GENETIC VARIATION OF WOOD PROPERTIES IN BALSAM POPLAR
(*Populus balsamifera* L.)

by
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Reader

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ABSTRACT

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Key Words: canonical variate analysis, coefficients of genetic prediction, genetic correlation, heritability, *Populus balsamifera,* provenance test, wood properties.

Genetic variation in wood properties among and within three provenances of balsam poplar was investigated. Between 1982 and 1984, clonal populations were sampled along the Longitude 90°W in North Wisconsin (Lat. 45°N to 46°N); Thunder Bay, Ontario (Lat. 48°N to 49°N); and Pickle Lake, Ontario (Lat. 50°N to 51°N). Rooted cuttings were planted in a field test near Lakehead University, Thunder Bay. In 1994, 30 clones from each provenance with 4 ramets per clone were measured for growth characteristics, and specimen disks were cut at tree base. Ring width, relative density, percent moisture content, fibre length, and vessel element length were determined in the laboratory. Univariate analyses of variance showed significant differences among the three provenances in growth rate and cell length. The southern provenance had the fastest growth rate and the longest cells. Provenance differences in relative density and moisture content of the wood were not statistically significant. Canonical multivariate analysis, using growth rate, relative density, and fibre length as dependent variables, showed differences between the southern and northern provenances, with the local source in an intermediate position. Estimates of broad sense heritability were different for each of the three provenances. Heritability was more uniform and higher for wood properties than for growth characteristics. Genetic correlations and coefficients of genetic prediction showed relative genetic independence of growth characteristics from relative density and moisture content. Phenotypically positive correlation between growth rate and cell length was genetically based in the northern provenance, while it was influenced more by environment in the local and southern provenance. Results justified selection based on growth characteristics, wood properties or a combination of these two.

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CHAPTER 1

INTRODUCTION

This thesis deals with genetic variation in wood properties and growth characteristics of balsam poplar (*Populus balsamifera* L). Balsam poplar is an almost transcontinental species, with a wide continuous range throughout Canada and in Lake States, USA. The most pronounced trends of variation within the range of the species are in a south-north direction (warm-cold trends). The genetic differentiation among latitudinal locations has been investigated in several provenance studies. The species has a continuous, so called "clinal", genetic variation, which implies an abundant gene interchange. No significant genetic differences were found among latitudinal provenances in isozyme characteristics (Farmer *et al.* 1988), rooting ability (Farmer *et al.* 1989), dormancy (Farmer and Reinholt 1985) and spring dehardening (Watson 1990). At the same time, leaf size was significantly smaller in northern sources (Penfold 1991). The rate of growth cessation in response to short photoperiods was higher in northern sources (Charrette 1990), which was one of the main reasons for differences in the shoot growth and tree height (Farmer 1993, Riemenschneider and McMahon 1993).

The main objectives of this study were:

- To determine the genetic pattern of wood quality variation in the south-north direction, along longitude 90^{o}, in North Wisconsin and North-West Ontario;

- To estimate the amount of variation present among clones within provenances, and among individual trees within clones. By comparing these two types of variation, to estimate the broad sense heritability of growth and wood characteristics;

- To examine correlations among growth and wood characteristics, and to determine the degree of genetic association between these characteristics;

- To put the results in the context of provenance testing of native poplars. By doing this, to provide for better knowledge of genetics of growth and wood properties in this genus.

LITERATURE REVIEW

Wood Properties in Tree Improvement Programs

Many authors have described the valuable qualities of poplar wood and importance of improving these by tree breeding has been realized for many years. In his publication on forest tree breeding and genetics Richens (1945) cited several papers which dealt with wood quality of poplar species. Selection for wood quality was advocated, i.e., the choice of breeding material with a higher cellulose content, more even growth, longer fibres, and greater pulp yield and strength.

In studies on the relationship of growth rate to wood quality in poplar hybrids, Johnson (1942) was concerned with the possibility of adverse wood characteristics arising from increased growth rate in hybrid trees. A general conclusion drawn from his studies was that, "... nothing has been found that would support a connotation that abnormally rapid growth is seriously detrimental to wood quality... Therefore, breeding work on the production of rapid growing forest trees will proceed with some assurance that rapid growth and good quality wood are not incompatible." Experimental pulp and paper tests did not reveal any very striking differences in quality between fast growing hybrid and slow growing parental trees. But the author warned that, "... to know the true commercial value of rapid growth (hybrid vigor in this case) the relation between growth rate and wood properties must be known."

The opportunity for improving wood properties is particularly attractive, since they are generally strongly inherited. In Chapter 11 of Zobel and Talbert (1984) entitled "Wood and Tree Improvement", the authors showed that most wood properties, as well as growth characteristics that affect wood, are inherited strongly enough to obtain rapid economic gains through genetic manipulation.

There are many examples of high inheritance of different wood properties in poplars (see *Tables* 1.3. and 1.7.).

Unfortunately, most tree improvement programs do not include improvement of wood quality, even though wood is the desired product (Zobel and van Buijtenen 1989).

Variation of Wood Properties in Balsam Poplar

According to Zobel and van Buijtenen (1989) variation of wood properties can be assessed at various levels:

First, there is variation among species, i.e., the highest level within a genus. Second, within-species variation can be subdivided into:

- geographic variation
- stand to stand variation
- among sites within stands
- variation among individual trees
- variation within individual trees.

Balsam poplar (*Populus balsamifera* L.) and black cottonwood (*Populus trichocarpa* Torr. and Gray) are the most widespread American poplars of the section *Tacamahaca*. Some botanists have had difficulty in categorizing black cottonwood and balsam poplar as separate species. Kellogg and Swan (1986) wrote, "It now appears to be generally recognized that they fit more closely to the criteria of subspecies within an individual species and that *Populus balsamifera* ssp. *trichocarpa* (Torr. and Gray) Brayshaw is correct nomenclature for black cottonwood." However, the old nomenclature is still more widely used. The balsam poplar is almost transcontinental from northern New England west to the Lake States and northwest across Canada to Alaska. The black cottonwood is western, growing from southern California north to Alaska.

Boreal America is a region of, so called, "clines", i.e., populations in which genetic variation is continuous or "clinal". In the species with wide continuous range there is an opportunity for abundant gene interchange and two segments of the range may not become very different genetically. For example, it has been suggested that very widespread aspen (*Populus tremuloides* Michx.) has a limited geographic variability throughout its range when compared to most species (Zobel and Talbert 1984). Balsam poplar is another typical example of a species with

continuous genetic variation pattern (Wright 1962). Genetic differentiation in balsam poplar is at least partially buffered by asexual regeneration. "Once established after migrating into an area, clones resulting from root suckering may persist for thousands of years, with clonal populations changing genetically only in response to strong, persistent selection pressures (Farmer *et al.* 1988)."

The most pronounced clinal trends vary in a north-south direction (cold-warm trends). This indicates the gradual change in a characteristic in conjunction with an environmental gradient. In the north temperate zone and boreal region, southern populations of the same species have a faster growth rate, as compared with northern.

For wood properties of some species, generally, the phenotypic variation pattern has been one of decreasing wood relative density (specific gravity) from south to north. Same as for relative density, cell length drops for trees grown at higher latitudes (Zobel and Talbert 1984). There are many exceptions to such general trends, and they are good reason for gathering data from actual sampling for each species, rather than relying on general trends observed. For example, phenotypic variation studies of aspen in Wisconsin and upper Michigan, by Einspahr and Benson (1967), confirmed existence of a south to north trend of decreasing relative density. On the other hand, they could not find such a pattern in fibre length variation.

In a range-wide phenotypic study of wood quality variation in balsam poplar grown in natural stands in Ontario Balatinecz and Peng (1984) found that:

- trees from northern locations showed generally slower growth rate than those from the south,
- relative density showed a slight negative correlation with growth rate,
- trees from the south had higher average fibre length than trees from the north, but with slightly smaller fibre diameter. Additionally, they noted that cell wall thickness showed little variation between locations.

Provenance tests

There are two types of studies involving wood properties:

- phenotypic, i.e., sampling trees from natural stands, and
- genetic, i.e., sampling trees grown in provenance tests.

"Provenance" is a synonym for origin or source of planting material. A "provenance test" is an experiment in which seeds (cuttings) are collected from a

number of widely scattered stands (usually natural), and the seedlings (propagules) are grown under similar conditions. Provenance testing is particularly necessary prior to introduction of an exotic, but is also desirable in native species. Genetic differences associated with the place of origin have often been several times as great as those among individual trees from the same stand. Natural selection has tended to produce natural populations that are well adapted to the conditions in which they evolved, but the adaptation has not been perfect. In many species local trees have not grown as well as trees from 50 to 500 km away (Wright 1976). A range-wide provenance test usually indicates the total range of genetic variation within a species and thus it gives a clue to the amount of improvement which may be expected from more intensive breeding work. We should be sure that we have the best provenance and the best clone before starting further crossing or plantation establishment. When grown in a common environment southern provenances of most species usually:

- grow faster,
- grow later and retain their leaves later in the fall,
- are less resistant to extreme winter cold (Wright 1976).

The pattern of genetic variation in wood properties, determined through provenance testing, has been different than phenotypic variation pattern. Zobel and van Buijtenen (1989) wrote, "The situation concerning wood properties of trees from plantations, as related to provenance, is very complicated and confusing and there are few evident clear-cut trends or relationships. Reports indicate that all types of wood property reactions related to provenance and environment have been reported for poplars."

Genetic Control - Inheritance of Wood Properties

To determine genetic variation in certain traits a test designed on statistical basis is necessary. Trees in the test plantation must be of known genetic origin and planted in a uniform environment. Genetic control is measured by subdividing the total variation in a characteristic into its components. The total phenotypic variance (σ^2_p) can be divided into two components: the genetic variance (σ^2_g) and environmental variance (σ^2_e) (Zobel and Talbert 1984).

In poplars it is possible to propagate individuals vegetatively. Thus, the simplest and most powerful way of determining genetic control is through clonal

tests. Since all ramets (vegetative propagules, replicates) of a clone have the identical genetic constitution, genetic and environmental variation can be clearly distinguished from each other. From the clonal test *broad sense heritability* (H^2) can be estimated by using the formula:

$$H^2 = \sigma^2_g / \sigma^2_p$$

Namkoong *et al.* (1988) stated that in this way, "... the full benefit of broad sense heritability is realized rather than only some portion of the narrow sense heritability. Furthermore, the tree breeder has the full control over the amount of genetic variance to be allowed into a forest planting."

In spite of this, to decide whether breeding is practical and to evaluate breeding alternatives, we need more precise data than those available now. Many reported heritabilities were from small experiments and often biased upward, because inadequate environmental sampling caused overestimation of the numerator and underestimation of the denominator (Namkoong *et al.* 1969). Also, very often investigators sampled a number of stems within each natural putative clone, and then used the ratio of variance among clones to total variance to estimate broad-sense heritability. In this case there is no true replication of a clone. Clone variation is confounded with site variation and other influences. The result is useful as a first approximation, but not genetically valid (Farmer 1990).

In general, the genetic experimental designs that provide efficient estimates of variance components can also provide estimates of their covariance (Namkoong 1981). In this case *genetic correlations* (r_g) among different traits can be computed. Genetic correlations indicate how we influence other traits by selection for one trait. Zobel and Talbert (1984) wrote, "... they play a role in determining the degree to which indirect selection, or selection for one trait in the hope of improving another trait, will be successful."

Analyses are similar to those for estimating components of variance in an analysis of variance (ANOVA), but instead of finding mean squares, mean cross products are computed in an analysis of covariance (ANCOVA). In such a way, it is possible to separate genetic and environmental components of covariance, and their effects.

Genetic correlations may be estimated as:

$$r_g = \frac{\hat{\sigma}_{cXY}}{\sqrt{\hat{\sigma}^2_{cY}}\ \sqrt{\hat{\sigma}^2_{cX}}}$$

r_g = genetic correlation
$\hat{\sigma}_{cXY}$ = clonal component of covariance for traits X and Y
$\hat{\sigma}^2_{cX}$ = clonal component of variance for trait X
$\hat{\sigma}^2_{cY}$ = clonal component of variance for trait Y

In addition, the very useful *coefficient of genetic prediction* (CGP) can be calculated. This coefficient is used to predict the response of trait Y to selecting for trait X (Fins *at al.* 1992).

$$CGP = \frac{\hat{\sigma}_{cXY}}{\sqrt{\hat{\sigma}^2_{pX}}\ \sqrt{\hat{\sigma}^2_{pY}}}$$

$\hat{\sigma}_{cXY}$ = clonal component of covariance for traits X and Y
$\hat{\sigma}^2_{pX}$ = phenotypic variance of trait X
$\hat{\sigma}^2_{pY}$ = phenotypic variance of trait Y

Relative Density of Balsam Poplar Wood

Relative density (specific gravity is the old term) is considered to be "by far the most important wood property" (Zobel and van Buijtenen 1989). The relationship between relative density and pulp yield, as well as other paper-making properties, is of great practical significance (Higgins *et al.* 1973, Panshin and de Zeeuw 1980, Zobel 1981, Zobel and Talbert 1984). For pulp and paper - making properties of aspen, van Buijtenen *et al.* (1962) found that both burst factor and tearing strength increase with increasing relative density. It is generally accepted that the optimum relative density for pulping, particle and waferboard production is around 0.400. Balsam poplar wood is desirable for waferboard for its low relative density, although, it can be difficult to waferize (Panning and Gertjejansen 1985). Also, it is well known that relative density plays a major role in the use of wood as an energy source. In addition to that, there is a

strong negative relationship between relative density and potential moisture content of wood (Farmer 1990). Because of these effects on wood quality and its high heritability, relative density is of the greatest importance for most tree improvement programs (Zobel and Talbert 1984).

Relative density is determined by different characteristics of wood anatomy, such as: amount of summerwood or latewood, cell size, and thickness of cell wall in cells of the same size. In hardwoods, relative density is affected not only by the cell wall dimension, but also by the relative amounts of ray and vessel elements (Zobel and Talbert 1984).

Poplars in general are low-density, fine textured, diffuse-porous hardwoods. Diffuse-porous means that vessels are more or less uniform in size and evenly distributed within a growth ring, as viewed in a cross section. Kennedy (1968) reported the tendency for fast-grown cottonwood to exhibit a semi-ring porous structure. This structure has a certain difference in vessel size between earlywood and latewood, i.e., vessels are more crowded in the early wood, decreasing gradually in size through the latewood. Panshin and de Zeeuw (1980) classified wood of balsam poplar as semi-ring- to diffuse-porous. Generally, in poplars vessels occupy approximately 20 to 33% of the cross section, and fibers 56 to 79% (Anon. 1958; MayerWegelin 1953). Percentage of fibre cells, their size, and thickness of their walls determine relative density (Farmer 1991, Kaiser and Boyce 1964, Scaramuzzi and Ferrari 1963). Mean values of relative density of some major North American poplars are given in *Table* 1.1.

Table 1.1. Relative density of some North American poplars

Species	Author	Relative density
Populus deltoides	Kennedy (1965)	0.352 (SD*=±0.038)
Populus deltoides	Farmer and Wilcox (1966a)	0.32-0.46 (tree to tree range)
Populus deltoides	Posey *et al.* (1969)	0.39 (increased 0.36-0.45 from E-W in Oklahoma)
Populus deltoides	Wood Handbook USDA (1987)	0.370
Populus tremuloides	Wilde and Paul (1959)	0.375 (range from 0.325-0.421)
Populus tremuloides	vanBuijtenen, Einspahr and Joranson (1959)	0.389 (range from 0.310-0.470 in northern Mich.)
Populus tremuloides	Kennedy (1965)	0.374 (SD= ± 0.024)
Populus tremuloides	Yanchuck *et al.* (1984)	0.32-0.40 (range of means for 15 putative clones in Alberta)
Populus tremuloides	Wood Handbook USDA (1987)	0.36
Populus trichocarpa	Markwardt and Wilson (1935)	0.32
Populus trichocarpa	Kennedy (1965)	0.295 (SD=± 0.027)
Populus trichocarpa	U.S. Dep. Agr., For. Ser. (1965)	0.31 (range 0.28-0.40)
Populus trichocarpa	Kellogg and Swan (1986)	0.338 (SD=±0.038)
Populus trichocarpa	Wood Handbook USDA (1987)	0.31
Populus balsamifera	Markwardt and Wilson (1935)	0.30

Table 1.1. continued

Species	Author	Relative density
Populus balsamifera	Clausen (1949)	0.319 (butt logs, near Aitkin, MN)
Populus balsamifera	Wallin (1954)	0.335 (Cloquet, MN butt logs 0.28-0.36, and top logs 0.30-0.41)
Populus balsamifera	Paul (1956)	0.301 (Vermont), 0.296 (coastal Alaska) 0.355 (inland Alaska)
Populus balsamifera	Irwin and Doyle (1961)	0.37 (Manitoba)
Populus balsamifera	Kennedy (1965)	0.372 (SD ± 0.032)
Populus balsamifera	Balatinecz and Peng (1984)	0.345 (average of 40 trees from different locations in Ontario)
Populus balsamifera	Kellogg and Swan (1986)	0.336 (SD=0.026) for ten trees: 0.338 in BC and 0.337 in Alberta
Populus balsamifera	Singh (1986)	0.387 (Northw. Terr. similar to aspen 0.388)
Populus balsamifera	Cyr and Laidler (1987)	0.37 (Alberta)
Populus balsamifera	Wood Handbook USDA (1987)	0.31
Populus balsamifera	Micko (1987)	0.293 (one mature-tree value, Alberta)
Populus balsamifera	Thomas (1987)	0.334 (Alberta)
Populus balsamifera	Pfaff (1988)	0.30 to 0.38 (range in Alberta)
Populus balsamifera	Kroll *et al.* (1992)	0.36 (0.34-0.39 rang of ten trees in MN.)
	(average of 16 means for *Populus balsamifera* is 0.336)	

* SD = standard deviation

Relative density - growth rate relationship

In some ring-porous hardwoods an approximately equal volume of vessels is produced each year regardless of the total growth during the year. This results in a higher proportion of heavier wood elements, fibres and hardwood tracheids, which causes a higher specific gravity of wood with wider rings. According to Zobel and Talbert (1984), in diffuse-porous hardwoods the number of vessels formed in an annual ring is closely related to the width of the ring, and radial growth rate has little direct effect on wood relative density. This appeared to be true in studies by Johnson (1942), Farmer and Wilcox (1966a), Guiher (1968), Farmer (1970b), Reddy and Jokela (1982), who could find no relationship between growth rate and relative density, in poplars.

On the other hand, Kennedy and Smith (1959), Paul (1956, 1963), Mutibarich (1967), Posey *et al.* (1969), Yanchuck *et al.* (1984), all found a negative correlation to be evident. Actually, all kinds of relationships have been reported for poplars (See *Table* 1.2.).

However, Kennedy (1968) noticed that some of the studies that could not reveal any relationship between growth rate and relative density dealt with only a narrow range of rapid growth rates. He concluded that, ..."effect of growth rate on specific gravity is not readily apparent unless a wide range of ring widths are available for study." Also all rings compared must be of the same age from the pith.

Table 1.2. Effect of growth rate on relative density in some North American poplars

Species	Author	Result
Populus spp.	Mutibarich (1967)	A slight negative correlation exists between growth rate and specific gravity of Euramerican poplars in Yugoslavia.
Populus spp. and hybrids	Paul (1956, 1963)	A negative linear relationship between growth rate and sp. gravity was found.
Populus spp. hybrids	Johnson (1942)	Correlations between growth rate (in terms of average annual increment in h,d or V) were not significant.

Table 1.2. continued

Species	Author	Result
Populus deltoides	Farmer and Wilcox (1966a)	Slight, non significant correlation (r_p=-0.20) was noted.
Populus deltoides	Farmer and Wilcox (1966b)	The genetic correlation of sp. gravity and diameter was (r_g=-0.07).
Populus deltoides	Farmer and Wilcox (1968)	Genetic correlatoins were (r_g=-0.32) on a silt loam and (r_g=-0.21) on a heavy clay were growth was poor.
Populus deltoides	Guiher (1968)	Rings per inch is not a good indication of specific gravity
Populus deltoides	Posey *et al* . (1969)	Specific gravity was negatively correlated (r_p=-0.49) with radial growth.
Populus deltoides	Farmer (1970a)	There was a slight positive genetic correlation (r_g=0.22).
Populus deltoides	Farmer (1970b)	There was essentially no phenotypic correlation (r_p=-0.08).
Populus deltoides	Reddy and Jokela (1982)	The phenotypic correlation was not statistically significant.
Populus deltoides	Olson *et al.* (1985)	A moderate negative genetic correlation was observed (r_g=-0.65)
Populus tremuloides	Wilde and Paul (1959)	For faster growing semi-mature aspen on soils with higher fertility sp. gravity was higher.
Populus tremuloides	Einspahr and Benson (1967)	There was no relationship between growth rate and specific gravity.
Populus tremuloides	Yanchuck *et al.* (1984)	The overall trend of a negative relationship was evident and it had a substantial genetic basis.
Populus trichocarpa	Kennedy and Smith (1959)	There was a modest negative relationship between growth and density.
Populus balsamifera	Balatinecz and Peng (1984)	Specific gravity showed a slight negative correlation with growth rate.
Populus balsamifera	Kroll *et al.* (1992)	There were no correlation between growth rate and SG.

Score: 8(-); 8(0); 2(+).

Most of the reports indicated a negative or insignificant influence of fast growth on relative density. Sometimes confusing results of the studies may be due to genetic influence. Therefore, growth rate may not be a reliable indicator of relative density of a genetically variable material (Guiher 1968, Kennedy 1968).

Variation and inheritance of wood relative density in poplars

Kennedy (1968) suggested that the possible deleterious influence of fast growth on wood density probably could be overcome by selection. Zobel and Talbert (1984) wrote, "Wood relative density is close to being the ideal characteristic for genetic manipulation in a breeding program. It combines a large tree to tree variability, strong heritabilty, low genotype by environment interaction, and its major effects on yield and wood quality." Farmer (1990) in his literature review on wood density - growth relationship in poplars concluded that broad sense heritability (H^2 - on ramet mean basis) was at least 0.50. That means that a relative density of 0.40 (an optimum for pulp and waferboard production) is quite achievable through clonal selection programs, and that it can be achieved without sacrificing growth rate. The heritability values for some North American poplars are given in *Table* 1.3.

Table 1.3. Inheritance of wood relative density in some North American poplars

Species	Author	Result
Populus deltoides	Farmer and Wilcox (1966b)	In a young half-sibling progeny test narrow sense heritability was h^2=0.62
Populus deltoides	Farmer and Wilcox (1968)	In one-year-old clones on two sites broad sense heritability was H^2 = 0.69 and H^2 = 0.70, respectively.
Populus deltoides	Farmer (1970a)	In three-year-old half-sibling progeny test narrow sense heritability was h^2=0.78
Populus deltoides	Farmer (1970b)	In one-year-old pot test of clones under stress H^2 = 0.76, and H^2 = 0.63 for control.

