Variation among the Offspring of Selected Lower Michigan Jack Pines[1])

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(Received December 1974 / January 1975)

Jack pine (*Pinus* banksiana LAMB.), one of Michigan's most important timber trees, grows rapidly and thrives on poor soils. But it is comparatively short-lived, tends to be branchy and often has poor form. The present project was undertaken to investigate the possibilities of genetically improving jack pine for several of these undesirable traits and increased height growth.

Previous inheritance data in jack pine pertinent to this study were derived from two experiments conducted in Minnesota. In the first, seeds were collected from 10 closed-cone and 18 open-cone trees in the fall of 1939. The seedlings were field planted in a replicated experiment and were measured in 1957 (RUDOLPH et al. 1957). The results showed that the ability to produce open-coned trees was strongly inherited; the proportion of trees which produced cones soon after ripening were 13% and 52% in the offspring of the closed-cone and open-cone trees respectively. The second experiment was a progeny test of normal and witches'-broom jack pines (JOHNSON et al. 1968). There was a 1 : 1 segregation ratio of normal to dwarf trees among the open-pollinated offspring of the witches'-broom trees, indicating that trait is governed by a single gene (or more probably a group of linked genes) which behaves in a dominant manner.

There have been two provenance tests of jack pine which included test plantations in Michigan. The first was started in 1951 by the Lake States Forest Experiment Station and was the subject of reports by AREND et al., 1961 and KING, 1964. The second was started in 1965 by the Petawawa (Ontario) Forest Experiment Station and included seed collected from natural stands in all parts of the species' range. Using stock grown from that seed, a series of test plantations was established in several parts of Michigan in 1966.

Data from both provenance tests indicated that trees grown from seed collected in Michigan's Lower Peninsula grew fastest when planted in Michigan (CANAVERA and WRIGHT 1973). For that reason Lower Peninsula trees were the source of all seed used in the present experiment.

This improvement project is very different than most improvement projects undertaken in northern Europe or southeastern United States, primarily because jack pine starts to flower when only 3—4 years old. In those other regions, important timber species do not flower until they are 12—40 years old whereas grafts taken from the tops of old trees flower in half that time. Consequently, breeders in those regions have usually selected plus trees, established grafted seed orchards, and then established progeny tests which provide inheritance data used to guide the thinning of the grafted seed orchards. Thus they can produce improved seed several years earlier than if they relied solely on seedlings. Because of the early flowering, grafting was necessary in jack pine. Consequently, the present project consists entirely of a series of progeny tests which can yield improved seed as well as inheritance data.

Material and Methods

In the summers of 1965 and 1966 natural stands of jack pine were located in the northern half of Michigan's lower Peninsula. A total of 60 stands were selected, all situated on state forests of the Michigan Department of Natural Resources. Most stands were 40—60 feet tall. Several had been selectively thinned by state foresters removing misshapen or small trees. Increment borings were made in all stands to insure that selected trees were within ±5 years of the stand average.

In those stands a total of 382 trees were selected for (or against) rapidity of growth, stem straightness and ability to produce cones which open soon after ripening. About 70% were selected for superiority and were 2 standard deviations or more above the stand average in height and stem straightness. The other 30% were selected for inferiority in those traits. Also, in a few stands which had been attacked heavily by jack pine budworm (*Choristoneura* pinus FREE.), trees were selected for resistance to this pest.

Each selected tree was judged in relation to others growing within a radius of 200 feet and was the best or poorest tree in that circle for 1, 2 or 3 traits.

The following data were recorded for each stand: age, location, density of stocking, average height, average diameter, stem straightness, and percent of trees attacked by the jack pine budworm. The following additional data were recorded for each selected tree: age, location, and degree of superiority (or inferiority) to the stand average in height, stem straightness, attack by jack pine budworm and quickness of cone opening. Degree of superiority was recorded in such a manner that it could be translated into standard deviations.

The selected trees were felled and their cones were collected by personnel of the Michigan Department of Natural Resources in September 1965 (199 trees in 40 stands) or September 1966 (183 trees in 20 stands) (Fig. 1). The cones were transported to East Lansing where the seeds were extracted separately for each parent and each seed lot was weighted.

