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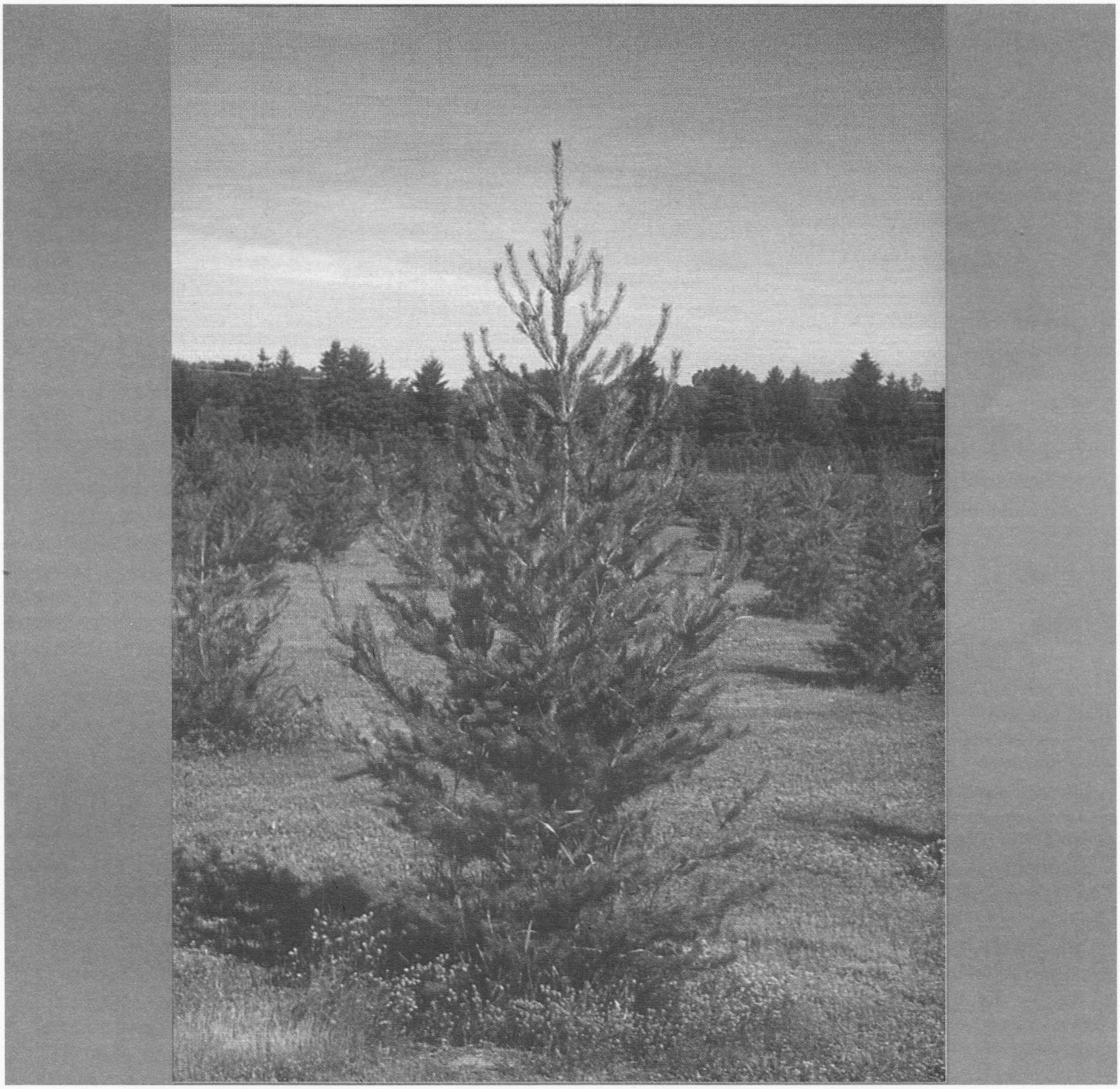
The Genetic Improvement of Jack Pine in Michigan



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INTRODUCTION

Jack pine (*Pinus banksiana* Lamb.) is a tree of the northern forests of the United States and Canada, commonly occurring as a fire-following species on less fertile, drier soils. In the Great Lakes states, jack pine is an important source of pulpwood, is requisite to maintaining viable Kirtland's warbler populations and is one of the few tree species suited to many of the outwash plains of northern Michigan. Consequently, it is widely planted by the Michigan Department of Natural Resources (MDNR). In 1995 alone, approximately 1,500 pounds of jack pine seed were processed by MDNR's State Tree Improvement Center and used in establishing nearly 6,000 acres. Jack pine is also a genetically diverse species amenable to genetic improvement (Rudolph, 1964; Jeffers and Nienstaedt, 1972). Jack pine's economic value, coupled with its genetic diversity, make it an excellent candidate for genetic improvement, and it has been the object of tree improvement efforts in Michigan since 1951.

