The Jack Pine Genetics Program at Petawawa Forest Experiment Station 1950-1970

by C. W. Yeatman

THE JACK PINE GENETICS PROGRAM AT PETAWAWA FOREST EXPERIMENT STATION 1950-1970

by

C.W. Yeatman
Research Scientist, Department of the Environment, Canadian Forestry Service, Petawawa Forest Experiment Station, Chalk River, Ontario

Résumé en français

DEPARTMENT OF THE ENVIRONMENT
Canadian Forestry Service
Publication No. 1331
Ottawa, 1974

Issued under the authority of the
Honourable Jack Davis, P.C., M.P.,
Minister, Environment Canada

INFORMATION CANADA
Catalogue No. Fo47-1331
OTTAWA, 1974

PRINTED IN CANADA

ABSTRACT

Planting and direct seeding of jack pine (*Pinus banksiana* Lamb.) in Canada is expected to reach 65,000 acres a year by 1985 and will require an estimated 3 tons of seed annually. This report describes results of 20 years of genetic research in jack pine in relation to seed-quality control and improvement.

Laboratory, nursery, and field studies of geographic variation have demonstrated broad clinal patterns of variation in physiological characteristics, and of growth cessation and maturation in particular, that determine survival and rate of growth. The primary choice of seed source must be based on matching latitude and climate.

Results further indicate that early gains of 5% to 10% can be expected if the better populations within geoclimatic regions are identified and used for seed production.

Progeny tests and trials of inter- and intraspecific hybrids have been established in support of theoretical and practical breeding objectives. In particular, lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) and its hybrids with jack pine are highly susceptible to sweet fern blister rust (*Cronartium comptoniae* Arth.) when grown in eastern Canada.

Plans for future research include continuing evaluation of existing field studies and new investigations in plus-tree selection, progeny- and stand-testing, and provenance hybridization. Regional breeding programs, including the maintenance *in situ* of selected gene pools, need to be establised now in conjunction with operational seed collection and reforestation.

RÉSUMÉ

On estime planter et ensemencer des Pins gris (*Pinus banksiana* Lamb.) sur 65,000 acres de terrain par année vers 1985, ce qui nécessitera environ trois tonnes de graines tous les ans. L'auteur décrit ici les résultats de vingt ans de recherches en génétique du Pin gris en rapport avec le contrôle et l'amélioration de la qualité des graines.

À la suite d'études en laboratoire, en pépinière et sur le terrain sur les variations géographiques de l'espèce, il appert que les caractères physiologiques varient largement de façon clinale, en particulier l'arrêt de croissance et la maturation, ce qui détermine les taux de survie et de croissance. On doit surtout choisir la source de graines d'après une latitude et un climat correspondant au lieu d'ensemencement.

De plus, des gains hâtifs de 5 à 10% peuvent être attendus si les meilleures populations dans chaque région géoclimatique étaient identifiées et utilisées pour la production de graines.

Les tests et les essais de progéniture des hybrides inter- et intraspécifiques furent mis au point d'après des objectifs de production théoriques et pratiques. En particulier, le Pin de Murray (*Pinus contorta* Dougl. var. *latifolia* Engelm.) et ses hybrides avec le Pin gris sont fortement vulnérables à la Rouille-tumeur *Cronartium comptoniae* Arth. lorsqu'ils poussent dans l'Est du Canada.

L'auteur se propose de poursuivre ses recherches par l'évaluation des études existantes sur le terrain et de nouveaux projets d'études sur le choix des arbres plus, les tests de progéniture et de peuplements, et l'hybridation des provenances. Les programmes régionaux de production, incluant le maintien *in situ* de banques de gènes choisis, doivent être maintenant mis en branle de concert avec la récolte opérationnelle de graines et le reboisement.

CONTENTS

LIST OF TABLES

LIST OF FIGURES

COVER PHOTO

Jack pine plus tree number 2610, Petawawa Plains, selected for superior height, diameter, stem straightness, branch form and budworm resistance.

Age (breast height) 47 years; height 62 feet; diameter (b.h.o.b.) 8.1 inches; crown diameter, 6 feet; branch angle, 60°.

THE JACK PINE GENETICS PROGRAM AT PETAWAWA FOREST EXPERIMENT STATION 1950-1970

INTRODUCTION

This report outlines genetic investigations of jack pine (*Pinus banksiana* Lamb.) initiated at Petawawa Forest Experiment Station during the 20-year period from 1950 to 1970. Published results derived directly from this program are reviewed briefly and new data are presented from early field experiments. The implications of this information for improving seed quality for planting and direct seeding are discussed, together with the need and direction for further genetic research and improvement in jack pine.

