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EVALUATION ON HEIGHT AND DIAMETER OF 9-YEAR-OLD PROGENY TEST OF NATIVE ASPENS AND THEIR HYBRIDS IN MICHIGAN

By

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ABSTRACT

EVALUATION ON HEIGHT AND DIAMETER OF 9-YEAR-OLD PROGENY TEST OF NATIVE ASPENS AND THEIR HYBRIDS IN MICHIGAN

By

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An evaluation on trembling aspen (*Populus tremuloides*), bigtooth aspen (*Populus grandidentata*) and their hybrids was undertaken at Water Quality Research Center, Ingham co., Michigan. Progenies of open- and controlled-pollination were generated from trees from Upper and Lower Peninsula. The progenies were planted in two-tree plot in a randomized complete block design with six replications.

The F1 hybrid of trembling and bigtooth aspen was able to establish as fast as their parents. Height and stem diameter of the hybrids was intermediate at the first- and second-year but superior at 7 and 9 years. Progenies with female parent from Lower Peninsula, especially central Lower Peninsula, grew faster than those from Upper Peninsula. Height and diameter was highly correlated. Age-age correlation among ages 1, 2, 7 and 9 years were significant.

An analysis using North Carolina I mating design identified a relatively high genetic variation. The composition of additive and dominance variance changed with age. At 7 and 9 years the genetic variance was dominated by the dominance variance.

To God,
The Almighty
Thank you.

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INTRODUCTION

Trembling aspen (Populus tremuloides) and bigtooth aspen (Populus grandidentata) are dominant species throughout the western Great Lakes area (Henry & Barnes 1977). These species grow sympatrically in Michigan and over a large portion of northeastern United State adjacent to Canada (Pregitzer & Barnes 1980).

Aspens are recognized as multiple-use species. They produce forage and cover for domestic livestock and wildlife, produce wood fiber for pulp, form protective firebreaks, yield high-quality of water, and are aesthetically attractive in the landscape (Debyle and Winokur 19..). Aspen is the most important pulpwood species in Michigan (Blyth & Smith 1982). However, the use of aspen in plantations has been avoided because genetically improved planting stock is not readily available (Reighard 1984). Another reason is the difficulty of cloning superior genotype or producing adequate seed for commercial nurseries (Dickmann 1992, personal communication).

Genetic variation of aspen is quite large. Large variation exists in height/diameter growth rate (Zahner & Crawford 1965, Barnes 1969, Einsphar & Benson 1967, Mitton

& Grant 1980), survival rate (Pauley 1963, Pauley et al. 1963) photoperiod responce (Vaartaja 1960), phenology (Barnes 1969, Brissette & Barnes 1984), specific gravity, fiber length, and chemical content of wood (Buijtenen et al. 1959, Einsphar & Benson 1967), suckering ability of roots (Schier & Chambell 1980, Barnes 1969), rooting ability (Schier 1974, Schier & Chambell 1980) and susceptibility to diseases and insects (Wall 1971, Copony & Barnes 1974).

Johnson (1942) had reported that selection for height and diameter growth appeared to have lack effect on wood quality. This lack of correlation might increase the efficiency of selection for these traits.

Trembling aspen and bigtooth aspen are easy to hybridize (Henry & Barnes 1977). Natural hybridization of these species has been reported by many authors (McComb & Hanson 1954, Einsphar & Joranson 1960, Andrejak & Barnes 1969, Wagner 1970). Natural hybrids were commonly found in extensively disturbed areas and grew together with their parents (Andrejak & Barnes 1969, Wagner 1970, Henry & Barnes 1977).

Artificial hybrids were first produced by Heimburger (1936) and later by Pauley (1963). The ease of hybridization might allow the possibility of enriching variation of these species with new sources of germplasm. The new germplasm may or may not be desirable. It is desired if it has beneficial effects, such as faster growth or more resistance to disease, but undesired if give the opposite effects.

Comparison between native aspen and their hybrids has been reported in flowering phenology (Pregitzer & Barnes, 1980), germination rate (Henry & Barnes 1977), and initial height & diameter growth (Henry & Barnes 1977, Brissette & Barnes 1984, Einsphar & Benson 1964, Reighard 1984). Various results from different studies of initial growth have been reported. Henry & Barnes (1977) reported that during the first 4 months hybrid seedlings grew faster than the progeny of either their parent, but at 6 months-old P.tremuloides was leading, followed by the hybrids, then P.grandidentata. Brissette & Barnes (1984) found that at the end of the first year P.tremuloides was the tallest followed by the hybrids then P.grandidentata, but at the end of the second year P.grandidentata was second and the hybrid was the shortest. A study by Reighard (1984) showed that at the first and second year measurements the hybrid was leading the progeny of either parent. Another study by Einsphar & Benson (1964) showed that, at one and four years old, P.tremuloides was the tallest followed by the hybrids, then P.grandidentata.

The increasing demands for aspens by the forest products industry have developed because of new technology to use aspen for products other than the traditional pulp and paper (Reighard 1984). The potency of aspen for genetic improvement (ease of hybridization and large genetic variation) and the lack of genetically improved planting stock for plantations are challenges for breeders to initiate an improvement program for this species.

In 1982 Michigan State University established a progeny test of aspen and their hybrids in Michigan. Many years will be required for testing and screening superior genotypes of these species to be released to the public as improved stock. However, by developing an early evaluation, improved stock could be ready for the release in the near future.

This study reports the 9-year-old results of a progeny test plantation in the MSU Water Quality Research Area, Ingham Co. Michigan.

The objectives of this study are:

1. To identify the fast-growing (height and stem diameter) aspen families and their hybrids.
2. To quantify genetic variation in the native aspen families and their hybrids.
3. To analyze age-age correlations of growth (height and stem diameter) of aspen families and their hybrids.

LITERATURE REVIEW

Aspen Distribution and Variation.

Populus tremuloides and *Populus grandidentata* are the only two of four native poplar in Michigan referred to as aspen (Graham et al. 1963). Trembling aspen (*Populus tremuloides*) is a boreal-temperate species and bigtooth aspen (*Populus grandidentata*) is a temperate mesic species (Fowell 1965). Trembling aspen is widely distributed on the North American continent. It grows from Alaska to northern Mexico, but is found mostly in north mid-western United States (Dickmann and Stuart, 1983). The southern range of its distribution extends along the Appalachian mountains to Georgia (Strotham and Zasada 1957). This species is more adaptable than bigtooth aspen (Graham et al.1963). It grows on more varieties of soil, but its growth is most satisfactory in well-drained loamy soils, and in land with a water table within 1.5 m of the surface (Dickmann and Stuart 1983, Graham et al. 1963).

The distribution of bigtooth aspen is much more restricted. It ranges from Maine and southern Canada to Tennessee and North Carolina (Graham et al. 1963). Bigtooth aspen is most often found in well-drained medium to coarse texture upland soils (Dickmann and Stuart 1983, Graham et al. 1963). When bigtooth and trembling aspen are growing together, bigtooth aspen often outgrows trembling aspen, however, due to its greater susceptibility to some juvenile diseases, bigtooth aspen is not likely to become established in some places (Graham et al. 1963).

Since trembling aspen and bigtooth aspen grow in a relatively wide range of environments, the existence of genetic variation can be expected. Some studies on natural variation have been reported from various authors.

Pauley (1963), studying aspen seedlings from various seed sources in Massachusetts, reported evidence of geographic variation on survival rate and growth. Survival rate and growth of seedlings from Lake states origin was similar to those from New England, but western seedlings from Arizona to the Yukon territory were weak and almost died by the age of 12 years.

Brissete & Barnes (1984), comparing phenology and growth of trembling aspen from Michigan and western North Americans growing in southeastern Michigan, documented that seedlings from western North American origin stopped growing earlier than those from Michigan. He also reported that after 2 years, the average height of the western progeny was only 26-38 percent of the height of Michigan progenies. The poor performance of western seedling origin was probably due to the problem of adaptation to photoperiod or temperature (Spurr & Barnes 1980, Brissete and Barnes 1984, Reighard 1984). Vartaaja (1960) found that daylength of the different latitudes was important for growth. Comparing seedlings from Wisconsin and northern Saskatchewan, he found that growth response to short-day condition between those sources of seedlings was very different. Brissete and Barnes (1984) reported that, in a high daily mean temperature condition, aspen from lower temperature showed low rate of photosynthesis and high rate of respiration.

Einsphar and Benson (1967), studying geographic variation of trembling aspen in Wisconsin and the Upper Peninsula of Michigan, reported a well-defined south-to-north trend of decreasing specific gravity of wood. Highly significant differences for a number of important growth and wood properties were obtained between clones within stand and stand within areas.

A similar result was also reported by Barnes (1975) from a study of phenotype of leaves representing western aspen from southern Utah and Colorado northward to the Canadian border. A tendency of smaller and narrower leaves following a clinal pattern from south to north was evident.

Einsphar, et al. (1963), studying natural variation in triploid aspen, reported that differences in tree volume, specific gravity, fiber length, fiber strength, crown volume, leaf size and shape appeared to be controlled genetically. A great deal of variation within areas was found, but differences between areas were more striking.

Several studies have also been carried out to document clonal variation in aspen. From various studies, Debyle & Winokur (19..) has compiled evidences of clonal variation of aspen for several characteristics, such as annual height and diameter growth, bursting of floral buds, timing of leaf flushing, suckering capacity, rooting, susceptibility to diseases and insects, flowering time and branching habit.

Barnes (1969), for example, identifying clones from populations in the northern Lower Peninsula of Michigan, reported that aspen exhibits an enormous amount of inter clonal variation, even in local populations on fragmentary parts of their range. Noticeable differences between clones occurred in growth rate, clone profile, density of ramets, and suckering ability. He also documented extensive inter-clonal variation in leaf morphology, size and shape. However, in some instances, intra-clonal leaf variation was more striking and greater than inter-clonal variation.

Mitton and Grant (1980), in the Colorado Front Range, found a significant positive correlation between clone heterozygosity and annual diameter growth. Another study by Zahner and Crawford (1965) documented large differences in growth of adjacent clones on the same site.

Genetic variation in other characteristics has also been studied. For example, Wall et al. (1971) noted that, in Manitoba, some clones became chlorotic on nutrient-deficient sites while other clones did not. Copony and Barnes (1974), studying four different sites in Michigan, reported that susceptibility to _Hypoxylon_ canker varied markedly among clones. Tew (1970) found different carbohydrate reserves in roots between aspen clones.

Aspen Hybrids.

Trembling aspen crosses readily with other species from the genus Populus within section Leuce, producing viable hybrids (DeByle and Winokur 19..). Successful crossing involving trembling aspen or bigtooth aspen as a parent, such as crossing with _Populus alba_, _P.sieboldii_, _P.adenopoda_, _P.trichocarpa_, _P.euramericana_ and _P.tremula_, has been reported (Zsuffa 1973, Dickmann and Stuart 1983). Natural hybrids between trembling aspen and bigtooth aspen was first reported and described by Victorin (Barnes 1961).

Although the flowering time of trembling aspen was earlier than that of bigtooth aspen, natural hybrids of trembling aspen and bigtooth aspen were not infrequent (Heimburger 1940, Pauley 1956). In central and eastern Massachusetts, Pauley (1956) observed scattered hybrid individuals and hybrid swarms of these species. In Michigan, natural hybrids of these species are not uncommon. Between 1956 and 1960, Barnes (1961) discovered natural hybrids of trembling and bigtooth aspen in 10 counties of Michigan. He found that the hybrid was apparently much more abundant in south-eastern Michigan than in the northern tip of the Lower Peninsula. This phenomenon might be caused by a condition, in an area of temperature inversion, where the flowering of female trembling aspen was retarded until it corresponded with the flowering time of neighboring bigtooth aspen (Pauley 1956).

Trembling aspen and bigtooth aspen are also easy to hybridize artificially. Einsphar and Benson (1964) described a simple procedure of hybridization technique known as the "cut-branch technique." The procedure is as follows; first, flower buds from the trees to be crossed were collected. The male flower buds are forced by placing the branch collection in a vase of tap water. The water is changed daily and a small disk from the end of each branch is clipped. After seven to ten days (at 65°F) the pollen will be already available to be collected and is then stored over calcium chloride at 38° to 40°F. Female branch collections are handled in a similar manner with the exception that after pollination, which is accomplished by applying the pollen with a small brush, the collections are placed in ice water to reduce the possibility of bacterial plugging. Then in 21 to 24 days the seed can collected and separated from the attached cotton.

Many experiments involving trembling aspen and bigtooth aspen hybrid had been reported (Heimburger 1940, Pauley et al. 1963a, Einspahr & Benson 1964, Henry & Barnes 1977, Brissete & Barnes 1984, Reighard 1984). Unfortunately only early growth analysis was available in most cases.