The objectives of this publication are fourfold:

1. Provide a brief history of tree improvement activities with jack pine in Michigan.
2. Discuss the genetic gains made to date.
3. Outline the short-term and long-term strategies employed to achieve these gains.
4. Discuss plans for continuing the genetic improvement of jack pine in Michigan.

HISTORICAL BACKGROUND

Provenance Tests - 1951

Genetic improvement efforts for forest tree species frequently begin with provenance testing. Provenance tests commonly consist of bulk seedlots collected from natural stands spanning all or much of the species' natural or naturalized range. Provenance tests provide basic information on the amount of genetic variability within a species and how that variability is distributed across the sampled portion of the species' range. Although provenance tests do not provide estimates of the genetic parameters required for designing and implementing a multigeneration improvement program, provenance test results can be used to direct seed collection to geographic areas or stands which exhibit above average performance.

In 1951, recognizing the value of potential genetic gains in the growth of jack pine, the USDA Forest Service initiated a regional improvement program for jack pine by establishing a provenance test of 29 seedlots collected from the Lake States region at 17 sites in Wisconsin, Minnesota and Michigan and one site in Ontario. Canada's Petawawa Forest Experiment Station at Chalk River, Ontario, initiated a more extensive rangewide provenance test consisting of 98 seedlots in 1962. Michigan State University's Department of Forestry was an active cooperator in both of these tests and was responsible for establishing and maintaining three plantings of the Lake States test and four plantings of the Petawawa test.

Both the Lake States and Petawawa provenance tests found significant differences in height growth among the seedlots (Alm and Jensen, 1969; Arend *et al.*, 1960; Jeffers and Jensen, 1980; Yeatman, 1974). Additionally, 10- and 15-year results of the Lake States test indicated that seedlots from lower Michigan were among the best in height growth (Rudolph and Yeatman, 1982). Twenty-year results of the Lake States test reported by Jeffers and Jensen (1980) found that seedlots from Michigan's Lower Peninsula averaged 16% above the mean for volume of all test sites and 25% above the mean for volume in the test's four Michigan plantations.

King (1966) and Jeffers and Jensen (1980) reported significant seedlot X test site interaction at ages 10 and 20 (respectively) for the Lake States test. Although none of these analyses provided evidence for the existence of geographic races within the Lake States jack pine population, there was a weak clinal pattern in the variation of height growth. The relative height of sources from the southeastern portion of the species' Lake States range (i.e., southern Michigan), tended to decline when moved north and west (i.e., to northern Wisconsin and Minnesota). Conversely, the relative performance of northern Minnesota sources tended to decline when moved south and east. King (1966) found that this pattern accounted for much of the seed source X site interaction in 10th-year height data.

Lower Michigan Half-sib Progeny Test - 1965

The excellent performance of lower Michigan seed sources in the Lake States and Petawawa provenance tests prompted MSU's Department of Forestry to intensify its tree improvement program for jack pine by initiating a half-sib progeny test using open-pollinated seed collected from phenotypically selected trees. The lower Michigan half-sib progeny test consists of 385 open-pollinated, single-tree seedlots (half-sib families) collected from 60 natural stands in the northern portion of Michigan's Lower Peninsula in 1965 and 1966. The 229 seedlots collected in 1965 were planted at four Michigan sites in 1968. The 156 seedlots collected in 1966 were planted at three other Michigan sites in 1969. The location of surviving plantings of the lower Michigan half-sib progeny test are given in Figure 1. The 1968 and 1969 plantings do not share any common seedlots.

Analyses of nursery data (Canavera, 1975) and ages 15 to 17 data (Howe *et al.*, 1983; Ernst *et al.*, 1983) from the lower Michigan progeny test reported significant differences among seedlots in height, diameter, biomass, form and specific gravity. Howe *et al.* (1983) reported that gains from phenotypic selection of wild maternal parents were minimal compared with gains from family selection based on performance in the progeny test. Ernst *et al.* (1983) analyzed a sample of well represented families in the Mackinac planting and estimated gains of 22% in wood mass when selecting for both volume and specific gravity. The lower Michigan progeny test was eventually used to pursue the MDNR's near-term needs for improved seed and is discussed in further detail later in this publication.

Figure 1. Plantation locations of the lower Michigan half-sib progeny test.