Jack pine has been third only to Douglas fir and eastern spruce (white, black, red) in acres artificially regenerated since 1900, and the annual rate is expected to reach 65,000 acres by 1985 (Cayford and Bickerstaff 1968). The wood is used extensively for pulp, poles, and lumber over much of the species' range, which extends from the Atlantic coast to the Mackenzie River valley (Fig. 2) (Critchfield and Little 1966). Large quantities of jack pine seed are required, particularly in Ontario, where more than 80% of planting and direct seeding of this species is conducted (Cayford and Bickerstaff 1968). It is expected that reforestation of jack pine will increase further as direct seedling increases in relation to planting (Hall 1970 Scott 1970). Assuming an annual planting rate of 25,000 acres (700 trees/acre) and 40,000 acres broadcast seeded ($2\frac{1}{2}$ oz or 20,000 seed/acre) (Scott 1970), it will be necessary to provide an estimated 6,750 lb of seed each year, which is equivalent to collecting cones from between 120 and 400 acres of jack pine forest (Roe 1963). The aim of genetic research is to ensure that only seed of the highest productive potential is used for regeneration (Carlisle 1970). It is necessary to determine and maintain the best sources among existing populations and, through further selection and breeding, to develop new strains of superior genetic quality for use in a diversity of environments (Yeatman and Teich 1969).

The purpose of the genetics research program in jack pine at Petawawa Forest Experiment Station is to determine the nature, extent, and applicability to reforestation of genetic variation and genotype-environment interaction. In the development of the program, seed and seedlings have been widely distributed in Canada and abroad to investigate the influence of seed origin on survival and growth in jack pine plantations under various climatic regimes. Additional tests of seed and seedlings have been made in nurseries and laboratories for early evaluation of provenance variation. More recently, progeny tests have been established for determination of heritability of growth, form, and resistance to diseases and insects of individual trees, and for assessment of variation within and among stands as the basis for selection and improvement. The value of early tests is being investigated for screening large numbers of seedlings for superior growth potential. Supporting research on techniques used in tree improvement has included investigations of growth acceleration, flower induction, and vegetative propagation.

SILVICS

Jack pine is a shade-intolerant two-needled tree found on a wide range of soils that are typically well drained and of low fertility. It commonly regenerates after fire when seed is released from serotinous cones and the burned forest floor provides a suitable seed bed (Rudolf 1958). Trees bearing open cones occur in varying proportions throughout the range of jack pine, and their numbers are particularly high in the southern parts of the range in the Lake States and Maritime Provinces (Schoenike 1962, Rudolph *et al.* 1957). Sporadic regeneration can occur from relatively small amounts of seed released from open cones. Failure of regeneration after harvesting has been attributed to unsuitable seed beds and inadequate release and distribution of seed from the closed cones in the felled tree tops. Planting or seeding following site preparation are frequently essential to ensure adequate stocking (Cayford *et al.* 1967). Jack pine is favored for reforestation because it has high early survival and rapid growth and does well in pure stands on sites of low fertility that require a minimum of preparation and tending, and because large areas of such terrain are accessible.

SEED ORIGIN

Geographic origin is the first factor to consider in selecting sources of seed for regeneration and breeding. Provenance experiments are necessary to determine the genetic influence of seed origin on survival and productivity and to form a basis for defining the spatial and ecological limits of seed collection and the distribution of seed and seedlings. Properly designed tests will reveal superior populations (stands) for immediate use for seed production and as foundation stocks for further improvement through selection and breeding.

The earliest tests of jack pine provenances at Petawawa were established from 1942 to 1945 when seven provenances of jack pine and nine provenances of lodgepole pine were planted in unreplicated plots on jack pine sites. Coastal lodgepole pine (*Pinus contorta* Dougl. var. *contorta*) was killed by frost, and provenances from the interior (*P. contorta* Dougl. var. *latifolia* Engelm.) were cold-hardy but succumbed to sweet fern blister rust (*Cronartium comptoniae* Arth.). Jack pine was hardy and grew appreciably more than the few surviving lodgepole pines (Cayford *et al.* 1967, p. 203).

