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GENETIC VARIATION IN EARLY FIELD PERFORMANCE OF WHITE SPRUCE (*PICEA GLAUCA* (MOENCH) (VOSS)) IN CENTRAL ALBERTA

BY

CHRISTINE RUTH HANSEN ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

DEPARTMENT OF FOREST SCIENCE

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled GENETIC VARIATION IN EARLY FIELD PERFORMANCE OF WHITE SPRUCE (*PICEA GLAUCA* (MOENCH) (VOSS)) IN CENTRAL ALBERTA submitted by Christine Ruth Hansen in partial fulfillment of the requirements for the degree of Master of Science.

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ABSTRACT

Height at age 8 and 10 years, average of 9- and 10-year height (mean increment), plant vigor and white pine weevil susceptibility of white spruce (Picea glauca (Moench) Voss) were assessed in a progeny test of 150 open-pollinated families at four test sites in north central Alberta. Both within and across sites, families differed significantly for all traits. However, the within-plot variation accounted for the largest component of the total variation, ranging from 50% to 72% of the total. The family-site interaction was also significant for all traits studied. However, except for plant vigor, the interaction effect was smaller than the main effect of families, accounting for from 1% to 4% of total variation. Eight- and 10-year heights were highly correlated (r_g=0.96) as were mean increment and 10-year height (r_g=0.88). Genetic correlation coefficients between site pairs ranged from 0.54 to 0.94 for age 10 height indicating a similar reaction of genotypes to environmental (site) differences. Narrow-sense heritability estimates were 0.19, 0.15, 0.17, 0.06 and 0.36 for age 10 height, age 8 height, mean increment, plant vigor and percent white pine weevil damage, respectively. The corresponding family heritability estimates were 0.74, 0.69, 0.72, 0.48 and 0.71, respectively.

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BACKGROUND

The Genetics and Tree Improvement Section, Alberta Land and Forest Services, has initiated a white spruce tree improvement program that is divided into five projects covering five different breeding regions. Within each region, superior trees are selected with the aim of developing superior strains of white spruce for the production of genetically improved seed in commercial quantities for reforestation purposes in each region. Major traits to be improved are

1) adaptability and hardiness including pest resistance
2) height and diameter growth
3) stem form and taper
4) crown and branching characteristics
5) wood quality (wood density and fibre length).

A fundamental principle of tree improvement by means of artificial selection is that natural variability must exist in the species to be improved. It is known that among provenances, or origins, white spruce varies clinally (Nienstaedt and Teich 1971). That is, the variation follows geographic gradients related to temperature, photoperiod and precipitation. On the basis of this clinal variation, the white spruce breeding regions in Alberta have been established to ensure that the base populations for each breeding program

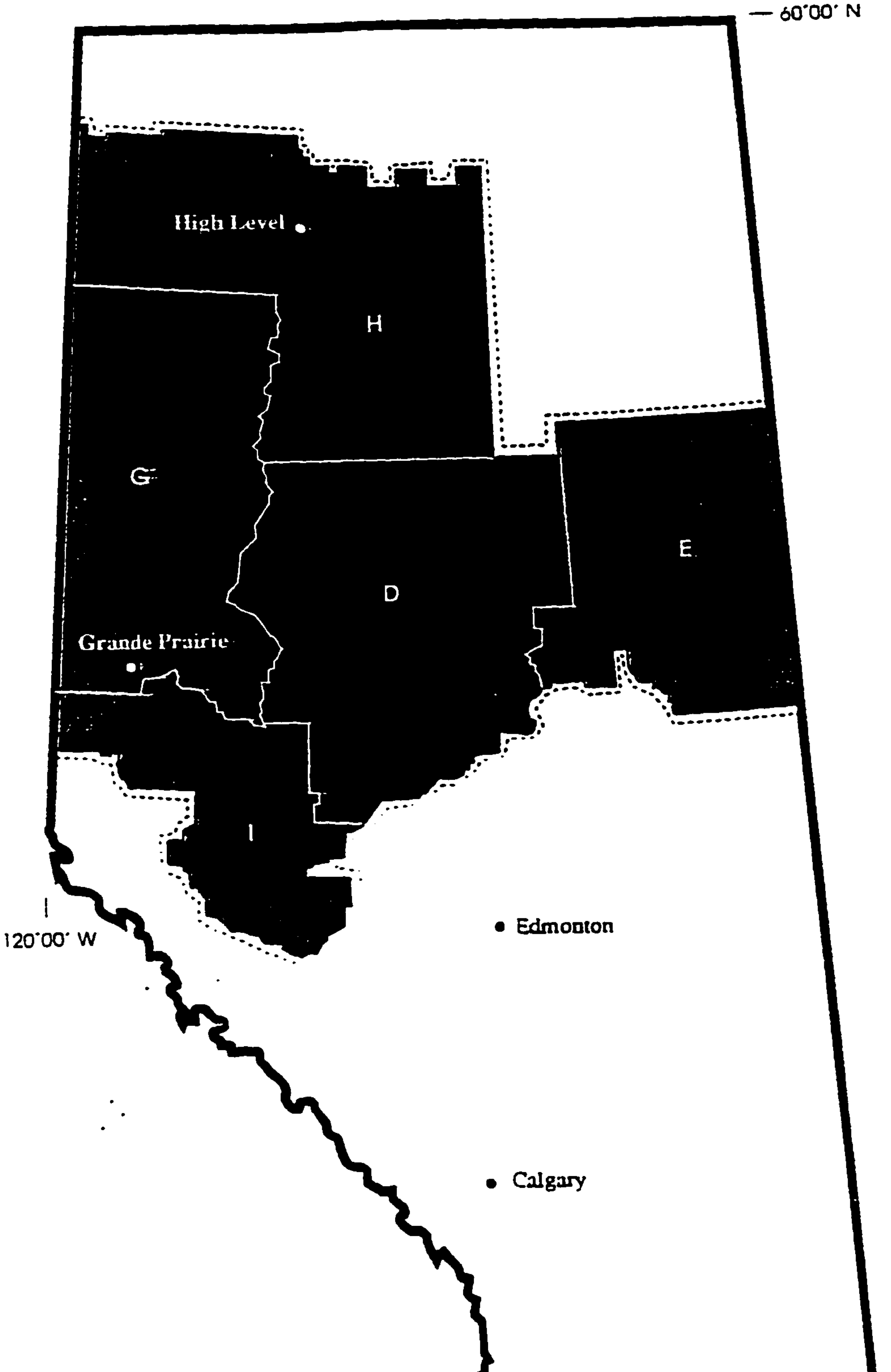


Figure 1. White spruce breeding regions in Alberta

are comprised of adapted material (Figure 1). However, it is the within-population or tree-to-tree variation that forms the basis of 'plus' tree selection and is the foundation of genetic improvement in white spruce (Yeatman 1989). In Alberta, not much is known about the nature and magnitude of this variation in white spruce as it relates to the traits listed above.

The area of focus for this study is central Alberta, designated as white spruce breeding region 'D', an area comprising about 4.6 million hectares. The main ecoregions are central mixedwood, dry mixedwood, upper foothills and lower foothills (Anonymous 1994).

The mixedwood ecoregions are typified by aspen forests and grey luvisol soils. The dry mixedwood region has a mean growing season temperature (June, July, August) of 15°C and mean annual precipitation of 380mm. The mean number of growing degree days above 5°C is 1150. Mean growing season temperature in the central mixedwood region is 14.8°C and mean annual precipitation is 397mm. The mean number of growing degree days above 5°C is 1143 (Strong 1992).

In the upper foothills region, forests of white spruce (Picea glauca(Moench)Voss), black spruce (Picea mariana(Mill.) B.S.P.), lodgepole pine (Pinus contorta Dougl.ex.Loud.) and subalpine fir (Abies lasiocarpa (Hook.)Nutt.) are typical. Predominant vegetation in the lower foothills region is forests of aspen (Populus tremuloides Michx.), balsam poplar (Populus balsamifera L., birch (Betula papyrifera Marsh.) white spruce and black spruce. Both regions are characterized by grey luvisol soils. The lower foothills region has a mean growing season temperature of 14°C and mean annual precipitation of 464mm. The mean number of growing degree days above 5°C is 1008. The upper foothills region has a mean growing season temperature of 12.7°C and mean annual precipitation of 538mm. The mean number of growing degree days above 5°C is 752 (Strong 1992). (Figure 2)

A potentially serious pest in the region is the white pine weevil (Pissodes strobi (Peck)). The weevil attacks the terminal growth of spruce, preferring vigorous trees from 1.5 to 9 meters in height with the sturdiest leaders (Wood and McMullen 1983). The leaders are seriously injured or killed resulting in crooked or bushy trees of low value. Each attack affects two or more years of growth and, consequently, repeated attacks result in reduced timber volume at maturity (Ives and Wong 1988).

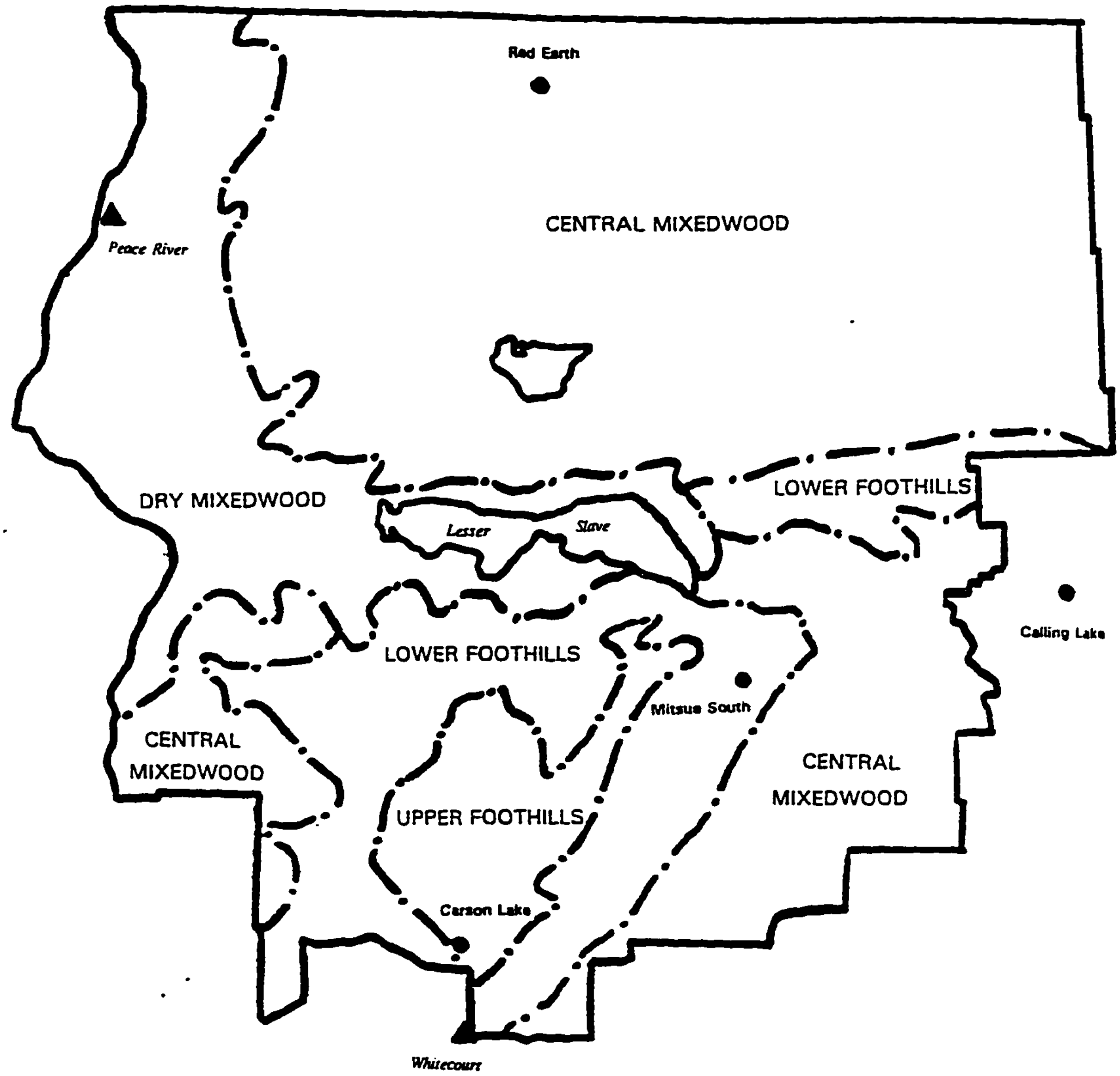


Figure 2. Ecoregions and Progeny Test Site Locations

STUDY OBJECTIVES

The study objectives were

1) To determine the magnitude and nature of variation for early growth performance and white pine weevil resistance in local white spruce populations

2) To estimate genetic parameters for selection and breeding of white spruce in central Alberta

3) To examine the relationship between observed variation for the trait studied and geographic origin

LITERATURE REVIEW

Silvics:

White spruce is one of the most important forest tree species in Canada's boreal forest and is found over a very wide geographical range (Figure 3). Outlier populations are found in southern Montana, in the Black Hills of Wyoming and South Dakota and in the Cypress Hills of Saskatchewan (Nienstaedt and Zasada 1990).

