Performance of Inter- and Intraprovenance Crosses of Jack Pine in Central Wisconsin

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Abstract

Inter- and intraprovenance crosses of jack pine (*Pinus banksiana* Lamb.) from six provenances across the natural range were planted in central Wisconsin and evaluated at age nine for height and pine-oak gall rust caused by *Cronartium quercum*. Survival was greater than 88% for all inter- and intraprovenance combinations except the intraprovenance cross from Big River, Saskatchewan (77% survival). Interprovenance hybrids showed no increased resistance to pine-oak gall rust infection. Trees representing provenances from Fife Lake, Michigan, and Petawawa Plains, Ontario, had higher rates of rust infection than trees representing other provenances. Trees representing provenances far from the planting site: Durell Island (Nova Scotia), Fort Smith (Northwest Territories), Big River (Saskatchewan); were shorter than provenances from the Lake States region: Mosinee (Wisconsin), Fife Lake (Michigan), Petawawa Plains (Ontario). Interprovenance hybrids had heights similar to the respective midparent values. No evidence of heterosis was found, suggesting that directional dominance in gene action is lacking. Variance component analysis revealed some large provenance effects but little or no family effect. The lack of family effect found is likely due to the mating design being insufficient to detect family differences. Interprovenance hybridization may be a useful technique for broadening the genetic base to increase population size, but heterosis is uncommon ,and adaptability imposes limits on the extent to which distant provenances can be used without sacrificing yield.

Key words: Jack pine, *Pinus banksiana*, interprovenance hybrids, heterosis.

Introduction

Provenance hybridization has been employed in forest genetics in attempts to capture hybrid vigor and/or to combine desirable parental characteristics, but past efforts have met with mixed results. Height growth in interprovenance hybrids of Norway spruce (*Picea abies* Karst) and of Scotch pine (*Pinus sylvestris* L.) expressed slight positive heterosis (Nilsson, 1973; Ekberg et al., 1982; Park and Gerhold, 1986). Interprovenance hybrids in red pine (*Pinus resinosa* Ait.) (Holst and Fowler, 1973) and jack pine (*Pinus banksiana* Lamb.) (Magnussen and Yeatman, 1988a) were found to be intermediate to the parental provenances. In white spruce (*Picea glauca* Moench Voss), however, interprovenance hybrids were 17% taller than local x local crosses (Ying, 1978), a finding attributed to reduced inbreeding. Wide crosses of loblolly pine (*Pinus taeda L.*) lacked hybrid superiority on good sites, but expressed significant heterosis when planted on poor sites (Woessner, 1972). Heterosis in the above examples was defined in the traditional sense of performance exceeding the midpoint between the two intraprovenance parental values (mid-parent value).

More success has been achieved in attempts to combine parental characteristics. Although results are variable, excellent crosses have been found in Norway spruce by combining the vigor of a Central European provenance with the winter-hardiness of a Swedish source (Nilsson, 1973). Coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) crossed with the inland variety (*Pseudotsuga menziesii* var. *glauca*) has yielded some hybrids having the vigor of the coastal variety with the winter-hardiness of the inland variety (Rehfeldt, 1986). More and more, research results suggest that the value of provenance hybridization lies in its combining of desirable parental traits and not in heterosis resulting from overdominance types of gene action (Namkoong et al., 1988).

Jack pine has a wide natural range, and is a likely candidate for provenance hybridization (Magnussen and Yeatman, 1988a). It is found from the Atlantic Coast in Nova Scotia and Maine, west to the Mackenzie Valley in the Northwest Territories ,and from central Wisconsin to north-central Quebec (Critchfield and Little, 1966). Distinct differences between Lake States and Canadian populations of jack pine for a variety of morphological and biochemical traits (Schoenike, 1962, 1976; Hyun, 1979; Skeates, 1979; Critchfield, 1985) suggest the existence of different geographic races in jack pine (Wright, 1972). The modern jack pine populations are thought to derive from three refugia which survived the last glaciation, two in the midcontinent and one in the Southeast (Critchfield, 1985). Thus, interprovenance hybrids between Lake States and Canadian populations would appear to incorporate the ends of the spectrum of variation in jack pine.

