VARIATION OF SYLLEPSIS IN ELEVEN TAMARACK [Larix laricina (Du Roi) K. Koch] PROVENANCES IN NORTHWESTERN ONTARIO AND ITS RELATION WITH HEIGHT GROWTH

Deng Shaotang©

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Major Advisor : Dr. R. E. Farmer
Committee: Dr. P. Knowles
Dr. W. H. Parker

Lakehead University
School of Forestry
Thunder Bay, Ontario

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A CAUTION TO THE READER

This M.Sc.F. thesis has through a formal process of review and comment by several members of the faculty of the School of Forestry, Lakehead University, as well as an external examiner.

It is made available for loan by the faculty for the purpose of advancing the practice of professional and scientific forestry.

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MAJOR ADVISOR'S COMMENTS

ABSTRACT

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Key Words: Broad-sense heritability, genetic correlation, genetic variation, Larix laricina (Du Roi) K. Koch, syllepsis, sylleptic long shoot.

Variation in syllepsis of tamarack and its relationship to juvenile height growth in eleven tamarack provenances from northwestern Ontario was evaluated in a four-year-old clonal test planted at Thunder Bay, Ontario. Significant provenance and clone-within-provenance effects were found for height growth, and occurrence and degree of syllepsis. There existed a south-north trend of decreasing provenance means for both height growth and degree of syllepsis. Degree of syllepsis was found to be moderately correlated with current-year height growth. Provenance broad-sense heritability estimates ranged from 0.22 to 0.23 for 1989 final height and 1989 height growth respectively, and they ranged from 0.11 to 0.13 for number and length of sylleptic branches on 1989 height growth. Clonal broad-sense heritability estimates ranged from 0.16 to 0.18 for 1989 final height and 1989 height growth respectively, and they ranged from 0.33 to 0.37 for number and length of sylleptic branches on 1989 height growth. Although syllepsis of tamarack has high phenotypic plasticity, the potential for its development on tamarack is heritable. Syllepsis of tamarack may be an evolutionary mechanism that permits tamarack trees to deal with environmental uncertainty.

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INTRODUCTION

Tamarack [Larix laricina (Du Roi) K. Koch] is a widely distributed native Nortrh American conifer that exhibits rapid juvenile growth on moist to moderately well-drained sites (Fowells, 1965). In the past, it has been largely neglected by foresters because of its low available wood volumes and susceptibility to damage by the larch sawfly (Pristiphora erichsonii Hartig) (Graham, 1956; Calvert,1977). As a result of the predicted wood supply shortage for the United States and Eastern Canada (Carter,1985), tamarack is now receiving attention as a potentially important reforestation tree species in Canada and the United States. Consequently, interest in use of this species in tree improvement programs is rising.

Calvert (1977) suggested that genetic improvement should be made through selection for rapid juvenile growth rate and good stem form within climatically adapted provenances. For this reason, the characters that can possibly influence juvenile growth rate and stem form are important to examine in any provenance or progeny study (Calvert, 1977; Carter,1985). Sylleptic shoots, defined as lateral shoots developing and elongating simultaneously with the parent shoot, might be one of these characters as suggested by Powell (1987).

Sylleptic shoots are commonly observed on the terminal leader of young tamarack trees. Syllepsis can modify the crown architecture, and growth of young tamarack trees is reported to be positively correlated with the amount of syllepsis (Remphrey and Powell, 1984; 1985). Further, trees with a large amount of syllepsis early in life are thought to have superior growth potential after passing the seedling stage (Powell,1987; Remphrey and Powell, 1984). There is also some evidence of genetic control over the degree of syllepsis (Remphrey and Powell, 1984). Together these characteristics of syllepsis suggest that it may be a useful character in early selection for growth in genetic improvement programs. Therefore, the goal of this thesis was to test the hypotheses that (1) the syllepsis of tamarack is a heritable trait, (2) it is genetically correlated with the juvenile growth rate, and (3) considerable variation of this trait exists both among the provenances and among clones within provenances in northwestern Ontario.

LITERATURE REVIEW

SILVICS AND ECOLOGY OF TAMARACK

Tamarack is a geographically widespread boreal conifer. The species occurs from Newfoundland and Labrador west along the northern limit of tree growth to the Yukon Territory and south to northeastern British Columbia and northern Maine (Fowells, 1965). Tamarack can pioneer under many conditions and can withstand high soil moisture, high acidity, and low soil temperature. However, growth performance of tamarack is sensitive to variation in site and competition (Jeffers, 1975). It occurs most commonly on wet to moist organic soils (Henry *et al.*, 1973) and grows best on moist but well-drained, loamy soils (Fowells, 1965; Rudolf, 1966).

Seedlings of tamarack are intolerant and require full light and an ample supply of water for rapid early establishment (Henry *et al.*, 1973; Park and Fowler, 1983). Because of this intolerance it can only survive as a dominant or co-dominant tree in a stand (Fowells, 1965).

Tamarack flowers at an early age (five to seven years) (Fowells, 1965). Seed production is low and infrequent (Fowells, 1965; Morgenstern *et al.*, 1984; Fowler ,1986). Large cone crops do not occur until trees are 40 or more years of age, and the frequency of a large seed crop ranges from 3 to 6 years (Fowells , 1965). Mature cones are small (1 to 2 cm in length). The small seeds generally are dispersed over distances of less than two tree heights (Duncan, 1954). Both germinative energy and capacity of the small seeds are low compared to most spruce and pine species (Armson, 1983; Farmer and Reinholt, 1986). However, rooting of cuttings of this species is relatively easy compared with other conifers (Morgenstern *et al.*,1984; Farmer *et al.*, 1986), and it is also possible to produce plantable grafts in 1 or 2 years (Fowler, 1986).

Tamarack will germinate on a wide range of seedbeds, but seedlings are susceptible to flooding and drought (Armson, 1983). In swamps and peatlands germination occurs on clumps of sphagnum moss (Beeftink, 1956). Tamarack is one of the most rapid growing of the boreal conifers. It outgrows most other native conifers (Fowells, 1965; Logan, 1966; Henry *et al.*, 1973; Mead, 1978; Hall, 1986).

Larch sawfly and spruce budworm (Choristoneura fumiferana (Clem)) attack larch foliage. Occasional widespread epidemics of larch sawfly can cause severe reductions in growth and mortality in tamarack (Fowells , 1965). However these two insects can be controlled successfully by chemical and biological insecticides (Vallee, 1983). More recently, concern has arisen for tamarack's vulnerability to attacks of European larch canker (Lachnellula willkommii Hartig), which is a serious pest in Europe. This disease has been reported in eastern Canada and the United States (Magasi and Pond, 1982; Ostaff and Newell, 1986).

Tamarack is suitable for both pulp and lumber (Hall, 1986; Yang and Hazenberg, 1987). Although tamarack has never been utilized on a large scale, it is now receiving attention as a potentially important reforestation species for fibre production in eastern Canada and the United States (Calvert, 1977; Morgenstern *et al.*, 1984; Carter, 1985; Hall, 1986; OMNR, 1987).

GENETICS OF TAMARACK

Although tamarack's life history and ecological characteristics are known in general way, its genetics have not been extensively investigated until recently, and literature is limited (Park and Fowler, 1983; Morgenstern *et al.*, 1984). Several researchers have found that a clinal pattern of variation in bud flushing, bud set, and height growth, typical of many wide ranging species, is also found in tamarack (Rehfeldt,1970; Cech *et al.*,1977; Riemenschneider and Jeffers, 1980). A cold hardiness study of tamarack populations from northern Ontario indicates that adaptive variation in cold hardiness is also clinal (Joyce,1987). Early fall hardiness is strongly correlated with latitude, longitude, and elevation of population origins.

No specific races are presently recognized in tamarack. The gene pool is thought to be highly variable and unsegmented (Rehfeldt, 1970; Cech *et al.*, 1977). However, a study comparing growth responses of seedlings from northern seed sources with those from a southern source indicates that tamarack contains photoperiodic ecotypes (Vaartaja, 1959).

Estimates of intrapopulation genetic variation based on common garden studies are relatively high (Rehfeldt, 1970; Jeffers, 1975; Park and Fowler, 1982;). Isozyme studies suggest that this is the case for many other northern conifers (*e.g.* Yeh and El-Kassaby, 1980; Yeh and O'Malley, 1980; Brown and Moran, 1981; Dancik and Yeh, 1983; Hiebert and Hamrick, 1983; Steinhoff, Joyce and Fins, 1983; Furnier and Adams, 1986). Fins and Seeb (1986) also found that most of the variation in allozymes of Western larch (<u>Larix occidentalis</u> Nutt.), occurred within rather than among populations. Furthermore, examination of allozyme variation in populations of eastern tamarack across northwestern Ontario did not reveal marked heterogeneity among the populations (Knowles and Perry, 1986; Liu, 1988).

Species of the genus <u>Larix</u> exhibit more deleterious effects of inbreeding than do most species in the family Pinaceae (Franklin, 1970), although Park and Fowler, (1982) found that tamarack is below average in selffertility and above average in number lethal equivalents. Rehfeldt (1970) observed three types of chlorophyll deficiencies (from both inter and intra-population crosses), and inferior performance of selfed progeny. Knowles *et al.* (1987) found that natural populations of tamarack in northern Ontario had lower outcrossing rates than those reported for other conifers. Significant heterozygote deficiencies occurred in most embryo populations, but few were observed in the adult populations.

Park and Fowler (1982) found a relatively high specific combining ability for early seedling height and suggested that non-additive effects would be the most important source of genetic variation throughout the life of tamarack.

Tamarack exhibits considerable phenotypic variation in stem form and branch habit (Fowler, 1986). Characteristics such as stem form, branching habit and wood quality, thought to be under relatively strong genetic control, also affect yields. However, to date no genetic data have been published on these characters.

DIVERSITY IN SHOOT GROWTH OF WOODY PLANTS

Predetermined growth and free growth of terminal shoots

Two patterns of terminal shoot growth are found in northern conifers. One is termed "predetermined growth" or "fixed growth" in which new leaf or stem unit initials are developed on a primordial shoot and extend together after a period of dormancy (*e.g.* overwinter) (Pollard and Logan, 1974). The other has been termed "free growth" (Jablanczy, 1971; Pollard and Logan, 1974, 1976), in which new stem units are initiated and extended without interruption on a continously expanding stem.

The pattern of shoot growth of trees has been the object of studies for a long time. The two modes of terminal shoot growth have been reported in Larix , Abies, Picea and Pinus species (Nienstaedt, 1966; Jablanczy, 1971; Pollard and Logan,1974; Von Wuhlisch and Muhs, 1986; Rudolph, 1964). Environmental conditions are found to have a distinct influence on predetermined growth and free growth (Rudolph, 1964; Von Wuhlisch and Muhs, 1986) and there are strong indications that the prevailing photoperiod and temperature can determine whether or not free growth begins (Pollard and Logan,1974; Von Wuhlisch and Muhs, 1986). Free growth of trees also decreases with increasing age, which causes a gradual change from free growth to predetermined growth until eventually nearly all shoot growth develops in the pattern of predetermined growth on adult trees (Busgen and Munch, 1929; Rudolph, 1964; Von Wuhlisch and Muhs, 1986).

Provenance differences have been found in both forms of growth (Jack pine (Pinus banksiana Lamb.), Rudolph, 1964; Black spruce (Picea mariana (Mill.) B. S. P), Pollard and Logan,1974; Sitka spruce (Picea sitchensis (Bong.) Carr.), Cannell and Johnstone, 1978; European spruce (Picea abies (L.) Karst.), Von Wuhlisch and Muhs, 1987). Pollard and Logan (1974) found that when grown at southern latitudes, southern provenances of black spruce are more likely to enter free growth than northern provenances at the same location. Rudolph (1964) found frequency of occurrence of free growth in jack pine varied with seed sources, indicating that the potential to form free growth is under genetic control. Cannell and Johnstone (1978) noted that provenances producing large amount of free growth at a favourable site tend to improve their height rankings during first few years after planting.

Sylleptic and proleptic growth of lateral shoots

Two alternative developmental possibilities similar to the free growth and predetermined growth of terminal leader also exist in the development of lateral shoots of woody plants. One is known as "sylleptic growth" in which a lateral branch develops simultaneously with its parent shoot without an intervening period of dormancy after bud formation. The other possibility is termed "proleptic growth", in which a lateral meristem, usually a bud, undergoes a period of dormancy after which it may extend to form a lateral meristem chronologically later than its supporting axis (Tomlinson,1978). The terms "syllepsis" and "prolepsis" have been adopted by Tomlinson & Gill (1973) to refer specifically to those two possibilities of lateral shoot development.

In the architecture of most trees the two types of branching can be distinguished by fairly consistent morphological features. Syllepsis produces a branch axis that (1) lacks basal bud scales or their persistent scars, (2) has a long basal internode, and (3) has little transition in leaf morphology and size at the first few nodes. Prolepsis produces a branch axis that has basal bud scales, initially congested nodes and a gradual transition in leaf morphology and size at the first few nodes (*e.g.* Halle *et al.*, 1978).

Syllepsis is predominantly a tropical phenomenon and is found to be infrequent in most temperate woody plants in the northern hemisphere (Halle *et al.*, 1978; Remphrey and Powell, 1985). It is only common in several northern woody genera under certain growing conditions or stages of development (Halle *et al.*, 1978; Nienstaedt, 1984; Remphrey and Powell, 1985). There is a trend of increasing frequencies of species with syllepsis from north to south (Tomlinson, 1978). Why syllepsis should be rare in a temperate flora is not obvious.

In northern woody plants, Halle *et al.* (1978) observed that Cornus alternifolia always bears sylleptic shoots, and Owens (1984) reported that syllepsis is a persistent feature of the lateral shoot development of species of Cupressaceae. Syllepsis can also be found on vigorous shoots of Tsuga (Mitchell, 1965; Owens and Molder, 1973), and is often observed on leaders of vigorously growing seedlings of Picea (Pollard and Logan, 1974, 1976; Cannell and Johnstone, 1978; Von Wuhlisch and Muhs, 1986), Betula (Kennedy and Brown, 1984), Cedrus (Mitchell, 1965) and Larix (Mitchell, 1965; Powell and Vescio, 1986).

Few detailed investigations of sylleptic branching have been conducted in temperate trees. There is evidence to suggest that the occurrence and amount of sylleptic branching are correlated with shoot vigor, in particular the rapidity of parental shoot extension (Halle *et al.*,1978; Kennedy and Brown, 1984; Remphrey and Powell 1985). Tomlinson and Gill (1973) suggested that a threshold determined by vigour changed conditions from a low state producing prolepsis to a higher state producing syllepsis, but between species and between-tree variability are considerable (Kennedy and Brown, 1984). Remphrey and Powell (1985) suggested that sylleptic growth is partly due to a tree's response to current year growing conditions.

Syllepsis in tamarack

Leaders of tamarack exhibit considerable developmental plasticity, as in other species of Larix. The prominent features of the plasticity include (1) the production (in axils of certain leaves) of short shoot buds in more proximal positions and long-shoot buds in more distal positions (Clausen and Kozlowski, 1970), (2) a remarkable potential for terminal leader free growth subsequent to growth of predetermined shoot elements (Remphrey and Powell, 1984), and (3) the capacity for production of sylleptic long shoots or short shoots (Remphrey and Powell,1985; Powell and Vescio, 1986). The capacity for free growth and sylleptic growth allows Larix leaders to respond to favorable growing conditions and to continue elongating late in the growing season (Mitchell, 1965; Powell and Vescio, 1986).

