A PROGENY TEST OF OTTAWA VALLEY JACK PINE - 6-YEAR RESULTS

Christopher W. Yeatman 1/

Abstract.-- Seed was collected from ten random trees in each of two stands from each of five areas along a 60-mile transect from Petawawa to Deux Rivieres. Tree height at the three test sites in the Valley reveal differences among progenies (trees) but not among stands or areas. The results are discussed in relation to delineation of populations, seed collection and improvement of jack pine.

Additional keywords: Height growth, heritability, genetic gain, *Pinus banksiana*.

Provenance research in the Lake States (Schantz-Hansen and Jensen 1952, Rudolph 1964, King 1966, Canavera 1969) and in Canada (Yeatman and Teich 1969, Yeatman 1974a) has shown a broad pattern of clinal variation associated with latitude and the duration and temperature of the growing season. Regional gains can be made by identifying the best populations for seed collection and improvement. This report examines sources of genetic variation within a limited area to determine population structure at the local level and estimate heritability of height growth from open-pollinated (half-sib) progenies.

AREA OF STUDY

Jack pine is found in pure and mixed stands growing on outwash and wind-blown sands along the Petawawa and Ottawa Rivers northwest of Pembroke, Ontario (fig. 1). Characteristically the distribution is discontinuous, interspersed with forests of white pine, spruce and hardwoods on the more fertile till soils and moist depressions. Even-aged jack pine stands originated from fire around the turn of the century but many have been cut in the past three decades to be replaced by scattered natural regeneration together with intolerant hardwoods. Remnants of older stands remain in roadside reserves and other special areas and these formed the basis for a systematic sampling in 1957 of jack pine stands along the Ottawa River between Petawawa and Deux Rivieres.

MATERIAL AND METHODS

Trees were sampled according to a nested or heirarchal system that included five areas, two stands in each area and ten trees in each stand for a total of 100 parent trees. The locations of areas (1 to 5) and stands in areas (1,2) are shown in figure 1. Trees were chosen from the dominant/co-dominant crown classes within mature, well stocked stands with closed canopy. Selection

---

1/Research Scientist, Canadian Forestry Service, Petawawa Forest Experiment Station, Chalk River, Ontario, Canada.

was exercised only to the extent that the stems were straight and without obvious defect, the trees were at least 50 feet from any roadway, stream or other break in the stand structure, and spaced at least 100 feet apart. Measurements of tree height, diameter, taper, age and crown characteristics were recorded and cones were collected from each tree sampled. Stand values for age, height and diameter (table 1) of the ten sample trees indicate all stands were site class 1 or better (Plonski 1960).

Table 1.--Mean (x) and standard deviation (s) of stump age (1 ft.), tree height and b.h. diameter (o.b) of 10 parent trees within each of 2 stands at 5 locations in the Ottawa Valley (fig. 1).

Location Name	Location No.	Stand No.	Age Years $\bar{x}$	Age Years s	Height m $\bar{x}$	Height m s	Diam. cm $\bar{x}$	Diam. cm s
Deux Rivieres	1	1	48	1	22.2	1.3	23	2
		2	64	6	24.7	0.4	27	3
Deep River	2	1	49	7	22.7	0.9	24	1
		2	49	3	20.6	1.5	25	3
Chalk River	3	1	46	2	20.1	1.5	21	1
		2	47	4	20.7	0.8	24	2
Petawawa River	4	1	75	7	23.4	0.9	27	3
		2	72	5	23.3	1.0	26	3
Petawawa Plains	5	1	68	3	22.2	1.3	25	2
		2	48	3	20.6	1.0	25	3

In 1968 seed was sown in rows with progenies randomized and replicated within uniformly prepared seed beds. The 2-0 seedlings were planted at two locations, Chalk River and Mackey, in May 1970, and 2-1 transplants were planted at a third location, Adelard, in May, 1971. At each site the test design included 6 replications of randomized split plots with stands as main plots and 10 5-tree progeny subplots within each main plot. The Chalk River and Adelard tests were planted at 5 ft. x 5 ft. spacing on typical jack pine sites with deep sands of medium to fine texture. The Mackey test was planted at 4 ft. x 4 ft. spacing on an old farm field in a small valley with sandy to gravelly soils and a high water table. Replications were arranged to conform to obvious variations in topography (Chalk River), ground cover (Adelard), and moisture regime (Mackey) as appropriate.

