HERITABILITY AND VARIATION OF 8th YEAR HEIGHT IN FOUR SUBPOPULATIONS OF LAKE STATES JACK PINE

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Abstract.--Analysis of height at age eight (from seed) in four "index populations" of Lake States jack pine showed significant differences among 1/2-sib families, and produced single-tree, narrow-sense heritability estimates ranging from 0.41 to 0.48. These estimates were substantially higher than heritabilities estimated previously for these populations from fifth year height data. Family X site interaction was significant in all of the populations. Spearman rank correlations of mean family performance among the sites indicated that family performance was most consistent between the two southernmost (r = 0.52) and the two northernmost Cr = 0.54) sites. Significant negative Pearson correlations existed between mean family performance and the latitude of family origin (r = -0.49 and r = -0.55) at the two southern sites, but this correlation decreased to insignificance at the northernmost site. The implications of these results on the genetic improvement of jack pine in the Lake States are discussed.

Additional keywords: *Pinus banksiana*, genotype X environment interaction, juvenile heritability.

INTRODUCTION

Jack pine (*Pinus banksiana* Lamb.) is an important source of pulpwood in the Lake States, where it is second only to aspen in total pulpwood production (Blyth and Smith, 1982). The economic importance of this resource prompted the U.S.D.A. Forest Service to initiate a provenance test of Michigan, Wisconsin, and Minnesota jack pine seed sources in 1951. All or portions of this test were analyzed in its fifth (Arend et al., 1960), tenth (King, 1966), and twentieth year in the field (Jeffers and Jensen, 1980). Significant differences among seed sources were found in all three analyses, and the source X site interaction was significant at ages ten and twenty. 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 to the variation of height growth. The relative height growth performance 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 tenth year height data.

In 1980, the U.S.D.A. Forest Service's Forestry Sciences Laboratory at

Rhinelander, Wisconsin initiated a Lake States Jack Pine Breeding Program in an effort to coordinate federal, state, and private programs involved in the genetic improvement of jack pine. The program's first objective was to establish a breeding population to be shared by cooperators throughout the region, and to outline a flexible, multi-generation breeding scheme to guide the management of research and improvement efforts.

The breeding scheme, as outlined by Riemenschneider (1979) was modeled after Kang's (1979) "coordinated population" concept, which initially divides the base breeding population into "index" and "breeding" subpopulations. The index populations are established in replicated plantations at several sites, and are the subject of intensive genetic research. Information from the index populations is intended to help guide and inform the management of the breeding populations. Each breeding population is established at a single site provided by one of the program's cooperators, and is managed primarily by, and according to the needs of that cooperator. The index populations are intended to provide information requisite to maximizing the efficiencies of breeding strategies applied to the breeding populations (Kang, 1977).

Riemenschneider (1985) examined the variation and heritability of height growth in the four index populations at age 5, and in the thirteen surviving breeding populations at age 3. Those analyses revealed no significant differences among the index populations (as expected, since they were random samples of the base population), significant family X site interactions, and narrow-sense heritabilities for each of the index populations ranging from 0.12 to 0.18. Heritabilities for the breeding populations ranged from 0 to 0.57. Riemenschneider (1985) suggested that the wide range of heritabilities among the breeding populations might be partially due to sampling variation resulting from the small size of the subpopulations. In light of the magnitude of the heritability estimates observed in the breeding populations, Riemenschneider recommended their immediate remeasurement to determine if the low heritabilities were a transitory, time-related phenomenon.

By 1987, flowering had begun in the breeding and index populations, and additional information was required to develop a breeding program for the index and breeding populations. Toward this end, height was measured at age eight in three of the index populations, and at age seven in the fourth. Analyses of that data, presented here, focused on the following objectives:

1) Provide basic information on the quantitative genetic parameters of the index and, by inference, breeding populations, and compare these results with Riemenschneider's (1985) analysis of fifth year height in the index populations and third year height in the breeding populations.

2) Examine family performance across the Lake States region, and provide information necessary for the selection of families for the second generation of improvement.

3) Determine if the geographic trends in height growth variation found in the provenance test (King, 1966; and Jeffers and Jensen, 1980) are duplicated in the index populations, and examine the effects of moving

seedlots across the breeding zone.

4) Reaffirm one of the primary assumptions of the breeding plan by verifying that no significant differences exist among the index populations.