Sylleptic long shoots and short shoots are commonly observed on leaders of young Tamarack (Remphrey and Powell, 1985). Compared with the sylleptic long shoot, the sylleptic short shoot is a "form of less sylleptic development occurring when a few of the first-formed lateral appendages of a new lateral axis differentiated as leaves, but with limited axil growth among leaf bases " (Powell and Vescio, 1986). Sylleptic long shoots in tamarack are easily recognized both in the year of their formation and for a few successive years according to three criteria: (1) its occurrence along elongating leader, (2) having smooth connection with its parent shoot or lacking bud scales at its base, and (3) lacking a cluster of basal leaves (*e.g.* Powell and Vescio, 1986).

Mitchell (1965) concluded that sylleptic shoots of Larix species were confined within the free growth part of its parent leader. This is reported to be true for certain hardwoods (Brown *et al.*, 1967). However, Remphrey and Powell (1984) found it unlikely that syllepsis of Tamarack was determined by the free growth of leaders. The occurrence and degree of syllepsis, are reported to bear a positive relationship with parental shoot length, and syllepsis is restricted to the transition zone between predetermined growth and free growth of parental leader in tamarack (Remphrey and Powell, 1985). This is usually along the lower half of the parental leader (Powell and Vescio, 1986). The occurrence of sylleptic short shoots, however, is not restricted to the zone where sylleptic long shoots appear (Powell and Vescio, 1986). Syllepsis is observed less frequently in mature trees (Von Wuhlisch and Muhs, 1985). Remphrey and Powell (1985) observed no syllepsis in tamarack trees over 25 years of age.

McCurdy and Powell (1987) suggested that the propensity for sylleptic branching of tamarack may be a part of an adaptive mechanism permitting exploitive development of as much photosynthetic surface as possible in order to compete successfully. Sylleptically initiated branches were reported bearing many more short and long shoots than did proleptic branches, and leaders with heavy syllepsis (21-39 shoots) elongated faster and longer than leaders without syllepsis (Remphrey and Powell,1984). Sylleptic long and short shoots greatly increased the numbers of leaves on the leaders (Powell, 1987). The initial superior growth of sylleptic leaders was generally associated with previous sylleptic shoot production (Powell and Vescio, 1986).

McCurdy and Powell (1987) found that there were positive correlations among annual wood ring production and total stem cross-sectional areas at various positions along the main stem of tamarack trees and the proleptic, sylleptic, and total branching components occurring above the positions. Wood production along the stem was found to be greater and more uniform, and the resultant stem more conical in heavily sylleptic saplings than in less sylleptic saplings. Therefore, McCurdy and Powell (1987) further suggested that in untended stands competition among trees would favour the more vigorous , sylleptic trees.

Powell (1987) found that the longevity of sylleptic shoots was shorter than that of proleptic shoots. Therefore, they suggested that the crown of a mature tree may not be overly branchy even though the tree had highly juvenile branchiness because of strong syllepsis. There was no association between leader crookedness and production of sylleptic long shoots (Powell,1987).

Powell and Vescio (1986) suggested that there existed genetic control over the development of syllepsis. They reported that certain plantation-grown trees from a single seed source did not exhibit any sylleptic branching although the component height growth increments were generally very vigorous. However, to date, no genetic data have been published.

GENETIC CORRELATION

According to Falconer (1981), the genetic correlation measures how strongly two characteristics are correlated genetically. It is defined as the ratio of the genetic covariance to the product of the two genetic standard deviations. It is expressed as:

$$r_{xy} = cov(xy) / \sqrt{var(x)} * \sqrt{var(y)}$$

where cov(xy) is the genetic covariance between character x and y, and var(x), var(y) are the genetic variance components for character x and y respectively. The genetic components of covariance for the two characters can be computed from an analysis of covariance (Falconer, 1981; Becker, 1984).

Estimates of genetic correlations are thought to be subject to rather large sampling errors and are therefore not very precise (Falconer, 1981). Furthermore, genetic correlations are strongly influenced by gene frequencies and therefore may differ markedly in different populations (Bohren *et al.*, 1966).

Therefore, estimates of genetic correlations only give a general impression of how strongly two characteristics are correlated genetically.

Two types of genetic correlation are designated (Burdon, 1977). One type is the genetic correlation obtained from both traits measured on the same individuals. The other type of genetic correlation is obtained from a single trait measured on different individuals within genetic groups in different environments, which is a special case of genetic correlation between environments.

Genetic correlations among traits are commonly used in determining the degree to which selection for one trait will be successful in improving another trait (Zobel and Talbert, 1984). Therefore it is of interest to tree breeders. Working with forest tree species, several researchers have used genetic correlation between juvenile and mature traits to judge the effectiveness of early family selection (Wakeley,1971; Ying and Morgenstern,1979; Lambeth,1980). Genetic correlation has also been used as a concept for studying genotype environment interaction in forest tree breeding (Burdon,1977).

HERITABILITY

The concept of heritability is widely used in quantitative genetics. It is expressed as the ratio of genetic variance to total variance, and is commonly thought of as an estimation of the degree of genetic determination (Falconer, 1981) or the ability for parents to pass their characteristics to their offspring (Zobel and Talbert, 1984). There are two kinds of heritability estimates: broad-sense heritability and narrow-sense heritability. Broad-sense heritability and narrow-sense heritability are expressed in the following two formulae:

Broad-sense: $h^2 = \sigma^2_G / \sigma^2_P = (\sigma^2_A + \sigma^2_{NA}) / (\sigma^2_A + \sigma^2_{NA} + \sigma^2_E)$

Narrow-sense: $h^2 = \sigma^2_A / \sigma^2_P = \sigma^2_A / (\sigma^2_A + \sigma^2_{NA} + \sigma^2_E)$

where σ^2_A, σ^2_{NA} and σ^2_E mean additive, non-additive and error variance components respectively. Therefore, heritability measures the relative importance of sources of variation which contribute to the determination of a phenotype.

Falconer (1981) explains that broad-sense heritability measures the extent to which an individual's phenotype is determined by its genotype, whereas the narrow-sense heritability estimates the relative importance of genes from parents in determining a phenotype.

METHODS

Genetic variation in syllepsis and juvenile growth of eastern tamarack in northwestern Ontario was studied in a clonal test established on a two hectare old-field site on Lakehead University land in Thunder Bay, Ontario.

EXPERIMENT MATERIALS

The area sampled to establish the experimental population was bounded by Long. 80° and 95° W and by Lat. 46° and 54° N (Table 1).

Table 1. Number designations of provenances used in the study.

Latitude	Longitude			
	80-82°	84-85°	90-91°	93-94°
46-47°	1	4	-	-
48-49°	2	5	8	-
50-51°	3	6	9	-
53-54°	-	7	10	11

Eleven provenances ranging from North Bay to Sandy Lake (Fig. 1), were included in the test. Each provenance was represented by twenty wildlings sampled from each of two stands. In each stand, sample trees were generally 20 meters or more apart and dispersed throughout the stand. These wildlings, ranging from 3 to 10 years of age, were used as ortets to produce planting stock for the test.

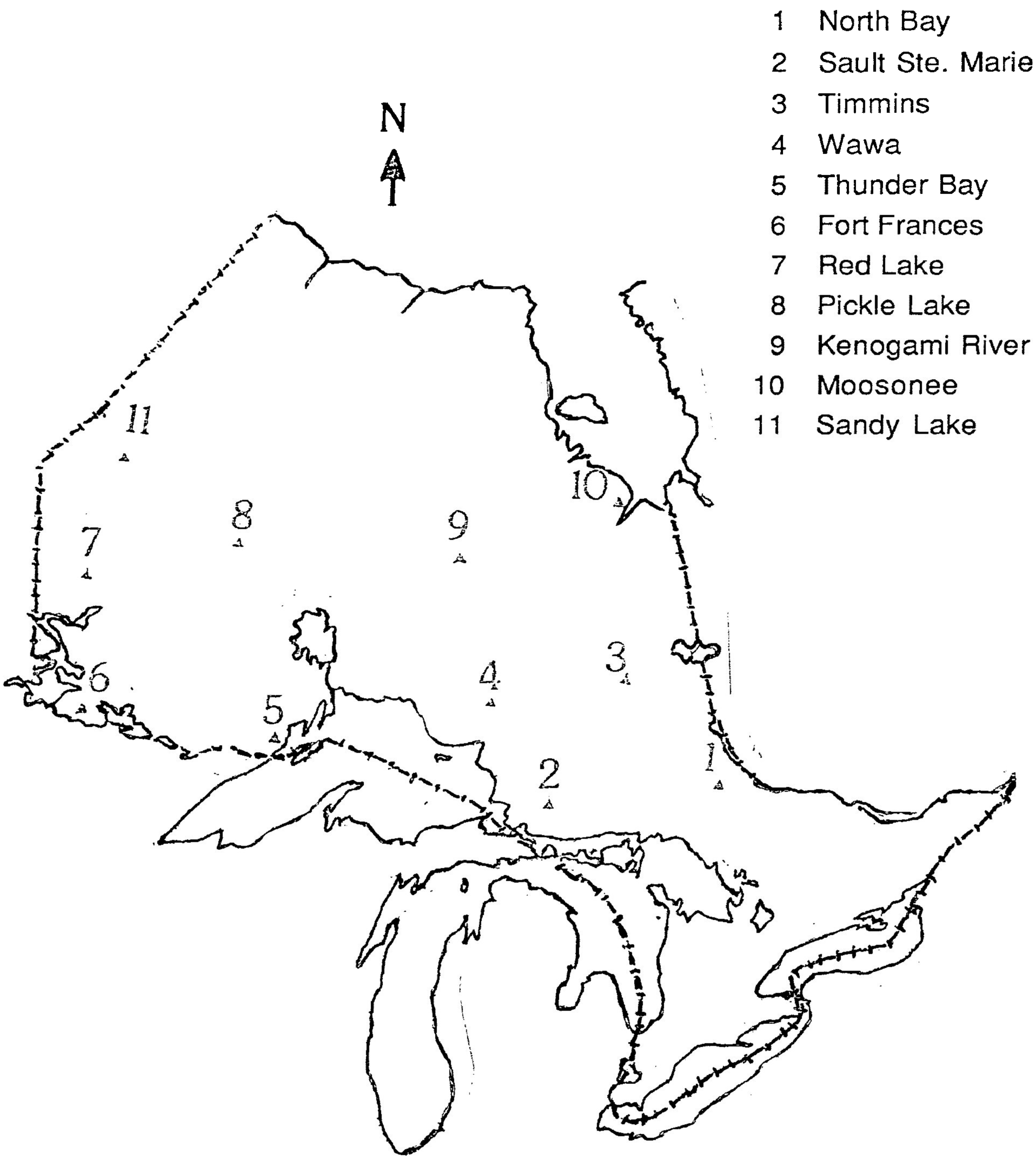

Figure 1. Location of collections of tamarack.

Wildlings were collected and transplanted during the spring and summer of 1984. These wildling transplants were excavated with soil in order to minimize disturbance to their root systems and planted in 6-liter pots filled with peat-vermiculite. Enough lateral shoots were developed to provide cuttings in the summer of 1984, and the cuttings were successfully rooted in Spencer-Lemaire containers (750 ml) via methods designed by Farmer *et. al.* (1986). The rooted ramets of these ortets were overwintered outdoors and brought into a greenhouse for forcing in January 1985. They were transferred to a lath-house in June where they remained until planted.

The soil on the test sites is not homogeneous, with a sandy loam in Blocks 1 and 2 and stony, shallow, sandy loam in Blocks 2 and 3. Before ramets were planted the sites were cleared with a brush saw. Then a glyphosate herbicide (Roundup) was applied to eliminate competing vegetation. In the fall of 1985, rooted cuttings were planted into Blocks 1 and 2. Cuttings were planted into Blocks 3 and 4 in the spring of 1986. During the first growing season after planting, every tree was covered with a plastic bag, then Roundup was sprayed to eliminate competing vegetation. In the later years, weed control was done manually using a brushsaw during growing seasons.

TEST DESIGN

The test is part of long-term provenance studies in eastern tamarack being conducted by the School of Forestry, Lakehead University. The test is aimed at determining the natural variation patterns of biologically important characteristics of tamarack, especially those with fitness values which vary along environmental gradients in northwestern Ontario (Farmer, 1983).

The test has a three level nested design (Table 2) with provenances as main plots, and stands within provenances, and clones within stands within provenances as subplots. Eleven provenance plots are randomly arranged in each of four replications. Three ramets from each of 20 clones per provenance are completely randomized within each provenance plot. The design allows for evaluation of genetic variance within each provenance, and for evaluation of provenance effects under the assumption that the restriction error on randomization of provenances is negligible.

Table 2: Design of Experiment.

Source	Degree of Freedom		Expected Mean Square
Bi	(Block)	3	$\sigma^2 + 3\sigma^2_{BC} + 30\sigma^2_{BS} + 60\sigma^2_{\omega} + 60\sigma^2_{BP} + 660\sigma^2_{\delta} + 660\phi_{(B)}$
$\delta_{(i)}$	(1st restriction error)	0	$\sigma^2 + 3\sigma^2_{BC} + 30\sigma^2_{BS} + 60\sigma^2_{\omega} + 60\sigma^2_{BP} + 660\sigma^2_{\delta}$
P_j	(Provenance)	10	$\sigma^2 + 12\sigma^2_{C} + 120\sigma^2_{S} + 60\ \sigma^2_{\omega} + 240\ \sigma^2_{P}$
BP_{ij}	(Block X Provenance)	30	$\sigma^2 + 3\sigma^2_{BC} + 30\ \sigma^2_{BS} + 60\ \sigma^2_{\omega} + 60\ \sigma^2_{BP}$
$\omega_{(ij)}$	(2nd Restriction error)	0	$\sigma^2 + 3\sigma^2_{BC} + 30\sigma^2_{BS} + 60\ \sigma^2_{\omega}$
$S_{(j)k}$	(Stand/ Provenance)	11	$\sigma^2 + 12\ \sigma^2_{C} + 120\ \sigma^2_{S}$
$BS_{i(j)k}$	(Block X St. /Prov.)	33	$\sigma^2 + 3\ \sigma^2_{BC} + 30\ \sigma^2_{BS}$
$C_{(jk)l}$	(Clone/ St. / Prov.)	198	$\sigma^2 + 12\ \sigma^2_{C}$
$BC_{i(jk)l}$	(Block X Clone/ St./ Prov.)	594	$\sigma^2 + 3\sigma^2_{BC}$
$E_{(ijkl)m}$	(Error)	1760	σ^2
Total		2639	

DATA COLLECTION

During early summer of 1989, the 1988 height increment was measured to the nearest 0.1 cm, and the number and length of sylleptic long shoots (>3cm) on 1988 apical shoots were recorded. Trees with severe terminal leader damage were excluded because of many abnormal adventitious shoots.

