	(<0.01)	(71.3)	(<0.01)
Rank_Med:Nutr_Med	β_{14}	44.4	<0.01	130.3	<0.01	152.4	<0.01	167.2	<0.01
Rank_Low:Nutr_Med	β_{15}	41.6	<0.01	118.5	<0.01	136.4	<0.01	142.3	<0.01
Rank_Good:Nutr_Rich	β_{16}	31.5	<0.01	92.1	<0.01	100.7	<0.01	119.7	<0.01
		(0.3)	(<0.01)	(32.8)	(<0.01)	(44.8)	(<0.01)	(85.2)	(<0.01)
Rank_Med:Nutr_Rich	β_{17}	38.5	<0.01	131.3	<0.01	155.3	<0.01	185	<0.01
		(-2.3)	(<0.01)	(25.1)	(<0.01)	(26.9)	(<0.01)	(63.1)	(<0.01)
Rank_Low:Nutr_Rich	β_{18}	24.5	<0.01	84.8	<0.01	92.5	<0.01	99.6	<0.01
		(-7.2)	(<0.01)	(8.5)	(<0.01)	(0.7)	(<0.01)	(28.5)	(<0.01)

	0.73	0.7	0.56	0.47
Model r^2	(0.68)	(0.80)	(0.73)	(0.82)

Abbreviations: Moi and Nutr are soil moisture and nutrient, respectively. Soil moisture is labeled as dry, med, and wet, and soil nutrient as poor, med, and rich. Rank contains three categorical levels: “good”, “med”, and “low”, based on height performance at 20 years. HT₅, HT₁₀, HT₁₅, HT₂₀ are height growth at 5, 10, 15, 20 years post-planting, respectively.

Chapter 4: Conclusions

4.1 Achieving objectives of the study

The first objective of the thesis was to estimate genetic parameters for growth traits and stem forking in black spruce first-generation family tests in New Brunswick, and explore their temporal trends. The study showed that growth in V, HT and DBH was highly genetically controlled. That control tended to increase with increasing ages of trials. The strong age-age genetic correlations for V, HT and DBH would allow genetic selection based on early tree growth, so that the length of the breeding cycle would be shortened. The positive and strong trait-trait genetic correlations among V and HT, and DBH would allow selecting for either one of these traits concurrently improving the other traits. Estimates of SF heritability were consistently low in both test series and at all trial ages. The negligible genetic correlation between SF and V implies that selection for V and for the other growth traits correlated with V would not influence SF in black spruce. SF would not be a worthy selection target in black spruce. The moderately high type-B genetic correlation estimates for all the traits (HT, V, DBH, and SF) implied the lower importance of genotype \times environment interactions.

The second objective of the thesis was to determine how and to what extent climatic and edaphic factors influence height growth of the black spruce families tested in the two trials. The study showed moderate seed transfer effects of temperature and heat accumulation (D_MAT, and D_GDD) on height growth but little effect of precipitation (D_MAP). Better height growth was on planting sites cooler than seed-source locations. This suggested that global warming might reduce opportunities for maximizing the growth of black spruce families planted in NB. In the limited geographic range of New Brunswick, the climate is not very diverse. It may be difficult to find planting sites cooler than those of the seed origin. Selecting superior trees from warmer, out-of province seed

sources may offer opportunities for reducing effects of global warming on growth of black spruce in New Brunswick. The greatest gains in height growth can be achieved by distributing the best of the black spruce families to planting sites on medium-rich and medium-moist soils.

4.2 New knowledge in this thesis

Earlier estimates of genetic parameters for black spruce in NB were either based on relatively small sampling sizes or on relatively short growth-time periods (Adam et al., 1994; Baltunis et al., 2010; Codesido & Fernández-López, 2008; Dieters, 1996; Hodge & Dvorak, 2001; Lu & Charrette, 2008; Mullin et al., 1995; 1992). For this study, a large dataset (285 open-pollinated families and more than 57,000 individual trees) and data from longer-term (up to 35 years) measurements were used, so better estimates of genetic parameters were obtained than in the previous studies.

The primary objective of New Brunswick black spruce tree improvement is enhanced growth performance but this benefit may be offset by SF, a serious bole-quality problem in many species (Dvorak et al., 2007; Ladrach & Lambeth, 1991; Schermann et al., 1997; Xiong, 2010; 2014), including black spruce (Krause & Plourde, 2008). But genetic studies on stem forking in black spruce have never been done in New Brunswick. Our study indicates that environmental rather than genetic effects are the major cause of SF in black spruce. Identifying and eliminating these environmental causes should be the priority rather than genetic selection.

The best growth can be achieved through distributing superior families to the most suitable planting sites that allow a full expression of their genetic potential (Falconer & Mackay, 1996; Griffiths et al., 2000). However, in current practice, black spruce families have been deployed across New Brunswick without considering climatic transfer effects (NBTIC, 1979, 1980). This study shows that best height growth can be achieved by

deploying black spruce to planting sites cooler than those of the seed origin. For optimal growth, the D_MAT and D_GDD should be 2°C and approximately 300 GDD less than at the seed source, respectively. This study also identifies the climate change as a potential factor reducing benefits from genetic selection in New Brunswick. The current climate is predicted to change vary rapidly (Houghton et al., 2001; Swansburg et al., 2004). Forest trees, including black spruce, adapting to changing climate may be challenging (Bronson et al., 2009; Farjat et al., 2015; Gamache & Payette, 2004; Gray et al., 2016; Joyce & Birdsey, 2000; Roberts, 1989; Wang et al., 2006). This study signals the need for preparing for effects of climate change on growth performance of black spruce in New Brunswick and indicates the direction for future research aiming at improving gains from genetic selection of trees.

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