Table 1.3. continued

Species	Author	Result
Populus deltoides	Herpka (1979)	In a three-year test of 117 clones $H^2 = \underline{0.86}$
Populus tremuloides	van Buijtenen *et al.* (1959)	Broad sense heritability within and among putative clones was esitmated to be $H^2 = \underline{0.17}$
Populus tremuloides	van Buijtenen *et al.* (1962)	A subsequent test of the previous sample gave estimate of $H^2 = \underline{0.43}$
Populus tremuloides	Einspahr *et al.* (1963)	Triploid clones in northern Michigan $H^2 = \underline{0.38}$ based on whole tree, and $H^2 = \underline{0.26}$ based on increment cores.
Populus tremuloides	Einspahr *et al.* (1967)	In a replicated test narrow sense heritability was estimated $h^2 = \underline{0.42}$
Populus tremuloides	Yanchuck *et al.* (1984)	For 15 putative clones, and 5-9 trees per clone estimate of $H^2 = \underline{0.35}$
Populus trichocarpa	Reck (1974)	For trees grown in West Germany $H^2 = \underline{0.56}$

Moisture Content of Balsam Poplar Wood

Standing poplar trees have a high moisture content. Kennedy (1968) cited two results that showed a decrease in average moisture content of aspen from winter (130% and 113%) to the summer months (65% and 80%) (Gibbs1935; Bendtsen and Rees 1962). This is not in agreement with the conclusion of Panshin and de Zeeuw (1980): "The total water content of the wood of a tree does not appear to fluctuate widely at different times during the year, although the distribution of the water within the stem may change from month to month, or from one season to another. In hardwoods there is commonly no such differences in moisture content between sapwood and heartwood, or with location in the stem as in conifers." Zobel and van Buijtenen (1989) wrote that, "Moisture content varies greatly from juvenile to mature wood and with height in the tree, and it is usually much higher in juvenile wood zone." Nevertheless, Yang (1990) used

variation in moisture content to determine boundary between heartwood and sapwood of aspen. A sharp decrease in moisture content dictated the demarcation between heartwood and sapwood.

Balsam poplar wood has also "wet heart" and sometimes "wet pockets", i.e., small volumes of exceedingly high moisture content. Wallin (1954) partitioned moisture content of aspen in three categories: sapwood, heartwood, and wetwood, with moisture content of 77%; 216%, and 250% respectively. He described "wetwood" as darkened in appearance and in watersoaked condition. Wetwood is associated with mixed populations of anaerobic bacteria (Kennedy 1974), however, the role of bacteria in formation of wetwood has not been ascertained. Wetwood is prevalent in balsam poplar (Ward and Pong 1980), although, it has been recorded in young aspen trees, as well (Hartley *et al.* 1961).

Moisture content is of a key importance in the drying process, as well as when the timber is bought or sold by green weight, or transported by weight. Balsam poplar is also difficult to thaw, presumably because of its high moisture content, and waferizing of frozen wood results in low quality wafers (Panning and Gertjejansen 1985). The variability in moisture content of wood might influence the processing parameters, flake formation uniformity, and thus surface features of wafers.

Micko (1987) examined several wood properties of aspen and balsam poplar in Alberta, and found that the most significant variation between two species was in the moisture content. In the middle of a radial section (ring section 30 -60 years) balsam poplar had significantly higher moisture content than aspen (117-136% vs. 67-73%). Moisture content of some major North American poplars is given in *Table* 1.4.

Moisture content was found to be strongly inherited in eucalipt species (Otegbeye and Kellison 1980), but no data are available for balsam poplar.

Table 1.4. Moisture content of some North American poplar wood

Species	Author	Moisture content
Populus tremuloides	Gibbs (1935)	130% average-winter and 65% - summer
Populus tremuloides	Bendtsen and Rees (1962)	113% average winter; 80%- summer

Table 1.4. continued

Species	Author	Moisture content
Populus trichocarpa	Kellogg and Swan (1986)	160% - average (SD*= ±23)
Populus balsamifera	Wallin (1954)	77% - sapwood 216% - heartwood, 250% - wetwood
Populus balsamifera	Balatinecz and Peng (1984)	150% in heartwood 80% in sapwood
Populus balsamifera	Panning and Gertjejansen (1985)	161% - average
Populus balsamifera	Kellogg and Swan (1986)	121% - average (SD=±17.5)
Populus balsamifera	Kroll *et al.* (1992)	140% (range 121-152% with a wet pocket 211%)

* SD = standard deviation

Cell Length in Balsam Poplar Wood

Cell length of hardwoods has been given less importance in tree improvement programs, because even a 10% gain would not mean much for paper characteristics (Zobel and van Buijtenen 1989). Accepted threshold values of pulp fibre length are 2 mm for tearing resistance, and 3 mm for bursting and tensile resistance, which is much above the cell length of balsam poplar or aspen. However, the use of aspen and balsam poplar for chemical pulping is increasing. Small vessel elements enhance smoothness and opacity, making poplars good species for the production of fine printing paper (Peterson and Peterson 1992). Even small differences in cell length and relative cell dimensions have a certain influence on the quality of pulp and paper products, and on solid products. For poplars, it is directly related to pulp strength, particularly burst and tear (van Buijtenen *et al.* 1962, Kennedy 1968). Average fibre and vessel element length of some North American poplars are given in *Tables* 1.5a. and 1.5b.

Table 1.5a. Fibre length of some North American poplars

Species	Author	Fibre length mm
Populus deltoides	Posey *et al.* (1969)	1.07 (range 0.94-1.28 in rings 6-7)
Populus tremuloides	Einspahr and Benson (1967)	0.895 (range 0.984-0.724) for trees 23-44 years old
Populus tremuloides	Yanchuck *et al.* (1984)	0.97-0.67 range 36 year-old trees
Populus tremuloides	Micko (1987)	0.98 (range 0.4-1.9) for a 119 year-old tree
Populus trichocarpa	Kennedy (1957)	0.95 -slow grown 1.21 -fast grown (10th ring)
Populus trichocarpa	Kellogg and Swan (1986)	1.237 (SD*=0.265) for mature trees
Populus balsamifera	Balatinecz and Peng (1984)	0.6-1.6 range for 10 mature trees
Populus balsamifera	Kellogg and Swan (1986)	1.032 (SD=±0.235) for mature trees
Populus balsamifera	Micko (1987)	1.07 (range 0.73-1.3) for a 119 year-old tree

Table 1.5b. Vessel element length of some North American poplars

Species	Author	Vessel elements mm
Populus tremuloides	Micko (1987)	0.71 (range 0.5-0.83) for a 119 year-old tree
Populus tremuloides	Thomas (1987)	0.50
Populus tremuloides	Panshin and de Zeeuw (1980)	0.67 (SD =± 0.18) and 0.58 (SD=±0.09)
Populus balsamifera	Micko (1987)	0.61 (range 0.44-0.82) for a 114 year-old tree

* SD = standard deviation

Cell length - growth rate relationship

Fiber length in poplars shows an unusual pattern in which faster growing trees have longer fibres (Kennedy 1957, Einspahr and Benson 1967). A usual relationship would be that hardwood tracheids and fibres are shorter in faster growing trees (Zobel and van Buijtenen 1989). This has been explained by Bannan (1967) through the dependence of cell length to the period of time cambial initials exist, before anticlinal division produce new cells. When growth is fast, the initials divide before they have a chance to reach their potential length. The length of cambial initials is of primary importance in controlling tracheid length in conifers. On the other hand, mature fibres of some hardwoods are four to five times longer than their cambial initial's (Panshin and de Zeeuw 1980). High growth rate causes shortening of the initials, but the subsequent greater elongation can produce longer fibres (Kennedy 1957).

Vessel element length is dictated by fusiform cambial initial length, and intrusive growth (subsequent elongation which occur during maturation of cells), is very little in the case of vessel elements (Carlquist 1988).

Effect of growth rate on cell length in some North American poplars is presented in *Table* 1.6.

Table 1.6. Effect of growth rate on cell length in some North American poplars

Species	Author	Result
Populus sp.	Liese and Ammer (1958)	Fiber length and growth rate were inversely correlated within any one ring.
Populus deltoides	Johnson (1942)	Fibers in fast growth annual rings were longer on the average than those in the slow growth rings. (Age from the pith not considered!)
Populus deltoides	Boyce and Kaeiser (1961)	Differences in tree diameter for rings of the same age accounted for only 3% of the variation in fibre length.
Populus deltoides	Posey *et al.* (1969)	Radial growth and fibre length were positively correlated r=0.50 (significant at 0.05% level of probability)
Populus tremuloides	Brown and Valentine (1963)	No influence of growth rate in control -ling fiber length.
Populus tremuloides	Yanchuck (1984)	Overall correlation was +0.311 (significant at 0.01% level), and genetic correlation was +0.577.
Populus trichocarpa	Kennedy (1957)	Fibre length was found to vary significantly with growth rate where faster growing trees had longer fibers
Populus trichocarpa	Kennedy and Smith (1959)	Fibre length was found to be positively correlated with growth rate.
Populus trichocarpa	Einspahr and Benson (1967)	Fibre length was significantly correlated with growth rate, and r=+0.336

Score: 1(-); 6(+); 2(0).

Variation and inheritance of cell length in poplars

A moderate to strong genetic influence on fibre length has been observed in poplars . Differences in fibre length among clones of the same species have been noted in many experiments (Kennedy 1968). Also, an exceptionally large increase in fibre length can be obtained through polyploidy (van Buijtenen *et al.* 1963, Einspahr *et al.* 1963). The results of some experiments with North American poplars are presented in *Table* 1.7.

Table 1.7. Inheritance of cell length in some North American Poplars

Species	Author	Result
Populus deltoides	Gabriel (1956)	Statistically significant within species differences were found among clones.
Populus deltoides	Farmer and Wilcox (1968)	In one-year-old clones on two sites broad sense heritability was $H^2 = \underline{0.36}$
Populus deltoides	Posey *et al.* (1969)	Strong clonal differences in fiber length occurred.
Populus tremuloides	van Buijtenen *et al.* (1963)	Increase in fiber length through polyploidy was 21-26%
Populus remuloides	Einspahr *et al.* (1963)	There was broad sense heritability of $H^2=\underline{0.86}$ for ring 30, and $\underline{0.50}$ on average in polyploids.
Populus tremuloides	Einspahr *et al.* (1967)	Fiber length was under moderate genetic control.
Populus trichocarpa	Gabriel (1956)	Statistically significant within species differences were found among clones.
Populus trichocarpa	Reck (1974)	For trees grown in West Germany $H^2 = \underline{0.71}$ was found for cell length.

The above values of broad sense heritability (gross heritability) include both, non-additive genetic component and additive genetic variance. Expected gains from breeding can be calculated by using those values.

Correlations among the Traits

The association that can be directly observed is the correlation of phenotypic values, i.e., measurements taken on different individuals. In genetic studies it is necessary to distinguish two causes of correlation between characteristics: genetic and environmental. Falconer (1981) wrote that correlated characteristics are of interest for two main reasons. First, genetic correlations can be caused by pleitropic action of genes (gene action affecting more than one characteristic in the phenotype). Pleitropy is a common property of major genes, and its effects should be considered in genetic studies of quantitative traits. Secondly, it is important to know how the improvement of one characteristic will affect other characteristics.

Some environmental causes of correlation may tend to cause a positive correlation, others a negative one. A large difference between genetic and environmental correlations, and particularly a difference in sign, shows that genetic and environmental sources of variation affect the characteristics through different physiological mechanisms. Considering the relation between heritability and correlation, Falconer (1981) concluded that if both characteristics have low heritability, then the phenotypic correlation is determined mostly by the environmental correlation; if they have high heritability, then the genetic correlation is more important.

Many experiments have shown significant phenotypic and also genetic correlations between wood and growth characteristics in poplars (see *Tables* 1.2. and 1.6.). Correlations among wood characteristics themselves are less often examined. Moisture content and relative density are considered to be negatively correlated (Farmer 1990). Olson *et al.* (1985) found highly significant phenotypic correlations, and also high genetic correlations between wood relative density and alpha-, and holo-cellulose content. Carlquist (1988) generalized that vessel element length always parallels fibre length.

CHAPTER 2

METHODS AND MATERIALS

Test Material

In 1982 and 1983 balsam poplar populations were sampled on a latitudinal transect that crosses the range of the species between longitudes 89° and 91° W. Three general locations used for this provenance study were: Rhinelander, northern Wisconsin (45°-46° N); Thunder Bay, Ontario (48°-49° N); and Pickle Lake, Ontario (50°-51° N) (*Figure* 2.1.). The sampled area in northern Wisconsin belongs to the Great Lakes - St. Lawrence forest region; Pickle Lake is in the boreal forest region; Thunder Bay is in the transition zone between these two regions. The average growing season temperature decreases from south to north. The number of degree-days ranges from 1400 in northern Wisconsin to about 1100 at Pickle Lake. (Growing season is represented by days with mean temperature above 5.5°C. The number of degree-days is the number of degrees accumulated for all days of the growing season.) There are approximately 100 frost free days in northern Wisconsin, 90 in Thunder Bay, and 80 in Pickle Lake (National Atlas of Canada 1974).

In each of these three locations cuttings were taken from upper lateral branches of 50 young dormant trees (ortets). Ortets were sampled randomly, but, at least 1 kilometre apart, to avoid the possibility of sampling more than one tree from a single naturally occurring clone. Cuttings were rooted in the greenhouse and transplanted to a nursery where several ramets (replications) of the sampled clones were grown for one season under the same environmental conditions.

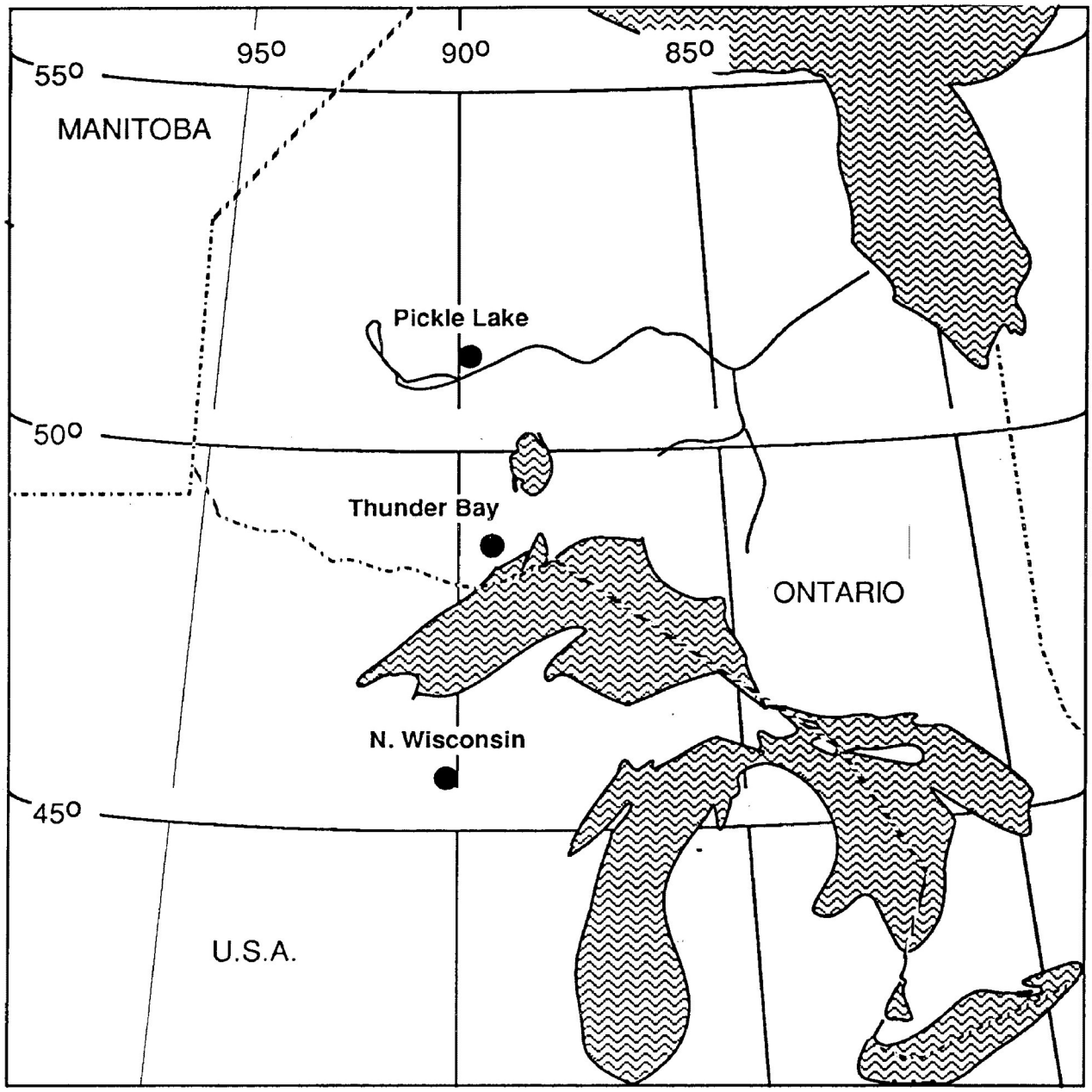

Figure 2.1. Three provenances of balsam poplar clones (●) used in the experiment.

In the spring of 1984 these primary ramets were used for secondary cloning (taking of cuttings). Cuttings were rooted in 750 ml Spencer - Le Maire containers filled with peat vermiculite mix. In June 1984 this material was used to establish a long-term clonal test in the field (Test I), near Lakehead University, Thunder Bay.

Soil was imperfectly drained, 20 - 30 cm deep loam to sandy loam, underlain by sand (Farmer 1993). Square provenance plots were randomly located within each block (replication). Clone ramets were planted randomly within provenance plots. Thus, the field test had a nested (or hierarchical) treatment-structure, and a variation of a randomized block design-structure.

In August 1986 additional replications of the design above were planted on an adjacent upland site, with uniform, deep, and well drained loam (Test II).

These two tests were grown for 10 (Test I) and 8 (Test II) years respectively. They were used for a number of different genetic and physiological experiments. In the spring of 1994 randomly chosen clones within each provenance were harvested for the investigation of genetic differences in wood properties.

Sampling for wood properties

When genetic variation is examined, wood samples from trees of different genetic origin are compared. At the same time, there are several other sources of variation in wood properties, which have to be eliminated or minimized, in order to obtain comparable samples.

Tree to tree variation. An exact determination of the wood properties of a species, or race, must take into account the magnitude of variability that is present. Usually, a minimum of 30 trees should be sampled before a good average value can be obtained. The results of limited sampling (only one or two trees) are often completely misleading. The chosen trees might be on the extremes of the variation. Therefore, tree to tree variation must always be kept in mind (Zobel and Talbert 1984). In this experiment, 30 clones in each provenance were sampled, and each clone was replicated in 4 blocks. This gave 120 trees per provenance.

Variation from the base to the top of the tree. A simple way of estimating whole tree values is to relate breast height to total tree values. These two values were found to be highly correlated (Farmer and Wilcox 1966a, Zobel and van Buijtenen 1989). To avoid this kind of within tree variation, wood samples (discs) for this experiment were taken at the same point in axial direction within each sample tree, i.e., at the base approximately 30 cm above the ground.

Variation from the pith to the bark. Generally, wood properties are found to vary considerably along the radius of the tree. The rule that *only wood of the same age can be compared* was obeyed. All wood samples were taken at the same age in radial direction. The rings sampled were the 5th, 6th, and 7th (*Figure* 2.2.). By sampling these three rings, it was possible to compare 10 year-old trees from Test I with 8 year-old trees from Test II. All wood samples were from the juvenile wood zone. (For the purpose of illustration, radial variation within one experimental tree was examined in a small independent study. Patterns of radial variation in growth rate, relative density, moisture content, cell length, and microfibril angle are presented in the Appendix 1.)

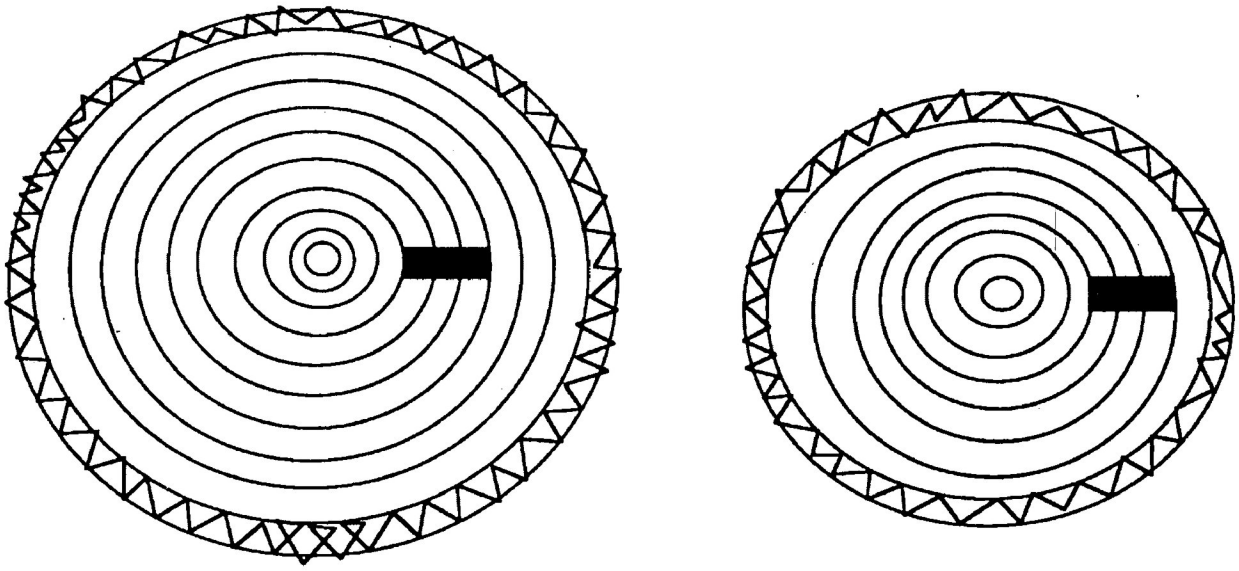

Figure 2.2. Three rings (5th, 6th, and 7th) sampled from 10 year - old and from 8 year - old trees.

Variation within a single growth ring. The properties of earlywood and latewood have been found to be significantly different in poplars, although the species can be classified as diffuse porous (Johnson 1942, Liese and Ammer 1958, Panshin and de Zeeuw 1980). Only the early wood portion of 7th growth ring was used for determination of fibre and vessel element length in this study.

Compass direction is sometimes considered to be of minor importance for diffuse porous woods (Yanchuck *et al.*1983); however, at high latitudes it is good

to have the control over this within - tree source of variation. Rings along the southern radius of each disc were sampled for the experiment.

Effect of tension wood. Tension wood, the form of reaction wood that occurs in hardwoods, is characterized by the formation of a gelatinous layer in the cell wall. The gelatinous layer is made of pure cellulose. Generally, in tension wood vessels are fewer and smaller (Zobel and van Buijtenen 1989), and relative density is higher (Lassen 1959, Kaiser and Boyce 1964). To avoid this effect, sample discs were taken only from straight portions of each tree stem. In spite of this measure, hairy radial surface occurred when sample strips were cut through the middle of the discs. This is the well known characteristic of tension wood. In balsam poplar tension wood is present to such an extent that it is practically impossible to avoid (Kroll *et al.* 1992).

Extractives have a major influence on wood properties, and certainly affect relative density of the wood (Panshin and de Zeeuw 1980). In spite of this, in studies with young trees, such as this study, extractive removal is not done. Values of relative density might be higher, but all values would be affected by approximately the same amount (Zobel and van Buijtenen 1989). It is assumed that comparable values can be obtained with unextracted wood.

Measurements in the Field

Height

Height of each tree was measured after harvesting. Measurements were taken from the root collar to the tree top, by using a metal measuring tape. Numbers were rounded to the closest centimetre. Tree height values were divided by tree age in order to obtain the mean annual height growth rate (HGR).