White spruce grows well under a wide variety of conditions and thrives in climates described as cool temperate and sub-arctic. The growing season varies from a maximum of 160 days in the south to a minimum of 20 to 25 days in the arctic areas

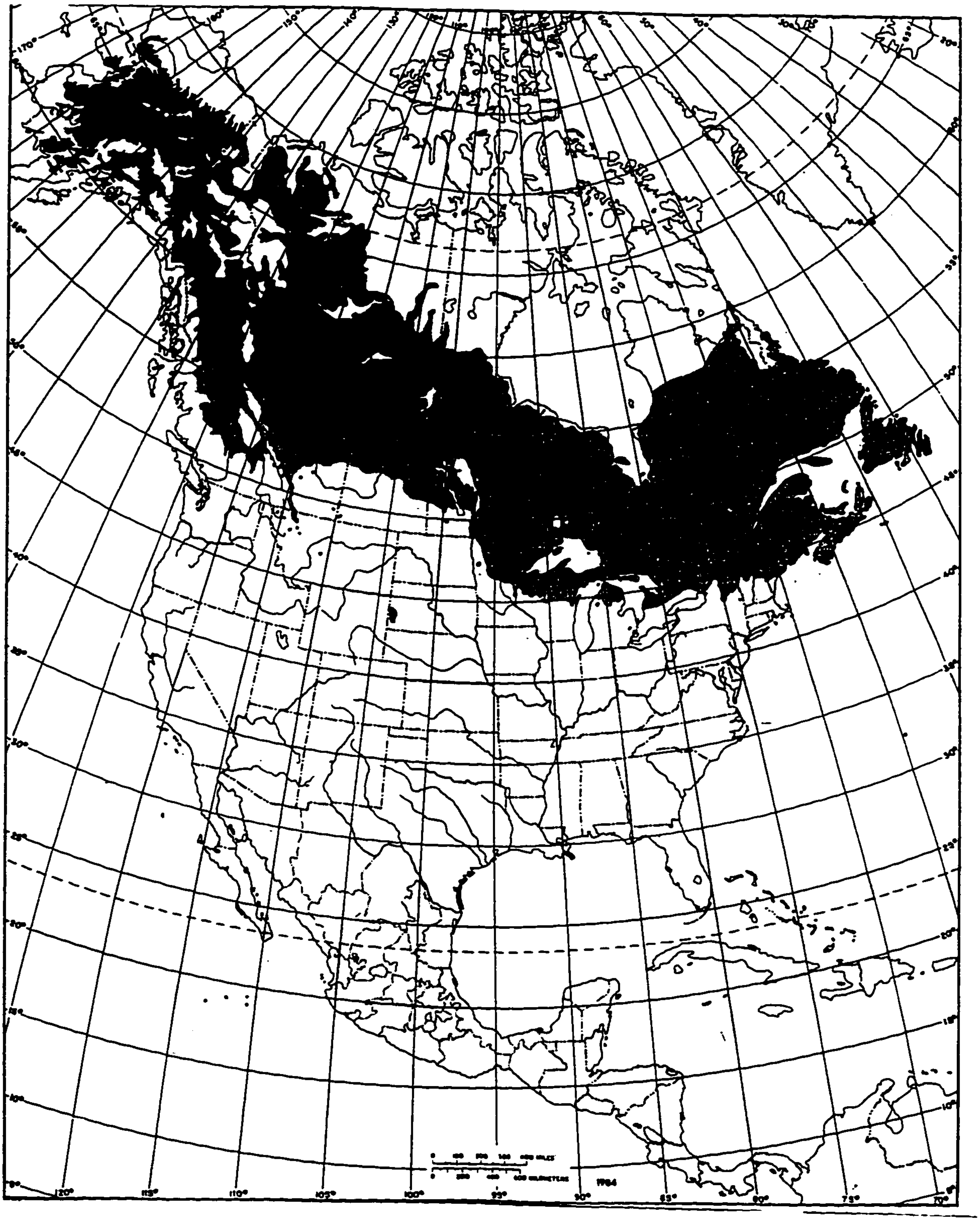


Figure 3. Geographical range of white spruce (after Nienstaedt and Zasada 1990)

of its range. In general, it grows south of a line delimiting a growing season of 60 days. Its elevational range is from sea level to about 5000 feet. Soil types throughout its range are glacial lacustrine, marine, alluvial, gray wooded, brown forest and podzolized and it grows well on all of these types (Fowells 1965).

White spruce is a characteristic species of the Boreal Forest Region that forms a continuous belt from Newfoundland to the Rocky Mountains and Alaska (Rowe 1972). In the eastern part of its range, white spruce is found in pure stands or mixed stands comprised of white and black spruce, balsam fir, trembling aspen and white birch. In the Maritime provinces and in the fog belt in Quebec and Labrador it is mainly confined to abandoned fields, but in other parts of eastern Canada it is more common and occurs to the tree line along Ungava Bay and Hudson Bay (Nienstaedt and Zasada 1990).

In the western part of its range, white spruce is an important constituent of the mixedwood subregion extending from southwestern Manitoba to northeastern British Columbia. Here it occurs with trembling aspen, balsam poplar, white birch and balsam fir in varying proportions. It is found in association with black spruce in the foothills, predominantly in older stands that have not been severely affected by fire. In its far northern range, white spruce is largely confined to river flood plains, well-drained benchlands, valleys and valley slopes with south and west aspects (Rowe 1972).

White spruce is a monoecious species. Separate male and female flowers are borne on the same tree on twigs of the previous year's growth. Female flowers are usually confined to the upper crown and male flowers to the middle crown, however overlapping does occur. Phenology of the species varies greatly according to geographical location. It flowers for three to five days in May/June with an overlap in pollen shedding and female receptivity. Cones ripen in August/September of the same year and the seed is shed in September/October. Seed in commercial quantities is usually not produced until trees are about thirty years old, and optimum production is reached at about sixty years. Cone crops are not produced annually. A good crop can be expected only every three to six years. The seed is strongly dormant and requires a stratification treatment or over-wintering in the forest soil to induce germination (Fowells 1965).

Time of flushing is temperature-dependent and, within a stand, flushing can differ by as much as three weeks between individual trees. The period of shoot elongation is short, lasting only for about four to six weeks. Shoot growth cessation is more dependent on photoperiod than temperature. On good sites, trees 100 to 250 years old are common, and trees 250 to 300 years old are often found on islands and wet upland areas protected from fire (Nienstaedt and Zasada 1990).

White spruce is intermediate in its tolerance to shade. It can, however, survive long periods of suppression while retaining an ability to respond to release (Fowells 1965; Nienstaedt and Zasada 1990).

The greatest use of white spruce is in pulpwood, but it is also used for lumber of all kinds, for veneer, and for specialty wood products such as sounding boards, paddles and oars. It is one of the most important species in the Canadian forest industry (Nienstaedt and Teich 1971).

Evolutionary History and Biogeography:

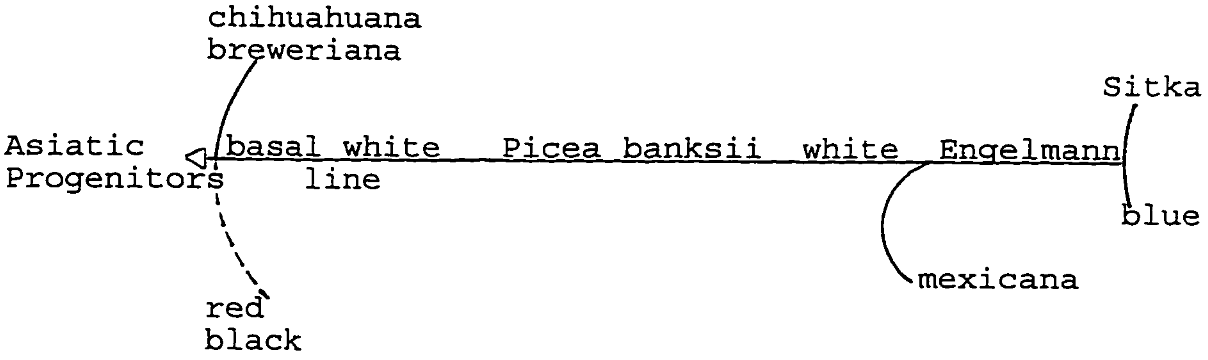
Approximately thirty species of the genus Picea exist today with the majority (sixteen) occurring in Japan and eastern China. It is, therefore, inferred that this is the centre of origin for the species (Ogilvie 1972). Although it is isolated genetically from other conifer genera, species of Picea are differentiated only by minor morphological characters. For example, differences in the chemical composition of the leaf extracts and leaf oil terpenes (Ogilvie and Rudloff 1968) and differences in cone scale morphology (Roche 1969) are virtually the only indications that white spruce and Engelmann spruce are two separate species.

The spruces are diploids with a chromosome number of 2n=24. There is no interspecific variation in chromosome number. Many species of spruce hybridize readily indicating they are not well isolated genetically (Ogilvie 1972; Roche 1969). For example, in western North America, hybridization has been reported among white spruce, Sitka spruce (Picea sitchensis (Bong.) Carr.), Engelmann spruce (Picea engelmannii Parry ex Engelm.) and blue spruce (Picea pungens Engelm.) suggesting close evolutionary relationships.

White spruce is possibly the link between the western group of North American spruces and the Asiatic spruces. Fossil cones dating to the late Miocene-early Pliocene found on Banks Island in the Canadian arctic, can only be differentiated from white spruce cones on the basis of mean cone size. This extinct spruce (Picea banksii) evolving into white spruce may, then, have led to the western group of spruces (Hills and Ogilvie 1970).

Three relict species of spruce exist. P. breweriana in California and P. chihuahuana in Mexico are of different stock than the other North American spruces and are similar to species in southern China. P. mexicana, also found in Mexico, is intermediate between Engelmann spruce and blue spruce and is close to the western group evolutionarily.

The possible phylogeny of North American spruces as proposed by Nienstaedt and Teich (1971) is illustrated below.



Evidence indicates white spruce can be divided into an eastern and a western population with the boundary at about longitude 95° W. (Nienstaedt and Zasada 1990). Monoterpenes in cortical samples, DNA content per cell and taxonomic characteristics such as needle color and length show distinct east-west variation patterns. This major division suggests that extant white spruce populations evolved from populations that survived both the Illinoian and Wisconsin glaciers in widely separated refugia. Barriers between these refugia resulted in the evolution of genetically distinct eastern and western populations (Wilkinson et al 1971; Miksche 1968).

Breeding System:

White spruce is predominantly a cross-pollinated species resulting in extensive genetic variation both within and among populations. Outcrossing allows for the recombination of different alleles occurring in the population and is also the means by which mutations are spread.

However, in white spruce selfing is a natural phenomenon due to the overlapping zones of male and female flowers on the same tree and because the periods of pollen shedding and maximum female receptivity coincide on the same tree. Since there is no mechanism that favors foreign pollen over pollen from the same tree, self-pollination can be very high under unfavorable conditions (Ying 1978). Therefore, white spruce may be considered to have a mixed mating system i.e. a system characterized by random outcrossing and selfing. For example, based on single locus estimates, King et al. (1984) reported an out-crossing rate of 0.9 (selfing=0.1) for a white spruce population in the present study area in central Alberta.

However, an allozyme study by Cheliak et al. (1985) revealed a slight excess of heterozygotes in the white spruce population studied. A mixed mating system would tend to produce a slight excess of homozygotes. The results suggest that all zygotes are not equally fit and that selfed individuals are being selected against as the result of an accumulation of lethal alleles in the homozygous condition. Such selection pressure would lead to an increased proportion of heterozygotes.

King et al. (1984) also concluded that mixed mating is not an appropriate model for white spruce. Although their allozyme study revealed a slight excess of homozygotes, this inbreeding structure could be explained by the spatial heterogeneity in the male gamete population and between the male and female gamete populations. They infer that mixed mating is just an ephemeral part of early zygote development and, therefore, that white spruce can best be described as predominantly outcrossing.

Given its outcrossing mating system and the fact that it is both wind pollinated and its seed is wind dispersed, the potential for long-distance gene flow in white spruce is very high. Nevertheless, inbreeding at levels less severe than selfing has a significant effect on the population structure of white spruce. Clusters of related trees are common in natural stands because seed often is not transported great distances from the maternal tree. In fact, the quantity of seed reaching a given area decreases drastically as distance increases from the seed source. For example, at 50, 100, 200 and 300 meters, seed rain may be as low as 7,4, 0.1 and 0.1

percent of that in the stand (Nienstaedt and Zasada 1990). Similarly, pollen density decreases rapidly with increasing distance from source (Bramlett, 1981). Consequently, various levels of inbreeding occur as a result of matings between closely related neighboring trees.

For example, using percent sound seed from controlled crosses as an indicator of inbreeding, Coles and Fowler (1976) determined that trees within a radius of about 100 meters could be relatives. They reported average (of percent sound seed and epicotyl length) relationship coefficients of $r=0.30$ and $r=0.23$ for trees within a 100 m radius in two New Brunswick white spruce stands.

In a related study, Park et al. (1984) estimated that in the same white spruce populations, the relationship of neighbouring trees approximates that of half-sibs (offspring inbreeding coefficient (F_0)=0.145 based on 7-year progeny height measurements). Although a comparison of percent full seed from open-pollinations and percent full seed from unrelated pollinations indicated that natural inbreeding exceeds that expected from half-sib pollinations ($F_0=0.16$ and $F_0=0.26$ for two stands), they concluded that reduced numbers of full seed, reduced germination, reduced growth and the occurrence of homozygous, recessive alleles removes most inbred individuals before they reach reproductive age resulting in an average half-sib relationship between individuals.

Finally, results of the allozyme study by Cheliak et al. (1985) suggest that effective pollen transmission distances can be measured only in tens of meters. The authors concluded that a distance of about 30-50 meters between trees should be maintained to avoid sampling close relatives.

Nevertheless, because of its large quantity and low sedimentation rate, pollen can be widely dispersed and its admixture can contain pollen from many trees (Koski 1973). For example, in Scots pine stands, most of the pollen received by individual trees comes from a distance of over fifty meters and a considerable portion has been carried by the wind for several kilometers (Sarvas 1962).

Genetic Variation:

Among populations

Among-population variation is usually assessed by provenance tests. These are replicated experiments comparing trees grown from seed collected in many parts of a species' natural range (Wright 1976). The objectives of such tests are to determine broad patterns of variation and to identify provenances or populations that will perform best on planting sites typical of a given region (Teich et al. 1975). Additionally, genecological information is obtained by relating patterns of variation to environmental conditions at provenance origins, and because the tests are usually replicated on several sites, information is gained on genotype x environment interaction (Nienstaedt 1979).

Knowledge of variation patterns is essential for the delineation of seed zones and breeding zones and to ensure the adaptiveness of planting provenances. Usually, the boundaries of these zones are drawn conservatively to minimize the risk of using unadapted seed. However, above-average productivity can be achieved by using the genetic variation both inside and outside these regions as revealed by provenance tests (Teich et al 1975).

Extensive provenance studies undertaken in eastern Canada and in the Lake States region of the United States have shown a high degree of variability in height growth among white spruce provenances at 10-25 years from seed (Teich 1970, 1973; Nienstaedt and Teich 1971; Teich et al. 1975; Khalil 1984; Hall 1986). Several fast growing sources that perform well under a wide range of environmental conditions have been identified from southeastern Ontario and the St. Lawrence Valley region of Quebec. For example, the most rapidly growing provenances in a series of experiments established in Ontario were 22% taller than the mean of all provenances studied and 21% taller than the provenance closest in origin to the plantation site. Hypothetically, improvement in height growth of about 20% could be achieved by superior provenance selection alone (Teich et al 1975).

A recently completed analysis of white spruce provenance trials in Alberta also revealed significant differences among provenances for height at age 15 years from seed (Morgenstern and Keenan 1993). Elevation and latitude were found to be important parameters in the delineation of this variation. The experiments also indicated that wide transfers of provenances were not possible and that the best growing trees on each test site were from seedlots within 2-3 degrees of latitude of the test site and within a narrow band of elevation (Morgenstern and Keenan 1993).

Provenance studies also reveal that much of the among-population variation in white spruce is clinal. That is, variation reflects adaptation to environmental gradients related to temperature, photoperiod and precipitation that vary continuously over the species' wide range (Stern and Roche 1974).

In a study of 2-year-old seedlings representing 27 Alberta provenances of white spruce, Dunsworth and Dancik (1983) found that among-provenance variation in relative dry matter (the ratio of dry weight to fresh weight) was typically clinal increasing continuously with latitude of source. The increase in dry matter with latitude is associated with increased winter hardiness.

