PROGENY TESTING OF NATIVE ASPENS AND THEIR HYBRIDS FOR BIOMASS PRODUCTION IN MICHIGAN

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ABSTRACT. Anaspen progeny test consisting of 206 families of trembling aspen (*Populus tremuloides*), bigtooth aspen (*P. grandidentata*), and their hybrids (P. *Xsmithii* and P. *Xrouleauiana*) was planted on five Michigan sites and evaluated after two growing seasons. Growth performance of trembling aspen families when compared with all aspen taxa was above average and increased with the latitude of the plantation site. Backcrosses of trembling aspen males to white poplar-bigtooth aspen (P. *Xrouleauiana*) females produced the fastest growing families at all Lower Peninsula plantations. Most hybrid aspen (P. *Xsmithii*) families had growth rates below the plantation means. Bigtooth aspen families had poor survival and growth at all plantations. Analyses of two nested mating designs showed that general combining ability (additive genetic variance) for height and diameter growth was present in the aspen population. Genotype x environment interaction was small at the family level.

INTRODUCTION

The aspens are fast-growing trees that have been studied by numerous poplar breeders, but unfortunately little progress has been made in improving the genetic base of the species. Large amounts of genetic variation in trembling aspen (*Populus tremuloides*) and bigtooth aspen (*Populus grandidentata*) have been reported (Pauley 1949, Einspahr and Benson 1967, Barnes 1969). This genetic variation provides an ample germplasm base for a tree improvement program. Furthermore, the ease of hybridization between the two species (Pauley 1956, Henry and Barnes 1977) permits the breeder to create additional variation in desired traits. The problem that geneticists have encountered when breeding aspen is how to quantify and "capture" the genetic variation found in the species. It has been difficult to establish test plantations for the species and to eliminate bias from genotype x environment interactions (Einspahr and Mohn, personal communication).

The objectives of this aspen progeny test were to: (1) quantify the genetic variation in the native aspen populations in Michigan, (2) create additional genetic variation by hybridizing the two native aspen species, (3) identify fast-growing aspen families for short-rotation biomass plantations, and (4) establish a progeny test on different sites in order to investigate genotype x environment interactions.

MATERIALS AND METHODS

Progeny Production and Mating Design

Seed and catkin-bearing branches of bigtooth and trembling aspen were collected from 43 counties in both peninsulas of Michigan during March and April of 1979 and 1980. Similar material from two putative white poplar-bigtooth aspen (P. *Xrouleauiana*) hybrids located in the southern Lower Peninsula of Michigan was also collected. Controlled-pollinations were made using the cut-branch technique (Einspahr and Benson 1964). Progenies from the pollinations represented 48 half-sib and 66 full-sib families of bigtooth and trembling aspen. In addition, 72 full-sib families of hybrid aspen (P. *Xsmithii* = P. *grandidentata* X P. *tremuloides*) and 20 F_1 backcrosses of bigtooth and trembling aspen to the putative white poplar hybrid, P. *Xrouleauiana* (P. *alba* X P. *grandidentata*), were produced.

The mating design used in the progeny test was a nested design (North Carolina Design 1) which later was reduced in size because of the failure of some crosses to produce sufficient seed. After adjustment for missing families, two nested designs were constructed from 46 of the 158 full-sib families that were well represented in the field tests. The first design had eight males (four each of bigtooth and trembling aspen) which were each crossed to two females of each species. Theoretically, random sampling of the population in the nested design would dictate that females be crossed only once, but in this test four females were used twice because of significant mortality in some families. The design comprised 32 families (8 males and 28 females) and was replicated six times in one plantation. The second design tested seven trembling aspen males which were each crossed with two different trembling aspen females. There were 14 families (7 males and 14 females) in this design, and they were replicated 16 times across three plantations.

Seed was sown in the nursery on May 26, 1981, and cultural procedures similar to those of Benson and Dubey (1972) were used to grow the seedlings. Insects were controlled with Orthene. The mean height for each family in the nursery was recorded before the seedlings were lifted the following March and placed in cold storage until the planting season started.