Diameter and circumference

Diameter and circumference were measured on each sample disc. Discs were cut at the same point in longitudinal direction within each sample tree (at the base of the tree, approximately 30 cm above the ground). Diameters were measured in the south - north direction, by using a ruler. Circumference was measured by using a metal measuring tape. Numbers were rounded to the closest millimetre. These values were divided by the age of the trees in order to obtain variables: mean annual diameter growth rate (DGR), and mean annual circumference growth rate (CGR).

Laboratory Studies

Radial growth rate

Mean annual radial growth rate (RGR) was defined as the average width (mm) of growth rings. Ring width could be determined by using a digital micrometer. After the cross-sections of the strips were smoothed by fine sand paper, water was applied to the surface in order to enhance the contrast of the growth rings. Yang (1987) wrote: "In diffuse porous species, poor contrast of the growth ring can be traced to the anatomical structure of the earlywood and latewood zones. The uniform size of the vessel element across most parts of the growth ring prohibits the contrast between two growth rings. The latewood zone is too narrow to stand out in contrast... A higher contrast image than that seen by the human eye can be obtained by using a photocopy machine." The measurement of ring width started from the pith outwards to the cambium. Average width of the 5^{th}, 6^{th}, and 7^{th} rings was taken to represent radial growth rate (RGR), and it was used for finding the correlation with relative density (RD) of these three rings. Cell length was determined only for the 7^{th} growth ring, and it was correlated to radial growth rate in 7^{th} year (RGR7). Accuracy of growth rate measurement, by using a digital micrometer, was around $\pm$ 0.01 mm.

Relative density

Relative density (RD) was determined by maximum moisture content method (Smith 1954):

$$RD = \frac{1}{\frac{Wmax - Wo}{Wo} + \frac{1}{1.53}}$$

RD - refers to basic relative density, determined on a green volume basis ($Wo / Vg * D_{H_2O}$)

Wmax - maximum weight, i.e., weight of wood with maximum moisture content

Wo - oven dry weight

1.53 - relative density of wood substance

V_g - green volume

D_{H_2O} - density of H_2O

After measuring ring width, the 5^{th}, 6^{th}, and 7^{th} ring together were cut from the cross - section strips . In order to determine the maximum weight (Wmax), these three-ring pieces were put into distilled water, and placed in a desiccator. To ensure that the wood reached the point of maximum moisture content, they had been left submerged until three subsequent measurements of weight were the same. It took 2 to 3 weeks to reach the maximum moisture content after complete submersion of the specimen. An analytical scale, with precision of $\pm$ 0.001g, was used for weight measurements. Just before weighing each piece, excess water was blotted with a damp paper towel to remove surface water but not water within the wood, as suggested by Gonzales and Kellogg (1978). (When some wood pieces were replaced in the water, surface water blotted again, and weighing repeated, agreement between two weights was within 0.5%.)

A constant maximum weight (Wmax) was obtained, and the three-ring sections were dried in the oven for 48 hours, at 105 $\pm$ 3 ^{o}C, to obtain the oven-dry weight (Wo). The ratio of maximum to oven-dry weight was calculated to two decimal places, and the appropriate value of relative density was found in Fogg's (1967) table (Table made by using the above formula).

Moisture content

After cutting in the field, specimen discs were placed in plastic bags, brought to the laboratory, and processed immediately. Moisture content (MC%) of the wood was expressed as a percentage of the oven dry weight of the wood :

$$M.C.\% = \frac{Wg - Wo}{Wo} \times 100$$

Wg - weight of wood with moisture
Wo - ovendry weight of wood

Cell length

After moisture content and relative density determination, the 7th - ring piece was separated, and further split into earlywood and latewood splints. Only earlywood cells were used in the study. Individual earlywood splints were macerated by Franklin's method (1945). The number of cells to be measured for each growth ring (n) was determined through preliminary sampling using Freese's (1986) formula :

$$n = \left[\frac{t * CV\%}{SE\%}\right]^2$$

where:

t - Student's t-value at the probability level $\alpha/2=0.01$,

CV% - coefficient of variation of preliminary sample, i.e., percent ratio of the standard deviation to the mean of preliminary sample,

SE% - allowable error set at 10%

The final number of measurements (n) was obtained through a series of iterations, by changing degrees of freedom for the t-value, without knowing the actual optimum sample size (n). Degrees of freedom were changed from those used as a first guessed value (n_0-1) in the preliminary sample of n_0 cells, to degrees of freedom n_1-1; n_2-1;...; and so on until two subsequent numbers for sample size (n) became equal. Value n_1 was obtained when Student's t was entered into the above formula with n_0-1 degrees of freedom; value n_2 was obtained when t had n_1-1 degrees of freedom etc. (CV%, SE%, and $\alpha/2$ level of probability were held constant.)

For both, fibre length and vessel element length sample size was rounded to 25 measurements per each growth ring. Van den Oever *et al.* (1981) also showed that "... standard deviation decreases very little if one bases a mean on more than 25 measurements." The image of a cell, magnified 100 times, was projected through a microscope onto a HIPAD digitizer connected to an Apple microcomputer (*Figure* 2.3.). Vessel elements were measured from tip to tip, so that the "tails" were included, even though some vessel elements had them while others lacked them in a single sample. This method is used by most research workers (Chalk and Chattaway 1934).

Figure 2.3. One fiber and one vessel element typical for balsam poplar wood

Data Analyses

Univariate analyses of variance

For the variables: mean annual height growth rate (HGR), mean annual diameter growth rate (DGR), mean annual circumference growth rate (CGR), average radial growth rate in fifth, sixth, and seventh year (RGR), growth rate in seventh year (RGR7), relative density (RD), fibre length (FL), and vessel element length (VEL) univariate analyses of variance (ANOVA) design and expected mean squares (EMS) are given in *Table* 2.1.

The design was nested, with a set of provenance plots randomized within blocks, and individual clones randomized within provenance plots. Such a design was considered to be a variation of randomized block design. The design reduced inter-provenance competition, which minimized within block variability for comparison within the set of provenances. Comparisons among provenances were imprecise, however, as main, provenance, plots were large, and the test had fewer degrees of freedom for error. Still, the analysis was appropriate since the clonal variation within provenances was of a greater interest (Fins *et al.* 1992).

At the first level of the design 3 provenances were replicated in 4 blocks. At the second level, because clones were nested within provenances (the first level factor), each provenance plot represented a block only for the clones from that particular provenance. There were 12 provenance plots, and they were divided among 3 provenances to give 4 plots (second level blocks) in which 30 clones from a single provenance were replicated (*Figure* 2.4.). Three independent ANOVA -s were performed at the second level of the test. One ANOVA was performed for clones within each of the three provenances.

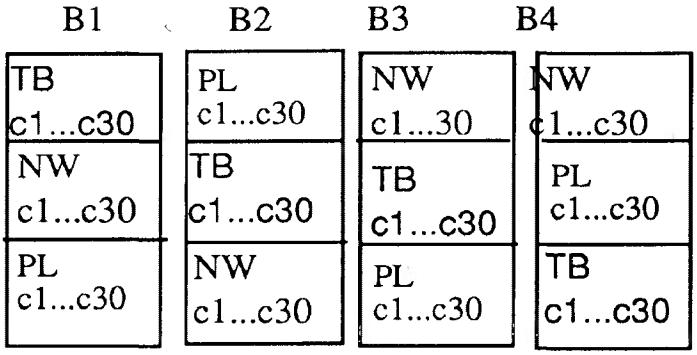

Figure 2.4. Schematic illustration of the provenance test layout (TB-Thunder Bay; PL-Pickle Lake; NW-North Wisconsin; B - block; P -provenance plot; c - clones)

The general linear model for the test was as follows:

$$Y_{ijkl} = \mu + B_i + \delta'(i) + P_j + BP_{ij} + \delta''(ij) + C(j)k + BC_{i(j)k} + \varepsilon(ijk)l$$
$$i = 1, 2, 3, 4;\ j = 1, 2, 3;\ k = 1, 2, ..., 30;\ l = 1.$$

where:

Y_{ijkl} = the value of any of 8 (above) variables observed on l^{th} tree from k^{th} clone within j^{th} provenance and i^{th} block

μ = the overall mean

B_i = the fixed effect of i^{th} block

$\delta'(i)$ = the (random) effect of the randomization of provenance plots within the i^{th} block (restriction error l)

P_j = the fixed effect of j^{th} provenance

BP_{ij} = the interaction effect of the i^{th} block with the j^{th} provenance

$\delta''(ij)$ = the (random) effect of the randomization of clones within the j^{th} provenance plot in the i^{th} block (restriction error 2)

$C(j)k$ = the random effect of the k^{th} clone within the j^{th} provenance

$BC_{i(j)k}$ = the interaction effect of the i^{th} block with the k^{th} clone

$\varepsilon(ijk)l$ = the random effect of the single tree from k^{th} clone within j^{th} provenance and i^{th} block. Assumed to be identically and independently distributed with $N(0,\sigma^2)$

Table 2.1. Analysis of variance format and expected mean squares for variables HGR, DGR, CGR, RGR, RGR7, RD, FL, and VEL.

Source of variation	df	EMS
Block (B)	3	$\sigma^2 + 90\emptyset_B$
Provenance (P)	2	$\sigma^2 + 120\emptyset_P$
Block X Prov.(BP)(error I)	6	$\sigma^2 + (30\sigma^2_{BP}$ - assumed to be 0)
* This stage of ANOVA was repeated 3 times, once for each provenance .		
Clone/Provenance (C)	29(*3)	$\sigma^2 + 4\sigma^2_C$
Block X Clone (BC)(error II)	87(*3)	$\sigma^2 + (\sigma^2_{BC}$ - assumed to be 0)
Within (ε)	0	σ^2
Total	359	

Only the variable moisture content (MC%) was analyzed in a smaller design with only two blocks, two provenances (Northern Wisconsin and Thunder Bay) and 15 clones per provenance. The design is outlined in *Table* 2.2. The general linear model was:

$$Y_{ijkl} = \mu + B_i + \delta'(i) + P_j + BP_{ij} + \delta''(ij) + C(j)k + BC_{i(j)k} + \varepsilon(ijk)l$$
$$i = 1, 2;\ j = 1, 2;\ k = 1, 2, ..., 15;\ l = 1.$$

where:

Y_{ijkl} = the value of variable moisture content observed on l^{th} tree from k^{th} clone within j^{th} provenance and i^{th} block

μ = the overall mean

B_i = the fixed effect of i^{th} block

$\delta'(i)$ = the (random) effect of the randomization of provenance plots within the i^{th} block (restriction error 1)

P_j = the fixed effect of j^{th} provenance

BP_{ij} = the interaction effect of the i^{th} block with the j^{th} provenance

$\delta''(ij)$ = the (random) effect of the randomization of clones within the j^{th} provenance plot in the i^{th} block (restriction error 2)

$C(j)k$ = the random effect of the k^{th} clone within the j^{th} provenance

$BC_{i(j)k}$ = the interaction effect of the i^{th} block with the k^{th} clone

$\varepsilon(ijk)l$ = the random effect of the single tree from k^{th} clone within j^{th} provenance and i^{th} block. Assumed to be identically and independently distributed with $N(0,\sigma^2)$

Table 2.2. Analysis of variance format and expected mean squares for the variable moisture content (MC%)

Source of variation	df	EMS
Block (B)	1	$\sigma^2 + 30\emptyset_B$
Provenance (P)	1	$\sigma^2 + 30\emptyset_P$
Block X Prov.(BP)(error I)	1	$\sigma^2 + (15\sigma^2_{BP}$ - assumed to be 0)
* This stage of ANOVA was repeated 2 times, once for each provenance .		
Clone /Provenance (C)	14(*2)	$\sigma^2 + 2\sigma^2_C$
Block X Clone (BC)(error II)	14(*2)	$\sigma^2 + (\sigma^2_{BC}$ - assumed 0)
Within (ε)	0	σ^2
Total	59	

Multiple comparisons of provenance means at the first level of analysis were done by using Fisher's LSD method. A significant F-test at 5% level of probability was required for the procedure to be used.

Multivariate analysis

Since the measured variables were correlated among themselves, the use of multivariate analysis was appropriate for comparison of the provenance means. One of the assumptions for multivariate analysis of variance (MANOVA) is that the variance-covariance matrices over cells are equal. In order to meet this requirement some of the variables had to be eliminated. On the basis of redundancy and linear dependence, only the variable radial growth rate (RGR) was chosen to represent five highly correlated growth characteristics. Also, vessel element length (VEL) was eliminated because it was highly correlated with fibre length (FL). The variables left in the analysis were radial growth rate (RGR), relative density (RD), and fibre length (FL). Bartlett's test of homgeneity of variance-covariance matrices still could not be satisfied. However, the multivariate analysis was performed assuming some robustness of the procedure to handle such discrepancies (Chatfield and Collins 1980).

Canonical variate analysis. Regardless of the fact that there were three variable means for each provenance, they could be defined by a plane, i.e., in a two dimensional space. Therefore, only two canonical variates were constructed. They explained most of the variation present in the original variables. Chatfield and Collins (1980) explained the process of deriving vectors of linear compounds, which , when multiplied by the vectors of provenance means, gave the coordinates of canonical means. The X axis in the plot represented the first canonical variate. The 95% confidence limit was drawn as a circle around the canonical mean of each provenance. Since canonical variates were normalized so that their variance was equal 1, the standard deviation of the means was simply $1/\sqrt{n}$, where n was the number of observations. Therefore, the radius of the circles was $k/\sqrt{n}$; where k was equal to 2, in order to represent 2 standard deviations which gave 95% confidence limits (k = 1 would have given 68% confidence limits).

Heritabilities

The broad sense (gross) heritability (H^2) was estimated for each variable, and within each provenance. It was estimated as a ratio of total genetic variation (σ^2_g) to the phenotypic variation (σ^2_p). In this case the total genetic variance was

represented by the clonal variance component (σ^2_c) (from ANOVA). The phenotypic variance was represented by the sum of the genetic and environmental variance, i.e., the clonal variance component (σ^2_c) plus the error variance component (σ^2):

$$H^2 = \frac{\sigma^2_g}{\sigma^2_p} = \frac{\sigma^2_c}{\sigma^2_c + \sigma^2}$$

In variance component analysis blocks are "nuisance" factors and they are omitted from the phenotypic variance, i.e., the denominator of heritability (White and Hodge 1989).

The clone and error components of variance were estimated from clone mean squares (MS_{clone}) and error mean squares ($MS_{error\ II}$) as follows:

$$\hat{\sigma}^2_c = \frac{MS_{clone} - MS_{errorII}}{4^*}$$

$$\hat{\sigma}^2_e = MS_{errorII}$$

(* denominator was equal to 2 for the variable moisture content MC%)

The (H^2) was estimated on an individual tree basis, i.e., based on measurements taken on individual trees. This is the most common way of estimating heritability (Fins *at al.* 1992, Falconer 1981, Namkoong *at al.* 1988, Becker 1985). The standard error of broad-sense heritability was obtained from the formula given by Falconer (1981):

$$S_{(H2)} = \sqrt{\frac{2[1+(n-1)H^2]^2 * (1-H^2)^2}{n(n-1)*(N-1)}}$$

where:

n - number of individuals per clone

N - number of clones

Genetic, environmental, and phenotypic correlations

"Overall" correlation included block source of variation, which is usually considered a "nuisance" and omitted from the phenotypic covariance. This correlation (or standardized covariance), was obtained by dividing the covariance of two characteristics by the product of their standard deviations:

$$r_{XY} = \frac{\sigma_{XY}}{\sqrt{\sigma 2_X}\ \sqrt{\sigma 2_Y}}$$

Genetic, environmental, and phenotypic correlations between the traits were obtained by methods similar to those used to estimate genetic variances and heritabilities. Expected mean cross-products (EMCP) were tabulated in an analysis of covariance (ANCOVA) table in the same manner as EMS were tabulated in an (ANOVA) table. The clone and error components of covariance were estimated from clone mean cross-products (MCP_{clone}) and error mean cross-products ($MCP_{error\ II}$),i.e., mean cross-products of block by clone interaction. The same coefficients for estimating variance components and components of covariance could be used in the both analyses (Becker 1985).

$$\hat{\sigma}_{cXY} = \frac{MCP_{clone} - MCP_{errorII}}{4^*}$$

$$\hat{\sigma}_{eXY} = MCP_{errorII}$$

(* denominator was equal to 2 for the variable moisture content MC%)

Clonal components of covariance and clonal variance components were used to estimate genetic correlations (r_g) (Becker 1985), by using the formula :

$$r_g = \frac{\hat{\sigma}_{cXY}}{\sqrt{\hat{\sigma}^2_{cX}}\ \sqrt{\hat{\sigma}^2_{cY}}}$$

where:

r_g = genetic correlation
$\hat{\sigma}_{cXY}$ = clonal component of covariance for traits X and Y
$\hat{\sigma}^2_{cX}$ = clonal component of variance for trait X
$\hat{\sigma}^2_{cY}$ = clonal component of variance for trait Y

Genetic correlations were calculated to be zero if the mean square component for clone was of the same sign and of a smaller magnitude than for error. Also, sometimes genetic correlations were greater than ± 1 because of the sampling error and mathematical approximation. However, in such a case they could be considered to be ± 1, considering the asymptotic nature of the normal distribution of correlation coefficients (ρ).

Environmental correlation included only the environmental portion of variation and covariation, i.e., error components of variance and covariance (Becker 1985). Environmental correlations (r_e) were estimated by using the formula:

$$r_e = \frac{\hat{\sigma}_{XY}}{\sqrt{\hat{\sigma}^2_{X}}\ \sqrt{\hat{\sigma}^2_{Y}}}$$

r_e = environmental correlation
$\hat{\sigma}_{XY}$ = error component of covariance for traits X and Y
$\hat{\sigma}^2_{X}$ = error component of variance for trait X
$\hat{\sigma}^2_{Y}$ = error component of variance for trait Y

Phenotypic correlation was calculated when block source of variation was removed. Phenotypic components of variance and covariance were obtained by adding clone to error components (Becker 1985). Phenotypic correlation (r_p) between variables X and Y was estimated from phenotypic (block effects are excluded) values as :

$$r_p = \frac{\hat{\sigma}_{pXY}}{\sqrt{\hat{\sigma}^2_{pX}}\ \sqrt{\hat{\sigma}^2_{pY}}}$$

r_p = phenotypic correlation
$\hat{\sigma}_{pXY}$ = covariance for traits X and Y (i.e. $\hat{\sigma}_{cXY} + \hat{\sigma}_{XY}$)
$\hat{\sigma}^2_{pX}$ = phenotypic variance of trait X (i.e. $\hat{\sigma}^2_{cX} + \hat{\sigma}^2_{X}$)
$\hat{\sigma}^2_{pY}$ = phenotypic variance of trait Y (i.e. $\hat{\sigma}^2_{cY} + \hat{\sigma}^2_{Y}$)

In addition the coefficient of genetic prediction (CGP) (Fins *et al.* 1992) was calculated :

$$CGP = \frac{\hat{\sigma}_{cXY}}{\sqrt{\hat{\sigma}^2_{pX}}\ \sqrt{\hat{\sigma}^2_{pY}}}$$

$\hat{\sigma}_{cXY}$ = clonal component of covariance for traits X and Y
$\hat{\sigma}^2_{pX}$ = phenotypic variance of trait X (i.e. $\hat{\sigma}^2_{cX} + \hat{\sigma}^2_{X}$)
$\hat{\sigma}^2_{pY}$ = phenotypic variance of trait Y (i.e. $\hat{\sigma}^2_{cY} + \hat{\sigma}^2_{Y}$)

Genetic Gain

The above parameters enabled us to calculate the predicted genetic gain (ΔG). Genetic gain is the function of the phenotypic variation present (σ_p), the amount of genetic variation (H^2), and the intensity of selection (i):

$$\Delta G = H^2 S = i\, H^2\, \sigma_p$$

where:
S = selection differential, i.e., mean (selected clones) - mean (population)

The selection differential (S) is not a good indicator of the amount of the selection pressure applied, if we deal with several characteristics at the same time. In that case, it is given in the standardized form, as the selection intensity (i):

$$i = S / \sigma_p$$

Also, it is often convenient to express the genetic gain as a percentage of the original population mean (Fins *et al.* 1992).

CHAPTER 3

RESULTS

Univariate Analyses

Provenance differences in mean annual height growth rate (HGR), mean annual diameter growth rate (DGR), mean annual circumference growth rate (CGR), average radial growth rate in fifth, sixth, and seventh year (RGR), growth rate in seventh year (RGR7), relative density (RD), moisture content (MC%), fibre length (FL), and vessel element length (VEL) were analyzed in univariate analyses of variance (ANOVA-s). The mean squares and their significance are presented in *Table* 3.1. (complete ANOVA tables are given in Appendix III).

Differences among provenance means, for each variable, were assessed by using Fisher's LSD method. Provenance means and appropriate ranges of clonal means are also presented in *Table* 3.1.

Clonal variation for each variable was analyzed in three separate ANOVA-s, one for each provenance. By using the results from these analyses, broad sense heritability (H^2) was also calculated separately for each provenance. Clonal mean squares for each source, their significance, and resulting broad sense heritability are presented in *Table* 3.2. (complete ANOVA tables are given in Appendix III).

Table 3. 1. a) The mean squares of the first (provenance) level analyses of variance for the 9 variables; b) provenance means, and ranges of clonal means.

a)		HGR	DGR	CGR	RGR	RGR7	RD	MC%	FL	VEL
Source of variation	[1]df	Mean squares								
Block	3	0.0727	0.0952	0.9139	5.9644	6.5594	0.00150	7774.8	0.00642	0.00196
Provenance	2	**0.0581***	**0.0858***	**0.8057***	**4.5481***	**6.2311^{NS}**	**0.00077^{NS}**	**5587.4^{NS}**	**0.00218***	**0.00144***
Error (B* P)	6	0.0105	0.0128	0.1152	0.8441	1.5409	0.00021	843.8	0.00042	0.00023

b)									
Provenance	Means (range of clonal means)								
	(m/year)	(cm/year)	(cm/year)	(mm/year)	(mm/year)		%	(mm)	(mm)
North Wisconsin	0.574 [2] a (0.827-0.441)	0.723 a (1.000-0.479)	2.309 a (3.156-1.557)	4.515 a (6.317-2.942)	5.011 a (6.875-2.950)	0.343 a (0.380-0.292)	139 a (185-102)	0.638 a (0.710-0.589)	0.349 a (0.413-0.314)
Thunder Bay	0.409 ab (0.559-0.287)	0.540 ab (0.783-0.368)	1.748 ab (2.567-1.324)	2.988 ab (4.417-2.025)	3.282 a (4.875-2.050)	0.357 a (0.408-0.287)	158 a (186-119)	0.632 a (0.707-0.556)	0.334 ab (0.387-0.289)
Pickle Lake	0.340 b (0.477-0.246)	0.433 b (0.575-0.277)	1.421 b (1.912-0.944)	2.462 b (3.392-1.133)	2.587 a (3.600-1.275)	0.371 a (0.399-0.331)	-	0.595 b (0.680-0.530)	0.311 b (0.395-0.266)

Note: Variable abbreviations are presented in the Materials and Methods section

* - Significant at 5% level of probability.

** - Significant at 1% level of probability.

[1] - For the variable MC% degrees of freedom were Block (1), Provenance(1), Error (1) .

[2] - Provenance means in a same column, with different letters in the superscript, are significantly different at 5% level of probability.