The earliest experiment involving aspen hybrid conducted in the United States was initiated in 1924 by Oxford Paper Company of Maine, under direction of A. B. Stout and E. J Schreiner (Einsphar & Benson 1964, Dickmann and Stuart 1983). The experiment included parental trees of three white poplars, five aspens, nine balsam poplars and seventeen black poplars and cottonwood (Dickmann and Stuart 1983). Unfortunately, there was no further report on the aspen of this experiment.

In 1935, Heimburger (1940), at Petawawa Forest Experiment Station of Ontario Canada, successfully crossed trembling aspen and bigtooth aspen. The objective of this experiment was to produce hybrid aspen suitable for reforestation in Ontario. The breeding goal included fast growth, hardiness, resistance to insects and disease, and improving rooting ability of stem cuttings (Dickmann and Stuart 1983). In this experiment Heimburger also crossed trembling aspen and bigtooth aspen with gray poplar (P.x canescens Sm). In 1937 the experiment showed that trembling aspen x bigtooth aspen hybrids had a good survival rate and a fair degree of resistance to rust caused by <u>Melampsora sp</u>, while bigtooth aspen x gray poplar hybrids had already perished (Heimburger 1940).

In 1954, an industry-sponsored program for the improvement of aspens in Lake states was initiated at the Institute Paper Chemistry of Appleton, Wisconsin, under direction of P. Joranson and D. Einsphar (Dickmann and Stuart 1983, Einsphar & Benson 1964). This program included selection of plus trees from natural stands, hybridization, and created polyploidy aspen to produce vigorous growth and better wood quality (Dickmann and Stuart 1983). At the early growth stage, much variation between crosses appeared in growth, tree form, and wood properties (Einsphar and Benson, 1964). The early growth of bigtooth aspen was relatively slower than either trembling aspen x bigtooth aspen hybrids or triploid hybrid produced by crossing natural diploid trembling aspen with tetraploid european aspen (<u>P.tremula</u>). The triploid hybrid grew more vigorously than the diploid trembling aspen.

From the same experiment, Benson & Einsphar (1967), comparing 4 years growth of triploid trembling aspen clones, triploid trembling aspen x european aspen hybrid, and diploid trembling aspen, reported a significant difference among taxa on some traits, such as on growth, specific gravity of wood, natural pruning, number of branches, branch angle, stem straightness and branch length.

Henry and Barnes (1977), comparing reproductive ability of bigtooth aspen, trembling aspen, and their hybrids in southern Michigan, reported that in some reproductive traits the hybrids were at lower degrees than the progeny of either their parent but intermediate in others. Seed production per shoot and seed germination of the hybrids were significantly lower than those of their parents. Initial height growth of the hybrid at four weeks was greater than the progeny of their parents. At eighteen weeks the hybrid is significantly lower than the progeny of trembling aspen but not significantly different from the progeny of bigtooth aspen.

Following height growth studied by Henry & Barnes (1977), Brissete and Barnes (1984) recorded that, at one year, trembling aspen were significantly taller than bigtooth aspen and their hybrid. The hybrid was in the middle and bigtooth aspen was the lowest. At second year, trembling aspen was still significantly taller than the others, but there was no significant difference between the hybrid and bigtooth aspen. This result might indicate that, at early growth, hybrids of bigtooth aspen and trembling aspen showed neither hybrid vigor nor marked growth inferiority, compared to their parents.

Brissete and Barnes (1984) also investigated inter- and intra-specific hybridization between trembling aspen from Utah and trembling aspen and bigtooth aspen native to

Michigan. They found that, at second year, the progeny of bigtooth aspen from Michigan crossed to trembling aspen from Utah was only 64% as tall as those crosses between Michigan aspens. Crosses between trembling aspen from Utah and those from Michigan were only 83% of mean height of those from Michigan. This indicates the importance of parental sources for hybridization for a specific location.

Reighard (1984), studying a two-year-old progeny test of trembling aspen, bigtooth aspen and their hybrids at five location in both peninsulas of Michigan, reported that maternal parent affected autumn leaf color, branchiness and bud morphology, more than paternal parent. The phenology of the hybrids, compared to their parents, was intermediate, but they suffered from a number of disorders more than their parents. The test also showed a significant difference in height, basal diameter and biomass production. Growth of trembling aspen was above bigtooth aspen and their hybrids. The growth increased with the latitude of plantation site. However, most of the hybrid's families had growth rate below the plantation means.

Age-age correlation.

The goal of an advance-generation tree breeding program is to maximize gain achieved per unit time (Zobel and Talbert, 1984). The breeder can increase efficiency of the overall program by eliminating poor trees and concentrating on potential superior trees. Therefore, early selection must be considered.

If early selection is to be successful, there must be evidence of high correlation between performance at rotation age and at a younger age. Unfortunately, juvenile-mature correlation in forest trees is usually low (Zobel and Talbert, 1984). The low juvenile-mature correlation has been reported in loblolly pines, ponderosa pines, Douglas fir, western white pines, slash pines, black walnut and various hardwood species (Wright 1976).

However, Mohrdiek (1979), evaluating 15 F_1 Leuce progeny trial among crosses of *Populus tremula*, *P. alba*, *P.x canescens* Sm, *P.tremuloides* and *P.grandidentata* from age one year to age twenty years, had reported high correlation of phenotypic growth across ages, he found that the age-age coefficient of correlation between age 20 years and ages 15, 11, 9, 3, 2, 1 years were 0.952, 0.934, 0.828, 0.554, 0.483 and 0.462, respectively. Mohrdiek also suggested that a test interval of eight years seems to be sufficient for F_1 Leuce progeny.

Reighard (1984), measuring age-age coefficient of correlation between nursery height growth at one year and height growth after two growing season in the plantation, reported r = 0.48. He indicated that, with this correlation coefficient, an early selection of F_1 progeny of aspen would be possible.

MATERIAL AND METHODS

Progeny Production

Progenies were produced by G. Reighard and the Michigan Cooperative Tree Improvement Program (MICHCOTIP) at MSU in 1981. Seeds and catkin-bearing branches of bigtooth and trembling aspen were collected during March and April 1979 and 1980 from most counties in both peninsulas of Michigan (Figure. 1). Similar material of a putative white poplar-bigtooth aspen hybrid (*P*.x *rouleauiana*) from southern lower peninsula were also collected. Controlled pollination was done using cut-branch technique (Einsphar & Benson 1964).

In addition to the seed obtained from open pollination, the progeny of controlled pollination represented 48 half-sib and 66 full-sib families of both bigtooth and trembling aspen, 72 full sib families of hybrid aspen (*P*.x *smithii* = *P*.*grandidentata* x *P*.*tremuloides*, reciprocally), and 20 full sib families of crosses of bigtooth and trembling aspen to the putative white poplar-bigtooth aspen hybrid.

Seed was sown in the nursery on May 26 1981. Cultural procedures similar to those mentioned in "Aspen seedling production in a commercial nursery" (Benson & Dubey, 1972)

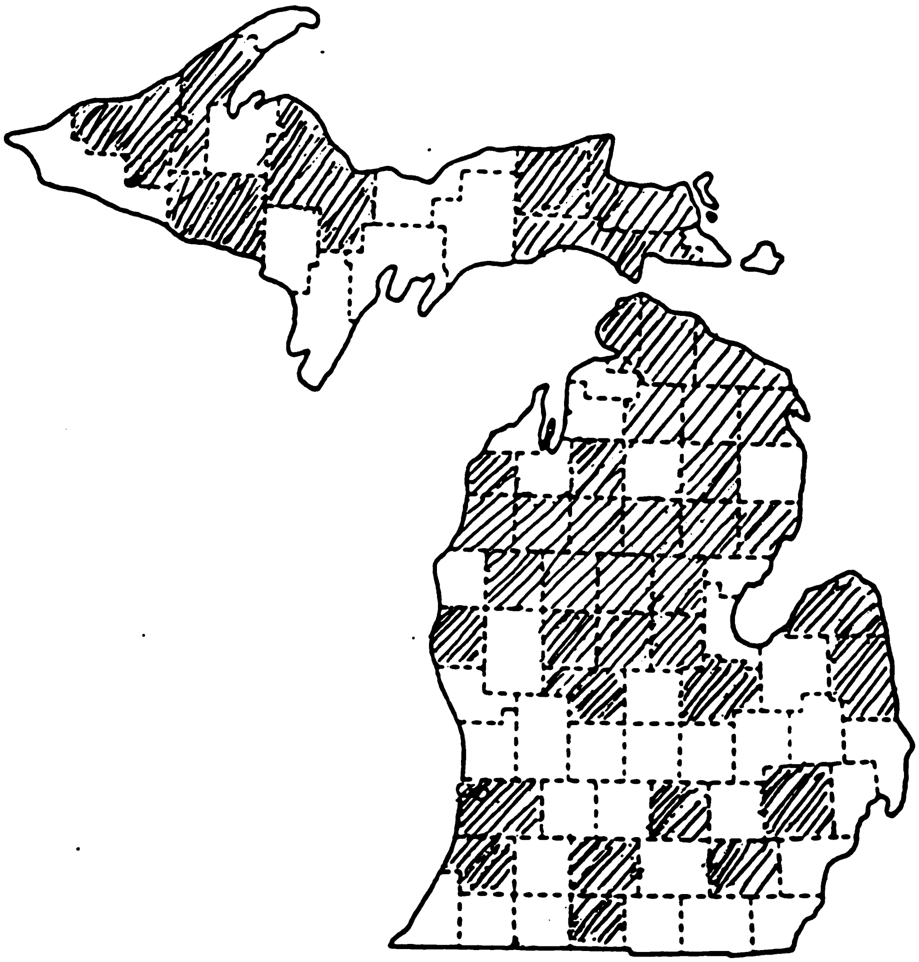

Figure 1. The location of seed and catkin-bearing branch collections

were used to grow the seedlings. Orthene was used to control insects. Seedlings were lifted the following March and placed in cold storage until the planting day.

<u>**Plantation Establishment**</u>.

Plantations were established on five sites, three in the Lower Peninsula and two in the Upper Peninsula. However, this study only deals with one plantation at the MSU Water Quality Research Center (Lower Peninsula, Ingham Co. Lat. 42.7N, Long 84.5W). The soil is well-drained and the texture is a fine sandy loam. The dominant vegetation on the site was grasses and perennial weeds.

Planting was done in April and May 1982. Seedlings were planted by machine in two-tree plots with spacing 1.8 meter between trees within rows and 2.4 meter between rows. The experimental design was a randomized complete block with six replications.

Site preparation consisted of mowing the existing vegetation with rotary mowed in August 1981 and spraying seven liters/ha of glyphosate in one-meter-wide strips three to four weeks later. At the following spring planting, 2.8 kg/ha of Simazine was applied over the tops of the seedlings and on to the glyphosate-sprayed strips. To control the invading grasses, Glyphosate was spot-sprayed once in 1982. Mowing was done once during each of the following years.

Data Collection.

Data were collected for survival rate, stem diameter and height. Stem diameter was measured in 1982 and 1983 (at five cm above ground), and in 1988 and 1990 (at breast height) to the nearest 2.5 cm. Height was measured in 1982 and 1983 (to the nearest 5 cm) and 1988 (to the nearest 1 cm). Survival rate was recorded as percentage from the original number of trees planted.

Data Analysis.

All analyses were done by using SAS Programe. Data were analyzed separately according to ages at measuring times. Since some trees were missing, all analyses, unless otherwise stated, utilize data from families that are at age 9 represented in least 4 replications. Analysis of variances and correlations were calculated for stem diameter and height at all ages measured.

1. *Phenotypic performance among taxa*,- Survival rates of each taxon were simply presented as percentages calculated from number of survived trees at measuring times divided by number of trees initially planted. Height and stem diameter growth were subjected to an analysis of variance (ANOVA), based on the tree-plot units as entries, following a linear model as:

$$Y_{ijk} = u + R_i + T_j + F_{k(j)} + E_{ijk}$$

where:

Y_{ijk} = performance of plot-unit of k^{th} family nested to jth taxa in the i^{th} replication;

u = overall mean;

R_i = effect of i^{th} replication;

T_j = effect of j^{th} taxa;

$F_{k(j)}$ = effect of the k^{th} nested to j^{th} taxa;

E_{ijk} = experimental error.

Form of the analysis of variance (ANOVA) is presented in Table 1. Taxa were considered as fixed, while families within taxa and replications as random. Means of taxa were compared to each other by using Duncan's multiple range test.

Table 1. Form of analysis of variance (ANOVA) model for analyzing height and stem diameter growth of taxa and families within taxa, based on tree-plot unit data.