Plantation Sites and Aspen Establishment Procedures

The five plantation sites chosen for this study were abandoned agricultural fields. Three plantations are in the Lower Peninsula of Michigan and two are in the Upper Peninsula. The Lower Peninsula plantations are at Michigan State University's (MSU) Russ Experimental Forest (Cass Co., Lat. 42.0°N, Long. 86.0°W), MSU Water Quality Research Area (Ingham Co., Lat. 42.7°N, Long. 84.5°W), and Michigan Consolidated Gas Company's gas storage fields near the town of Six Lakes (Mecosta Co., Lat. 43.5°N, Long. 85.2° W). The soil textures of the Russ Forest, Water Quality, and Six Lakes sites are a sandy loam, a fine sandy loam, and a sandy loam, respectively. Grasses and perennial weeds were the dominant vegetation on these sites.

The two Upper Peninsula plantations are at the Michigan State agricultural field station near Chatham (Alger Co., Lat. 46.3°N, Long. 86.9°W) and on Neebish Island (Chippewa Co., Lat. 46.3°N, Long. 84.2°W). The Chatham plantation is on a former alfalfa field which has a fine sandy loam soil texture. The Neebish Island plantation was a clover and timothy field with a heavy clay soil which was mottled at a depth of 20 cm. The soils at all plantations except Neebish Island were well-drained.

Site preparation for each of the five plantations consisted of mowing the existing vegetation with a rotary mower in August, 1981 and spraying seven liters/ha of glyphosate in one-meter-wide strips three to four weeks later. In April and May of 1982, the seedlings were planted at these five Michigan locations. The seedlings were machine-planted in two-tree plots with a spacing of 1.8 meters between trees within rows, and 2.4 meters between rows. The experimental design was a randomized block with six replications at each plantation. Following spring planting, 2.8 kg/ha a.i. of simazine was applied over the tops of the seedlings and onto the glyphosate-sprayed strips. The planting strips in the Water Quality and Six Lakes plantations were spot-sprayed once with glyphosate in July, 1982 to control invading grasses.

Data Analyses

Height, basal diameter, and survival of the families in all the plantations except Neebish Island were tallied in 1982 and 1983. The diameters were squared and then multiplied by the heights to give an index of biomass production (=biomass production index). Analyses of variance and correlations were calculated for all height, basal diameter, biomass production index, and other growth measurements. Family performances in all analyses were based on the plot mean of each family which was expressed in percent of the block (replicate) mean. Family and species performances within, and between geographical regions of Michigan were evaluated for trends and genotype x environment interactions. Heritability estimates for height and diameter were derived from analyses of variance of the first nested design. Male and female effects were tested and evaluated for the parents used in both nested designs. Age-age correlations were calculated for the relationship of first-year nursery height to the two-year-old plantation height data.

RESULTS AND DISCUSSION

Family Performance Among Plantations

Two-year survival of the families within each cross (taxon) is listed in Table 1 for the three best plantations. The Russ Forest and Neebish Island plantings were not listed because mortality was greater than 50% due to herbicide damage and drought. Survival increased with decreasing latitude of the plantations. Survival at the Chatham plantation was seven and 11 percent less than that at Six Lakes and Water Quality (East Lansing), respectively. The freeze-free period or growing season at Chatham is 100 days compared to 126 days at Six Lakes and 151 days at East Lansing (Mich. Dept. Agric. 1971). The shorter growing season and other environmental stresses significantly reduced the survival of P. Xsmithii families at Chatham. Survival of the two native aspens varied little across the three plantations.

Rapid juvenile growth is positively correlated with aspen survival (Pauley et al. 1963a, Hattemer and Seitz 1967, Melchior and Seitz 1966, Mohrdiek 1979a). The fastest growing families in this test also had the lowest mortality. Bigtooth aspen and the hybrids grew poorly on the Chatham site and consequently, suffered significantly higher mortality than the trembling aspen families. These initially slow-growing species and hybrids should not be planted in areas with severe climatic conditions because early mortality is likely to be high. However, if some of these families become fast growers once they are established, the early mortality can be compensated for by planting at higher densities.

