GENETIC VARIATION AND GAINS OF SPECIFIC GRAVITY AND WOODY BIOMASS IN A JACK PINE HALF-SIB PROGENY TEST IN MICHIGAN

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Abstract -- Specific gravity and growth characters were analyzed in a half-sib progeny test of jack pine (*Pinus banksiana* Lamb.) located in the Upper Peninsula of Michigan and comprised of northern Lower Peninsula families. Significant family differences were found for specific gravity, diameter, volume and wood mass. Combined selection at both the family and within-family levels for single and multiple trait indexes were evaluated using gains in woody biomass for comparison. Combined selection for volume at the family level and specific gravity within families may produce the most efficient gain in woody biomass when costs of evaluation are considered.

Additional keywords: Heritability, combined selection, Pinus banksiana.

INTRODUCTION

Jack pine (*Pinus banksiana* Lamb.) is second only to aspen in industrial roundwood production in the Lake States -- Michigan, Minnesota and Wisconsin. Because jack pine is so widely utilized, has such a high degree of phenotypic and genetic variation, and so many sites in the Lake States are essentially restricted to the production of jack pine, this species has been given high priority in the Michigan State Cooperative Tree Improvement Program (MICHCOTIP) tree improvement effort.

As part of the MICHCOTIP improvement plan for jack pine, half-sib progeny tests established in 1968 and 1969 are currently being analyzed so that one or more may be rogued and utilized as a first-generation seed orchard and breeding arboretum for genetically improved seed in Michigan. These plantations are composed of northern Lower Peninsula sources which have been shown to have superior growth potential in both the Upper and Lower Peninsulas of Michigan (Canavera and Wright 1973; Jeffers and Jensen 1980). Volume production, form, and perhaps specific gravity and cone morphology will be criteria used in determining the roguing recommendations. Specific gravity has been shown to have sufficiently high variability and heritability in jack

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pine to warrant its consideration as a selection criterion in maximizing genetic gains in wood biomass (Okwuagwu and Guries 1981). With a specific gravity of 0.350 grams per cubic centimeter, a reasonable average for jack pine (Okwuagwu and Guries 1981), each increase of 0.010 in specific gravity will yield 57 additional pounds per ton of pulpwood.

The importance of specific gravity in tree improvement programs has been assessed for various species (e.g., Jett and Talbert 1982) and selection indexes with specific gravity as a component trait developed and evaluated (Bridgwater et al. 198_). Also, juvenile and mature wood specific gravities have been shown to be highly correlated in loblolly pine (*Pinus taeda* L.) (Talbert et al. 198_). Sufficient gains in specific gravity are achievable in only one generation of selection when establishing a base breeding population to warrant consideration of specific gravity in selection programs (Jett and Talbert 1982).

The objectives of this study were:

1. To determine the extent of variation in specific gravity of selected families of jack pine in Michigan.
2. To determine the relationships between wood quality and growth characteristics of these selected families and the most efficient means for obtaining genetic gains in woody biomass.

MATERIALS AND METHODS

The jack pine half-sib progeny test plantation sampled for analysis of growth and wood quality traits is located in Mackinac County, Michigan, and was planted with 2-1 nursery stock. It is one of four such plantations planted in Michigan as part of a northern Lower Peninsula collection and test of plus-tree selection -- see Canavera (1975) and Howe et al. (1983) for a description of the collection procedures and mother-tree data. The plantation contains 169 families from 40 stands, planted in a randomized complete block design with six replications (blocks) using four-tree plots and 2.5 x 2.5 m (8 foot) spacing. Present survival in the plantation is 98 percent.

Individual-tree height and diameter measurements and form observations were made in the plantation in the fall of 1981, 12 years from planting and 15 years from seed. Poor form was scored if the tree had a crook which offset the stem by more than one-half its diameter, and the percentage of defective trees within each family was calculated.

Only 50 of the 169 families occur in each of four of the same replications, and only these families and replications were sampled for specific gravity to maintain a balanced data set. Two trees per four-tree plot were sampled for specific gravity, using as first choice the two middle trees. However, to minimize effects of poor form and growth (suppression) on specific gravity measurements, an outside tree of the four-tree plot was used when warranted by poor form or diameter growth. The resulting bias toward better growing trees was negligible (see Table 4) and no adjustments were made. A total of 400 trees, 50 families x 4 replications x 2 trees per replication, were sampled for specific gravity. Increment cores (5 mm) were taken at breast height (1.2 m) and placed in straws which were then labeled and kept in a freezer until analysis. Increment cores Were taken only from the north side of the tree to minimize the effects of compass bearing (Olson et al. 1981).