Sources	df[1]	MS	Ftest	EMS[1] [2]
Replicate.	r-1	MSR	--	
Taxa	t-1	MST	MST/MSF(T)	$V^2_e + rV^2_{f(t)} + rfV^2_t$
Family within taxa	t(f-1)	MSF(T)	MSF(T)/MSE	$V^2_e + rV^2_{f(t)}$
Error	(tf-1)(r-1)	MSE	--	V^2_e
Total	trf-1	---		

[1] r, t and f refer to number of replications, taxa and harmonic mean number of families/taxa respectively.

[2] V^2_e, $V^2_{f(t)}$ and fV^2_t refer to variance error, variance family within taxa and variance among taxa, respectively.

2. *Geographic significance of parent*,- Effects of parental origin were analyzed for height and stem diameter. Geographic parental origins were simply grouped into four regions: 41.8 N to 43.0 N, 43.0 N to 44.2 N, 44.2 N to 45.4 N, and 45.4 N to 46.8 N. The first three regions represent parental trees from the Lower Peninsula, while the last one represents parental trees from the Upper Peninsula.

Since the parents of the trihybrid were only from two regions, this taxa was excluded from the analysis. Analysis of variance was conducted for height and stem diameter following a linear model as:

$$Y_{ijk} = u + R_i + T_j + Z_k + E_{ijk}$$

where: Y_{ijk} = performance of entries of j^{th} taxa at k^{th} regions in the i^{th} replication;

u = overall mean;

R_i = effect of i^{th} replication;

T_j = effect of j^{th} taxa;

Z_k = effect of the k^{th} regions.

E_{ijk} = experimental error.

Form of the ANOVA model is presented in Table 2. Both taxa and regions were considered to be fixed.

Since numbers of trees of the treatments at each replication were different, analysis was conducted based on means of trees on the treatments (taxa and region) at each replication.

Contrast comparison tests were used for comparing trees with Upper Peninsulas parental origin to those from Lower Peninsula, while Duncan's multiple range test was used for comparing means of height and stem diameter trees among regions

Table 2. Form of analysis of variance (ANOVA) for analyzing effect of geographic of parental origin.

Sources	df[2]	SS	MS	Ftest
Replicate	r-1	SSR	MSR	---
Taxa	t-1	SST	MST	MST/MSE
Regions	z-1	SSZ	MSZ	MSZ/MSE
-UppervsLower Peninsulas[1]	1	SSC	MSC	MSC/MSE
Error	tz(r-1)	SSE	MSE	
Total	tzr-1			

[1] Upper and Lower Peninsulas were compared using contrast comparison test.
[2] t, z and r refer to number of taxa, regions and replications respectively.

3. ***Heritability and variance components estimate***.-

Since the population in this test is a mix of families (half-sib and full-sib families from controlled pollination, and half-sib families from open pollination), direct estimates of variance components and heritabilities cannot be done. Variance component and heritability were only approached from the controlled pollinated families together (regardless of taxa), by constructing a nested design (North Carolina design I).

After adjusting for missing families/trees, there were available 78 progenies of 27 male families that had been mated with at least 2 female families. Samples of 15 male families and 30 female families (in which each male was crossed into 2 females) were selected randomly without repetition. The progenies represent 30 families, 5 families of *P. grandidentata*, 9 families of *P. x smithii* (*P. grandidentata* x *P. tremuloides*), 6 families *P.x smithii* (*P. tremuloides* x *P. grandidentata*) and 10 families of *P. tremuloides*.

An analysis of variance, by using the mating design, was conducted according to Becker (1984) following a linear model as:

$$Y_{hij} = u + R_i + M_j + F_{k(j)} + E_{ijk}$$

where: Y_{hij} = plot-unit mean within the j^{th} male parent and the k^{th} female parent;

u = overall mean;

R_i = effect of i^{th} replication;

M_j = effect of j^{th} male parent;

$F_{k(j)}$ = effect of the k^{th} female parent mated to j^{th} male parent;

E_{ijk} = environmental and remainder of genetic variance among plots.

Replicate is considered as fixed while male parents and females within male parent as random.

Since some trees within plot were missing, an estimate of the individual variance within plots was obtained from individual trees by using the formula (Becker, 1984):

$$Y_{fk} = u + P_f + E_{fk}$$

where: Y_{fk} = individual observation on k^{th} individual of f^{th} plot;

u = overall mean;

P_f = effect of the f^{th} plot;

E_{fk} = environmental and genetic variance among trees within plot

The form of the ANOVA model and the expected means square (EMS) are presented at Table 3 & 4.

Table 3. Form of ANOVA and EMS of NC mating design I for analyzing male and female parent and variance component estimate of all population (base on plot mean data)

Sources	df[1]	MS	Ftest	EMS[2]
Replicate	r-1	MSR	--	
Male	m-1	MSM	MSM/MSF(M)	$V^2_e+rV^2_{f(m)}+rfV^2_m$
Female (male)	m(f-1)	MSF(M)	MSF(M)/MSE	$V^2_e+rV^2_{f(m)}$
Male-female crosses x rep. (error pooled)	(mf-1)(r-1)	MSE	--	V^2_e
Total	rmf-1	MST		

[1] r, m and f refer to number of replications, male parent and number of female parent mating to male parent respectively.

[2] V^2_e, $V^2_{f(m)}$ and fV^2_m refer to variance error pooled, variance among female within male and variance among male parent, respectively

Table 4. Form of ANOVA and its expected mean square for analyzing within plot component of variance (based on individual-tree data)

Sources	df[1/]	SS	MS	EMS[2/]
Between plot	rmf-1	SS	--	--
Within plot	rfm(t-1)	SS_w	MSW	V^2_w

[1/] r, m, f and t refer to number of replications, male parent and number of female parent mating to male parent and harmonic mean of number of trees per plot, respectively.
[2/] V^2_w variance among trees within plot.

With the assumption of no occurrence of epistasis, the variance among male parent (V^2_m) was considered equal to 1/4 of additive genetic variance, and variance among female within male parent ($V^2_{f(m)}$) was considered equal to 1/4 additive variance plus 1/4 dominance variance (Hallauer & Miranda 1981, Namkoong 1979). Then the narrow-sense heritability estimate was formulated according to Hallauer & Miranda (1981) as presented at Table 5.

Table 5. Formula for calculating narrow-sense heritabilities utilizing variance components derived from NC I mating design.

Family based heritability	Single tree based heritability
$h^2 = \dfrac{4\ V^2_m}{V^2_e/r + 4\ V^2_{f(m)}}$	$h^2 = \dfrac{4\ V^2_m}{V^2_w + V^2_e + V^2_m + V^2_{f(m)}}$

where:

h^2 = narrow-sense heritability
V^2_w = variance among tree within plot
V^2_e = variance of pooled error
V^2_m = variance among male parent
$V^2_{f(m)}$ = variance among female parent within male parent.

4. *Correlation*,- Correlations between height and diameter were analyzed at ages 1, 2, and 7 years. Age-age correlations of phenotypic performance of height and stem diameter were analyzed at all years measured. All correlation analyses were calculated based on family means by utilizing Pearson product-moment correlation formula as follows (Snedechor & Cochran, 1967):

$$r_{xy} = \frac{\sum (X-\bar{X})\ (Y-\bar{Y})}{\sqrt{\sum (X-\bar{X})^2\ \sum (Y-\bar{Y})^2}}$$

where:

r_{xy} =coefficient of correlation
X, Y =observation unit
$\bar{X}, \bar{Y}$ =means of observation units

RESULTS AND DISCUSSION

Phenotypic Performance among Taxa.

1. *Survival rate*,- Survival rate at ages 1-, 2-, 7-, and 9-years old of the families within each aspen taxon are presented in Table 6.

Table 6 : Survival rate of each aspen taxon at ages 1, 2, 7 and 9 years (in percentages).

Taxa	no. of families	1st year	2nd year	7th year	9th year
P.grandidentata x P.grandidentata	24	84	76	75	70
P.tremuloides x (P.x rouleauiana)	10	99	99	71	65
P.tremuloides x P.grandidentata	24	95	91	84	80
P.grandidentata x P.tremuloides	21	92	87	76	74
P.tremuloides x P.tremuloides	69	98	92	87	83
All together	148	94	89	82	78

*) Percentages were calculated from number of survive tree at the measured years divided by number of trees initially planted.

At the 1st & 2nd year old, the survival rate of the trihybrid (P.x rouleauiana x P. tremuloides) was the highest (99%, 99%), followed by P. tremuloides (98%, 92%), P. tremuloides x P. grandidentata (txg crosses) (95%, 91%), P. grandidentata x P. tremuloides (gxt crosses) (92%, 87%), then P. grandidentata as the lowest (84%, 76%).

At the age 7 & 9 years, the survival rate of trihybrid families dropped into the lowest (71%, 65%), while the other taxa remained in the same order. P. tremuloides was the highest (87%, 83%) followed by txg crosses (84%, 80%), gxt crosses (76%, 74%) then P. grandidentata (75% and 70%).

The drastic drop of survival rate of the trihybrid might be caused by the attack of the poplar gall beetle (Saperda inornata). This insect was the most destructive insect in this progeny test. At two years of age, it attacked and produced galls on trihybrid trees at twice the rate as on bigtooth aspen (Reighard 1984).

2. Stem diameter and height,- After testing the homogeneity of variances among families across taxa, analysis of variances for stem diameter and for height at all ages measured were conducted. The analysis of variances showed significant differences ($P<0.01$) among taxa and among families within taxa at all ages (Table 7).

Table 7. F value of analysis of variance of stem diameter and height among taxa and among family within taxa.

Source	Diameter				Height		
	1st year	2nd year	7th year	9th year	1st year	2nd year	7th year
Rep.	7.04**	5.24**	10.55**	8.07**	6.47**	12.25**	17.54**
Taxa	10.59**	8.66**	5.30**	4.56**	23.49**	19.77**	5.29**
Family (Taxa)	2.28**	1.84**	2.18**	2.53**	2.20**	1.89**	2.08**
MS Error	0.0974	0.3420	2.4978	4.5410	831.10	2283.89	21194.75

**. Significant at $P<0.01$

Means stem diameter of each taxa at ages 1, 2, 7 and 9 years are presented in Table 8 and Figure 2; means for height at ages 1, 2, and 7 years are presented in Table 9 and Figure 3.

At one-year-old, the mean diameter of the trihybrid (1.40) was significantly larger and different from the means of other taxa. _P_. _tremuloides_ (1.35) was significantly larger than txg crosses (1.23) and _P_._grandidentata_ (1.07), but not significantly larger than gxt crosses (1.28). The reciprocal hybrids (txg and gxt crosses) were not significantly different from each other but significantly larger than _P_. _grandidentata_. _P_. _grandidentata_ was the smallest and significantly different from other taxa.

At second year, again the trihybrid was the largest (2.40) and _P_. _grandidentata_ was the smallest (1.91). The trihybrid was significantly different from txg crosses (2.20) and _P_. _grandidentata_ (1.91), but not significantly different from _P_._tremuloides_ (2.39) and gxt crosses (2.28). Reciprocal hybrids (gxt and txg crosses) were not significantly different from each other, but they were significantly different from _P_. _grandidentata_. _P_. _grandidentata_ was the smallest and significantly different from other taxa.

At age 7 and 9 years old, the order, based on stem diameter, was gxt cross (6.08 and 8.94) as the largest, followed by txg cross (5.84 and 8.58), _P. tremuloides_ (5.81 and 8.46), trihybrid (5.83 and 8.40), then _P. grandidentata_ (4.69 and 7.14). Those four former taxa were not significantly different from each other but were significantly different from _P. grandidentata_.

The pattern of height growth was similar to that of diameter. At the first year the trihybrid and _P. tremuloides_ were significantly taller than the hybrids (gxt and txg) or _P. grandidentata_. The hybrids (gxt and txg) were not significantly different from each other, but significantly different from _P. grandidentata_. At the second year, _P. tremuloides_ was the tallest and different from other taxa. The trihybrid and gxt hybrid were second, followed by txg hybrid, then _P. grandidentata_ as the lowest. At 7 years, the highest was gxt hybrid. The gxt hybrid was significantly different from the trihybrid and _P. grandidentata_, but not from txg hybrid and _P. tremuloides_. _P. grandidentata_ was significantly shorter than other taxa.

Graham et al. (1963) reported that, when growing together, _P. grandidentata_ outgrows _P. tremuloides_. In contrast, this test showed that at all years measured _P. tremuloides_ always outgrew _P. grandidentata_. This result is similar to a previous study by Brissette and Barnes (1984) of two-year-old aspens in southeastern Michigan.

Table 8. Means of stem diameter of each aspen taxon at ages 1, 2, 7 and 9 years.