After trees ceased growing in late summer of 1989, the following were recorded: (1) the total number of sylleptic long shoots, (2) the total length of those shoots, (3) 1989 height growth and (4) mortality for each provenance. Total heights in 1989 were derived by adding 1989 height growth to 1988 total height. The total heights for 1987 and 1988 were available from previous measurements.

DATA ANALYSES

Since up to 25 percent missing entries caused problems in matrix manipulation, multivariate analysis of variance was not used. Univariate analyses of variance were done using individual tree data for each of the following attributes:

1. The total number of sylleptic long shoots on 1989 growth.
2. The total length of sylleptic long shoots on 1989 growth.
3. Number of sylleptic long shoots per cm of 1989 growth.
4. Length of sylleptic long shoots per cm of 1989 growth.
5. Total height in September 1988.
6. Height growth for 1988.
7. Height growth for 1989.
8. Total height in September 1989.

All the analyses of variance were carried out according to the following model:

$$Y_{ijklm} = \mu + B_i + \delta_{(i)} P_j + BP_{ij} + \omega_{(ij)} + S_{(j)K} + BS_{i(j)k} + C_{(jk)l} + BC_{i(jk)l} + E_{(ijkl)m}$$

Where:

Y_{ijklm} =the m^{th} observation of the l^{th} clone of k^{th} stand of j^{th} provenance in i^{th} block

μ = overall effects

B_i = block effects (fixed), i=1,2,3,4;

$\delta_{(i)}$ = first restriction error (due to blocking)

P_j = provenance effects (random), j=1,2,··········11;

BP_{ij} = block X provenance interaction effect

$\omega_{(ij)}$ = second restriction error (due to provenances.within blocks)

$S_{(j)k}$ = effect of the k^{th} stand within the J^{th} provenance (random)

$BS_{i(j)k}$ = block X stand interaction effect, k=1,2;

$C_{(jk)l}$ = clonal effect (random), l=1,2,··········10;

$BC_{i(jk)l}$ = block X clone interaction effect

$E_{(ijkl)m}$ = random effect, m=3;

All analyses of variance were done using the Excel spreadsheet on a McIntosh microcomputer. The procedures for the calculation of unbalanced data for a nested design described by Sokal and Rohlf (1981) were followed.

The variance components were calculated following the design shown in Table 1. Since there were missing data entries, the coefficients in the expected mean square table were estimated using Sokal and Rohlf's (1981) procedure for an unbalanced nested design (Appendix I).

Although it is unusual to use provenance test to estimate broad-sense heritability it is permissible here because both among provenance and within provenance variation can be estimated with this test design Broad-sense heritability for both provenances and clones within provenances are estimated using the following formulae (Falconer, 1981; Zobel and Talbert, 1981) :

$$h^2_P = \sigma^2_P / \sigma^2_{BP} + \sigma^2_S + \sigma^2_{BS} + \sigma^2_C + \sigma^2_{BC} + \sigma^2$$

$$h^2_C = \sigma^2_C / \sigma^2_C + \sigma^2_{BC} + \sigma^2$$

Where: h^2_P and h^2_C represent the broad-sense heritability for provenances and clones within provenances respectively;

σ^2_P, σ^2_S and σ^2_C are variance components due to provenances, stands and clones within provenances respectively;

σ^2_{BP}, σ^2_{BS} and σ^2_{BC} stand for variance components due to block X provenance interactions, block X stand interactions and block X clone interactions respectively;

σ^2 stands for the variance component due to random error;

Due to the nature of the clonal test design, it is possible to analyze individual provenances separately as for a randomized complete block design (Table 3) using the model:

$$Y_{ijk} = \mu + B_i + \delta_{(i)} + C_j + BC_{ij} + E_{(ij)k}$$

Where:

Y_{ijk} =the k^{th} ramet of the j^{th} clone in i^{th} block

μ = overall effects

B_i = block effects (fixed), i=1,2,3,4;

$\delta_{(i)}$ = first restriction error (due to blocking)

C_j = clone effect (random), j=1,2,··········20;

BC_{ij} = block by clone interaction effect

$E_{(ij)k}$ = random effect, k=3;

Therefore, clonal broad-sense heritability of a trait in an individual provenance can be estimated from the individual provenance analysis of variance.

Table 3. Design for analysing height growth and syllepsis of individual provenances.

Source of Variation [1/]	Degree of Freedom	Expected Mean Square
B_i (Block)	3	$\sigma^2 + 3\,\sigma^2_{BC} + 60\sigma^2_{\delta} + 60\phi_{(B)}$
$\delta_{(i)}$ (Restriction error)	0	$\sigma^2 + 3\sigma^2_{BC} + 60\,\sigma^2_{\delta}$
C_j (Clone)	19	$\sigma^2 + 12\,\sigma^2_C$
BC_{ij} (Block X Clone)	57	$\sigma^2 + 3\,\sigma^2_{BC}$
$E_{(ij)k}$ (Error)	160	σ^2
Total	239	

1/. Site within provenances had no significant effect (at 0.05 level of probability) on variation of any traits in analyses of variance using all provenances. Therefore, it was not included in this analysis.

Because of the importance of interrelationships among height growth characteristics and branching habits in selection and breeding programs, correlation analyses were applied to investigate the possible relationships among these attributes. Phenotypic correlations were calculated between all characters recorded at the individual tree level using Pearson product-moment correlations. The calculations were carried out using the SPSS-X statistical package on a MicroVax II computer system.

Genetic correlations among traits give information useful in determining effects of selection for one trait on other trait. Genetic correlation at the clonal level can be estimated as

$$r(g)_C = COV(XY)_C / \sqrt{V(XX)_C} * \sqrt{V(YY)_C}$$

where: $COV(XY)_C$ = clonal genetic covariance for trait X and Y.

$V(XX)_C$ = clonal genetic variance of trait X.

$V(YY)_C$ = clonal genetic variance of trait Y.

In this study, the procedures of covariance analysis for a nested design described by Becker (1984) were followed. Genetic correlations were investigated for the following pairs of traits:

1. Total height for 1988 vs total number and length of 1989 sylleptic long shoots and 1989 total height.
2. Height growth for 1988 vs. total number and length of 1989 sylleptic long shoots and 1989 total height.
3. Height growth for 1989 vs. total number and length of 1989 sylleptic long shoots and 1989 total height.
4. Height growth for 1989 vs. 1989 total height.
5. Total number of 1989 sylleptic long shoots vs. total length of 1989 sylleptic long shoots and 1989 total height.

RESULTS

MORTALITY

Mortality at the end of 1989 growing season averaged 22 percent and ranged from 7 percent for North Bay to 46 percent for Pickle Lake (Table 4). There is a trend of increasing provenance mortality from south to north. But there is no indication that this trend is statistically significant. Correlations between mortality of each provenance and mean provenance height growth for 1988 and 1989 were high (average $r=-0.84$; $\alpha=0.01$). However, mortality of the Thunder Bay provenance was significantly higher than the average for provenances at the lower latitudes.

Despite the geographic trend in mortality for provenances, the mortality occurred randomly among clones within provenances. Only eleven clones were excluded from analyses of variance due to high mortality during 1988 (Table 4).

Table 4. Mortality and occurrence of syllepsis in 1988 and 1989.

Provenance	Mortality percent 1989	Number of clones excluded from analyses	Percent of clones with syllepsis 1988	Percent of clones with syllepsis 1989	Percent of trees with syllepsis 1988	Percent of trees with syllepsis 1989
(1) North Bay	7	0	55	95	1.20	61
(2) Sault S Marie	18	0	10	100	0.10	47
(3) Timmins	20	1	30	90	0.90	35
(4) Wawa	19	1	30	95	0.30	34
(5) Thunder Bay	31	1	35	95	0.35	48
(6) Fort Frances	15	0	75	95	1.60	51
(7) Red Lake	29	0	10	90	0.35	38
(8) Pickle Lake	46	2	5	65	0.05	22
(9) Kenogami R.	21	1	10	70	0.20	23
(10) Moosonee	40	4	10	45	0.10	14
(11) Sandy Lake	22	1	35	90	0.65	35

HEIGHT

There is a significant provenance effect on height growth, as is the effect of clones within provenances (Table 6). However, no significant stand effect was detected. Comparisons among provenance means were made for 1988 and 1989 height growth and 1989 final height using Tukey-Kramer's multiple-range comparison method. The ranking of the eleven provenances indicates a north-south trend of increasing provenance means in height growth (Table 5). All southern provenances (Nos. 1 through 6) rank higher than northern provenances for both height growth and final height in 1989. Among southern provenances, the North Bay and the Fort Frances provenances are superior in height growth. Among northern provenances, the most northern provenance, Sandy Lake, exhibited the best height growth. The variance components for provenance were larger than those for clones within provenances for height growth traits, with the exception of 1988 height growth (Table 7). Variance components for provenance also increased with time, from 6.2 percent of total variance in 1988 height growth to 23 percent in 1989. The same relationship is true for final height. In contrast, there was little increase in clonal variance components between 1988 and 1989 (Table 7).

Table 5. Ranked provenance means and the range of clone means (in parentheses) for height growth (cm) traits. Provenance means followed by different letter suffixes are significantly different at the 0.05 level of probability.

Provenance	Height growth, 1988	Final height, 1988	Height growth, 1989	Final 1/ height, 1989
(8) Pickle Lake	18.4	61.5	34.3 **a**	95.5 **a**
	(10.0-29.7)	(39.4-81.6)	(21.1-44.9)	(60.9-126.4)
(10) Moosonee	20.9	67.9	36.3 **a**	104.1 **b**
	(16.2-27.4)	(48.4-89.7)	(22.2-47.7)	(74.7-131.7)
(7)Red Lake	20.3	66.5	42.8 **b**	109.0 **bc**
	(11.7-31.9)	(44.1-89.4)	(22.6-65.9)	(68.3-146.5)
(9) Kenogami R.	22.8	71.0	43.1 **b**	114.0 **cd**
	(14.5-34.2)	(52.1-98.3)	(30.1-65.3)	(81.4-152.6)
(11) Sandy Lake	26.2	71.6	46.4 **b**	117.6 **d**
	(16.7-43.0)	(54.6-113.1)	(33.1-57.3)	(87.6-156.3)
(3) Timmins	25.2	77.6	52.4 **c**	129.1 **e**
	(17.6-39.7)	(64.5-101.6)	(41.7-72.8)	(108.8-174.4)
(4) Wawa	25.6	82.2	50.1 **c**	132.3 **ef**
	(16.7-30.7)	(65.6-101.3)	(35.7-59.7)	(108.1-154.8)
(2) Sault S. M.	24.8	85.7	53.8 **cd**	139.4 **fg**
	(19.6-31.4)	(67.0-105.0)	(37.8-65.0)	(109.7-162.5)
(5) Thunder Bay	27.0	89.8	53.3 **cd**	143.2 **g**
	(19.4-35.3)	(71.8-104.9)	(33.0-72.6)	(107.6-175.0)
(6) Fort Frances	29.5	90.3	56.8 **d**	146.6 **g**
	(18.8-40.3)	(63.2-121.1)	(43.9-68.7)	(115.9-186.9)
(1) North Bay	30.9	99.9	68.7 **e**	168.5 **h**
	(19.1-47.3)	(82.7-129.5)	(53.3-91.7)	(140.1-204.4)

1/. Provenances are ranked by this attribute.

Table 6. Analyses of variance for height growth traits.

Source of Variation	DF	Height growth, 1988	Final height, 1988	Height growth, 1989	Final height, 1989
		Mean Square			
Block	3	16170.24 n	72294.26 n	3990.66 n	104469.09 n
Provenance	10	2285.30 *	24065.71 **	16895.39 *	79617.35 **
Block X Prov.	30	1163.12 *	5250.45 *	3216.41*	15140.32 *
Stand	11	254.51 ns	1762.18 ns	356.93 ns	2879.12 ns
Block X Stand	33	157.82 ns	514.15 ns	192.75 ns	1069.01 ns
Clone	187	231.86 **	1311.04 **	599.62 *	2860.80 **
Block X Clone	528	104.25 ns	549.23 ns	187.56 ns	983.26 ns
Error	1191	98.99	508.44	192.59	1006.73

* and **, significant at 5% and 1% levels of probability respectively, ns, not significant, n, no valid test for block effect.

Table 7. Variance components and percent of variance (in parentheses) for growth characters..

Source of Variation	Height growth, 1988	Final height, 1988	Height growth, 1989	Final height, 1989
Block	30.2(16.6)	134.9(13.8)	1.6(0.39)	179.8(8.5)
Provenance	11.2(6.2)	123.4(12.6)	90.1(22.9)	424.4(20.0)
Block X Prov.	22.2(12.3)	104.0(10.6)	66.9(17.0)	311.5(14.7)
Stand	0.2(0.1)	4.5(0.5)	0	0
Block X Stand	2.4(1.3)	0 1/	0	2.8(0.1)
Clone	14.0(7.7)	84.6(8.7)	42.9(10.9)	195.4(9.2)
Block X Clone	2.2(1.2)	17.2(1.7)	0	0
Error	99.0(54.5)	508.4(52.0)	192.6(48.9)	1006.7(47.5)

1/. " 0 " stands for negative or zero variance component .

OCCURRENCE OF SYLLEPTIC SHOOTS

Percentage of living trees and clones with sylleptic long shoots increased greatly between the 1988 and 1989 growing seasons (Table 4). In 1988, only 5.4 percent of trees and 27 percent of living clones developed sylleptic long shoots. In 1989, 37 percent of trees exhibited syllepsis and 79 percent of the living clones (220) had one or more ramets with syllepsis.

Occurrence of sylleptic growth gradually decreased from southern to northern provenances. In 1988, the trees with sylleptic growth were mostly in southern provenances, such as Fort Frances (1.6%) and North Bay (1.2%), and the number of clones with sylleptic growth was greater in southern provenances (Provenances 1-6, average 7 clones) than that in northern provenances (Provenances 7-13, average 3 clones) (Table 4). An exception to this relationship is seen in the Sandy Lake provenance which, at Latitude 53°30', is the most northern provenance in the test. In 1988, it had seven clones with one or more sylleptic ramets, which is almost equal to the average of all southern provenances. The Sandy Lake provenance also had 0.65 percent of trees with sylleptic growth in 1988, which is a higher percentage than for trees from Sault Ste Marie (Lat. 46°48'N), Wawa (Lat. 48°49'N), and Thunder Bay (Lat. 48°24'N) (Table 4).

The south-north trend of decreasing potential for sylleptic growth for tamarack is clearer in 1989 than in 1988. In 1989, North Bay had the highest percentage of trees with syllepsis (61 percent), while Moosonee had only 14 percent (Table 4). Differences among the more southern provenances with regard to the percent of clones that had developed syllepsis are minor in 1989, when over 90 percent of clones exhibited sylleptic growth (Table 4). The northern provenances were more variable in this respect, with a range of 45 to 90 percent of clones exhibiting some syllepsis. However, provenance means for percentage of ramets with syllepsis ranged widely among both northern and southern provenances (Table 4).