The 1965 seeds were sown May 23—24, 1966 in Michigan State University's Tree Research Center at East Lansing. The 1966 seeds were sown there May 15—16, 1967. Each year's experiment consisted of a randomized complete block design with 4 replications. A plot consisted of one 4-ft. row containing 20 evenly spaced seeds; the plots were 1 ft. apart.

Germination was prompt and averaged 90%. Losses after germination were negligible. The seedbeds were kept well watered, weed-free and were mulched with sawdust the first winter. At age 2 the east half of each plot was lifted to provide planting stock for a series of permanent test plantations. The remaining seedlings were discarded after growing an additional 2 years in the seedbeds.

All data from this report were obtained from the trees remaining in the seedbeds. Heights were measured to an accuracy of ¼ inch (2-year-old seedlings) or ½ inch (3-

[1]) The work reported here was supported by the Forestry Division, Michigan Department of Natural Resources. The author expresses his appreciation to Hans NIENSTAEDT, Ralph A. READ, T. D. RUDOLPH and J. W. WRIGHT for their critical review of the manuscript.

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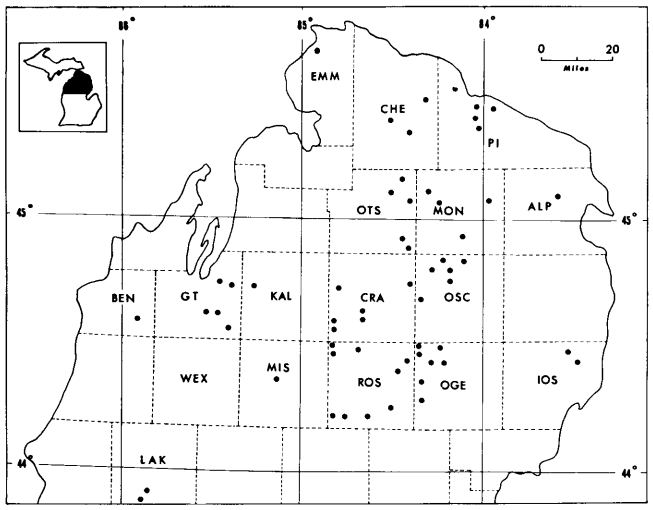

Fig. 1. — Distribution of the parental stands (black dots) from which the half-sib progenies were obtained. The black portion in the upper left insert shows the area of Michigan which was sampled. County names are as follows: EMM = Emmet, CHE = Cheboygan, PI = Presque Isle, OTS = Otsego, Mon = Montmorency, ALP = Alpena, BEN = Benzie, GT = Grand Traverse, KAL = Kalkaska, CRA = Crawford, OSC = Oscoda, WEX = Wexford, MIS = Missaukee, ROS = Roscommon, OGE = Ogemaw, IOS = Iosco and LAK = Lake.

year-old seedlings). The proportion of trees having lammas growth or female flowers were determined by simple counts of the numbers of trees with and without the trait. Autumnal foliage color was scored on the basis of grades 1 (= purple) to 10 (= green). Stem straightness was not measured because practically all trees were straight.

An analysis of variance was calculated for each set of data, using plot means as item. For the 1966 experiment which contained the offspring of 199 single parents located in 40 stands, the degrees of freedom and expected mean squares were as follows:

Source of Variation	Degrees of freedom	Expected mean squares
Parent tree	198	
Between stands	39	$\sigma^2_e + 4\sigma^2_p + 20\sigma^2_s$
Within stands	159	$\sigma^2_e + 4\sigma^2_p$
Replication	3	
Error	594	σ^2_e
Total	795	

Simple correlations were calculated, using family means as items.

Results

The results are summarized by stand of origin in *Tables 1* and *2*, which also include data on the location and length of growing season for each parental stand. In both tables the stands are arranged by county in an approximate north-south manner to facilitate geographic comparisons.

Growth rate. The trees grew well. When the final height measurements were made in 1968, the 3-year-old seedlings in the 1966 experiment averaged 23.5 in. (60 cm) tall; the 2-year-old seedlings in the 1967 experiment averaged 7.5 in. (19 cm) tall. There had been no insect damage and all trees were straight.

The best families grew 27% faster than the experimental average whereas the poorest were 28% shorter than average. The statistical analyses showed that these differences

Table 1. Data on orgin of parents and growth of offspring for half-sib progeny test of Michigan jack pine sown in 1966, by stand of origin.