Taxa	1st year		2nd year		7th year		9th year	
	cm	(%)*)	cm	(%)*)	cm	(%)*)	cm	(%)*)
P. grandidentata x *P. grandidentata*	1.07 ^{d}	(83)	1.91 ^{c}	(84)	4.69 ^{b}	(82)	7.14 ^{b}	(86)
P. tremuloides x (*P.* x *rouleauiana*)	1.48 ^{a}	(115)	2.40 ^{a}	(105)	5.83 ^{a}	(102)	8.40 ^{a}	(101)
P. tremuloides x *P. grandidentata*	1.23 ^{c}	(95)	2.20 ^{b}	(96)	5.84 ^{a}	(103)	8.58 ^{a}	(103)
P. grandidentata x *P. tremuloides*	1.28 ^{bc}	(99)	2.28 ^{ab}	(100)	6.08 ^{a}	(107)	8.94 ^{a}	(107)
P. tremuloides x *P. tremuloides*	1.35 ^{b}	(105)	2.39 ^{a}	(105)	5.81 ^{a}	(102)	8.46 ^{a}	(101)
All together	1.29	(100)	2.28	(100)	5.69	(100)	8.34	(100)

*)-Percentage was measured from mean total (all together).
-Any two means in the same year with the same letter are not significantly different at alpha = 0.05.

Table 9. Means of height of each aspen taxon at ages 1, 2, and 7 years.

Taxa	1st year		2nd year		7th year	
	cm	(%)*)	cm	(%)*)	cm	(%)*)
P.grandidentata x P.grandidentata	86 ^{c}	(75)	159 ^{d}	(79)	614 ^{c}	(89)
P.tremuloides x (P.x rouleauiana)	126 ^{a}	(110)	202 ^{b}	(101)	687 ^{b}	(99)
P.tremuloides x P.grandidentata	106 ^{b}	(92)	187 ^{c}	(94)	714^{ab}	(103)
P.grandidentata x P.tremuloides	113 ^{b}	(98)	195^{bc}	(98)	733 ^{a}	(106)
P.tremuloides x P.tremuloides	127 ^{a}	(110)	217 ^{a}	(109)	694^{ab}	(101)
All together	115	(100)	200	(100)	690	(100)

*) -Percentage was measured from mean total (all together).
-Any two means in the same year with the same letter are not significantly different at alpha = 0.05

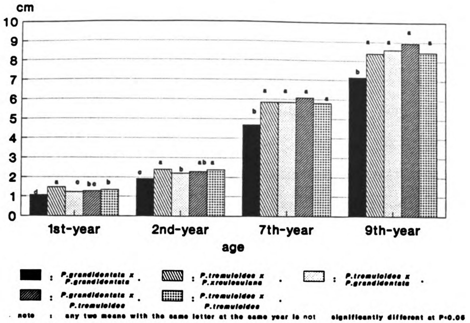

Figure 2. Means of stem diameter at ages 1, 2, 7 and 9 years

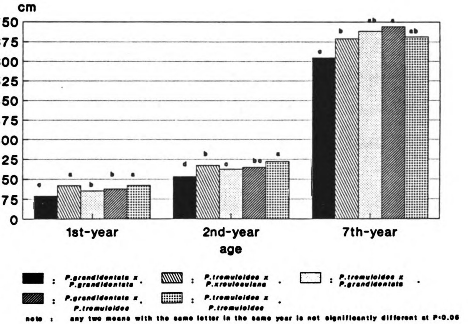

Figure 3. Means of height at ages 1, 2 and 7 years.

A rapid juvenile growth is positively correlated with aspen survival rate (Reighard 1984, Pauley 1963, Hattemer and Seitz 1967, Morhdiek 1979). In this test, the correlation appeared only in the early growth (first year) and became obscure in the following (2nd, 7th and 9th) years. At the 1st year, the fastest growing taxa was the highest in survival rate and the slowest growing taxa was also the lowest in survival rate. At the 2nd year the relationship somewhat degraded and at the age 7 and 9 this relationship no longer held true. This phenomenon might be caused by the attack of some diseases or insects that had different severeness and preferences regarding taxa. As reported by Reighard (1984) some diseases and insects, such as Venturia tremulia, Saperda inornata and Janus abbreaviatus, were evidence at age two years. He reported that V.tremulia infected mostly trembling aspen; it was intermediate in the hybrid and less in bigtooth aspen. S.inornata attacked the trihybrid twice as much as bigtooth aspen. Compared to other taxa, J.abbreviatus mostly damaged P.x smithii. At older age, there were also other insects and pathogens at work in this plantation. For example, after about 5 years, cancer diseases became very important.

Brissete and Barnes (1984) reported that the F_1 hybrid of P. tremuloides and P. grandidentata showed neither hybrid vigor nor marked growth inferiority compared with progeny of their parents. The hybrid of P. tremuloides and

P. grandidentata is intermediate in most morphological characteristics (Pauley 1963, Barnes 1961) and has a tendency to approach, but not exceed, typical rapid growth of *P. tremuloides* in height (Pauley 1963, Einsphar & Benson 1964, Henry & Barnes 1977, Brissete & Barnes 1984).

The performance of this progeny test showed similar results at the first- and the second-year. The height and stem diameter of *P. tremuloides* x *P. grandidentata* hybrids (reciprocal) were intermediate between progenies of either of their parents. However, at ages 7 and 9 years the results were somewhat different. The mean stem diameter and height of the hybrids exceeded, although not significantly, *P. tremuloides*.

Moreover, following growth of each taxa for several years (Figure 2 & 3) and number of families of each taxa that comprised 15 (10%) best families (Table 10), it seemed that dominancy of *P. tremuloides* as the fastest growing families at the early growth was replaced by the hybrids (txg and gxt crosses) at the older ages.

Even though, at age 9 years, the analysis of variance still did not show significant difference (P>0.05) between *P. tremuloides* and the hybrids, the mean value of stem diameter and height showed that the hybrids, which were smaller than *P. tremuloides* at ages 1 and 2 years, gradually became larger at ages 7 and 9 years. The dominancy of *P. tremuloides* families in the 15 best families at the first-year decreased with the time. On the other hand, the hybrid (gxt and txg crosses) families, that were less representative in the 1st year, increased along the years and became dominant at the 7th and 9th years.

Table 10. Number of families of each aspen taxon that comprise 15 (10%) of the best families in height and stem diameter at ages 1, 2, 7 and 9 years.

Taxa	No. of families planted	Diameter				Height		
		1st yr.	2nd yr.	7th yr.	9th yr.	1st yr.	2nd yr.	7th yr.
P.grandidentata x P.grandidentata	24	0	0	0	0	0	0	0
P.tremuloides x (P.x rouleauiana)	10	3	1	1	1	2	1	2
P.tremuloides x P.grandidentata	24	2	3	5	5	1	2	5
P.grandidentata x P.tremuloides	21	2	2	5	6	0	2	4
P.tremuloides x P.tremuloides	69	8	9	4	3	12	10	4

These results suggest that until age 9 years the superiority of the hybrids did not appear clearly, but indicated that hybrid vigor of the aspens' family might show up at an older age.

In relation to the composition of additive and dominance variance within genetic variance (see heritability and components of variance page 46-56), the growth superiority of the hybrids seems to be affected by non-additive (dominant variance) genetic variance. Johnson and Larsen (cit. by Reighard 1984) also reported that non-additive genetic variance was responsible for the growth superiority of hybrids between geographically isolated aspen species.

The largest family mean diameters of trembling aspen, bigtooth aspen, trihybrid aspen, txg crosses and gxt crosses at age 9 years were 10.6 cm, 9.8 cm, 10.9 cm, 13.4 cm and 12.1 cm (Table 11). The tallest families at age 7 years were 875 cm, 788 cm, 826 cm, 1020 cm, and 923 cm, respectively (Table 12). These families are 25% to 56% larger than the average stem diameter and 20% to 42% taller than the average height of each taxa. They are 17% to 61% (in diameter) and 14% to 48% (in height) larger than the average of all families. The averages of the 15 (10%) best families in diameter (11.2 cm) and height (870.8 cm) were 35% and 26% larger than the average of all families, respectively.

In line with the result at two-years-old reported by Reighard (1984), at 7-years-old, the early growth of these families was still comparable or greater than those reported for promising trembling aspen, hybrid aspen, triploid hybrid aspen, white poplar-bigtooth aspen hybrids and white poplar-aspen trihybrids (Pauley 1963b, Pauley 1963, Benson & Einsphar 1967).

Table 11. Stem diameter (cm) and percentage ranking of the best family and the best individual of each aspen taxon at ages 1, 2, 7 and 9 years.

Taxa	Best family (mean)				Best individual			
	1st year	2nd year	7th year	9th year	1st year	2nd year	7th year	9th year
_P._ _grandidentata_ x _P._ _grandidentata_	1.6	2.6	7.1	9.8	2.2	4.5	10.2	15.2
	149%[1/]	136%	151%	137%	205%	236%	217%	213%
	124%[2/]	114%	125%	117%	170%	197%	179%	182%
_P._ _tremuloides_ x (_P._ x _rouleauiana_)	1.7	2.9	7.3	10.9	2.8	4.6	11.2	16.3
	114%	120%	125%	130%	189%	192%	192%	194%
	131%	127%	128%	131%	228%	202%	197%	195%
_P._ _tremuloides_ x _P._ _grandidentata_	1.9	3.1	9.8	13.4	2.7	4.2	11.9	16.3
	154%	141%	168%	156%	219%	191%	196%	190%
	147%	136%	172%	161%	210%	184%	209%	195%
_P._ _grandidentata_ x _P._ _tremuloides_	1.6	3.3	8.5	12.1	2.7	5.6	13.2	17.0
	125%	145%	140%	135%	211%	246%	217%	190%
	124%	145%	150%	145%	210%	246%	232%	203%
_P._ _tremuloides_ x _P._ _tremuloides_	1.9	3.1	7.7	10.6	2.6	5.3	10.9	14.7
	140%	130%	132%	125%	193%	222%	187%	174%
	147%	136%	135%	127%	201%	231%	191%	176%

[1]) percentages were calculated based on means of each taxon respectively.
[2]) percentages were calculated based on grand means (means of all together).

Table 12. Height (cm) and percentage ranking of the best family and the best individual of each aspen taxon at ages 1, 2, and 7 years.

Taxa	Best family (mean)			Best individual		
	1st year	2nd year	7th year	1st year	2nd year	7th year
P. grandidentata x	129	233	788	220	350	1030
P. grandidentata	150%[1]	147%	128%	256%	220%	168%
	112%[2]	166%	114%	191%	175%	149%
P. tremuloides x	159	254	826	235	360	1152
(_P._ x _rouleauiana_)	126%	126%	120%	186%	178%	167%
	138%	127%	120%	204%	180%	167%
P. tremuloides x	172	271	1020	250	420	1160
P. grandidentata	162%	145%	142%	236%	224%	162%
	150%	136%	148%	217%	210%	168%
P. grandidentata x	143	275	923	200	435	1200
P. tremuloides	127%	141%	125%	177%	223%	164%
	124%	138%	134%	174%	218%	174%
P. tremuloides x	163	275	875	235	400	1120
P. tremuloides	128%	127%	126%	185%	184%	161%
	142%	138%	127%	204%	200%	162%

1) percentages were calculated based on means of each taxon respectively.
2) percentages were calculated based on grand means (means of all together).

Geographic Significance of Parent.

Selection of parents is an important point for providing improved seed sources. The importance of parental selection in progeny performance of forest trees species has been recognized (Duffield 1958, Hyun 1976, Little andTrew 1976). In Massachusetts, Pauley et al. (1963) reported that trembling aspen from the Lake states origin survived and grew better than those from Washington and Yukon territory. Progeny of European aspen (P. tremula) from central Europe grew faster than those from northern Europe (Pauley et al. 1963a).

Reighard (1984), analysing all five plantations of this test at two years old, reported that the female parent showed a significant effect on progeny performance, but not the male parent. Based on this result, analysis of variance of geographic parental origin was conducted only for the female parent. The analysis showed that there was a significant difference in diameter ($P<0.05$) but not in height among progeny from different female parent origins (Table 13).

Nine-year-old performance of this test showed that the best progenies of these aspens have their maternal parent from the central Lower Peninsula. In contrast to these results, under greenhouse conditions, western Upper Peninsula sources of bigtooth and trembling aspen grew faster than those from other sources (Okafo, 1976).