Initial survival exceeded 95% and stood at 95%, 96% and 92% for the respective test plantations at the time of height measurement in 1973 when the trees had grown through six growing seasons since sowing.

RESULTS

Analyses of variance and calculations of variance components were made from the data of each test separately and combined over locations. The appropriate models for analysis were:

Single test location;

$$X_{jklm} = \mu + R_j + A_k + S(A)_{kl} + R.AS_{jkl} + F(AS)_{klm} + R.F(AS)_{jklm}$$

Combined over locations;

$$X_{ijklm} = \mu + T_i + R(T)_{ij} + A_k + S(A)_{kl} + T.A_{ik} + T.S(A)_{ikl} + R(T).AS_{ijkl} + F(AS)_{klm} + T.F(AS)_{iklm} + R(T).F(AS)_{ijklm}$$

where,	X - plot mean height		
	μ - general mean		
effect	T - test locations,	i = 1, ...3	
"	R - replications in T,	j = 1, ...6	
"	A - areas,	k = 1, ...5	
"	S - stands in A	l = 1, ...2	
"	F - families in S	m = 1, ...10	

All effects were treated as random variables (Bliss 1967, Steel and Torrie 1960). Partition of the degrees of freedom and the expected mean squares are set out in table 2 for the combined model.

Mean height growth differed among test locations (tables 3 and 4), with the best growth at Adelard. The poorest growth was at Mackey, where the results were also least consistent as reflected by the relatively large components of variance for error (table 5). Differences among areas or stands within areas were small (table 3) and were not consistent within tests or when pooled over locations (table 4) .

