HERITABILITY AND INTERTRAIT CORRELATIONS IN BREEDING SUBPOPULATIONS OF JACK PINE

Don E. Riemenschneider[1]

Abstract.--Twenty breeding populations of jack pine were established in 1979 and 1980 in Minnesota, Wisconsin, and Michigan. Four populations were index populations and were each established at 4 locations by research cooperators. Sixteen populations were applied breeding populations and were established at single locations by public and private cooperators. Combined analysis of height at age 5 in index populations at three locations indicated little genotype x environment interaction and heritability of 0.19. Separate analysis of index populations indicated that the amount of genotype x environment interaction varied in relation to main effect family variance but was never more than 50 percent of the family variance. Heritability estimates for height at age 3 in 13 surviving breeding populations varied from 0 to 0.57. Population related differences in heritability may have been due to sampling variation, environmental differences, or both. The data suggested a need for remeasurement of the 13 surviving breeding populations which are currently 6 years old. Heritability in most populations is sufficient to recommend that selection and breeding to produce the second generation be initiated now. Selection of parents at age 5 or 6 has previously been shown to be effective in many species of *Pinaceae*.

Additional keywords: Population size, genotype x environment interaction, crown form, branch size, branch angle.

The concept of subdividing tree breeding populations (Kang 1980) has been applied to loblolly pine (*Pinus taeda* L.) in Texas (Low and van Buijtenen 1981) and jack pine (*Pinus banksiana* Lamb.) in the Lake States (Riemenschneider 1981). Multiple, subdivided populations are expected to have several advantages in comparison with large, single populations. First, several cooperators each managing one or two small populations distributes the breeding work load. For example, breeding to maintain an effective populations size of 20 can be done with as few as 10 controlled crosses in a single pair mating design. Second, inbreeding in multiple small populations can be encouraged in order to increase heritability (Lindgren and Gregorious 1976). And, inbreeding can be easily relieved by crossing unrelated individuals (Rudolph 1981) in separate populations to produce depression-free orchard trees. Third, genetic diversity and thus gene conservation is facilitated because each subpopulation samples a unique environment and is subjected to different natural selection pressures.

It has become axiomatic that the amount of response to selection in each generation partly depends on the heritability of the selection criterion (often

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[1] Research Plant Geneticist, USDA, Forest Service, North Central Forest Experiment Station, Forestry Sciences Laboratory, P.O. Box 898, Rhinelander, Wisconsin.

tree height). However, the possible influences of population size on heritability estimates are unknown. Previous estimates of heritability for tree height in jack pine (Yeatman, 1975; Canavera, 1969, 1975; Riemenschneider, 1979) were based on large populations and, therefore, may not apply to smaller, subdivided populations. The formulation and testing of hypotheses concerning alternative breeding strategies, such as subdivided populations, may be profoundly influenced if heritability for selection criteria varies among small populations. Thus, the purpose of the present research was to determine the magnitude of population related variation in heritability, genotype x environment interactions, and selected genetic intertrait correlations.

This paper presents heritability estimates for early height growth in 4 index populations and 13 breeding populations of jack pine in the Lake States. Genotype x environment interactions were estimated for the 4 index populations that were established at multiple locations. Additionally, genetic correlations between several characteristics related to crown form were estimated in two index populations at Rhinelander, WI.

MATERIALS AND METHODS

Open-pollinated seed from 400 phenotypically select wild trees in Minnesota, Wisconsin, and Michigan was used to produce foundation breeding populations. Seedlots were subdivided at random into 20 populations of 20 families each. Of the 20 populations, 4 were designated 'index populations' to be managed by research organizations (Universities of Minnesota and Wisconsin, Michigan State University, and Forestry Sciences Laboratory, Rhinelander, WI). The remaining 16 populations were designated 'breeding populations' to be managed by USFS Region 9; the Minnesota, Wisconsin, and Michigan Departments of Natural Resources; Potlatch Corporation, Cloquet, MN; Consolidated Papers, Rhinelander, WI; and Mead Corporation, Escanaba, MI.

Seedlings for the four index populations were grown in the greenhouse at Rhinelander from February to May 1979 and outplanted in May and June, 1979 at Cloquet, Minnesota (University of Minnesota), Rhinelander, Wisconsin (Forestry Sciences Laboratory), Hancock, Wisconsin (University of Wisconsin), and Wellston, Michigan (Michigan State University). Seedlings for the 16 breeding populations were grown in the greenhouse one year later and outplanted in May and June 1980. Breeding populations were planted at only one location per population. Most plantings shared a common randomized complete block experimental design with 12 replications of 4-tree plots. Index populations planted at Cloquet, Minnesota contained 10 replications of 4-tree plots.