DEGREE OF SYLLEPSIS

Provenance means for number and total length of sylleptic long shoots per tree, and the number and total length of sylleptic long shoots per cm height increment in 1989 are presented in Table 8. A strong statistically significant (Table 9) provenance effect is shown. Multiple comparison among provenances indicates an apparent south-north trend of decreasing provenance means. The North Bay provenance had the highest number of shoots (7.5); Moosonee had the lowest of (0.8). There also exists the same trend of decreasing provenance means for the other three attributes. In fact, provenance means for these four attributes are strongly correlated with each other (average $r=0.98$ $p<0.01$), and have identical ranges. Generally, southern provenances (Nos. 1-6) exhibit larger number and length of sylleptic shoots per cm of height growth than northern provenances (Table 8). Provenance means for number of sylleptic shoots per cm of 1989 height growth ranged from 0.016 to 0.091, while provenance means for length of sylleptic shoots per cm of 1989 height growth ranged from 0.048 to 1.022. The analyses of variance also indicate that the effect of clones within provenances was statistically significant for the four sylleptic branching traits. However, the effect of stands within provenance was not significant for any traits (Table 9). Variance components (Table 10) were calculated using the expected mean squares presented in Appendix I. Clone and provenance effects accounted for an average of 39 percent of the total variance for sylleptic branching traits. Clones within provenance contributed more variance than provenance for the four sylleptic branching traits. The average ratio of clonal variance to provenance variance is 2.9.

Table 8. Ranked provenance means and the range of clone means (in parentheses) for 1989 sylleptic branch traits. Provenance means followed by different letter suffixes are significantly different at the 0.05 level of probability, Tukey-Kramer multiple range test.

Provenance	Total [1/] number of sylleptic shoots	Total length of sylleptic shoots, cm	Number of sylleptic shoots per cm height growth	Length (cm) of sylleptic shoots per cm height growth
10 Moosonee	0.8 **a**	2.6 **a**	0.016 **a**	0.05 **a**
	(0.0-5.0)	(0.0-19.2)	(.000 - .084)	(0.00-0.32)
8 Pickle Lake	1.0 **a**	4.3 **b**	0.021 **a**	0.09 **b**
	(0.0-3.5)	(0.0-22.8)	(0.00-0.069)	(0.00-0.40)
9 Kenogami R.	1.0 **a**	5.4 **b**	0.018 **a**	0.09 **b**
	(0.0-5.0)	(0.0-21.8)	(.000 - .079)	(0.00-0.37)
11 Sandy Lake	1.7 **b**	7.7 **c**	0.03 4**b**	0.14 **c**
	(0.0-5.0)	(0.0-24.3)	(.000- .098)	(0.00-0.43)
4 Wawa	2.0 **b**	11.5 **d**	0.035 **b**	0.18 **cd**
	(0.0-6.8)	(0.0-55.4)	(.000 - .103)	(0.00-0.74)
7 Red Lake	2.2 **bd**	11.5 **d**	0.047 **c**	0.25 **de**
	(0.0-7.7)	0.0-35.1	(.000 - .135)	(0.00-1.03)
3 Timmins	2.7 **de**	19.2 **e**	0.043 **c**	0.28 **ef**
	(0.0-13.8)	(0.0-129.2)	(.000 - .173)	(0.00-1.56)
5 Thunder Bay	3.1 **e**	21.0 **e**	0.049 **cd**	0.30 **f**
	(0.1-8.8)	(2.1-62.9)	(<.001- .146)	(<0.01-0.95)
2 Sault S. M.	3.4 **e**	20.5 **e**	0.054 **d**	0.31 **f**
	(0.2-11.6)	(0.3-74.1)	(<.001- .198)	(<0.01-1.18)
6 Fort Frances	4.5 **f**	40.4 **f**	0.063 **e**	0.52 **g**
	(0.0-19.1)	(0.0-173.8)	(.000- .262)	(0.00-2.20)
1 North Bay	7.5 **g**	89.4 **g**	0.091 **f**	1.02 **h**
	(0.0-26.4)	(0.0-369.0)	(.000 - .268)	(0.00-3.59)

1/. Provenances are ranked by this attribute.

Table 9. Analyses of variance.for 1989 sylleptic branching traits.

Source of Variation	DF	Total number of sylleptic shoots	Total length of sylleptic shoots	Number of sylleptic shoots per cm height growth	Length of sylleptic shoots per cm height growth
		Mean Square			
Block	3	202.28 no	22724.67 no	0.147 no	1.44 no
Provenance	10	763.56 **	132733.29 *	0.096 *	16.17 **
Block X Prov.	30	120.28 **	27508.54 **	0.019 **	3.06 **
Stand	11	120.52 ns	6637.30 ns	0.025 ns	1.15 ns
Block X Stand	33	12.55 ns	1556.51 ns	0.003 ns	0.22 ns
Clone	187	113.84 *	14687.86 **	0.021 **	1.85 **
Block X Clone	528	19.31 ns	2729.73 ns	0.004 ns	0.34 ns
Error	1191	16.06	2137.10	0.003	0.27

* and **, significant at 5% and 1% levels of probability respectively.
no, no valid test for block effect.
ns, not significant.

Table 10. Variance components and percent of variance (in parenthesis) for sylleptic branching characters.

Source of Variation	Total number of sylleptic shoots	Total length of sylleptic shoots	Number of sylleptic shoots per cm height growth	Length of sylleptic shoots per cm height growth
Block	0.165(0.5)	± 0[1/]	0.00026(4.0)	0
Provenance	3.557(10.5)	650.63(13.3)	0.00039(6.1)	0.079(13.1)
Block X Prov.	2.233(6.6)	548.07(11.2)	0.00032(5.0)	0.060(10.0)
Stand	0.035(0.1)	0	0.00005(0.8)	0
Block X Stand	0	0	0	0
Clone	10.303(30.5)	1322.53(26.9)	0.00178(27.6)	0.166(27.6)
Block X Clone	1.368(4.1)	250.05(5.1)	0.00035(5.4)	0.028(4.6)
Error	16.064(47.6)	2137.09(43.5)	0.00329(51.1)	0.269(44.7)

1/ " 0 " stands for negative or zero variance component .

HERITABILITY

Broad-sense heritabilities based on variance components for provenances and clones within provenance are presented for each attribute in Table 11. For sylleptic branching characters, heritabilities based on clonal variance were generally larger than those based on provenance variance. For growth characters, the opposite is true. Clonal heritabilities for sylleptic branch characters were the highest in the test (average h^2=0.36).

Table 11. Broad-sense heritabilities based on provenance and clonal variance.

Traits	Heritability Provenance	Heritability Clone
Number of sylleptic shoots on 1989 height growth	0.11	0.37± 0.02 1/
Number of sylleptic shoots /cm 1989 height growth	0.06	0.33± 0.03
Total length of sylleptic shoots on 1989 height growth	0.13	0.36± 0.02
Length of sylleptic shoots /cm 1989 height growth	0.13	0.36± 0.03
Height Growth,1988	0.07	0.12± 0.03
Final Height,1988	0.15	0.14± 0.04
Height Growth, 1989	0.23	0.18± 0.04
Final Height,1989	0.22	0.16± 0.03

1/ . Standard errors were calculated using the method described by Falconer (1981).

Clonal broad-sense heritability estimates for individual provenances are listed in Table 12. They range widely for both 1989 height growth and sylleptic branching traits. The Red Lake provenance exhibits the highest clonal broad-sense heritabilities for height growth traits (average h^2=0.42), which is twice as large as the clonal broad-sense heritability estimates using all provenances. The Sault Ste. Marie, Wawa and Sandy Lake provenances exhibit very low clonal broad-sense heritabilities. The clonal broad-sense heritabilities for individual provenances vary from 0.11 to 0.52 for total number of sylleptic shoots in 1989 and from 0.10 to 0.44 for total length of sylleptic shoots in 1989. Apparently, those provenances which have low clonal broad-sense heritabilities for height growth also tend to have low heritabilities for sylleptic branching traits.

Table 12. Broad-sense heritability estimates based on clonal variance from analyses of variance for individual provenances.

Provenance	Height growth, 1989	Final height, 1989	Total number of sylleptic shoots,1989	Total length of sylleptic shoots,1989
North Bay	0.25± 0.08	0.15± 0.06	0.50± 0.09	0.44± 0.09
Sault Ste. Marie	0 1/	0	0.21± 0.07	0.10± 0.05
Timmins	0.14± 0.06	0.10± 0.05	0.45± 0.09	0.39± 0.09
Wawa	0	0.09± 0.05	0.17± 0.07	0.19± 0.07
Thunder Bay	0.21± 0.07	0.16± 0.07	0.30± 0.08	0.18± 0.07
Fort Frances	0.20± 0.07	0.16± 0.07	0.52± 0.09	0.43± 0.09
Red Lake	0.37± 0.09	0.48± 0.09	0.21± 0.07	0.14± 0.06
Pickle Lake	0.13± 0.06	0.13± 0.06	0.11± 0.05	0.16± 0.07
Kenogami River	0.31± 0.09	0.27± 0.08	0.37± 0.09	0.27± 0.08
Moosonee	0.24± 0.08	0.40± 0.09	0.36± 0.08	0.37± 0.09
Sandy Lake	0.08± 0.04	0.08± 0.05	0.16± 0.06	0.11± 0.06

1/. Clonal effect is not significant. Therefore, estimation of broad-sense heritability is zero.

CORRELATIONS

Pearson product-moment correlation coefficients based on individual tree data for eight traits are shown in Table 13. The correlations were all positive and statistically significant. In most cases, they were moderate, except for those correlations between the 1989 sylleptic branching traits and the 1988 height traits, which were about 0.3. The number and total length of sylleptic shoots developed during the 1989 growing season were only moderately correlated with 1989 height increment.

Genetic correlations were calculated for several pairs of traits important to selection (Table 13). Genetic correlations between 1989 final height and other traits are similar, in most cases, to the equivalent Pearson product-moment correlations. Genetic correlations remain low between sylleptic branching in 1989 and 1988 final height (average r=0.28). However, the genetic correlations between sylleptic branching in 1989 and 1988 height growth are much higher than equivalent Pearson product-moment correlations.

Table 13. Phenotypic and genetic correlations (in parentheses) among eight traits. All the Pearson product-moment correlations are significant at the 0.01 probability level.

	(1)[1/] FHT88	(2) HIN88	(3) HIN89	(4) SY89	(5) LSY89
(2) HIN88	0.78				
(3) HIN89	0.58	0.59			
(4) SY89	0.24(.29)	0.24(.46)	0.54(.57)		
(5) LSY89	0.32(.27)	0.34(.50)	0.53(.55)	0.88(.95)	
(6) FHT89	0.93(.93)	0.78(.83)	0.83(.86)	0.40(.45)	0.45(.43)

[1/] (1): Final height, 1988.
(2): Height growth,1988.
(3): Height growth,1989.
(4): Total number of sylleptic long shoots on 1989 height growth.
(5): Total length of sylleptic long shoots on 1989 height growth.
(6): Final height, 1989.

DISCUSSION

MORTALITY

The south-north trend of increasing mortality for provenances indicates that mortality in the test is not occurring randomly among the eleven provenances. Results of other provenance studies with tamarack also are similar to my results (Cech *et al.*, 1977; Jeffers, 1975). Why northern provenances generally have higher mortality than southern provenances is not apparent. It may be because northern provenances are more adapted to northern environments. When they are moved to lower latitudes they simply can not compete as successfully as provenances from lower latitudes. The high negative correlations between mean provenance mortality and height growth for 1988 and 1989 (average $r=-0.84$; $\alpha<0.01$) suggest that the survival of a provenance is at least partly associated with good early height growth. However, the fact that the Thunder Bay provenance, the local provenance, had a significantly higher mortality than two higher latitude provenances (*i.e.* Sandy Lake and Kenogami River) seems to suggest that the genetic constitution of a provenance may play an important role in provenance mortality. The genetic constitution of some provenances may result in their being able to exhibit good height growth but may also make them more resistant to many mortality factors such as root disease. Provenances may also interact with test location to generate this exception to south-north trend of mortality.

HEIGHT GROWTH

The main reason for the decreasing provenance means from south to north for both 1988 and 1989 height growth may be that tamarack trees from different provenances respond to the local photoperiod differently. Southern provenances have a longer shoot elongation period than northern provenances. The influence of photoperiod on growth and dormancy in woody plants has been demonstrated by many researchers (Ekberg *et al.*, 1976; Pollard and Logan, 1976; Heide, 1983). Generally, the higher the latitude, the longer the critical photoperiod for apical growth cessation (Heide, 1983). Variation in photoperiodic responses of tamarack has been reported in several studies. Vaartaja (1959) reported photoperiodic ecotypes between two geographically distant populations. Charrette (1990) found that tamarack provenances displayed significant variation in the critical daylength for inducing growth cessation. In the clonal test reported here, provenances from higher latitudes were found to set buds earlier than provenances from lower latitudes (G. O'Reilley, personal observation). Thus, provenances from higher latitudes have a shorter shoot elongation period.

Since a large proportion of leader extension is accomplished by free growth in tamarack seedlings (Mitchell, 1965; Remphrey and Powell, 1984) photoperiod may influence height growth by decreasing the free growth of northern provenances and enhancing the free growth of southern provenances. Changes in photoperiod from that of provenance origins are reported to have drastic effects on free growth of woody plants (Pollard and Logan, 1974; Von Wuhlisch and Muhs, 1985,1987). Pollard and Logan (1974) demonstrated that free growth of black spruce diminished when local photoperiod was shorter than that at provenance origin.

From the point of view of ecological genetics the height growth differentiation of provenances caused by differential photoperiodic response reflects the adaptation of each provenance to its origin environment. Rehfeldt (1983) concluded that variation in height growth is a result of selection for height growth potential in mild environments and selection for cold hardiness in relatively severe environments. For tamarack, it is also the balance between selection for height growth and selection for cold hardiness that leads to photoperiodic ecotypes. On one hand, the species is shade intolerant (Fowells, 1965) and biological competition as a natural selection force would select fast growing trees. On the other hand, early autumn frost as a natural selection force may lead to selection for photoperiodic types that cease growing early enough to avoid severe frost damage.

Generally, variance components for provenances were larger than for clones within provenances (Table 6) and made up an increasingly large proportion of variance as tamarack trees aged. This increasing provenance variance with age of trees seems to suggest that the differences in height growth among provenances may increase with advancing tree development. The increasing provenance variance also results in increases in broad-sense heritability estimates of provenances for height growth from 1988 to 1989. The moderate broad-sense heritability estimate of provenances for 1989 height growth indicates that substantial genetic gain will result from selecting southern provenances.

Significant variation among clones within provenances for both 1988 and 1989 final height and height growth clearly indicates that clonal variation is also an important source of variation in the height of tamarack. When analyses of variance are done for each provenance separately using 1989 final height and height increment data, clonal effects are statistically significant for most of the provenances. This confirms the significance of clonal variation in height growth noted in the overall analysis of variance. However, the large differences in clonal variance components among provenances and the resulting variable broad-sense heritability estimates for individual provenances indicate that the clonal variance component estimates for individual provenances are unstable. Several factors may possibly contribute to this. Because the estimates of clonal heritability are from a single test location they may be biased by the clone-location interaction. Since there were only 20 genotypes sampled for each of the eleven provenances the large differences in clonal variation may be partly caused by sampling errors in the test. It may also be partly due to the fact that there may exist more variation in photoperiodic response in some provenances than others. Consequently, shoot elongation period may differ widely. Unpublished phenology data from the test indicate, for example, that clones in Red Lake, Moosonee and North Bay provenances respond to the same photoperiod more variably than clones in Sault Ste. Marie and Wawa provenances. However, there are exceptions to this relationship, and the phenology data were only recorded for ten clones within each provenance. Therefore, the clonal variance component estimates and the clonal broad-sense heritability estimates for individual provenances may not be generally representative. Larger samples must be included for individual provenances to obtain reliable clonal broad-sense heritability estimates for them.