Table 3.2. The mean squares of the second (clonal) level analyses of variance for 9 variables in the three provenances

North Wisconsin		Mean Squares								
Source of variation	[1]df	HGR	DGR	CGR	RGR	RGR7	RD	MC%	FL	VEL
Block	3	1.84016	2.29043	20.8145	168.880	225.825	0.02968	1748.03	0.07720	0.04249
Clone	29	**0.01998***	**0.06774****	**0.6577***	**3.588***	**4.598***	**0.00229****	**1040.99***	**0.00418***	**0.00231***
Error (B* C)	87	0.01067	0.03503	0.3510	1.897	2.806	0.00052	301.96	0.00257	0.00139
Broad sense heritability		0.18±0.09	0.19±0.10	0.18±0.10	0.18±0.09	0.14±0.09	0.46±0.10	0.55±0.19	0.13±0.09	0.14±0.09
Thunder Bay										
Block	3	0.24952	0.41995	4.1529	21.392	26.909	0.00405	6870.53	0.05597	0.00933
Clone	29	**0.01322^{NS}**	**1.12524^{NS}**	**0.4164^{NS}**	**1.443^{NS}**	**2.596^{NS}**	**0.00360****	**604.03****	**0.00756****	**0.00221^{NS}**
Error (B* C)	87	0.01197	3.11570	0.3736	1.579	2.372	0.00078	83.46	0.00282	0.00148
Broad sense heritability		0.03±0.08	0.00±0.00	0.03±0.08	0.00±0.00	0.02±0.08	0.47±0.10	0.76±0.11	0.30±0.10	0.11±0.09
Pickle Lake										
Block	3	0.72210	0.91236	9.3634	39.962	32.145	0.02331	-	0.08356	0.02111
Clone	29	**0.01171****	**0.02110****	**0.2374***	**0.899***	**0.972^{NS}**	**0.00151****	-	**0.00560****	**0.00288****
Error (B* C)	87	0.00431	0.00972	0.0952	0.451	0.677	0.00040	-	0.00215	0.00091
Broad sense heritability		0.30±0.10	0.24±0.11	0.27±0.10	0.20±0.10	0.10±0.09	0.41±0.10	-	0.29±0.10	0.35±0.10

* - Significant at 5% level of probability.

** - Significant at 1% level of probability.

[1] - For the variable MC% degrees of freedom were Block(1), Clone(14), Error (14).

Height growth rate

Provenance differences in mean annual height growth rate (HGR) were significant at the 0.05 level of probability. The mean values in metres per year (m/year), compared by using Fisher's LSD method, showed a steady decrease in the south-north direction. Height growth rate was the highest for the southern, North Wisconsin provenance (*Table* 3.1.).

The magnitude of clonal variation differed from population to population. The most significant clonal variation, and therefore, the highest heritability of mean annual height growth rate was found in the northern clonal population, from the Pickle Lake provenance. On the other hand, the local, Thunder Bay clonal population, had a very low heritability (*Table* 3.2.).

Diameter growth rate

Differences in mean annual diameter growth rate (DGR) among the provenances were found significant at 0.05 level of probability. The southern North Wisconsin had again the highest and the Pickle Lake provenance the lowest mean value (*Table* 3.1.).

Variation in mean annual diameter growth rate among clones, analyzed in three separate ANOVA-s, showed different results for each provenance. The highest broad sense heritability had the clones from the Pickle Lake provenance, while it was close to 0 for the Thunder Bay clones (*Table* 3.2).

Circumference growth rate

For mean annual circumference growth rate (CGR), provenance differences were found significant at 0.05 level of probability. Mean circumference growth rate, in centimetres per year (cm/year), decreased from southern to northern provenances (*Table* 3.1.).

Clonal variation in mean annual circumference growth rate and broad sense heritability are given for each provenance separately in *Table* 3.2. Clones from the Pickle Lake provenance had the highest broad sense heritability.

Radial growth rate

Mean radial growth rate in the 5th, 6th, and 7th year (RGR) showed significant provenance differences at 0.05 level of probability. ANOVA mean squares and their significance are presented in *Table* 3.1. Provenance mean values and ranges of clonal means, in millimetres per year (mm/year) are given also. A decrease from southern to northern provenances was evident.

Mean squares from analyses of variance for the variable, on the clonal level of the experiment are presented in *Table* 3.2. The heritability of radial growth rate in Thunder Bay provenance was found to be 0.

Radial growth rate in the 7th year

Provenance differences in radial growth rate in the 7th year (RGR7) were not found significant at 0.05 level of probability. Still, provenance mean values in millimetres per year (mm/year) and ranges of clonal means showed a decrease from southern to northern provenances (*Table* 3.1.).

Clonal variation for this characteristic was analyzed for each provenance separately, and heritability was found to be low for the clones from all three provenances. North Wisconsin had the highest, and Thunder Bay the lowest value of broad sense heritability (*Table* 3.2.).

Relative density

Provenance differences in relative density (RD) were not significant at 0.05 level of probability. Relative density was the highest for Pickle Lake, Thunder Bay was in the middle, and the lowest relative density occurred in the clones from North Wisconsin. Again, these differences were not statistically significant (*Table* 3.1.).

Clonal variation for each provenance was analyzed in three independent ANOVA-s, and broad sense heritability of relative density was calculated separately for each provenance. It was moderate, but relatively high in comparison to heritability of growth characteristics. Also, it was roughly equal for all three provenances (*Table* 3.2).

Moisture content

For the variable moisture content (MC%) provenance differences were not significant at 0.05 level of probability. However, the ANOVA F-test had only 1/1 degrees of freedom. Average percent moisture content for provenances and ranges of clonal means are given in *Table* 3.1.

Clonal variation of percent moisture content was analyzed, and broad sense heritability calculated separately for two provenances (*Table* 3.2). The broad sense heritability of moisture content was high for both analyzed provenances. It was higher for Thunder Bay clones than for North Wisconsin ones.

Fibre length

Provenance differences in fibre length (FL) were statistically significant at 0.05 level of probability. Fibres were the longest in trees originally from North Wisconsin; however, Thunder Bay trees had fibres which were not significantly (statistically) shorter. Only trees from the Pickle Lake provenance had significantly shorter fibres (*Table* 3.1.).

Clonal variation of fibre length was analyzed separately for each provenance. Broad sense heritability was found to be higher in Thunder Bay and Pickle Lake than in the North Wisconsin provenance (*Table* 3.2).

Vessel element length

Provenance differences in vessel element length (VEL) were significant at 0.05 level of probability. Comparisons of means showed that mean vessel element length decreased in a south-north direction (*Table* 3.1).

Clonal variation in vessel element length was analyzed in three separate ANOVA-s, and broad sense heritability calculated for each provenance separately (*Table* 3.2.). Clones from the Pickle Lake provenance showed again the highest broad sense heritability for this characteristic.

Multivariate Analysis

Results of the multivariate analysis of variance are presented in *Table* 3.3. The three most important response variables (see Chapter 2): radial growth rate (RGR), relative density (RD), and fibre length (FL) were analysed together. None of the four tests were significant for the overall differences between provenances. This could have been the consequence of either, the very low number of degrees of freedom for error, or the real lack of variation. The low number of degrees of freedom for error was a disadvantage of the experimental design, at the first (provenance) level. However, canonical variates (CV) were derived and the canonical variate 1 was plotted. Although, MANOVA F-tests were not significant, the difference between North Wisconsin and Pickle Lake provenances can be seen in the plot (*Figure* 3.1.).

Table 3.3. Multivariate tests of significance for the differences between the three provenances.

Test Name	Value	F	Hypoth. DF	Error DF	Sig. of F
Pillai's	1.12677	2.15	2	10	0.136
Hotelling's	2.96306	1.48	2	6	0.323
Wilks'	0.17595	1.84	2	8	0.207
Roy's	0.68457				

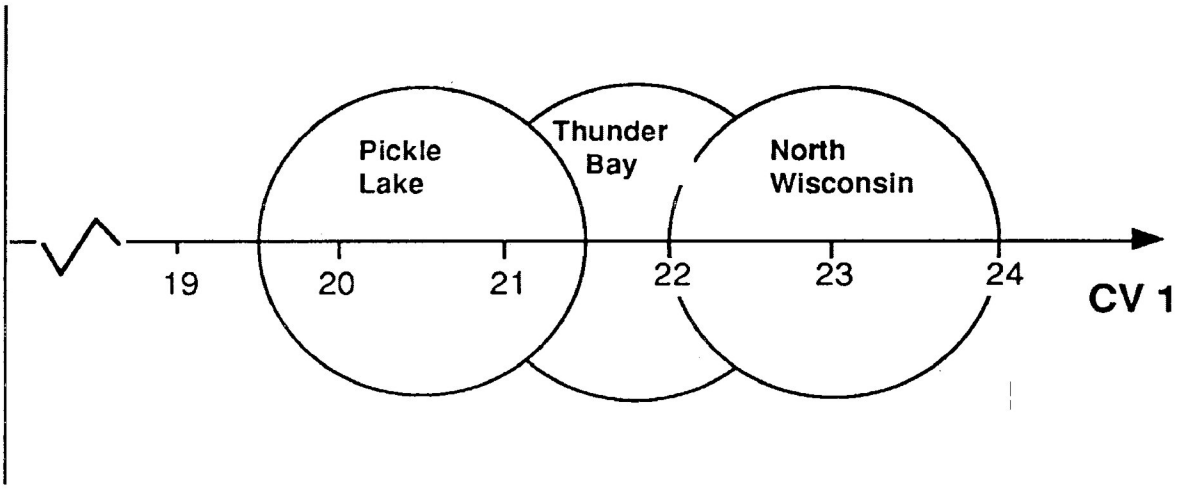

Figure 3.1. Canonical means and 95% confidence limits for the three provenances projected on the first canonical variate axis.

Correlation among the Traits

First, the "overall" correlations among 9 variables were calculated for the entire sample (*Table* 3.4). All growth characteristics were highly positively correlated among themselves, and with cell length. They were highly negatively correlated with relative density, and uncorrelated with moisture content. Relative density was negatively correlated with moisture content and cell length. Moisture content was uncorrelated with fibre length, but somewhat correlated with vessel element length. Fibre and vessel element length were highly positively correlated.

Table 3.4. Overall correlations among 9 characteristics calculated for the entire sample, by using all observed values.

	HGR	DGR	CGR	RGR	RGR7	RD	MC%	FL	VEL
HGR	1								
DGR	.93**	1							
CGR	.93**	1.00**	1						
RGR	.93**	.95**	.95**	1					
RGR7	.89**	.93**	.93**	.97**	1				
RD	-.64**	-.62**	-.61**	-.65**	-.63**	1			
MC%	.02	.00	.01	.13	.17	-.35**	1		
FL	.64**	.63**	.64**	.58**	.52**	-.40**	.19	1	
VEL	.65**	.64**	.64**	.61**	.57**	-.54**	.27*	.76**	1

* - Significant at 5% level of probability;
** - Significant at 1% level of probability

Second, four types of correlation were calculated within each provenance separately. The overall correlation included block (a "nuisance") source of variation, which is usually omitted from the phenotypic covariance. It was calculated for the North Wisconsin provenance (first row in the horizontal cells of *Table* 3.5.). Growth characteristics were highly positively correlated among themselves, and with cell length. As for the entire sample, they were highly negatively correlated with relative density, and uncorrelated with moisture content. Relative density was again negatively correlated with moisture content, and with cell length. Moisture content was uncorrelated with fibre length, but significantly and positively correlated with vessel element length .

Genetically, growth characteristics were highly positively correlated among themselves, but in this provenance, negatively correlated with cell length. Growth characteristics were negatively correlated with relative density, and slightly positively correlated with moisture content. Relative density was not negatively genetically correlated with cell length. Moisture content was uncorrelated with cell length. Fiber and vessel element length were positively genetically correlated. (Second row in the horizontal cells of *Table* 3.5.)

Table 3.5. Overall, genetic, environmental, and phenotypic correlations calculated for the North Wisconsin provenance

	HGR	DGR	CGR	RGR	RGR7	RD	MC%	FL	VEL
HGR	1	**a**.92** **b**.87** **c**.80** **d**.82**	.91** .85** .81** .82**	.93** .76** .78** .78**	.89** .81** .67** .69**	-.70** -.00 -.50** -.33**	.33 .18 .00 .05	.65** -.98** .56** .32**	.69** -.43** .51** .36**
	DGR	1	.99** 1.00** .99** .99**	.96** .94** .89** .90**	.94** .95** .84** .85**	-.66** -.29** -.37** -.33**	.35* .39* -.04 .06	.60** -.82** .52** .30**	.65** -.29** .47** .34**
		CGR	1	.95** .92** .89** .90**	.93** .89** .84** .84**	-.66** -.26** -.38** -.33**	.33 .39* -.04 .05	.60** -.72** .52** .32**	.66** -.24** .49** .36**
			RGR	1	.97** .98** .91** .92**	-.72** -.41** -.45** -.42**	.41* .44* -.02 .09	.57** -.89** .41** .20**	.65** -.34** .43** .31**
				RGR7	1	-.69** -.45** -.35** -.35**	.28 .32 -.06 .03	.52** -1.00** .30** .13	.60** -.33** .29** .21*
					RD	1	-.41* -.34 -.04 -.09	-.38** .66** .00 .04	-.60** -.06 -.01 -.32**
						MC%	1	.25 .08 .02 .03	.49** .26 .05 .15
							FL	1	.74** .44** .01 .59**
								VEL	1

a - Overall correlation
b - Genetic correlation
c - Environmental correlation
d - Phenotypic correlation (block effects excluded)
* - Significant at 5% level of probability;
** - Significant at 1% level of probability

Environmental correlations in the provenance North Wisconsin were as follows: growth characteristics were highly positively correlated among themselves, and with cell length. They were highly negatively correlated with relative density , and uncorrelated with moisture content. Relative density was not environmentally correlated with moisture content or cell length. Moisture content was uncorrelated with cell length. Fiber and vessel length were not environmentally correlated.(Third row in the horizontal cells of *Table* 3.5.)

Generally, phenotypic correlations were similar to overall ones, but of a much less magnitude. (Fourth row in the horizontal cells of *Table* 3.5.)

For the North Wisconsin provenance coefficients of genetic prediction were significantly different from 0 only between the diameter growth rate and two other characteristics of radial growth (*Table* 3.6.).

Table 3.6. Heritabilities and coefficients of genetic prediction for the North Wisconsin provenance.

	HGR	DGR	CGR	RGR	RGR7	RD	MC%	FL	VEL
HGR	[a].18*								
DGR	.16	**.19***							
CGR	.16	.19*	**.18***						
RGR	.14	.18*	.17	**.18***					
RGR7	.13	.15	.15	.15	**.14***				
RD	.00	-.08	-.08	-.12	-.11	**.46****			
MC%	.05	.09	.08	.11	.07	-.06	**.55****		
FL	-.15	-.13	-.12	-.14	-.14	.16	.02	**.13**	
VEL	-.07	-.05	-.04	-.05	-.05	-.01	.13	.06	**.14***

a - Values on the diagonal are trait heritabilities
* - Significant at 5% level of probability
** - Significant at 1% level of probability

Overall correlations were calculated for the Thunder Bay provenance (first row in the horizontal cells of *Table* 3.7.). Growth characteristics were highly positively correlated among themselves, and with cell length. They were negatively correlated with relative density, and uncorrelated with moisture content. Relative density was again negatively correlated with moisture content, and with cell length. Moisture content was uncorrelated with cell length.

Table 3.7. Overall, genetic, environmental, and phenotypic correlations calculated for the Thunder Bay provenance.

	HGR	DGR	CGR	RGR	RGR7	RD	MC%	FL	VEL
HGR	1	**a**.92** **b**.13 **c**.93** **d**.91**	.92** .12 .92** .90**	.89** .00 .85** .86**	.85** .85** .82** .82**	-.41** -.59** -.38** -.34**	.24 .00 .04 .02	.57** -.55** .54** .40**	.44** -1.84** .43** .30**
	DGR	1	.99** 1.02** .99** .99**	.93** .00 .92** .92**	.91** .53** .90** .89**	-.37** -.18* -.39** -.29**	.04 -1.14** .05 -.01	.56** -.01 .54** .45**	.45** -1.04** .43** .35**
		CGR	1	.92** .00 .92** .91**	.90** .15 .90** .88**	-.35** -.01 -.39** -.28**	.03 -.47** .04 -.01	.57** -.10 .54** .46**	.44** -.68** .41** .34**
			RGR	1	.94** .00 .94** .94**	-.44** -.00 -.42** -.37**	.34 .17 .06 .06	.51** -.00 .52** .36**	.39** -.00 .37** .27**
				RGR7	1	-.45** -.57** -.45** -.38**	.14 .01 .05 .03	.43** -.91** .47** .31**	.35** -1.96** .37** .25**
					RD	1	-.63** -.42* -.06 -.27	-.18* .21* .00 -.07	-.33** -.04 -.01 -.27**
						MC%	1	.27 -.22 .08 -.05	.16 -.51** .05 .00
							FL	1	.68** 1.45** .00 .12
								VEL	1

a - Overall correlation
b - Genetic correlation
c - Environmental correlation
d - Phenotypic correlation (block effects excluded)
* - Significant at 5% level of probability
** - Significant at 1% level of probability

Genetic correlations among growth characteristics within the Thunder Bay provenance were not important since heritability was close to zero (Falconer 1981). Relative density was negatively correlated with moisture content and fibre length. Moisture content was negatively genetically correlated with cell length. Fibre and vessel element length were positively genetically correlated. (Second row in the horizontal cells of *Table* 3.7.)

Environmentally, growth characteristics were highly positively correlated among themselves, and with cell length. They were negatively correlated with relative density , and uncorrelated with moisture content. Relative density was not environmentally correlated with moisture content, or cell length. Moisture content was uncorrelated with cell length. Fibre and vessel length were not environmentally correlated.(Third row in the horizontal cells of *Table* 3.7.)

Generally, phenotypic correlations were similar to overall ones, but of a less magnitude for most of the characteristics. (Fourth row in the horizontal cells of *Table* 3.6.)

For the Thunder Bay provenance coefficients of genetic prediction (*Table* 3.8.) were significantly different from 0 only between fibre and vessel element length.

Table 3.8. Heritabilities and coefficients of genetic prediction for the Thunder Bay provenance.

	HGR	DGR	CGR	RGR	RGR7	RD	MC%	FL	VEL
HGR	[a]**.02**								
DGR	.00	**.02**							
CGR	.00	.02	**.03**						
RGR	.01	.00	-.01	**.02**					
RGR7	.02	.01	.00	.01	**.02**				
RD	-.06	-.02	.00	-.06	-.06	**.47****			
MC%	.00	-.04	-.04	.02	.00	-.24	**.76****		
FL	-.05	.00	.01	-.08	-.08	.08	-.09	**.30****	
VEL	-.10	-.05	-.04	-.08	-.10	-.01	-.03	.26**	**.11**

[a] - Values on the diagonal are trait heritabilities
* - Significant at 5% level of probability
** - Significant at 1% level of probability

Overall correlations calculated for the Pickle Lake provenance were highly significant for all characteristics (first row in the horizontal cells of *Table* 3.9.). Growth characteristics were positively correlated among themselves, and with cell length. As for the previous two provenances they were highly negatively correlated with relative density. Relative density was again negatively correlated with cell length. Correlations with moisture content were not calculated for this provenance. Fibre length was significantly and positively correlated with vessel element length .

Genetically, growth characteristics were highly positively correlated among themselves and with cell length. Three growth characteristics (DGR, CGR, RGR7) were negatively correlated, while other two (HGR, RGR) were uncorrelated with relative density. Relative density was negatively genetically correlated with cell length. Fibre and vessel element length were highly - positively genetically correlated. (Second row in the horizontal cells of *Table* 3.9.)

Environmentally, growth characteristics were highly positively correlated among themselves, and with cell length. They were negatively correlated with relative density. Relative density was not environmentally correlated to cell length. Fiber and vessel length were not environmentally correlated.(Third row in the horizontal cells of *Table* 3.9.)

Generally, phenotypic correlations were similar to overall ones, but of less magnitude. (Fourth row in the horizontal cells of *Table* 3.9.)

Table 3.9. Overall, genetic, environmental, and phenotypic correlations calculated for the Pickle Lake provenance.

	HGR	DGR	CGR	RGR	RGR7	RD	FL	VEL
HGR	1	**a** .94**	.94**	.93**	.86**	-.67**	.75**	.65**
		b .80**	.80**	.84**	1.01**	.16	.74**	.67**
		c .84**	.84**	.76**	.65**	-.45**	.48**	.50**
		d .83**	.83**	.78**	.69**	-.23**	.56**	.55**
	DGR	1	1.00**	.96**	.89**	-.69**	.77**	.68**
			1.00**	.93**	1.19**	-.29**	.91**	.80**
			.99**	.87**	.72**	-.39**	.48**	.48**
			.99**	.88**	.78**	-.35**	.59**	.57**
		CGR	1	.96**	.89**	-.69**	.77**	.68**
				.91**	1.12**	-.27**	.88**	.77**
				.88**	.72**	-.39**	.47**	.47**
				.88**	.77**	-.34**	.59**	.56**
			RGR	1	.94**	-.67**	.72**	.65**
					1.07**	-.11	.89**	.86**
					.85**	-.41**	.36**	.41**
					.87**	-.32**	.48**	.52**
				RGR7	1	-.66**	.66**	.60**
						-.29**	1.15**	1.03**
						-.39**	.27**	.34**
						-.34**	.41**	.45**
					RD	1	-.55**	-.52**
							-.33**	-.35**
							.00	.00
							-.28**	-.36**
						FL	1	.83**
								.97**
								.01
								.78**
							VEL	1

a - Overall correlation
b - Genetic correlation
c - Environmental correlation
d - Phenotypic correlation (block effects excluded)
* - Significant at 5% level of probability
** - Significant at 1% level of probability

Coefficients of genetic prediction in the Pickle Lake provenance were generally the most significant. Also, the values of broad sense heritability were the highest (*Table* 3.10.).

Table 3.10. Heritabilities and coefficients of genetic prediction for the provenance Pickle Lake.

	HGR	DGR	CGR	RGR	RGR7	RD	FL	VEL
HGR	[a]**.30****							
DGR	.21*	**.24****						
CGR	.23**	.25**	**.27****					
RGR	.20*	.20*	.21*	**.20***				
RGR7	.17	.18*	.18*	.15	**.10**			
RD	.06	-.09	-.09	-.03	-.06	**.41****		
FL	.22*	.24**	.24**	.21*	.19*	-.11	**.29****	
VEL	.22*	.23**	.24**	.23**	.19*	-.13	.31**	**.35****

[a] - Values on the diagonal are trait heritabilities
* - Significant at 5% level of probability
** - Significant at 1% level of probability

CHAPTER 4

DISCUSSION

Differences among Provenances

For growth characteristics the provenance test indicated a more or less continuous variation pattern: the rate of growth decreased in a south-north direction. This is in accordance with Farmer's (1993) findings for height growth of balsam poplar. The author concluded that, "Generally, material moved south exhibits less growth than local material, and plants moved north of the origin grow more than local trees." Since geographic source does not always influence the time of bud break, one of the reasons for such a variation pattern could be because northern clones stop their growth earlier in the season. (Pauley and Perry 1954, Farmer1993).

In this study, the low significance of tests for provenance differences may be the result of insensitivity of the ANOVA (*Table* 3.1.), at its first provenance-plot level. If a higher number of blocks, or provenance-plot replications within each block had been used, a higher number of degrees of freedom associated with error would have been obtained. In that case, it would be reasonable to expect the significance of provenance differences in growth rate to be higher (Fins *et al.* 1992, Brown 1993).