Lake States Half-sib Progeny Test - 1979

A major advance occurred in the USDA Forest Service's regional program in 1979, when the Forestry Sciences Laboratory at Rhinelander, Wis., initiated the Lake States Jack Pine Breeding Program. This program is a regional effort designed to coordinate federal, state and private programs involved in the genetic improvement of jack pine. The program's first-generation field trials are a variation on traditional half-sib progeny tests and contain 458 half-sib seedlots collected from Michigan, Minnesota and Wisconsin established in four primary or index plantations (Figure 2) and 16 secondary or local breeding populations. Each index population is randomly divided into four subpopulations of 20 half-sib families each. A detailed description of the structure and content of this test is given by Riemenschneider (1979).

In 1974, MSU's Department of Forestry organized and began administering the Michigan State Cooperative Tree Improvement Program (MICHCOTIP). MICHCOTIP assumed responsibility for all of the MSU Department of Forestry's genetic plantations and for directing the department's ongoing tree improvement research. MICHCOTIP participated in the Lake States Jack Pine Breeding Program, establishing one of the test's four primary plantations at Wellston, Mich., in 1980. This test figures prominently in the MDNR's pursuit of long-term objectives and is discussed at length below.

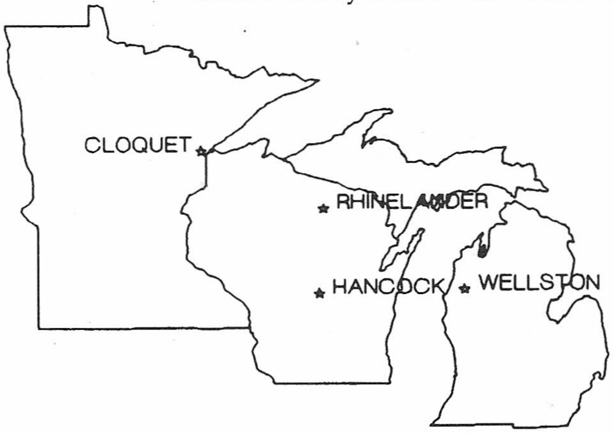

Figure 2. Locations of the primary (index) plantations in the Lake States half-sib progeny test.

PURSUIT OF NEAR-TERM OBJECTIVES

In 1982, the MDNR decided to pursue the immediate production of improved jack pine seed for use in its planting program. Working cooperatively, MDNR and MICHCOTIP reviewed the genetics tests existing in Michigan and decided that the most expedient means of producing improved seed was to thin one or more plantations of the Lower Michigan progeny test. MDNR contracted with MICHCOTIP to analyze the lower Michigan progeny test and used the results of these analyses to select superior families and thin one or more of the test plantations.

Roguing the Allegan Plantation for Seed Production

Because of its size and its proximity to available labor, the Allegan County planting was the first chosen for thinning. To provide the information necessary to select the trees to be removed from the plantation during thinning, height and diameter at breast height (DBH) were measured in the Allegan planting (1982) and in two of its companion plantings in Antrim (1982) and Mackinac counties (which had been measured in 1981 prior to the MDNR's initiative). Volume estimates were computed using the prediction equation used by Jeffers and Jensen (1980) in their analysis of 20-year USFS provenance test data:

$$\mathrm{Vol}\ (\mathrm{ft}^3) = (.1781 + .3361(\mathrm{DBH})^2)\ (\mathrm{Height} - (.01/\mathrm{DBH})).$$

Analysis

Analyses of variance (ANOVAs), following the model in Table 1, were performed on the height, DBH and volume data. ANOVAs provide significance tests (F-tests) for sources of variation included in the model and quantify those sources of variation by partitioning the total variation into components. Variance components estimate how much of the total observed variation is due to specific effects. The variance components of interest in the model used include variation due to families (σ_f^2), site (σ_s^2), family X site interaction (σ_{fs}^2) and error (σ_e^2).

Variance components were estimated by equating expected mean squares (Table 1) to observed mean squares (produced by ANOVAs) and solving for the desired variance components.

Variance component estimates are needed for the calculation of heritabilities. Heritabilities estimate the percentage of the total variation due to genetic factors. Two types of narrow-sense heritabilities were calculated: family heritabilities (h_f^2) and single-tree heritabilities (h_t^2). Family heritabilities were used to estimate the portion of the variation among family means due to additive genetic factors. They are used to predict genetic gain when selecting entire families. Single-tree heritabilities estimate the portion of the total variation due to additive genetic factors. Single-tree heritabilities are used to estimate genetic gain when selecting individual trees. All heritability estimates presented here were calculated per Wright's (1976) formulae.