Total tree height was measured in all breeding populations in 1982 after completion of seasonal growth. Trees in the index populations at Hancock, Wisconsin; Rhinelander, Wisconsin; and Wellston, Michigan were measured in 1983. Trees in the index populations at Cloquet, Minnesota were measured in 1981.

Components of crown form were measured in two populations at Rhinelander in the fall of 1983 (tree height, leader length and diameter, number of whorls, number of branches per whorl, branch length angle).

Missing plot estimates for tree height in all breeding and index populations were computed according to Snedecor and Cochran (1967) and variance components were estimated via analysis of variance using plot means. Within-plot variance was estimated separately and combined with the plot mean analysis after correcting for scale. Variances due to families, families x locations, and whole-plot and subplot error were estimated by equating expected mean squares to observed mean squares, and then solving for the appropriate variance component. Heritability was estimated on an individual basis in the single location breeding populations as:

$$h^2 = \frac{4 * V_f}{V_f + V_{rf} + V_w}$$

where h^2 is heritability on an individual tree basis

V_f is the variance among half sib families

V_{rf} is the reps x families whole-plot error

and V_w is within plot error.

Heritability was estimated from multiple location combined analysis of the index populations as:

$$h^2 = \frac{4 * V_f}{V_f + V_{f1} + V_{rf} + V_w}$$

where h^2, V_f, V_{rf}, V_w are as before

and V_{f1} is variance due to families x location interaction.

Components of variance and covariance were estimated assuming a completely random design in order to simlify estimation of genetic intertrait correlations. Genetic intertrait correlations were estimated as:

$$r_g = \frac{COV_{1j}}{(V_1 * V_j)^{1/2}}$$

where COV_{1j} is the family covariance between trait i and trait j.

Standard errors for estimates of genetic correlations were also calculated (Tallis 1959).

RESULTS

Heritability and Genotype x Environment Interaction

Combined analysis of tree height in 4 index populations grown at 3 locations in Wisconsin and Michigan showed significant differences between families, and significant family x location interactions (table 1). Combined analysis of the two locations in Wisconsin, however, indicated non-significant variation due to family x location interaction. Heritability for height at age 5 was estimated to be 0.19 for all sites and 0.22 when only the Wisconsin sites were analyzed. The higher heritability obtained by excluding the Michigan location was primarily due to increased family variance and the lack of family x location interaction.

Table 1.--Combined analyses of variance for height (cm) at age 5 in 4 index populations of jack pine at 2 locations in Wisconsin and 1 location in the Lower Peninsula of Michigan. Each index population consisted of 20 open-pollinated families of jack pine in 12 replications of 4-tree plots.

Source of Variation	2 Wisconsin sites only			3 sites in Wisconsin and Michigan		
	df	MS	f	df	MS	f
Locations	1	320,751	7.49 ns	2	1,676,590	26.40 *
Populations	3	83,796	1.96 ns	3	33,118	0.52 ns
Pop. x Locations	3	42,796	16.91 **	6	63,496	29.73 **
Reps./Pop./Location	88	2,531		132	2,136	
Families/Pop.	76	2,345	4.09 **	76	2,509	3.73 **
Locations x Families/Pop.	88	573	0.99 ns	152	673	1.25 *
Reps. x Families /Pop./Loc.	1672	600	1.90 **	2508	539	1.92 **
Within plot	4072	316		5902	281	

ns = not significant
* = significant at $P < 0.05$
** = significant at $P < 0.01$

Family x location interaction differed significantly between index populations (table 2). Interactions were significant ($P < 0.01$) in population 3 but not in the others. Heritability varied from 0.12 in populations 2 and 4 to 0.18 in populations 1 and 3. Family x location interaction varied in relation to main effect family variance. The interaction was approximately one half the main effect in populations 2 and 3 but much smaller in populations 1 and 4.

Heritability for tree height varied with index population location, although family differences were always significant (table 3). Heritability varied from 0.14 to 0.44 over the three locations in Wisconsin and Michigan. Heritability for tree height at age 3 in Minnesota was 0.37.

Table 2.--Combined analyses of variance for tree height at age 5 in 4 index populations of jack pine planted at Rhinelander, WI; Hancock, WI; and Wellston, MI. Each population contained 20 open-pollinated families of jack pine in 12 replications of a randomized complete design with 4-tree plots.