OCCURRENCE AND DEGREE OF SYLLEPSIS

Occurrence and the degree of sylleptic growth in the 1988 and 1989 growing seasons provide some insight into genetic control of syllepsis. Powell and Vescio (1986) conclude that vigorously growing tamarack trees have more potential for exhibiting syllepsis. The increasing percentage of both clones and ramets within each provenance exhibiting syllepsis from 1988 to 1989 also supports this conclusion. The increasing vigor of tamarack trees between 1988 and 1989 was clearly demonstrated by the 1989 height increment of trees in the clonal test. The Pearson product-moment correlations between the percentage of clones with syllepsis and height increment in 1988 and 1989 (average r=0.84, α <0.03), and between the percentage of ramets with syllepsis and height increment in 1988 and 1989 (average r=0.85, α <0.03) further indicate that the occurrence of syllepsis in provenances is generally associated with their height growth.

The correlation between height growth and occurrence of syllepsis and the fact that syllepsis only occurs during the most rapid elongation period (Powell, 1987), suggest that when an apical shoot of tamarack grows vigorously, its apical dominance is diminished. However, the mechanism by which the development of syllepsis is controlled seems to be more complex than apical dominance in which lateral buds are released from inhibition by decapitation of apical buds. In apical dominance, removal of an actively growing apical bud will release one or more upper axillary buds which become the dominant shoots. In development of syllepsis, on the other hand, lateral meristem growth is generally associated with actively elongating apical buds.

It is known that growth hormones play important roles in apical dominance (Zimmermann and Brown, 1980; Wareing and Phillips, 1981). However, the way in which hormones cause the inhibition of axillary bud growth is not fully understood. There are two major theories to explain the phenomenon of apical dominance. One is known as the 'Direct Theory', in which diffusible auxin, produced in young leaves of apical buds, is believed to have a direct inhibitory effect on lateral buds. The other theory is the 'Nutritive Theory', in which apical buds are believed to be able to command a preferential supply of metabolites as these move along their concentration gradients, and auxin only has an indirect role (*i.e.* directing the transport of metabolites to apical buds). Neither of these two theories can adequately explain the development of syllepsis. Powell (1987) suggests that occurrence of syllepsis in tamarack is due to the attainment of two or three thresholds of some kind determined by the vigor of the parent shoot. But no studies have been done to find out exactly what these thresholds are and how they control the developmental process of syllepsis. As there is evidence that cytokinin is involved in release of lateral buds from inhibition (Wareing and Phillips, 1981), it is reasonable to believe that the development of syllepsis is not only a function of overall vigor and nutrition, but also involves the interactions of other growth factors, especially cytokinin.

Although in 1989, most of the clones exhibited the potential for sylleptic growth, the degree of syllepsis (*i.e.* total number and length of sylleptic long shoots) for each provenance was highly variable. Southern environments seem to be more conducive to the formation of large numbers of sylleptic shoots. This can be seen from the fact that southern provenances always bear significantly more sylleptic branches than northern provenances when growing at a southern location. Probably, a large number of sylleptic branches in trees from southern provenances has fitness value in that it allows trees to compete more successfully. As mentioned earlier, tamarack is an early successional species which is unable to tolerate shade (Fowells, 1965). For such a pioneer species, individual trees which are able to produce superior height growth and produce shoot structure rapidly, might have some advantage in competition. Remphrey and Powell (1985) also suggest that in untended stands, competition tends to favour the survival of constantly sylleptic trees. Therefore, it is possible that the larger degree of syllepsis in southern provenances is a result of natural selection for syllepsis.

Syllepsis is a trait of great phenotypic plasticity, and environmental factors apparently have a profound effect on the occurrence and degree of syllepsis in tamarack. This can be seen from the fact that for most of the provenances, a large percent of ramets within clones did not develop syllepsis during the 1989 growing season despite existing potential. For example, 100 percent of clones within the Sault Ste Marie provenance had one or more ramets with sylleptic growth, only 47 percent of ramets exhibited syllepsis. This observation is similar to a study of Norway spruce (Von Wunlish and Muhs, 1987), in which factors influencing height growth could also affect the both free growth and sylleptic branching.

The plastic response of tamarack trees in terms of syllepsis may have some evolutionary significance. "Phenotypic plasticity" means that genetically identical organisms may show different characteristics under different conditions (Stearns, 1989). Plasticity of a trait is thought to be a trait itself, evolved to deal with environmental changes (Schlichting, 1989). In tamarack, the occurrence and degree of syllepsis is sensitive to environmental changes. It responds to favorable growing environments and is thought to be part of an adaptive and exploitive mechanism that allows tamarack to display maximal photosynthesizing surface (Remphrey and Powell, 1985). The plasticity of tamarack trees to environmental change manifested in syllepsis possibly evolved to deal with environmental uncertainty.

The correlations between syllepsis and height growth of tamarack clearly demonstrate the relationship between syllepsis and juvenile height growth. Clearly, it is the greater height growth that results in the large amount of syllepsis. Syllepsis may enhance the height growth of tamarack in a later year. But it is unlikely that syllepsis on current-year shoots is the reason for the vigorous parent shoot growth.

Since significant clonal effects were also found for the eleven provenances, and broad-sense heritability estimates were moderate for both provenances and clones within provenances, selection for sylleptic branches should yield a good response. Further, the strong genetic correlation between degree of syllepsis and parent shoot growth indicates that if selection for propensity for syllepsis is made the correlated gains in height growth may also be large.

IMPLICATIONS IN TREE IMPROVEMENT

The results of this study have provided valuable information for guiding tamarack tree improvement programs in northwestern Ontario. First, the information about mortality seems to suggest that selection for trees with superior height growth potential may improve the survival of tamarack plantations. One important objective in forest tree improvement studies is to find out how much genetic variation exists both among and within populations with regard to the traits to be improved. This study shows that tamarack in northwestern Ontario is highly variable both within and among populations with regard to height growth and syllepsis traits. Therefore, selecting both provenances and individual trees within provenance should be stressed. Since height growth and production of sylleptic branches are strongly correlated, use of height growth as the selection criterion would probably be sufficient. However, it would be more reliable to combine height growth with production of sylleptic branches as the selection criterion because: (1) the difference in the production of sylleptic branches is easy to see and (2) a large amount of syllepsis in a tamarack tree is partly a response to a good environment, and therefore, tamarack trees with good potential of producing syllepsis are of more developmental plasticity and should have an advantage over those without or with little potential of producing syllepsis when environmental opportunity is high.

CONCLUSIONS

The results of my study of tamarack syllepsis and its relation to height growth indicates:

1) lower latitude provenances of tamarack will generally have survival advantage over higher latitude provenances when both are planted in a southern location.

2) tamarack in northwestern Ontario is highly variable both within and among provenances with regard to both height growth and sylleptic branching traits.

3) degree of syllepsis of tamarack trees has genetic correlation with the growth of parent leaders, and selection for heavy syllepsis in a tamarack population should result in superior height growth.

4) there is some evidence to suggest that syllepsis of tamarack has fitness value and enables the species to be opportunistic.

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APPENDICES

APPENDIX I

EXPECTED MEAN SQUARE TABLE WITH ADJUSTED COEFFICIENTS

Source of Variation	DF	Expected Mean Square
Block (B_i)	3	$\sigma^2 + 2.46\sigma^2_{BC} + 22.71\sigma^2_{BS} + 45.17\,\sigma^2_{\omega} + 45.17\,\sigma^2_{BP} + 496.87\sigma^2_{\delta} + 496.87\phi_{(B)}$
Provenance (P_j)	10	$\sigma^2 + 9.85\sigma^2_{C} + 90.86\sigma^2_{S} + 45.17\,\sigma^2_{\omega} + 180.70\,\sigma^2_{P}$
Block X Provenance (BP_{ij})	30	$\sigma^2 + 2.46\sigma^2_{BC} + 22.71\sigma^2_{BS} + 45.17\sigma^2_{\omega} + 45.17\sigma^2_{BP}$
Stand $(S_{(j)k})$	11	$\sigma^2 + 9.83\,\sigma^2_{C} + 90.04\,\sigma^2_{S}$
Block X Stand $(BS_{i(j)k})$	33	$\sigma^2 + 2.46\,\sigma^2_{BC} + 22.51\,\sigma^2_{BS}$
Clone $(C_{(jk)l})$	187	$\sigma^2 + 9.49\,\sigma^2_{C}$
Block X Clone $(BC_{i(jk)l})$	528	$\sigma^2 + 2.37\,\sigma^2_{BC}$
Error $(E_{(ijkl)m})$	1191	σ^2
Total	1993	

APPENDIX II

ANALYSES OF VARIANCE, VARIANCE COMPONENTS AND HERITABILITY CALCULATIONS FOR HEIGHT TRAITS

Height growth, 1988

Source of variation	Sums of squares	Degrees of freedom	Mean square	Variance components	Percent of variance	Herit-ability
Block	48510.72	3	16170.24	30.203	16.6	
Provenance	22852.95	10	2285.30	11.236	6.2	0.07
Block X Prov.	34893.60	30	1163.12	22.246	12.3	
Stand	2799.64	11	254.51	0.199	0.1	
Block X Stand	5207.92	33	157.82	2.371	1.3	
Clone	43357.98	187	231.86	14.001	7.7	0.12
Block X Clone	55044.12	528	104.25	2.219	1.2	
Error	117898.38	1191	98.99	98.991	54.6	
Total	330565.31					

Final height, 1988

Source of variation	Sums of squares	Degrees of freedom	Mean square	Variance components	Percent of variance	Herit-ability
Block	216882.78	3	72294.26	134.932	13.8	
Provenance	240657.11	10	24065.71	123.398	12.6	0.15
Block X Prov.	157513.53	30	5250.45	104.862	10.7	
Stand	19383.98	11	1762.18	4.691	0.5	
Block X Stand	16966.99	33	514.15	-1.627	-0.2	
Clone	245164.66	187	1311.04	84.573	8.7	0.14
Block X Clone	289992.78	528	549.23	17.209	1.8	
Error	605556.12	1191	508.44	508.443	52.1	
Total	1792117.95					

Appendix II Continued

Height growth, 1989						
Source of variation	Sums of squares	Degrees of freedom	Mean square	Variance components	Percent of variance	Herit-ability
Block	11972.00	3	3990.67	1.558	0.4	
Provenance	168953.88	10	16895.39	91.533	23.4	0.24
Block X Prov.	96492.37	30	3216.41	66.939	17.1	
Stand	3926.18	11	356.93	-2.857	-0.7	
Block X Stand	6360.74	33	192.75	0.239	0.1	
Clone	112128.40	187	599.62	42.890	11.0	0.18
Block X Clone	99031.01	528	187.56	-2.123	-0.5	
Error	229375.71	1191	192.59	192.591	49.3	
Total	728240.28					

Final height, 1989						
Source of variation	Sums of squares	Degrees of freedom	Mean square	Variance components	Percent of variance	Herit-ability
Block	313407.27	3	104469.09	179.783	8.5	
Provenance	796173.52	10	79617.35	424.653	20.1	0.22
Block X Prov.	454209.63	30	15140.32	311.502	14.8	
Stand	31670.34	11	2879.12	-0.534	0.0	
Block X Stand	35277.24	33	1069.01	3.849	0.2	
Clone	534969.36	187	2860.80	195.371	9.3	0.16
Block X Clone	519161.80	528	983.26	-9.901	-0.5	
Error	1199010.38	1191	1006.73	1006.726	47.7	
Total	3883879.52					

APPENDIX III

ANALYSES OF VARIANCE, VARIANCE COMPONENTS AND HERITABILITY CALCULATIONS FOR SYLLEPTIC BRANCHING TRAITS

Total number of sylleptic shoots, 1989

Source of variation	Sums of squares	Degrees of freedom	Mean square	Variance components	Percent of variance	Herit-ability
Block	606.86	3	202.29	0.165	0.5	
Provenance	7635.62	10	763.56	3.557	10.6	0.11
Block X Prov.	3608.45	30	120.28	2.386	7.1	
Stand	1325.69	11	120.52	0.035	0.1	
Block X Stand	414.28	33	12.55	-0.305	-0.9	
Clone	21287.21	187	113.84	10.303	30.7	0.37
Block X Clone	10192.91	528	19.30	1.368	4.1	
Error	19131.83	1191	16.06	16.064	47.8	
Total	64202.86					

Total lenght of sylleptic shoots,1989

Source of variation	Sums of squares	Degrees of freedom	Mean square	Variance components	Percent of variance	Herit-ability
Block	68174.06	3	22724.69	-9.628	-0.2	
Provenance	1327332.94	10	132733.29	698.102	14.5	0.14
Block X Prov.	825256.06	30	27508.54	574.776	11.9	
Stand	73010.30	11	6637.30	-94.405	-2.0	
Block X Stand	51364.94	33	1556.51	-53.120	-1.1	
Clone	2746629.55	187	14687.86	1322.525	27.4	0.36
Block X Clone	1441296.91	528	2729.73	250.057	5.2	
Error	2545279.83	1191	2137.09	2137.095	44.3	
Total	9078344.59					

Appendix III continued

Number of sylleptic shoots per cm height growth, 1989						
Source of variation	Sums of squares	Degrees of freedom	Mean square	Variance components	Percent of variance	Herit-ability
Block	0.44	3	0.15	0.000257	4.0	
Provenance	0.96	10	0.10	0.000393	6.1	0.06
Block X Prov.	0.56	30	0.02	0.000353	5.5	
Stand	0.28	11	0.03	0.000050	0.8	
Block X Stand	0.09	33	0.00	-0.000057	-0.9	
Clone	3.77	187	0.02	0.001780	27.7	0.33
Block X Clone	2.17	528	0.00	0.000348	5.4	
Error	3.92	1191	0.00	0.003293	51.3	
Total	12.21	1993				

Length of sylleptic shoots per cm height growth, 1989						
Source of variation	Sums of squares	Degrees of freedom	Mean square	Variance components	Percent of variance	Herit-ability
Block	4.33	3	1.44	-0.00326	-0.6	
Provenance	161.72	10	16.17	0.08317	14.0	0.14
Block X Prov.	91.93	30	3.06	0.06293	10.6	
Stand	12.62	11	1.15	-0.00842	-1.4	
Block X Stand	7.35	33	0.22	-0.00508	-0.9	
Clone	345.61	187	1.85	0.16638	28.1	0.36
Block X Clone	176.64	528	0.33	0.02758	4.7	
Error	320.58	1191	0.27	0.26917	45.4	
Total	1120.76					