Table 1. Format of the analyses of variance used to test for family differences and significant family X site interactions and to estimate variance components in the lower Michigan and Lake States half-sib progeny tests.

Source	DF	Expected Mean Squares
Site	S-1	$\sigma_e^2 + F\,\sigma_b^2 + B\,\sigma_{fs}^2 + BF\,\sigma_s^2$
Block (site)	S(B-1)	$\sigma_e^2 + F\,\sigma_b^2$
Family	F-1	$\sigma_e^2 + B\,\sigma_{fs}^2 + BS\sigma_f^2$
Family X site	(F-1)(B-1)	$\sigma_e^2 + B\,\sigma_s^f$
Error	FS(B-1)	σ_e^2

Results

Significant variation among families ($\alpha \leq 0.01$) was found for height, DBH and volume (Table 2). The magnitude of family and single-tree heritabilites indicated that these characters are under relatively strong genetic control (Table 2).

Significant family X site interactions were found for height ($\alpha \leq 0.01$) and volume ($\alpha \leq 0.02$). This indicated that there were significant differences in family rankings for height and volume growth across the three test sites. Significant family X site interactions dictate the choice of one of two selection strategies: 1) select families or individuals based on their performance in specific environments or breeding zones and initiate separate breeding programs for each environment, or 2) select broadly adapted families which perform well across all sites tested. Option 2 was chosen for thinning the Allegan plantation because the delineation of breeding zones and development of corresponding breeding populations would have been prohibitively expensive. It was also unwarranted because broadly adapted families could be identified.

It was determined that trees to be retained for seed production in the Allegan planting could be selected on the basis of their individual performance (mass selection), on the basis of their family's performance (family selection), or on a combination of individual and family performance (combined selection). Family selection was chosen because the family heritability values were high

Table 2. Error (σ_e^2), family (σ_f^2) and family X site (σ_{fs}^2) variance component estimates, and family (h_f^2) and single tree (h_t^2) estimates for height, DBH and volume in the Allegan, Antrim and Mackinac plantings of the lower Michigan half-sib progeny test at age 16 years.

Character	σ_e^2	σ_f^2	σ_{fs}^2	h_f^2	h_t^2
Height	30.62	1.63*	3.53*	0.43	0.18
DBH	17.36	3.34*	0.56	0.82	0.56
Volume	9.0×10^7	$1.4 \times 10^{7*}$	$5.1 \times 10^{6*}$	0.77	0.52

* Significant at $\alpha \leq 0.01$.

(Table 2), and it allowed the selection of broadly adapted families whose average volume growth exceeded the test mean across all three test sites. Family selection is also less expensive than mass or combined selection because the identification and removal of entire half-sib plots within the test plantation is less costly than marking and removing individual trees within the plots. Mass selection was not a viable option because of the significance of family X site interactions (trees selected for their performance at one site may represent a gene combination that would perform poorly at another site).

Applying Results

An initial thinning level of 50% was chosen for roguing the Allegan planting. Although a heavier thinning would have produced greater genetic gain, this gain was outweighed by the increased risk of wind damage incurred by opening the plantation too quickly. Volume was chosen as the variable upon which selection was based, as it most accurately reflects economic value. Family averages for volume across the three tests were computed. Families which averaged below the test mean were marked by MICHCOTIP personnel in 1983 and removed by MDNR personnel during the summers of 1983 and 1984. To avoid creating large holes in certain parts of the plantation, several plots of below average families were retained until the plantation became wind firm.

Expected genetic gains from the current roguing and subsequent thinnings to the top 33% and 25% are reported in Table 3. Initial expected gains for progeny produced by the Allegan planting are low because of the low selection intensity (only the bottom 50% was removed). However, genetic gains should increase substantially after a second roguing. Also, note that the gains reported in Table 3 do not include the 16% to 25% gain already realized by selecting northern Lower Peninsula seedlots. Plans for a second roguing of the Allegan plantation have not yet been formalized.

Roguing the Emmet Plantation for Seed Production

Cone production in the Allegan plantation increased slowly following the initial roguing, and limited amounts of seed were produced for several years. In 1986, MDNR and MICHCOTIP decided to thin another plantation in the northern lower Michigan progeny test to supplement seed production at Allegan. The Emmet County planting was chosen because it had excellent survival and was located on a fertile, upland hardwood site, which should aid in the development of live crown and flower production after thinning.