Interprovenance hybrids of jack pine have been created on at least two occasions (Magnussen and Yeatman, 1988a, b) to examine the feasibility of capturing "hybrid vigour," or of combining desirable parental traits in such wide crosses. Analyses through age 15 suggests that interprovenance hybrids of jack pine have yielded intermediate progeny relative to parental provenances in terms of height growth (Magnussen and Yeatman, 1988a). However, Magnussen and Yeatman (1988b) report some examples of jack pine provenance hybrids that exhibit "statistically significant heterosis," although they do not outperform the superior parent.

The study reported here includes data from 73 families representing six provenances and their hybrids from throughout the natural range of jack pine. Based on measurements made at age nine, we look at possible explanations for absence of heterosis in height, discuss the validity of provenance and family variance estimates in height, and consider heritability estimates derived from this data.

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We also compare survival and rust infection among these populations (planted at this site).

Materials and Methods

Provenances and mating design

Inter- and intraprovenance controlled pollinations were made between 1971 and 1974 using a subset of six provenances drawn from a rangewide seed source study of jack pine (*Table 1*). Pollinations were made at two locations, the Forestry Sciences Laboratory, USDA Forest Service, Rhinelander, Wisconsin (set 1), and the Petawawa National Forestry Institute, Chalk River, Ontario (set 2). Progeny from these controlled crosses were planted at Wisconsin Rapids in central Wisconsin (the study reported here), and in east central Minnesota (rust incidence reported in Stewart et al., 1987). Crosses of the families in set 2 were also planted at three sites in Ontario, Canada (Magnussen and Yeatman, 1988b). The central Wisconsin trees were evaluated at nine years from seed for survival, total height, and incidence of pine-oak gall rust caused by *Cronartium quercum.* Interprovenance tree heights were compared to their midparent values and variance components were obtained from analysis of variance. For analysis, set 1 is separated into two series: series A includes male and female parents from each of Nova Scotia (NS)) Ontario (ON), Wisconsin (WI), and Michigan (MI); series B includes males from each of the above provenances but females from only Saskatchewan (SA) and Northwest Territories (NT).

The mating design employed two paternal trees from each provenance crossed with a different maternal tree from each provenance (*Figure 1*). Each maternal tree was used only once throughout the design whereas each paternal tree was crossed with six maternal trees. Series A has inter- and intraprovenance crosses whereas series B has only interprovenance crosses. Of the 48 potential full-sib families (6 provenances x 8 crosses/provenance), 47 were completed.

The pollinations for set 2 were made on trees originating from On, MI, and SA. Provenance origin is the same as for like provenances in set 1. Three paternal trees from each provenance were crossed with a different maternal tree from each provenance. Of the 27 potential full-sib families (3 provenances × 9 crosses/provenance), 26 were completed.

Planting and measurements

Seeds were processed and sown at the Hugo Sauer Nursery, Forestry Sciences Laboratory, Rhinelander, Wisconsin. In May 1980, 2-year-old, bare-root seedlings were hand-planted near Wisconsin Rapids in Wood County, Wisconsin. The site was of Plainfield sand (Typic Udipsamment) and was previously fallow though cropped in earlier years. The site for set 1 was plowed and disked; the site for set 2 received no site preparation. Four-tree row plots were planted at 2.4 m x 2.4 m spacing in a randomized complete block design with five replications. A single border row surrounded the study. Tree heights were measured to the nearest centimeter at 9 years from seed. At the same time, trees of set 1 were evaluated for the presence or absence of pine-oak gall rust, but no attempt was made to evaluate severity of infection.

Analysis

For survival, rust incidence, and height, no significant differences were found between any reciprocal provenance crosses (data not shown). Therefore, for all analyses, the reciprocal cross pairs are pooled and analysed. For convenience we will refer to interprovenance hybrid populations as "hybrids" and intraprovenance populations as "provenances". We will use the term "population" to indicate both hybrids and provenances.

Percent survival was evaluated for each hybrid provenance and provenance. The proportion of pine-oak gall rust infected trees was calculated for each full-sib family, hybrid provenance, and provenance. These provenances were ranked by percent rust infection, and correlations between percent rust infection and mean family height were determined.

Individual tree heights were used to calculate mean height for each cross and for hybrid provenances and provenances. Heterosis was tested for in those matings with both inter- and intraprovenance crosses (series A of set 1 and all of set 2) by using t-tests to compare the heights of the hybrids with the mid-point between the heights of the parent provenances (mid-parent values).