	PARENTAL DATA					PROGENY DATA			
							Trees with		
Stand no., no. of parents per stand and county of origin (a)			North Lat.	West Long.	Frost free days	Height Age 3	Lammas growth Age 2	Female flowers Age 3	Female flowers per 100 trees
			°	°	no.	% of mean	%	%	no.
1	7	EMM	45.68	84.68	130	97	27	16	22
2	6	CHE	45.47	84.32	125	95	13	10	13
3	5	CHE	45.38	84.45	126	101	14	13	22
4	2	CHE	45.35	84.55	125	95	17	8	14
5	6	PI	45.70	83.98	129	96	14	13	21
6	5	PI	45.32	84.22	129	99	16	16	20
7	3	PI	45.29	83.95	130	86	17	8	9
8	4	PI	45.28	84.08	130	98	16	18	28
9	5	PI	45.25	84.09	128	98	30	14	24
10	10	OTS	45.15	84.45	96	101	20	13	19
11	4	OTS	44.90	84.48	90	99	5	23	29
12	6	OTS	44.83	84.40	96	96	20	13	21
13	4	BEN	44.45	85.58	106	106	14	10	16
14	3	GT	44.72	85.38	105	105	9	2	4
15	3	GT	44.71	85.38	103	103	28	16	23
16	4	KAL	44.72	85.22	120	104	10	12	13
17	6	CRA	44.70	84.37	90	97	18	7	10
18	6	CRA	44.58	84.62	85	102	20	17	22
19	8	CRA	44.58	84.82	85	95	13	10	10
20	4	CRA	44.53	84.84	85	103	17	22	33
21	5	OSC	44.83	84.20	90	106	14	17	28
22	5	OSC	44.83	84.13	90	93	29	12	18
23	4	OSC	44.80	84.32	90	96	17	25	33
24	14	OSC	44.70	84.20	90	102	13	11	17
25	4	MIS	44.37	85.15	107	106	21	14	20
26	5	ROS	44.32	84.80	100	104	22	22	32
27	5	ROS	44.53	85.89	130	100	11	10	13
28	4	ROS	44.47	84.37	92	99	16	13	18
29	4	ROS	44.47	84.65	80	99	14	12	18
30	3	ROS	44.45	84.46	100	96	15	16	23
31	2	ROS	44.33	84.80	81	106	11	9	20
32	5	ROS	44.27	84.48	98	99	20	11	14
33	5	ROS	44.18	84.64	100	106	17	21	32
34	5	OGE	44.48	84.25	96	95	16	12	22
35	5	OGE	44.47	84.35	98	104	15	9	14
36	5	OGE	44.43	84.30	97	104	11	14	26
37	5	OGE	44.40	84.33	99	102	14	18	28
38	5	OGE	44.32	84.28	100	101	17	16	23
39	4	IOS	44.48	83.37	129	106	11	16	23
40	4	IOS	44.47	83.45	129	105	13	23	26

(a) Key to county names: BENzie, CHEboygan, CRAwford, EMMet, Grand Traverse, IOSco, KALkaska, MISsaukee, OGEmaw, OSCoda, OTSego, Presque Isle, ROScommon.

Table 2. Data on Origin of parents and growth of offspring for half-sib progeny test of Michigan jack pine sown in 1967, by stand of origin.

	PARENTAL DATA					PROGENY DATA		
Stand No., no. of parents per stand and county of origin (a)			North Lat.	West Long.	Frost free days	Height Age 2	Autumn Foliage Color Age 2	Trees with Lammas growth Age 2
			°	°	no.	% of mean	0=purple 10=green	%
41	16	OTS	45.13	84.48	96	101	7	8
42	5	OTS	44.87	84.87	90	96	8	6
43	7	MON	45.13	84.32	95	86	6	14
44	15	MON	45.08	84.23	95	94	8	7
45	7	MON	45.08	84.03	95	94	7	9
46	10	MON	44.93	84.11	98	98	8	11
47	4	ALP	45.12	84.63	86	86	4	4
48	9	GT	44.63	85.47	109	109	8	13
49	11	GT	44.63	85.45	101	101	88	10
50	8	GT	44.62	85.40	108	108	6	16
51	8	CRA	44.58	84.93	85	96	7	17
52	11	CRA	44.57	84.52	85	101	7	9
53	11	OSC	44.87	84.22	90	109	8	10
54	2	OSC	44.80	84.27	90	90	8	7
55	12	ROS	44.38	84.40	99	94	9	10
56	11	ROS	44.22	84.78	100	102	8	12
57	16	OGE	44.48	84.35	98	97	8	12
58	7	OGE	44.42	84.22	97	92	8	12
59	4	LAK	43.98	85.80	100	120	8	15
60	9	LAK	44.03	85.78	100	108	9	15