MATERIALS AND METHODS

Seedling production and plantation establishment

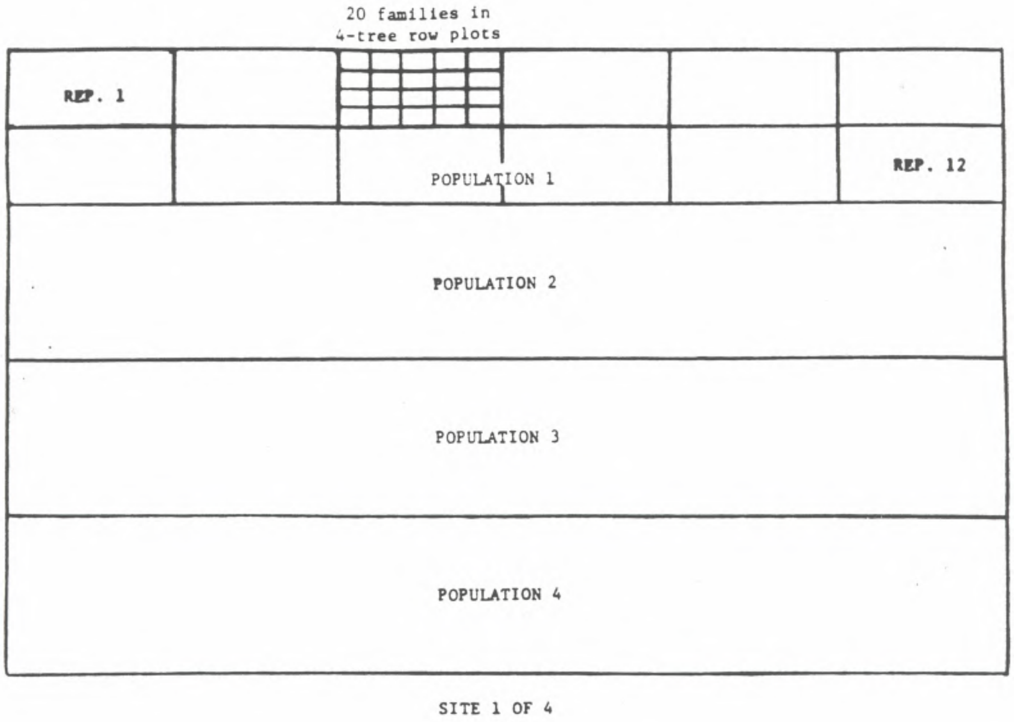
A collection of 458 1/2-sib families of jack pine from Michigan, Wisconsin, and Minnesota was assembled by the Forestry Sciences Laboratory. Seedlots were sown December, 1979 on wet perlite and transplanted into 30 cubic inch Tinus Rootrainers containing 3 peat : 1 perlite : 1 vermiculite following germination. Macro-nutrients were supplied by slow release fertilizer, and micronutrients were supplied by periodic application in solution. Seedlings were grown in the greenhouse four months, and distributed to cooperating agencies as containerized greenhouse stock.

The base collection of 458 families was divided into twenty subpopulations by randomly selecting, without replacement, twenty families for each subpopulation (58 families were therefore, excluded from the program). Sixteen subpopulations were randomly designated as breeding populations and distributed to various cooperators across the region for planting in replicated tests on single sites. The other four subpopulations were designated as index populations and established as replicated tests at four locations (Table 1). Each of these populations was planted in a randomized complete block design with 12 replications (except the Cloquet, Minnesota site which has 10 replications) of 4-tree row-plots. The index populations were planted in discrete blocks at each site (Figure 1). The location of each index population at each site was randomly assigned.

Table 1. The locations and managing cooperators of the four sites where index populations are established.

Site Name	State	Managing Cooperator	Latitude	Longitude
Wellston	MI	Michigan St. Univ.	44° 12'	85° 58'
Hancock	WI	Univ. of Wisconsin	44° 8'	89° 31'
Rhinelander	WI	Forestry Sciences Lab.	45° 40'	89° 25'
Cloquet	MN	Univ. of Minnesota	46° 42'	92° 25'

Figure 1. Field design of the index populations at each site.



Measurements and analyses

Height was measured in the Wellston, Hancock, and Cloquet plantations after the end of the 1986 growing season (age eight from seed). Height was measured in the Rhinelander plantation at the end of the 1985 growing season (age seven from seed). The one year disparity between the measurements at Rhinelander and the other sites was treated as a simple site effect, as it was assumed that no significant changes in family rankings occurred between ages 7 and 8.

An analysis of variance (based on plot means) following the design outlined in Table 2 was performed to determine if significant differences existed among the four index populations. All analyses of variance were computed using Type III sums of squares produced by the GLM procedure of the SAS statistical package (SAS, 1882). Data were restricted to ten replications in this analysis, and all subsequent analyses, to match the data from the Cloquet site.