The analyses of variance showed that differences in height, basal diameter, and biomass production index were significant ($P<.05$) for individual families and families-within-taxa at all plantations in years 1982 and 1983. The highest family means for two-year height and diameter at the best plantation (Water Quality) were 2.8 meters and 3.3 cm., respectively (Table 2). The height and diameter of the five top families when averaged over four plantations were 1.6 meters and 1.9 cm., respectively. Early growth of these families was comparable or greater than that reported for promising families of trembling aspen (Pauley et al. 1963b), hybrid aspen (Pauley et al. 1963c), triploid hybrid aspen (Benson and Einspahr 1967), white poplar-bigtooth hybrids (Johnson 1942), and white poplar-aspen trihybrids (Maynard 1977).

Table 1. Two-year survival in percent for aspen taxa at three plantations.

Taxa (Female X Male)	Plantation Site		
	Chatham	Six Lakes	Water Quality
Populus tremuloides X P. tremuloides	92	90	97
P. tremuloides X P. grandidentata	68	89	91
(P. Xrouleauiana) X P. tremuloides	84	88	99
P. grandidentata X P. grandidentata	72	73	75
P. grandidentata X P. tremuloides	72	86	87
(P. Xrouleauiana) X P. grandidentata	64	63	79
All Crosses Combined	79	86	90

[1] Replicates 4-6 were not included because of herbicide overdose.

To evaluate the growth potential of these families, the biomass production index, basal diameter squared times height, was used. Correlations of height to basal diameter within plantations ranged from .73 to .89 and were significant at the one percent probability level. Mohrdiek (1979a) summarized the findings of many Populus genetic studies and concluded that height is highly correlated with diameter for all poplars. Since the correlation between height and diameter is high in poplars, the biomass production index was considered a valid measure of biomass productivity.

Table 2. Two-year growth performance of the best family and individual of each aspen taxon at the Water Quality plantation.

Aspen Taxon	Best Family (Mean) 1983 Ht[1] (cm)	Best Family (Mean) 1983 Diam[2] (cm)	Best Individual 1983 Ht (cm)	Best Individual 1983 Diam (cm)
Populus tremuloides	273	3.1	395	4.6
P. grandidentata	232	2.6	345	3.8
P. Xsmithii	275	3.3	435	5.6
(P. Xrouleauiana) X P. tremuloides	254	2.9	360	4.6

[1] Heights were measured to the nearest 5 cm.
[2] Diameters measured at 5 cm above the soil surface

The biomass production index of each taxon at four plantations is shown in Table 3. The number of families of each taxon that were among the top 25 families in biomass production index at each plantation are summarized in Table 4. The number of trembling aspen families in the top 25 increased with increasing latitude of the plantation site, while the number of hybrid and trihybrid families increased with decreasing latitude. Trembling aspen families comprised 19 of the 25 best families overall. Families of trembling aspen and the trihybrid were best in terms of biomass production index over all four plantations. The best family, a trihybrid, averaged 28% above the mean biomass production index for all families at age two.

Family x Site Interaction

Correlations between taxon performance (biomass production index) at each plantation with its respective performance over all plantations are listed in Table 5. The performance of individual families at each plantation site was significantly correlated with their average performance over the four sites (r= .68 to .77), although bigtooth aspen families at Six Lakes were an exception. The correlation data implied that although genotype x site interactions were present, they were not strong at the family level under the particular conditions of this test. These findings agree with those of Hattemer and Seitz (1967) who reported that family x site interactions for height data of hybrid aspen in Germany were non-significant. The results suggest that most aspen families had good correspondence in performance at two years across the environments tested. Therefore, the fast-growing genotypes expressed growth superiority in different environments.