The data was partitioned into groups, each "group" consisting of all of the full-sib families of two prove-

Table 1. — Provenance origin.

Prov. abbr.	Provenance	Latitude (N)	Longitude (W)
NS	Durell Island, Nova Scotia	45° 21'	61° 01'
ON	Petawawa Plains, Ontario	45° 54'	77° 17'
MI	Fife Lake, Michigan	44° 35'	85° 21'
WI	Mosinee, Wisconsin	44° 47'	89° 43'
SA	Big River, Saskatchewan	53° 50'	107° 01'
NT	Fort Smith, Northwest Territories	60° 00'	111° 53'

Set 1

FEMALE PROVENANCE	(tree)	MALE PROVENANCE NS 1	NS 2	ON 1	ON 2	WI 1	WI 2	MI 1	MI 2
Series A									
NS	3	X							
	4		X						
	5			X					
	6				X				
	7					X			
	8						X		
	9							X	
	10								X
ON	3	X							
	4		X						
	5			X					
	6				X				
	7					X			
	8						X		
	9							X	
	10								X
WI	3	X							
	4		X						
	5			X					
	6				X				
	7					X			
	8						X		
	9							X	
	10								X
MI	3	X							
	4		X						
	5			X					
	6				X				
	7					X			
	8								
	9							X	
	10								X
Series B									
SA	3	X							
	4		X						
	5			X					
	6				X				
	7					X			
	8						X		
	9							X	
	10								X
NT	3	X							
	4		X						
	5			X					
	6				X				
	7					X			
	8						X		
	9							X	
	10								X

Set 2

FEMALE PROVENANCE	(tree)	MALE PROVENANCE ON 1	ON 2	ON 3	MI 1	MI 2	MI 3	SA 1	SA 2	SA 3
ON	4	X								
	5		X							
	6			X						
	7				X					
	8					X				
	9						X			
	10							X		
	11								X	
	12									X
MI	4	X								
	5		X							
	6			X						
	7				X					
	8					X				
	9						X			
	10							X		
	11									
	12									X
SA	4	X								
	5		X							
	6			X						
	7				X					
	8					X				
	9						X			
	10							X		
	11								X	
	12									X

Prov. abbr.	Provenance
NS	Durell Island, Nova Scotia
ON	Petawawa Plains, Ontario
MI	Fife Lake, Michigan
WI	Mosinee, Wisconsin
SA	Big River, Saskatchewan
NT	Fort Smith, Northwest Territories

Figure 1. — Mating design and provenance identification.

nances. The four families of the hybrids plus the four families of the provenances make up one "group". As an example, the NS-ON group includes the 2 families of each of the following crosses: NS x ON, ON x NS, NS x NS and ON x ON. The provenances are each included in several different groups. For each group, the variance components were estimated using SAS Procedure Varcomp (SAS Institute, 1987) with the restricted maximum likelihood method option. In addition, SAS General Linear Models Procedure using type III analysis was run on plot means to determine statistical significance of estimates. The overall error was used to test all the factors in the F-test.

The model used is:

$$Y_{ijklm} = u+r_i+m_j+p_k+mp_{jk}+rm_{ij}+rp_{ik}+rmp_{ijk}+h_l(p_k)+rh_{il}(p_k)+f_m[h_l(p_k)]+rf_{im}[h_l(p_k)]+e_{ijklm}$$

where u = the experimental mean,
r_i = i^{th} replicate effect,
m_j = j^{th} maternal provenance effect,
p_k = k^{th} paternal provenance effect
mp_{ik} = interaction between j^{th} maternal provenance and k^{th} paternal provenance,
rm_{ij} = interaction between i^{th} replicate, and j^{th} maternal provenance,
rp_{ik} = interaction between i^{th} replicate, k^{th} paternal provenance,
rmp_{ijk} = interaction between i^{th} replicate, j^{th} maternal provenance, and k^{th} paternal provenance,
$h_l(p_k)$ = l^{th} half-sib family effect within k^{th} paternal provenance,
$rh_{il}(p_k)$ = interaction between i^{th} replicate with l^{th} half-sib family within k^{th} paternal provenance,
$f_m[h_l(p_k)]$ = m^{th} full-sib family within l^{th} half-sib family within k^{th} paternal provenance,
$rf_{im}[h_l(p_k)]$ = interaction between i^{th} replicate and m^{th} full-sib family within l^{th} half-sib family within k^{th} paternal provenance, and
e_{ijklm} = within full-sib family error.