Analysis

DBH and branch angle were measured in the Emmet plantation in 1987. Branch angle was measured because the MDNR suspected that jack pine with more upright branch angles recover more quickly from terminal leader damage caused by the white pine weevil (*Pissodes strobi*). (White pine weevil damage to jack pine has become a major concern in Michigan over the past decade.) Height could not be measured accurately because of crown closure in the Emmet plantation. This prevented the estimation of volume growth. The Emmet planting's two companion plantations could not be measured because of extensive snow damage (Kalkaska) and poor survival (Higgins Lake).

Analyses of variance performed on DBH and branch angle followed a format similar to the design in Table 1. Site and family X site terms could not be tested because data were collected from a single site. Variance components, family heritabilities and single-tree heritabilities were estimated from the analyses of variance.

Results

Variation among families was significant for DBH $\alpha \leq 0.05$) and branch angle $\alpha \leq 0.01$). Family heritability estimates for both traits were substantially higher than single-tree heritabilities (Table 4). Family and single-tree heritability estimates for DBH calculated from the Emmet plantation data (Table 4) were

Table 3. Estimated genetic gains (% above test mean) from family selection for height, DBH and volume for progeny produced from the Allegan planting of the lower Michigan half-sib progeny test.

Character	Select Top 50%	Select Top 33%	Select Top 25%
Height	0.4	0.5	1.0
DBH	2.0	3.7	5.0
Volume*	5.6	7.6	11.5

* Variable used to rogue the Allegan planting.

Table 4. Variance components and family (h_f^2) and single-tree (h_t^2) heritability estimates for DBH and branch angle in the Emmet plantation of the lower Michigan half-sib progeny test at age 20 years.

Character	σ_e^2	σ_f^2	h_f^2	h_t^2
DBH	71.07	3.12*	0.44	0.16
Branch angle	72.2	2.21**	0.38	0.15

* Significant at $\alpha \leq 0.05$
** Significant at $\alpha \leq 0.01$

substantially lower than family and single-tree heritability estimates computed from data collected in the Allegan, Antrim and Mackinac plantings (Table 2). However, the Emmet plantation was established on a high quality upland hardwood site, a site on which the MDNR would not normally plant jack pine. On such a high quality site, every seedlot may grow to its fullest potential, thereby minimizing differences among seedlots and reducing heritability estimates.

Applying Results

Removal of 50% of the trees in the Emmet planting was deemed necessary to allow adequate light into the plantation for crown development and flower production while minimizing the risk of wind damage. As in the Allegan planting, family selection was chosen because the significance of family X site interactions could not be determined, family heritabilities were high, and it was less costly than mass or combined selection.

A selection index which placed equal weight on family means for DBH and branch angle was used to select families for removal. Families were ranked by index score, and the lower 50% were marked for removal by MICHCOTIP personnel in fall 1987. Because of the relatively narrow range of variability of DBH in the Emmet planting, the loss of fast-growing families was undesirable, so families in the top quartile for DBH were retained even if their index score specified their removal (five families were retained by this criterion). Giving DBH more selection weight than branch angle in these five cases was also justified on the grounds that current evidence linking branch angle to recovery from weevil attack was anecdotal and not based on replicated field studies. The thinning was performed by MDNR personnel in summer 1989.

Continued selection for both DBH and branch angle will result in marginal improvement of both traits (Table 5). Future selection efforts based solely on DBH would produce substantially larger, though modest, gains in DBH, while effectively realizing no gain or loss in branch angle (Table 5). Although the 2 to 3% gain resulting from family selection for DBH is modest, it would probably produce much larger gains in volume. In previously discussed analyses of the Allegan, Antrim and Mackinac plantations, estimated gains in volume were nearly twice the size of corresponding gains in DBH. Relatively small gains in diameter usually translate into much larger gains in volume because diameter values are squared in volume calculations.

PURSUIT OF LONG-TERM OBJECTIVES

While economically significant genetic gains in volume growth are anticipated from second thinnings of the Allegan and Emmet plantations, a second-generation progeny test was required to continue the improvement of jack pine in Michigan. In addition to producing a population for selection and seed production, a second-generation progeny test generally produces higher genetic gains because selection intensity can be increased by restricting the number of trees chosen to parent the next generation. In 1989, MDNR and MICHCOTIP again reviewed the status of existing jack pine genetic tests in Michigan and faced the option of progeny testing selected trees in the lower Michigan half-sib progeny test or the Lake States half-sib progeny test. The Lake States test was chosen because it was established on a wide range of sites, current data were readily available, and trees in the test had full live crowns with adequate cone production.