Table 3. Biomass production index (diameter^2 X height) in % of plantation mean for five aspen taxa in four Michigan plantations.

		Taxon (Female X Male)				
Plantation	Latitude	AGxT[1]	TT[2]	TG, GT[3]	AGxG[4]	GG[5]
		%				
Chatham	46.3°N.	114	133	74	66	46
Six Lakes	43.5°N.	125	116	81	86	51
Water Quality	42.7°N.	123	116	94	74	61
Russ Forest	42.0°N.	160	108	76	86	76
Combined		122	120	84	77	56

[1] (Populus alba x P. grandidentata) x P. tremuloides

[2] P. tremuloides x P. tremuloides

[3] P. tremuloides x P. grandidentata and the reciprocal cross

[4] (P. alba x P. grandidentata) x P. grandidentata

[5] P. grandidentata x P. grandidentata

Table 4. Number of families of each taxon that comprise the 25 families with the highest biomass production indices at each plantation.

Taxon (Female X Male)	Plantation Site: Chatham	Six Lakes	Water Quality	Russ Forest	Combined
Populus tremuloides X P. tremuloides	20	16	12	11	19
(P. Xrouleauiana) X P. tremuloides	2	4	4	6	4
P. Xsmithii (plus reciprocal)	2	5	7	6	2
(P. Xrouleauiana) X P. grandidentata	-	-	1	1	-
P. grandidentata X P. grandidentata	1	-	1	1	-

Table 5. Correlations of taxon performance (biomass production index) at each plantation with mean performance of each taxon for all plantations.

Taxon (Female X Male)	Number of Families	Plantation Site[1] Chatham	Six Lakes	Water Quality	Russ Forest
		---------r-----------			
Populus tremuloides X *P. tremuloides*	73	.63	.61	.62	.74
P. tremuloides X *P. grandidentata*	37	.73	.58	.86	.78
P. grandidentata X *P. grandidentata*	34	.68	-.05 ns	.70	.90
P. grandidentata X *P. tremuloides*	35	.31 *	.75	.58	.67
All Taxa Combined	179	.77	.74	.68	.71

[1] All correlation coefficients without asterisks are significant at the 1 percent level.
*Significant at the 5 percent level.
ns Non-significant at the 5 percent level.

Trembling aspen and trihybrid families had similar biomass production indices and exhibited growth rates that exceeded the mean at all plantations. However, trembling aspen families were superior in growth and survival to all other aspen taxa at Chatham (Upper Peninsula), whereas trihybrid families grew the best at the three Lower Peninsula plantations. Trembling aspen families did well in the Upper Peninsula because the species is more adapted to northern climates than the other taxa tested. Performance of trembling aspen families in relation to the other aspen taxa increased with increasing latitude of the plantation site.

The performance of trembling aspen families from site to site differed from those of big tooth aspen and the trihybrid, P. *Xrouleauiana* X P. *tremuloides*. The P. *Xrouleauiana* backcrosses were not well adapted to the shorter growing season and colder temperatures at Chatham. The P. *alba* lineage in this cross probably originated in Central or Southern Europe and was less ecologically adaptable in the Upper Peninsula than the native aspens. This hybrid did perform well in the Lower Peninsula plantations, possibly because of the milder climate. All other hybrid taxa performed below the mean at the four sites. These hybrids may be late starters, or are more site specific since their performance varied markedly with site. Bigtooth aspen grew poorly at all sites, but growth was 65 percent better at the southernmost plantation (Russ Forest) than at the northernmost one (Chatham). In general, trembling aspen families grew best on northern Michigan sites, and hybrid and bigtooth aspen families grew better on southern Michigan sites.

The unidirectional clines in relative performance of trembling, bigtooth, and trihybrid aspen from northern to southern plantations were undoubtedly influenced by the latitude and climate of the planting site. Once the appropriate species or hybrid is chosen for a specific climatic region, family selection can then be based on the average performance for all plantations within that region. From this study, trembling aspen families would be selected for the Upper Peninsula and cold regions of the Lower Peninsula, whereas trihybrid families would be planted throughout the other areas of the Lower Peninsula.