To asses the impact of ignoring the provenance effect, a reduced model was also used:

$$Y_{ilm} = u+r_i+h_l+rh_{il}+f_m(h_l)+rf_{im}(h_l)+ e_{ilm}$$

where u = the experimental mean,
r_i = i^{th} replicate effect,
h_l = l^{th} half-sib family effect,
rh_{il} = interaction between i^{th} replicate and l^{th} half-sib family,
$f_m(h_l)$ = m^{th} full-sib family within l^{th} half-sib family,
$rf_{im}(h_l)$ = interaction between i^{th} replicate and m^{th} full-sib family within l^{th} half-sib family, and
e_{ilm} = within full-sib family error.

Results

Survival and rust infection

Survival for populations in set 1 ranged from 89% to 100% (*Table 2*). In set 2,SAxSA had the lowest survival (77%) while the remaining populations ranged from 94% to 100% survival. Therefore, with the one exception of SAxSA, the populations had no differences in survival.

Rust infection among full-sib families ranged from 0% to 79% and among hybrids and provenances ranged from 8.4% to 72% (*Table 2*). No superior rust resistance was identified for any hybrid. Populations consisting of at least one parent from MI or ON had higher average rates of infection (44.7%) than populations with one or both parents from NS or WI (23.8%). These results concur with those of Stewart et al (1987).

Table 2. — Percent rust infection (Set 1), percent survival, mid-parent values (of hybrid populations in Set 1 series A and Set 2), mean height and percent difference between mid-parent value and mean height.

				height comparison		
	population	% rust infection	percent survival	mid-parent value(cms)	mean ht (cms)	percent difference
Set 1	NS x NS	8.4	93		190	
	NS x WI	10.8	91	271	287	5.9^{NS}
	NS x NT	13.1	98		226	
	WI x MI	16.9	97	362	367	1.1^{NS}
	WI x WI	21.2	93		354	
	NS x SA	23.6	95		238	
	ON x WI	32.0	98	349	353	1.4^{NS}
	NT x WI	32.9	98		292	
	NS x MI	33.1	89	282	280	-0.7^{NS}
	NS x ON	33.8	95	269	275	2.2^{NS}
	SA x WI	35.6	98		345	
	SA x MI	38.2	98		324	
	NT x ON	40.0	100		278	
	SA x ON	45.0	100		313	
	MI x MI	57.5	100		373	
	ON x ON	60.6	95		350	
	MI x ON	62.1	91	360	366	2.5^{NS}
	NT x MI	72.0	98		316	
Set 2	SA x SA		77		273	
	MI x ON		94	351	351	0^{NS}
	SA x MI		95	328	332	1.2^{NS}
	ON x ON		97		340	
	SA x ON		97	317	315	-0.6^{NS}
	MI x MI		100		362	

NS: Not significant. A series of t-tests found that none of the differences between mean height and mid-parent value were significant at the 5% level of probability.

Rust infection of full-sib families was positively correlated with the mean family height (r=0.43). A moderate correlation between incidence of gall rust infection and height was also noted by Stewart et al. (1987) who reported a correlation coefficient of 0.456. Nevertheless, they indicated that growth rate was not a dominant factor in determining rust infection, citing as an example that the WI populations were among the tallest but had low rust incidence. The same is true for our study trees.

Hybrids and provenance heights

In set 1, mean tree heights of populations with both parents from the Lake States Region, (ON, MI, WI) were very similar, ranging only from 350 cms (ON x ON) to 373 cms (MI x MI) (*Figure 2*). The NS x NS provenance was considerably shorter (190 cms). Hybrids with NS resulted in progeny heights close to the mid-parent values (*Table 2*). The WI x NS hybrid expressed the largest deviation from the mid-parent values with a differences of +5.9%. The hybrids including SA and NT (series B) were shorter than the series A hybrids (*Figure 2*).