A range-wide greenhouse experiment conducted by Khalil (1986) revealed clinal variation in seed quality and juvenile characters of white spruce. Strong north-south trends were noted in seed weight, hypocotyl length and four-month seedling height. Seed weight also displayed a strong east-west trend. Significant variation was found to exist both between and within provenances for characters of germinative energy, germination percent, cotyledon numbers and four-month seedling height.

Studies also revealed large provenance differences in the wood density of white spruce (Taylor et al 1982; Corriveau et al 1987). However, clinal gradients are not as readily discernable for wood quality traits as they are for traits such as growth rate that are very closely related to adaptation. Considering the extent of the variation, selecting populations of high wood density could significantly improve the structural qualities of wood. However, negative correlations between growth rate and wood density indicate that selection for rapid growth rate may result in reduced wood density and vice versa (Corriveau et al 1987).

Ecotypic variation has also been reported in white spruce. Unlike clinal variation, ecotypic variation is discontinuous and originates from the discontinuous distribution of environments of a species such as the distribution of certain soil types. A species reacts to this by forming discrete races (Stern and Roche 1974).

For example, Teich and Holst (1974) conducted an experiment with twelve white spruce provenances, 6 from areas with limestone parent material and 6 from areas with granitic parent material. These provenances were planted on two experimental sites, one with limestone and one with granitic parent material. At fifteen years from seed, the limestone provenances were 10% taller than the granitic provenances on the limestone site and, at the granitic site, the granitic provenances were 9% taller than the limestone provenances. The results suggest that limestone ecotypes evolving by natural selection occur in white spruce.

Within populations

To assess within-population variation and in order to predict the potential genetic improvement of desirable traits, progeny tests are conducted. Test plantations are established with the open-pollinated progeny of individual, phenotypically superior trees. Replicated within and over several environmentally diverse sites, these tests allow for the partitioning of environmental variance and, consequently, for the discernment of genetic differences between open-pollinated families (Wright 1975).

In general, progeny studies conducted in eastern Canada, the Lake States region of the United States and British Columbia indicate that white spruce is a good candidate species for 'plus' tree selection (mass selection) followed by family and individual selection based on progeny test results (Teich 1975; Ying and Morgenstern 1979; Kiss and Yeh 1988; Nienstaedt 1985).

Characteristics found to be under fairly strong genetic control are crown and stem form and branch angle (Merrill and Mohn 1985; Morgenstern 1974; Cahalan 1981) and time of budburst (Yeatman and Venkatesh 1974; Nienstaedt 1985; Pollard and Ying 1979b). Traits under weaker genetic control are height and stem diameter (Dhir 1975; Li et al 1993; Ying and Morgenstern 1979; Merrill and Mohn 1985). Therefore, phenotypic mass selection of trees superior in highly heritable traits i.e. traits under strong genetic control, should be followed by progeny testing to reveal the significant family and individual differences in lower heritability traits of economic importance.

Although among family differences are usually highly statistically significant, variance analyses of progeny trial measurements usually reveal that the within-plot, or within-family, component contributes the most to the total variance (Khalil 1978; Ying and Morgenstern 1979; Kiss and Yeh 1988; Li et al 1993).

For example, Ying and Morgenstern's (1979) analysis of height and DBH at four individual progeny trials at 8, 11 and 22 years from seed revealed that variation within families accounted for over 70% of the total variation in all experiments. Similarly, in Li et al's (1993) study of genetic variation in juvenile growth and phenology in white spruce, the within-plot (within-family) variance accounted for approximately 60% of the total variance. Differences between provenances and families were statistically significant also but accounted for only 3.1% and 2.9%, respectively, of the total variance.

Large within-population variation is the result of many factors. It is indicative of a large number of effective pollen parents (Kiss and Yeh 1988), variable degrees of inbreeding among seedlings from each mother tree (Khalil 1978) and the environmental heterogeneity encountered by white spruce occupying individual sites.

Two greenhouse studies were conducted by Pollard and Ying (1979a,b) to examine variation in flushing and response to declining photoperiod in a southeastern Ontario white spruce population. In both experiments, variation among families within stands was highly significant and variation between stands was not significant. Because of the wide range in date of occurrence of the first fall frost and the last spring frost, sometimes more than 50 days, they concluded that natural selection would favor the maintenance of high within-stand variation in these traits.

Allozyme studies also indicate a high degree of tree-to-tree variation in white spruce. These studies offer more precision in the estimation of genetic variation for several reasons. Firstly, homozygote and heterozygote individuals can be readily distinguished because the expression of allozyme variants is usually codominant. Secondly, zymograms produced from gel electrophoresis procedures make the direct quantification of the number of allozyme loci being studied possible. With traditional provenance and progeny tests, the morphological traits studied are usually controlled by an unknown number of loci. Finally, allozyme expression is not mediated by epistatic or environmental effects as is often the case with morphological traits (Yeh 1979).

Allozyme variation is usually quantified by calculating the expected heterozygosity and Wright's fixation index (F). The former is calculated with the formula $1-\Sigma p^2$ where 'p' is the frequency of the ith allele at the locus. The latter, which indicates the proportional increase or decrease in heterozygosity relative to that expected under Hardy-Weinberg equilibrium, is calculated by taking the ratio of observed to expected heterozygotes and subtracting from 1. A negative F value indicates an excess of heterozygotes in the population and a positive value indicates an excess of homozygotes (Cheliak et al 1985).

Assaying 14 allozyme loci in a sample of 47 white spruce trees from a 19 ha natural mixedwood stand, Cheliak et al (1985) reported a mean expected heterozygosity of 0.183 and a mean F value of -0.063. The filial population had a mean expected heterozygosity of 0.298 and a mean F value of -0.066 based on 5 loci. King et al (1984) reported a mean expected heterozygosity of 0.14 and a mean F value of 0.039 based on 20 loci studied in a sample of 37 trees from a 40 ha natural even-aged white spruce stand in north central Alberta. Finally, 22 seed sources from a range-wide white spruce provenance test in Minnesota studied by Furnier et al (1991) had a mean expected heterozygosity of 0.290 and a mean F value of -0.051 based on 6 loci. The low fixation indices indicate no significant difference from Hardy-Weinberg equilibrium in the populations assessed. The expected heterozygosities, then, are illustrative of the high inherent genetic diversity in white spruce (King et al 1984).

The possibility of using allozyme data to develop sampling strategies for gene conservation has been investigated. In the study previously referred to, Furnier et al (1991) compared geographic variation in allozymes and height growth in white spruce. Significant differences were found in allele frequencies among populations but, the among-population variation was only 3.8% of the total. In contrast, 48% and 54% of height variation at ages 9 and 19 respectively was due to differences among populations. Additionally, the height data exhibited definite geographic trends whereas the allozyme data did not. Furnier hypothesized that selection was a significant force defining the genetic variation in height growth but not in allozyme loci. The latter are likely selectively neutral and the low among-population variation may reflect sufficient gene flow to prevent population differentiation for neutral alleles. The same gene flow levels would be insufficient to prevent population differentiation for loci under strong selective constraints such as those associated with height growth. Provenance and progeny tests, then, must continue to be the primary tools for delineating the patterns of variation in selectively important traits such as height growth both for gene conservation purposes and for tree improvement programs (Furnier et al 1991).

In summary, the genetic variation pattern found in white spruce is the result of a predominantly outcrossing mating system with a relatively small proportion of selfing and relative matings. This results in high tree-to-tree and within-population variation. The high potential for long distance gene flow also tends to reduce variation among populations. However, because the species range extends continuously over large areas and crosses different ecological boundaries, both clinal and ecotypic variation are characteristic of white spruce. These types of variation lead to significant variation among populations.

Genetic Parameters:

Genetic parameters of primary interest to tree breeders are heritability, selection differential and intensity, genetic gain, genotype x environment interaction and genetic correlation.

Estimates of these parameters may be based on analyses of variance computations. The total variation associated with a particular trait is partitioned into components attributable to different causes of variation. Of most interest from a tree improvement perspective are (after van Buijtenen 1992)

1) phenotypic variance (V_P), the total variance among all phenotypes in the population,

2) genetic variance (V_G), the portion of phenotypic variance associated with the genetic differences among all trees in the population,

3) additive genetic variance (V_A), the proportion of genetic variance due to the cumulative effects of alleles at all gene loci influencing a trait (Zobel and Talbert 1984),

4) non-additive genetic variance (V_{NA}), the proportion of genetic variance due to dominance effects (interaction of alleles at a gene locus) and epistatic effects (interactions among gene loci) (Zobel and Talbert 1984),

5) environmental variance(V_E), the proportion of phenotypic variance associated with environmental effects only.

Using these components, heritabilities can be estimated. The ratio V_A/V_P, is called heritability in the narrow sense(h^2) and it expresses the extent to which phenotypes are determined by the genes transmitted from the parents (Falconer 1989). Narrow-sense heritability is used for species and programs in which sexual recombination occurs and additive effects are most important (van Buitjenen 1992). Heritabilities are defined relative to a specific trait and a specific population.

The selection differential (S) is the mean of the selected individuals minus the population mean (Becker 1975). Because the standard deviation provides a common scale unit which facilitates comparison of different traits, the selection differential is usually expressed in terms of the phenotypic standard deviation (σ_P). This standardized selection differential (S/σ_P) is called the selection intensity (i) (Falconer 1989).

With an estimate of heritability for a given trait and the selection intensity, genetic gain (ΔG) can be predicted with the following formula

$$\Delta G = ih^2\sigma_P$$

The gain that can be obtained by selection in a given population is, then, a function of the amount of variation present (σ_P), the proportion of the variation that is genetic (h^2) and the intensity of selection in the population (i) (van Buijtenen 1992).

An additional component of variation is often significant when multiple locations or sites are used in genetic testing. Variation due to genotype x environment interaction occurs when the relative performance of families differs when they are grown under different environments (Zobel and Talbert 1984). Commonly, the best and worst families are stable across environments but the mid-range families change ranks quite dramatically from site to site (van Buijtenen 1992).

The consequences of not accounting for the g x e interaction i.e. of planting genetic tests on only one site, are over-estimation of the additive genetic variance and, concomitantly, over-estimation of heritabilities, and, use of suboptimal genotypes in environments different from the test environment (Zobel and Talbert 1984).

Options for dealing with severe g x e interaction involve developing stable genotypes that perform well on a broad range of sites or matching specific genotypes to specific sites.

When considering multiple traits, it is necessary to know if improvement in one character will result in simultaneous changes in another. To examine correlations between two traits, the covariance is partitioned into additive and non-additive components just as the variance can be partitioned for single traits. The correlation is the ratio of the covariance of two traits to the product of their respective standard deviations:

$r_{12} = \mathrm{cov}_{12}/\sigma_1\sigma_2$ (Falconer 1989).

The phenotypic covariance of two traits includes all genetic and environmental variation. A positive phenotypic correlation indicates that the two traits vary in the same direction. Genetic covariance is analogous to additive genetic variance and includes only the component of covariance related to the genetic differences among families. A positive correlation indicates that an increase in one trait due to genetic manipulation will result in a simultaneous increase in the other. A negative correlation means that one trait decreases as the other increases (van Buijtenen 1992).

MATERIALS AND METHODS

Sampling of the Region D white spruce population was completed in 1976 and 1979. One hundred and fifty superior trees were selected throughout the region based on stem straightness, good crown form and branching characteristics and height superiority relative to any dominant tree within a 300 meter distance. A minimum distance of 2 kilometers was maintained between selected trees to ensure non-relatedness and to distribute selections throughout the breeding region. The trees were felled and cones collected.

Seedlings used for establishing field trials were plug+2 transplants. The stock was seeded in March 1983 into 60cc Spencer-Lemaire containers, greenhouse grown for 4 months, hardened-off in shade frames during July and transplanted into bareroot beds in early August, 1983. Seedlings remained in the bareroot beds for the 1984 and 1985 growing seasons and were lifted and packed for transplanting in April, 1986.

Test plantations were established in May, 1986 at four sites representative of the environmental diversity that will form the context of future reforestation projects (Figure 2). Site particulars are given in Table 1 and climatic information from the weather station closest to each site is presented in Table 2.

Table 1. Description of test plantations

Test Site	Lat (°N)	Long (°W)	Elev (m)	Soil Type	Site prep
Calling Lake	55.17	113.09	625	luvisol clay-loam	disced
Mitsue South	55.06	114.32	762	luvisol sandy clay loam	disced
Red Earth	56.34	115.19	518	luvisol clay clay-loam	disced
Carson Lake	54.24	115.34	1006	luvisol clay loam	disced

Table 2. Climatic conditions at test plantations

Station	Elev (m)	distance from site (km)	mean temp (°C) *	mean precip (mm) *	FFP *	DD > 10° C*
Calling Lake Ranger Sta.	594	8.5	14.7	243	88	143
Flattop Lookout	1030	17.5 from Mitsue South	13.3	326	112	112
Red Earth Lookout	610	16	14.3	225	96	129
Whitecourt Lookout	1201	45 from Carson Lake	12.8	326	103	99

* mean temp. and precip. for June, July and August
FFP=frost free period in days
DD= mean degree days greater than 10°C for June, July and August

The experimental design was a randomized complete block with six replications and 6-tree row plots. Calling Lake, however, has only 5-tree row plots due to space limitations. Additionally, all 150 seedlots could not be planted on every site because of stock shortages. At both Mitsue South and Red Earth all 150 seedlots are represented. However, Calling Lake has only 146 seedlots and Carson Lake 147. Post-planting survival was excellent and no mortality replacements were done.

The number of families from each ecoregion is as follows:

Ecoregion	Number of Seedlots
Central Mixedwood	73
Dry Mixedwood	18
Lower Foothills	41
Upper Foothills	18

In the fall of 1993, the following traits were measured or assessed.