APPENDIX IV

CALCULATIONS OF COVARIANCE COMPONENTS

Total length of 1989 sylleptic shoots vs.total height,1988

Source	Sums of covariance	Degrees of freedom	Mean covariance	Covariance components
Block	95788.18	3	31929.39	95.91
Provenance	471787.85	10	47178.79	258.93
Block X Prov.	-471787.85	30	-15726.26	-809.43
Stand	4337.11	11	394.28	-7.72
Block X Stand	681570.03	33	20653.64	909.40
Clone	197929.78	187	1058.45	91.29
Block X Clone	96838.11	528	183.41	-3.68
Error	228812.99	1191	192.12	192.12
Total	1305276.19			

Total length of 1989 sylleptic shoots vs.height growth,1988

Source	Sums of covariance	Degrees of freedom	Mean covariance	Covariance components
Block	51238.42	3	17079.47	43.54
Provenance	136699.72	10	13669.97	70.92
Block X Prov.	-136699.72	30	-4556.66	-243.93
Stand	9371.22	11	851.93	1.07
Block X Stand	211388.35	33	6405.71	278.87
Clone	136943.97	187	732.32	67.60
Block X Clone	67067.28	528	127.02	15.27
Error	108183.10	1191	90.83	90.83
Total	584192.35			

Appendix IV Continued

Total length of 1989 sylleptic shoots vs. height growth,1989

Source	Sums of covariance	Degrees of freedom	Mean covariance	Covariance components
Block	9674.25	3	3224.75	34.52
Provenance	417817.49	10	41781.75	225.84
Block X Prov.	-417817.49	30	-13927.25	-722.68
Stand	10735.37	11	975.94	-6.56
Block X Stand	612253.12	33	18553.12	814.50
Clone	284626.12	187	1522.06	131.12
Block X Clone	116684.95	528	220.99	-23.92
Error	330732.13	1191	277.69	277.69
Total	1364705.94			

Total length of sylleptic shoots, 1989 vs. total height, 1989

Source	Sums of covariance	Degrees of freedom	Mean covariance	Covariance components
Block	104691.80	3	34897.27	129.99
Provenance	890689.27	10	89068.93	484.77
Block X Prov.	-890689.27	30	-29689.64	-1534.71
Stand	16244.26	11	1476.75	-12.62
Block X Stand	1296499.04	33	39287.85	1727.55
Clone	474869.89	187	2539.41	216.78
Block X Clone	213120.69	528	403.64	-33.13
Error	574236.13	1191	482.15	482.15
Total	2679661.81			

Appendix IV Continued

Number of sylleptic shoots, 1989 vs. 1989 height growth

Source	Sums of covariance	Degrees of freedom	Mean covariance	Covariance components
Block	-2192.29	3	-730.76	0.77
Provenance	33427.52	10	3342.75	17.63
Block X Prov.	-33427.52	30	-1114.25	-56.24
Stand	1727.31	11	157.03	0.14
Block X Stand	46657.18	33	1413.85	61.71
Clone	26178.10	187	139.99	11.98
Block X Clone	13147.62	528	24.90	-0.59
Error	31334.75	1191	26.31	26.31
Total	116852.68			

Number of sylleptic shoots, 1989 vs. total height, 1988

Source	Sums of covariance	Degrees of freedom	Mean covariance	Covariance components
Block	-9353.19	3	-3117.73	-3.74
Provenance	37833.14	10	3783.31	20.55
Block X Prov.	-37833.14	30	-1261.10	-63.37
Stand	776.18	11	70.56	-0.30
Block X Stand	52383.23	33	1587.37	70.06
Clone	17649.93	187	94.38	8.67
Block X Clone	5457.54	528	10.34	-0.74
Error	14411.83	1191	12.10	12.10
Total	81325.51			

Appendix IV Continued

Number of sylleptic shoots, 1989 vs.1988 height growth				
Source	Sums of covariance	Degrees of freedom	Mean covariance	Covariance components
Block	-4073.94	3	-1357.98	-2.01
Provenance	10739.46	10	1073.95	5.29
Block X Prov.	-10739.46	30	-357.98	-18.39
Stand	1301.39	11	118.31	0.64
Block X Stand	15465.16	33	468.64	20.55
Clone	11058.78	187	59.14	5.53
Block X Clone	3251.75	528	6.16	-0.20
Error	7911.75	1191	6.64	6.64
Total	34914.89			

Number of sylleptic shoots, 1989 vs.total length of 1989 sylleptic shoots				
Source	Sums of covariance	Degrees of freedom	Mean covariance	Covariance components
Block	-2418.45	3	-806.15	4.98
Provenance	98481.71	10	9848.17	49.76
Block X Prov.	-98481.71	30	-3282.72	-176.10
Stand	9440.69	11	858.24	-4.37
Block X Stand	152867.72	33	4632.36	197.40
Clone	226938.97	187	1213.58	111.17
Block X Clone	99136.02	528	187.76	12.30
Error	188901.88	1191	158.61	158.61
Total	674866.83			

Appendix IV Continued

Number of sylleptic shoots, 1989 vs.total height, 1989

Source	Sums of covariance	Degrees of freedom	Mean covariance	Covariance components
Block	-11523.37	3	-3841.12	-2.95
Provenance	71326.44	10	7132.64	38.11
Block X Prov.	-71326.44	30	-2377.55	-119.76
Stand	2697.63	11	245.24	0.09
Block X Stand	99180.74	33	3005.48	131.94
Clone	43039.90	187	230.16	20.10
Block X Clone	18873.15	528	35.74	-1.54
Error	46908.08	1191	39.39	39.39
Total	199176.14			

APPENDIX V

EXAMPLE OF VARIANCE COMPONENT CALCULATIONS: NUMBER OF SYLLEPTIC BRANCHES

1). Error variance component

$\sigma^2 = 16.06$

2). Variance component for block X clone interaction

$\sigma^2_{BC} = (MS_{BC} - MS_{Error}) / 2.37 = (19.30-16.06)/2.37 = 1.368$

3). Clone variance component

$\sigma^2_{C} = (MS_{C} - MS_{Error}) / 9.49 = (113.84-16.06)/9.49 = 10.303$

4). Variance component for Block X Stand interaction

$\sigma^2_{BS} = (MS_{BS} - MS_{Error} - 2.46\ \sigma^2_{BC}) / 22.51$

$= (12.55-16.06-2.46^{*}\ 1.368)/22.51 = -0.305$

5). Stand variance component

$\sigma^2_{S} = (MS_{S} - MS_{Error} - 9.83\ \sigma^2_{C}) / 90.04$

$= (120.52-16.06-9.83^{*}\ 10.303)/90.04 = 0.035$

6). Variance component for block X provenance interactions

$\sigma^2_{BP} = (MS_{BP} - MS_{Error} - 2.46\ \sigma^2_{BC} - 22.71\ \sigma^2_{BS}) / 45.17$

$= (120.28-16.06-2.46^{*}1.368-22.71^{*}0)/45.17 = 2.386$

7). Provenance variance component

$\sigma^2_{P} = (MS_{P} - MS_{Error} - 9.85\ \sigma^2_{C} - 98.06\ \sigma^2_{S}) / 180.7$

$= (763.56-16.06-9.85^{*}10.303-90.86^{*}0.035)/ 180.7 = 3.557$

8). Block variance component

$\sigma^2_{B} = (MS_{B} - MS_{Error} - 2.46\ \sigma^2_{BC} - 22.71\ \sigma^2_{BS} - 45.17\ \sigma^2_{BP}) / 496.87$

$= (202.29-16.06-2.46^{*}1.368-22.71^{*}0-45.17^{*}2.386)/496.87$

$= 0.165$

APPENDIX VI

CLONE MEANS FOR HEIGHT GROWTH, CM

CLONE	Height growth, 1988	Final height, 1988	Height growth, 1989	Final height, 1989
101213	30.92	102.00	72.25	173.00
101223	27.59	95.09	71.91	167.00
101233	27.33	88.46	60.17	148.63
101293	32.86	103.73	53.45	157.18
101313	19.05	90.05	56.23	146.27
101323	35.75	129.54	74.83	204.38
101333	25.18	88.14	71.36	159.50
101343	41.00	121.00	80.25	201.25
101363	27.95	97.59	76.64	174.23
101373	34.29	108.75	79.63	188.38
102223	35.36	110.09	78.09	188.18
102253	23.42	100.63	65.50	166.13
102263	47.32	115.36	78.41	193.77
102273	25.45	87.73	63.27	151.00
102293	31.21	82.67	64.54	147.21
102323	33.18	115.00	66.09	181.09
102333	30.33	88.61	56.94	145.56
102343	24.73	91.91	59.27	151.18
102353	36.82	94.00	91.73	185.73
102383	28.28	86.78	53.28	140.06
201213	20.32	85.73	59.73	145.45
201243	30.41	91.59	58.82	150.41
201263	25.91	81.05	55.82	136.86
201273	28.55	105.00	52.65	157.65
201283	26.42	90.25	59.13	148.00
201303	27.50	101.71	60.79	162.50
201323	20.92	71.83	37.83	109.67
201333	19.82	69.73	54.45	124.18
201363	22.45	81.09	51.64	132.73
201373	23.27	80.32	58.41	138.73
202213	31.35	92.00	48.80	140.80
202233	28.30	91.35	42.30	133.65
202253	19.60	74.40	48.55	122.95
202263	22.28	67.00	54.50	121.50
202273	24.31	91.88	52.25	144.13
202303	21.60	88.10	49.90	138.00
202323	25.60	87.65	59.85	147.50
202333	24.55	87.45	53.75	141.20
202353	22.13	81.75	52.04	133.79
202363	30.50	93.43	65.00	158.43

Appendix VI Ccontinued

301253	21.72	64.67	51.17	115.83
301263	39.70	101.60	72.80	174.40
301273	26.91	75.86	41.73	117.59
301283	25.32	76.55	51.82	128.36
301293	24.09	82.64	54.64	137.00
301303	21.82	84.86	57.41	140.82
301333	27.44	82.56	59.63	142.19
301343	28.68	75.36	52.77	128.14
301353	34.40	84.50	56.00	140.50
302213	19.05	67.50	53.00	120.50
302223	17.64	74.77	42.91	117.23
302263	21.83	71.17	55.25	126.42
302283	17.56	64.50	44.33	108.83
302293	26.88	66.06	52.31	118.06
302303	26.50	77.13	45.75	110.13
302323	25.90	87.70	48.70	136.40
302343	25.00	75.96	50.88	126.67
302353	23.70	82.80	54.40	137.20
302363	25.00	77.28	49.78	127.06
401223	16.75	70.40	48.60	119.00
401243	20.05	65.59	42.68	108.27
401263	22.05	75.91	49.73	125.64
401283	24.22	85.06	53.06	138.11
401293	28.23	94.00	49.09	143.09
401303	30.73	95.50	56.59	152.09
401313	24.63	87.25	53.08	140.33
401333	28.44	76.89	45.94	122.83
401343	24.06	79.69	44.50	124.19
401363	25.95	75.64	43.73	119.36
402233	27.23	101.27	53.50	154.77
402243	21.30	68.40	56.60	123.60
402253	29.40	92.75	56.20	148.95
402263	28.08	89.13	59.71	148.83
402273	28.55	86.59	53.32	139.91
402283	22.20	76.90	53.40	130.30
402303	29.67	72.33	35.72	108.06
402343	25.45	83.73	47.09	130.82
402353	28.79	85.21	49.75	134.96
501223	27.85	103.25	53.05	156.30
501253	24.44	79.75	51.81	131.56
501263	32.61	101.94	51.94	154.22
501273	29.79	101.38	62.79	164.17
501283	29.95	86.86	64.09	150.95
501293	35.28	102.78	63.00	165.78
501313	25.42	79.13	51.25	130.38
501333	23.18	74.55	61.14	135.68
501343	19.44	71.75	35.81	107.56
502213	21.33	75.17	33.00	108.17

Appendix VI Continued

502233	33.43	101.36	49.57	150.93
502263	25.55	83.00	54.50	137.50
502273	30.29	102.07	55.57	157.64
502283	23.17	92.25	37.67	129.92
502293	26.50	102.35	72.60	174.95
502313	28.55	104.86	60.68	165.64
502323	20.06	82.50	47.00	129.50
502333	28.38	78.00	56.50	134.50
502343	27.00	83.83	50.92	134.75
601213	26.00	82.73	45.45	128.18
601243	31.86	98.36	52.79	151.14
601253	34.63	96.56	68.75	165.31
601263	29.00	87.25	55.05	142.30
601293	34.27	102.36	66.59	156.59
601303	29.95	100.68	58.32	159.00
601323	18.78	76.17	49.11	125.28
601333	34.08	121.08	65.79	186.88
601343	26.18	101.95	57.73	159.68
601353	32.36	86.91	55.23	142.14
602223	26.41	75.86	56.77	132.64
602243	31.75	86.46	58.75	145.21
602253	23.00	63.21	51.50	115.88
602293	36.00	102.56	63.39	165.94
602303	21.50	77.55	43.90	121.45
602323	40.32	110.41	67.59	178.00
602333	25.44	74.28	51.06	125.33
602353	33.75	84.13	59.69	143.81
602363	24.05	80.85	53.90	134.75
602373	30.45	96.00	55.45	151.45
701213	20.57	71.21	41.36	112.57
701223	21.93	65.14	46.93	112.07
701243	13.75	58.08	31.67	89.75
701263	19.14	63.36	37.91	101.27
701283	21.50	79.72	44.56	121.39
701323	16.86	58.09	37.09	95.18
701333	15.00	66.45	39.64	106.09
701343	11.69	50.94	34.13	85.06
701373	22.39	72.33	49.67	122.44
701383	14.33	44.08	29.75	73.83
702243	31.86	80.57	65.93	146.50
702253	29.70	89.40	55.70	145.10
702263	23.40	82.70	48.80	131.50
702273	26.45	86.05	51.64	138.59
702283	19.89	63.06	45.50	107.56
702313	16.70	56.10	43.60	99.70
702323	15.25	46.56	22.63	68.31
702333	22.56	66.06	44.22	110.17
702353	25.59	81.00	50.73	131.73

Appendix VI Continued

702383	17.50	48.43	33.57	82.00
801223	18.11	59.67	40.56	100.22
801233	20.38	63.25	21.13	84.38
801243	13.88	45.25	40.00	85.25
801253	19.56	63.39	34.44	97.83
801263	13.70	54.00	34.40	88.40
801283	14.50	39.38	21.50	60.88
801303	29.69	81.56	44.88	126.44
801313	20.45	57.59	35.95	93.55
801323	14.38	68.19	30.50	98.69
801363	18.50	61.67	42.25	103.92
802213	17.88	65.81	35.13	100.19
802243	10.00	42.30	25.40	67.70
802273	19.45	65.00	39.10	99.80
802293	25.67	78.33	32.25	110.58
802323	14.00	58.63	28.44	87.06
802333	19.69	62.94	38.63	101.56
802353	20.06	72.50	27.67	100.17
802363	21.88	66.88	44.75	111.63
901213	18.45	60.64	35.27	95.77
901223	24.81	78.94	45.38	124.31
901243	29.04	85.79	46.75	132.54
901253	22.63	79.83	40.83	120.58
901283	23.65	76.90	35.75	112.65
901313	34.23	98.27	54.36	152.64
901343	27.50	79.89	65.33	145.22
901373	24.50	70.21	51.25	122.38
901403	19.82	71.82	33.73	104.86
901413	20.25	60.35	45.60	105.95
902233	16.57	62.79	34.93	97.71
902253	26.15	67.25	42.45	109.70
902313	22.06	68.72	39.78	108.50
902323	15.14	52.07	30.21	81.36
902343	19.67	52.83	38.56	91.39
902353	25.42	73.17	54.63	127.79
902363	23.41	67.00	41.23	108.23
902403	25.45	81.32	52.50	133.14
902413	14.50	61.42	30.08	91.83
1001223	23.00	74.00	44.61	118.61
1001233	19.21	52.79	28.36	81.14
1001283	26.45	89.65	39.40	129.05
1001303	17.90	56.90	31.50	90.00
1001333	19.50	64.35	39.25	103.70
1001353	21.35	80.65	32.60	110.75
1001363	23.70	74.95	40.30	115.05
1002223	16.15	52.55	22.15	74.70
1002233	17.59	57.82	35.86	93.77
1002243	22.95	80.50	35.25	115.75