Those crosses with NS were the shortest in series B (mean=232 cms) and were even shorter than the NS hybrid provenances in series A (mean=280 cms). The shortest hybrids, SA x NS and NW x NS, represent the widest crosses. Populations with both parents from the Lake States (set 2), had similar heights (*Figure 2*). The "SA x SA" provenance was considerably shorter than the Lake States provenances, and hybrid provenances resulted in progeny very close to the midparent values (*Table 2*). When t-tests were made on each of the groups with both inter- and intraprovenance crosses, no significant differences between mean heights and mid-parent values ($P<0.05$) were found.

Variance component analysis

In set 1, the variance component analysis yielded low variance estimates for the half-sib and full-sib family

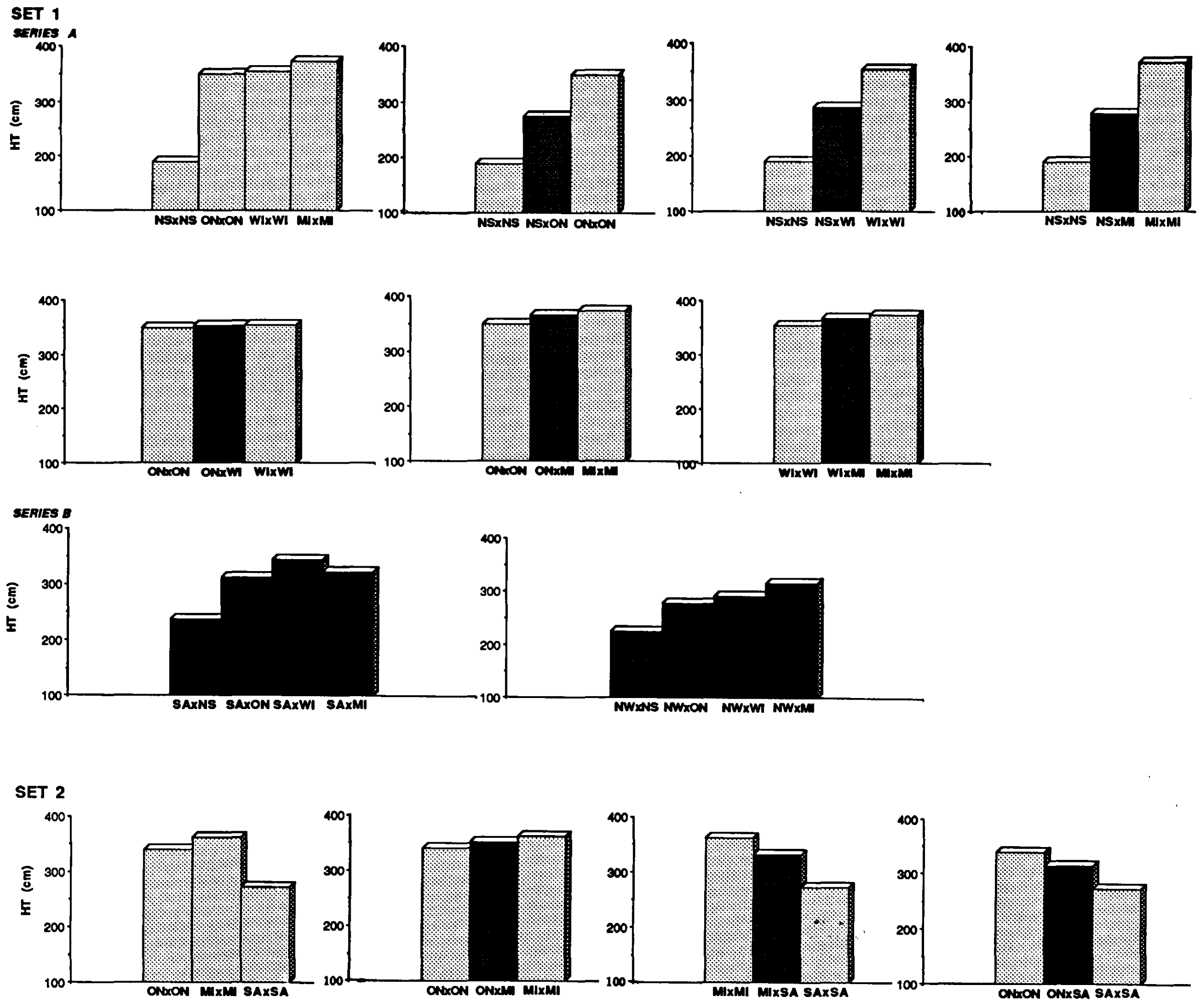

Figure 2. — Mean tree heights at age 9 of provenances (light areas) and hybrids (dark areas).