- height at age 10 (H10) - measured to the tip of the terminal bud and taken to the nearest centimeter

- height at age 8 (H8) - measured to the second branch whorl down from the terminal bud and taken to the nearest centimeter

- mean increment (MI) - average of 9- and 10-year height growth (MI=H10-H8/2)

- vigor - assessment of the general adaptiveness of each tree with classes as follows

    1-dying or seriously unhealthy
    2-significantly unhealthy
    3-fairly healthy (<u>i.e.</u> may be competitive) but showing signs of dieback
    4-healthy, minor injury
    5-vigorous, no signs of dieback, needle loss, chlorosis or other damage
    6-exceptionally vigorous

- survival - expressed as a percent of living trees calculated on a plot mean basis

- white pine weevil susceptibility (WPW) - expressed as a percent of trees damaged by white pine weevil calculated on a plot mean basis

Statistical Analysis:

The data were summarized according to family means, and analyses of variance completed to determine statistical significances and to compute the variance components of the appropriate sources of variation. The analyses were done on a within individual site basis and then a combined analysis of all sites was completed (see Appendices A-I for ANOVA tables). The analysis of variance format is as follows:

Individual Site:

Model: $Y = \mu + R_j + G_k + F_{l(k)} + \epsilon$

Source	d.f.	EMS*
Rep (R)	R-1	$\frac{\sigma^2_w}{T} + \sigma^2_e + GF\sigma^2_R$
Region (G)	G-1	$\frac{\sigma^2_w}{T} + \sigma^2_e + R\sigma^2_F + Q_G$
Family(Region) (F)	G(F-1)	$\frac{\sigma^2_w}{T} + \sigma^2_e + R\sigma^2_F$
Pooled error	(R-1)(G-1) (R-1)G(F-1)	$\frac{\sigma^2_w}{T} + \sigma^2_e$
Within plots	RGF(T-1)	σ^2_w

Where R=number of replications (6)
G=number of ecoregions (4)
F=number of families per ecoregion (73,41,18,18)
T=number of trees per plot (6 at 3 sites; 5 at 1 site)

N=5400

Combined Sites:

Model: $Y = \mu + S_i + R_{j(i)} + G_k + SG_{ik} + F_{l(k)} + SF_{il(k)} + \epsilon$

Source	d.f.	EMS*
Site (S)	S-1	$\frac{\sigma^2_w}{T} + \sigma^2_e + R\sigma^2_{SF} + RF\sigma^2_{SG} + GF\sigma^2_R + RGF\sigma^2_S$
Rep(site) (R)	S(R-1)	$\frac{\sigma^2_w}{T} + \sigma^2_e + GF\sigma^2_R$
Region (G)	G-1	$\frac{\sigma^2_w}{T} + \sigma^2_e + R\sigma^2_{SF} + SR\sigma^2_F + RF\sigma^2_{SG} + Q_G$
Site*Region	(S-1)(G-1)	$\frac{\sigma^2_w}{T} + \sigma^2_e + R\sigma^2_{SF} + RF\sigma^2_{SG}$
Family(Region) (F)	G(F-1)	$\frac{\sigma^2_w}{T} + \sigma^2_e + R\sigma^2_{SF} + SR\sigma^2_F$
Site*Family(Region)	G(F-1)(S-1)	$\frac{\sigma^2_w}{T} + \sigma^2_e + R\sigma^2_{SF}$
Pooled error	S(R-1)(G-1) G(F-1)S(R-1)	$\frac{\sigma^2_w}{T} + \sigma^2_e$
Within plots	SRGF(T-1)	σ^2_w

Where
S=number of sites (4)
R=number of replications per site (6)
G=number of ecoregions (4)
F=number of families per ecoregion (73,41,18,18)
T=number of trees per plot (6 at 3 sites; 5 at 1 site)

N=20,700

* based on SAS GLM procedure with Region as a fixed variable and all other variables random

Subsequent to the analyses of variance, univariate statistics were generated on residual values for all traits on individual sites and on all sites combined to determine if the data were normally distributed. Normal probability plots and plots of predicted versus residual values indicate that assumptions of normality and constant variance are valid. Due to the low mortality on all sites, the data for survival were skewed and, consequently, an arcsine square root transformation was used to make it conform more closely to a normal distribution. Data for white pine weevil were also slightly skewed but an arcsine square root transformation did not alter the data appreciably so the original data were used in the analysis.

Due to mortality, the data are unbalanced and, consequently, Type III sums of squares were used in the analysis. Although missing cells are present also, Type III and Type IV sums of squares are the same. The extent of the missing data is as given in Table 3.

Table 3. Missing plots at each site

Site	Total plots	plots empty	plots with one tree
Calling Lake	876	3	10
Mitsue South	900	1	0
Red Earth	900	0	0
Carson Lake	882	3	19

Plot means were used to estimate site, replicate, region and family variances and the between plot error variance. The within-plot variance was estimated on an individual tree basis. This method provides variance component estimates that are very similar to an analysis based entirely on individual tree data and requires much less computational time and computer resources (Stonecypher 1992).

All analyses were done using SAS PROC GLM with one exception. Due to insufficient computer memory, PROC ANOVA was used to obtain the within-plot variance estimate for the combined sites analysis.

In calculating heritabilities, the variance component for open-pollinated families was assumed to estimate one-quarter of the additive genetic variance (Wright 1976). Individual tree (h^2_i) and family mean heritabilities (h^2_f) for all sites combined were estimated using the following formulas.

$$h^2_i = \frac{4\sigma^2_F}{\sigma^2_w + \sigma^2_e + \sigma^2_{SF} + \sigma^2_F}$$

$$h^2_f = \frac{\sigma^2_F}{\frac{\sigma^2_w}{SRT} + \frac{\sigma^2_e}{SR} + \frac{\sigma^2_{SF}}{S} + \sigma^2_F}$$

The terms are as defined in the analysis of variance format presented above.

For number of trees per plot, harmonic means were used as follows:

Calling Lake - 4.506
Red Earth - 5.75
Mitsue South - 5.62
Carson Lake - 4.284
All Sites - 4.963
Calling Lake/Red Earth (for calculating weevil damage h^2) - 5.06

For the calculation of genetic correlations, SAS PROC VARCOMP was used to generate the variances of individual traits and their sums, and the covariance was estimated using the formula

$$COV_{xy} = (\sigma^2_{(x+y)} - \sigma^2_x - \sigma^2_y)/2$$ (Stonecypher 1992).

Genetic correlations were calculated using the following formula

$$r_G = \frac{Cov_{xy}}{\sqrt{\sigma^2_x} * \sqrt{\sigma^2_y}}$$ (Becker 1975).

The hypotheses being tested were as follows:

1) The mean performance of white spruce does not vary from test site to test site.
2) The mean performance of white spruce from four ecoregions does not vary from test site to test site.
3) The mean performance of white spruce families does not vary on any of the four test sites.

4) There is no interaction between test sites and ecoregions.

5) There is no interaction between test sites and families of any ecoregion.

RESULTS

Survival:

Survival was excellent at Calling Lake, Mitsue South and Red Earth and good at Carson Lake (Table 4). Statistical comparison of mean survival using Duncan's Multiple Range Test indicated Carson Lake was significantly different from all other sites.

Table 4. Mean Survival (%)

	TEST SITES				
	Calling Lake	Mitsue South	Red Earth	Carson Lake	All Sites
No. of trees	4380	5400	5400	5292	20472
Mean	95	96	97	81	92
Range	70-100	72-100	75-100	53-100	53-100

All sites were similarly prepared and received essentially the same post-planting care. However, Carson Lake is variable topographically in comparison to the other sites and, being located in the Upper Foothills Region, is dissimilar climatically from the other sites as well. Calling Lake and Red Earth are both in the Central Mixedwood Region and Mitsue South is in the Lower Foothills Region.

Lower survival at Carson Lake may be associated with the varied topography at the site because most of the mortality occurred on the higher, more exposed areas. Planting shock can be excluded as a primary cause as many of the trees had reached 1 metre or more in height before dying i.e. 3-4 years post-planting. Armillaria root rot is a major disease of white spruce and could have been a significant factor in the mortality. However, none of the dead trees were excavated to determine if the fungus was present. Heavy grass is also present on portions of the site and likely caused some mortality by out-competing young seedlings for nutrients and light.

Analysis of variance revealed no significant ecoregion or family differences in survival and also no significant interaction between sites and families for survival. The only significant source of variation is sites.

Height:

The best height growth occurred at Carson Lake and the poorest at Calling Lake (Table 5). After 8 and 10 years of growth, mean height at Calling Lake was 60% and 61%, respectively, of the mean height at Carson Lake.

Table 5. Mean and Standard Error of Families for 4 Growth Traits

Test Site		Traits			
		H10	H8	MI	VIG
Calling Lake	Mean	106	84	11	3
	Std Err	0.43	0.36	0.08	0.006
Mitsue South	Mean	145	109	18	4
	Std Err	0.54	0.40	0.13	0.008
Red Earth	Mean	143	112	16	3
	Std Err	0.60	0.44	0.10	0.008
Carson Lake	Mean	174	139	18	4
	Std Err	0.71	0.58	0.15	0.009
All Sites	Mean	142	111	16	3
	Std Err	0.34	0.26	0.06	0.004

H10=mean height at age 10 (cm)
H8=mean height at age 8 (cm)
MI=mean of 9- and 10-year height growth (cm)
VIG=mean plant vigor score

Variance components and heritabilities for the individual site analyses and for the combined site analysis are given in Tables 6 and 7, respectively.

At the site level, height growth at both age 8 and age 10 differed significantly according to family. Across sites, significant variation in height is attributable to site and family. The site by family interaction is also highly significant accounting for 36% and 30% (Table 7 σ^2_{SF}/σ^2_F) of the between family variance at age 8 and age 10, respectively.

Ecoregions did not contribute to height variation either within or across sites.

Typically, within plot variation (σ^2_w) accounted for the largest component of the total variation in height, comprising about 50% of the total variation in the combined site analysis for both age 8 and age 10 (Table 7). In comparison, family variation (σ^2_F) accounted for 2% and 3% of the total variation in the combined site analysis for age 8 and 10, respectively.

The site by family interaction indicates the rank shifting occurring across the four test sites. Of the 146 families that were common to all sites, 27 showed above average performance on all sites for height at age 10. If Carson Lake is excluded, the number performing above average on the remaining three sites is 36. Of the seedlots performing below average for

Table 6. Growth Trait Variance Components and Heritabilities for Individual Sites

H10	σ^2_w	%	σ^2_e	%	σ^2_F	%	σ^2_R	%	h^2_i	h^2_f
Calling Lake	684	87	33	4	64	8	3	0	.33	.67
Mitsue South	1180	77	227	15	81	5	42	3	.22	.52
Red Earth	1210	64	506	27	125	6	55	3	.27	.50
Carson Lake	1702	78	300	14	132	6	49	2	.25	.49
H8	σ^2_w	%	σ^2_e	%	σ^2_F	%	σ^2_R	%	h^2_i	h^2_f
Calling Lake	456	86	26	5	45	8	6	1	.34	.68
Mitsue South	645	76	136	16	35	4	36	4	.17	.44
Red Earth	720	67	265	25	70	6	24	2	.26	.51
Carson Lake	1120	79	215	15	47	3	39	3	.14	.33
MI	σ^2_w	%	σ^2_e	%	σ^2_F	%	σ^2_R	%	h^2_i	h^2_f
Calling Lake	24	90	2	7	0.7	3	.07	0	.11	.38
Mitsue South	75	86	7	9	5	6	.4	0	.25	.61
Red Earth	34	68	12	25	2	4	1.5	3	.15	.37
Carson Lake	86	87	3	3	9	9	.6	1	.38	.69
VIG	σ^2_w	%	σ^2_e	%	σ^2_F	%	σ^2_R	%	h^2_i	h^2_f
Calling Lake	.12	75	.03	19	.006	4	.004	2	.16	.42
Mitsue South	.31	86	.03	9	.014	4	.002	1	.15	.49
Red Earth	.23	70	.08	24	.014	4	.007	2	.17	.41
Carson Lake	.32	82	.05	13	.014	4	.005	1	.14	.35

H10=height age 10 (cm)
H8=height age 8 (cm)
MI=mean of 9- and 10-year height growth (cm)
VIG=plant vigor score

σ^2_w=variation within plots
σ^2_e=variation between plots error
σ^2_F=family(reg) variation
σ^2_R=rep variation
h^2_i=individual tree heritability
h^2_f=family mean heritability

Table 7. Growth Trait Variance Components and Heritabilities for All Sites

Trait	σ^2_w	%	σ^2_e	%	σ^2_{SF}	%	σ^2_F	%	$\sigma^2_{R/S}$	%	σ^2_S	%	h^2_i	h^2_f
H10	1198	51	269	11	23	1	77	3	38	2	753	32	.19	.74
H8	731	50	165	11	13	1	36	2	26	2	502	34	.15	.69
MI	55	72	6	8	1.5	3	2.8	4	.7	1	10	13	.17	.72
VIG	.25	66	.04	11	.007	2	.005	1	.005	1	.07	19	.06	.48

H10=height age 10 (cm)
H8=height age 8 (cm)
MI=mean of 9- and 10-year height growth (cm)
VIG=plant vigor score
h^2_i=individual tree heritability
h^2_f=family mean heritability

σ^2_w=variation within plots
σ^2_e=variation between plots error
σ^2_{SF}=site*family(reg) variation
σ^2_F=family(reg) variation
$\sigma^2_{R/S}$=rep(site) variation
σ^2_R=replicate variation
σ^2_S=site variation
NOTE: σ^2_{SG} not included in table because it did not contribute to total variation

height at age 10, 32 were common to all four sites and 38 to all sites except Carson Lake.

However, in spite of the significant site by family interaction, the estimates of family mean correlation for height at age 10 between pairs of sites are all positive and statistically significant. The corresponding genetic correlations are much larger (Table 8) indicating a substantial portion of the genotype x environment interaction is due to factors other than differential genetic performance from site to site (Nelson and Mohn 1991).

The coefficients illustrate the dissimilarity between Carson Lake and the Central Mixedwood sites (Red Earth and Calling Lake). The lowest coefficients are between these sites. A north/south trend is also apparent with lower coefficients between Red Earth, the most northerly site, and Mitsue South and Carson Lake, the most southerly.

These trends are again apparent in the genetic correlation coefficients between site pairs for height at age 8 (Table 9). In addition, the coefficients increase from age 8 to age 10 with the exception of Red Earth/Carson Lake.

Table 8. Simple, Rank and Genetic Correlation Coefficients between site pairs for Family Height at age 10

Test Site		Mitsue South	Red Earth	Carson Lake
Calling Lake	simple	0.53	0.54	0.33
	rank	0.53	0.52	0.31
	genetic	0.88	0.89	0.54
Mitsue South	simple	-	0.38	0.51
	rank	-	0.34	0.51
	genetic	-	0.70	0.94
Red Earth	simple	-	-	0.35
	rank	-	-	0.33
	genetic	-	-	0.63

Table 9. Genetic Correlation Coefficients between site pairs for Family Height at age 8

Test Site	Mitsue South	Red Earth	Carson Lake
Calling Lake	.79	.87	.39
Mitsue South	-	.60	.92
Red Earth	-	-	.78

Individual and family heritabilities are given in Tables 6 and 7. For Carson Lake and Mitsue South, the trend is for both individual and family heritabilities to increase with age indicating the increasing influence of genetic factors in height performance as age increases. However, for Calling Lake and Red Earth, this trend is absent and heritabilities essentially remain the same for height at both ages. These static heritabilities are likely the result of white pine weevil infestations that have obscured the expression of greater family variance in height. The percent family variance reflects this situation. For Calling Lake and Red Earth, the proportion of family variance remains the same for both ages at 8% and 6%, respectively. However, the percent increases for Mitsue South and Carson Lake going from 3% to 6% for the former and from 4% to 5% for the latter.

Strong genetic correlations both within and across sites between age 8 and age 10 heights indicate that selection for height at the younger age is feasible. The coefficients are 0.99, 0.88, 0.97 and 0.90 for Calling Lake, Mitsue South, Red Earth and Carson Lake, respectively. The coefficient for all sites combined is 0.96.

Mean Increment:

Mean increment displays the same trend as heights, with Carson Lake showing the best performance and Calling Lake the poorest (Table 5).