For wood properties, a pattern of decrease in cell length from southern to northern sources was found. It paralleled the growth rate pattern. On the other hand, relative density and moisture content were not significantly different among the three provenances. Faster growth rate was generally negatively correlated with relative density. However, when block source of variation was removed, the negative correlation within the provenances was greatly reduced. Thus, the faster growth of the southern provenance, in comparison with the other two, did not

cause a significant loss in relative density.

Despite the fact that F-tests of *multivariate analysis* were not significant, it suggested the existence of a variation pattern in the south-north direction. A significant difference between the southern and northern source, and an intermediate position of the local source can be seen from the plot of the first canonical variate (*Figure* 3.1.).

The best performance in terms of growth rate and cell length, without a significant loss in relative density, or a change in moisture content, favours the North Wisconsin source over the other two, for the use in selection. This is especially because no serious frost injuries have been observed so far among the trees from the southernmost provenance. Riemenschneider *et al.* (1993) considered selection of foundation breeding populations. They sampled natural stands in Wisconsin, Minnesota, and Michigan, and developed multiple-trait selection-methods to increase growth and pest resistance.

Differences among Clones within Provenances

At the second level of analysis of variance the precision was greatly improved. This provided a better basis for estimating variance components, and eventually heritability of the traits. Also, it was possible to obtain these estimates for each of the three provenances separately. Clonal variance components, and their relative contribution to the total (phenotypic) variation, differed from provenance to provenance. This relation between sources of variation determined heritability of the traits within each provenance.

Heritability of the traits

Despite the widespread use of broad sense heritability, Suzuki *et al.* (1986) pointed out its special and limited meaning: "In general, the heritability of a trait is different in each population and in each set of environments; it cannot be extrapolated from one population and set of environments to another." These considerations proved to be important for this experiment, especially for heritability of growth characteristics. The northern, Pickle Lake, provenance had much higher heritability of growth characteristics than the North Wisconsin and Thunder Bay provenances. This was because in populations with a

developmentally stable genotype the environmental variance could be smaller. In other words, the most northern genotype, which was more conservative and stopped growth earlier in the fall, could have a reduced sensitivity to changes in the environment (Farmer 1993). At the same time, genetic variance components were relatively close in magnitude among the three provenances.

Heritability of wood properties was generally more uniform among the provenances, as well as higher than that of growth characteristics. In this study, balsam poplar relative density had a moderate heritability, which was roughly equal among the three provenances. In comparison with heritabilities reported for cottonwood (*P. deltoides)* (Farmer and Wilcox 1968, Farmer 1970a, Farmer 1970b, etc.) it was considerably lower. The values were closer to those reported for aspen (*P. tremuloides*) and black poplar (*P. trichocarpa*) (van Buijtenen. *et al.* 1962, Einspahr *et al.* 1967, Reck 1974, etc.). No reports were found on heritability of relative density in balsam poplar, to use for comparison.

Heritability of wood moisture content in this study was high. No data for poplars were available to use for comparison.

Cell length heritability was, generally, more variable among the three provenances than the other wood properties. No pattern in heritability could be detected among provenances, for fibre and vessel element length. Heritability values obtained in this experiment were much lower than those reported for cottonwood (*P. deltoides)* (Farmer and Wilcox 1968), aspen (*P. tremuloides*) (Einspahr *et al.* 1963) or black poplar (*P. trichocarpa*) (Reck 1974, etc.)

By comparing heritability values from this study with results from other experiments (listed in *Tables* 1.3. and 1.7), we can learn which values are generally associated with a particular wood property. Because of the considerable variation in heritabilty from population to population, especially for cell length, more data should be obtained for balsam poplar. Only after that, will it be possible to evaluate breeding alternatives, and to give a general recommendation whether to include wood properties in future tree improvement programs.

Correlation among the Traits

There is an abundance of literature on correlation between growth and wood properties in poplars. Still, only a few attempts to separate genetic from environmental effects can be found (Zobel and van Buijtenen 1989). In this study

four different types of correlation (overall, phenotypic, environmental, and genetic) were calculated among growth characteristics, between them and wood properties, and among wood properties.

Correlation among growth characteristics

Phenotypic and environmental correlations among growth characteristics were positive and highly significant in all three provenances. At the same time, genetic correlations varied considerably from provenance to provenance. This could be explained by the fact that if both characteristics have low heritability, the phenotypic correlation is determined mainly by the environmental correlation; if they have high heritability, then the genetic correlation is more important (Falconer 1981). In the Pickle Lake provenance, where heritability of growth characteristics was much higher than in the other two, genetic correlation was positive and highly significant, as was expected (*Table* 3.9.). Nevertheless, genetic correlations are only estimates, usually subject to large sampling errors and seldom very precise. They are also strongly influenced by gene frequencies (Falconer 1981).

Correlation between growth and wood properties

A highly significant negative correlation between growth rate and relative density was obtained from directly observed values. This so called "overall" correlation included block effects. However, in the experiments where genetic differences are sought, environmental variation should be reduced to a minimum, and this is usually done by blocking. When block effects, as a source of correlation, were removed, the negative correlation between growth and relative density was of considerably less magnitude. This "phenotypic" correlation was then used for comparison with other types of correlation (genetic and environmental) within each provenance, and with "phenotypic" correlation coefficients in other provenances. On the other hand, the "overall" correlation covered a wider range of values for both growth characteristics and relative density, and it gave a better general estimate of the correlation between these values.

The negative phenotypic correlation between growth and relative density was genetically based only for characteristics of radial growth, but not for the

height growth (*Table* 3.9.). Still, this genetic correlation might not have been strong (r_g = 0.11 - 0.29 for the Pickle Lake provenance). It did not mean that clones with both fast radial growth rate and high relative density could not be selected. For example, two clones from the Thunder Bay provenance were compared (*Figure* 4.1.). Both clones had approximately equal radial growth rate; negative overall correlation between radial growth and relative density was evident; but clone 2. had genetically higher relative density.

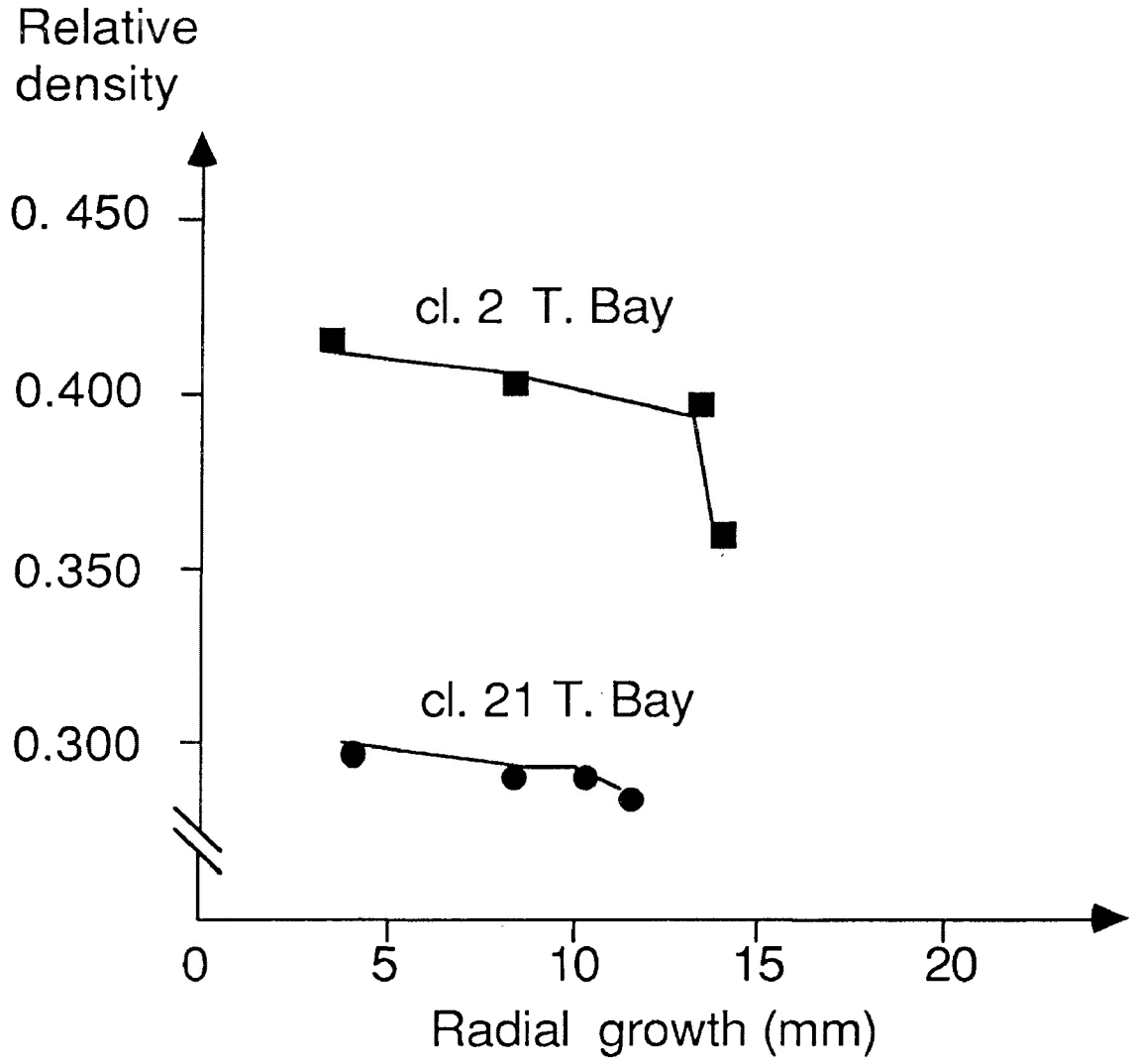

Figure 4.1. Radial growth (in 5th, 6th, and 7th year) - relative density relationship for two clones (with four ramets each) from the Thunder Bay provenance.

Either a weak or no phenotypic correlation between moisture content and growth rate was found. This may be due to having the samples taken early in the spring before shoot growth started.

Between cell length and growth characteristics, phenotypic and environmental correlations were significantly positive. This kind of phenotypic correlation had been observed by many authors, and Kennedy (1968) first emphasized it as a peculiarity of poplars. In this study, the extent to which the correlation was genetically based was not entirely clear, because of somewhat ambiguous results for different provenances. Negative genetic correlation obtained in the North Wisconsin and Thunder Bay provenances may not be important because heritabilities of both traits were low. At the same time, in the Pickle Lake provenance, where heritability of growth characteristics and cell length was higher than in the other two, genetic correlation was positive and highly significant, as was expected (*Table* 3.9.).

Correlation among wood properties

The evident negative phenotypic correlation between relative density and moisture content was more genetically than environmentally influenced (*Tables* 3.5. and 3.7.).

Relative density seemed to be more negatively correlated to vessel element than to fibre length. The negative phenotypic correlation between relative density and cell length was also more genetically than environmentally influenced. In the Pickle Lake provenance, where heritability of cell length was generally higher, negative genetic correlation was more important than environmental correlation (*Table* 3.7. and 3.9.).

Moisture content also seemed to be more correlated to vessel element length than to fibre length, although, this correlation was not uniform among the provenances.

Carlquist's (1988) statement that, "vessel element length always parallels fibre length" was supported again. Moreover, it was found that this kind of relationship had a strong genetic basis and it was not influenced by the environment.

Coefficients of genetic prediction and genetic gain

For the Pickle Lake provenance, in which heritability was generally the highest, coefficients of genetic prediction were also of higher significance (*Table* 3.10.). However, they were not proportional to heritability of two characteristics examined. (Coefficients of genetic prediction were not significant between growth and relative density, although, the latter had a high heritability. A similar result was obtained between relative density and moisture content of the wood.) Significantly positive values of coefficients of genetic prediction were found among some growth characteristics, as well as between growth and cell length in the Pickle Lake provenance. Still, selection would not be made within this provenance, because of its poor performance.

On the whole, the North Wisconsin provenance was the one with the best performance. The average height growth was 40%, and radial growth over 50% better than in the Thunder Bay provenance, while relative density was only 4% less (*Table* 3.1.). Therefore, clones from North Wisconsin should be used for selection. If the clones had been selected so that they had growth rate one standard deviation above their population average, the *genetic gain* would be the standard deviation times appropriate heritability. The *correlated response* in, for example, relative density would be one standard deviation in relative density times appropriate coefficient of genetic prediction. By using heritabilities and coefficients of genetic prediction (*Tables* 3.6.), genetic gain was estimated for selection in some growth and wood characteristics, within the North Wisconsin provenance:

- for selection in height or radial growth rate percent genetic gain would be around 8% and 10% of the population mean, respectively,

- for selection in relative density, it would be approximately 6%, and for cell length less than 2%.

None of the genetic changes caused by above selections would significantly influence potential of other characteristics, since all the CGP were insignificant.

Conclusions

Presently, balsam poplar has a low commercial value. However, there is some interest in the hybrid of this species and eastern cottonwood for intensive plantation establishment in the boreal region. To develop such hybrids, adapted parents with superior shoot growth should be selected. A combination of provenance and individual clone selection before hybridization would be useful (Farmer 1993). A recent study suggested that multiple-trait selection could increase both tree height and pest resistance (Riemeschneider *et al.* 1992).

Results presented here show that selection for faster growth would not necessarily have a significantly negative genetic influence on relative density or moisture content of the wood. Moreover, selection for growth potential would not affect the highly positive phenotypic correlation between faster growth and cell length.

Combined selection for growth and wood properties is an opportunity for tree improvement. It could simultaneously improve growth rate and relative density (or moisture content) of the wood, without significantly affecting cell length.

Selection concentrated on wood density or moisture content could also give satisfying results.

Even though these conclusions cannot be taken as final and general recommendations, further research of balsam poplar genetics is in progress. More reports can be expected (Farmer 1990). By comparing different studies, we will be able to learn more about this native species, whose importance for forestry practice is increasing.

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APPENDICES

APPENDIX 1

Patterns of Radial Variation in Juvenile Wood Zone of Balsam Poplar

Introduction

Importance

Radial variation of wood properties, or variation from the pith to the bark, has been studied by many authors in this century. It is one of the best known patterns of variation that occur within the tree stem. This kind of variation is closely related to the presence of juvenile wood in the first 5-20 growth rings near the tree center. Zobel and van Buijtenen (1989) wrote that, "The radial patterns are reflected in the concept of juvenile and mature wood, which is a crude but useful way of understanding the within tree patterns of variation." Also, they emphasized that, "...one fact is sometimes misunderstood, i.e., relative density stabilizes more rapidly than cell length, thus, juvenile zones are not the same for both characteristics within a given tree." Generally, juvenile wood has shorter and thinner walled fibers, and they consequently have larger micro fibril angles (Wheeler 1987).

In an anatomical sense, these changes result from the process called "maturation of cambium", where the size and survival of newly formed fusiform initials depend on the age of cambium. Also, the frequency of anticlinal divisions of these initials is higher near the pith. Eventually, these processes determine the character and dimensions of the wood cells formed (Panshin and de Zeeuw 1980).

Relative density

In many experiments done with poplars, which are low density diffuse-porous hardwoods, radial variation of relative density was found to be significant. For aspen, Valentine (1962) found that the major portion of variation in relative density across the radius of the tree was related to distance from the pith. The pattern of radial variation in poplars, cannot be generalized easily. Zobel and van Buijtenen (1989) concluded: "Poplars seem to have somewhat higher density near the pith, although some have a uniform density from pith to bark."

Moisture content

Moisture content varies greatly from juvenile to mature wood and with height in the tree (Zobel and van Buijtenen 1989). In hardwoods there are commonly no such differences in moisture content between sapwood and heartwood, or with location in the stem as in conifers (Panshin and de Zeeuw 1980). However, balsam poplar wood often has "wet heart", and "wet pockets", which are small volumes of exceedingly high moisture content (Wallin 1954, Balatinecz and Peng 1984).

Cell length

The most elementary form of variation in cell length occurs within a single growth ring, where, in poplars, latewood fibers are found to be 10-20% longer than those of earlywood (Kennedy 1968, Johnson 1942). The much more significant variation is due to the number of rings from the pith. Kennedy (1957) found a rapid increase in fiber length with increasing age in the first 15 rings for black cottonwood (*Populus trichocarpa* L.). In a more recent study Micko (1987) had similar findings, when he examined black cottonwood and aspen. Both, fibre and vessel length increased with the distance from the pith in the juvenile wood zone. These findings were the same in both species. The radial variation of cell length in the juvenile zone can be especially important, if poplars are grown in short rotation plantations.

Microfibril angle

Microfibril angle is the mean helical angle that the microfibrils of S_2 layer of the secondary cell wall form with the longitudinal axis of the cell. Normally, the fibrils in S_2 are oriented almost parallel to the cell axis, but when large fibril angles occur (flat fibrils) excess longitudinal shrinkage (up to 9%) occurs (Zobel and van Buijtenen 1989, Panashin de Zeeuw 1980). "As hydrogen bonded water is lost from between the crystalline chains within the microfibrillar structure, shrinkage takes place in approximate direct proportion to the volume of water lost, and more or less in direction perpendicular to the orientation of the crystalline chains," explained Megraw (1985).

This is of great importance especially for solid wood products, where the fibril orientation has a major effect on the stability of wood upon drying and following manufacture. When a board contains wood with both normal and flat fibril angles, the board is unstable and will crack, wrap, and check because of differential shrinkage within the board (Harris and Meylan 1965). Juvenile wood has shorter and thinner walled fibers with increased microfibril angles. Angles over 25-30^{o} result in a high longitudinal shrinkage that makes solid wood products so unstable (Meylan 1968).

Effect of growth rate

Effect of growth rate (ring width) should not be ignored whenever we are dealing with wood properties, because it can have a significant contribution as a source of variation in relative density and cell length. However, this effect should be distinguished from the effect of juvenile wood. Panshin and de Zeeuw (1980) wrote, " Juvenile wood in plantation-grown trees can be related to the fast growth near the pith, but, wide rings are not necessarily associated with juvenile wood in all trees."

Experimental Methods

Specimens

In order to determine the pattern of radial variation in wood properities, specimen was taken from one balsam poplar tree. This tree belonged to a clone, originally from North Wisconsin, U.S.A., grown for ten years in the experimental plantation close to Lakehead University, Thunder Bay. It was harvested in April, 1994. Specimen disk was taken at approximately 40 cm above the ground. Wood strip 1.5 cm wide and 2 cm high was cut in the north-south direction through the center of the disc. The south-side half was used for laboratory studies.

Laboratory studies

Radial growth rate, relative density, moisture content and cell length were defined and their measurment was described earlier in the text (Chapter 3). The only difference was that these characteristics were determined for each growth ring from 1^{st} to 10^{th} , in this study.

In addition, *microfibril angle* (MFA) was measured for each ring. Direction and angle of the helix of the microfibrillar orientation can be determined by the: direction of striations on the surface on the cell wall, orientation of slitlike openings of the pit apertures, orientation of the fracture of cell wall, depositions of minute crystals of metals and iodine in the fine cavities of the cell wall, preferential attack of fungal hiphae, special optical and X-ray methods, and electron microscopy.

The more recent method, that uses pit apertures as windows to measure microfibril angle can be applied to softwoods, however, hardwood fibres do not have large pit apertures through which measurements can be made (Donaldson 1991, Panshin and deZeeuw 1980).

In this experiment the method of measuring the orientation of pit apertures, was used. The orientation follows more or less the microfibril angle of the S_2 layer. (Measurement of orientation of the fracture of cell wall was unsuccessful, because fractures could not be produced by drying the fibers in maceration at 150°C in the oven for 30 min). Slitlike pit apertures of libriform fibres represent openings in the wall parallel to the cellulose microfibrils that compose the wall. Because the microfibrillar structure is merely pushed apart by the aperture and the

microfibrils are not broken at that point little strength is lost giving libriform fibers greater mechanical strength than tracheids. Nevertheless, even in tracheids elliptical pit apertures may be seen (Carlquist 1988). Donaldson (1991) stated that, although the orientation of pit apertures can be used to determine microfibril angle, there are also some problems in using this approach. One of them is that microfibril angle can be distorted by the presence of a pit, and this may lead to biased results.

However, a preliminary sample was taken, and an optimum sample size of 25 fibres was obtained, to represent the variation in microfibril angle within one growth increment. Therefore, one angle was measured on each of 25 fibres from a single growth ring. Measurements were taken at the same relative location within a particular fibre, in order to avoid within fibre variation. This sampling method gave an estimate of mean microfibril angle for each of 10 growth rings. In order to follow the radial variation within the stem, all growth rings from the 1st to 10th year were sampled.

In the first few rings pit apertures were smaller and angles were measured by using a special microscopic eye-lens with a grid. Pit orientation in the squared field was used to estimate the angles, by using a simple trigonometric transformation. In the rest of the rings cells were measured from the magnified, projected image.

Data analyses

Data for each wood property parameter were plotted against ring number (RN) in order to follow the radial variation, and to find possible unusual observations. Regression equations were derived between the ring number (or age from the pith) as an independent variable and various wood property parameters as dependent variables. A correlation matrix was obtained for all variables, and it was used to determine the association between variables along the radius of stem.

Results

A summary of data for the experiment is given In *Table* A.1. Radial growth rate (RGR), moisture content (MC%), relative density (RD), cell length and microfibril angle are presented as measurements on each growth ring.

Table A.1. Radial variation of several wood characteristics - summary of the data.

Ring No.	Rad. Growth Rate (mm/year)	% Moisture	Relative Density	Length of Fibre (mm)	Length of Vessel (mm)	Microfibril Angle
1	0.5	250	0.374	0.371	0.211	48.7
2	0.8	194	0.384	0.377	0.204	46.6
3	3.3	192	0.346	0.533	0.238	39.1
4	4.9	171	0.337	0.685	0.274	38.5
5	7.1	172	0.314	0.587	0.266	38.1
6	6.2	171	0.341	0.694	0.289	39.1
7	10.3	153	0.348	0.638	0.279	36.8
8	10.3	61	0.335	0.779	0.333	33.7
9	8.4	62	0.342	0.848	0.349	32.9
10	6.7	70	0.332	0.906	0.389	29.6

Radial variation in growth rate

Ring width increased from the pith up to 7^{th} and 8^{th} year, when it reached a maximum (of over 10mm). After that radial growth rate decreased with age from the pith (*Figure* A.1.).