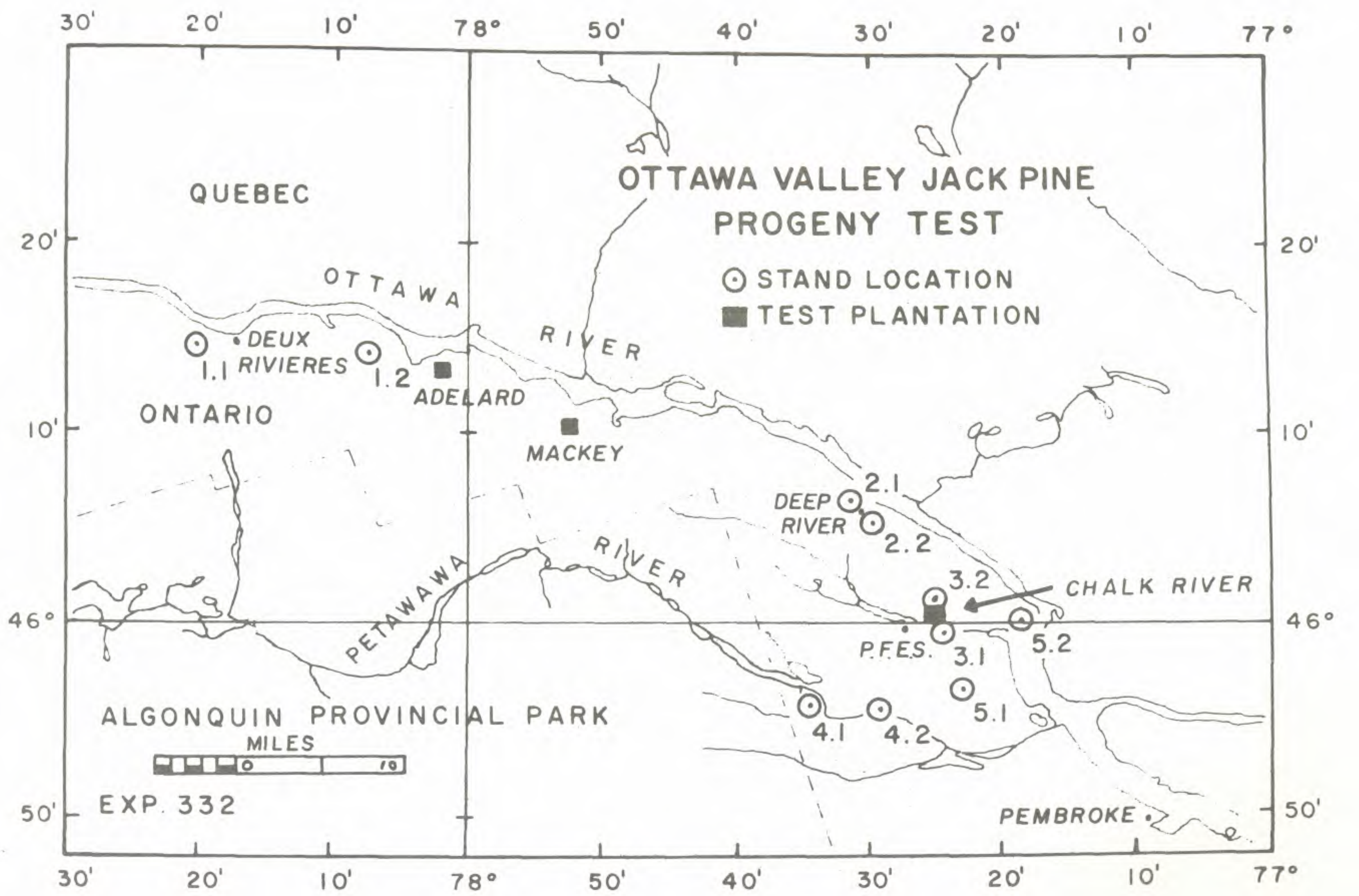

Figure 1. Location of jack pine stands, areas and test plantations in the Upper Ottawa Valley.

Table 2.-- Expected mean squares used in the analysis of tree height of 100 jack pine progenies pooled over three test locations (after Bliss 1967 and Stonecypher et al. 1973).

Source of variation	Degrees of freedom[a]	Coefficients in expected mean squares[b]									
		COMPONENTS									
		$\sigma_w^2/k+\sigma_{r(t)f(as)}^2$	$\sigma_{tf(as)}^2$	$\sigma_{f(as)}^2$	$\sigma_{r(t)as}^2$	$\sigma_{ts(a)}^2$	σ_{ta}^2	$\sigma_{s(a)}^2$	σ_a^2	$\sigma_{r(t)}^2$	σ_t^2
Test locations	t-1	1	r		f	rf	rsf			asf	rasf
Replications in T	t(r-1)	1			f					asf	
Areas	a-1	1	r	tr	f	rf	rsf	trf	trfs		
Stands in A	a(s-1)	1	r	tr	f	rf		trf			
T X A	(t-1)(a-1)	1	r		f	rf	rsf				
T X S/A	(t-1)a(s-1)	1	r		f	rf					
Error 1	t(r-1)(as-1)	1			f						
Families in S in A	as(f-1)	1	r								
T X F/S/A	(t-1)as(f-1)	1	r								
Error 2	t(r-1)as(f-1)	1									
Total	trasf-1	______									
Within plot	$\sum_{i=1}^{trasf} (n_i-1)$	σ_w^2									

a/ t = no. test locations
r = no. replications per test
a = no. areas sampled
s = no. stands in each area
f = no. families (trees) in each stand

b/ k = harmonic mean of plants per plot
σ_i^2 = components identified by subscripts: an expected mean square is found as the sum of products of the coefficients and appropriate components.