effects for almost all groups (*Table 3* columns 8 and 10). Groups with both provenances from the Lake States region all had non-significant maternal and parental provenance variance estimates, whereas those families with one or both provenances from NS all had significant provenance variation estimates (cols. 2 and 3). Similar results were found in set 2, where half-sib variance estimates were small for all groups, but full-sib variances were generally larger than in set 1. Again, the Lake States Region group (MI x ON) had low provenance variance. For both sets, the full-sib variance, when present, is small compared to provenance variances. Furthermore, the interaction between maternal and paternal provenances is also small.

Discussion

Absence of heterosis

Failure of the hybrids to exceed mid-parent values for height (*Table 2*) indicates that no hybrid vigor for height is expressed by these crosses. Hybrid vigor is usually explained by the presence of either directional dominance or overdominance gene action (Crow, 1984). Additionally, increase (or excess) in the level of heterozygosity is necessary for the expression of hybrid vigor (Falconer, 1989). Therefore, it is necessary to determine the level of heterozygosity in the hybrid populations, in order to determine the presence or absence of (over)dominance gene action (when two unrelated populations are crossed).

When crossing two populations with the same, or similar, allele frequencies, but which are inbred, their hybrids will contain more heterozygotes than the average of the parental populations. When two populations with different allele frequencies are crossed, as might occur with geographically separated populations, then these hybrids will produce a transient excess of heterozygotes (Robertson, 1965). Thus, regardless of the allele frequencies of the parents, there is a good chance that the hybrids will have excess heterozygotes when compared to the mean of the parental populations. In the case of jack pine, if all provenances had similar allele frequencies for loci influencing, for example, tree height, then all the provenances would be expected to have similar heights. However, the presence of significant height differences in jack pine suggests that the parental populations are likely to have different allele frequencies with respect to height. If we assume that all the provenances have the same mode of gene action, then the magnitude of the differences in allele frequencies between parents determines the level of heterozygosity. The height differences observed (*Table 2*) do not display clear trends to substantiate this point. However, if the hybrids indeed have substantial excess of heterozygotes originating from allele frequency differences, then the small absolute

Table 3. — Variance component estimates of groups with interprovenance crosses.

column	1	2	3	4	5	6	7	8	9	10	11	12
prov. groups	rep	mat. prov.	pat. prov.	mxp	repxm	repxp	repxmxp	hs(p)	rxhs(p)	fs(hs(p))	rxfs(hs(p))	err
Set 1												
series A												
NS-WI	0	3036^{+}	3210^{+}	170	0	15	0	136	66	0	425	994
MI-NS	31	4690^{+}	3566^{+}	0	97	0	164	0	0	109	204	1501
NS-ON	0	2439^{+}	3649^{+}	0	6	0	247	0	391	0	237	941
ON-WI	0	0	0	0	153	1	31	0	40	0	419	873
MI-WI	0	36	20	0	0	97	0	0	0	0	0	1691
MI-ON	0	0	19	0	0	148	0	0	0	82	673	1103
Set 2												
MI-ON	0	0	152*	0	0	95	0	37	123	197	180	1375
MI-SA	40*	1016^{+}	687^{+}	206	0	214	0	0	199	108	56	1276
ON-SA	0	511^{+}	529^{+}	0	38	45	50	0	0	72	336	1361

rep = r = replicate
mat. prov. = m = maternal provenance
pat. prov = p = paternal provenance
hs=half-sib family (common father)
fs=full-sib family
*) significant at the 5% level of probability
+) significant at the 0.05% level of probability

differences and the lack of clear trends could be interpreted as indicating that the amount of directional dominance gene action involved is small.

Provenance vs family variance

The presence of large provenance effects in the groups containing NS (of set 1) and SA (of set 2), indicates that there are sizable genetic effects. However, given the negligible half-sib and full-sib family variances in most groups, we are tempted to conclude that there are no family related gene effect differences, either additive or non-additive, with respect to height in jack pine (*Table* 3).