Jack pine was among the first species to be investigated when the present genetics program was initiated in 1950. A provenance experiment (No. 40) was sown in 1951 with seed from 12 Ontario jack pine sources supplied by the Ontario Department of Lands and Forests. Seed sown 2 years later from five Ontario and four Quebec seed sources (Exp. No. 82) extended the sampling range of the earlier experiment west and east (Fig. 1). In 1955, plants of 16 Lake States provenances (Exp. No. 125) were provided by the Institute of Forest Genetics, Rhinelander, Wisconsin, in a cooperative experiment including plantations at 17 locations in the Lake States. The first sowing of a range-wide collection of 99 jack pine provenances (Exp. No. 255, Fig. 2) was made at Petawawa in 1962. Investigations of this collection have included laboratory studies of seed and seedlings, nursery evaluations of seedlings, and tests of performance in plantations at Petawawa and at other locations in Canada and abroad.

Ontario - Exp. No. 40

The first replicated tests of Ontario provenances were made with seed of known origin from the Angus Tree Seed Plant, Ontario. The objective was to initiate provenance work with material immediately available. Few details of seed origin are known other than the forest offices from which the cones were shipped, and two seedlots collected in southern Ontario from southern plantations of unknown seed origin were included for comparison with collections from natural stands.

At 2 years of age significant height differences were recorded among the provenances growing in the nursery at Petawawa. In 1954, 12 provenances were planted as 1-2 transplants in an open field at 4 x 4 feet spacing in four replications of 100 tree plots (Exp. No. 40, Fig. 1, Table 1). The soil was a podsolic fine sand of moderate fertility for jack pine. Growth in the nursery and field experiments during the first 8 years was positively correlated with length of growing season of the area of seed origin and was less well associated with mean summer temperature (Holst and Yeatman 1961).

Mean heights of the 12 Ontario provenances differed significantly (P = .01) at each of five assessments from 1955 to 1969 (Table 2). Regressions were calculated to determine whether the height at 19 years (1969) could be predicted by mean heights of the provenances in early years. Seedling height in the nursery at 5 years was ineffective in predicting tree height at 19 years. In the field test, 71% of the variation in height at 19 years was accounted for by height at 11 years (1961). Provenance performance at 11 years provided a sound basis for selection of the better seed sources and elimination of the poorer provenances when the trees were grown at Petawawa. Stevens, from a northern location with a short, cool growing season, was always the shortest. In contrast, the Angus-plantation provenance was significantly taller than all other provenances in 1961, but not in 1969. Changes in rank were accompanied by a reduction in the difference between shortest and tallest provenances relative to the tallest, from a difference