Specific gravity was determined in the laboratory using an oven-dry versus green volume ratio. Upon removal from the freezer the year of juvenile/mature wood transition, as indicated by opacity differences, was determined on a light table. Cores were then split into two sections corresponding to 1975-1981 and pith-1974 growth and immersed in water for at least 24 hours to insure saturation. Volume was determined by water displacement, wish each core immersed three times to establish precision to 0.001 cm (or g). Cores were then dried in a circulating oven at 105 C for at least 12 hours and weighed to the nearest 0.001 g. Single-tree wood volumes were calculated using a formula similar to one developed for biomass estimates by Green and Grigal (1978) from jack pine of similar size in the Lake States. Estimates of single-tree wood biomass were calculated by multiplying the volume of a tree by its specific gravity (1975-1981 increment).

The analysis of variance tabulation for replication and family effects is as follows:

Source of Variation	df	MS	F	Expected Mean Squares
Replication	r-1	M_1	M_1/M_3	$\sigma^2_W + t\sigma^2_{RF} + ft\sigma^2_R$
Family	f-1	M_2	M_2/M_3	$\sigma^2_W + t\sigma^2_{RF} + rt\sigma^2_F$
Rep x Family	(r-1)(f-1)	M_3	M_3/M_4	$\sigma^2_W + t\sigma^2_{RF}$
Within-plot (pooled)	rf(t-1)	M_4		σ^2_W
Total	rft-1			

where r = number of replications, f = number of families, and t = number of trees sampled in each plot. Heritability estimates and standard errors (Hallauer and Miranda 1981) for height, diameter, specific gravity (1975-1981 increment), volume and mass were

2 Volume (cm^2m) = $(DBH(cm))^{1.828}\ (HT(m))^{0.859}$

calculated on a family-plot, within-family and individual-tree basis. Heritability estimates for height, diameter, volume and mass were calculated using all four trees in a plot (t = 4), versus two trees per plot (t = 2) for specific gravity, due to the greater precision afforded by the larger sample. For analysis of variance, family means for specific gravity were used in calculating individual-tree mass. This reduced within-plot variance and increased variation among families for this trait, and these effects will be noted in analyzing the comparisons. Genetic gains for family, within-family and individual tree selection were calculated for each of the traits singly and in combination with other traits as a form of index selection, using gains in mass as the ultimate goal and common comparison. The top 10 of 50 (20%) families, based on family means, and the top 2 of 8 (25%) trees within these better families were the selection intensities used. Correlation analysis of growth characters on a family-mean basis was also performed.

RESULTS

Specific gravity of 1975-1981 wood was fairly well correlated with specific gravity of the juvenile wood (pith-1974) on a family-mean basis (r = 0.50, Table 1). Also specific gravity of the 1975-1981 increment was considered to be the more valuable parameter because juvenile wood constitutes such a small portion of the merchantable volume at the normal rotation age of 40 years for jack pine pulpwood in the Lake States. Therefore only the 1975-1981 specific gravity data will be used in the remaining analyses and comparisons.

Families having high percentages of trees with good form tended to exhibit better height growth (r = 0.34) and higher specific gravity (r = 0.31), although these relationships were not very strong. Height and diameter were only mildly correlated (r = 0.28) in this plantation among the 50 sampled families. Specific gravity showed no linear trends with either diameter or height (Table 1). The synthetic variable volume and mass exhibited strong correlations only with those variables from which they were estimated (diameter, height and specific gravity). Families having higher percentages of trees with compression wood showed some tendencies toward higher specific gravities (r = 0.36).

All traits but tree height exhibited significant family differences in the analyses of variance (Table 2), while only height exhibited a significant replication x family interaction. Strong replication effects were evident for all traits. Variance components extracted from results of analyses of variance and calculated heritabilities and standard errors are listed in Table 3. No heritability estimate was calculated for height due to the lack of significant differences among family means for that trait. All traits but height exhibited negative replication x family variance

Table 1. Correlations among growth and wood quality variables on a family mean basis (significances in parentheses), based on a sample of 50 half-si jack pine familiesfrom a plantation in the Upper Peninsula of Michigan.

	CPWD[a]	SGA	SGB	HT	DBH	VOL	MASS
FORM	0.16 (0.141)	0.31 (0.014)	0.38 (0.003)	0.34 (0.008)	-0.20 (0.080)	-0.05 (0.362)	0.07 (0.322)
CPWD		0.36 (0.005)	0.16 (0.141)	-0.04 (0.389)	0.04 (0.392)	0.00 ----	0.12 (0.208)
SGA			0.50 (0.001)	0.05 (0.353)	0.00 ----	0.01 (0.466)	0.37 (0.004)
SGB				0.16 (0.141)	-0.13 (0.190)	-0.08 (0.298)	0.12 (0.204)
HT					0.28 (0.023)	0.56 (0.001)	0.54 (0.001)
DBH						0.94 (0.001)	0.87 (0.001)
VOL							0.93 (0.001)

[a]Variables are:

FORM = percentage of trees in a family exhibiting good form.