Source of variation		Population 1		Population 2		Population 3		Population 4	
	df	MS	Variance component	MS	Variance component	MS	Variance component	MS	Variance component
Locations	2	390,400		777,164		1,054,689		172,172	
Reps./Locations	33	3,590		1,665		1,372		1,919	
Families	19	2,891 **	65	2,201 **	42	3,123 **	62	1,822 **	36
Fam. x Loc.	38	564 ns	0	675 ns	16	910 **	30	592 ns	7
Reps. x Fam./Loc.	628	644 **	644	481 **	481	522 **	522	457 **	457
Within plot [1]	5902	281	736	281	736	281	736	281	736
Heritability		0.18		0.12		0.18		0.12	

1. Common within plot error mean square taken from combined ANOVA of all sites in table 1.

ns = mean square not significant

* = mean square significant at $P < 0.05$

** = mean square significant at $P < 0.01$

Table 3.--Analyses of variance for tree height in 4 index populations of jack pine in Minnesota, Wisconsin, and Michigan. All index populations consisted of 20 open-pollinated families. Experimental design at Wisconsin and Michigan locations was 12 replications of randomized complete blocks with 4-tree plots. Populations at Cloquet, Minnesota contained 10 replications.

Source of Variation	Cloquet Minnesota[1] df	Cloquet Minnesota[1] MS	Hancock Wisconsin df	Hancock Wisconsin MS	Rhinelander Wisconsin df	Rhinelander Wisconsin MS	Wellston Michigan df	Wellston Michigan MS
Populations	3	3,443	3	83,519	3	73,946	3	52,646
Reps./Populations	36	255	44	1,346	44	1,564	44	3,499
Families/Pop.	76	384 **	76	847 **	76	1,727 **	76	1,292 **
Reps. x Fam./Pop.	684	94 **	836	415 **	836	836 **	836	366 **
Within plot	2353	65	2588	277	1484	497	1830	187
Variance Components								
Families		29	36			74	76	
Reps. x families		29	188			339	179	
Within plot		254	778			1045	432	
Heritability		0.37	0.14			0.20	0.44	

1. Trees at Cloquet Minnesota were measured in 1981 at age 3. Trees at other locations were measured in 1983 at age 5.

** = mean square significant at $P < 0.01$

Heritability varied more in the 13 surviving breeding populations established at single locations (table 4). Estimates ranged from 0 to 0.57, and there was no apparent association of heritability or its components to mean plantation growth or any environmental variable. Standard errors for heritability in the 16 breeding populations ranged from 0.15 to 0.25.

Table 4.--Heritability for height growth at age 3 in breeding populations of jack pine. Each population consisted of 20 open-pollinated families of jack pine in a randomized complete block design with 12 replications of 4-tree plots.

Population number	Cooperator	Height (cm)	Additive Variance	Phenotypic Variance	Heritability
5[1]	USFS Region 9				
6	"	142.5	6.60	11.56	0.57
7	"	87.4	0.88	7.57	0.12
8	"	105.6	0.79	6.80	0.12
9	"	132.0	2.26	4.29	0.53
10	Wisconsin DNR[2]	124.5	2.06	7.93	0.26
11	"	136.7	2.76	6.71	0.41
12[1]	Minnesota DNR[2]				
13	"	97.1	0.55	5.46	0.10
14	Michigan DNR[2]	95.2	1.98	4.33	0.46
15	"	70.0	0.72	2.31	0.31
16	Consolidated	134.1	0.03	1.26	0.02
17	"	101.8	0.13	0.54	0.24
18[1]	Mead Corp.				
19	"	102.4	0.02	5.26	0.00
20	Potlatch Corp.	116.2	0.24	6.43	0.04

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1. Population abandoned due to poor survival or loss of family identity.
2. Department of Natural Resources.

Inter-trait correlations

A genetic correlation was declared significant if it was at least 1.96 times the associated standard error (table 5). Total tree height was significantly correlated with leader length (r_g=0.824) and leader diameter (r_g=0.529). There was little variation between populations for these two correlations. Tree height was not correlated with number of whorls. Height was significantly correlated with whorl 1 branch length (r_g=0.694) and whorl 2 branch angle (r_g=-0.477).

DISCUSSION

In the present study estimates of heritability and genotype x environment interaction for tree height in the 4 index populations were comparable to previous estimates (Yeatman 1974, Riemenschneider 1979). Yeatman (1974) found single location heritabilities of 0.14 to 0.18 at three locations and a combined heritability of 0.15. The genotype x environment interaction was not significant. Riemenschneider (1979) found that heritability for tree height at comparable ages in Minnesota ranged from 0.08 to 0.17 over two locations and two years, and from 0.14 to 0.18 in combined analyses. Again, the genotype x envrionment interaction was not significant.