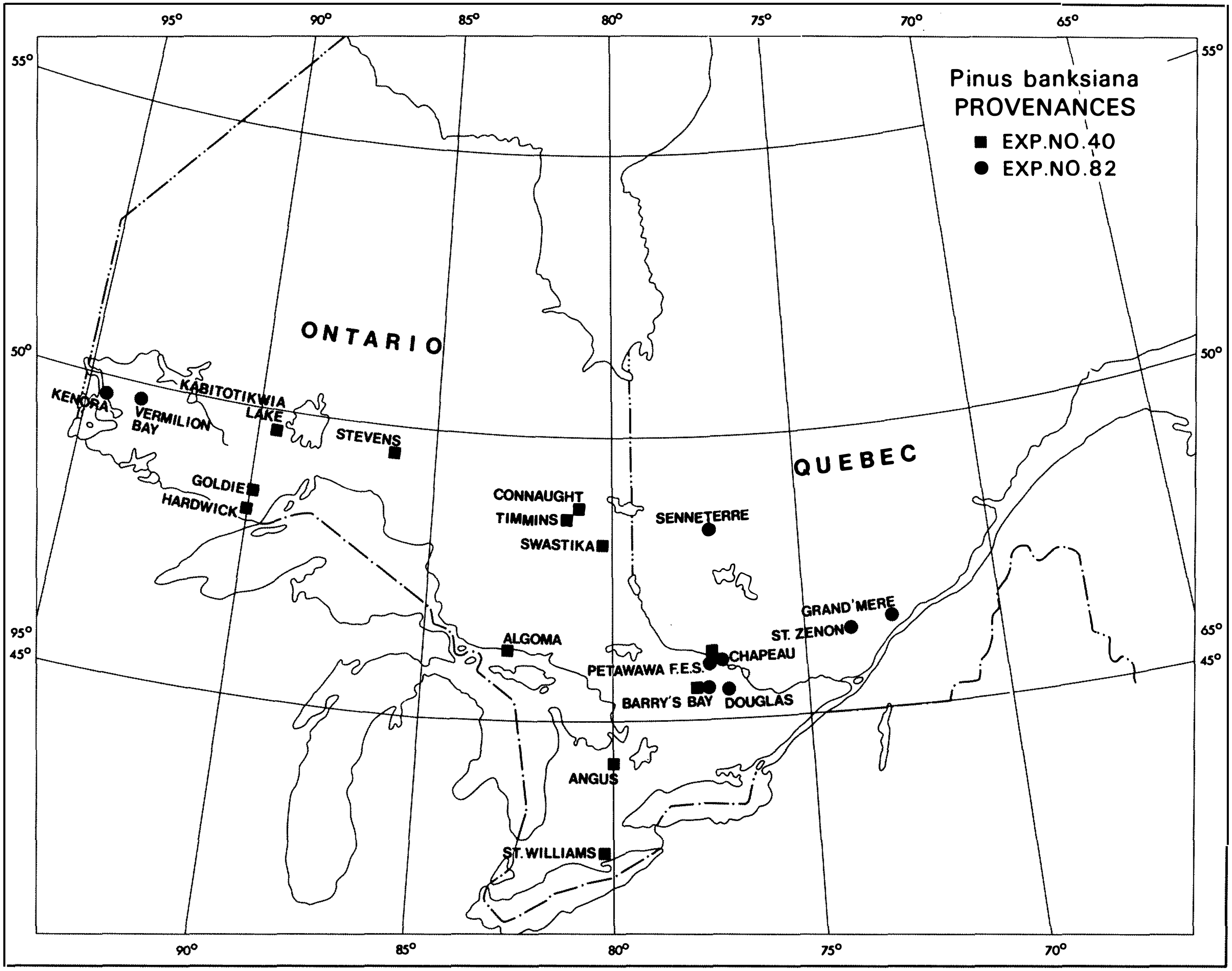

Figure 1. Distribution of jack pine provenances included in experiments 40 and 82 planted at Petawawa Forest Experiment Station in 1954 and 1957 respectively.