Geographic Significance of Parent

Pauley et al. (1963a) found that P. *tremula* families from Central Europe grew faster than Northern European families in Weston, Massachusetts. In this test, the 20 best families overall were produced by 35 parents (17 females and 18 males) representing 26 widely dispersed counties. Families from the 206 in the progeny test that included a trembling aspen parent from northern Lower Michigan (above Lat. 43.8°N) grew two percent larger than families with Upper Peninsula trembling aspen parents, and five percent larger than families with southern Lower Michigan (below Lat. 43.8°N) trembling aspen parents. Families that had bigtooth aspen parents from southern Lower Michigan grew two to ten percent larger than families with bigtooth aspen parents from northern Lower Michigan and the Upper Peninsula. The best hybrid families (P. *Xsmithii*) were produced from parents of both species that were located in southern Lower Michigan. These families grew two to eight percent larger than did hybrids with parents from northern Lower Michigan and the Upper Peninsula.

Finding an existing natural aspen population (50-100 clones) with superior growth would increase the gain that would be achieved in the first breeding cycle. However, the clonal nature of aspen (Barnes 1966, Kemperman 1976) and its large genetic variability would necessitate a sample size so large that it would be impractical to progeny test. This study contained half-sib and full-sib progeny from 125 clones representing 43 counties. The number of families (206) used in this test was inadequate to estimate the within, and between stand variation of the two species. Furthermore, the failure of some 50 other clones to produce progeny reduced the efficacy of the mating designs to detect genetic variation.

Even though superior aspen stands were not identified, the general geographic location of the parents was important to the performance of the crosses. Okafo (1976) found that western Upper Peninsula sources of bigtooth and trembling aspen grow faster under greenhouse conditions than other Michigan sources. Other aspen researchers (Barnes 1959, Pauley et al. 1963a, Johnsson 1976, Melchior and Seitz 1966) have found that aspen parents from specific geographic regions produce the best progeny. In this study, the best bigtooth and trembling aspen parents came from northern and southern Lower Michigan, respectively. Since trembling aspen is a boreal species, the climate and soils of northern Lower Michigan are similar to the northern range of the species. Southern Lower Michigan, however, has soils and climate that are less representative of the boreal habitat of trembling aspen. Generally, Populus progenies from northern latitudes grow poorly at lower latitudes because the shorter photoperiod and warmer temperatures are thought to induce growth cessation (Pauley and Perry 1954). This trend was apparent in some families, but was relatively insignificant due to the large variation in phenology within each geographic population. However, only one of the four measured plantation sites was in the Upper Peninsula; consequently, the two percent lower growth rate of families with trembling aspen parents from the Upper Peninsula may partially be attributed to this latitudinal effect.

In contrast to trembling aspen, bigtooth aspen grows on drier sites and tolerates warmer temperatures. Bigtooth aspen appears to occur more frequently than trembling aspen on the farmland of Michigan's southern tier counties (Reighard, personal observation). The higher growth rates of bigtooth families from southern Michigan may be due to the commonly observed genetic trend that southern populations of many tree species sacrifice cold hardiness for faster growth rates (Wright 1976), or it may be that the longer leaf retention of the southern sources (Reighard, unpublished data) is an advantage because of autumn photosynthesis.

The best hybrid families had parents of both species from southern Lower Michigan. Barnes (1961) and Andrejak and Barnes (1969) have reported that natural hybridization is currently occurring between bigtooth and trembling aspen in southern Michigan. Due to this gene flow between the two species, the southern Michigan populations of these species probably share more genes than do their northern Michigan populations. This introgression may reduce the degree of chromosome non-homology in hybrid families that are produced from southern Michigan parents because many non-vigorous hybrids in the plantations suffered from a dysgenesis syndrome which included chlorophyll breakdown, bud abortion, and shoot or whole tree death. Pauley et al. (1963c) found a similar type of physiological breakdown when he reported that 39 of 41 progeny of a hybrid aspen family died at age eight from unknown causes. These physiological abnormalities and Peto's (1938) findings that hybrid aspen progenies commonly have chromosomal irregularities such as univalents and trivalents casts suspicion on the fitness of hybrid aspen over an entire rotation period.