Relation was approximated with the curvilinear regression equation:

$$RGR = 1.10 + 0.300(RN) + 0.068(RN)^2$$

and the coefficient of determination was $R^2 = 95.4\%$

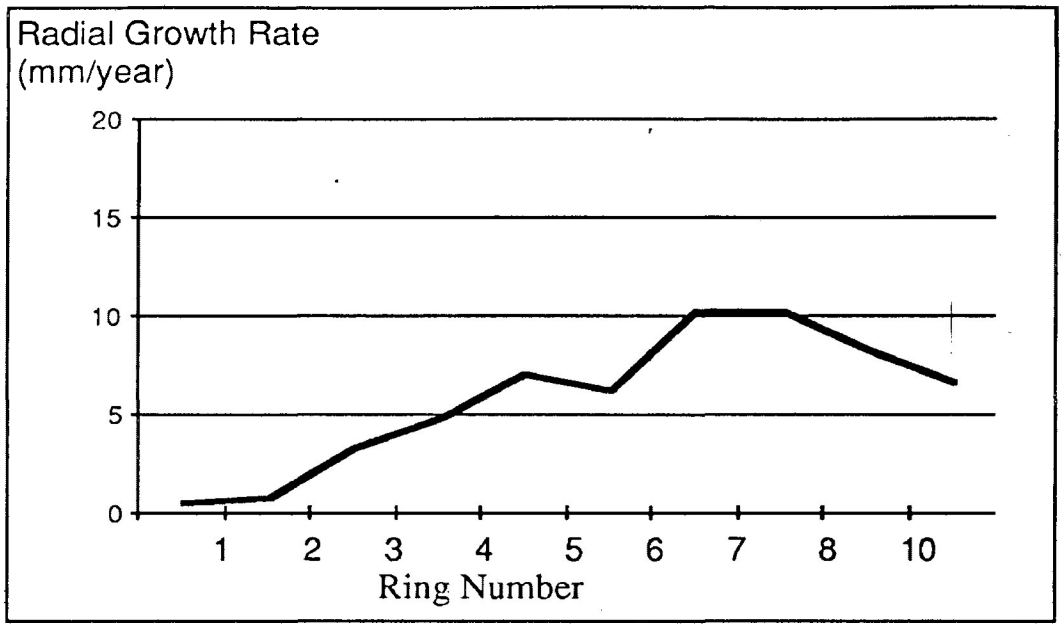

Figure A.1. Radial variation of growth rate in the juvenile wood zone

Relative density

The highest relative density was found near the pith. It was 0.384 in the 2nd ring, after the 3rd ring relative density dropped under 0.350 and varied only between 0.300 and 0.350. (*Figure* A.2.)

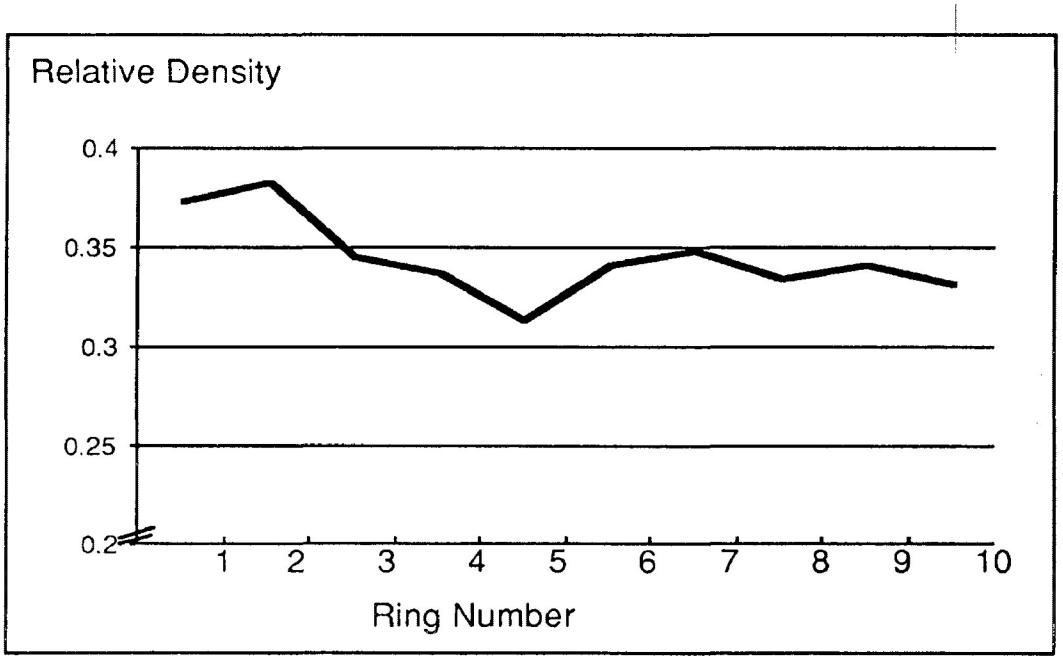

Figure A.2. Radial variation of relative density in the juvenile wood zone

Neither straight-line nor curvilinear relationship between relative density and ring number (or age from the pith) could be established at 5% probability level.

Moisture content

Very high moisture content was found in the first growth ring, i.e., 250%. Moisture content decreased towards the bark, and a sudden drop in 7th year was noticeable. After 7th year of age moisture content settled down under 100% (*Figure* A.3.).

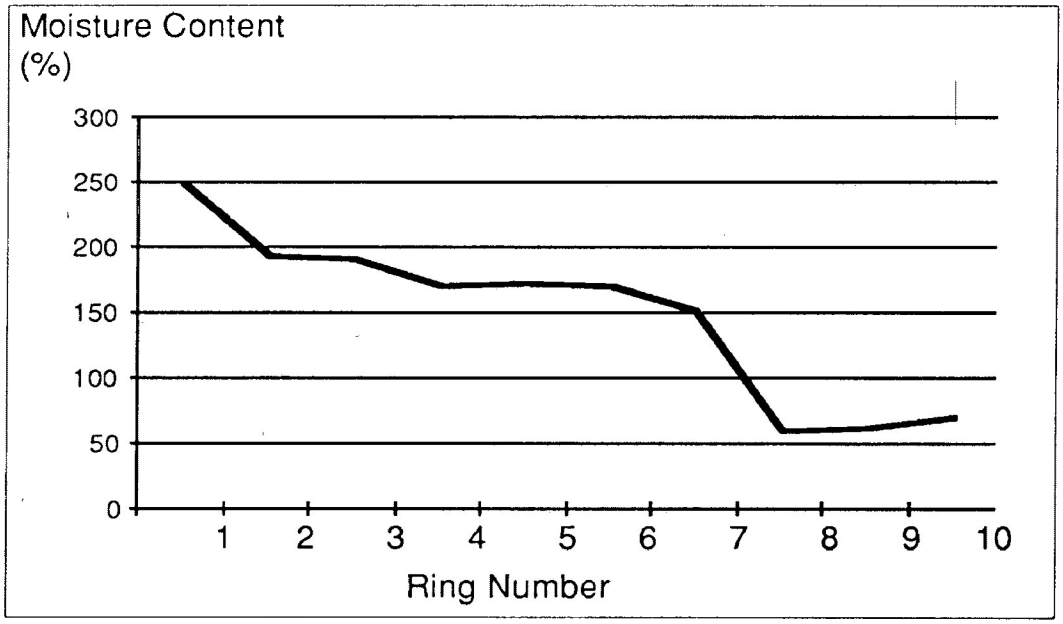

Figure A.3. Radial variation in moisture content in the juvenile wood zone.

Regression equation was:

$$MC\% = 258 - 19.7(RN)$$

with a coefficient of determination $R^2 = 86.4\%$

Cell length

Both, fibre length and vessel element length increased steadily from the pith towards the bark (Figure A.4.). Patterns were not exactly parallel. Differences in length of two cell types increased in older growth rings. The rate of increase was given in regression coefficients, i.e., the slope of regression line was (b_f = 0.0564) for the fibre length, and only (b_v = 0.0190) for the vessel element length. No signs of stabilization in cell length could be observed in first ten growth rings.

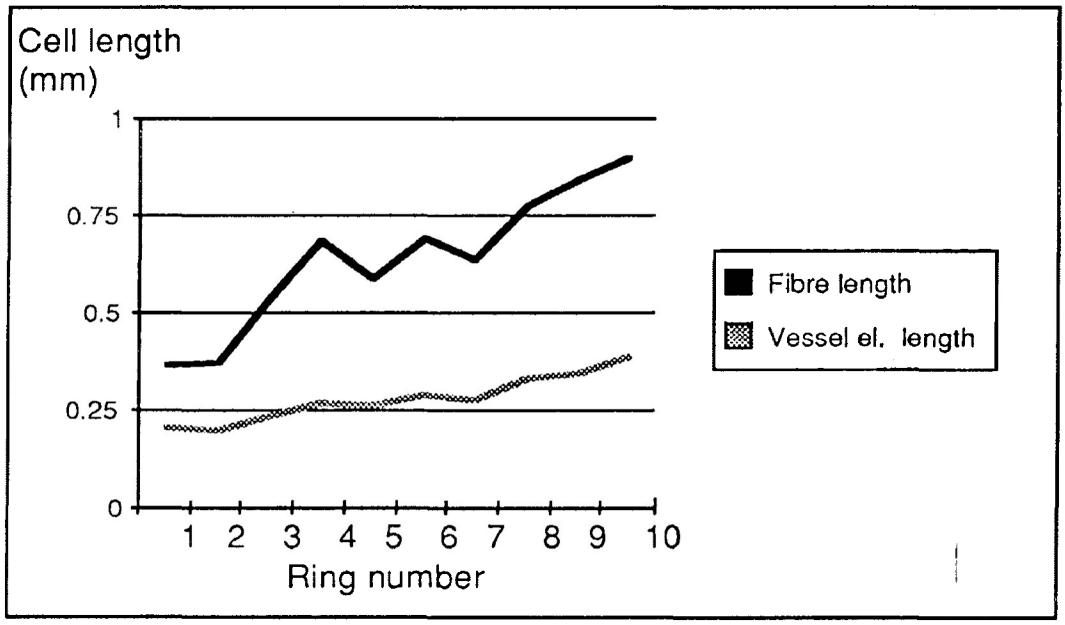

Figure A.4. Radial variation of cell length in the juvenile wood zone.

The regression equations were:

$$FL = 0.332 + 0.0564\ (RN)$$

with R^2 = 89.3%; and,

$$VEL = 0.179 + 0.0190\ (RN)$$

with R^2 = 92.9%.

Microfibril angle

MFA decreased steadily with the age from the pith. It was nearly 50° degrees in the 1st growth ring, but, in 10th it dropped under 30° with a tendency to approach normal values, more parallel with cell axis (25-30°) (*Figure* A.5.)

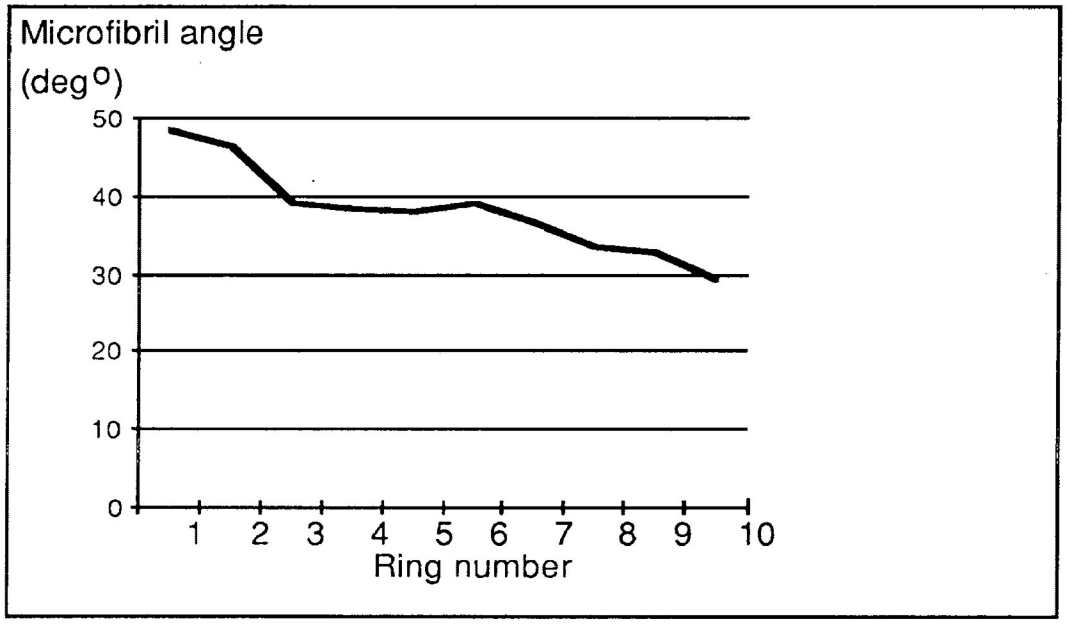

Figure A.5. Radial variation of microfibril angle in the juvenile wood zone.

Regression equation was:

$$MFA = 48.3 - 1.81\ (RN)$$

with $R^2 = 88.3\%$.

Correlations among the wood properties along the radius

As we can see from *Table* A.2. all wood characteristics were correlated with each other. The highest correlation with the ring number from the pith had the cell length and microfibril angle (negative correlation). A highly significant negative correlation was found between the fiber length and microfibril angle. The relative density was more independent of other characteristics than the cell length.

Table A.2. Correlation among the wood properties along the radius.

	RN	RGR	MC%	RD	FL	VEL
RGR	0.836**					
MC%	-0.929**	-0.754**				
RD	-0.604*	-0.686*	0.506			
FL	0.945**	0.759**	-0.900**	-0.686*		
VEL	0.964**	0.721*	-0.922**	-0.619*	0.976**	
MFA	-0.940**	-0.806**	0.898**	0.750**	-0.956**	-0.938**

* - significant at 0.05 level of probability
** - significant at 0.001 level of probability

Discussion

Relative Density

The pattern of variation could be described as, the highest near the pith, although, it was highly variable throughout the juvenile zone. The findings are in agreement with the generalization given by Zobel and van Buijtenen (1989): "Poplars seem to have somewhat higher density near the pith, although, some have a uniform density from pith to bark." High variability, that was found, could be accounted for by other influences, such as tension wood (very common in balsam poplar) or extractives. It was also negatively influenced by growth rate.

For all these reasons, it is hard to connect this pattern with stabilization of variation, in the transition zone from juvenile to mature wood. Relative density could be expected to stabilize more rapidly than fibre length.

Moisture Content

Moisture content showed a decreasing pattern from pith to bark. Fairly steady decrease up to certain age and then a sudden drop was result of a "wet heart". (Kroll *et al.* 1992, Yang 1990, Wallin 1954). The transformation of sapwood into heartwood was found to take place at or after 5 years of age in aspen (Yang and Hazenberg 1991). Moisture content correlations to other wood properties along the radius had here little meaning. It could have been expected to be negatively correlated with relative density, but that was not the case. High negative correlation with cell length was the consequence of the wet heart, since the first few growth rings had the shortest cells.

Cell Length

The pattern of increasing fibre and vessel element length in the juvenile wood zone is common in poplars (Kennedy 1957, Micko 1987). These two patterns were similar for the experimental tree. This is in agreement with general statement of Carlquist (1988) that vessel element length always parallels fibre length. Nevertheless, increase was more rapid for fibre length, which could be the result of subsequent elongation of fibre initials after anticlinal division. There was

no sign of transition from juvenile to mature wood for cell length, i.e., no stabilization of length.

Both lengths were positively correlated with growth rate, and this is not unusual in poplars (Kennedy 1957, Einspahr and Benson 1967). A negative correlation with relative density could imply that longer cells had thinner walls. It is assumed that in diffuse-porous hardwoods the number of vessels formed in an annual ring is closely related to the width of the ring, and that has little direct effect on wood relative density (Zobel and Talbert 1984).

Microfibril Angle

The expected pattern of radial variation in microfibril angle is: the highest angle near the pith with a decrease toward the bark, in the juvenile zone. The pattern in this experiment was almost perfect, hopefully, not as a result of biased measuring. High negative correlation between microfibril angle and fibre length can be expected as a rule. Megraw (1985) wrote that since cellular elongation has essentially ceased by the time deposition of the S_2 wall layer begins, it must be assumed that it is fibril angle that is influenced by fibre length, rather then other way around. Microfibril angle was positively correlated with relative density, but, this relationship was not strong. Since only earlywood fibres were examined in the experiment, it was hard to connect this to variation in cell wall thickness.

In conclusion, it should be emphasized that all wood characteristics were correlated with age from the pith (ring number) in the juvenile zone. These correlations were highly significant, and either positive (radial growth rate, fibre and vessel element length), or negative (moisture content, microfibril angle). Only relative density showed a less significant negative correlation.

All results presented were for specimen taken at the base of the tree, and at higher positions within the stem patterns of radial variation might have been somewhat different.

APPENDIX II

"RAW" EXPERIMENTAL DATA

Cl. No.	HGR	DGR	CGR	RGR	RGR7	Bl.	Prov.	RD	FL	VEL
1	0.70000	0.8625	2.9750	6.0333	6.40	1	1	0.301	.769	.395
2	0.27375	0.2750	1.0125	1.2000	1.40	1	1	0.435	.648	.298
3	0.43500	0.4000	1.3875	2.9333	3.20	1	1	0.359	.675	.323
4	0.50250	0.5125	1.5625	4.1333	4.50	1	1	0.339	.638	.351
5	0.59250	0.7375	2.2750	5.4667	4.90	1	1	0.340	.629	.346
6	0.50875	0.6625	1.9375	4.2333	4.20	1	1	0.326	.758	.394
7	0.53625	0.7625	2.4375	5.0000	5.00	1	1	0.312	.705	.372
8	0.57500	0.6000	1.9125	3.5333	3.30	1	1	0.349	.735	.325
9	0.56875	0.7250	2.2875	4.7333	4.80	1	1	0.364	.626	.352
10	0.69375	0.9125	2.7875	6.5333	6.90	1	1	0.275	.755	.416
11	0.59375	0.7750	2.5250	5.0000	6.00	1	1	0.340	.672	.348
12	0.65250	0.9125	2.9375	5.8333	6.70	1	1	0.313	.824	.444
13	0.54500	0.5250	1.6625	3.5000	3.10	1	1	0.284	.636	.373
14	0.31875	0.3125	0.9625	1.6667	1.70	1	1	0.388	.714	.341
15	0.32375	0.3500	1.1000	1.7333	1.90	1	1	0.405	.635	.340
16	0.39125	0.5375	1.7500	2.4667	2.20	1	1	0.348	.653	.314
17	0.51000	0.6000	1.9875	3.6000	3.00	1	1	0.368	.710	.374
18	0.55500	0.7375	2.2750	5.2667	5.50	1	1	0.324	.682	.325
19	0.58375	0.8625	2.7500	6.0667	5.90	1	1	0.401	.667	.296
20	0.50250	0.5750	1.8750	2.0667	1.90	1	1	0.358	.720	.324
21	0.51625	0.7500	2.3875	4.0333	4.50	1	1	0.334	.692	.368
22	0.47875	0.6250	2.0000	4.0333	3.70	1	1	0.378	.720	.353
23	0.32750	0.2750	1.0875	1.9333	2.10	1	1	0.359	.693	.363
24	0.50250	0.7750	2.5125	4.2333	4.60	1	1	0.339	.805	.417
25	0.46625	0.7125	2.2000	4.3667	5.00	1	1	0.285	.568	.351
26	0.86000	1.3000	4.6250	7.3667	8.00	1	1	0.312	.640	.322
27	0.38875	0.5375	1.6500	2.8667	2.70	1	1	0.383	.631	.339
28	0.62875	0.8375	2.6500	5.3000	5.00	1	1	0.332	.751	.376
29	0.19625	0.3125	1.0625	1.3000	1.80	1	1	0.350	.649	.302
30	0.54125	0.7375	2.3750	3.7000	4.10	1	1	0.334	.605	.366
1	0.54500	0.7500	2.3875	3.9667	3.90	1	2	0.302	.697	.370
2	0.54500	0.6125	1.9875	3.6667	3.00	1	2	0.370	.746	.354
3	0.70875	0.8750	2.7500	5.7667	6.20	1	2	0.313	.765	.406
4	0.62500	0.7875	2.6000	4.6333	4.90	1	2	0.346	.678	.311
5	0.54875	0.5375	1.7625	2.9333	3.50	1	2	0.375	.650	.308
6	0.72125	0.7875	2.5375	5.3667	5.50	1	2	0.320	.678	.380
7	0.42625	0.5000	1.6125	3.3333	3.40	1	2	0.346	.648	.312
8	0.52500	0.6125	1.9625	4.4333	3.90	1	2	0.308	.635	.328
9	0.53625	0.6375	2.0250	3.8333	3.50	1	2	0.352	.677	.324
10	0.67125	0.8000	2.6000	5.5667	5.70	1	2	0.328	.649	.384
11	0.52250	0.5500	1.7750	3.4333	3.60	1	2	0.334	.581	.330
12	0.51875	0.5125	1.6750	3.7000	4.70	1	2	0.313	.556	.303
13	0.53625	0.5125	1.6625	2.6667	3.20	1	2	0.331	.678	.332
14	0.68750	0.7750	2.4125	5.2000	4.80	1	2	0.335	.722	.391
15	0.68500	0.8125	2.5625	4.5000	3.80	1	2	0.335	.610	.355
16	0.52125	0.6125	1.9500	3.3333	3.40	1	2	0.303	.629	.328
17	0.57250	0.5875	1.9375	3.5333	3.10	1	2	0.378	.665	.335
18	0.68625	0.7750	2.5500	5.4000	4.60	1	2	0.342	.748	.375
19	0.57625	0.9000	2.9625	5.3667	4.60	1	2	0.333	.686	.358
20	0.70250	0.9375	3.1375	5.9333	4.80	1	2	0.333	.707	.363
21	0.68500	0.9000	3.0375	5.5333	6.40	1	2	0.298	.749	.431
22	0.75375	0.9125	3.0375	4.5667	3.70	1	2	0.305	.693	.342
23	0.41250	0.5250	1.7625	3.1000	3.40	1	2	0.366	.646	.340
24	0.40250	0.4500	1.5250	2.3000	2.10	1	2	0.333	.601	.291

25	0.46625	0.6875	2.2625	3.9667	3.70	1	2	0.308	.723	.379
26	0.56125	0.8625	2.7875	4.9333	4.60	1	2	0.301	.694	.361
27	0.40750	0.5125	1.7000	2.7333	3.30	1	2	0.333	.582	.302
28	0.45250	0.5875	1.9000	3.0000	3.30	1	2	0.339	.699	.294
29	0.53125	0.6500	2.1375	3.6333	3.50	1	2	0.312	.712	.382
30	0.59125	0.7875	2.5250	5.2000	5.70	1	2	0.332	.682	.367