One explanation for such a phenomenon is that the allele frequencies diverged in the different populations and different alleles became fixed within those populations, with the result that no variability is detected for half-sib or full-sib variance. If such populations having fixed alleles were then crossed to form hybrids, these hybrids also would show little variability and the variance estimates may be similar to those shown in *Table 4.* However, there is no evidence for gene fixation in different populations. In fact, the data available from various electrophoretic studies (Wheeler, 1981; O'Malley and Guries, 1983) indicate that jack pine, like most conifers, appears to share the same alleles at approximately the same frequencies over large geographic areas.

A lack of family effects could also occur if the planting was poorly blocked and environmental variation was not minimized within replicates. Although this is a possible factor in minimizing family genetic effects, the prominent provenance variances observed indicate that the family variance would have remained relatively small even if the experiment was not well blocked. The particular planting site used was apparently very homogeneous in terms of soil, aspect, site preparation and other variables.

The mating design employed in this study could also be a factor which limits our ability to detected family effects. There is only one family for every female parent and only two half-sib families for every male parent within the same group. Thus, there are only two full-sib families for every provenance cross (four full-sib families when reciprocals are included). Therefore, although the analysis shows no half-sib family effects in most groups, we may not conclude that there is no genetic variance for height in jack pine.

Of the three possible explanations as to why there are no detectable full-sib or half-sib family differences between groups, we believe the chief factor to be the limitation of the mating design. The first possible explanation, that different alleles were fixed in the different populations, is unlikely since heritabilites of height in jack pine have been found in other studies (Riemenschneider, 1989; Rudolph et al., 1989). The explanation that poor blocking of the site was responsible is unlikely because the site was very uniform. Thus, it is likely that the inability to discern family effects is due to the mating design which provides very few families in any one group.

Reduced statistical model

To determine if significant provenance effects observed could be transferred to family effects, and to understand the potential consequences of eliminating provenance effects, a reduced model of the same data was used which ignores provenance effects. The use of this reduced model

Table 4. — Variance component estimates without provenance effects. This table provides variance component estimates from the restricted maximum likelihood procedure, which does not require analysis of variance as an intermediate step.

column	1	2	3	4	5	6
prov. groups	rep	hs	rep*hs	fs(hs)	rep*fs(hs)	err
Set 1 - series A						
NS-WI	0	758	60	3166	476	988
MI-NS	90	84	0	4748	419	1499
NS-ON	0	1225	264	2392	609	940
ON-WI	21	0	0	0	609	873
MI-WI	21	0	17	19	0	1760
MI-ON	28	0	0	99	781	1104
Set 2						
MI-ON	0	115	213	198	187	1375
MI-SA	121	0	359	1270	41	1281
ON-SA	0	51	0	578	442	1373

hs=half-sib family (common father)
rep=replicate
fs=full-sib family

yielded sizable full-sib and half-sib family variances only in those groups which had provenance effects in the full model (*Table 4*). It is evident that these supposed full-sib and half-sib effects are actually provenance effects. Nevertheless, if we used this reduced model as the primary basis for our analysis, we would have concluded that there were substantial non-additive gene effects in those groups which included NS and SA. This would counter our conclusion regarding directional dominance gene action, and we would recommend breeding based on expensive reciprocal recurrent selection instead of simple selection, the latter approach being sufficient for capturing additive genetic variance.

Heritability

Heritabilities calculated from this data would be zero for all but two groups due to the lack of family variances (*Table 3*, column 9). Does this mean that there would be no genetic gain achieved if selections were made within these groups? Consider, for example, the group "NS-ON", in which we have the hybrid (ON x NS) and two provenances (NS x NS, ON x ON). The populations in this group have different means but there is no overall family variance. Because family variance is used to estimate heritability (h^2), the h^2 would be zero. However, our heritability estimate assumes that all the variances originate from a single intermating population. In this case, however, there are three populations, each with its own genetic mean and variance. Thus, even if h^2 estimate is zero, we could achieve gain from selection. On the other hand this selection is likely to result in individuals exclusively from ON x ON, which defeats the original intention of population crossing (Kang and Nienstaedt, 1987). This is an extreme example demonstrating the potential problems associated with estimation of heritabilities and selection in population crossings. While heritability is a useful concept, it is critical to clearly define the context within which this measure is to be used (Rudolph et al., 1989).