Geographic Separation of Parent Stands

Certain fast-growing hybrid aspen progenies (ie. P. *alba* X P. *grandidentata* or P. *glandulosa*; P. *tremula* X P. *tremuloides*) have been produced by crossing Leuce poplars that were geographically and ecologically disjunct (Zsuffa 1973). Highly productive families have also been produced by hybridizing the sympatric species P. *alba* and P. *tremula* (Mohrdiek 1979b) and allopatric populations of P. *tremula* (Johnsson 1956). In this study, there were no apparent trends in the biomass production indices of the full-sib families of trembling and hybrid aspen in relation to the geographic distance between their parents (Table 6). However, there was a small decrease in the biomass production index of bigtooth aspen families with increasing geographic distance between the parents. This trend had a significant ($P<.05$) correlation of -.25.

Johnsson (1956) and Muhle Larsen (1970) have assumed that non-additive genetic variance (heterosis) was responsible for the growth superiority of hybrids between geographically isolated aspen species and populations. The absence of heterosis in the progeny that were produced by crossing geographically distant populations of trembling aspen may be attributed to gene flow occurring between the trembling aspen populations in Michigan. On the other hand, additive genetic variance (Mohrdiek 1980) has been reported in growth traits of aspen. If additive effects were indeed important in the performance of outstanding hybrid families, the variation within Michigan's aspen populations may have been equal to or greater than the variation between populations. The large genetic variation within aspen populations has been well documented by Barnes (1969), Cheliak and Dancik (1982), and many others. Therefore, maximum genetic gain could be achieved from selecting within one large, genetically tested population.

The slower growth of many P. *Xsmithii* families when compared to promising aspen hybrids such as P. *Xrouleauiana* may be indirectly the result of the phenological isolation of bigtooth and trembling aspen (Pregitzer and Barnes 1980) over much of their Michigan ranges. This phenological barrier to introgression exerts upon each species a form of assortative mating which has been demonstrated by Gregorius (1980) to be a process that increases the rate of chromosome evolution via allelic mutations and ultimately leads to changes in chromosomal homology between two populations or species. The chromosomal irregularities in this hybrid were probably responsible for its inferior fitness in the progeny test. However, another explanation for the lack of vigor in P. Xsmithii is that both parent species may have evolved under similar environmental conditions in eastern North America, and therefore, may be more alike genetically than other aspen species used to produce hybrids. We do not know why increased geographic distance between bigtooth parents reduced progeny performance, but sampling error due to the low number (34) of families analyzed cannot be ruled out.

Table 6. Biomass production index in % of replicate mean of families-within-taxa in relation to the geographic distance between parents.

Distance (Km) Between Parents	Parental Taxon: P. tremuloides X P. tremuloides	P. grandidentata X P. grandidentata	P. Xsmithii
Open-pollinated	114	77	
1-175	132	50	84
176-325	121	46	90
326-650	130	45	76
Average	121	59	84

Open-pollinated families of trembling aspen (Table 6) did not perform as well as full-sib families. The opposite was true for bigtooth aspen. The biomass production index of the open-pollinated families of trembling aspen was 13 percent below the mean biomass production index of its full-sibs. In contrast to trembling aspen, the open-pollinated families of bigtooth aspen grew 29 percent better than its full-sibs. Farmer and Barnes (1978), however, found that open-pollinated families of trembling aspen showed no more genetic variation than full-sib families. Since open-pollinated families usually have more than one male parent and full-sib families are fathered by one male parent, it would be expected that half-sib families would show more variation in phenotypic traits. We do not know why the number of pollen parents per family affected each species in a different manner.