Analysis of Lakes States Half-sib Progeny Test

Height was measured in the Wellston, Hancock and Cloquet plantations at the end of the 1986 growing season (age 8 from seed) and in the Rhinelander plantation at the end of the 1985 growing season (age 7 from seed). As discussed, each of these plantations is divided into four populations of 20 families each. Consequently, separate ANOVAs were computed for each population, in addition to an ANOVA combining the data from all four populations. All ANOVAs followed the format outlined in Table 1. Pearson correlations were computed to assess any linear relationships between family performance at each of the sites and the latitude and longitude of family origin.

Results

Significant differences ($\alpha \leq 0.01$) among families and significant family X site interactions were found within each of the four index populations and in the combined data set.

Table 5. Estimated genetic gains (% above plantation mean) from family selection for DBH and branch angle for progeny produced from the Emmet planting of the lower Michigan half-sib progeny test.

Character	Select for DBH and Branch Angle			Select for DBH	
	Top 50%	Top 33%	Top 25%	Top 33%	Top 25%
DBH	1.0	1.7	1.7	2.5	3.0
Branch angle	1.0	1.2	1.5	0.3	0

Table 6. Variance components and family (h_f^2) and single-tree (h_t^2) heritability estimates for each of the index populations and for all populations combined for 8th-year height in the Lake States half-sib progeny test.

	σ_e^2	σ_{fs}^2	σ_f^2	h_f^2	h_t^2
Population 1	1062	120	163	0.74	0.48
Population 2	763	89	115	0.73	0.48
Population 3	799	43	96	0.75	0.41
Population 4	743	53	92	0.74	0.41
Combined	1027	317	106	0.50	0.29

Variance components, family heritabilities and single-tree heritabilities are reported in Table 6. Both family and single-tree heritability estimates were quite consistent among the index populations. The heritability estimates from the combined analysis were lower than the heritabilities estimated for each index population individually (Table 6). This decrease was due primarily to a large relative increase in the family X site variance component, suggesting that although a sample size of 20 families was adequate for the detection of significant family X site interactions, a larger sample may be necessary to accurately estimate this term's magnitude.

The significant family X site interactions within each index population and in the combined analysis are consistent with King's (1966) and Jeffers' and Jensen's (1980) analysis of provenance test data and indicate that care must be taken when moving seed across the Lake States region. The relative size of the family X site variance component has increased since age 5. At age 8, the family X site variance was more than 50% of the family variance in three of the four index populations, while it was less than 50% of family variance in all four of the index populations at age 5 (Riemenschneider, 1985).

Pearson correlations between family performance at each site and the latitude and longitude of family origin (Table 7) reveal a pattern similar to that reported by Jeffers and Jensen (1980) for provenance test data. A strong negative correlation exists between family performance and latitude of family origin at the two southern sites r = -0.49 at Wellston and r = -0.55 at Hancock). This negative correlation weakens as the families are moved north to Rhinelander r = - 0.22) and eventually becomes statistically insignificant (albeit weakly positive, r = 0.14) at Cloquet (the northernmost site). A similar though weaker pattern occurs between family performance and longitude of family origin. Pearson correlations indicate that lower Michigan families tend to perform well in the southern portion of the Lake States range of jack pine but tend to lose their advantage as they are moved north and west.

It should be noted that the Pearson correlations are simply indicative of general trends in the data, and an examination of the performance of individual families reveals many exceptions to the patterns. One glaring example is family 8223, which originated in lower Michigan (Lake County). This family was the top performer at all sites (indeed, it is the only seedlot in the test to maintain its rank across all sites) and, contrary to the previously mentioned geographic trends, actually increased its advantage at Cloquet.

Developing an Improvement Strategy for the 2nd-generation Progeny Test

The magnitude of the family X site interaction term again dictated the selection of trees from broadly adapted families (i.e., families that performed well at all four test sites) for parents of the second-generation progeny test. Although performance at all test sites was considered when selecting families, emphasis was given to their growth at Wellston, Mich., because this site is most typical of Lower Peninsula sites commonly managed for jack pine by the MDNR. Families whose combined average across all four sites was 2% above average and whose growth at Wellston was at least 7% above the plantation mean were considered for selection. Secondary emphasis was given to balanced family

Table 7. Pearson correlations for mean family performance (8th-year height) at each test site of the Lake States half-sib progeny test sites and the latitude and longitude of family origin.

Site	Latitude	Longitude
Wellston	-0.49*	-0.42*
Hancock	-0.55*	-0.26*
Rhinelander	-0.22	-0.15
Cloquet	0.14	0.07

*Significant at $\alpha \leq 0.01$

Table 8. Mean performance (average percentage of site mean for 8th-year height) of selected families in the Lake States half-sib progeny test.