Concluding remarks

Incidence of rust infection, and a correlation between height and the rust incidence found in different provenances, were consistent with the findings of Stewart et al (1987). There was little difference in height performance among provenances from the Lake States Region (Rudolph and Yeatman, 1982). The apparent lack of heterosis shown in this study is also concordant with that found by Magnussen and yeatman (1988a). We hypothesize that the lack of hybrid vigor was primarily due to a lack of directional dominance gene actions, but the hybrids would have excess heterozygotes primarily due to different allele frequencies among the provenances. The findings regarding tree height of jack pine support the rationale used to establish the multiple breeding populations of jack pine in the Lake States (Kang, 1980; Riemenschneider, 1981), namely that the gene actions involved in the jack pine height are likely to be primarily additive, and that little differences existed among the average heights of jack pine populations from Lake States, excepting the trees from northeastern Minnesota. An unexpected outcome of this study is that little or no family variance was found in most of the groups. This could lead us to a contradiction that there is no genetic variance, yet the populations (provenances) have diverged. The only genetically plausible conclusion is that most of the loci in the provenances are fixed for different alleles. This conclusion is, however, unrealistic because moderate heritabilities in height were found in other reports (Riemenschneider, 1989; Rudolph et al., 1989). We consider this as a case in point which underscores the importance of careful mating design and analysis in forest genetics experiments.

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Clonal Variation in a Four-Year-Old Plantation of Triplochiton scleroxylon K. Schum. and its Relation to the Predictive Test for Branching Habit

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Summary

Considerable clonal variation is reported in the size and form of the West African tree *Triplochiton scleroxylon* K. Schum. after four years of growth in plantations near Ibadan, Nigeria. At normal spacing (2.4 m) mean heights ranged from 5.9 m to 8.1 m, whilst at wide spacing (4.9 m) the range was 5.1 m to 7.8 m, although the trunks had a greater diameter. Form varied considerably, some clones having straight monopodial stems while others were multi-stemmed, much-forked or heavily branched. The relationship between these characteristics and the result of a Predicitive Test for Branching Habit is reported. This test is based on genetic variation in apical dominance following decapitation and is made on very young plants in the nursery, 3 to 4 weeks after removal of the terminal bud. There were correlations between field characters (extent of branching, the incidence of heavy branching, and the diameter of the stem) and indices obtained from the test. The possibility is discussed of using the test to screen young seedlings for those which, following vegetative propagation, are likely to give clones with a low branching frequency and high harvest index.

Key words: apical dominance, correlative inhibition, clonal variation, branching, decapitation, screening test, tree improvement, Triplochiton scleroxylon.

Introduction

Triplochiton scleroxylon K. Schum. (Sterculiacase) is an important forest tree of West Africa. For much of this century it has accounted for more of the timber extracted annually from the region than any other species (Hall and Bada, 1979). In the early 1960s it was realised that the quality and quantity of the remaining resource had been diminished by over-exploitation, and so a programme of tree improvement began at Ibadan, Nigeria, known as the West African Hardwoods Improvement Project (Howland and Bowen, 1977). Methods of vegetative propagation of *T. scleroxylon* were rapidly developed and clonal trial plantations were established in 1975 and 1976.

The first purpose of the present paper is to describe the clonal variation in some of the main morphometric attributes of 4-year-old trees and to relate these to a physiological characteristic measured in very young plants. It is possible that undesirable traits, like forking, multiple stem growth and heavy branching, may be related to inherent features of apical dominance which persist throughout the life of the tree. Earlier studies have demonstrated that decapitation of young plants breaks apical dominance and reveals clonal variation in bud outgrowth (Leakey and Longman, 1986; Ladipo, Leakey and Grace, 1991 and in press b). It is hypothesised that this phenomenon provides a prediction of the branching habit inherent to each clone. We have therefore called this assessment of asical dominance and branching frequency the Predictive Test for Branching Habit.

The second aim of the present work is to search for relationships between the result of the Predictive Test in young clonal plants at the nursery stage and the size and form of the same clones after several years' growth in plantation. If such relationships exist, it should be pos-

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