Family is a highly significant source of variation at each individual site. Considering all sites combined, sites, families and the site x family and site x ecoregion interactions are all significant sources of variation.

Variation due to sites is less important for mean increment than it is for height. It accounts for only 13% of the total across-site variation in comparison to 34% and 32% for height at age 8 and 10, respectively. The within-plot variation is concomitantly higher at 72% of the total, in comparison to 50% and 51% for height at age 8 and 10, respectively. In other words, differences between trees contribute considerably more to increment variation than differences between sites.

Rank and genetic correlation coefficients between site pairs for family mean increment are given in Table 10. Again, a north/south trend is revealed with the lowest correlations between Red Earth/Carson Lake and Red Earth/Mitsue South. Genetic correlations between Calling Lake/Mitsue South and Mitsue South/Carson Lake are in the region of unity.

Table 10. Rank and Genetic Correlation Coefficients between site pairs for Family Mean Increment

Test Site		Mitsue South	Red Earth	Carson Lake
Calling Lake	rank	.48	.31	.40
	genetic	1.08	.88	.73
Mitsue South	rank	-	.26	.67
	genetic	-	.63	1.06
Red Earth	rank	-	-	.25
	genetic	-	-	.49

Strong genetic correlations between height at age 10 and mean increment indicate that simultaneous selection is possible for these two traits. The coefficients are 0.79, 0.80, 0.93, and 0.86 for Calling Lake, Mitsue South, Red Earth and Carson Lake, respectively. For all sites, the coefficient is 0.88.

Heritabilities for mean increment are indicated in Tables 6 and 7. Values range from 0.11 to 0.38 (h^2_i). Lower heritabilities for Calling Lake and Red Earth are indicative of a smaller family variance component, 3% and 4% of the total, respectively. In comparison, the family variance component accounts for 6% of the total at the other two sites. This is indicative of the greater environmental variation at Calling Lake and Red Earth resulting from white pine weevil infestations and subsequent pruning.

Plant Vigor:

Mitsue South and Carson Lake were rated the most vigorous of the four sites (Table 5). This is largely due to the fact that both sites were relatively free of white pine weevil.

The only significant source of variation at individual sites was family. Site, family and the site*family interaction were all highly significant in the combined sites analysis. Ecoregion variation was not significant either within or across sites.

As with mean increment, the contribution of sites to variation in vigor is not as large as it is for height variation. The between tree differences account for more than half of the variation in vigor for all sites combined.

Genetic correlations between site pairs are given in Table 11. Overall, the correlations are not as strong as they are for the growth traits. Additionally, some of the previously noted trends are reversed. For example, Mitsue South and Carson Lake have the strongest genetic correlations over all other site pairs for both age 8 and 10 height, and for mean increment, the correlation is in the area of unity. However, for vigor, the correlation is only 0.50 and other site pairs have stronger correlations. Most notably, Calling Lake and Carson Lake, which have the lowest correlation coefficients for both age 8 and 10 height and the third lowest for increment, have the second highest coefficient for vigor (0.60).

Table 11. Genetic Correlation Coefficients between site pairs for plant vigor

Test Site	Mitsue South	Red Earth	Carson Lake
Calling Lake	0.62	0.45	0.60
Mitsue South	-	0.38	0.50
Red Earth	-	-	0.42

Heritabilities for plant vigor are given in Tables 6 and 7. They are essentially the same at all four sites with family differences contributing equally (4%) to total variation in vigor at all sites. Higher variation between replications at Calling Lake and Red Earth relates to the variable effects of white pine weevil across these sites.

White Pine Weevil:

White pine weevil damage at Calling Lake and Red Earth was wide spread with 33% and 27% of living trees, respectively, being affected. However, only 6% and 5% of living trees were affected at Mitsue South and Carson Lake, respectively (Table 12) Only the former two sites were used in the analysis because the family differences in white pine weevil susceptibility are obscured if all four are included due to the low numbers affected. Pruning of leaders killed by weevils was undertaken at both Calling Lake and Red Earth in June, 1992 and 1993. The number of trees affected is indicated in Table 12. Trees attacked by weevils and not pruned had either recovered from the attack and established a new leader or, had not yet developed symptoms of weevil attack when pruning was done.

The variable analyzed is family mean percent with white pine weevil damage. Variance components and heritabilities are given in Table 13. In the combined analysis of the two sites, percent white pine weevil damage differed significantly according to family. The site x family interaction is also significant and the interaction variance is approximately one-half of the family variance (Table 14). The genetic correlation between the two sites for this trait is positive with a coefficient of 0.66 and a rank correlation coefficient of 0.30.

For individual sites, family is the only significant source of variation in white pine weevil damage percentage.

Table 12. Number and Percent of trees affected by White Pine Weevil and Number and Percent of trees pruned due to White Pine Weevil

Test Site	Total trees	no wpw	%[1]	wpw/np	%[1]	wpw/p	%[1]	living	%[2]
Calling Lake	4380	2800	67	740	18	618	15	4158	95
Mitsue South	5400	4865	94	33	1	279	5	5177	96
Red Earth	5400	3824	73	438	8	973	19	5235	97
Carson Lake	5292	4093	95	210	5	3	-	4306	81

wpw=white pine weevil
np=not pruned
p=pruned
%[1]=percent of living trees
%[2]=percent of total trees

Heritabilities and variance components are given in Tables 13 and 14. The high heritabilities indicate the higher family variance components for this trait, both for individual and combined sites, in comparison to the family variance components for the growth traits. For the latter, family variance accounts for only 2-4% of the total on a combined site basis and for white pine weevil damage percentage, it comprises 8% of the total.

Genetic correlations were calculated between height at age 10 and white pine weevil damage percentage. Trees that had been pruned were excluded from the analysis to avoid biasing the results. For Calling Lake, the correlation is very low with a coefficient of 0.09. However, for Red Earth, the correlation

Table 13. Variance Components and Heritabilities for Percent White Pine Weevil Damage at Calling Lake and Red Earth

Test Site	σ^2_e*	%	σ^2_F	%	σ^2_R	%	h^2_i	h^2_f
Calling Lake	559	86	71	11	19	3	.45	.77
Red Earth	435	79	81	15	32	6	.63	.87

*component being estimated is $(\sigma^2_w/T)+\sigma^2_e$

Table 14. Variance Components and Heritabilities for Percent White Pine Weevil Damage Calling Lake and Red Earth Combined

σ^2_e*	%	σ^2_{SF}	%	σ^2_F	%	$\sigma^2_{R/S}$	%	σ^2_S	%	h^2_i	h^2_f
496	82	25	4	51	8	26	4	7	1	.36	.71

*component being estimated is $(\sigma^2_w/T)+\sigma^2_e$
σ^2_{SG} not included in table because it did not contribute to total variation

coefficient is -0.52. The negative correlation suggests that white pine weevil percent and 10-year height may be confounded, i.e. weevil damaged trees are shorter on average than those not attacked because the leader has been killed and the tree has not yet recovered.

Nevertheless, as indicated in Table 15, the incidence of weevil damage in the top 50% of families for age 10 height is considerably lower than the site average for weevil damage. The difference is particularly striking for the Red Earth site.

Table 15. Comparison of the Mean Percent Damage of the top 50% of Families for age 10 height and the Site

Test Site	Mean % WPW Damage Site	Mean % WPW Damage above average families
Calling Lake	33	18
Red Earth	27	6

Geographic Trends:

No significant trends related to latitude, longitude and elevation were observed in any of the growth traits studied. Simple correlation coefficients are presented in Table 16.

Table 16. Simple Correlation Coefficients of Family Growth Trait Means with Latitude, Longitude and Elevation

	H10	H8	MI	VIG
LATITUDE	-0.10	-0.07	-0.14	-0.05
LONGITUDE	-0.03	-0.03	0.01	-0.02
ELEVATION	0.007	-0.02	0.08	0.06

Latitude modified by elevation according to the rule given by Wiersma (1964) is also not significantly correlated with family mean height at age 10. Wiersma states that, with regard to the length of the growing season, a displacement of one degree of latitude to the north is equivalent to a displacement of 100 meters upwards (i.e. modified lat. = lat. + (elev./100)). He found significant correlations between mean 19 year height and modified latitude for a Picea abies provenance trial (R=-0.60). However, in the test he analyzed, the range of latitudes was approximately 20° whereas the range of latitudes in this study is only 2°. The R value for mean height at age 10 and modified latitude is -0.04.

Simple correlations between location and white pine weevil incidence were calculated separately for the Calling Lake and Red Earth sites. For the Calling Lake site, family mean percent white pine weevil damage is not significantly correlated with location. However, latitude and mean percent white pine weevil damage are significantly correlated for the Red Earth site. Coefficients are tabulated below.

Table 17. Simple Correlation Coefficients of Family Mean Percent White Pine Weevil with Latitude, Longitude and Elevation

	Calling Lake	Red Earth
LATITUDE	-0.11	-0.21*
LONGITUDE	0.17	0.16
ELEVATION	0.03	0.12

*significant at 0.01 level

The negative correlation indicates that the families from more northerly provenances have lower mean percent white pine weevil damage.

DISCUSSION

Validity of Null Hypotheses:

1) The mean performance of white spruce does not vary from test site to test site.

Site was a significant source of variation in all traits studied except percent white pine weevil damage. Consequently, the null hypothesis is rejected.

Significant variation attributable to site is indicative of the heterogeneity in climate and topography to be found throughout the breeding region. Site was a particularly important source of variation for height growth accounting for 34% and 32% of the total variation for height at age 8 and 10, respectively. Similar results were reported by Kiss and Yeh (1988). In a study of an interior spruce progeny test established on three sites in British Columbia, they reported that site accounted for 27%, 30% and 9% of the total variation in height at age 6, 9, and 13 years from seed, respectively.

2) The mean performance of white spruce from four ecoregions does not vary from test site to test site.

Performance of white spruce from each ecoregion did not vary significantly for any of the traits studied. The ecoregion classification system for Alberta has just recently been re-defined (Anon 1994) and the relative absence of significant performance variation by ecoregion may reflect the need for further refinements in the system. Alternatively, the lack of ecoregion variation may, in fact, indicate no ecotypic difference within white spruce in this breeding region. The null hypothesis is not rejected.

3) The mean performance of white spruce families does not vary on any of the four test sites.

Family variation was highly significant for all traits studied except survival. The null hypothesis is rejected.

For height and increment, family variance accounted for 4-5% of the phenotypic variation across sites and 2-4% of the total variation. This is comparable to other reported results for genetic variation in height growth. For white spruce, Kiss and Yeh (1988) report family variance components of 9.4%, 6.2% and 6.5% of total variation for height at age 6, 9 and 13 years from seed, respectively. Nienstaedt and Riemenschneider (1985) report 4.0% and 6.2% of phenotypic variation for height at age 9 and 15, respectively, and Li et al (1993) reported 2.4% of total variation for 8-year height. For black spruce, Nelson and Mohn (1991) reported 3% of phenotypic variation for 7, 10 and 12 year heights. Finally, Yeh and Rasmussen (1985) reported family variance of 1.4% of total for sitka spruce (Picea sitchensis(Bong.)Carr.) 10-year height.

For percent white pine weevil damage, family variance accounted for 8% of the total variation for combined sites. Kiss and Yanchuk (1991) reported the same percent family variance in a study of genetic variation of weevil resistance in white spruce in British Columbia.

4) There is no interaction between test sites and ecoregions.

Ecoregions were generally stable over sites. Consequently, the null hypothesis is not rejected.

The only significant site x ecoregion interaction occured for mean increment in the combined sites analysis at the 5% level. However, this interaction term is very small amounting to only 0.2% of the total variation for mean increment.

5) There is no interaction between test sites and families of any ecoregion.

Interaction between sites and families is significant for all traits studied except survival. The null hypothesis is, therefore, rejected.

Although it is significant, the interaction effect for height is still smaller than the main effect of families. For age 8 and 10 the interaction variance component is 36% and 30%, respectively, of the between family component. Over all sources, the site x family interaction accounts for 1% of the total variation in height for both age 8 and age 10.

Results of other studies differ regarding the magnitude of the site x family variance component relative to the between family component with increasing age. In this study, it decreases with age, as it does in Nienstaedt and Riemenschneider's (1985) study. In the latter, it decreased from 28% at age 9 to 12% at age 15. In Kiss and Yeh's study (1988), the site x family component increased from 18% of the between family variance at age 6 to 24% at age 9. At age 13, however, the site x family component decreased to 20% of the between family variance. Nelson and Mohn (1991) reported a similar trend in black spruce with the site x family component increasing relative to the between family component between age 7 and 10 and then decreasing between 10 and 12 years. These trends suggest that starting at about 10 years, family differences in height become more defined. In this study, the generally increasing genetic correlation coefficients for height between site pairs from age 8 to age 10 (Tables 8 and 9) appear to support this suggestion.

Additional trends in site x family interaction are discernable in the genetic correlations between site pairs for height (Tables 8 and 9). The coefficients between Carson Lake and Calling Lake, 0.39 and 0.54 for height at age 8 and 10, respectively, are markedly lower than the others suggesting differential performance of genotypes on these sites i.e. high performance on one site requires a different set of genes than on the other (Falconer 1989). The coefficients suggest that the Carson Lake site may belong in a different breeding region.

For mean increment, the interaction component is 54% of the between family component (Table 7). The rank shifting suggested is confirmed by the rank correlation coefficients between site pairs (Table 10). Of the six site pairs, increment correlations are lower than height correlations in four. However, the high genetic correlation coefficients suggest that factors other than differential genetic performance are playing an important role in the rank changes in increment between sites. A primary factor in this case is likely differential white pine weevil attacks.

The site x family interaction component for plant vigor is larger than the between family component and the genetic correlation coefficients are smaller than the corresponding coefficients for height and increment. These factors suggest that plant vigor is not the best criterion to use for selection because of pronounced rank shifting for this trait across sites.

Heritabilities:

Heritabilities for height are comparable to those quoted in the literature for white spruce. For example, heritabilities of 0.10 (individual) and 0.45 (family) for 8-year height (Li et al 1993), 0.36 (individual) and 0.73 (family) for 9-year height, 0.29 (individual) and 0.67 (family) for 13-year height (Kiss and Yeh 1983), 0.43 (individual) for 8-year height, 0.51 (individual) for 9-year height (Nienstaedt 1985) have been reported.

For increment, Li et al (1993) reported 0.12 (individual) and 0.37 (family) for 3-year height increment, and Nienstaedt (1985) reported an individual heritability of 0.49 for 7-year terminal growth.

Kiss and Yanchuk (1991) reported 0.18 (individual) and 0.77 (family) heritabilities for percent white pine weevil damage.

For height at both age 8 and 10, Calling Lake, the least productive site, has the highest heritabilities. Nienstaedt and Riemenschneider (1985) reported the same phenomenon in their white spruce progeny test study. However, this trend is reversed for mean increment. Carson Lake, the site with the highest productivity, has the highest heritabilities for this trait.

At Carson Lake, family differences for height are somewhat obscured by the interaction between replications and families, i.e. by the environmental variation (σ^2_e=14%). At Calling Lake, the variation attributable to environment is very low (σ^2_e=4%) and family differences are better expressed.