Cl. No.	HGR	DGR	CGR	RGR	RGR7	Bl.	Prov.	RD	FL	VEL
1	0.79250	1.1500	3.5375	8.6000	9.80	1	3	0.327	.692	.433
2	0.95375	1.0250	3.3000	7.8000	8.40	1	3	0.314	.678	.387
3	0.63125	0.8875	2.6250	5.7000	7.30	1	3	0.316	.684	.343
4	0.99375	1.2000	4.0125	8.4667	8.50	1	3	0.301	.760	.418
5	0.76625	0.7750	2.4500	5.2333	6.80	1	3	0.327	.751	.367
6	1.02250	1.2750	3.9750	11.5333	13.10	1	3	0.247	.629	.406
7	0.77750	0.7625	2.3375	4.3667	3.50	1	3	0.319	.769	.446
8	1.07500	1.2375	3.8125	10.3333	10.30	1	3	0.281	.711	.398
9	0.94625	1.2125	3.7500	9.5333	12.90	1	3	0.270	.627	.392
10	0.94125	1.0125	3.2625	8.0333	8.20	1	3	0.295	.777	.456
11	1.02750	1.0875	3.4375	7.9000	7.20	1	3	0.301	.734	.386
12	0.91500	1.3000	4.1875	9.6333	10.20	1	3	0.296	.693	.368
13	0.97750	0.8000	2.4125	6.7667	7.60	1	3	0.284	.657	.384
14	0.93750	0.7625	2.4625	6.1667	7.50	1	3	0.321	.653	.363
15	0.94250	1.0000	3.0750	8.1333	8.20	1	3	0.298	.721	.422
16	1.01375	1.2500	3.9000	8.9000	8.80	1	3	0.269	.681	.390
17	0.84125	1.1750	3.7000	8.0333	9.60	1	3	0.316	.786	.444
18	0.82375	1.1625	3.6125	9.2000	8.90	1	3	0.257	.809	.467
19	1.03125	1.4875	4.6125	10.3333	13.30	1	3	0.289	.684	.473
20	0.70750	0.8250	2.5375	4.2667	5.10	1	3	0.317	.732	.426
21	1.00250	1.0750	3.5375	6.8333	7.50	1	3	0.339	.770	.394
22	0.95500	1.0125	3.1625	7.3667	6.80	1	3	0.272	.807	.402
23	0.84625	1.0000	3.0625	5.7333	8.60	1	3	0.349	.679	.292
24	1.01875	1.4125	4.3750	10.5000	11.40	1	3	0.291	.699	.436
25	0.95125	1.4000	4.1125	8.5667	8.90	1	3	0.276	.672	.411
26	0.98125	1.1875	3.6875	7.8333	9.20	1	3	0.268	.739	.445
27	0.97375	1.0500	3.3500	6.6667	7.00	1	3	0.316	.690	.396
28	1.04500	1.2875	4.1375	8.2333	8.10	1	3	0.290	.734	.454
29	0.94000	1.2625	4.0250	9.2333	11.60	1	3	0.321	.709	.312
30	0.63500	0.6750	2.1875	3.7333	5.30	1	3	0.336	.626	.365
1	0.29000	0.3200	1.0200	1.2667	1.10	2	1	0.381	.584	.330
2	0.29700	0.4400	1.4300	2.5667	2.70	2	1	0.407	.577	.314
3	0.40700	0.4600	1.5200	2.2000	2.60	2	1	0.351	.589	.280
4	0.28100	0.3400	1.1100	1.8000	2.00	2	1	0.342	.524	.308
5	0.36900	0.4800	1.6200	2.5667	2.80	2	1	0.439	.560	.295
6	0.44200	0.7800	2.6500	4.9000	4.70	2	1	0.318	.703	.381
7	0.44500	0.6000	1.9900	3.4000	4.80	2	1	0.305	.566	.316
8	0.34700	0.4100	1.3300	1.7333	1.90	2	1	0.311	.564	.293
9	0.30200	0.3500	1.0900	1.6000	1.80	2	1	0.378	.503	.239
10	0.33300	0.3400	1.1200	1.5667	1.60	2	1	0.384	.588	.282
11	0.26500	0.3000	0.9800	1.2667	1.40	2	1	0.416	.495	.226
12	0.33000	0.4100	1.2900	1.8333	1.50	2	1	0.340	.655	.311
13	0.25100	0.2600	0.8200	1.4000	1.70	2	1	0.296	.530	.262
14	0.34700	0.4100	1.2800	2.0333	2.70	2	1	0.374	.619	.265
15	0.39100	0.4900	1.6400	2.5333	2.70	2	1	0.404	.628	.330
16	0.33400	0.4700	1.5500	2.2000	2.40	2	1	0.349	.709	.396
17	0.20300	0.2200	0.7400	0.9667	1.00	2	1	0.434	.606	.316
18	0.39500	0.5500	1.7800	2.4667	2.30	2	1	0.374	.667	.333

19	0.45200	0.5300	1.7700	2.4667	2.90	2	1	0.343	.645	.320
20	0.41500	0.4500	1.4400	2.0667	1.80	2	1	0.374	.700	.333
21	0.37600	0.5100	1.7800	2.5333	2.50	2	1	0.380	.638	.334
22	0.39900	0.5500	1.8200	2.0000	2.00	2	1	0.350	.723	.416
23	0.26700	0.3700	1.3000	1.8667	2.40	2	1	0.448	.660	.376
24	0.44800	0.6500	2.1600	3.2000	3.70	2	1	0.348	.693	.433
25	0.39200	0.4600	1.4100	2.1333	2.60	2	1	0.309	.582	.397
26	0.25000	0.3400	1.1200	2.0000	2.30	2	1	0.368	.578	.379
27	0.32100	0.4500	1.4800	2.3333	2.10	2	1	0.434	.677	.310
28	0.62300	0.9000	3.0000	4.8000	5.20	2	1	0.331	.666	.350
29	0.24200	0.3200	1.1000	1.4000	1.70	2	1	0.367	.672	.364
30	0.38500	0.4700	1.5400	2.2667	2.00	2	1	0.374	.547	.336

Cl. No.	HGR	DGR	CGR	RGR	RGR7	Bl.	Prov.	RD	FL	VEL
1	0.34300	0.4500	1.5100	2.8000	3.30	2	2	0.323	.603	.311
2	0.22300	0.2500	0.8500	1.8667	2.00	2	2	0.412	.534	.286
3	0.34700	0.4600	1.4700	2.7667	3.40	2	2	0.383	.600	.323
4	0.23400	0.3000	0.9700	1.7333	2.10	2	2	0.425	.559	.266
5	0.22700	0.2500	0.7800	1.2000	1.60	2	2	0.393	.578	.293
6	0.48800	0.5000	1.7100	3.1667	4.10	2	2	0.374	.626	.335
7	0.24300	0.3300	1.0800	2.1000	2.90	2	2	0.374	.539	.293
8	0.16200	0.2000	0.6400	1.1000	1.10	2	2	0.376	.572	.305
9	0.32500	0.4500	1.4000	2.7667	3.40	2	2	0.394	.580	.292
10	0.25200	0.3000	1.0000	1.8667	1.90	2	2	0.429	.494	.230
11	0.24700	0.2900	0.9500	1.3667	1.70	2	2	0.415	.504	.289
12	0.20500	0.2300	0.7800	1.2333	1.20	2	2	0.411	.532	.260
13	0.23500	0.2700	0.8500	1.3333	1.50	2	2	0.364	.601	.317
14	0.25300	0.1800	0.9000	1.6667	1.70	2	2	0.398	.532	.275
15	0.26400	0.3600	1.1700	2.2667	3.30	2	2	0.381	.583	.306
16	0.30500	0.4700	1.5300	2.5000	2.70	2	2	0.323	.595	.305
17	0.23400	0.2900	1.0100	1.6667	1.80	2	2	0.403	.523	.258
18	0.32100	0.4000	1.3600	1.9333	2.40	2	2	0.371	.593	.271
19	0.27200	0.4100	1.3200	2.2333	3.90	2	2	0.373	.549	.265
20	0.20800	0.2400	0.8300	1.2000	1.10	2	2	0.392	.504	.256
21	0.33900	0.4600	1.5600	3.2000	2.40	2	2	0.357	.675	.366
22	0.31000	0.3000	1.0500	1.6000	2.00	2	2	0.386	.596	.314
23	0.22800	0.3200	1.0700	1.8667	2.60	2	2	0.370	.597	.297
24	0.28100	0.2100	0.6900	0.5000	0.80	2	2	0.370	.543	.252
25	0.18200	0.2300	0.8000	1.1000	0.80	2	2	0.367	.545	.271
26	0.16400	0.2500	0.9500	1.1000	1.10	2	2	0.413	.512	.246
27	0.26500	0.3700	1.2400	2.1667	2.80	2	2	0.366	.555	.266
28	0.27600	0.4600	1.4300	2.2667	3.00	2	2	0.348	.579	.270
29	0.20300	0.2900	1.0000	1.6667	1.90	2	2	0.357	.597	.285
30	0.17000	0.1900	0.6200	0.9000	0.70	2	2	0.395	.482	.237
1	0.38400	0.6000	1.9300	3.5000	4.30	2	3	0.395	.696	.342
2	0.23100	0.2800	0.9400	0.7333	0.80	2	3	0.396	.556	.281
3	0.37000	0.4300	1.4400	2.2333	2.20	2	3	0.344	.558	.295
4	0.51500	0.6700	2.1600	4.5333	4.00	2	3	0.367	.610	.294
5	0.31400	0.3500	1.1700	2.3333	2.00	2	3	0.359	.599	.300
6	0.26200	0.3500	1.1800	1.9667	1.50	2	3	0.352	.541	.295
7	0.20500	0.1500	0.8300	1.1333	0.90	2	3	0.358	.601	.350
8	0.25200	0.4400	1.5000	3.3333	3.70	2	3	0.390	.470	.240
9	0.25500	0.3000	1.0100	1.0000	1.00	2	3	0.357	.565	.301
10	0.28300	0.4000	1.2900	1.9667	2.20	2	3	0.404	.541	.277
11	0.19000	0.2700	0.8200	0.9667	0.60	2	3	0.404	.564	.251
12	0.31500	0.5500	1.9200	3.0667	3.70	2	3	0.416	.690	.278

13	0.25500	0.2800	1.0000	1.0333	1.00	2	3	0.371	.574	.275
14	0.29200	0.3300	1.0600	1.0333	1.10	2	3	0.414	.583	.338
15	0.27600	0.3200	1.0500	1.4000	1.30	2	3	0.436	.640	.335
16	0.39800	0.5100	1.6500	2.9000	2.20	2	3	0.304	.567	.361
17	0.35900	0.6200	2.0600	3.4667	3.30	2	3	0.395	.650	.345
18	0.36000	0.5500	1.7700	2.8667	3.20	2	3	0.383	.605	.293
19	0.45600	0.6000	2.0600	3.4000	3.30	2	3	0.380	.666	.351
20	0.49700	0.6200	2.0200	2.9000	2.80	2	3	0.332	.646	.380
21	0.32400	0.3400	1.1000	0.9333	0.60	2	3	0.378	.634	.327
22	0.30700	0.4000	1.3400	1.6333	1.50	2	3	0.342	.678	.361
23	0.45200	0.5400	1.7400	2.4000	1.80	2	3	0.375	.622	.314
24	0.41800	0.6400	2.1600	3.1667	2.10	2	3	0.393	.613	.384
25	0.36400	0.4200	1.3500	1.8333	1.90	2	3	0.358	.615	.323
26	0.28300	0.3600	1.1400	1.9000	1.60	2	3	0.377	.642	.299
27	0.21300	0.2300	0.7400	0.6667	0.90	2	3	0.413	.559	.299
28	0.30300	0.3100	1.0000	1.4333	1.20	2	3	0.390	.587	.276
29	0.16900	0.3700	1.2400	1.4333	1.10	2	3	0.361	.535	.271
30	0.39000	0.4200	1.4500	1.9667	2.10	2	3	0.325	.697	.379

Cl. No.	HGR	DGR	CGR	RGR	RGR7	Bl.	Prov.	RD	FL	VEL
1	0.29500	0.4000	1.2400	2.5333	3.30	3	1	0.328	.565	.326
2	0.52000	0.8100	2.5900	4.9333	6.00	3	1	0.360	.688	.372
3	0.52200	0.7500	2.3800	4.7333	6.70	3	1	0.306	.609	.310
4	0.21000	0.2900	0.9700	1.2667	1.10	3	1	0.403	.535	.330
5	0.25100	0.2700	0.8500	1.2667	1.90	3	1	0.398	.561	.364
6	0.21700	0.3400	1.1000	1.0667	1.30	3	1	0.386	.636	.378
7	0.29300	0.4800	1.4800	2.0667	2.00	3	1	0.317	.678	.360
8	0.41500	0.5800	1.7600	3.7667	4.50	3	1	0.307	.654	.372
9	0.30300	0.4300	1.3200	3.2667	2.80	3	1	0.403	.538	.248
10	0.20000	0.2300	0.7200	2.1000	1.60	3	1	0.297	.587	.312
11	0.37100	0.4700	1.5100	3.0333	3.90	3	1	0.313	.529	.282
12	0.24600	0.3400	1.0600	1.7000	2.90	3	1	0.319	.619	.332
13	0.44100	0.5900	1.8600	3.7000	3.70	3	1	0.280	.579	.359
14	0.21700	0.2400	0.7600	1.3667	1.70	3	1	0.328	.505	.292
15	0.22700	0.3100	0.9700	2.2000	2.10	3	1	0.426	.586	.277
16	0.29700	0.4500	1.5200	2.5667	2.40	3	1	0.373	.631	.348
17	0.18900	0.2500	0.8500	1.0667	1.20	3	1	0.409	.498	.262
18	0.28600	0.3200	1.0600	1.8000	1.90	3	1	0.370	.521	.267
19	0.49000	0.7000	2.4200	4.1333	5.30	3	1	0.349	.597	.301
20	0.32900	0.4400	1.4300	2.1333	2.20	3	1	0.383	.612	.301
21	0.27300	0.3100	1.0400	1.9667	1.81	3	1	0.392	.519	.291
22	0.48500	0.5900	1.9500	3.3667	4.50	3	1	0.406	.625	.254
23	0.33700	0.3400	1.1200	1.4333	1.90	3	1	0.416	.559	.284
24	0.19700	0.2900	1.0100	1.2000	1.60	3	1	0.398	.573	.330
25	0.32500	0.4900	1.5400	2.8667	3.20	3	1	0.350	.574	.310
26	0.24600	0.3100	1.0200	1.4000	1.30	3	1	0.398	.524	.288
27	0.33900	0.4700	1.5800	1.8333	2.20	3	1	0.409	.632	.321
28	0.38800	0.4800	1.5200	1.7000	1.60	3	1	0.349	.594	.334
29	0.24600	0.3400	1.1200	1.3000	1.10	3	1	0.471	.578	.242
30	0.24900	0.3600	1.2000	2.5333	1.40	3	1	0.364	.638	.346
1	0.29900	0.3300	1.0200	1.8667	2.30	3	2	0.354	.553	.305
2	0.25600	0.3500	1.0900	1.4000	1.40	3	2	0.419	.673	.345
3	0.33700	0.5000	1.5200	2.6000	2.70	3	2	0.385	.670	.395
4	0.16900	0.3000	1.0000	1.2333	1.20	3	2	0.412	.610	.300
5	0.26900	0.3200	1.0600	1.5667	1.40	3	2	0.434	.625	.292
6	0.30000	0.3500	1.1300	1.7000	1.60	3	2	0.446	.599	.300

7	0.13300	0.2200	0.6900	1.2000	1.00	3	2	0.456	.487	.284
8	0.12700	0.1700	0.5800	1.4667	2.10	3	2	0.337	.554	.284
9	0.25400	0.3700	1.1500	2.3667	2.40	3	2	0.365	.544	.290
10	0.23800	0.3200	1.0900	2.0000	1.50	3	2	0.394	.491	.268
11	0.19500	0.2400	0.9200	1.7667	2.00	3	2	0.421	.468	.257
12	0.25300	0.3100	1.0000	1.8667	2.10	3	2	0.418	.561	.233
13	0.23500	0.2800	0.9100	1.7667	1.70	3	2	0.363	.553	.298
14	0.20600	0.3000	0.9700	1.3667	1.50	3	2	0.408	.565	.300
15	0.17200	0.2500	0.7800	1.3000	1.10	3	2	0.413	.532	.269
16	0.32600	0.5800	1.8400	2.4333	2.70	3	2	0.362	.616	.319
17	0.11100	0.1700	0.5700	1.0000	0.80	3	2	0.414	.476	.288
18	0.24400	0.2700	0.9500	1.2333	1.60	3	2	0.430	.629	.365
19	0.27200	0.3700	1.2400	1.8667	2.00	3	2	0.386	.587	.318
20	0.21600	0.4300	1.4600	2.7667	3.30	3	2	0.430	.568	.276
21	0.41200	0.5000	1.6200	2.4667	3.00	3	2	0.373	.651	.404
22	0.23100	0.3200	1.1100	1.8667	1.90	3	2	0.421	.598	.282
23	0.24100	0.3700	1.2300	2.0667	2.00	3	2	0.380	.581	.314
24	0.15900	0.2300	0.7900	0.9333	1.30	3	2	0.390	.514	.255
25	0.25800	0.3000	0.9800	1.8000	2.00	3	2	0.380	.596	.327
26	0.22900	0.2800	0.9700	1.7000	1.50	3	2	0.340	.543	.320
27	0.21800	0.2800	0.9700	1.1333	1.00	3	2	0.401	.533	.267
28	0.30900	0.4600	1.5200	1.9333	3.30	3	2	0.387	.628	.373
29	0.31000	0.4700	1.5300	2.8333	2.60	3	2	0.348	.730	.391
30	0.22700	0.3300	1.1100	1.8333	1.60	3	2	0.380	.705	.384

Cl. No.	HGR	DGR	CGR	RGR	RGR7	Bl.	Prov.	RD	FL	VEL
1	0.49400	0.6100	1.7200	3.7000	4.20	3	3	0.342	.662	.354
2	0.49600	0.6400	1.9200	2.9667	2.90	3	3	0.411	.675	.296
3	0.58400	0.7200	2.2300	4.6000	4.80	3	3	0.305	.564	.298
4	0.64100	0.7700	2.3000	4.5000	4.60	3	3	0.359	.601	.326
5	0.27800	0.3000	0.9800	1.3667	2.10	3	3	0.367	.560	.292
6	0.52900	0.7200	2.1400	4.8333	5.10	3	3	0.362	.581	.353
7	0.55100	0.6500	1.9500	4.2333	4.10	3	3	0.305	.754	.420
8	0.64900	0.8200	2.5500	5.5000	5.80	3	3	0.307	.585	.332
9	0.57000	0.8100	2.3800	4.3333	5.60	3	3	0.331	.644	.373
10	0.70500	0.9500	3.0200	5.4000	7.70	3	3	0.354	.744	.370
11	0.56200	0.7900	2.3700	4.5667	4.60	3	3	0.381	.648	.331
12	0.45600	0.4200	1.3500	2.4000	3.40	3	3	0.352	.617	.288
13	0.61500	0.7500	2.2300	4.6333	5.20	3	3	0.303	.627	.312
14	0.48000	0.5500	1.7400	3.0000	3.50	3	3	0.389	.635	.314
15	0.54300	0.6000	1.8200	3.4333	3.60	3	3	0.389	.643	.328
16	0.55900	0.6600	2.1600	4.9667	6.30	3	3	0.303	.551	.330
17	0.49900	0.5600	1.7800	2.9667	3.00	3	3	0.375	.638	.353
18	0.25800	0.3000	1.0500	1.8333	2.40	3	3	0.295	.611	.322
19	0.58000	0.6100	1.9800	3.1667	3.50	3	3	0.425	.655	.320
20	0.38300	0.4700	1.5700	3.4667	3.70	3	3	0.361	.567	.332
21	0.52100	0.6100	2.0200	3.3000	3.10	3	3	0.362	.666	.350
22	0.60700	0.8900	2.8500	5.0667	5.80	3	3	0.316	.674	.386
23	0.66600	0.8700	2.8200	5.3000	6.70	3	3	0.348	.602	.320
24	0.78100	1.3600	4.4000	7.0667	7.30	3	3	0.319	.712	.390
25	0.65700	0.8000	2.5400	4.8333	5.40	3	3	0.330	.608	.350
26	0.56200	0.6800	2.2500	3.1333	4.70	3	3	0.314	.622	.369
27	0.45700	0.4800	1.5700	2.8333	3.60	3	3	0.333	.585	.354
28	0.59000	0.8300	2.6000	4.7333	5.20	3	3	0.348	.647	.418
29	0.60400	0.7500	2.4200	5.4667	5.20	3	3	0.336	.579	.340
30	0.53800	0.6200	2.1500	3.9000	4.00	3	3	0.325	.687	.366

1	0.39500	0.5000	1.6000	2.2667	2.30	4	1	0.368	.688	.392
2	0.71100	0.9900	2.9900	4.3667	5.20	4	1	0.398	.704	.407
3	0.31800	0.3000	0.9800	1.6000	1.90	4	1	0.364	.529	.278
4	0.55000	0.6600	2.1300	3.0667	4.50	4	1	0.343	.570	.382
5	0.31900	0.3100	1.0200	2.3667	2.50	4	1	0.354	.530	.299
6	0.25500	0.3000	0.9800	1.1000	1.90	4	1	0.368	.567	.382
7	0.35000	0.3400	1.0300	2.4000	3.30	4	1	0.301	.512	.307
8	0.55600	0.6900	2.2200	3.5333	3.90	4	1	0.352	.685	.356
9	0.44700	0.5600	1.7700	2.9667	4.10	4	1	0.373	.557	.318
10	0.53800	0.5100	1.6200	2.7333	3.60	4	1	0.332	.642	.335
11	0.53700	0.9700	2.9400	5.3667	6.70	4	1	0.359	.565	.313
12	0.56000	1.0200	3.1700	6.3000	8.40	4	1	0.342	.694	.340
13	0.33300	0.5000	1.6200	2.8000	3.40	4	1	0.288	.575	.326
14	0.46800	0.5100	1.7000	3.1333	4.00	4	1	0.352	.621	.345
15	0.45400	0.6000	2.0100	2.7667	3.50	4	1	0.399	.688	.365
16	0.55600	0.8800	2.9700	3.8333	5.00	4	1	0.335	.836	.437
17	0.44900	0.5100	1.7200	3.0667	3.00	4	1	0.367	.666	.362
18	0.60200	0.9800	3.0400	5.7667	8.90	4	1	0.323	.694	.367
19	0.71300	1.0400	3.3300	5.0000	6.80	4	1	0.313	.699	.361
20	0.40700	0.4600	1.5200	2.7333	2.70	4	1	0.352	.746	.326
21	0.29000	0.4800	1.6300	2.1333	2.30	4	1	0.361	.578	.334
22	0.49300	0.7900	2.5500	4.4667	5.50	4	1	0.353	.715	.355
23	0.43900	0.6800	2.1200	3.5333	4.10	4	1	0.404	.646	.344
24	0.38900	0.5600	1.8100	2.6333	1.70	4	1	0.353	.629	.369
25	0.34000	0.4400	1.4500	2.2000	3.40	4	1	0.296	.617	.282
26	0.48100	0.6700	2.0800	3.6000	3.90	4	1	0.355	.590	.307
27	0.53200	0.8800	2.8200	4.7667	6.10	4	1	0.393	.657	.322
28	0.47000	0.6100	2.2500	4.0000	5.80	4	1	0.342	.661	.341
29	0.46400	0.7500	2.3500	4.1000	4.50	4	1	0.349	.747	.322
30	0.42200	0.5100	1.6300	2.2333	3.10	4	1	0.337	.606	.297

Cl. No.	HGR	DGR	CGR	RGR	RGR7	Bl.	Prov.	RD	FL	VEL
1	0.35000	0.4600	1.5500	2.0000	2.40	4	2	0.346	.603	.318
2	0.36400	0.4200	1.3700	2.3000	2.10	4	2	0.387	.617	.374
3	0.25000	0.3100	1.0300	1.5667	1.80	4	2	0.372	.596	.321
4	0.20600	0.3000	0.9700	1.3667	1.80	4	2	0.380	.612	.295
5	0.38500	0.4500	1.4200	2.3667	3.10	4	2	0.366	.545	.308
6	0.40000	0.4500	1.4700	2.7333	2.60	4	2	0.388	.604	.347
7	0.18300	0.2200	0.6700	1.0667	1.30	4	2	0.379	.486	.246
8	0.17000	0.2000	0.6900	1.9000	1.90	4	2	0.351	.494	.257
9	0.19800	0.2700	0.8600	1.2333	1.00	4	2	0.395	.458	.253
10	0.25600	0.2600	0.8600	1.1000	1.30	4	2	0.423	.488	.272
11	0.34400	0.4200	1.3800	1.7000	2.00	4	2	0.360	.597	.317
12	0.39600	0.4800	1.5800	2.4000	2.50	4	2	0.368	.606	.267
13	0.27600	0.4300	1.3600	2.4000	2.40	4	2	0.376	.613	.364
14	0.24000	0.3000	1.0000	1.7667	1.70	4	2	0.437	.516	.264
15	0.32000	0.3600	1.1700	2.5000	3.20	4	2	0.388	.581	.288
16	0.23400	0.3200	1.1100	2.1333	2.20	4	2	0.339	.496	.260
17	0.19000	0.2700	0.8700	1.2667	1.10	4	2	0.401	.539	.290
18	0.27300	0.4000	1.3200	1.9000	1.50	4	2	0.378	.555	.331
19	0.31400	0.4100	1.3200	2.0000	1.90	4	2	0.380	.619	.305
20	0.36300	0.4700	1.5200	2.5333	2.20	4	2	0.395	.633	.322
21	0.30600	0.4400	1.4300	2.3667	2.60	4	2	0.346	.646	.381
22	0.42000	0.5200	1.7300	3.3000	3.50	4	2	0.399	.580	.284
23	0.22900	0.4500	1.3600	2.3667	2.30	4	2	0.375	.490	.290
24	0.21300	0.2200	0.7700	0.8000	0.90	4	2	0.386	.527	.289