(a) Key to county names: ALPena, CRAwford, Grand Traverse, LAKe, MONtmorency, OGEmaw, OSCoda, OTSego, ROScommon.

were significant and showed further that approximately 17% (1966 experiment) or 39% (1967 experiment) of the total variance in height was attributable to the seed parents *(Table 3)*.

Special analyses of the data were made to determine why the offspring of some trees faster than others, with the following results.

Table 3. Statistical summary of the two progeny tests of jack pine.

Item	Height	Trees with Lammas growth	Trees with Female flowers	Female flowers per 100 trees	Autumn foliage color (10=greenest)
Experiment sown in 1966, measured at age 2 (Lammas growth) or age 3 (other traits)					
Average	23.4 in.	16%	14%	20	--
Range in seedlot means	18-30 in.	0-50%	0-50%	0-93	--
F value	1.83**	1.32	1.25	1.28	--
% of total variance due to					
Stand or origin	0**	5	0	0	--
Parent within stand	17	2	5	7	--
Error	83		95	93	--
Experiment sown in 1967, measured at age 2					
Average	7.5 in.	10%	--	--	grade 7.6
Range in seedlot means	5-10 in.	0-33%	--	--	grade 1-10
F value	3.30**	1.17	--	--	1.85**
% of total variance due to					
Stand of origin	7	0	--	--	12**
Parent within stand	23**	4	--	--	11**
Error	61	96	--	--	77

** = statistically significant at 1% level.

Seed size. There was no relation between seed weight and height of seedlings. Hence the between-family differences are presumed to be genetic.

Parental selection. Offspring of the 214 "plus" trees which had been selected for superior height or form or both grew only 0.4% faster that the offspring of the 168 "average" or "minus" parents. This difference was not statistically significant and parental selection was presumed to be ineffective.

Stand of origin. Three stands in Presque Isle County were of the same age and grew on seemingly similar Rubicon sandy soils. They were 39, 50 and 61 feet tall and their offspring were 23.3, 22.6 and 22.9 inches tall respectively at age 3. In other words, seeds collected from the tallest stand did not grow the fastest. This is a single example but the conclusions were confirmed by analysis of the variance components for all stands in both experiments *(Table 3).* The superiority of seeds from certain stands was due to chance.

Latitude of origin. Approximately half the seeds were collected north and half were collected south of latitude 44.6°. In the combined data from both experiments, southern seedlings grew 1.8% faster than northern seedlings. That difference was statistically significant (5% level) and indicates that a small amount of gain might be expected by collecting seed from the central rather than the northern part of the lower Peninsula.

Length of growing season at place of origin. There was no statistically significant (10% level) relationship between length of growing season at place of origin and growth of the seedlings in the nursery.

Lammas growth. Approximately 15% of the seedlings developed Lammas growth during their second summer. These shoots, which developed in midsummer, hardened off properly and suffered no apparent winter injury. Consequently there was no relationship between the amount of Lammas growth and form or height.

Although the proportion of trees with Lammas growth varied from 0—50% in different families, the between-family differences were not statistically significant and this trait must be considered as of minor importance.

Early flowering. Jack pine is noted for its early production of flowers. It preserved its reputation in the present experiments, where 14% of the trees flowered by age 3. The differences among families were not statistically significant. Observations made in 1970 and 1971 on the permanent plantations showed that nearly all trees produced pollen and cones by ages 4—5.

Autumn foliage color. In provenance tests which include seedlings from very distant areas, north-south trends in foliage color are evident (RUDOLF, 1957; CANAVERA and WRIGHT, 1973). In such experiments young seedlings grown from seed collected in cold northern areas turn purple in the autumn whereas seedlings of southern origin remain green.

Autumn foliage color was studied in the second experiment only. There was a possible north-south trend in that trees from one of the most northern stands, in Aplena County, were much more purple than the others.