Table 5.--Genetic correlations between tree height at age 5 and form-related traits for two jack pine index populations at Rhinelander, Wisconsin. Each population consisted of 20 open-pollinated families in a randomized complete block design with 12 replications of 4-tree plots. A pooled genetic correlation was considered significant if it was at least 1.96 times the associated standard error.

Trait	Population 1	Population 2	Pooled (Standard Error)
Leader length (cm)	0.638	0.408	0.824 (0.304)
Leader diameter (mm)	0.385	0.397	0.529 (0.270)
No. of whorls	0.057	0.041	-0.224 (0.253)
Cycle 1			
No. branches	-0.038	-0.062	-0.202 (0.247)
Branch length (cm)	1.030	0.230	0.694 (0.325)
Branch diameter (mm)	0.076	0.180	0.416 (0.345)
Branch angle (degrees)	-0.428	-0.147	-0.463 (0.250)
Cycle 2			
No. branches	0.156	0.177	-0.197 (0.216)
Branch length (cm)	0.567	0.195	0.001 (0.195)
Branch diameter (mm)	0.713	0.260	0.270 (0.278)
Branch angle (degrees)	-0.560	-0.206	-0.477 (0.222)

The weak genotype x environment interactions between index population plantings in this study were expected because of the method used to establish the foundation populations. It is known that seed sources from Northeastern Minnesota contribute strongly to genotype x environment interactions in Lake States jack pine seed source tests (Jeffers and Jensen 1980; Riemenschneider 1983). Few of these sources were included in the index and breeding populations. The absence of strong genotype x environment interactions in the jack pine index populations indicates that breeding for broadly adapted populations may be possible.

Heritability differences in the 13 surviving breeding populations may cause concern for some cooperators, particularly those who have populations with little family variation. The differences may be partly due to the large sampling variation which resulted from small population size. However, even those populations with low heritability contain progenies of geographically diverse origin. Thus it should not be concluded that populations with low heritability are impoverished with regard to additive genetic variation.

Population related variation in heritability may be site related. It is known that variation between seed sources of jack pine is site-dependent (Jeffers and Jensen 1980). Also, heritability is known to be age-dependent in conifers (Franklin 1979). Site-related developmental differences may explain observed variation in heritability estimates if age-related variation in heritability is dependent on physiological age as opposed to chronological age. Remeasurement of breeding populations at several ages would provide data with which to test this hypothesis.

Heritability differences may be important if an index based on the performance of relatives is used as a selection criterion. Weights assigned to the individual and its family are computed based on estimates of additive and phenotypic variances (Burdon 1982). A different index should be computed for each population if these parameters differ greatly, as they did in this study. The tools required for index construction -- analysis of variance, variance component estimation, and minor matrix manipulation -- have been research tools in the past but will need to become common management tools (Kang 1980).

Many families are required to estimate genetic intertrait correlations with low standard errors (Tallis 1959). In this study a confidence interval of 2 standard errors would be 0.5 to 0.6 for most traits. Genetic correlations between tree height, and leader and branch traits were mostly consistent between two populations, at least in sign, in spite of large estimation errors. Correlated responses to selection for tree height will probably include larger whorl 1 branches and more acute branch angles.

It is interesting to note that whorl 1 branch length was well correlated with tree height while whorl 2 branch length was not. This was most likely due to differences in lateral shoot development patterns (Van Den Berg and Lanner 1971). For example, assume all lateral long shoot buds are initiated in year n. Then all but the top-most buds are elongated in year n+1. Thus the top-most buds continue development during year n+1 and are elongated during year n+2 as the basal whorl. This development pattern is more like that of the terminal bud than that of other lateral long shoots and may be the cause of the correlations observed in this study.

RECOMMENDATIONS

The 13 breeding populations should be remeasured immediately and appropriate genetic and phenotypic variances should be reestimated. This additional information will indicate whether the low heritability observed in some breeding populations in the present study is a transitory, time-related phenomenon. Selection at about age 5 or 6 has been recommended for conifers (Lambeth 1980). Since trees in the jack pine breeding populations are now 6 years old, parents should be selected, and breeding to produce the next generation should be initiated. Selection of a mating scheme has little impact on the long term response to selection (Kang and Namkoong 1979, 1980; Kang 1983) and thus each population may be advanced with as few as 10 single pair matings.

Attention should be paid to logistics related to the current geographic distribution of the breeding populations. In many cases populations are remote from the cooperator's facilities which may delay timely completion of breeding work. It may prove profitable to designate a limited number of locations (5 or 6) in the Lake States where breeding populations could be concentrated and work could be jointly supported by all cooperators.

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