Appendix VI Continued

1002253	17.06	60.67	32.11	92.78
1002293	19.67	66.25	42.83	109.08
1002303	17.50	48.40	28.80	77.20
1002343	18.88	61.44	33.00	94.44
1002353	26.33	84.00	47.72	131.72
1002363	27.40	81.40	46.50	127.90
1301213	32.45	77.55	49.05	126.60
1301233	24.27	65.55	43.45	109.00
1301243	16.65	70.00	38.60	108.60
1301273	24.00	68.88	41.75	110.63
1301293	22.64	66.32	44.95	111.27
1301303	22.06	58.94	57.33	116.28
1301313	25.22	68.00	45.06	113.06
1301323	23.35	59.65	37.70	97.35
1301343	31.41	81.50	51.00	132.50
1302213	28.32	73.59	51.50	125.09
1302223	19.69	54.56	33.06	87.63
1302233	26.21	82.14	41.64	124.07
1302243	29.50	75.10	52.70	127.80
1302253	29.00	73.25	50.17	123.00
1302263	43.00	113.08	43.25	156.33
1302273	22.29	66.54	50.83	117.38
1302283	28.83	80.71	54.25	128.29
1302293	25.22	58.44	51.44	109.89
1302303	23.38	65.92	43.63	109.54

APPENDIX VII

CLONE MEANS FOR SYLLEPTIC BRANCHING TRAITS

Clone	Total number of sylleptic shoots 1988	Total number of sylleptic shoots 1989	Total length of sylleptic shoots, cm 1988	Total length of sylleptic shoots, cm 1989	Number of sylleptic shoots per cm height growth 1989	Length of sylleptic shoots per cm height growth 1989
101213	0.17	5.58	0.42	56.33	0.072	0.693
101223	0.09	8.18	0.64	115.41	0.097	1.336
101233	0.00	5.58	0.00	58.21	0.079	0.768
101293	1.00	4.73	3.86	44.14	0.074	0.638
101313	0.00	2.18	0.00	16.45	0.029	0.209
101323	0.25	5.83	1.00	84.04	0.077	0.966
101333	0.82	8.45	3.45	82.09	0.102	0.930
101343	0.33	6.58	0.63	62.54	0.082	0.745
101363	0.00	4.18	0.00	41.55	0.050	0.493
101373	1.83	19.83	12.25	264.04	0.207	2.924
102223	0.27	9.45	2.18	107.50	0.118	1.358
102253	0.00	1.08	0.00	15.00	0.013	0.172
102263	4.91	19.18	51.68	258.14	0.228	2.895
102273	0.00	7.45	0.00	53.09	0.098	0.648
102293	2.33	12.00	5.08	122.96	0.169	1.565
102323	0.00	2.64	0.00	28.77	0.035	0.356
102333	0.00	0.22	0.00	5.00	0.005	0.111
102343	0.00	0.55	0.00	2.77	0.009	0.042
102353	1.36	26.36	10.36	368.95	0.268	3.592
102383	0.00	0.00	0.00	0.00	0.000	0.000
201213	0.00	5.45	0.00	51.73	0.067	0.590
201243	0.00	2.18	0.00	13.91	0.033	0.206
201263	0.00	2.09	0.00	15.64	0.033	0.234
201273	0.00	2.20	0.00	12.45	0.032	0.179
201283	0.00	6.33	0.00	46.38	0.102	0.774
201303	0.00	7.43	0.00	35.36	0.118	0.529
201323	0.00	0.33	0.00	0.33	0.008	0.008
201333	0.00	11.55	0.00	74.14	0.198	1.184
201363	0.00	4.27	0.00	17.95	0.072	0.304
201373	0.00	6.18	0.00	29.73	0.098	0.445
202213	0.30	1.30	0.60	6.95	0.021	0.106
202233	0.00	0.30	0.00	1.90	0.004	0.023
202253	0.00	4.80	0.00	16.45	0.092	0.296
202263	0.00	0.22	0.00	1.00	0.004	0.015
202273	0.00	1.38	0.00	7.63	0.019	0.106
202303	0.00	1.10	0.00	9.25	0.023	0.208
202323	0.00	0.20	0.00	0.90	0.003	0.014

Appendix VII Continued

202333	0.00	2.70	0.00	14.85	0.046	0.262
202353	0.00	1.92	0.00	11.58	0.030	0.179
202363	0.14	5.43	0.43	42.00	0.074	0.569
301253	0.00	0.11	0.00	0.56	0.002	0.009
301263	1.80	13.80	10.25	129.20	0.173	1.560
301273	0.00	0.73	0.00	2.32	0.012	0.039
301283	0.00	3.09	0.00	20.32	0.046	0.299
301293	0.09	7.27	0.45	36.95	0.115	0.544
301303	0.00	4.27	0.00	18.77	0.064	0.277
301333	0.00	8.63	0.00	61.06	0.138	0.972
301343	0.00	0.91	0.00	4.41	0.017	0.080
301353	0.00	2.40	0.00	15.95	0.048	0.342
302213	0.00	3.82	0.00	28.41	0.065	0.434
302223	0.00	0.45	0.00	1.86	0.008	0.032
302263	0.00	0.25	0.00	1.00	0.005	0.022
302283	0.00	0.00	0.00	0.00	0.000	0.000
302293	1.25	1.00	11.63	4.25	0.018	0.069
302303	0.25	2.63	0.38	24.50	0.043	0.389
302323	0.00	1.30	0.00	8.00	0.033	0.221
302343	0.08	0.75	1.50	3.38	0.013	0.057
302353	0.20	0.50	2.00	2.70	0.008	0.043
302363	0.00	0.11	0.00	0.22	0.002	0.004
401223	0.00	0.10	0.00	0.65	0.002	0.010
401243	0.00	4.73	0.00	11.05	0.103	0.224
401263	0.00	1.91	0.00	12.14	0.032	0.194
401283	0.00	1.89	0.00	12.00	0.034	0.211
401293	0.00	0.18	0.00	1.64	0.005	0.044
401303	0.00	0.18	0.00	0.18	0.003	0.003
401313	0.17	1.83	0.42	8.83	0.027	0.121
401333	0.00	0.00	0.00	0.00	0.000	0.000
401343	0.63	1.75	0.81	10.63	0.031	0.181
401363	0.09	1.82	0.09	9.18	0.034	0.165
402233	0.55	2.73	2.36	26.55	0.045	0.390
402243	0.00	1.00	0.00	5.10	0.018	0.088
402253	0.00	4.10	0.00	18.75	0.070	0.310
402263	1.50	6.83	12.58	55.38	0.094	0.737
402273	0.00	1.55	0.00	8.05	0.027	0.126
402283	0.00	1.20	0.00	7.85	0.020	0.126
402303	0.00	0.33	0.00	2.00	0.011	0.074
402343	0.00	3.73	0.00	17.91	0.063	0.295
402353	0.58	2.08	3.58	11.25	0.037	0.183
501223	0.00	2.30	0.00	21.50	0.030	0.276
501253	0.63	5.13	1.88	33.81	0.089	0.585
501263	0.00	2.89	0.00	15.67	0.048	0.256
501273	0.00	2.00	0.00	14.17	0.027	0.191
501283	0.55	7.82	1.64	49.64	0.113	0.658
501293	0.11	1.22	0.78	5.78	0.021	0.089
501313	0.00	2.83	0.00	16.63	0.055	0.276

Appendix VII Continued

501333	0.00	8.82	0.00	51.50	0.146	0.806
501343	0.00	0.75	0.00	7.50	0.013	0.129
502213	0.00	2.00	0.00	9.67	0.057	0.241
502233	0.43	3.29	1.86	19.14	0.052	0.293
502263	0.45	0.91	3.27	6.41	0.021	0.142
502273	0.00	0.14	0.00	2.14	0.018	0.093
502283	0.00	0.50	0.00	2.25	0.013	0.056
502293	0.80	2.70	7.55	22.90	0.039	0.277
502313	0.00	8.64	0.00	62.86	0.000	0.000
502323	0.00	0.78	0.00	4.89	0.138	0.950
502333	0.00	2.63	0.00	22.50	0.013	0.076
502343	1.58	3.42	7.67	30.83	0.037	0.313
601213	0.00	0.45	0.00	5.82	0.060	0.515
601243	0.71	1.00	3.00	6.21	0.009	0.112
601253	2.63	10.00	4.69	110.00	0.014	0.084
601263	0.00	0.00	0.00	0.00	0.127	1.308
601293	0.00	8.27	0.00	82.64	0.000	0.000
601303	0.27	5.36	1.55	45.73	0.112	1.048
601323	0.22	1.22	0.56	3.17	0.082	0.644
601333	0.67	3.58	5.04	44.21	0.026	0.065
601343	0.00	4.64	0.00	39.64	0.047	0.561
601353	2.18	3.55	28.45	39.55	0.069	0.521
602223	0.55	0.64	4.73	6.64	0.048	0.524
602243	3.50	5.08	20.42	31.71	0.008	0.088
602253	0.08	0.58	1.25	6.58	0.093	0.487
602293	1.00	8.11	7.61	75.94	0.009	0.095
602303	0.00	1.20	0.00	14.40	0.110	0.949
602323	5.82	19.09	24.14	173.77	0.015	0.171
602333	0.00	0.33	0.00	2.89	0.262	2.175
602353	0.63	1.50	5.25	12.50	0.005	0.041
602363	0.80	7.10	2.75	48.45	0.025	0.175
602373	2.64	7.36	10.64	58.55	0.130	0.832
701213	0.00	5.00	0.00	25.57	0.127	1.027
701223	0.00	2.57	0.00	16.79	0.125	0.639
701243	0.00	1.50	0.00	6.83	0.051	0.289
701263	0.00	2.45	0.00	9.82	0.030	0.137
701283	0.00	0.11	0.00	0.33	0.052	0.192
701323	0.00	1.64	0.00	5.91	0.003	0.009
701333	0.00	1.73	0.00	6.64	0.040	0.133
701343	0.00	0.25	0.00	1.00	0.033	0.126
701373	0.00	0.11	0.00	1.17	0.006	0.024
701383	0.00	0.00	0.00	0.00	0.002	0.019
702243	0.00	0.86	0.00	4.14	0.000	0.000
702253	0.80	3.80	3.40	29.50	0.013	0.061
702263	0.00	6.40	0.00	32.30	0.063	0.484
702273	0.00	2.36	0.00	16.77	0.105	0.523
702283	0.00	1.33	0.00	7.06	0.036	0.249
702313	0.00	3.20	0.00	11.10	0.031	0.180

Appendix VII Continued

702333	0.00	2.44	0.00	9.06	0.000	0.000
702353	1.64	7.73	3.14	35.09	0.043	0.154
702383	0.00	1.14	0.00	4.00	0.135	0.568
801223	0.44	0.67	0.56	2.22	0.022	0.078
801233	0.00	0.00	0.00	0.00	0.013	0.044
801243	0.00	1.25	0.00	4.38	0.000	0.000
801253	0.00	1.44	0.00	5.00	0.026	0.089
801263	0.00	0.00	0.00	0.00	0.026	0.090
801283	0.00	0.00	0.00	0.00	0.000	0.000
801303	0.00	2.25	0.00	5.94	0.000	0.000
801313	0.00	1.27	0.00	6.00	0.045	0.120
801323	0.00	3.50	0.00	18.88	0.024	0.110
801363	0.00	0.17	0.00	0.67	0.069	0.368
802213	0.00	0.00	0.00	0.00	0.003	0.013
802243	0.00	0.40	0.00	0.50	0.000	0.000
802273	0.00	3.50	0.00	22.75	0.013	0.017
802293	0.00	0.33	0.00	2.50	0.062	0.390
802323	0.00	1.38	0.00	3.38	0.008	0.056
802333	0.00	0.00	0.00	0.00	0.041	0.101
802353	0.00	0.67	0.00	2.28	0.000	0.000
802363	0.00	0.75	0.00	3.63	0.022	0.078
901213	0.00	0.18	0.00	0.45	0.012	0.058
901223	0.00	1.25	0.00	4.63	0.003	0.008
901243	0.00	0.00	0.00	0.00	0.021	0.076
901253	0.00	0.00	0.00	0.00	0.000	0.000
901283	0.00	0.00	0.00	0.00	0.000	0.000
901313	1.18	2.45	4.36	18.95	0.000	0.000
901343	1.33	5.00	5.11	21.78	0.034	0.255
901373	0.00	3.08	0.00	16.13	0.079	0.328
901403	0.00	0.36	0.00	0.91	0.056	0.270
901413	0.00	0.30	0.00	1.10	0.009	0.023
902233	0.00	1.86	0.00	9.21	0.006	0.021
902253	0.00	0.20	0.00	1.60	0.037	0.177
902313	0.00	0.00	0.00	0.00	0.004	0.030
902323	0.00	0.14	0.00	0.21	0.000	0.000
902343	0.00	0.00	0.00	0.00	0.003	0.005
902353	0.00	3.58	0.00	21.71	0.000	0.000
902363	0.00	0.00	0.00	0.00	0.050	0.305
902403	0.00	0.91	0.00	5.05	0.000	0.000
902413	0.00	0.00	0.00	0.00	0.017	0.090
1001223	0.00	1.89	0.00	7.78	0.000	0.000
1001233	0.00	0.00	0.00	0.00	0.036	0.148
1001283	0.20	0.00	0.40	0.00	0.000	0.000
1001303	0.00	0.80	0.00	0.80	0.000	0.000
1001333	0.00	0.10	0.00	0.90	0.024	0.024
1001353	0.00	1.80	0.00	4.65	0.002	0.018
1001363	0.00	0.90	0.00	2.90	0.062	0.125
1002223	0.00	0.00	0.00	0.00	0.015	0.046