For mean increment, environmental variation is greatly reduced at Carson Lake (σ^2_e=3%), allowing for more pronounced expression of family variance in mean increment. For Calling Lake, relatively low mean increment heritabilities are the result of increased between-tree (σ^2_w) and environmental variation and a correspondingly lower family variance component.

The topographical variability at the Carson Lake site is likely the primary factor in the relatively large replicate x family interaction. In contrast, Calling Lake is quite uniform. However, the topography at the Carson Lake site apparently does not interfere with the expression of family differences in mean increment. The increased between-tree and replication x family variance at Calling Lake is probably due to the effects of white pine weevil.

Trends with age in height heritabilities also reflect the effects of white pine weevil. Heritabilities at Mitsue South and Carson Lake increased from age 8 to age 10 and those at Calling Lake and Red Earth remained essentially the same. At the latter sites, where weevils caused widespread damage, the family variance component has stayed the same from age 8 to 10. In contrast, at Mitsue South and Carson Lake, the family variance component increased between the two ages and, in fact, doubled for the Carson Lake site. Concomitantly, environmental variance tended to decrease. These trends suggest that expression of family differences in height growth is being obscured by the effects of weevil attacks at Calling Lake and Red Earth.

Correlations:

For white spruce, high age-to-age correlations for height are widely reported in the literature. For example, a genetic correlation of 1.05 for 8- and 3-year heights was reported in Li et al's progeny test study (1993), Kiss and Yeh (1988) reported a family mean correlation of 0.96 for 6- and 10-year height assessments, and Nienstaedt and Riemenschneider (1985) reported age-9 and -15 family mean correlations of 0.943 and 0.930, respectively, for two progeny test sites. These are comparable to the age-8 and -10 correlations for this study. The genetic correlation coefficient of 0.96 for all sites combined indicates that progress in the improvement of white spruce can be accelerated by selection at age-8 rather than 10.

Genetic correlations between mean increment and height at age-10 are not as strong as height correlations, but indicate that simultaneous selection for superior height and increment is feasible. The genetic correlation coefficient of 0.88 for all sites combined is comparable to those reported in other studies. For example, Nienstaedt (1985) reported correlations of 0.729 and 0.753 between 8-year total height and terminal growth of the previous year and between 8-year total height and terminal growth of the same year, respectively. For 8-year height and 3-year height increment, Li et al (1993) reported a genetic correlation of 0.77.

The genetic correlation coefficient of -0.52 for percent weevil damage and age-10 height for the Red Earth site is very close to that reported by Kiss and Yanchuk (1991) for 10-year height and percent weevil damage of white spruce at 16 years (r_g=-0.51). Ledig and Smith (1981) reported a similar value of -0.50 for family mean height and weevil attack in eastern white pine plantations.

In this study, the negative correlation is likely due to the fact that weevil attacks have severely reduced the growth of affected trees. However, in Kiss and Yanchuk's (1991) study height growth data and weevil damage were not confounded and they suggested that the negative correlation indicates genetic composition of individual trees is more important in weevil susceptibility than length and diameter of the leader. Their data support this suggestion. In their study, the incidence of damage in the top 25% of families for 10-year height is consistently less than the plantation average for weevil damage. This trend is also apparent for the Calling Lake and Red Earth sites and most particularly for the latter. The top 50% of families at Red Earth have only 6% mean percent weevil damage compared to a site average of 27%.

In Ledig and Smith's (1981) study, progeny from white pine stands selectively thinned to remove weeviled trees had superior height growth to progeny from untreated weeviled stands indicating selection for weevil resistance does not constitute selection against rapid height growth. They suggested, as did Kiss and Yanchuk (1991), that weevil susceptibility is not solely related to leader height and vigor. They found that weevils preferentially attacked the tallest trees within families, but that this relationship was not necessarily true between families.

Genetic Gain:

The progeny test data analyzed in this study will be used to identify superior parents in an unrogued seed orchard. Selection, then, is for particular half-sib families. The top 50% of families will be retained. Based on these criteria, genetic gain (ΔG) is calculated as follows.

$$\Delta G = i * \frac{.25\sigma^2_A}{\sigma_p} \quad \text{(Namkoong et al 1966)}$$

where i = selection intensity expressed in standard deviations

$.25\sigma^2_A$ = one-quarter of the additive genetic variance

$= \sigma^2_F$

σ_p = phenotypic standard deviation

$$= \sqrt{\frac{\sigma^2_w}{TRS} + \frac{\sigma^2_e}{RS} + \frac{\sigma^2_{FS}}{S} + \sigma^2_F}$$

(see Table 7 for symbol definitions).

Using the genetic parameters for 10-year height, genetic gain is

$$\Delta G = \frac{0.9 * 77}{10} = 7 \text{ cm}$$

where $i = \dfrac{\overline{X}_{selected} - \overline{X}_{overall}}{\sigma_p} = \dfrac{151 - 142}{10} = 0.9$

$\sigma^2_F = 77$ (Table 7)

$\sigma_p = \sqrt{\dfrac{1198}{6*6*4} + \dfrac{269}{6*4} + \dfrac{23}{4} + 77} = 10$ (Table 7).

Relative to the unselected population, expected gain in 10-year height is (7/142)*100 = 5%. In comparison, Li et al

(1993) reported an expected genetic gain of 7.7% in 8-year height if the best 20% of families were selected from 285 open-pollinated white spruce families from Ontario and Quebec and Kiss and Yeh (1988) reported an expected genetic gain of 12.1% in height at 13 years if the top 40% of families were retained from 174 open-pollinated white spruce families from British Columbia.

CONCLUSIONS AND IMPLICATIONS

Prior to completion of this study, virtually no information was available on the magnitude and nature of the genetic variation in growth traits, plant vigor and weevil resistance for Alberta white spruce populations.

Results indicate that in the white spruce population delimited by breeding region 'D', there is substantial within- and among-family genetic variation in the traits studied.

Family heritabilities are high (0.74 for age-10 height, 0.72 for mean increment and 0.71 for percent white pine weevil damage) and gains of about 5% in height growth are predicted following selection of the top 50% of families. The high positive correlation between mean increment and age-10 height (0.88 for all sites combined) indicates simultaneous gains can be made in total height and growth rate. Between-family variance components of 3% of total variation for height at age 10, 4% for mean increment and 8% for percent weevil damage indicate significant family differences in these traits.

The within-family variance components, however, account for the greatest amount of total variability in all traits studied (51% for age-10 height, 72% for mean increment and 82% for percent white pine weevil damage). There is, therefore, wide scope for further improvement by selecting the best individual trees within families.

Individual tree heritabilities are low for the growth traits (0.19 for age-10 height, 0.17 for mean increment) and moderate for percent weevil damage (0.36). However, the large number of families (150) and the large family size (138) allow for a high selection intensity within families. Further gains of approximately 11.5% are predicted for height growth as indicated in the following calculations.

$$\frac{2.78*(3*77)}{39} * \frac{1}{142} = 11.5\%$$

where 2.78 is the selection intensity expressed in standard deviations (Becker 1975) with the proportion selected being 1/138=.007, 77 is σ^2_F ($.25\sigma^2_A$) for age 10 height (Table 7), 39 is $\sqrt{\sigma^2_w + \sigma^2_c + \sigma^2_{FS}}$ for age 10 height (Table 7) and 142 is the mean height of the unselected population. Since $\sigma^2_F = .25\sigma^2_A$, multiplying by 3 accounts for the remaining three-quarters of the additive variance utilizable when within-family selection is practiced.

However, the likelihood that these heritabilities are inflated should be considered. For this progeny trial, families consisted of 138 individuals. To be true half-sibs, they all must have had a different pollen parent. Since it is not likely that this condition has been fulfilled, the genetic correlation among offspring is probably somewhat larger than

0.25, the correlation between true half-sib families (Squillace 1974).

A possibly more appropriate genetic correlation value was estimated by Cheliak et al (1985) on the basis of an allozyme study of a white spruce population covering an area of 19 ha. The estimated ratio of genetically effective males to females in their sample of 47 trees was approximately 0.4. They concluded that a figure of 0.37 was more realistic than 0.25 as the proportion of additive genetic variance represented by the among-family component of variance. This would be applicable for progeny arrays of 40 or less from one tree.

Squillace (1974) estimated the correlation to be 0.30 for a family size of 100, assuming a selfing level of 0% and assuming five equally effective local pollen parents. Using 0.30 in the heritability calculations for this study would have the effect of reducing the age-10 height individual tree heritability for combined sites from 0.19 to 0.16.

Calculation of the genetic correlation among offspring requires accurate information on number of pollen parents, number of offspring sired by each pollen parent and selfing rates (Squillace 1974). As this information is generally unavailable for the region of Alberta under study, it seems more appropriate to use the 0.25 coefficient, with the knowledge that estimates of heritability and gain are somewhat inflated rather than to use an estimate that is based on information not specific to the area under study.

Ecoregion and geographic location effects for any of the traits studied were essentially not significant. This is likely more a result of the restricted geographic area of the study and the very broad definitions of ecoregions than a lack of provenance and ecoregion variation in white spruce families. In fact, an Alberta range-wide white spruce provenance study (Morgenstern and Keenan 1993) found highly significant provenance effects for height at 15 years.

The significance of the site x family interaction may have implications for the selection of broadly adapted genotypes that perform well on all sites in the breeding region. Nevertheless, of the above average families over all, 84% are also above average at Calling Lake, 79% at Red Earth, 75% at Mitsue South, and 78% at Carson Lake. Additionally, the high genetic correlation coefficients between site pairs, excluding the Calling Lake/Carson Lake coefficient, indicate that absolute and relative differences in environmental and genetic variances between sites may be playing a larger role in the site x family interaction than differential genetic performance of families (Nelson and Mohn 1991) (Searle 1961).

Although this study has provided insights into the nature of genetic variation in central Alberta populations of white spruce, it has also raised many questions that require additional research.

The relationship between height growth and white pine weevil resistance should be explored further. Definitive conclusions could not be made from this study because height and weevil damage were confounded. Further investigation is also warranted in ecoregion variation in white spruce. Since this study was not specifically designed to test variation in white spruce according to the new ecoregion classification system, the lack of significant ecoregion variation should not be considered conclusive.

Given the young age of the progeny test plantations, the information provided in this study should be regarded as preliminary. Continued monitoring of changes in the magnitude of variance components and in the nature of the relationships between different components with increasing age will further define the nature of genetic variation in white spruce. Such changes affect heritabilities and correlations and, consequently, have a direct impact on the tree improvement program and genetic gain calculations. Therefore, remeasurement of the progeny trials is planned at regular intervals in order to further refine the tree improvement program and to explore additional aspects of genetic variation in white spruce.

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APPENDICES

APPENDIX A.
Analyses of Variance Tables for Calling Lake

Table A1. Analysis of Variance of Age-10 Height at Calling Lake - Plot Mean Basis

Dependent Variable: age-10 height

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	150	84970.30	566.46	3.07	0.0001
Error	722	133267.09	184.58		
Total	872	218237.40			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
REP	5	2961.53	592.30	3.21	0.0071
REG	3	1329.79	443.26	0.78	0.5076
FAMILY(REG)	142	80776.33	568.84	3.08	0.0001

Table A2. Analysis of Variance of Age-8 Height at Calling Lake Plot Mean Basis

Dependent Variable: age-8 height

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	150	62313.12	415.42	3.26	0.0001
Error	722	92137.17	127.61		
Total	872	154450.30			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
REP	5	4644.69	928.93	7.28	0.0001
REG	3	1111.01	370.33	0.93	0.4287
FAMILY(REG)	142	56612.36	398.67	3.12	0.0001

Table A3. Analysis of Variance of Mean Increment at Calling Lake - Plot Mean Basis

Dependent Variable: mean increment

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	150	1774.92	11.83	1.62	0.0001
Error	722	5258.18	7.28		
Total	872	7033.11			

Source	DF	Type III SS	Mean Square	F-Value	Pr > F
REP	5	86.05	17.21	2.36	0.0384
REG	3	27.24	9.08	0.78	0.5089
FAMILY(REG)	142	1660.04	11.69	1.61	0.0001

Table A4. Analysis of Variance of Plant Vigor at Calling Lake Plot Mean Basis

Dependent Variable: plant vigor

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	150	13.73	0.09	2.48	0.0001
Error	722	26.61	0.03		
Total	872	40.35			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
REP	5	3.16	0.63	17.16	0.0001
REG	3	0.006	0.002	0.03	0.9928
FAMILY(REG)	142	10.55	0.07	2.02	0.0001

Table A5. Analysis of Variance of Age-10 Height for Calling Lake - Individual Tree Basis

Dependent Variable: age-10 height

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	872	1000782.33	1147.69	1.68	0.0001
Error	3279	2242097.60	683.77		
Total	4151	3242879.93			

Table A6. Analysis of Variance of Age-8 Height for Calling Lake - Individual Tree Basis

Dependent Variable: age-8 height

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	872	714885.75	819.82	1.80	0.0001
Error	3259	1486104.25	456.00		
Total	4131	2200990.00			

Table A7. Analysis of Variance of Mean Increment for Calling Lake
Individual Tree Basis

Dependent Variable: mean increment

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	872	31816.18	36.48	1.49	0.0001
Error	3259	79911.75	24.52		
Total	4131	111727.93			

Table A8. Analysis of Variance of Plant Vigor for Calling Lake Individual Tree Basis

Dependent Variable: plant vigor

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	872	183.16	0.21	1.76	0.0001
Error	3285	391.16	0.11		
Total	4157	574.33			

Table A9. Expected Mean Squares for age-10 and age-8 height, mean increment and plant vigor for Calling Lake

Source	Type III Expected Mean Square
REP	Var(Error) + 145.4 Var(REP)
REG	Var(Error) + 5.9822 Var(FAMILY(REG)) + Q(REG)
FAMILY(REG)	Var(Error) + 5.9791 Var(FAMILY(REG))

APPENDIX B.