Practical Application

To present seed procurement practices: Only growth rate differences can be considered at the present time because the seedlings were too young to provide data on form or branch size.

Other experiments have shown that Michigan's Lower Peninsula is the source of the fastest growing jack pine, at least for Michigan. Within that area, about a 2% gain can be expected from collecting seed in the central rather than the northern counties.

To further improvement by mass and stand selection. The data indicate that further parental mass selection of the same intensity as practiced in these studies for height will be ineffective in natural stands. The environmental influences appear to be so great as to mask genetic differences.

Even stand selection appears to be ineffective. In both the 1966 and 1967 experiments, a negligible portion of the total variance was due to stand of origin (7 and 0%, respectively).

To improvement possibilities by combined family and mass selection in the progeny-test seed orchards. To practice family selection over a longer period than was possible in the nursery experiment, the 199 families in the 1966 experiment were field planted in 1968 and the 183 families in the 1967 experiment were field planted in 1969. Three permanent plantations were established in the Lower Peninsula each year, using 2—0 stock. Each plantation contains 40 to 50 trees per family and 4 to 6 replications, with 8 × 8 foot spacing between trees. As of the summer of 1974, survival in the six plantations varied from 85 to 96%. The trees averaged 10 to 12 feet tall and were almost uniformly good form.

It was the original intent of the project to convert the progeny tests into seed orchards by removing 50% of the poorest parent tree families by age 9 based on average family performance. The remaining families would then be subject to later thinnings which would remove the poorest individuals and leave only the best. However, measurement of the progeny tests at ages 7—8 revealed that F values for height differences between parent tree families varied from a low 0.77 to a high of 1.79. These F values are too low to guarantee that families left after thinning are in fact the best material that can be retained in the progeny-test seed orchards. Therefore, to maximize genetic gain initial selection of families will be based not only on aver-

age family performance but also on the range of variation and type of distribution that exists (normal or skewed) within the families.

This selection scheme will not only retain superior individuals that would otherwise be removed, but also permit retention of a larger number of parent tree families with fewer individuals per family. Thus a broader genetic base can be maintained within the seed orchard and provide maximum genetic gain from second generation controlled pollination seed orchards. The full-sib progeny test seed orchards will come into bearing about the time the first-generation orchards become too tall for easy cone collection.

Summary

Seed was collected in two successive years from individual jack pine (*Pinus banksiana* Lamb.) trees in each of 60 natural stands in the Lower Peninsula of Michigan. Second and third year height growths showed that 17% (first year's selections) and 39% (second year's selections) of the total variation was attributable to the parent trees. However, the field selection of both superior trees and stands proved to be ineffective. The half-sib families have been field planted and will be converted to seed orchards. These progeny-test seed orchards will be rogued not only on the basis of average family performance, but also on the degree and distributional patterns of the variation existing within families. An immediate gain of 2% in height growth can be realized by collecting seeds from the southern and central parts of the Lower Peninsula.

Key words: heritability, genetic gain, *Pinus banksiana* Lamb.

Zusammenfassung

In den Jahren 1965 und 1966 wurden auf insgesamt 60 autochthonen Standorten in Lower Peninsula of Michigan Einzelbäume von *Pinus banksiana* Lamb. ausgewählt und von diesen Saatgut geerntet, welches später zur Aussaat gelangte. Die daraus angezogenen Einzelbaum-Nachkommenschaften zeigten im zweiten und dritten Jahr, daß 17% aus der Ernte 1965 und 39% aus der Ernte 1966 in der Gesamtvariation des Höhenwachstums den Mutterbäumen zugeordnet werden konnten. Die Selektion von jeweils vorwüchsigen Einzelbäumen und Beständen war jedoch nicht erfolgreich, was die Leistung der Nachkommenschaften betrifft.

Die Halbgeschwister-Familien sind ausgepflanzt worden, um später in Samenplantagen umgewandelt zu werden. Solche Samenplantagen aus dem Nachkommenschaftstest sollen nicht nur nach der Leistung des Familiendurchschnitts ausgewählt werden, sondern auch nach dem Variationsmuster innerhalb der Familien. Ein unmittelbarer Gewinn von 2% an Höhenwachstum kann dadurch erzielt werden, daß Saatgut aus den südlichen und zentralen Teilen von Lower Peninsula gewonnen wird.

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