Table 13. F value of analysis of variance of height and stem diameter among maternal parent origin.(Entries are means of families at each region)

Source	Diameter				Height		
	1st year	2nd year	7th year	9th year	1st year	2nd year	9th year
Rep.	4.71^{**}	1.92^{**}	3.87^{**}	3.46^{**}	4.24^{**}	4.24^{**}	6.10^{**}
Taxa	7.96^{**}	4.85^{**}	7.87^{**}	6.73^{**}	13.83^{**}	9.63^{**}	6.98^{**}
Region	4.40^{**}	1.95^{*}	3.74^{*}	4.12^{**}	2.26^{ns}	1.85^{ns}	2.01^{ns}
Upper vs lower pens.	12.08^{**}	5.24^{*}	5.78^{*}	6.54^{*}	4.98^{*}	2.06^{ns}	1.04^{ns}
MS Error	0.0287	0.1266	0.9676	1.6260	246.00	757.99	7004.29

* . Significant at P<0.05
**. Significant at P<0.01
ns. Non significant at P<0.05

Southern seedlots from the same species usually grow faster than the northern ones (Wright 1976). This phenomenon is also evident in this test. Mean stem diameter of families with maternal origin from the Lower Peninsula was relatively larger than those from Upper Peninsula. At age 9 years, the mean diameter of families with maternal origin from the Lower Peninsula overall was 7% larger than those from Upper Peninsula.

Duncan's Multiple Range Tests showed significant difference between central Lower Peninsula and Upper Peninsula parental origin, but not between northern & southern Lower Peninsula and Upper Peninsulas. However, mean stem diameter and height of families from the northern, central and southern Lower Peninsula were 6%, 12%

and 3% larger than those from Upper Peninsula, respectively (Table 14 & Figure 4). This is consistent with (but less than) results reported by Wright (1976). He reported that trees from the Lower Peninsula grow 10% to 20% faster than those from Upper Peninsula if tested in Lower Peninsula.

Although, there was no significant difference in height among families with different maternal origin, the 15 best families in height at 7 years were dominated by families that have maternal origin from the Lower Peninsula (Table 17). A similar result was also evident for stem diameter at 9 years old (Table 16). These results may indicate that for a plantation in the Lower Peninsula, a maternal parent from the Lower Peninsula, especially the central Lower Peninsula, will give a better progeny than those from the Upper Peninsula.

The different growth between progenies with maternal parents from the Upper Peninsula and Lower Peninsula might be caused by several reasons. Trees from the Upper Peninsula were separated from those from the Lower Peninsula by the Strait of Mackinaw that forms a natural restriction for gene exchange. Therefore, different natural selection pressures could result in development of races that are more or less distinct (Wright 1976). Trees are genetically adapted to photoperiod of their native habitat (Spurr & Barnes 1980). The growing season in northern latitudes has longer days than the southern

Table 14. Mean of stem diameter of aspen families among geographic areas at ages 1, 2, 7 and 9 years.

Region	Latitude	1st year	2nd year	7th year	9th year
Lower Peninsula	41.8°-43.0°N	1.32 [a] (116%)	2.24 [a] (106%)	5.53 [ab] (103%)	8.08 [ab] (103%)
	43.0°-44.2°N	1.26 [a] (111%)	2.23 [a] (106%)	6.10 [a] (114%)	8.83 [a] (112%)
	44.2°-45.4°N	1.25 [a] (110%)	2.27 [a] (108%)	5.60 [ab] (104%)	8.37 [ab] (106%)
	combined	1.28 (112%)	2.25 (107%)	5.76 (107%)	8.43 (107%)
Upper Peninsula	45.4°-46.6°N	1.14 [b] (100%)	2.11 [a] (100%)	5.37 [b] (100%)	7.86 [b] (100%)

-Percentages were calculated based on the mean diameter of families from Upper Peninsula.
-Any two means in the same years with the same letter are not significantly different at alpha=0.05 according to Duncan's multiple range test.

Table 15. Mean of height of aspen families among geographic areas at 1, 2 and 7 years .

Region	Latitude	1st year	2nd year	7th year
Lower Peninsula	41.8°-43.0°N	113.57 [a] (106%)	187.98 [a] (97%)	674.19 [a] (97%)
	43.0°-44.2°N	108.30 [a] (101%)	194.91 [a] (101%)	724.27 [a] (104%)
	44.2°-45.4°N	112.13 [a] (104%)	199.46 [a] (103%)	684.30 [a] (98%)
	combined	111.29 (103%)	193.25 (100%)	694.64 (100%)
Upper Peninsula	45.4°-46.6°N	107.58 [a] (100%)	192.98 [a] (100%)	697.00 [a] (100%)

-Percentages were calculated based on the mean height of families from Upper Peninsula.
-Any two means in the same years with the same letter are not significantly different at alpha=0.05 according to Duncan's multiple range test.

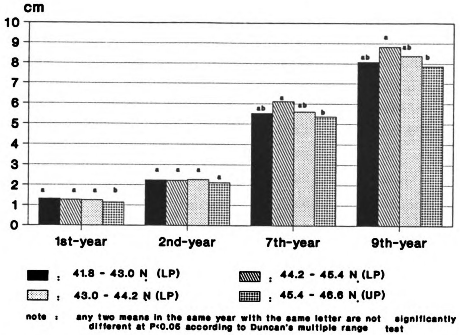

Figure 4. Means of stem diameter among geographic areas at ages 1, 2, 7 and9 years

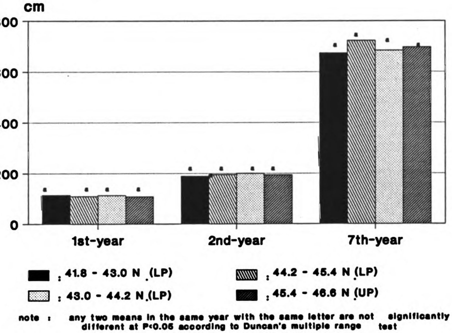

Figure 5. Means of height among geographic areas at ages 1, 2, and 7 years.

Table 16. The fifteen best aspen families (in diameter) at age 9 year.

Accession number	Diameter (cm)	Parental origin			
		Maternal parent		Paternal parent	
		County	Region	County	Region
70071[e]	10.25	Montcalm	II	Sanilac	II
*90105[d]	10.39	Lake	II	Chippewa	IV
90038[d]	10.53	Lake	II	*) open pollination	
*70057[e]	10.71	Calhoun	I	Iron	IV
70033[c]	10.77	Marquette	IV	Oakland	I
70070[e]	10.77	Moncalm	II	Van Buren	I
60001[a]	10.87	Calhoun	I	Alpena	III
*90125[d]	10.89	Wexford	II	Kalkaska	III
*70044[c]	11.13	Roscommon	II	Oakland	I
70079[e]	11.17	Van Buren	I	Oscoda	III
*70081[e]	11.31	Wexford	II	Benzie	III
*70024[c]	12.03	Iosco	III	Gladwin	II
*70078[e]	12.07	Van Buren	I	Iron	IV
*70004[c]	12.41	Branch	I	Clare	II
*70043[c]	13.43	Roscommon	II	Ingham	I

*.also excellent in height at 7 years

b.P.tremuloides x (P.x rouleauiana)
c.P.tremuloides x P.grandidentata
d.P.tremuloides x P.tremuloides
e.P.grandidentata x P.tremuloides

Table 17. The fifteen best aspen families (in height) at age 7 year.

Accession number	Height (cm)	Parental origin			
		Maternal parent		Paternal parent	
		County	Region	County	Region
60004[b]	818.42	Calhoun	I	Iron	IV
60008[b]	826.33	Calhoun	I	Oscoda	III
70005[c]	831.63	Branch	I	Marquette	IV
70071[e]	835.67	Montcalm	II	Sanilac	II
*70057[e]	836.90	Calhoun	I	Iron	IV
90117[d]	845.92	Oceana	II	Huron	II
*90105[d]	851.80	Lake	II	Chippewa	IV
*70081[e]	852.20	Wexford	II	Benzie	III
90106[d]	853.25	Lake	II	Emmet	III
*90125[d]	874.92	Wexford	II	Kalkaska	III
*70044[c]	876.60	Roscommon	II	Oakland	I
*70004[c]	887.00	Branch	I	Clare	II
*70078[e]	923.50	Van Buren	I	Iron	IV
*70024[c]	928.67	Iosco	III	Gladwin	II
*70043[c]	1019.75	Roscommon	II	Ingham	I

*.also excellent in stem diameter at 9 years

b.*P.tremuloides* x (*P*. x *rouleauiana*)
c.*P.tremuloides* x *P.grandidentata*
d.*P.tremuloides* x *P.tremuloides*
e.*P.grandidentata* x *P.tremuloides*

latitudes. Therefore, if planted in southern latitudes, northern trees will stop growing sooner than southern trees due to the shorter daylength. Reduced daylength will trigger growth cessation (Vaartaja 1960). Trees also genetically adapted to the temperature regime of their native habitat (Perry 1962). Brissete and Barnes (1984) reported that aspen from lower summer daily mean temperature habitats exhibit low rates of photosynthesis and high rates of respiration, when preceded by higher daily mean temperature. Therefore, when planted in the Lower Peninsula, aspen progeny from the Upper Peninsula may grow slower than those from the Lower Peninsula. Summer daily mean temperature at high latitude habitats is lower than those at lower latitude.

Heritability and Variance Components Estimate.

In agreement with the result reported by Reighard (1984) from the same plantation at age two years, but with different sample, analysis of variance using the nested design in Table 3 showed that the variance component of female-within-male was significant ($P<0.05$), but not the male component (Table 18).

The component of variation associated with male parent, female-within-male parent, error pooled and trees-within-plot of stem diameter and height for all years measured are presented in Table 19 and Figure 6 & 7.

Table 18. F-value of ANOVA derived from the nested design (NC design 1) at Table 3.

Sources	Diameter				Height		
	1st year	2nd year	7th year	9th year	1st year	2nd year	7th year
Rep.	4.05^{**}	1.88^{ns}	5.92^{ns}	3.08^{*}	2.85^{*}	2.25^{*}	8.73^{**}
Male	1.67^{ns}	1.83^{ns}	1.21^{ns}	1.04^{ns}	2.22^{ns}	1.90^{ns}	1.11^{ns}
Female (male)	2.32^{**}	2.16^{**}	2.99^{**}	3.11^{**}	2.85^{**}	2.44^{**}	3.09^{**}
MS Error	0.093	0.310	2.376	4.367	704.05	1954.06	18832.95

*) Significantly different at alpha level =0.05
**) Significantly different at alpha level =0.01
ns) Non significantly different at alpha level =0.05

Male variances of stem diameter and height were small and not significant at all years measured. The trend of male variance was decreasing along years. It ranged from 8% at age two years to 1% at age nine years for diameter, and from 12% at first year to 1% at age seven years for height. On the other hand, female variance was relatively larger than male variance and significant at all years measured. The female variance seemed to increase with the age. It ranged from 10% at the first year to 15% at age nine years (for diameter), and from 13% and 11% at the first- and second-year to 16% at age seven years (for height).

These results showed that variation in progeny of aspen were affected more by the female parent than by the male parent. It also indicates the importance of selecting female parents in a mating design. However, Other research

Table 19. Components of variance of stem diameter and height derived from NC 1 mating design.

Sources	Diameter[1/]				Height[1/]		
	1st year	2nd year	7th year	9th year	1st year	2nd year	7th year
Var. male	.013 (6%)	.052 (8%)	.142 (2%)	.058 (1%)	222.28 (12%)	406.15 (9%)	614.58 (1%)
Var. female (male)	.023 (10%)	.068 (10%)	.912 (13%)	1.789 (15%)	236.78 (13%)	529.61 (11%)	7378.15 (16%)
Var. error (pooled)	.094 (40%)	.310 (46%)	2.376 (34%)	4.367 (36%)	704.05 (39%)	1954.06 (42%)	18322.95 (41%)
Var. tree (plot)	.103 (44%)	.248 (36%)	3.643 (51%)	5.751 (48%)	643.59 (36%)	1752.55 (38%)	18744.90 (42%)

1/ Percentages were based on the total of Var.male, Var. female(male), Var.Error (pooled), and Var. tree(plot).