Analyses of variance among families (based on plot means) within each of the index populations were computed following the design outlined in Table 3. The same design was used in an analysis of variance of differences among families across all four index populations. Family (h^2_f) and single-tree (h^2_t) heritabilities were calculated for each index population, and for all populations combined, using variance components estimated by equating expected mean squares to observed mean squares and solving for the desired variance components. Heritability estimates followed Wright's (1976) formulae.

Table 2. Format of the analysis of variance used to detect difference among the index populations.

SOURCE	DF	EXPECTED MEAN SQUARES
Site	S-1	$\sigma_e^2 + N\sigma_{sp}^2 + NP\sigma_s^2$
Population	P-1	$\sigma_e^2 + N\sigma_{sp}^2 + NS\sigma_p^2$
Site X Population	(S-1) (P-1)	$\sigma_e^2 + N\sigma_{sp}^2$
Error	SP (N-1)	σ_e^2

Where: S = # of Sites
P = # of Populations
N = (# of families/rep) X (# of reps/pop/site).

Table 3. Format of the analyses of variance used to estimate variance components for the index populations.

SOURCE	DF	EXPECTED MEAN SQUARES
Site	S-1	$\sigma_e^2 + F\sigma_r^2 + R\sigma_{fs}^2 + RF\sigma_s^2$
Rep(Site)	S(R-1)	$\sigma_e^2 + F\sigma_r^2$
Family	F-1	$\sigma_e^2 + R\sigma_{fs}^2 + RS\sigma_f^2$
Family X Site	(F-1)(S-1)	$\sigma_e^2 + R\sigma_{fs}^2$
ERROR	FS(R-1)	σ_e^2

Where: S = # of sites
R = # of reps./site
F = # of families

Analyses of variance among families were also performed on each population at each site (i.e. each of the sixteen population-site combinations) to simulate Riemenschneider's (1985) single-site analyses of the breeding populations, and examine the possible effects of sampling variation on the estimation of variance components and heritabilities. These analyses were based on single-tree data, and followed Zobel and Talbert's (1984) single-plantation model. Narrow-sense heritabilities and the requisite variance components were computed as previously described.

Family performance at each site was standardized by dividing the plot means of each family by their respective replicate means, and averaging these percentages across all ten replications. The resulting percentages became the scale by which family performance was judged and analyzed. Spearman rank correlations were computed for family performance at the four sites to assess the magnitude and distribution of any existing family X site interaction across the sites.

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 AND DISCUSSION

No significant differences were found among the four index populations. Thus, subsequent analyses are not confounded by unexpected differences among the index populations. This result was expected since each index population is a random sample of the base population.

Significant differences among the families, and significant family X site interactions were found within each of the four index populations at the 0.99 level of confidence. Variance components, family heritabilities, and single-tree heritabilities are reported in Table 4. The heritability estimates were quite consistent among the index populations, ranging from 0.41 to 0.48.

Since there were no significant differences among the populations, the index populations were included in a combined analysis of variance among families. The heritability estimate from this analysis was lower than the heritabilities estimated for each index population individually (Table 4). This decrease was due primarily to a large increase in the family X site variance component. This suggests that although a sample size of 20 families was adequate for the detection of significant family X site interactions, a larger sample size may be necessary to accurately estimate this term's magnitude.

Heritabilities reported here are higher than those reported by Riemenschneider (1985) for height at age five in the index populations. Franklin (1979) proposed a model for temporal changes in genetic variance in North American conifers in which additive genetic variance peaks once during the juvenile phase of plantation development, and again during the mature phase of plantation development. Similarly, Foster (1986) reported a peak in heritability estimates for height growth in loblolly pine (Pinus taeda L.) at age five. The heritabilities reported here may correspond to the juvenile peak described by Franklin.

Results of the analyses of variance among families within each of the index populations at each site were consistent with the analyses of each population across the sites. Single-tree heritabilities estimated from these analyses are shown in Table 5. Again, heritability estimates were generally higher than those reported at age five, and, assuming the index populations are representative of the breeding populations, much more consistent than the heritabilities estimated for the breeding populations at age three. It appears that the genetic parameters of the subpopulations have stabilized over time, and that the inconsistency of the heritability estimates for the breeding populations was indeed transitory (confirming Riemenschneider's [1985] hypothesis). Continued monitoring of the genetic parameters of the index populations is necessary to examine the relationship between tree and stand development and genetic variance in Lake States jack pine.