Table 3.--Mean tree height at 6 years of age for sample areas and stands within areas by test locations and combined over all.

Sample	Test Location: Chalk River cm	Adelard cm	Mackey cm	Combined locations cm
Area 1.	106	118	101	108
2.	107	118	103	109
3.	107	114	99	107
4.	109	116	103	109
5.	106	118	107	110
Stand 1.1	109	118	104	110
1.2	104	117	98	106
2.1	109	118	101	109
2.2	105	118	105	110
3.1	110	116	100	109
3.2	105	113	98	105
4.1	106	117	104	109
4.2	111	115	102	109
5.1	104	120	105	110
5.2	109	116	108	111
All progenies	107	117	103	109

Families (single-tree progenies) within stands within areas differed in mean height at the 5% level of significance at each location. Differences were significant at the 1% level when families were pooled over locations (table 4). The relative values of the variance components and their standard errors substantiate these family effects (tables 5 and 6). Estimates of heritability from each test location and from combined locations are listed in table 7 and predicted and calculated gains are given in table 8 for two levels of mass selection.

DISCUSSION

The lack of genetic discrimination among areas or stands indicates that stand selection would be ineffective at the local level within the area sampled. Canavera (1969) found a similar situation to exist in jack pine sampled in Lower Michigan. Stands that share a common history of migration, gene exchange and climate have not become differentiated in the post-glacial period. In the Ottawa

Table 4.-Variance ratios (F)a/ from analyses of variance of tree height (5-tree Diot means) at three test locations and combined over locations

Source	df	Test Locations: Chalk River F	Adelard F	Mackey F
Replications	5	7.05**	13.77**	3.88**
Areas	4	0.19ns	1.60ns	1.86ns
Stand/Areas	5	1.22ns	0.65ns	0.79ns
Error 1	45			
Families /stands/areas	90	1.53*	2.11**	1.48*
Error 2	450			
Total	599			

Combined

Source	df	F
Test locations	2	9.97**
Replications/locations	15	6.94**
Areas	4	1.05ns
Stands/areas	5	0.76ns
Locations x areas	8	0.94ns
Locations x stands/areas	10	1.01ns
Error 1	135	
Families/stands/areas	90	4.20**
Locations x families/stands/areas	180	0.82ns
Error 2	1350	

Levels of significance: **, 1%; *5%; ns, not significant

a/ Variance ratios and associated degrees of freedom calculated after Bliss 1967, p. 371-372.

Valley the sampled stands all belong to the Petawawa provenance which ranks consistently among the best in local provenance plantations (Yeatman 1974a and unpublished data). Thus any large stand of good site quality within the provenance area is suitable for bulk collection of seed and identification as Petawawa provenance. To retain the adaptive advantage of the local population it is recommended that a particular stand or stands be designated and managed for seed collection, preservation of the gene pool and genetic improvement in seedling seed orchards (Yeatman 1972, 1974b).

Table 5.--Variance components of tree height within test locations

Source		Test Location		
		Chalk River σ^2(s.e.)[a/]	Adelard σ^2(s.e.)	Mackey σ^2(s.e.)
Replications	σ^2_r	26.7(19.7)	30.5(20.8)	15.9(13.5)
Areas	σ^2_a	-4.4	1.0(2.1)	3.3(5.6)
Stands/areas	$\sigma^2_{s(a)}$	2.4(4.9)	-2.6	-2.7
Error 1	σ^2_{ras}	30.8(9.3)	14.3(5.1)	39.8(11.6)
Families /stands/areas	$\sigma^2_{f(as)}$	11.7(5.3)	17.8(5.2)	12.2(5.8)
Error 2	$\sigma^2_{rf(as)}$	43.7(9.3)	23.8(6.7)	53.8(10.5)
Within plot	σ^2_w	417.7(12.4)	346.8(10.3)	430.7(13.2)
Harmonic mean of no. trees per plot	k[b/]	4.7	4.8	4.4

a/ Standard error calculated after Comstock and Moll 1963.

b/ k = harmonic mean where $\frac{1}{k} = \frac{1}{n} \Sigma\left(\frac{1}{X_i}\right)$,

n = number of plots, i = 1 to n, X_i = number of trees in the ith plot.