25	0.33800	0.5300	1.7600	2.8333	2.90	4	2	0.347	.600	.357
26	0.32400	0.5000	1.6500	2.6000	2.80	4	2	0.329	.656	.359
27	0.25500	0.3700	1.2200	1.7667	1.60	4	2	0.367	.555	.313
28	0.21100	0.3000	1.0000	1.3667	1.50	4	2	0.380	.481	.287
29	0.32700	0.5600	1.7800	3.3000	4.10	4	2	0.380	.537	.275
30	0.33600	0.4800	1.5000	2.5000	2.60	4	2	0.362	.541	.267
1	0.31100	0.4200	1.3200	2.5000	2.30	4	3	0.380	.579	.326
2	0.46300	0.5600	1.8400	2.6333	3.10	4	3	0.396	.678	.294
3	0.48600	0.6000	1.9800	3.8333	5.50	4	3	0.331	.607	.327
4	0.79500	1.3600	4.1500	7.7667	10.30	4	3	0.334	.638	.279
5	0.40700	0.4900	1.1630	2.8333	3.40	4	3	0.364	.610	.315
6	0.61700	0.8600	2.8200	6.5333	7.10	4	3	0.281	.662	.403
7	0.46100	0.4900	1.6900	2.8667	3.30	4	3	0.330	.715	.436
8	0.67800	0.9700	3.2300	5.9333	6.60	4	3	0.318	.605	.344
9	0.61600	0.9200	2.8500	5.6667	8.00	4	3	0.308	.616	.381
10	0.73400	1.2400	4.0400	7.1000	7.60	4	3	0.354	.685	.400
11	0.32100	0.3700	1.2200	2.2333	2.90	4	3	0.414	.601	.326
12	0.45700	0.5900	2.0100	3.4000	3.90	4	3	0.352	.649	.400
13	0.60200	0.6700	2.1300	4.3667	4.70	4	3	0.343	.552	.303
14	0.67800	0.6700	2.1800	4.4000	5.00	4	3	0.398	.718	.429
15	0.53900	0.7500	2.4200	4.2000	5.40	4	3	0.389	.642	.341
16	0.61700	0.8300	2.5900	5.6667	5.80	4	3	0.292	.558	.300
17	0.46500	0.5400	1.7500	3.2333	3.00	4	3	0.364	.590	.301
18	0.36300	0.5600	1.8800	3.1000	3.70	4	3	0.336	.556	.324
19	0.34100	0.3700	1.2300	2.4333	3.00	4	3	0.408	.501	.275
20	0.48900	0.5700	1.8700	2.7000	3.80	4	3	0.326	.494	.304
21	0.65200	0.9400	3.1200	6.5000	7.60	4	3	0.406	.673	.364
22	0.47800	0.8400	2.7100	5.4333	6.10	4	3	0.330	.643	.330
23	0.43800	0.5500	1.7500	2.5333	2.80	4	3	0.364	.562	.342
24	0.40200	0.4600	1.4900	2.3333	2.70	4	3	0.350	.506	.309
25	0.66400	0.9500	3.1300	5.1667	6.50	4	3	0.313	.567	.367
26	0.64000	1.0800	3.5000	6.8667	8.50	4	3	0.312	.671	.392
27	0.45000	0.4800	1.5600	3.2333	3.50	4	3	0.347	.587	.313
28	0.46700	0.4000	1.3400	1.6333	1.70	4	3	0.358	.538	.301
29	0.47800	0.7100	2.3400	3.0667	2.90	4	3	0.363	.603	.332
30	0.29100	0.5100	1.6700	3.6667	4.00	4	3	0.361	.565	.277

APPENDIX III

ANALYSES OF VARIANCE FOR THE 9 VARIABLES

Table A 3.1a. The first (provenance) level analysis of variance for the variable height growth rate (HGR)

Source	DF	SS	MS	F	p
Block	3	0.2182	0.0727	no test	
Provenance	2	0.1162	0.0581	5.54	0.043
Error (BxP)	6	0.0629	0.0105		
Total	11	0.3973			

Table A.3.1b. The second (clonal) level analyses of variance for the variable height growth rate (HGR) in each of the three provenances

	Source	DF	SS	MS	F	p
North Wisconsin						
	Block	3	5.52049	1.84016	no test	
	Clone	29	0.57936	0.01998	1.87	0.014
	Error (BxC)	87	0.92860	0.01067		
	Total	119	7.02846			
Thunder Bay						
	Block	3	0.74857	0.24952	no test	
	Clone	29	0.38339	0.01322	1.10	0.352
	Error (BxC)	87	1.04149	0.01197		
	Total	119	2.17346			
Pickle Lake						
	Block	3	2.16629	0.72210	no test	
	Clone	29	0.33956	0.01171	2.72	0.000
	Error (BxC)	87	0.37508	0.00431		
	Total	119	2.88093			

Table A.3.2a. The first (provenance) level analysis of variance for the variable diameter growth rate (DGR)

Source	DF	SS	MS	F	p
Block	3	0.2855	0.0952	no test	
Provenance	2	0.1716	0.0858	6.68	0.030
Error (BxP)	6	0.0770	0.0128		
Total	11	0.5341			

Table A.3.2b. The second (clonal) level analyses of variance for the variable diameter growth rate (DGR) in each of the three provenances

	Source	DF	SS	MS	F	p
North Wisconsin						
	Block	3	6.87129	2.29043	no test	
	Clone	29	1.96459	0.06774	1.93	0.010
	Error (BxC)	87	3.04747	0.03503		
	Total	119	11.88335			
Thunder Bay						
	Block	3	1.25986	0.41995	no test	
	Clone	29	1.12524	1.12524	1.08	0.376
	Error (BxC)	87	3.11570	3.11570		
	Total	119	5.50080			
Pickle Lake						
	Block	3	2.73708	0.91236	no test	
	Clone	29	0.63789	0.02110	2.26	0.002
	Error (BxC)	87	0.84550	0.00972		
	Total	119	4.22048			

Table A.3.3a. The first (provenance) level analysis of variance for the variable circumference growth rate (CGR)

Source	DF	SS	MS	F	p
Block	3	2.7418	0.9139	no test	
Provenance	2	1.6115	0.8057	6.99	0.027
Error (BxP)	6	0.6911	0.1152		
Total	11	5.0441			

Table A.3.3b. The second (clonal) level analyses of variance for the variable circumference growth rate (CGR) in each of the three provenances

	Source	DF	SS	MS	F	p
North Wisconsin						
	Block	3	62.4436	20.8145	no test	
	Clone	29	19.0734	0.6577	1.87	0.014
	Error (BxC)	87	30.5376	0.3510		
	Total	119	112.0547			
Thunder Bay						
	Block	3	12.4588	4.1529	no test	
	Clone	29	12.0762	0.4164	1.11	0.341
	Error (BxC)	87	32.5011	0.3736		
	Total	119	57.0362			
Pickle Lake						
	Block	3	28.0903	9.3634	no test	
	Clone	29	6.8834	0.2374	2.49	0.001
	Error (BxC)	87	8.2787	0.0952		
	Total	119	43.2525			

Table A3..4a. The first (provenance) level analysis of variance for the variable radial growth rate (RGR)

Source	DF	SS	MS	F	p
Block	3	17.8931	5.9644	no test	
Provenance	2	9.0963	4.5481	5.39	0.046
Error (BxP)	6	5.0649	0.8441		
Total	11	32.0543			

Table A.3.4b. The second (clonal) level analyses of variance for the variable radial growth rate (RGR) in each of the three provenances

	Source	DF	SS	MS	F	p
North Wisconsin						
	Block	3	506.639	168.880	no test	
	Clone	29	104.045	3.588	1.89	0.012
	Error (BxC)	87	165.083	1.897		
	Total	119	775.767			
Thunder Bay						
	Block	3	64.175	21.392	no test	
	Clone	29	41.838	1.443	0.91	0.596
	Error (BxC)	87	137.367	1.579		
	Total	119	243.380			
Pickle Lake						
	Block	3	119.885	39.962	no test	
	Clone	29	26.073	0.899	1.99	0.008
	Error (BxC)	87	39.269	0.451		
	Total	119	185.227			

Table A.3.5a. The first (provenance) level analysis of variance for the variable radial growth rate in 7th year (RGR7)

Source	DF	SS	MS	F	p
Block	3	19.6781	6.5594	no test	
Provenance	2	12.4623	6.2311	4.04	0.077
Error (BxP)	6	9.2454	1.5409		
Total	11	41.3858			

Table A.3.5b. The second (clonal) level analyses of variance for the variable radial growth rate in 7th year (RGR7) in each of the three provenances

	Source	DF	SS	MS	F	p
North Wisconsin						
	Block	3	677.475	225.825	no test	
	Clone	29	133.338	4.598	1.64	0.041
	Error (BxC)	87	244.083	2.806		
	Total	119	1054.896			
Thunder Bay						
	Block	3	80.726	26.909	no test	
	Clone	29	75.293	2.596	1.09	0.364
	Error (BxC)	87	206.409	2.372		
	Total	119	362.429			
Pickle Lake						
	Block	3	96.435	32.145	no test	
	Clone	29	28.194	0.972	1.44	0.102
	Error (BxC)	87	58.930	0.677		
	Total	119	183.559			

Table A.3.6a. The first (provenance) level analysis of variance for the variable relative density (RD)

Source	DF	SS	MS	F	p
Block	3	0.00449	0.00150	no test	
Provenance	2	0.00154	0.00077	3.73	0.089
Error (BxP)	6	0.00124	0.00021		
Total	11	0.00727			

Table A.3.6b. The second (clonal) level analyses of variance for the variable relative density (RD) in each of the three provenances

	Source	DF	SS	MS	F	p
North Wisconsin						
	Block	3	0.08906	0.02968	no test	
	Clone	29	0.06642	0.00229	4.41	0.000
	Error (BxC)	87	0.04522	0.00052		
	Total	119	0.20070			
Thunder Bay						
	Block	3	0.01214	0.00405	no test	
	Clone	29	0.10433	0.00360	4.61	0.000
	Error (BxC)	87	0.06796	0.00078		
	Total	119	0.18443			
Pickle Lake						
	Block	3	0.06963	0.02331	no test	
	Clone	29	0.04388	0.00151	3.75	0.000
	Error (BxC)	87	0.03514	0.00040		
	Total	119	0.14865			

Table A.3.7a. The first (provenance) level analysis of variance for the variable moisture content (MC%)

Source	DF	SS	MS	F	p
Block	1	7774.8	7774.8	no test	
Provenance	1	5587.4	5587.4	6.62	0.236
Error (BxP)	1	843.8	843.8		
Total	3	14206.0			

Table A.3.7b. The second (clonal) level analyses of variance for the variable moisture content (MC%) in two provenances

	Source	DF	SS	MS	F	p
North Wisconsin						
	Block	1	1748.03	1748.03	no test	
	Clone	14	14573.87	1040.99	3.45	0.014
	Error (BxC)	14	4227.47	301.96		
	Total	29	20549.37			
Thunder Bay						
	Block	1	6870.53	6870.53	no test	
	Clone	14	8456.47	604.03	7.24	0.000
	Error (BxC)	14	1168.47	83.46		
	Total	29	16495.47			

Table A.3.8a. The first (provenance) level analysis of variance for the variable fibre length (FL)

Source	DF	SS	MS	F	p
Block	3	0.01926	0.00642	no test	
Provenance	2	0.00437	0.00218	5.26	0.048
Error (BxP)	6	0.00249	0.00042		
Total	11	0.02612			

Table A.3.8b The second (clonal) level analyses of variance for the variable fibre length (FL)in each of the three provenances

	Source	DF	SS	MS	F	p
North Wisconsin						
	Block	3	0.23160	0.07720	no test	
	Clone	29	0.12125	0.00418	1.63	0.044
	Error (BxC)	87	0.22373	0.00257		
	Total	119	0.57659			
Thunder Bay						
	Block	3	0.16792	0.05597	no test	
	Clone	29	0.21926	0.00756	2.68	0.000
	Error (BxC)	87	0.24514	0.00282		
	Total	119	0.63232			
Pickle Lake						
	Block	3	0.25068	0.08356	no test	
	Clone	29	0.16234	0.00560	2.60	0.000
	Error (BxC)	87	0.18709	0.00215		
	Total	119	0.60011			

Table A.3.9a The first (provenance) level analysis of variance for the variable vessel element length (VEL)

Source	DF	SS	MS	F	p
Block	3	0.00587	0.00196	no test	
Provenance	2	0.00288	0.00144	6.28	0.034
Error (BxP)	6	0.00138	0.00023		
Total	11	0.01014			

Table A.3.9b. The second (clonal) level analyses of variance for the variable vessel element length (VEL) in each of the three provenances

	Source	DF	SS	MS	F	p
North Wisconsin						
	Block	3	0.12748	0.04249	no test	
	Clone	29	0.06690	0.00231	1.66	0.037
	Error (BxC)	87	0.12075	0.00139		
	Total	119	0.31512			
Thunder Bay						
	Block	3	0.02799	0.00933	no test	
	Clone	29	0.06415	0.00221	1.49	0.081
	Error (BxC)	87	0.12915	0.00148		
	Total	119	0.22129			
Pickle Lake						
	Block	3	0.06332	0.02111	no test	
	Clone	29	0.08362	0.00288	3.17	0.000
	Error (BxC)	87	0.07921	0.00091		
	Total	119	0.22615			

APPENDIX IV

VARIANCE-AND COVARIANCE-COMPONENTS

Mean squares (MS), variance components (V.C.), sum of squares cross products (SSCP), mean squares cross products (MSCP), and covariance component (COV.C.) for the PICKLE LAKE provenance:

	MS clone	MS-V.C. error	V.C. clone	sqrt V.C. error	sqrt V.C. clone
H	0.01171	0.00431	0.00185	0.06566	0.04301
D	0.02200	0.00972	0.00307	0.09858	0.05540
C	0.23736	0.09516	0.03555	0.30848	0.18855
GR	0.89910	0.45140	0.11192	0.67186	0.33455
GR7	0.97220	0.67740	0.07370	0.82304	0.27148
RD	0.00151	0.00040	0.00028	0.02010	0.01665
FL	0.00560	0.00215	0.00086	0.04637	0.02936
VL	0.00288	0.00091	0.00049	0.03017	0.02221
	SSCP clone	SSCP error	MSCP clone	MSCP-V.C. error	COV. C. clone
HD	0.37770	0.47240	0.01302	0.00543	0.00190
HC	1.24521	1.47282	0.04294	0.01693	0.00650
HGR	2.37120	2.92826	0.08177	0.03366	0.01203
HGR7	2.39674	3.07299	0.08265	0.03532	0.01183
HRD	-0.00358	-0.05137	-0.00012	-0.00059	0.00012
HFL	0.15099	0.12719	0.00521	0.00146	0.00094
HVL	0.10249	0.08621	0.00353	0.00099	0.00064
DC	2.08000	2.61308	0.07172	0.03004	0.01042
DGR	3.66848	5.01993	0.12650	0.05770	0.01720
DGR7	3.76608	5.05025	0.12986	0.05805	0.01795
DRD	-0.05343	-0.06673	-0.00184	-0.00077	-0.00027
DFL	0.23453	0.18948	0.00809	0.00218	0.00148
DVL	0.15541	0.12486	0.00536	0.00144	0.00098
CGR	11.92130	15.83690	0.41108	0.18203	0.05726
CGR7	11.93740	15.92720	0.41163	0.18307	0.05714
CRD	-0.16860	-0.20810	-0.00581	-0.00239	-0.00086
CFL	0.75950	0.58890	0.02619	0.00677	0.00486
CVL	0.50330	0.38330	0.01736	0.00441	0.00324
GRGR7	24.85840	40.79300	0.85719	0.46889	0.09708
GRRD	-0.23470	-0.48430	-0.00809	-0.00557	-0.00063
GRFL	1.34210	0.96840	0.04628	0.01113	0.00879
GRVL	0.97960	0.71670	0.03378	0.00824	0.00639
GR7RD	-0.33940	-0.55810	-0.01170	-0.00641	-0.00132
GR7FL	1.36080	0.90530	0.04692	0.01041	0.00913
GR7VL	0.96410	0.72820	0.03324	0.00837	0.00622
RDFL	-0.02580	-0.02100	-0.00089	-0.00024	-0.00016
RDVL	-0.02150	-0.01990	-0.00074	-0.00023	-0.00013
FLVL	0.10150	0.08380	0.00350	0.00096	0.00063

Mean squares (MS), variance components (V.C.), sum of squares cross products (SSCP), mean squares cross products (MSCP), and covariance component (COV.C.) for the THUNDER BAY provenance:

	ms clon	ms-v.c error	v.c clon	sqrt v.c. error	sqrt v.c. clon
H	0.01322	0.01197	0.00031	0.10941	0.01767
D	0.03880	0.03581	0.00075	0.18924	0.02733
C	0.41642	0.37358	0.01071	0.61121	0.10349
GR	1.44270	1.57890	-0.03405	1.25654	#NUM!
GR7	2.59630	2.37250	0.05595	1.54029	0.23654
RD	0.00360	0.00078	0.00070	0.02795	0.02653
FL	0.00756	0.00282	0.00119	0.05308	0.03444
VL	0.00221	0.00148	0.00018	0.03853	0.01349
	sscp clon	sscp error	msscp clon	msscp err-v.c	cov.c. clon
HD	0.56337	1.66750	0.01943	0.01917	0.00006
HC	1.81643	5.37310	0.06264	0.06176	0.00022
HGR	3.58485	10.12830	0.12362	0.11642	0.00180
HGR7	4.43818	12.07650	0.15304	0.13881	0.00356
HRD	-0.06575	-0.10120	-0.00227	-0.00116	-0.00028
HFL	0.05212	0.27270	0.00180	0.00313	-0.00033
HVL	0.00157	0.15720	0.00005	0.00181	-0.00044
DC	3.65592	9.96580	0.12607	0.11455	0.00288
DGR	6.28928	19.09410	0.21687	0.21947	-0.00065
DGR7	7.97479	22.74190	0.27499	0.26140	0.00340
DRD	-0.07460	-0.17720	-0.00257	-0.00204	-0.00013
DFL	0.15745	0.47630	0.00543	0.00547	-0.00001
DVL	0.04554	0.27050	0.00157	0.00311	-0.00038
CGR	19.88830	61.16170	0.68580	0.70301	-0.00430
CGR7	24.88300	73.40750	0.85803	0.84376	0.00357
CRD	-0.19350	-0.57400	-0.00667	-0.00660	-0.00002
CFL	0.55190	1.53460	0.01903	0.01764	0.00035
CVL	0.17010	0.84020	0.00587	0.00966	-0.00095
GRGR7	53.86030	158.00900	1.85725	1.81620	0.01026
GRRD	-0.76090	-1.27200	-0.02624	-0.01462	-0.00290
GRFL	0.26110	3.02500	0.00900	0.03477	-0.00644
GRVL	0.05170	1.55800	0.00178	0.01791	-0.00403
GR7RD	-0.98200	-1.70000	-0.03386	-0.01954	-0.00358
GR7FL	0.25260	3.33900	0.00871	0.03838	-0.00742
GR7VL	-0.09100	1.90600	-0.00314	0.02191	-0.00626
RDFL	0.01200	-0.03200	0.00041	-0.00037	0.00020
RDVL	-0.01350	-0.03600	-0.00047	-0.00041	-0.00001
FLVL	0.06719	-0.03212	0.00232	-0.00037	0.00067

Mean squares (MS), variance components (V.C.), sum of squares cross products (SSCP), mean squares cross products (MSCP), and covariance component (COV.C.) for the NORTH WISCONSIN provenance:

	ms clon	v.c. error	v.c clon	sqrt v.c. error	sqrt v.c. clon
H	0.01998	0.01067	0.00233	0.10332	0.04823
D	0.06774	0.03503	0.00818	0.18716	0.09043
C	0.68370	0.35100	0.08317	0.59245	0.28840
GR	3.58770	1.89750	0.42255	1.37750	0.65004
GR7	4.59800	2.80600	0.44800	1.67511	0.66933
RD	0.00229	0.00052	0.00044	0.02280	0.02104
FL	0.00418	0.00257	0.00040	0.05071	0.02006
VL	0.00231	0.00139	0.00023	0.03725	0.01516
	sscp clon	sscp error	msscp clon	msscp err-v.c	cov.c. clon
HD	0.89230	1.35140	0.03077	0.01553	0.00381
HC	2.81078	4.32480	0.09692	0.04971	0.01180
HGR	5.98500	9.70710	0.20638	0.11158	0.02370
HGR7	6.35586	10.01490	0.21917	0.11511	0.02601
HRD	-0.03386	-0.10290	-0.00117	-0.00118	0.00000
HFL	-0.02502	0.25600	-0.00086	0.00294	-0.00095
HVL	0.02045	0.17150	0.00071	0.00197	-0.00032
DC	6.19810	9.52960	0.21373	0.10954	0.02605
DGR	13.11070	20.00260	0.45209	0.22991	0.05554
DGR7	14.25480	22.77570	0.49154	0.26179	0.05744
DRD	-0.10920	-0.13760	-0.00377	-0.00158	-0.00055
DFL	-0.02990	0.43020	-0.00103	0.00494	-0.00149
DVL	0.04870	0.28410	0.00168	0.00327	-0.00040
CGR	41.06770	63.31860	1.41613	0.72780	0.17208
CGR7	44.07310	72.16540	1.51976	0.82949	0.17257
CRD	-0.33210	-0.45010	-0.01145	-0.00517	-0.00157
CFL	-0.02640	1.36310	-0.00091	0.01567	-0.00414
CVL	0.18950	0.93160	0.00653	0.01071	-0.00104
GRGR7	110.16700	182.38800	3.79886	2.09641	0.42561
GRRD	-1.05300	-1.22200	-0.03631	-0.01405	-0.00557
GRFL	-0.52200	2.46900	-0.01800	0.02838	-0.01159
GRVL	0.26200	1.93600	0.00903	0.02225	-0.00330
GR7RD	-1.12800	-1.17100	-0.03890	-0.01346	-0.00636
GR7FL	-0.81600	2.24600	-0.02814	0.02582	-0.01349
GR7VL	0.14200	1.59500	0.00490	0.01833	-0.00336
RDFL	0.02600	-0.01900	0.00090	-0.00022	0.00028
RDVL	-0.01300	-0.03300	-0.00045	-0.00038	-0.00002
FLVL	0.04920	0.10057	0.00170	0.00116	0.00014