Table 4. Variance components and family (h^2_f) and single-tree (h^2_t) heritability estimates for each of the index populations, and for all populations combined.

	$\hat{\sigma}^2_e$	$\hat{\sigma}^2_{fs}$	$\hat{\sigma}^2_f$	h^2_f	h^2_t
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

* All family and family X site variance components are significant at $P > 0.01$.

Table 5. Single-tree heritabilty estimates for each population at each site.

	Wellston	Hancock	Rhinelander	Cloquet
Population 1	0.41	0.29	0.33	0.40
Population 2	0.41	0.43	0.35	0.35
Population 3	0.34	0.38	0.26	0.29
Population 4	0.66	0.30	0.24	0.16

The significant family X site interactions within each index population, and in the analysis combining all populations, is consistent with King's (1966), and Jeffers' and Jensen's (1980) analysis of provenance test data, and indicates 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 five. At age eight, the family X site variance is more than 50% of the family variance in three of the index populations, while it was less than 50% of the family variance in all four of the index populations at age five (Riemenschneider, 1985).

Spearman rank correlations (Table 6) indicate that family performance was most consistent between the two southernmost sites (r = 0.52 for the Hancock and Wellston sites), and the two northernmost sites (r = 0.54 for the Rhinelander and Cloquet sites). Family performance was least consistent between the northwestern and southeastern extremes of the plantation locations (r = 0.19 for family performance at the Wellston and Cloquet sites). This indicates that family selections made at any one site will tend to perform similarly at other sites, but that this pattern will deteriorate as the distance between the plantations increases, particularly at the northwestern and southeastern corners of the region.

Table 6. Spearman rank correlations for mean family performance at each of the test sites.

	Hancock	Rhinelander	Cloquet
Wellston	0.52	0.36	0.19*
Hancock		0.46	0.35
Rhinelander			0.54

*Significant at $P < 0.10$, all others significant at $P < 0.01$.

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 insignificant (albeit weakly positive) at Cloquet (r = 0.14). A similar, though weaker, pattern occurs between family performance and longitude of family origin. The Pearson correlations indicate that southern 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.

Table 7. Pearson correlations for mean family performance at each test site and the latitude and longitude of family origin.

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

*Significant at or above $P < 0.01$.

It should be noted that both the Spearman rank and 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 southern Michigan. This family was the top performer at all sites (indeed, it the only seedlot in the test to maintain its rank across all sites), and, in contradiction to the previously mentioned trends, actually improved its advantage at the Cloquet site. Examples of good, average, and poor families which performed relatively consistently across the sites is shown in Table 8.

Table 8. Mean family performance (average percentage of rep. mean) of selected families.

Family #	Origin	Mean Family Performance			
		Wellston	Hancock	Rhinelander	Cloquet
		----Above Average Families----			
8223	MI(LP)*	1.14	1.15	1.12	1.18
9813	MI(LP)	1.10	1.11	1.08	1.05
8345	WI	1.02	1.04	1.07	1.06
		----Average Families----			
8874	WI	0.99	0.98	0.96	0.97
8609	MN	0.97	0.95	1.00	0.98
		-----Below Average Families----			
8356	MI(UP)*	0.90	0.91	0.97	0.93
9757	MN	0.91	0.90	0.92	0.92

* LP = Lower Peninsula; UP = Upper Peninsula.

CONCLUSIONS

The heritability estimates of height growth in the four index populations increased between ages five and eight. Assuming the performance of the index populations accurately reflects the performance of the breeding populations, heritabilities for height in the breeding populations have also increased and become more consistent. If the populations follow Franklin's (1979) model, heritabilities can be expected to continue to change as the plantations mature. The magnitude of heritability estimates are more than adequate to support continued tree improvement efforts with jack pine. The consistency among the index populations of the variance component and heritability estimates indicates that this information can be applied with confidence to the breeding populations. Family height rankings from eighth year data have already been used to begin breeding programs in the index populations at Cloquet and Hancock.

Significant family X site interaction exists in Lake States jack pine at age eight. However, this does not pose an immediate problem to cooperative jack pine improvement efforts in the region, as no exchange of genetic materials among cooperators is planned in the immediate future. Following Riemenschneider's (1979) breeding plan, each cooperator will effect the first few generations of selection and breeding according to the intra-regional interests which each cooperator represents. If the adverse effects of inbreeding depression become apparent, the subpopulations can be outcrossed and the resulting progeny may be broadly adapted to Lake States sites (Kang, 1980). Until that time, continued monitoring of the index populations is necessary to determine if family X site interaction continues to be a significant component of the total variation as the plantations mature.

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