Table 6.--Variance components of tree height over all test locations, based on plot means.

Source		Component (s.e.)	Percent of total
Test locations	σ^2_{t}	48.1(52.7)	19.5
Replications/T	$\sigma^2_{r(t)}$	24.1(10.4)	9.5
Areas	σ^2_{a}	.1(30.1)	.1
Stands/A	$\sigma^2_{s(a)}$	-.1	0
T x A	σ^2_{ta}	-.2	0
T x S/A	$\sigma^2_{ts(a)}$	.1(3.0)	.0
Error 1	$\sigma^2_{r(t)as}$	28.3(5.0)	11.5
Families/S/A	$\sigma^2_{f(as)}$	18.1(3.6)	7.4
T x F/S/A	$\sigma^2_{tf(as)}$	-4.2	0
Error 2	$\sigma^2_{r(t)f(as)}$	40.9(4.9)	16.6
Within plot	σ^2_{w}/k	86.0(3.1)	35.0
			100.0
Harmonic mean of no. trees per plot	k	4.6	

Genetic improvement will be achieved by selection and breeding within the population, as indicated by the significance of family effects in the analyses of variance shown in table 4. A heritability (h 2/f) of 0.49 was derived from the regression of progeny mean height (relative to the mean of all 100 progenies over all tests) on parental mean height (relative to the mean of the 10 trees sampled in each stand) ($b = \frac{1}{2}h^2$, Falconer 1960, p. 169). By using a selection intensity of 1/10 among dominants and codominants of mature Ottawa Valley jack pine, a gain of 4% is redicted in mean tree height at 6 years of age ($\Delta G = i \sigma ph^2$ i=1.75, σp=4.7%, h2 = 0.49, Falconer 1960, p.193). An average gain of 3.4% (range -2.0% to 7.5%) was realised in these tests by progenies of the
of 3.4% (range -2.0% to 7.5%) was realised in these tests by progenies of the

Table 7.--Heritability estimates of individual tree height at 6 years of age, from three test locations and over all locations

	Test Location			Combined
	Chalk River	Adelard	Mackey	locations
Heritability, h_i^2	0.099 [a]	0.184	0.098	0.145 [b]

a/ Location $h_i^2 = \dfrac{4\sigma^2_{f(as)}}{\sigma^2_w + \sigma^2_{rf(as)} + \sigma^2_{f(as)}}$

b/ Combined $h_i^2 = \dfrac{4\sigma^2_{f(as)}}{\sigma^2_w + \sigma^2_{r(t)f(as)} + \sigma^2_{tf(as)} + \sigma^2_{f(as)} + \sigma^2_{r(t)as} + \sigma^2_{ts(a)} + \sigma^2_{ta} + \sigma^2_{s(a)} + \sigma^2_a}$

tallest tree of the 10 sampled at random in each of 10 stands. This value is in close agreement with the improvement predicted.

Heritability estimates on the basis of individual tree height (h_i) are listed in table 7 for each test and from data combined over locations. These values are of the same order as have been found for other pines at young ages, eg. 0.18 and 0.26 for loblolly pine at 6 and 7 years (Stonecypher *et al*. 1973) and 0.17 for jack pine at 3 years (Canavera 1969). The gains predicted for mass selection based on progeny test results are listed in table 8 at two levels of selection and based on single test sites and combined locations. The phenotypic superiority of the best progeny (1/100) or progenies (1/10) is shown for comparison. The predictions are conservative relative to the observed gains but indicate that substantial improvement in tree height can be achieved in a single stage of selection.