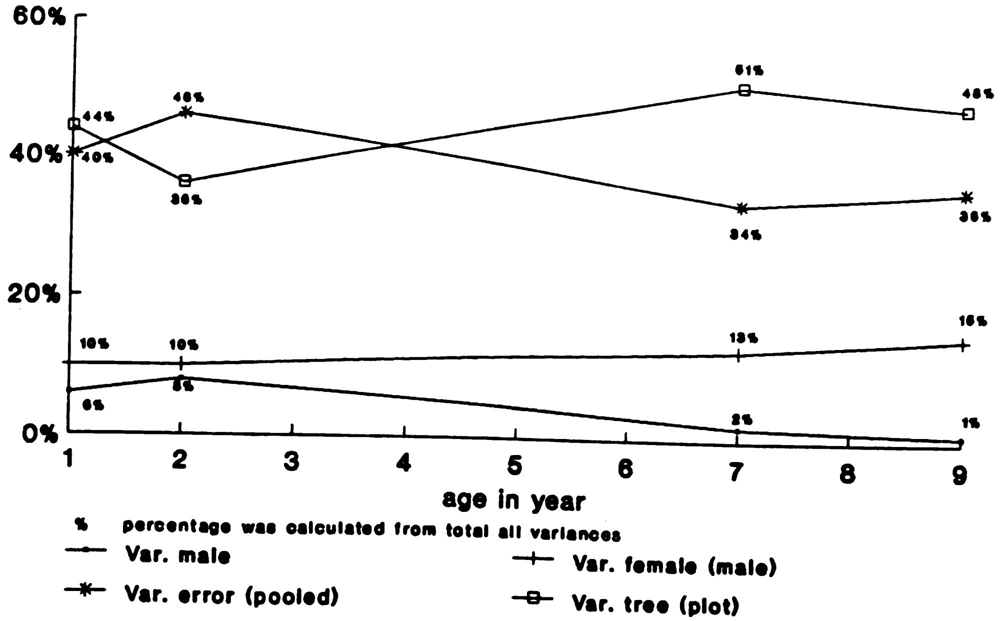

Figure 6. Components of variance of stem diameter at ages 1, 2, 7 and 9 years derived from NC 1 mating design (in percentage).

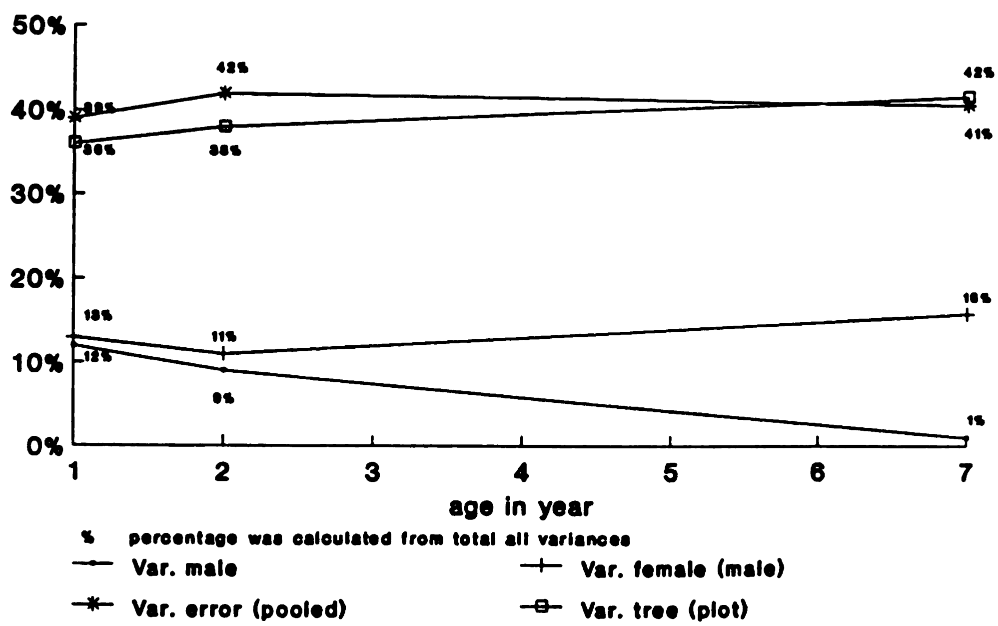

Figure 7. Components of variance of height at ages 1, 2, and 7 years derived from NC 1 mating design (in percentage).

by Mohrdiek (1979), who crossed _P. tremula_ with _P. tremuloides_, indicated that selection of either male or female parent was very important.

The non-significance of the male parent in this test could be caused by the strong effect of maternal parent or by experimental error (Reighard 1984). The variance caused by experimental error were relatively high. It ranged from 82% to 86% for diameter, and 75% to 83% for height. A further test by using reciprocal parents (male parent nested to female parent) might be worthwhile.

Assuming that there was no epistasis in the genetic variance, the estimate of additive and dominance component variances and the narrow sense heritability were calculated and presented in Table 20 and Figure 8 to 11.

Heritability estimates apply only to a particular population, in a particular environment and in a particular point in time (Zobel and Talbert 1984). Einsphar et al.(1967) reported narrow-sense heritabilities of 0.24 (height) and 0.35 (diameter) for full-sib families of trembling aspen. Reighard (1984), using the same plantation of this test with a different set of samples, found narrow-sense heritabilities of 0.31 (height) and 0.39 (diameter) at the second year. In this test, narrow-sense family based heritabilities for diameter and height were high at the first year (0.50 for diameter, 0.83 for height) and second years (0.63 for diameter, 0.66 for height), but it changed

Table 20. Genetics and environmental variance and narrow-sense heritability of stem diameter and height derived from NC 1 mating design.

Sources	Diameter 1/				Height 1/		
	1st year	2nd year	7th year	9th year	1st year	2nd year	7th year
				Genetic variance			
Additive (A)	.053 (18%)	.209 (25%)	.569 (5%)	.232 (1%)	889.10 (39%)	1624.59 (28%)	2458.31 (4%)
Dominance (D)	.037 (13%)	.063 (8%)	3.080 (32%)	6.925 (40%)	58.02 (2%)	493.85 (8%)	27054.29 (40%)
Genetic (A + D)	.090 (31%)	.272 (33%)	3.659 (38%)	7.157 (41%)	947.12 (41%)	2118.44 (36%)	29512.60 (44%)
				Environmental variance			
Error (pooled)	.094 (33%)	.310 (37%)	2.376 (25%)	4.367 (25%)	704.05 (31%)	1954.06 (34%)	18322.95 (28%)
Tree (plot)	.103 (36%)	.248 (30%)	3.643 (37%)	5.751 (33%)	643.59 (28%)	1752.55 (30%)	18744.90 (28%)
				Narrow-sense heritability			
Family based 2/	.495	.632	.139	.029	.826	.653	.074
Single-tree based 2/	.228	.308	.080	.019	.492	.350	.054

1/ Percentages were based on the total of Var.genetic, Var.Error(pooled), and Var. tree(plot).
2/ Heritabilities were calculated by using formula according to Hallauer and Miranda (1981).

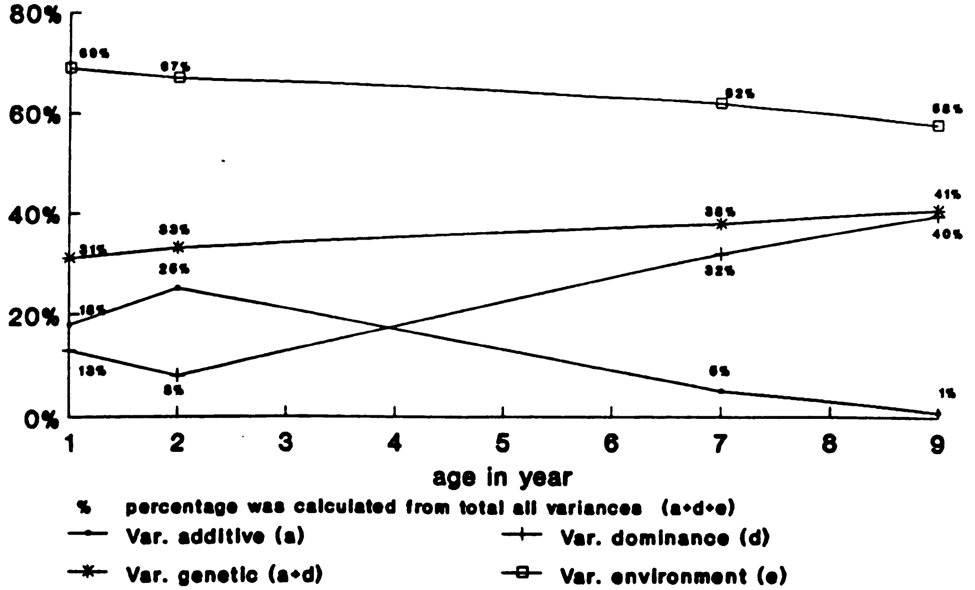

Figure 8. Genetic and environmental variance estimates of stem diameter at ages 1, 2, 7 and 9 years (in percentage).

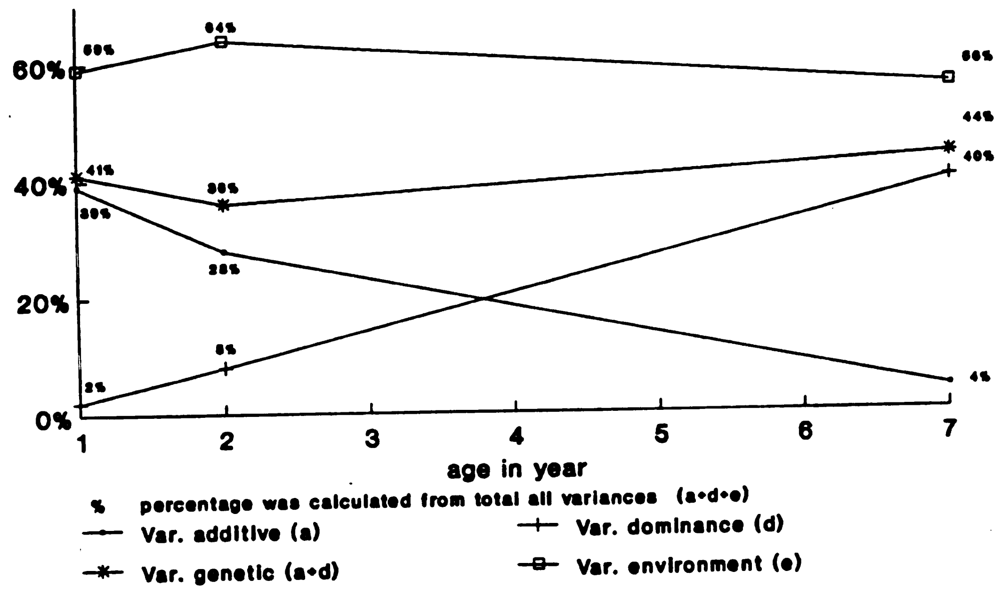

Figure 9. Genetic and environmental variance estimates of height at ages 1, 2, and 7 years (in percentage).

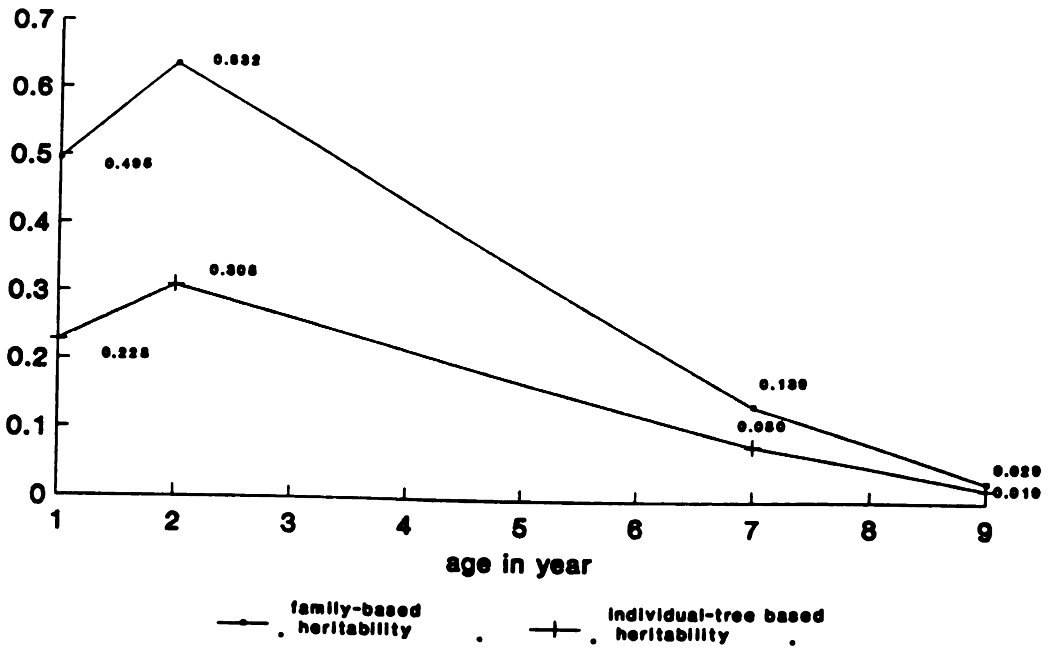

Figure 10. Family- and individual tree-based heritability of stem diameter at ages 1, 2, 7 and 9 years.