Analyses of Variance Tables for Mitsue South

Table B1. Analysis of Variance of Age-10 Height at Mitsue South - Plot Mean Basis

Dependent Variable: age-10 height

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	154	169758.88	1102.33	2.52	0.0001
Error	744	325193.54	437.08		
Total	898	494952.42			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
REP	5	33630.33	6726.06	15.39	0.0001
REG	3	1698.83	566.28	0.61	0.6072
FAMILY(REG)	146	134738.22	922.86	2.11	0.0001

Table B2. Analysis of Variance of Age-8 Height at Mitsue South Plot Mean Basis

Dependent Variable: age-8 height

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	154	95676.59	621.27	2.48	0.0001
Error	744	186708.14	250.95		
Total	898	282384.74			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
REP	5	28434.06	5686.81	22.66	0.0001
REG	3	375.01	125.00	0.27	0.8453
FAMILY(REG)	146	67036.46	459.15	1.83	0.0001

Table B3. Analysis of Variance of Mean Increment at Mitsue South - Plot Mean Basis

Dependent Variable: mean increment

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	154	8460.54	54.93	2.72	0.0001
Error	744	15052.97	20.23		
Total	898	23513.51			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
REP	5	421.55	84.31	4.17	0.0010
REG	3	289.34	96.44	1.82	0.1468
FAMILY(REG)	146	7753.88	53.10	2.62	0.0001

Table B4. Analysis of Variance of Plant Vigor for Mitsue South Plot Mean Basis

Dependent Variable: plant vigor

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	154	27.25	0.17	2.08	0.0001
Error	745	63.42	0.08		
Total	899	90.67			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
REP	5	2.10	0.42	4.94	0.0002
REG	3	0.67	0.22	1.35	0.2616
FAMILY(REG)	146	24.47	0.16	1.97	0.0001

Table B5. Analysis of Variance of Age-10 Height for Mitsue South - Individual Tree Basis

Dependent Variable: age-10 height

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	898	2714950.88	3023.33	2.56	0.0001
Error	4213	4971161.80	1179.96		
Total	5111	7686112.68			

Table B6. Analysis of Variance of Age-8 Height for Mitsue South - Individual Tree Basis

Dependent Variable: age-8 height

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	898	1550936.84	1727.10	2.68	0.0001
Error	4212	2716273.12	644.89		
Total	5110	4267209.96			

Table B7. Analysis of Variance of Mean Increment for Mitsue South - Individual Tree Basis

Dependent Variable: mean increment

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	898	132503.59	147.55	1.96	0.0001
Error	4212	317143.07	75.29		
Total	5110	449646.67			

Table B8. Analysis of Variance of Plant Vigor for Mitsue South Individual Tree Basis

Dependent Variable: plant vigor

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	899	504.95	0.56	1.82	0.0001
Error	4277	1317.45	0.30		
Total	5176	1822.40			

Table B9. Expected Mean Squares for age-10 and age-8 height and mean increment for Mitsue South

Source	Type III Expected Mean Square
REP	Var(Error) + 149.8 Var(REP)
REG	Var(Error) + 5.9929 Var(FAMILY(REG)) + Q(REG)
FAMILY(REG)	Var(Error) + 5.9933 Var(FAMILY(REG))

Table B10. Expected Mean Squares for plant vigor for Mitsue South

Source	Type III Expected Mean Square
REP	Var(Error) + 150 Var(REP)
REG	Var(Error) + 6 Var(FAMILY(REG)) + Q(REG)
FAMILY(REG)	Var(Error) + 6 Var(FAMILY(REG))

APPENDIX C.
Analyses of Variance Tables for Red Earth

Table C1. Analysis of Variance of Age-10 Height at Red Earth Plot Mean Basis

Dependent Variable: age-10 height

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	154	263637.36	1711.93	2.39	0.0001
Error	745	533800.12	716.51		
Total	899	797437.48			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
REP	5	45274.15	9054.83	12.64	0.0001
REG	3	4094.35	1364.78	0.93	0.4280
FAMILY(REG)	146	214268.85	1467.59	2.05	0.0001

Table C2. Analysis of Variance of Age-8 Height for Red Earth Plot Mean Basis

Dependent Variable: age-8 height

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	154	140120.46	909.87	2.33	.0001
Error	745	290934.26	390.51		
Total	899	431054.72			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
REP	5	19732.81	3946.56	10.11	0.0001
REG	3	2131.59	710.53	0.88	0.4545
FAMILY(REG)	146	118256.05	809.97	2.07	0.0001

Table C3. Analysis of Variance of Mean Increment at Red Earth Plot Mean Basis

Dependent Variable: mean increment

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Mo	154	5503.82	35.73	1.99	0.0001
Error	745	13347.85	17.91		
Total	899	18851.68			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
REP	5	1221.26	244.25	13.63	0.0001
REG	3	51.15	17.05	0.59	0.6236
FAMILY(REG)	146	4231.40	28.98	1.62	0.0001

Table C4. Analysis of Variance of Plant Vigor at Red Earth Plot Mean Basis

Dependent Variable: plant vigor

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	154	37.04	0.24	2.05	0.0001
Error	745	87.43	0.11		
Total	899	124.48			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
REP	5	7.59	1.51	12.95	0.0001
REG	3	0.20	0.06	0.34	0.7970
FAMILY(REG)	146	29.24	0.20	1.71	0.0001

Table C5. Analysis of Variance of Age-10 Height for Red Earth Individual Tree Basis

Dependent Variable: age-10 height

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	899	4623713.45	5143.17	4.25	0.0001
Error	4328	5238328.35	1210.33		
Total	5227	9862041.80			

Table C6. Analysis of Variance of Age-8 Height at Red Earth Individual Tree Basis

Dependent Variable: age-8 height

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	899	2441158.09	2715.42	3.77	0.0001
Error	4238	3052254.23	720.21		
Total	5137	5493412.32			

Table C7. Analysis of Variance of Mean Increment for Red Earth Individual Tree Basis

Dependent Variable: mean increment

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	899	107450.52	119.52	3.53	0.0001
Error	4238	143473.81	33.85		
Total	5137	250924.33			

Table C8. Analysis of Variance for Plant Vigor for Red Earth Individual Tree Basis

Dependent Variable: plant vigor

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	899	721.76	0.80	3.53	0.0001
Error	4335	985.38	0.22		
Total	5234	1707.14			

Table C9. Expected Mean Squares for age-10 and age-8 height, mean increment and plant vigor for Red Earth

Source	Type III Expected Mean Square
REP	Var(Error) + 150 Var(REP)
REG	Var(Error) + 6 Var(FAMILY(REG)) + Q(REG)
FAMILY(REG)	Var(Error) + 6 Var(FAMILY(REG))

APPENDIX D.
Analyses of Variance Tables for Carson Lake

Table D1. Analysis of Variance of Age-10 Height at Carson Lake Plot Mean Basis

Dependent Variable: age-10 height

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	151	253441.23	1678.41	2.41	0.0001
Error	727	506670.96	696.93		
Total	878	760112.19			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
REP	5	39504.35	7900.87	11.34	0.0001
REG	3	1211.05	403.68	0.27	0.8157
FAMILY(REG)	143	212338.139	1484.882	2.13	0.0001

Table D2. Analysis of Variance of Age-8 Height for Carson Lake Plot Mean Basis

Dependent Variable: age-8 height

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	151	144147.78	954.62	2.00	0.0001
Error	727	346763.54	476.97		
Total	878	490911.33			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
REP	5	31122.62	6224.52	13.05	0.0001
REG	3	4436.64	1478.88	1.95	0.1239
FAMILY(REG)	143	108302.62	757.36	1.59	0.0001

Table D3. Analysis of Variance of Mean Increment for Carson Lake - Plot Mean Basis

Dependent Variable: mean increment

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	151	12066.54	79.91	3.43	0.0001
Error	727	16959.69	23.32		
Total	878	29026.23			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
REP	5	563.34	112.66	4.83	0.0002
REG	3	289.85	96.61	1.23	0.3006
FAMILY(REG)	143	11214.74	78.42	3.36	0.0001

Table D4. Analysis of Variance of Plant Vigor for Carson Lake Plot Mean Basis

Dependent Variable: plant vigor

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	151	34.81	0.23	1.80	0.0001
Error	727	92.99	0.12		
Total	878	127.81			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
REP	5	4.39	0.87	6.88	0.0001
REG	3	0.42	0.14	0.68	0.5645
FAMILY(REG)	143	30.00	0.20	1.64	0.0001

Table D5. Analysis of Variance of Age-10 Height for Carson Lake - Individual Tree Basis

Dependent Variable: age-10 height

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	878	3552767.16	4046.43	2.38	0.0001
Error	3371	5738953.90	1702.45		
Total	4249	9291721.06			

Table D6. Analysis of Variance of Age-8 Height for Carson Lake Individual Tree Basis

Dependent Variable: age-8 height

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	878	2214905.92	2522.67	2.25	0.0001
Error	3359	3763575.07	1120.45		
Total	4237	5978480.98			

Table D7. Analysis of Variance of Mean Increment for Carson Lake - Individual Tree Basis

Dependent Variable: mean increment

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	878	135290.90	154.09	1.80	0.0001
Error	3359	287866.50	85.70		
Total	4237	423157.40			

Table D8. Analysis of Variance of Plant Vigor for Carson Lake Individual Tree Basis

Dependent Variable: plant vigor

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	878	585.73	0.66	2.12	0.0001
Error	3426	1078.73	0.31		
Total	4304	1664.47			

Table D9. Expected Mean Squares for age-10 and age-8 height, mean increment and plant vigor for Carson Lake

Source	Type III Expected Mean Square
REP	Var(Error) + 146.4 Var(REP)
REG	Var(Error) + 5.9826 Var(FAMILY(REG)) + Q(REG)
FAMILY(REG)	Var(Error) + 5.9793 Var(FAMILY(REG))

APPENDIX E.

Analyses of Variance Tables for All Sites Combined

Table E1. Analysis of Variance of Age-10 Height for All Sites Combined - Plot Mean Basis

Dependent Variable: age-10 height

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	612	2767753.51	4522.47	8.86	0.0001
Error	2938	1498931.73	510.19		
Total	3550	4266685.24			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	3	1465283.43	488427.81	103.82	0.0001
REP(SITE)	20	121370.39	6068.52	11.89	0.0001
REG	3	1554.89	518.30	0.21	0.8905
SITE*REG	9	6208.89	689.88	1.06	0.3911
FAMILY(REG)	146	359868.69	2464.85	3.78	0.0001
SITE*FAMILY(REG)	431	280390.54	650.56	1.28	0.0003

Table E2. Analysis of Variance of Age-8 Height for All Sites Combined - Plot Mean Basis

Dependent Variable: age-8 height

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	612	1754713.31	2867.18	9.19	0.0001
Error	2938	916543.13	311.96		
Total	3550	2671256.44			

Source	DF	Type III SS	Mean Square	F Value	P > F
SITE	3	976148.64	325382.88	98.29	0.0001
REP(SITE)	20	83934.19	4196.71	13.45	0.0001
REG	3	2837.11	945.70	0.69	0.5646
SITE*REG	9	4706.00	522.88	1.34	0.2115
FAMILY(REG)	146	182264.22	1248.38	3.21	0.0001
SITE*FAMILY(REG)	431	167575.62	388.80	1.25	0.0009

Table E3. Analysis of Variance of Mean Increment for All Sites Combined - Plot Mean Basis

Dependent Variable: mean increment

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	612	53699.22	87.74	5.09	0.0001
Error	2938	50618.70	17.22		
Total	3550	104317.93			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	3	19141.27	6380.42	52.49	0.0001
REP(SITE)	20	2292.21	114.61	6.65	0.0001
REG	3	147.39	49.13	0.40	0.7512
SITE*REG	9	506.17	56.24	2.14	0.0254
FAMILY(REG)	146	13467.73	92.24	3.51	0.0001
SITE*FAMILY(REG)	431	11336.94	26.30	1.53	0.0001

Table E4. Analysis of Variance of Plant Vigor for All Sites Combined - Plot Mean Basis

Dependent Variable: plant vigor

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	612	291.89	0.47	5.18	0.0001
Error	2939	270.47	0.09		
Total	3551	562.36			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	3	131.39	43.79	63.76	0.0001
REP(SITE)	20	17.26	0.86	9.38	0.0001
REG	3	0.10	0.03	0.14	0.9355
SITE*REG	9	1.15	0.12	0.97	0.4640
FAMILY(REG)	146	36.83	0.25	1.91	0.0001
SITE*FAMILY(REG)	431	57.02	0.13	1.44	0.0001

Table E5. Analysis of Variance of Age-10 Height for All Sites Combined - Individual Tree Basis

Dependent Variable: age-10 height

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3550	21629687.7	6092.9	5.09	0.0001
Error	15191	18190541.7	1197.5		
Total	18741	39820229.4			

Table E6. Analysis of Variance of Age-8 Height for All Sites Combined - Individual Tree Basis

Dependent Variable: age-8 height

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3550	13268623.5	3737.6	5.11	0.0001
Error	15068	11018206.7	731.2		
Total	18618	24286830.2			

Table E7. Analysis of Variance of Mean Increment for All Sites Combined - Individual Tree Basis

Dependent Variable: mean increment

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3550	538475.86	151.68	2.76	0.0001
Error	15068	828395.15	54.97		
Total	18618	1366871.02			

Table E8. Analysis of Variance of Plant Vigor for All Sites Combined
Individual Tree Basis

Dependent Variable: plant vigor

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3551	2929.65	0.82	3.35	0.0001
Error	15323	3772.73	0.24		
Total	18874	6702.39			

Table E9. Expected Mean Squares for age-10 and age-8 height and mean increment for All Sites Combined

Source	Type III Expected Mean Square
SITE	Var(Error) + 5.9927 Var(SITE*FAMILY(REG)) + 160.56 Var(SITE*REG) + 107.01 Var(REP(SITE)) + 642.04 Var(SITE)
REP(SITE)	Var(Error) + 147.9 Var(REP(SITE))
REG	Var(Error) + 5.9895 Var(SITE*FAMILY(REG)) + 23.502 Var(FAMILY(REG)) + 193.63 Var(SITE*REG) + Q(REG)
SITE*REG	Var(Error) + 5.9894 Var(SITE*FAMILY(REG)) + 193.86 Var(SITE*REG)
FAMILY(REG)	Var(Error) + 5.9865 Var(SITE*FAMILY(REG)) + 23.658 Var(FAMILY(REG))
SITE*FAMILY(REG)	Var(Error) + 5.9875 Var(SITE*FAMILY(REG))

Table E10. Expected Mean Squares for plant vigor for All Sites Combined

Source	Type III Expected Mean Square
SITE	Var(Error) + 5.9939 Var(SITE*FAMILY(REG)) + 160.6 Var(SITE*REG) + 107.03 Var(REP(SITE)) + 642.17 Var(SITE)
REP(SITE)	Var(Error) + 147.95 Var(REP(SITE))
REG	Var(Error) + 5.9911 Var(SITE*FAMILY(REG)) + 23.508 Var(FAMILY(REG)) + 193.71 Var(SITE*REG) + Q(REG)
SITE*REG	Var(Error) + 5.9912 Var(SITE*FAMILY(REG)) + 193.94 Var(SITE*REG)
FAMILY(REG)	Var(Error) + 5.9884 Var(SITE*FAMILY(REG)) + 23.666 Var(FAMILY(REG))
SITE*FAMILY(REG)	Var(Error) + 5.9892 Var(SITE*FAMILY(REG))

APPENDIX F.