Heritability and General Combining Ability

Height and diameter analyses of the two nested designs showed that the female-within-male variance component was significant (P<.01), but the male component was not. Narrow-sense heritabilities for height (h^2=.31) and diameter (h^2=.39) were obtained from the variance components of the first nested design which included data from a single plantation. Heritabilities could not be obtained from the second design which included data from three plantations because of negative mean squares from insufficient observations in the sampling procedures.

The first nested design gave relatively large narrow-sense heritabilities (additive genetic variance) for height and diameter. The true heritability of these traits is much less because the genotype x environment interaction variance could not be partitioned out. Einspahr et al. (1967) reported similar narrow-sense heritibilities of .24 (height) and .35 (diameter) for full-sib families of trembling aspen. Likewise, their heritabilities were based on a single test plantation.

The nested design analyses show that selection of the female parent was important in the mating design. The choice of the male parent, however, was not found to be statistically important. This may be due to a strong maternal effect or experimental error. The latter is assumed because Mohrdiek (1979b) reported that both the maternal and paternal parents were important in crosses of P. tremula and P. tremuloides, and in the nested designs, the better males possessed good general combining ability (GCA). The top male in designs 1 and 2 had a general combining ability (GCA) of 18.5 and 7.9 units above the mean, respectively. In Germany, Hattemer and Seitz (1967) found the GCA of paternal aspen parents to be three to five times the GCA of the maternal aspen parents in diallel crosses. These analyses and the the narrow-sense heritability data suggest that mating designs that screen for additive genetic variance should be used to improve the breeding population of Leuce poplars.

Age-age Correlations

Age-age correlations between nursery height and the average two-year field height within each cross are presented in Table 7. Mohrdiek (1979a) found positive age-age correlations of .46 between years one and 20 and .83 between years nine and 20 for growth traits in aspen. After evaluating data from 36 aspen progeny trials, he recommended the eighth year as the earliest time to begin intensive selection. The age-age correlation in this study between nursery height growth and the height growth after two field growing seasons for all aspen families as a group was significant ($P<.05$) but somewhat low ($r=.48$).

Families of trembling aspen and the trihybrid had significant age-age correlations, in contrast to non-significant ones for bigtooth aspen families. Taxa with bigtooth aspen as the female parent were not significantly correlated, but the opposite was true for trembling aspen as the female parent. The age-age correlation of families with a trembling aspen female was less significantly correlated ($P<.05$) if the male parent was bigtooth aspen. One explanation for the data is that families of trembling aspen and the trihybrid were fast growers the first few years from seed, whereas bigtooth aspen was a slow grower for the first two years. In the second growing season in the field (three years from seed), bigtooth aspen began to grow as rapidly as trembling aspen. This initial slow start would explain why taxa with bigtooth aspen parents had low and non-significant age-age correlations at an early age. Hybrids containing European white poplar (P. alba) parentage had the largest age-age correlation of all the taxa and were the fastest growing in the nursery and the field plantings.

Table 7. Age-age correlations of the mean family height in the nursery with the mean family height averaged over four plantations.

Taxon (Female X Male)	Families Per Taxon	Correlation
		- - - - - r - - - - - - -
Populus tremuloides X P. tremuloides	59	.38 **
P. tremuloides X P. grandidentata	18	.51 *
P. grandidentata X P. grandidentata	14	.33 n.s.
P. grandidentata X P. tremuloides	19	.28 n.s.
(P. Xrouleauiana) X Populus species	17	.64 **
All Taxa	127	.48 **

*/** Significant at the 5 and 1 percent levels, respectively.

For short-rotation biomass plantations, selection within this progeny test at age three may be effective at the species level (ie., eliminate bigtooth families), but selection at the family level would only be partially effective until approximately year eight. By the eighth year, many families would be flowering (Valentine 1975). Therefore, the high age-age correlations for growth traits and precocious flowering found in the aspens might permit an eight-year breeding cycle which is considerably shorter than many other tree species.

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