The highest estimates of gain were at Adelard, which reflects larger family and smaller error and within-plot contributions to total variance (table 5). Best overall height and survival were recorded for the Adelard test. It was established with 2-1 transplants which at the time were considered superior planting stock to the 2-0 seedlings planted at Petawawa and Mackey in the previous year.

Table 8.--Predicted gains from mass selection and values realized by the best progenies relative to means of all progenies at selection levels of 1/100 and 1/10.

Proportion Selected	Gain[a]	Test Locations: Chalk River	Adelard	Mackey	Combined locations
1/100 $i = 2.66$	Predicted (genetic) (cm)	5.3	9.4	5.8	8.1
	(%)	4.9	8.0	5.6	7.4
	Phenotypic (cm)	13.3	17.8	14.8	9.6
	(%)	12.4	15.2	14.4	8.8
1/10 $i = 1.75$	Predicted (genetic) (cm)	3.5	6.2	3.8	5.3
	(%)	3.2	5.3	3.7	4.9
	Phenotypic (cm)	10.8	10.4	11.5	8.4
	(%)	10.0	8.0	11.3	7.8

[a] $\Delta G = i \, \sigma_p \, h_i^2$

i = selection intensity for proportion selection (Shelbourne 1969).

σ_p = standard deviation of trait (Stonecypher *et al* 1973).

h_i^2 = heritability.

Commonly the best genetic discrimination among progenies or provenances is found on the best sites (Ledig 1973). In view of the marked absence of family x test (genotype x environment) interaction (table 6), it would appear that subsequent genetic selection in this area could safely and economically be based on progeny tests established at a single location of good site quality. Every care should be exercised in design and establishment to minimise uncontrolled environmental and cultural effects within replicates and family plots.

Prediction of gain from applied breeding is estimated best from data combined over the three test locations. Seedling seed orchards are well suited to improvement of jack pine (Yeatman 1974b) by combining family and individual tree selection to maximise gains. Estimated gain for selection of one family in ten tested is 5.1% and gain for selection of the best individual in 5-tree plots is estimated as 2.9% 1/. When phenotypic selection in the forest is followed by genotypic selection based on progeny tests and phenotypic selection of second generation parents in the seed orchard, the total gain in height at 6 years of age over that of the original population is estimated by the sum of their effects, viz:

Phenotypic (parental generation 1)	4.0%
Genotypic (progeny)	5.1%
Phenotypic (parental generation 2)	2.9%
	12.0%

This is a realistic estimate of genetic gain and could be achieved within ten years of initiating an improvement program in jack pine.

CONCLUSION

1. Jack pine in the Upper Ottawa Valley is not differentiated in terms of early growth by ecotypic variation nor by isolation of separate stands that apparently share a common gene pool.

2. Plus tree selection may be spread throughout the area of the provenance. Emphasis should be placed on the results of progeny tests to establish a new breeding population for seed production and continuing selection and improvement.

3. An early gain of at least 12% in height growth can be achieved by multi-stage selection and seed production in seedling seed orchards. The stages include phenotypic selection in natural stands, family selection from the results of progeny tests, and phenotypic selection within the selected families growing in a seedling seed orchard.

4. Progeny tests need to be planted on good jack pine sites with uniformly high standards of design and establishment. Negligible family by location interaction in this study indicates that a single test will provide early and reliable estimates of genetic worth of trees and families. Tests at two or more typical sites are needed to derive realistic estimates of heritability and genetic gain.

1/ $\Delta G = i_2 1/4 \frac{\sigma^2_{A'}}{\sigma_2} x \frac{100}{\bar{X}} + i_3 3/4 \frac{\sigma^2_{A''}}{\sigma_3} x \frac{100}{\bar{X}}$, where $i_2 = 1.75$, $\sigma^2_{A'} = 62.3$, $\sigma_2 = 4.87$,

$i_3 = 1.40$, $\sigma^2_{A''} = \sigma^2_A = 72,4$, $\sigma_3 = 23.8$, $\bar{X} = 108.8$ (after Namkoong et al. 1966, Shelbourne 1969).