Analyses of Variance Tables for Percent Survival All Sites Combined

Table F1. Analysis of Variance of Percent Survival for All Sites Combined

Dependent Variable: (% survival (transformed with arcsine percent)

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	612	136682.47	223.33	2.76	0.0001
Error	2945	238456.96	80.97		
Total	3557	375139.43			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	3	45104.61	15034.87	19.58	0.0001
REP(SITE)	20	20369.32	1018.46	12.58	0.0001
REG	3	237.90	79.30	0.88	0.4880
SITE*REG	9	815.18	90.57	1.02	0.4230
FAMILY(REG)	146	12822.77	87.82	0.99	0.5239
SITE*FAMILY(REG)	431	38277.90	88.81	1.10	0.0968

Source	Type III Expected Mean Square
SITE	Var(Error) + 6 Var(SITE*FAMILY(REG)) + 160.76 Var(SITE*REG) + 107.14 Var(REP(SITE)) + 642.82 Var(SITE)
REP(SITE)	Var(Error) + 148.25 Var(REP(SITE))
REG	Var(Error) + 6 Var(SITE*FAMILY(REG)) + 23.543 Var(FAMILY(REG)) + 194.11 Var(SITE*REG) + Q(REG)
SITE*REG	Var(Error) + 6 Var(SITE*FAMILY(REG)) + 194.34 Var(SITE*REG)
FAMILY(REG)	Var(Error) + 6 Var(SITE*FAMILY(REG)) + 23.712 Var(FAMILY(REG))
SITE*FAMILY(REG)	Var(Error) + 6 Var(SITE*FAMILY(REG))

APPENDIX G.
Analyses of Variance Tables for Percent White Pine Weevil Damage at Calling Lake

Table G1. Analysis of Variance and Expected Mean Squares for Percent White Pine Weevil Damage at Calling Lake

Dependent Variable: % weevil damage

			Sum of	Mean	
Source	DF	Squares	Square	F Value	Pr > F
Model	150	159072.02	1060.48	1.90	0.0001
Error	722	403921.69	559.44		
Total	872	562993.72			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
REP	5	16458.67	3291.73	5.88	0.0001
REG	3	2478.52	826.17	0.84	0.4753
FAMILY(REG)	142	140015.76	986.02	1.76	0.0001

Source	Type III Expected Mean Square
REP	Var(Error) + 145.4 Var(REP)
REG	Var(Error) + 5.9822 Var(FAMILY(REG)) + Q(REG)
FAMILY(REG)	Var(Error) + 5.9791 Var(FAMILY(REG))

APPENDIX H.

Analyses of Variance Tables for Percent White Pine Weevil Damage at Red Earth

Table H1. Analysis of Variance and Expected Mean Squares for Percent White Pine Weevil Damage at Red Earth

Dependent Variable: % weevil damage

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	154	162388.77	1054.47	2.42	0.0001
Error	745	324228.55	435.20		
Total	899	486617.33			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
REP	5	26466.81	5293.36	12.16	0.0001
REG	3	1395.69	465.23	0.50	0.6795
FAMILY(REG)	146	134526.27	921.41	2.12	0.0001

Source	Type III Expected Mean Square
REP	Var(Error) + 150 Var(REP)
REG	Var(Error) + 6 Var(FAMILY(REG)) + Q(REG)
FAMILY(REG)	Var(Error) + 6 Var(FAMILY(REG))

APPENDIX I.

Analyses of Variance Tables for Percent White Pine Weevil Damage for Calling Lake and Red Earth Combined

Table I1. Analysis of Variance and Expected Mean Squares for Percent White Pine Weevil Damage for Calling Lake and Red Earth Combined

Dependent Variable: % weevil damage

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	305	335410.63	1099.70	2.22	0.0001
Error	1467	728150.25	496.35		
Total	1772	1063560.88			

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SITE	1	7785.26	7785.26	2.23	0.1627
REP(SITE)	10	42925.48	4292.54	8.65	0.0001
REG	3	1361.83	453.94	0.32	0.8069
SITE*REG	3	2367.75	789.25	1.22	0.3039
FAMILY(REG)	146	82464.66	1249.75	1.93	0.0001
SITE*FAMILY(REG)	142	91681.41	645.64	1.30	0.0130

Source	Type III Expected Mean Square
SITE	Var(Error) + 5.9938 Var(SITE*FAMILY(REG)) + 158.71 Var(SITE*REG) + 105.77 Var(REP(SITE)) + 634.64 Var(SITE)
REP(SITE)	Var(Error) + 147.7 Var(REP(SITE))
REG	Var(Error) + 5.991 Var(SITE*FAMILY(REG)) + 11.773 Var(FAMILY(REG)) + 193.6 Var(SITE*REG) + Q(REG)
SITE*REG	Var(Error) + 5.9911 Var(SITE*FAMILY(REG)) + 191.36 Var(SITE*REG)
FAMILY(REG)	Var(Error) + 5.9889 Var(SITE*FAMILY(REG)) + 11.814 Var(FAMILY(REG))
SITE*FAMILY(REG)	Var(Error) + 5.9886 Var(SITE*FAMILY(REG))

APPENDIX J.
List of Seedlots and Locations

LIST OF SEEDLOTS AND LOCATIONS

LOC	ELEV (m)	LAT ^{0}N	LONG ^{0}W	ECOREG	FAMILY
Marten Hills	793	55.30	113.53	low_fthl	120
Marten Hills	793	55.30	113.55	low_fthl	121
Marten Hills	793	55.30	114.02	low_fthl	122
Marten Hills	793	55.30	114.02	low_fthl	123
Marten Hills	793	55.30	114.02	low_fthl	124
Marten Hills	793	55.30	114.10	low_fthl	125
Marten Hills	731	55.30	114.12	low_fthl	126
Marten Hills	731	55.30	114.12	low_fthl	127
Marten Hills	731	55.30	114.21	low_fthl	128
Marten Hills	731	55.30	114.21	low_fthl	129
Marten Hills	731	55.30	114.21	low_fthl	130
Marten Hills	731	55.27	114.21	low_fthl	131
Marten Hills	834	55.27	114.25	low_fthl	132
Marten Hills	731	55.27	114.05	cen_mxwd	133
Marten Hills	834	55.27	114.31	low_fthl	134
Marten Hills	834	55.27	114.31	low_fthl	135
Marten Hills	640	55.23	114.40	dry_mxwd	136
Marten Hills	640	55.23	114.40	dry_mxwd	137
Marten Hills	640	55.23	114.40	dry_mxwd	138
Marten Hills	640	55.23	114.40	dry_mxwd	139
Marten Hills	640	55.23	114.40	dry_mxwd	140
Marten Hills	640	55.23	114.40	dry_mxwd	141
Marten Hills	640	55.23	114.40	dry_mxwd	142
North Wabasca	579	56.12	113.52	cen_mxwd	143
North Wabasca	579	56.12	113.52	cen_mxwd	144
North Wabasca	579	56.12	113.52	cen_mxwd	145
North Wabasca	579	56.12	113.52	cen_mxwd	146
North Wabasca	579	56.12	113.52	cen_mxwd	147
North Wabasca	579	56.12	113.52	cen_mxwd	148
North Wabasca	579	56.12	113.52	cen_mxwd	149
North Wabasca	579	56.12	113.52	cen_mxwd	150
North Wabasca	579	56.12	113.52	cen_mxwd	151
North Wabasca	579	56.12	113.52	cen_mxwd	152
Nipisi	701	55.40	115.10	cen_mxwd	153
Nipisi	701	55.40	115.10	cen_mxwd	154
Nipisi	701	55.40	115.10	cen_mxwd	155
Nipisi	701	55.40	115.10	cen_mxwd	156
Nipisi	701	55.40	115.10	cen_mxwd	157
Nipisi	701	55.40	115.10	cen_mxwd	158
Nipisi	701	55.40	115.10	cen_mxwd	159
Nipisi	701	55.40	115.10	cen_mxwd	160
Nipisi	701	55.40	115.10	cen_mxwd	161
Nipisi	701	55.40	115.10	cen_mxwd	162
Nipisi	701	55.40	115.10	cen_mxwd	163
Nipisi	701	55.40	115.10	cen_mxwd	164
Nipisi	701	55.40	115.10	cen_mxwd	165
Nipisi	701	55.40	115.10	cen_mxwd	166

LOC	ELEV (m)	LAT ^{0}N	LONG ^{0}W	ECOREG	FAMILY
Nipisi	701	55.40	115.10	cen_mxwd	167
Nipisi	701	55.40	115.10	cen_mxwd	168
Smith	640	55.12	113.52	cen_mxwd	169
Smith	640	55.17	113.52	cen_mxwd	170
Smith	640	55.20	113.52	cen_mxwd	171
Smith	579	55.15	114.02	cen_mxwd	172
Smith	579	55.15	114.02	cen_mxwd	174
Smith	579	55.15	114.12	cen_mxwd	175
Smith	579	55.15	114.20	cen_mxwd	176
Smith	579	55.15	114.20	cen_mxwd	177
Mitsue S. Road	610	55.01	114.23	cen_mxwd	178
Mitsue S. Road	610	55.01	114.23	cen_mxwd	179
Mitsue S. Road	610	55.01	114.23	cen_mxwd	180
Mitsue S. Road	610	55.01	114.23	cen_mxwd	181
Mitsue S. Road	610	55.01	114.23	cen_mxwd	182
Mitsue S. Road	610	55.01	114.23	cen_mxwd	183
Mitsue S. Road	610	55.01	114.23	cen_mxwd	184
Mitsue S. Road	610	55.01	114.23	cen_mxwd	185
Mitsue S. Road	610	55.01	114.23	cen_mxwd	186
Mitsue S. Road	610	55.01	114.23	cen_mxwd	187
Mitsue S. Road	610	55.01	114.23	cen_mxwd	188
Mitsue S. Road	610	54.58	114.23	cen_mxwd	189
Mitsue S. Road	610	54.58	114.23	cen_mxwd	190
Mitsue S. Road	610	54.58	114.23	cen_mxwd	191
Mitsue S. Road	610	55.01	114.23	cen_mxwd	192
Mitsue S. Road	610	55.01	114.23	cen_mxwd	193
Mitsue S. Road	610	55.03	114.23	cen_mxwd	194
Mitsue S. Road	731	55.04	114.30	low_fthl	195
Mitsue S. Road	731	55.08	114.30	low_fthl	196
Mitsue S. Road	731	55.08	114.30	low_fthl	197
Mitsue S. Road	731	55.08	114.30	low_fthl	198
Mitsue S. Road	731	55.12	114.30	low_fthl	199
Mitsue S. Road	731	55.23	114.30	cen_mxwd	200
Kinuso, S. Lake	701	55.20	115.17	dry_mxwd	201
Kinuso, S. Lake	701	55.18	115.17	dry_mxwd	202
Kinuso, S. Lake	701	55.16	115.17	dry_mxwd	203
Kinuso, S. Lake	701	55.13	115.17	dry_mxwd	204
Kinuso, S. Lake	701	55.13	115.17	dry_mxwd	205
Kinuso, S. Lake	701	55.08	115.17	low_fthl	206
Kinuso, S. Lake	701	55.03	115.17	low_fthl	207
Kinuso, S. Lake	701	55.03	115.17	low_fthl	208
Kinuso, S. Lake	701	55.00	115.17	low_fthl	209
Wabasca	580	55.53	114.00	cen_mxwd	1579
Wabasca	580	55.53	114.00	cen_mxwd	1580
Wabasca	580	55.53	114.00	cen_mxwd	1581
Wabasca	580	55.52	114.00	cen_mxwd	1582
Wabasca	580	55.53	114.00	cen_mxwd	1583
Wabasca	580	55.54	114.02	cen_mxwd	1584
Wabasca	580	55.54	114.02	cen_mxwd	1585

LOC	ELEV (m)	LAT °N	LONG °W	ECOREG	FAMILY
Wabasca	580	55.54	114.02	cen_mxwd	1586
Wabasca	580	55.54	114.02	cen_mxwd	1587
Wabasca	580	55.54	114.02	cen_mxwd	1588
Whitecourt	876	54.29	115.13	low_fthl	1912
Whitecourt	876	54.30	115.14	low_fthl	1913
Whitecourt	892	54.30	115.16	low_fthl	1914
Whitecourt	899	54.29	115.17	low_fthl	1915
Whitecourt	1066	54.28	115.25	up_fthl	1916
Whitecourt	1066	54.28	115.25	up_fthl	1917
Whitecourt	1066	54.28	115.25	up_fthl	1918
Whitecourt	1066	54.28	115.25	up_fthl	1919
Whitecourt	1066	54.28	115.25	up_fthl	1920
Whitecourt	1066	54.28	115.25	up_fthl	1921
Whitecourt	1066	54.28	115.25	up_fthl	1922
Whitecourt	884	54.19	115.36	low_fthl	1923
Whitecourt	1066	54.22	115.37	up_fthl	1924
Whitecourt	830	54.13	115.54	cen_mxwd	1949
Whitecourt	808	54.18	115.50	low_fthl	1950
Whitecourt	803	54.19	115.49	low_fthl	1951
Whitecourt	881	54.16	116.05	low_fthl	1952
Whitecourt	853	54.16	116.05	low_fthl	1953
Whitecourt	853	54.16	116.05	low_fthl	1954
Whitecourt	975	54.36	115.37	up_fthl	1974
Whitecourt	945	54.35	115.35	up_fthl	1975
Whitecourt	884	54.34	115.28	up_fthl	1976
Whitecourt	754	54.14	115.26	cen_mxwd	1977
Whitecourt	762	54.15	115.26	low_fthl	1978
Whitecourt	777	54.16	115.27	low_fthl	1979
Whitecourt	792	54.17	115.28	low_fthl	1980
Whitecourt	823	54.18	115.28	low_fthl	1981
Whitecourt	1052	54.28	115.37	up_fthl	1982
Whitecourt	884	54.23	115.40	up_fthl	1983
Whitecourt	732	54.08	115.20	dry_mxwd	1984
Whitecourt	884	54.19	115.43	up_fthl	1985
Whitecourt	1036	54.26	115.34	up_fthl	1986
Whitecourt	991	54.25	115.30	up_fthl	1987
Whitecourt	914	54.34	115.31	up_fthl	1988
Whitecourt	960	54.29	115.21	up_fthl	1989
Saddle Hills	845	55.29	119.34	cen_mxwd	2045
Slave Lake	740	55.05	114.28	low_fthl	2096
Slave Lake	765	55.12	114.33	low_fthl	2098
Slave Lake	625	55.20	115.12	dry_mxwd	2101
Slave Lake	610	55.21	115.11	dry_mxwd	2102
Slave Lake	610	55.21	115.04	dry_mxwd	2103
Slave Lake	595	55.20	114.55	dry_mxwd	2105
Slave Lake	580	55.19	114.54	dry_mxwd	2106
Slave Lake	610	55.15	114.43	cen_mxwd	2107
Slave Lake	600	55.15	114.43	cen_mxwd	2108
Slave Lake	600	55.14	114.41	cen_mxwd	2109

LOC	ELEV (m)	LAT ^{0}N	LONG ^{0}W	ECOREG	FAMILY
Slave Lake	610	55.13	114.39	low_fthl	2110
Slave Lake	670	55.13	114.25	cen_mxwd	2111
Slave Lake	610	55.13	114.24	cen_mxwd	2112
Slave Lake	625	55.11	114.21	cen_mxwd	2113
Slave Lake	605	55.10	114.16	cen_mxwd	2114