CPWD = percentage of trees in a family exhibiting compression wood.

SGA = specific gravity of 1975-1981 increment.

SGB = specific gravity of pith-1974 increment.

HT = tree height.

DBH = diameter at breast height.

VOL = tree merchantable volume.

MASS = tree wood biomass.

Table 2. Results from the analyses of variance for five growth and wood quality traits based on a sample of 50 half-sib jack pine families from a plantation in the Upper Peninsula of Michigan.

	Mean Squares -- larger sample (4 trees per plot t = 4)					Mean Squares (t = 2)	
Source	df	Height (m)	Diameter (cm)	Volume ($cm^2 m$)	Mass (kg)	df	Specific Gravity ($g/cm^3 \times 1000$)
Replication	3	8.368***[a]	12.82**	113,487***	114.38**	3	1673**
Family	49	0.690[ns]	5.04*	26,285*	37.01***	49	1294***
Rep x Family	146	0.782***	3.48[ns]	19,834[ns]	20.26[ns]	147	542[ns]
Residual (Pooled within-plot error)	556	0.438	3.83	19,921	20.54	200	550

[a]Significances of F-ratios:

*** = significant at P > 0.99

** = significant at 0.99 > P > 0.95

* = significant at 0.95 > P > 0.90

ns = not significant

Table 3. Estimates of variance components and heritabilities, with standard errors in parentheses, based on a sample of 50 half-sib jack pine families from a plantation in the Upper Peninsula of Michigan.

	Height	Diameter BH	Volume	Mass	Sp. Gravity
σ^2_F	-0.0058 (0.010)	0.098 (0.071)	403 (355)	1.05 (0.48)	94.0 (33.0)
σ^2_{RF}	0.086	-0.089	-21.8	-0.07	-2.0
σ^2_W	0.438	3.83	19,921	20.5	550
$\sigma^2_{\bar{P}}$	----	0.315	1,643	2.31	162
σ^2_P	----	3.84	20,302	21.5	642
h^2_F	----	0.31 (0.23)	0.25 (0.22)	0.45 (0.21)	0.58 (0.20)
h^2_W	----	0.08 (0.06)	0.06 (0.05)	0.15 (0.07)	0.51 (0.18)
h^2_I	----	0.10 (0.07)	0.08 (0.07)	0.19 (0.09)	0.58 (0.21)

σ^2_F = variance among half-sib families

σ^2_{RF} = variance of replication x family interaction

σ^2_W = within-plot (error) variance

$\sigma^2_{\bar{P}}$ = phenotypic variance among half-sib families = $\sigma^2_F + \sigma^2_{RF}/t + \sigma^2_W/rt$[a]

σ^2_P = phenotypic variance among individuals = $\sigma^2_F + \sigma^2_{RF} + \sigma^2_W$

h^2_F = heritability on a half-sib family basis = $\sigma^2_F/\sigma^2_{\bar{P}} = 1/4\ \sigma^2_A/\sigma^2_P$

h^2_W = heritability on a within-family basis = $3\ \sigma^2_F/\sigma^2_W = 3/4\ \sigma^2_A/\sigma^2_W$

h^2_I = heritability on an individual-tree basis = $4\ \sigma^2_F/\sigma^2_P = \sigma^2_A/\sigma^2_P$

[a]Heritability components from Namkoong (1979).

Table 4. Genetic gains of pertinent comparisons and related information for four growth and wood quality traits, based on a sample of 50 half-sib jack pine families from a plantation in the Upper Peninsula of Michigan.

Parameter[a]	Mass (kg)	Volume $(cm^2 m)$ I[b]	Volume $(cm^2 m)$ II[b]	Diameter (cm)	Sp. Gravity (g/cm^3)
$\bar{x}_P$	13.5	420	420	11.4	0.321
ΔG_F	3.76	63.2	63.2	1.00	0.036
ΔG_W	0.97	11.6	0.021	0.20	0.019
ΔG_T	4.73	74.8	----	1.20	0.055
$\Delta G_F/\Delta G_W$(%)	388 %	545 %	----	500 %	189 %
ΔG_{MASS}	4.73	2.18	3.02	2.12	2.08
% Gain in Mass (F)	35 %	16 %	22 %	16 %	15 %
$\bar{x}_P$ (t = 4)	12.7	395		11.0	----

[a]Parameter descriptions:

$\bar{x}_P$: Plantation mean; 50 families, 4 replications, 2-tree plots (f = 50, r = 4, t = 2)

ΔG_F: Genetic gain of family selection = $4 i_F h^2_F \sigma_F$, where i = 1.371 (Becker 1975; 10/50).

ΔG_W: Genetic gain of within-family selection = $4/3\ i_W h^2_W \sigma_W$, where i = 1.138 (Becker 1975; 2/8).