Appendix VII Continued

1002233	0.00	1.09	0.00	3.09	0.000	0.000
1002243	0.00	0.10	0.00	0.10	0.024	0.068
1002253	0.00	0.00	0.00	0.00	0.002	0.002
1002293	0.00	5.00	0.00	19.17	0.000	0.000
1002303	0.00	0.00	0.00	0.00	0.084	0.316
1002343	0.00	0.00	0.00	0.00	0.000	0.000
1002353	0.00	0.00	0.00	0.00	0.000	0.000
1002363	0.80	0.50	3.30	1.60	0.009	0.026
1301213	4.70	2.40	31.10	10.20	0.049	0.206
1301233	0.00	2.18	0.00	9.27	0.044	0.158
1301243	0.00	1.30	0.00	2.80	0.029	0.063
1301273	0.00	0.00	0.00	0.00	0.000	0.000
1301293	0.09	1.00	0.27	2.18	0.021	0.045
1301303	0.00	0.56	0.00	1.72	0.012	0.035
1301313	0.00	3.89	0.00	15.50	0.075	0.274
1301323	0.00	0.20	0.00	2.30	0.003	0.035
1301343	0.82	1.73	4.73	5.27	0.037	0.112
1302213	1.18	3.45	5.82	19.73	0.070	0.321
1302233	0.00	0.86	0.00	1.29	0.022	0.033
1302243	1.00	1.70	4.05	5.55	0.037	0.116
1302253	0.25	1.67	0.25	10.19	0.029	0.183
1302263	2.33	0.83	21.33	16.67	0.015	0.303
1302273	0.42	5.00	0.83	24.25	0.098	0.428
1302283	0.00	1.58	0.00	4.83	0.028	0.085
1302293	0.00	2.11	0.00	6.56	0.038	0.114
1302303	0.00	2.08	0.00	8.58	0.040	0.160

APPENDIX VIII

ANALYSIS OF VARIANCE OF INDIVIDUAL PROVENANCES FOR HEIGHT GROWTH TRAITS

Height growth, 1989

Provenance	Source of Variation	Sums of Squares	Degrees of Freedom	Mean Square	Variance Comp-onent	Percent of variance
North Bay	Block	23205.69	3	7735.23	109.12	24.29
	Clone	22571.40	19	1187.97	83.54	18.60
	B X C	10767.97	57	188.91		0.00
	Error	36684.92	143	256.54	256.54	57.11
	Total	93229.98	222	419.95		
Sault.	Block	2632.14	3	877.38	11.28	4.61
Ste.	Clone	6521.03	19	343.21	9.96	4.07
Marie	B X C	9177.43	56	163.88		0.00
	Error	26396.13	118	223.70	223.70	91.33
	Total	44726.72	196	228.20		
Timmins	Block	4550.34	3	1516.78	22.35	9.05
	Clone	8610.17	18	478.34	30.42	12.31
	B X C	11091.38	54	205.40	7.95	3.22
	Error	21613.96	116	186.33	186.33	75.42
	Total	45865.84	191	240.14		
Wawa	Block	7076.39	3	2358.80	43.79	16.13
	Clone	6143.58	18	341.31	13.06	4.81
	B X C	9350.71	52	179.82		0.00
	Error	25751.75	120	214.60	214.60	79.06
	Total	48322.44	193	250.38		
Thunder Bay	Block	5404.57	3	1801.52	23.05	5.69
	Clone	14902.46	17	876.62	73.07	18.05
	B X C	15514.50	45	344.77	34.09	8.42
	Error	27179.04	99	274.54	274.54	67.83
	Total	63000.58	164	384.15		

Appendix VIII Continued

Height growth, 1989

Provenance	Source of Variation	Sums of Squares	Degrees of Freedom	Mean Square	Variance Component	Percent of variance
Fort Frances	Block	30329.53	3	10109.84	187.10	50.77
	Clone	9894.87	19	520.78	36.69	9.95
	B X C	8028.60	57	140.85		0.00
	Error	18094.42	125	144.76	144.76	39.28
	Total	66347.42	204	325.23		
Red Lake	Block	1588.85	3	529.62		0.00
	Clone	15549.48	19	818.39	79.73	33.45
	B X C	9734.88	53	183.68	21.99	9.22
	Error	12983.71	95	136.67	136.67	57.33
	Total	39856.92	170	234.45		
Pickle Lake	Block	3554.09	3	1184.70	31.23	15.91
	Clone	4730.54	17	278.27	20.78	10.59
	B X C	5521.58	45	122.70		0.00
	Error	9086.79	63	144.23	144.23	73.50
	Total	22893.00	128	178.85		
Kenogami R.	Block	11950.67	3	3983.56	70.00	22.53
	Clone	13417.98	18	745.44	63.31	20.38
	B X C	11832.03	53	223.25	33.37	10.74
	Error	16560.17	115	144.00	144.00	46.35
	Total	53760.85	189	284.45		
Moosonee	Block	14502.06	3	4834.02	142.87	45.29
	Clone	6902.41	16	431.40	41.46	13.15
	B X C	5515.81	42	131.33	0.30	0.09
	Error	10855.38	83	130.79	130.79	41.47
	Total	37775.66	144	262.33		
Sandy Lake	Block	3670.02	3	1223.34	18.92	7.66
	Clone	6810.66	18	378.37	17.89	7.24
	B X C	8856.84	51	173.66		0.00
	Error	24169.46	115	210.17	210.17	85.09
	Total	43506.98	187	232.66		

Appendix VIII Continued

Total Height, 1989

Provenance	Source of Variation	Sums of Squares	Degrees of Freedom	Mean Square	Variance Comp-onent	Percent of variance
North Bay	Block	182569.59	3	60856.53	937.48	34.28
	Clone	86549.72	19	4555.25	273.56	10.00
	B X C	88778.75	57	1557.52	18.81	0.69
	Error	215228.88	143	1505.10	1505.10	55.03
	Total	573126.94	222	2581.65		
Sault. S. M.	Block	19798.80	3	6599.60	106.07	9.54
	Clone	27846.01	19	1465.58	41.83	3.76
	B X C	47321.76	56	845.03		0.00
	Error	113702.25	118	963.58	963.58	86.69
	Total	208668.82	196	1064.64		
Timmins	Block	38556.35	3	12852.12	233.44	16.17
	Clone	39732.22	18	2207.35	115.91	8.03
	B X C	57179.03	54	1058.87		0.00
	Error	126969.71	116	1094.57	1094.57	75.81
	Total	262437.31	191	1374.02		
Wawa	Block	46449.70	3	15483.23	292.16	20.10
	Clone	36392.69	18	2021.82	98.89	6.80
	B X C	45136.83	52	868.02		0.00
	Error	127510.96	120	1062.59	1062.59	73.10
	Total	255490.18	193	1323.78		
Thunder Bay	Block	54992.18	3	18330.73	406.05	21.28
	Clone	55086.22	17	3240.37	242.32	12.70
	B X C	57494.07	45	1277.65	16.50	0.86
	Error	123122.38	99	1243.66	1243.66	65.16
	Total	290694.85	164	1772.53		
Fort Frances	Block	261274.60	3	87091.53	1620.87	50.36
	Clone	76413.88	19	4021.78	262.07	8.14
	B X C	57912.26	57	1016.00		0.00
	Error	166950.04	125	1335.60	1335.60	41.50
	Total	562550.78	204	2757.60		

Appendix VIII Continued

Total Height, 1989

Provenance	Source of Variation	Sums of Squares	Degrees of Freedom	Mean Square	Variance Comp-onent	Percent of variance
Red Lake	Block	702.85	3	234.28		0.00
	Clone	89800.77	19	4726.36	490.62	42.26
	B X C	43882.97	53	827.98	138.67	11.95
	Error	50500.08	95	531.58	531.58	45.79
	Total	184886.67	170	1087.57		
Pickle Lake	Block	2109.74	3	703.25		0.00
	Clone	22308.95	17	1312.29	101.58	13.39
	B X C	26911.40	45	598.03		0.00
	Error	41396.38	63	657.09	657.09	86.61
	Total	92726.47	128	724.43		
Kenogami R.	Block	32183.85	3	10727.95	165.81	14.18
	Clone	56799.23	18	3155.51	257.67	22.04
	B X C	42283.43	53	797.80	37.97	3.25
	Error	81377.58	115	707.63	707.63	60.53
	Total	212644.09	189	1125.10		
Moosonee	Block	53231.86	3	17743.95	470.44	30.91
	Clone	44547.75	16	2784.23	318.24	20.91
	B X C	39537.45	42	941.37	256.20	16.83
	Error	39591.58	83	477.01	477.01	31.34
	Total	176908.65	144	1228.53		
Sandy Lake	Block	75747.37	3	25249.12	526.72	33.20
	Clone	31162.24	18	1731.24	79.96	5.04
	B X C	48001.09	51	941.20		0.00
	Error	112660.54	115	979.66	979.66	61.76
	Total	267571.24	187	1430.86		

APPENDIX IX

ANOVA OF INDIVIDUAL PROVENANCES FOR SYLLEPTIC BRANCHING TRAITS

Total number of sylleptic shoots, 1989

Provenance	Source of Variation	Sums of Squares	Degrees of Freedom	Mean Square	Variance Comp-onent	Percent of variance
North Bay	Block	713496.97	3	237832.32	2109.38	9.11
	Clone	2043369.03	19	107545.74	8652.71	37.35
	B X C	843136.25	57	14791.86	1335.91	5.77
	Error	1582726.96	143	11068.02	11068.02	47.78
	Total	5182729.20	222	23345.63		
Sault. S. M.	Block	3497.90	3	1165.97		0.00
	Clone	76521.29	19	4027.44	192.83	10.11
	B X C	53962.82	56	963.62		0.00
	Error	202195.04	118	1713.52	1713.52	89.89
	Total	336177.05	196	1715.19		
Timmins	Block	6529.88	3	2176.63		0.00
	Clone	170987.39	18	9499.30	852.10	36.27
	B X C	94342.23	54	1747.08	178.29	7.59
	Error	153025.42	116	1319.18	1319.18	56.15
	Total	424884.92	191	2224.53		
Wawa	Block	4671.52	3	1557.17		0.00
	Clone	32759.57	18	1819.98	129.62	18.72
	B X C	27123.42	52	521.60		0.00
	Error	67521.25	120	562.68	562.68	81.28
	Total	132075.75	193	684.33		
Thunder Bay	Block	437.18	3	145.73		0.00
	Clone	54340.94	17	3196.53	247.06	17.55
	B X C	51382.20	45	1141.83		0.00
	Error	114910.58	99	1160.71	1160.71	82.45
	Total	221070.90	164	1347.99		

Appendix IX Continued

Total number of sylleptic shoots, 1989

Provenance	Source of Variation	Sums of Squares	Degrees of Freedom	Mean Square	Variance Comp-onent	Percent of variance
Fort Frances	Block	145103.87	3	48367.96	489.28	8.27
	Clone	370423.18	19	19495.96	1681.01	28.41
	B X C	345540.41	57	6062.11	1481.54	25.04
	Error	283206.79	125	2265.65	2265.65	38.29
	Total	1144274.25	204	5609.19		
Red Lake	Block	10904.85	3	3634.95	33.01	2.99
	Clone	42253.36	19	2223.86	152.60	13.81
	B X C	31500.29	53	594.35		0.00
	Error	87318.54	95	919.14	919.14	83.20
	Total	171977.05	170	1011.63		
Pickle Lake	Block	1516.77	3	505.59		0.00
	Clone	5845.58	17	343.86	28.92	8.76
	B X C	17509.37	45	389.10	143.72	43.55
	Error	9913.08	63	157.35	157.35	47.68
	Total	34784.81	128	271.76		
Kenogami	Block	2222.14	3	740.71		0.00
	Clone	11965.42	18	664.75	54.47	23.28
	B X C	11864.87	53	223.87	32.26	13.79
	Error	16932.33	115	147.24	147.24	62.93
	Total	42984.77	189	227.43		
Moosonee	Block	720.11	3	240.04	1.04	1.36
	Clone	2464.82	16	154.05	17.26	22.45
	B X C	3474.69	42	82.73	29.71	38.63
	Error	2397.42	83	28.88	28.88	37.56
	Total	9057.04	144	62.90		
Sandy Lake	Block	4328.93	3	1442.98	20.74	7.37
	Clone	8709.27	18	483.85	28.22	10.03
	B X C	12825.29	51	251.48	14.01	4.98
	Error	25132.41	115	218.54	218.54	77.63
	Total	50995.90	187	272.71		

Appendix IX Continued

Total length of sylleptic long shoots, 1989

Provenance	Source of Variation	Sums of Squares	Degrees of Freedom	Mean Square	Variance Comp-onent	Percent of variance
North Bay	Block	1823.34	3	607.78	0.79	0.84
	Clone	10453.13	19	550.16	45.30	47.82
	B X C	3137.11	57	55.04	3.58	3.78
	Error	6442.83	143	45.05	45.05	47.56
	Total	21856.41	222	98.45		
Sault. Ste.	Block	168.41	3	56.14		0.00
	Clone	1691.10	19	89.01	5.64	20.86
	B X C	848.52	56	15.15		0.00
	Error	2522.67	118	21.38	21.38	79.14
	Total	5230.69	196	26.69		
Timmins	Block	75.37	3	25.12		0.00
	Clone	2315.12	18	128.62	11.89	40.41
	B X C	1176.32	54	21.78	3.04	10.32
	Error	1681.67	116	14.50	14.50	49.28
	Total	5248.48	191	27.48		
Wawa	Block	231.40	3	77.13	0.91	6.09
	Clone	628.01	18	34.89	2.40	15.95
	B X C	612.90	52	11.79	0.05	0.36
	Error	1398.83	120	11.66	11.66	77.61
	Total	2871.14	193	14.88		
Thunder Bay	Block	214.66	3	71.55		0.00
	Clone	1278.98	17	75.23	7.10	29.77
	B X C	573.97	45	12.75		0.00
	Error	1658.00	99	16.75	16.75	70.23
	Total	3725.61	164	22.72		
Fort Frances	Block	464.08	3	154.69		0.00
	Clone	4214.85	19	221.83	19.85	44.71
	B X C	1951.22	57	34.23	6.20	13.96
	Error	2293.50	125	18.35	18.35	41.33
	Total	8923.64	204	43.74		

Appendix IX Continued

Total length of sylleptic long shoots, 1989

Provenance	Source of Variation	Sums of Squares	Degrees of Freedom	Mean Square	Variance Comp-onent	Percent of variance
Red Lake	Block	504.13	3	168.04	2.72	11.91
	Clone	980.39	19	51.60	4.17	18.21
	B X C.	809.10	53	15.27		0.00
	Error	1518.67	95	15.99	15.99	69.88
	Total	3812.29	170	22.43		
Pickle Lake	Block	114.04	3	38.01	0.77	7.27
	Clone	165.65	17	9.74	0.68	6.42
	B X C.	512.38	45	11.39	3.73	35.32
	Error	338.83	63	5.38	5.38	50.99
	Total	1130.90	128	8.84		
Kenogami R	Block	109.74	3	36.58	0.26	3.95
	Clone	396.04	18	22.00	1.96	29.36
	B X C	317.50	53	5.99	1.11	16.65
	Error	384.83	115	3.35	3.35	50.04
	Total	1208.11	189	6.39		
Moosonee	Block	103.65	3	34.55	0.63	9.98
	Clone	176.71	16	11.04	1.22	19.38
	B X C	264.42	42	6.30	2.27	35.98
	Error	181.33	83	2.18	2.18	34.65
	Total	726.11	144	5.04		
Sandy Lake	Block	406.50	3	135.50	2.61	24.32
	Clone	312.92	18	17.38	1.19	11.12
	B X C	403.76	51	7.92	0.74	6.90
	Error	710.67	115	6.18	6.18	57.66
	Total	1833.85	187	9.81		