ACKNOWLEDGEMENT

Field experiments with forest trees always require team effort, with attention to detail at all stages. In this work special credit is due J.B. Santon for the nursery stage, P. Viidik for plantation establishment, T. Nieman for tree measurement and data processing and W.A. Kean for programming the analyses and working them through the PDP-8 computer. The critical reviews received from colleagues at Petawawa and at Rhinelander are greatly appreciated.

LITERATURE CITED

Bliss, C.I. 1967. Statistics in biology. Volume 1. McGraw-Hill, New York. 558 p.

Canavera, D.S. 1969. Geographic and stand variation in jack pine (*Pinus banksiana* Lamb.). Ph.D. Thesis, Michigan State University. 100 p.

Comstock, R.E., and Moll, R.H. 1963. Genotype-environment interactions. *In* W.D. Hanson and H.F. Robinson (eds.) Statistical genetics and plant breeding, p. 164-194. National Acad. Sci. - National Res. Council, Washington, D.C. Pub. 982.

Falconer, D.S. 1960. Introduction to quantitative genetics. The Ronald Press, New York. 365 p.

King, J.P. 1966. Ten year height growth variation in Lakes States jack pine. U.S. Forest Serv. Res. Pap. NC-6:84-88.

Ledig, T.F. 1973. The application of mass selection in tree improvement. Proceed. 20th. Northeastern Forest Tree Improv. Conf., Univ. New Hampshire, Durham, N.H., 1972. p. 69-83.

Namkoong, G., Snyder, E.B., and Stonecypher, R.W. 1966. Heritability and gain concepts for evaluating breeding systems such as seedling orchards. Silvae Genet. 15:76-84.

Plonski, W.L. 1960. Normal yield tables for black spruce, jack pine, aspen, white birch, tolerant hardwoods, white pine and red pine for Ontario. Ont. Dept. of Lands and Forests, Silv. Series Bull. No. 2. 39.

Rudolph, T.D. 1964. Lammas growth and prolepsis in jack pine in the Lake States. Forest Sci. Monogr. 6. 70 p.

Schantz-Hansen, T., and Jensen, R.A. 1952. The effect of source of seed on growth of jack pine. J. Forestry 50:539-544.

Shelbourne, C.J.A. 1969. Tree breeding methods. New Zealand Forest Serv. Forest Res. Inst. Tech. Pap. No. 55. 43 p.

Steel, R.G.D., and Torrie, J.H. 1960. Principles and Procedures of statistics. McGraw-Hill, New York. 481 p.

Stonecypher, R.W., Zobel, B.J., and Blair, R. 1973. Inheritance patterns of loblolly pines from a nonselected natural population. North Carolina Agric. Exp. Sta. Tech. Bul. No. 220. 60 p.

Yeatman, C.W. 1972. Gene pool conservation for applied breeding and seed production. In: Proceedings IUFRO Genetics - SABRAO Joint Symposia, p. B-8(V), 1 to 6. The Government Forest Exp. Sta. of Japan, Tokyo.

Yeatman, C.W. 1974a. The jack pine genetics program at Petawawa Forest Experiment Station 1950-1970. Dept. Environment, Can. Forest. Serv. Pub. No. 1331. 30 p.

Yeatman, C.W. 1974b. Seedling seed orchards for jack pine. In: Proc. 21st Northeastern Forest Tree Improv. Conf., Fredericton, N.B., 1973. p. 69-71.

Yeatman, C.W., and Teich, A.H. 1969. Genetics and breeding of jack and lodgepole pines in Canada. Forest. Chron. 15:428-433.