Family #	Origin	Wellston	Hancock	Rhinelander	Cloquet	Combined
8223	MI(LP)*	1.14	1.15	1.12	1.18	1.15
9813	MI(LP)	1.10	1.11	1.08	1.05	1.09
8214	MI(LP)	1.14	1.05	1.05	1.05	1.07
8224	MI(LP)	1.07	1.07	1.04	1.05	1.06
8268	MI(LP)	1.11	0.98	1.06	1.05	1.05
8246	MI(LP)	1.10	1.03	1.02	1.06	1.05
8845	WI	1.07	1.09	1.02	1.01	1.05
9748	MI(LP)	1.12	1.03	1.01	1.01	1.04
8228	MI(LP)	1.10	1.08	0.98	0.99	1.04
8797	MI(LP)	1.12	1.00	0.98	1.04	1.03
8222	MI(LP)	1.12	1.02	1.01	0.93	1.02
Site means (m)		2.37	3.29	3.19	3.51	3.08

*LP= Lower Peninsula

performance across the other three non-Michigan sites. Eleven families were selected using these criteria. The mean performance at each site for the selected families is reported in Table 8. From each of these 11 families, the tallest two individuals at the Wellston planting were selected to form the breeding population. A third tree from the best two families was chosen to fill out the mating design.

Selecting a Breeding Design

After selecting the parents of the next generation, a breeding design for progeny testing the selected trees and producing a seed orchard was needed. Breeding designs vary in simplicity and cost from simple half-sib designs to elaborate full-sib designs. Half-sib designs require only the collection of open-pollinated seedlots (flowers are fertilized by the ambient pollen cloud) from selected trees, and they produce half-sib families with a known maternal parent and unknown paternal parents. Full-sib designs require controlled-pollinations (flowers are isolated in bags and fertilized by hand with known pollen lots) and produce full-sib families with known maternal and paternal parents. Half-sib designs are relatively inexpensive; full-sib designs are more costly yet provide more detailed information on genetic parameters. Available funding permitted the use of controlled-pollinations, so a full-sib mating design, the disconnected partial diallel (DPD), was chosen. This design efficiently provides estimates of additive genetic variance and general and specific combining ability, yet it requires relatively few crosses. The DPD design also provides a genetically diverse population to serve as the next breeding population.

The DPD design employed here consisted of eight partial diallels. Each partial diallel contained six parents and produced nine full-sib families. One of the partial diallels is diagramed in Table 9 as an example. Four of the partial diallels were executed in 1990, and the remaining four were conducted in 1991. A total of 48 parents were used to produce 72 full-sib families.

Table 9. Diagram of one of the eight partial diallels used to create a second-generation full-sib progeny test. Each X denotes a completed controlled-pollination and the production of a full-sib family.

Male Parent #	Female Parent					
	1611	2455	327	2319	652	1534
1611			X	X	X	
2455				X	X	X
327					X	X
2319						X
652						
1534						

Establishing the Progeny Test

The primary function of the progeny test is to evaluate the genetic value (breeding value) of each of the trees selected in the Wellston plantation. Seed from the controlled-pollinations was collected in October 1991 and September 1992. In addition to the full-sib families, open-pollinated seedlots were collected from every tree used as a parent in the DPD breeding design. Inclusion of the half-sib families provided the opportunity to evaluate the relative effectiveness of half-sib vs. full-sib breeding designs in realizing genetic gain. While it is given that half-sib progeny tests provide less detailed information, in jack pine it is not known if genetic gains realized in the next generation justify the additional expense and time required to complete a full-sib progeny test. Several lower Michigan stand collections were procured from the MDNR's State Tree Improvement Center to serve as check lots and provide a standard against which the test lots could be measured.

Including the full-sib families, half-sib families and check lots, a total of 129 seedlots were sown at the MSU Tree Research Center greenhouse in January 1993.

Figure 3. Locations of plantings in the second-generation full-sib and half-sib jack pine progeny test.

Seedlings were bare-rooted in spring 1994 and out-planted at three Michigan sites (Figure 3). Each plantation follows a randomized block design, with four blocks at each site and four single-tree plots per seedlot per block.

Establishing a Seedling Seed Orchard

A seed orchard was needed to produce large quantities of seed for use in the MDNR's planting program. The first decision required in designing a seed orchard is to choose either grafted or seedling planting stock. The advantages of grafted seed orchards include:

1. Clonal duplication of the selected population—i.e., each graft is an exact genetic copy of the flowering portion (above the graft union) of the selected tree; this usually results in higher genetic gain and the ability to multiply specific genotypes within the orchard.
2. Accelerated flowering in species which do not flower for 10 to 20 years after out-planting; if scions are collected from mature trees, seed production begins earlier in grafted orchards because grafts tend to retain the physiological age of the scion parents.