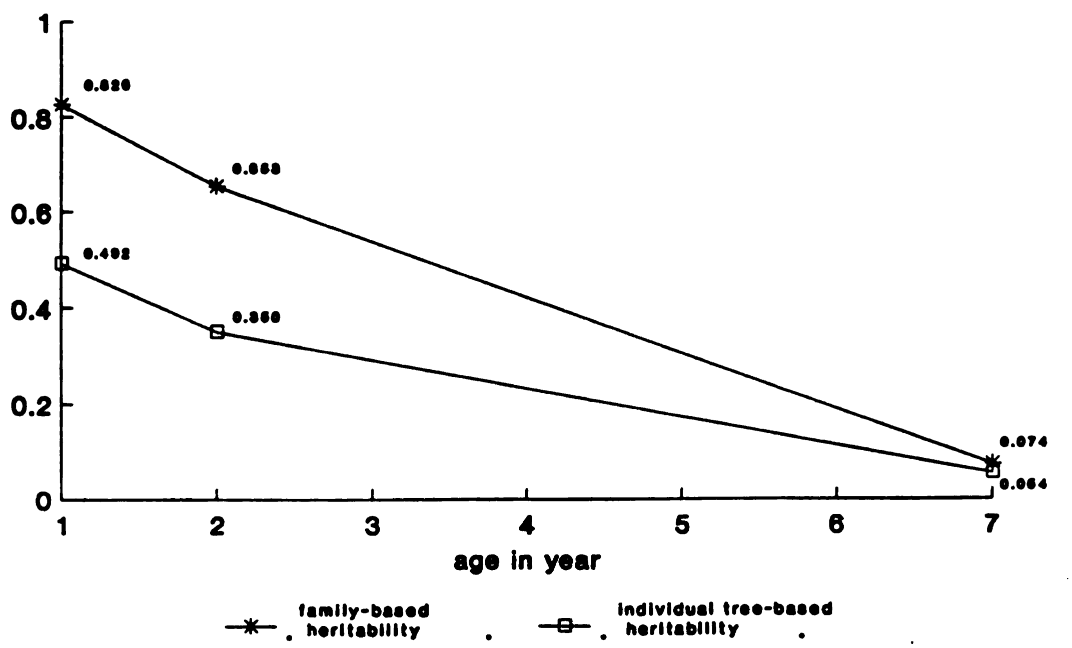

Figure 11. Family- and individual tree-based heritability of height at ages 1, 2 and 7 years.

drastically at 7 years (0.14 for diameter, 0.07 for height) and at 9 years (0.03 for diameter). A similar result also showed up for single-tree based heritability, but all single-tree based heritabilities were smaller than those based on family.

The decrease of heritabilities might be caused by the change of composition of additive and dominant variance within genetic variance, and by environmental effects. As trees mature, the heritability changed markedly due to environmental change and composition change in genetic control of the characteristics (Zobel and Talbert 1981).

In this test, the genetic control (genetic variance) of stem diameter was relatively high and slightly increased with ages (from 31% in the first year to 41% at nine years old). For height, the genetic variances were also high, moving from 41% at the first year to 36% at the second year and then up to 44% at 7 years. The composition of additive and dominance variances within genetic variance also changed with the age. The additive variance component dominated genetic variance at the first and second year but decreased markedly with age (from 18% at the first year to 1% at 9 years for diameter, and 39% at first year to 4% at 7 years for height). On the other hand dominance variance components that were less pronounced in the first and second years increased with the age (from 13% at the first year to 40% at 9 years for diameter, and from 2% at the first year to 40% at 7 years for height). Since narrow-sense heritability is based on additive variance, the decrease in additive variance decreased the heritability.

The decline of additive variance with ages often occurs in forest trees species (Franklin 1979). Namkoong and Conkle (1976) showed a marked decrease of additive variance (in height) between ages 5 and 7 years in half-sib families of Ponderosa pine. Gill (1987) reported a decline of additive variance between height at 8 or 11 years and 22 years in half-sib families of white spruce. This problem should be a major concern for a tree breeding program, because if there is no additive variance at a certain time there will not be any prospect for improving general combining ability by doing selection at those times (Wright and Talbert 1984).

The declining of additive variance in this test might be caused by the interaction between inter-tree competition and expression of genetic variance. Franklin (1979) mentioned that inter-tree competition is a major causal factor in the behavior of additive genetic variance when the stand is developing. The increased growth of trees may increase inter-tree competition, influencing the additive genetic variance.

Cannell (1982) also showed evidence, in open pollinated Sitka spruce, that the decline of additive variance was caused by the increasing inter-tree competition. However, the phenomenon of interaction between competition and genetics has not yet been widely studied in forest tree breeding.

The contribution of components of variance containing non-genetic factors (var.error and var.trees-within-plot) to the total variation was relatively large (ranging from 69% to 58% for diameter and 64% to 56% for height). This large non-genetic variance may indicate that silvicultural practices for increasing growth is important.

It should be noted that these components of variance were derived from a specific population involving a mixture of inter- and intra-specific crosses. An analysis based on inter- or intra-specific crosses separately might give a different result.

Correlations

1. Stem Diameter - Height Correlation,-
The coefficient of correlations between stem diameter and height at ages 1, 2, and 7 years, for all taxa together and for each taxa separately, showed that stem diameter and height were significantly correlated (Table 21 & Fig 12).

The coefficient of correlation ranged from 0.88 to 0.90 for all taxa together, and from 0.73 to 0.97 for each taxa separately, except for *P.tremuloides* x *P.grandidentata* at the first year (0.44). Reighard (1984), analyzing all five plantations in Michigan at two years old, found a

Table 21. Coefficient of correlation between stem diameter and height at ages 1, 2, and 7 years.

Taxa	1st year	2nd year	7th year
P.grandidentata x *P.grandidentata*	0.83**	0.86**	0.90**
P.tremuloides x (*P.*x *rouleauiana*)	0.89**	0.97**	0.73**
P.tremuloides x *P.grandidentata*	0.44**	0.79**	0.89**
P.grandidentata x *P.tremuloides*	0.73**	0.90**	0.89**
P.tremuloides x *P.tremuloides*	0.87**	0.82**	0.84**
All together	0.89**	0.88**	0.90**

**) Significantly correlated at alpha = 0.01.

range of coefficient correlations from 0.73 to 0.89. Another study on Leuce progenies by Mohrdiek (1979) also showed that height and stem diameter were highly correlated.

The high correlation between stem diameter and height is an advantage for a tree improvement program. It gives a possibility to estimate height by only measuring stem diameter, or vice versa.

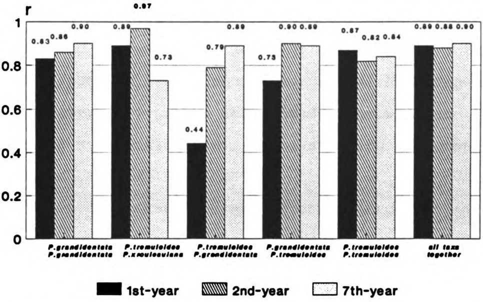

Figure 12. Coefficient of correlation between stem diameter and height at ages 1, 2 and 7 years

2. ***Age-age correlation.-*** Age-age correlation of a trait is a principal tool in forest genetics for calculating the gain from juvenile selection to a future breeding program (Zobel and Talbert 1984, Namkoong 1979). Age-age correlations are influenced by growth rate (Namkoong and Conkle 1976), site, stocking and competition (Franklin 1979).

The age-age coefficients of correlation of family-mean diameter between ages 1, 2, 7, and 9 year, and those of height between ages 1, 2, and 7 years are presented in Table 22.

The correlation of phenotypic performances between ages 9, 7, 2, years and age 1 year (for diameter) and between ages 7 & 2, years and age 1 year (for height) of all taxa combined as a group, were significance ($P<0.05$). However, the coefficient of correlation gradually decreased along with the distance between ages measured (Figure 13).

Based on age 9 years for diameter, the coefficients of correlation for ages 7, 2, and 1 were 0.94, 0.66 and 0.54 respectively. Based on 7 years for height, the coefficients of correlation for ages 2 and 1 were 0.62 and 0.52 respectively. These results are similar to those from Leuce progeny reported by Mohrdiek (1984). He found numbers of 0.952, 0.934, 0.828, 0.554, 0.483 and 0.462 for correlation between age 25 to 15, 11, 9, 3, 2, and 1, respectively. Reighard (1984), found a coefficient correlation of 0.48 between one-year-old trees in the nursery and 2-year-old trees in the field. The significance of the correlation may give a possibility to do an indirect selection, based on height or diameter, earlier than 9 years old.

Analysis for each taxa, separately, showed that families of bigtooth aspen, trembling aspen and the P. tremuloides x P. grandidentata hybrid had significant correlations for all ages, but not for the trihybrid and the P. grandidentata x P. tremuloides hybrid. This may indicate that, if early selection will be done based on families of each taxa separately, it will only be partially effective for bigtooth aspen, trembling aspen and P. tremuloides x P. grandidentata, but not for the trihybrid and hybrid P. grandidentata x P. tremuloides.

Tabel 22. Phenotypic coefficient of correlation of stem diameter and height among ages 1, 2, 7 and 9 years.

	Diam.1	Diam.2	Diam.7	Diam.9
Diam.1	1	a. 0.76** b. 0.82** c. 0.88** d. 0.82** e. 0.84**	a. 0.62** b. 0.19^{ns} c. 0.57** d. 0.26^{ns} e. 0.74**	a. 0.68** b. 0.39^{ns} c. 0.42* d. 0.10^{ns} e. 0.68**
Diam.2	f. 0.88**	1	a. 0.54** b. 0.58^{ns} c. 0.81** d. 0.55** e. 0.74**	a. 0.62** b. 0.54^{ns} c. 0.67** d. 0.38^{ns} e. 0.72**
Diam.7	f. 0.64**	f. 0.73**	1	a. 0.82** b. 0.77** c. 0.94** d. 0.92** e. 0.93**
Diam.9	f. 0.54**	f. 0.66**	f. 0.94**	1

	Hgt.1	Hgt.2	Hgt7
Hgt.1	1	a. 0.76** b. 0.75* c. 0.86** d. 0.70** e. 0.80**	a. 0.36^{ns} b. 0.38^{ns} c. 0.52** d. 0.38^{ns} e. 0.58**
Hgt.2	f. 0.86**	1	a. 0.54** b. 0.80** c. 0.69** d. 0.81** e. 0.62**
Hgt.7	f. 0.52**	f. 0.62**	1

note : a. <u>Populus grandidentata</u> x <u>P.grandidentata</u>.
b. <u>P.tremuloides</u> x <u>P.xrouleaniana</u>
c. <u>P.tremuloides</u> x <u>P.grandidentata</u>
d. <u>P.grandidentata</u> x <u>P.tremuloides</u>
e. <u>P.tremuloides</u> x <u>P.tremuloides</u>
f. combined all taxa.
*. Significant at $P<0.05$
**. Significant at $P<0.001$
ns. Non significant at $P<0.05$

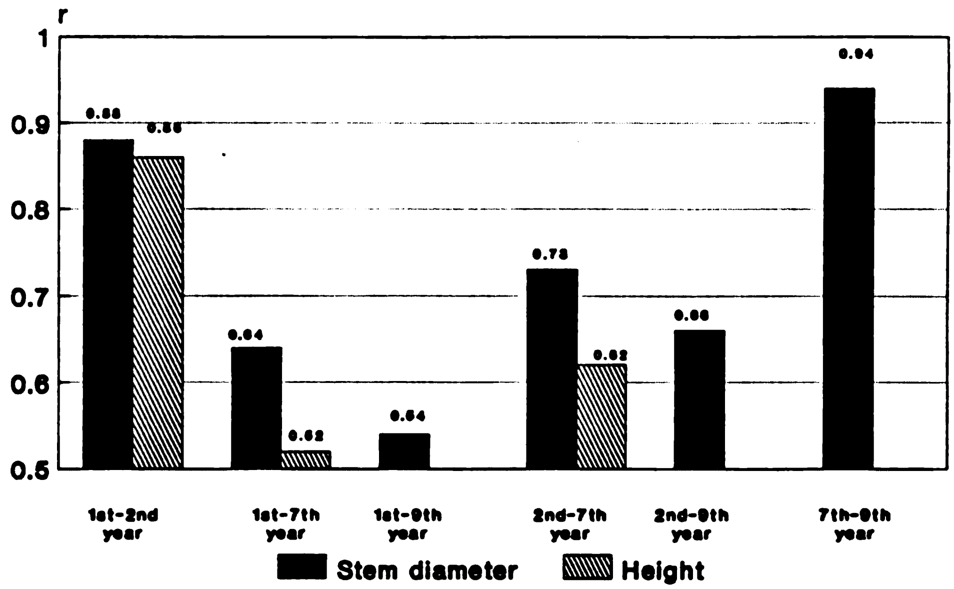

Figure 13. Age-age coefficient of correlation of stem diameter and height among ages 1, 2, 7 and 9 years.