ΔG_T: Total genetic gain = $\Delta G_F + \Delta G_W$.

$\Delta G_F/\Delta G_W$: Ratio of family and within-family genetic gains as a percent.

ΔG_{MASS}: Genetic gain in mas for family and within-family selection based on gains achieved in given trait(s).

% Gain in Mass (F): Gain in mass relative to plantation mean for combined family selection, in percent.

$\bar{x}_P$ (t = 4): Plantation mean; 50 families, 4 replications, 4-tree plots (f = 50, r = 4, t = 4); data used in analyses of variance for height, diameter, volume and mass.

[b]I : Selection among and within families for volume.
II: Selection among families for volume and within families for specific gravity.

components, an indication of the lack of replication x family interaction among the 50 sampled families and possible sampling anomalies (Searle 1971).

Selection among and within families on single traits or a mixture of traits (other than mass) were inferior to selection directly for mass or volume (Table 4). Within-family selection, while generating larger potential selection differentials and contributing to overall gain, was less effective than family selection for all traits.

DISCUSSION

While the lack of significant family differences for height precluded its use in genetic gains comparisons, the other traits exhibited heritabilities consistent with, although somewhat lower than, those reported elsewhere for jack pine (Okwuagwu and Guries 1981; Riemenschneider 1981) and southern pines (Bridgwater et al. 198_; Meier and Goggans 1977). Relatively large standard errors, negative variance components and large within-plot variance components indicate some sampling anomalies may be evident in the data (Searle 1971). All traits were normally distributed on both a two-tree and four-tree plot basis. The heritability estimates may be somewhat inflated because genotype x environment interaction variance (σFE) was not accounted for in estimating the additive variance components *(σA)*, as measurements were taken in only one plantation. However, analysis of three of the plantations in this jack pine half-sib progeny test indicated no significant genotype x environment interaction for height, diameter or biomass. Potential biases in results for wood mass because specific gravity family means were used in calculating individual-tree mass data used in analysis of variance and heritability estimates seem small. Heritabilities for wood mass were intermediate between those for volume and specific gravity, and the consistency and general conservativeness of the estimates justifies consideration of these values as reasonable estimates.

Combined selection based on single or multiple component variables was clearly less effective than selecting directly for wood mass (Table 4). Bridgwater et al. (198_) found combined selection for height was more effective in increasing gains for dry weight in loblolly pine than combined selection directly for dry weight. This resulted because heritabilities for height were greater than those for dry weight: h2F = 0.54 vs. 0.46, and h2I = 0.28 vs. 0.19, respectively, or height and dry weight at the family and individual-tree level. However, in the same study gain in dry weight based on selection for diameter was relatively ineffective. While height could not be used in this study, diameter was also less effective as a selection criterion, as was volume. Selection based only on specific gravity was less effective in increasing wood mass, but in combination with selection for volume at the family level was the most efficient selection index relative to selection directly for wood mass (Table 4). Even with this restricted sample population, specific gravity exhibited large selection differentials and a high degree of heritability.

Overall, with large numbers of families (>150) from which to make initial selections, combined selection using volume as the criterion at the family level, based on height and diameter measurements, and specific gravity within those better families may prove to be the most efficient means of increasing wood mass in jack pine. Selecting directly for mass obviates the need to obtain specific gravity information for each tree, which is an expensive and time-consuming task. However, selection within better volume-producing families for specific gravity requires specific gravity data only for trees within those better families. Also, among those families having higher growth potential, further family roguing might be accomplished using specific gravity indexes based on the reported high degree of general combining ability for specific gravity in jack pine (Okwuagwu and Guries 1981). Form considerations may also be included as an additional within-family selection criterion based on the general high degree of heritability for form in jack pine (Polk 1974) and the positive correlation between form and specific gravity experienced in this study. Based on the positive correlation in this study between specific gravity and incidence of compression wood and the detrimental effects of compression wood in the pulping process (Panshin and de Zeeuw 1970), the effects of compression wood should also be assessed and removed if necessary from future selection efforts. Gains in wood mass and its component traits are clearly achievable, and these should be compared with concomitant economic gains to determine the desirability and intensity of selection efforts. Also, following growth and wood quality traits through rotation age in this and other plantations should yield more conclusive data on heritability and juvenile/mature relationships for these traits in jack pine.

CONCLUSIONS

Specific gravity exhibited substantial family and within-family variability in the jack pine half-sib progengy test plantation measured in this study. Selecting for volume at the family level and specific gravity at the within-family level resulted in the most efficient means of increasing wood mass because fewer specific gravity determinations were required. Overall a 22% gain in wood mass was achieved when selecting for both volume and specific gravity in this manner, versus a 35% gain when selecting directly for wood mass. Further gains may be possible if the number of families and number of trees per plot or family in the sample population is increased.

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