Disadvantages of grafted seed orchards include increased costs incurred by labor-intensive grafting and the risk of graft incompatibility, which in some species can result in poor growth or mortality. Advantages of seedling seed orchards include greatly reduced cost and no risk of losses due to graft incompatibility.

Jack pine is well suited for seedling orchards because its rapid juvenile growth and sexual precocity result in substantial seed production at a young age. Despite the potential for greater gains, the cost of grafting is not warranted because grafted jack pine have exhibited slow juvenile growth and lagged well behind seedling plantings in seed production (Rudolph and Yeatman, 1982). The MDNR's planting program uses approximately 1,000 pounds of jack pine seed annually, and establishing a grafted seed orchard that would meet that need would be prohibitively expensive.

The choice of a seedling seed orchard was clear, and MICHCOTIP and MDNR decided to use all surplus seedlings from the half- and full-sib families of the progeny test to establish a seed orchard. Placement of the families within the orchard was determined by the Seed Orchard Management and Design (SOMAD) software developed by the USDA Forest Service. Although there are many different seed orchard designs (Faulkner, 1975), there are two common goals: to minimize inbreeding by spatially separating members of the same clone or family, and to maximize outcrossing by giving members of each clone or family an equal opportunity to mate with all other clones or families in the orchard (a condition termed panmixia).

Family placement is critical to equalizing each family's contribution (via pollen or ovule contribution) to the seed crop. It is also critical to the management of inbreeding, which can result if family members are not sufficiently separated. Inbreeding can seriously reduce seedling vigor and growth and reduce genetic gain. SOMAD creates a permutated neighborhood design which separates members of families or clones to minimize inbreeding while simultaneously shifting the mix of neighbors around a given family or clone to maximize panmixia.

The MDNR's State Tree Improvement Center near Brighton, Mich., was chosen as the site for the seedling seed orchard. The State Tree Improvement Center is well south and east of the natural range of jack pine in Michigan, limiting contamination of the orchard's seed crop by foreign pollen from wild trees outside the orchard. The State Tree Improvement Center also has extensive cone processing, seed cleaning and seed storage facilities and currently processes virtually all of the seed collected by the MDNR.

After determining how much area was available for orchard development at the Tree Improvement Center, a map for the orchard was generated using SOMAD and the planting locations were staked with corresponding family numbers. Seedlings were hand planted in spring 1994 on a 10- by 20-ft. hexagonal spacing. Over 5,000 seedlings representing 83 half- and full-sib families were used to plant 26 acres. Data collected from the second-generation progeny test will be used to evaluate each of the families in the Brighton orchard and guide future thinning of the orchard to maximize genetic gain.

SUMMARY

Provenance and progeny test data clearly indicate that lower Michigan seed sources are superior for use in Michigan's Lower Peninsula. Gains of 16 to 25% in volume growth over the Lake States average can be realized in lower Michigan simply by collecting seed from natural stands in this area. Additional genetic gains can be realized by collecting seed from the rogued Allegan and Emmet plantings of the lower Michigan half-sib progeny test. Seed currently collected from the Allegan and Emmet plantings should produce progeny that average 5% and 2% (respectively) above the mean volume of lower Michigan seed sources. A second roguing in these plantations could increase these gains to 11% (at Allegan) and 6% (at Emmet).

While near-term needs are met by the thinnings in the Allegan and Emmet plantings, long-term needs have been addressed by establishing a 26-acre seedling seed orchard at the MDNR's State Tree Improvement Center. A combined full- and half-sib second-generation progeny test has been established at three Michigan sites to evaluate the performance of families included in the seed orchard. The progeny test will also empirically evaluate the efficiency of half-sib and full-sib breeding strategies. Over the next 5 to 10 years, seed collection will shift from the Allegan and Emmet plantings to the Brighton orchard as it comes into full production. Conservative seed production estimates (Schopmeyer, 1974) indicate that, even with a future roguing of 50%, the Brighton orchard should be able to meet the MDNR's current annual target of 1,000 pounds. During that same period, estimates of the genetic gains realized by progeny of the Brighton orchard will be empirically refined using data collected from the progeny test. These data will also guide future thinnings of the Brighton orchard, which will further increase genetic gain. The progeny test will also provide the parents for the third-generation breeding population and initial estimates of the amount of genetic gain to be expected from a third-generation breeding program, should the MDNR and MICHCOTIP decide to continue pursuing the genetic improvement of jack pine in Michigan.

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