CONCLUSION

The results of this study indicate that the hybrids between *P. tremuloides* and *P. grandidentata* were able to establish themselves as readily as either *P. grandidentata* or *P. tremuloides*. For the families used in the experiment, the survival rate of the hybrids and the trihybrid, especially at the first and second year (87-99%), were high and almost equal to the progeny of their parent. However, the survival rate of the trihybrid at 7 and 9 years of age (71% and 65%) as slightly less than the progeny of either *P. grandidentata* or *P. tremuloides*.

P. grandidentata was the least competitive among the taxa investigated. Height and stem diameter growth of the hybrids were initially intermediate between *P. tremuloides* and *P. grandidentata*. However, at ages 7 and 9 years the hybrids surpassed either of their parents. The hybrids, which were initially not dominant among the 10% best families, became dominant at ages 7 and 9 years.

These results indicated that hybrid vigor might exist in aspen families. The superiority of the hybrids might not appear early on, but rather show up in lates years. Further study of this test at an older age might be worthwhile.

Variation of the progeny was affected more by female parent than by male parent. The male parent variance was small, not significant, and decreased with age. On the other hand, the female parent variances were significant and tended to increase with age. The performance of the progeny was also affected by geographical origin of the female parent, in term of stem diameter but not height. For plantations in the Lower Peninsula, female parent from the Lower Peninsula had better progeny than those from the Upper Peninsula. Among female parents from the Lower Peninsula regions, those from the central Lower Peninsula generated better progeny.

Narrow-sense heritability estimates of stem diameter and height traits were relatively high in the early growth but decreased extremely with age. The family-based heritability was relatively high at the first-year (50% for diameter and 83% for height) but declined to below 10% at 7 years (for height) and 9 years (for diameter). The individual tree-based heritability had a similar pattern and was always smaller than the family-based heritability.

The proportion of genetic variances for stem diameter (31%-41%) and height (36%-44%) was relatively large and slightly increased with age. This is an advantage for tree improvement program. However, composition of additive and dominance variance within the genetic variance changed with time. The additive variance decreased along the years and was very small at ages 7 years and 9 years. The dominance variance increased with the ages, and at age 7 years and 9 years became the major proportion of the genetic variance.

The proportion of non-genetic variance (environmental variance) was relatively high (range from 69% to 56%) and slightly decreased with age.

Stem diameter and height traits were highly correlated to each other. The coefficien of correlation for all taxa, combined, ranged from 0.88 to 0.90. Age-age correlation among ages 1, 2, 7 and 9 years (for stem diameter) and ages 1, 2 and 7 years (for height) were also significantly evident for all taxa together. These results provide some justification for doing indirect selection at an early age.

RECOMMENDATIONS

The objective of a tree improvement program is the development of improved trees and mass production of improved seed or propagules at any stage of their development, for immediate need (Zobel and Talbert 1984).

The progeny test in this experiment showed that hybrid vigor seemed to appear in the F1 hybrids of trembling aspen x bigtooth aspen (reciprocal). It means that, for plantation in southern Lower Peninsula of Michigan, production of this hybrid could be more beneficial. However, since the superiority of the hybrids seemed to be controlled by non-additive genetic variance, the F2 progeny of the best F1 hybrids could not be guaranteed to be better than the F1 itself, they might even be worse (Wright, 1962).

Based on these reasons, mass production of selected F1 hybrids by clonal means or other plantings of parental species will be better than production of untested F2 hybrids from the best F1 hybrids. Mass production of the selected F1 hybrids may be accomplished through several methods.

In aspen, vegetative propagation of the F1 hybrids is a possibility. Aspen is noted for its ability to regenerate vegetatively by adventitious shoots or suckers that arise on its long lateral roots (Debyle and Winokur 19..). An average of two suckers can be produced from 2.5 lineal centimeters of 0.63 cm to 1.27 cm diameter root cuttings (Schier and Campbell 1980). Vegetative propagation also has the advantages of perpetuating preferred genotypes.

Another way to produce selected F1 hybrids is by establishing seed orchard that consists of parental trees of the selected F1 hybrids, followed by controlled pollination of specified parental combinations. Parental trees should be collected clonally, while pollination can be done by using the cut-branch method (Einsphar and Benson 1964), or by using a wind-pollination method. By manipulating trees arrangement in a specific design, pollination can be directed for specific parents.

The cut-branch method has generally been used in artificial seed production of aspen hybrids. This method may produce a large number of seeds. Benson (1972) reported that 700 seeds per catkin can be produced with this method, but the average production ranged from 150 to 300 seeds per catkin. The cut-branch method is also easy to handle and gives a guarantee in producing pure seed from specified parental combination. Another advantage in using cut-branch method is that we do not need to design any specific lay out for parental trees in the seed orchard. However, this method might need a high capital input for collecting catkin-bearing branches and for other expenses.

When wind-pollination is a preference, a chessboard distribution design is recommended (Klaehn 1960, Giertych 1975). This design simply alternates two selected clones (one pair of parents of a selected F1 hybrid) in each row and column of the orchard. To avoid intra-specific hybridization, only one pair of parents (two clones) is allowed in an orchard. Since aspen is a dioecious species, selfing will not be a problem.

When more than one pair of selected parents are needed, a group of small orchards in which each orchard has difference pairs of parent might be an alternative. In this case, the distance between orchards should be far enough, or the orchards should be isolated to each other, such that unwanted crossing can be avoided.

Since aspen is prolific and produces tremendous seeds per individual seed-bearing female (Graham, et al. 1963), a small number of selected female parents at each orchard may produce a huge number of improved seeds.

The wind-pollination method offers the simplest and cheapest route to production F1 hybrids seed production. However, since the flowering time of trembling aspen and bigtooth aspen is slightly different, this method must be recommended with caution.

Another alternative for producing improved seed in the next generation is by testing the F2 hybrids. Selected F1 hybrids can be crossed to each other such that a sufficient wide genetic base of F2 hybrids can be made. A progeny test on the F2 hybrids could be done at an early year. By this time good combining F1 hybrid parents can be identified. If the genetic variance is dominated by non-additive components, a similar method for producing F1 hybrids can be applied for producing improved F2 hybrids. If the genetic variance is dominated by additive components, clonal seed orchards from F2 hybrid can be established.

While producing improved seed for short-term objectives, continuous improvement program can be done by simultaneously increasing the additive genetic variance in the parents (based on the F1 Hybrids) that have exhibited the best specific combining ability and then mating these improved parents for subsequent generations of F1 hybrids. Namkoong (1979) suggested that direct recurrent selection based on general combining ability would be easier and just as effective as method based on specific combining ability.

Continuous observation and evaluation of phenotypic performance and the behavior of the genetic control of growth traits at older years would be valuable. Concurrently, improvement on other traits such as pest and diseases resistance, stem-straightness, and flowering time should also be done.

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A P P E N D I C E S

Table A1. Families that at age 9 years represent at least at four replications.

Families Accession number	Counties origin	
	Maternal Parent	Paternal Parent
10001	Allegan	open-pollination
10004	Branch	open-pollination
10009	Clare	open-pollination
10014	Ingham	open-pollination
10015	Ingham	open-pollination
10034	Ogemaw	open-pollination
10037	Oscoda	open-pollination
10045	Van Buren	open-pollination
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10048	Branch	Ingham
10049	Branch	Calhoun
10050	Branch	Sanilac
10051	Branch	Marquette
10052	Calhoun	Ingham
10054	Calhoun	Midland
10055	Clare	Oakland
10056	Ingham	Chippewa
10057	Ingham	Clare
10058	Ingham	Sanilac
10060	Ingham	Marquette
10062	Iosco	Gladwin
10069	Ogemaw	Ontonagon
10070	Ogemaw	Marquette
10071	Saginaw	Oakland
10072	Saginaw	Missaukee
60001	Calhoun	Alpena
60003	Calhoun	Ingham
60004	Calhoun	Iron
60006	Calhoun	Marquette
60007	Calhoun	Midland
60008	Calhoun	Oscoda
60010	Ingham	Isabella
60011	Ingham	Isabella
60012	Marquette	Isabella
60015	Roscommon	Isabella

cont'd.

table A1 (cont'd.)

	Maternal Parent	Paternal Parent
70004	Branch	Clare
70005	Branch	Marquette
70008	Chippewa	Kalkaska
70012	Gladwin	Chippewa
70013	Gladwin	Calhoun
70016	Ingham	Chippewa
70017	Ingham	Midland
70020	Ingham	Roscommon
70021	Ingham	Roscommon
70022	Iosco	Branch
70024	Iosco	Gladwin
70027	Lake	Marquette
70028	Marquette	Ingham
70029	Marquette	Clare
70030	Marquette	Oakland
70031	Marquette	Marquette
70032	Marquette	Clare
70033	Marquette	Oakland
70035	Oceana	Clare
70038	Oceana	Sanilac
70039	Ontonagon	Clare
70043	Roscommon	Ingham
70044	Roscommon	Oakland
70045	Washtenaw	Otsego
70047	Allegan	Huron
70048	Branch	Presque Isle
70050	Branch	Oscoda
70051	Branch	Mackinac
70052	Branch	Ingham
70054	Branch	Marquette
70056	Calhound	Wexford
70057	Calhound	Iron
70059	Clare	Kalkaska
70060	Ingham	Sanilac
70062	Ingham	Midland
70069	Marquette	Marquette
70070	Montcalm	VanBuren
70071	Montcalm	Sanilac
70072	Montcalm	Alpena
70074	Saginaw	Huron
70075	Saginaw	Alpena
70076	Saginaw	Chippewa
70078	VanBuren	Iron
70079	VanBuren	Oscoda
70081	Wexford	Benzie

cont'd.

table A1 (cont'd).

	Maternal parent	Paternal parent
90001	Allegan	open-pollination
90003	Alpena	open-pollination
90004	Alpena	open-pollination
90005	Alpena	open-pollination
90010	Branch	open-pollination
90011	Branch	open-pollination
90013	Chippewa	open-pollination
90014	Chippewa	open-pollination
90016	Clare	open-pollination
90019	Gladwin	open-pollination
90020	Gladwin	open-pollination
90021	Gladwin	open-pollination
90026	Ingham	open-pollination
90028	Ingham	open-pollination
90029	Ingham	open-pollination
90037	Lake	open-pollination
90038	Lake	open-pollination
90039	Luce	open-pollination
90043	Marquette	open-pollination
90044	Marquette	open-pollination
90045	Marquette	open-pollination
90051	Missauke	open-pollination
90053	Montmorency	open-pollination
90054	Montmorency	open-pollination
90056	Oakland	open-pollination
90057	Oakland	open-pollination
90059	Oceana	open-pollination
90063	Ogemaw	open-pollination
90065	Oceola	open-pollination
90066	Oceola	open-pollination
90067	Osceola	open-pollination
90068	Oscoda	open-pollination
90076	Wexford	open-pollination
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90078	Allegan	Gladwin
90079	Allegan	Manistee
90082	Branch	Ingham
90083	Branch	Ingham
90084	Branch	Emmet
90085	Chippewa	Huron
90086	Chippewa	Oscoda
90088	Gladwin	Gladwin
90089	Gladwin	Luce
90091	Ingham	Sanilac
90093	Iron	Iron

cont'd.

table A1 (cont'd)

	Maternal Parent	Paternal Parent
90094	Ingham	Montcalm
90095	Ingham	Marquette
90096	Ingham	Mackinac
90097	Ingham	Washtenaw
90098	Ingham	Emmet
90099	Iosco	Gladwin
90100	Lake	VanBuren
90101	Lake	Benzie
90103	Lake	Emmet
90104	Lake	Alpena
90105	Lake	Chippewa
90106	Lake	Emmet
90107	Marquette	Ingham
90108	Marquette	Ingham
90109	Mecosta	Montmorency
90114	Oceana	Iron
90116	Oceana	Marquette
90117	Oceana	Huron
90118	Ontonagon	Wexford
90119	Ontonagon	Iron
90120	Osceola	Sanilac
90121	Osceola	Midland
90123	Roscommon	Marquette
90124	Wexford	Midland
90125	Wexford	Kalkaska

Table A2. Families that were used for constructed NC-1 mating design.

Accession Number		
Male parent	Female parent	Progeny
10032	10040 90043	10071 70030
10029	10006 90026	10054 70017
10008	10014 90021	10056 70012
10027	10004 90038	10051 70038
10013	10017 90033	10062 70024
10010	90045 90064	70032 70039
10039	90027 90028	70020 70021
90025	10002 90062	70047 90117
90069	10045 90014	70079 90086
90034	10044 90060	70078 90114
90036	10009 90076	70059 90124
90072	10031 90067	70071 90120
90047	10023 90071	70069 90123
90031	90009 90044	90082 90108
90017	90037 90029	90103 90097