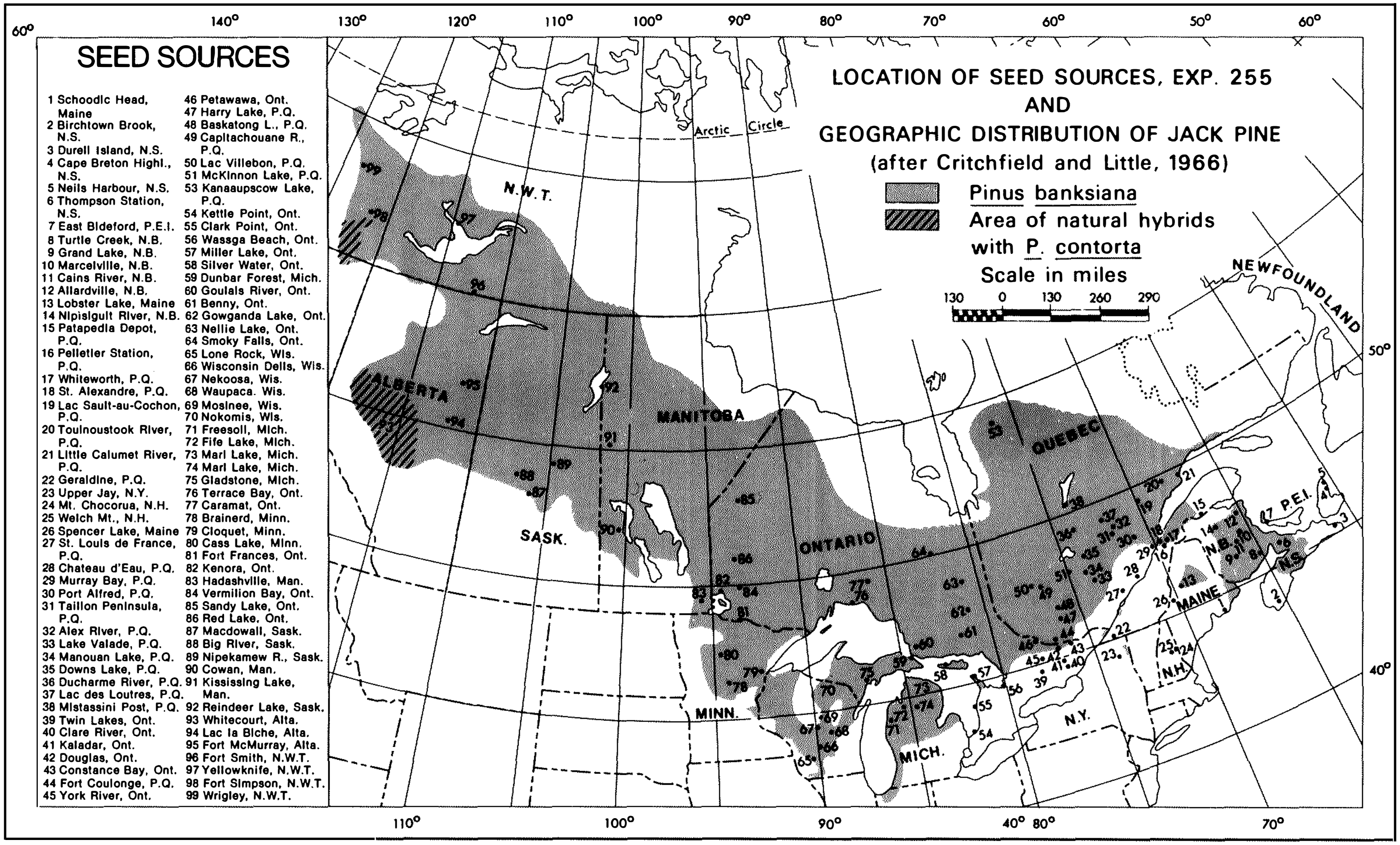

Figure 2. Botanical range of jack pine and names and locations of jack pine provenances of the all-range collection, Experiment 255.

TABLE 1. TWELVE ONTARIO JACK PINE PROVENANCES PLANTED AT PETAWAWA FOREST EXPERIMENT STATION IN 1954 (EXP. NO. 40, FIG. 1)

Seed origin	Location Lat. N Deg	Min	Long. W Deg	Min	Forest section[1]	Growing deg-days[2] number
Barry's Bay	45	25	77	30	L4C	2,700
Algoma	46	38	83	00	L4e	2,800
Angus[3]	44	19	79	53	-	-
Hardwick	48	10	90	05	L11	2,500
Petawawa	46	00	77	28	L4c	3,000
Timmins	48	28	81	20	B4/B7	2,050
Goldie	48	35	89	50	L11/B11	2,300
Connaught	48	38	80	56	B4	2,000
Swastika	48	07	80	06	L8/B7	2,200
Kabitotikwia L.	49	40	89	11	B10	2,100
St. Williams[3]	42	50	80	30	-	-
Stevens	49	33	85	50	B8	1,850

[1]Rowe 1959.
[2]Chapman and Brown 1966.
[3]Seed collected in jack pine plantations of unknown seed origin.

of 30% in 1958, to 24% in 1961, to 11% in 1969. The range tests (Table 2) also indicate that differences among provenances became less well defined with time, particularly among the faster-growing seed sources.

Differences in stem diameter (breast height over bark) among provenances were significant at 19 years of age but were less well defined than for tree height and followed a similar rank order (Table 3). Mean tree volume for the St. Williams-plantation provenance was 30% less than that for Barry's Bay, the top-ranking seed source. Mean tree volume for Barry's Bay exceeded that of the local Petawawa provenance by 10%, but the difference was not statistically significant.

Tree size in 1969 was significantly related to growing degree-days above 42°F (5.6°C) at the seed origin and accounted for 55% and 58% of the mean tree height and volume respectively of the 10 provenances from natural stands. On this basis, seed for Angus-plantation trees probably came from a southern location with a relatively warm climate. Seed for trees in the St. Williams-plantation probably were collected in a boreal location with a decidedly cool climate similar to that at Stevens, northern Ontario. This 19-year test clearly shows the importance of careful selection of seed source for artificial regeneration of jack pine. The performance of trees derived from plantations of unknown origin cannot be predicted, and collection of seed from such plantations must be avoided unless field tests demonstrate conclusively its genetic superiority over seed from selected natural populations.

TABLE 2. MEAN TREE HEIGHTS AND RANGE TESTS BY YEARS OF MEASUREMENT OF 12 ONTARIO JACK PINE PROVENANCES PLANTED IN A NURSERY EXPERIMENT (1951) AND A FIELD EXPERIMENT (1954) AT PETAWAWA FOREST EXPERIMENT STATION (EXP. NO. 40)

Seed origin	Field experiment 1969[1] m	1961[2] m	1960[2] m	1958[2] m	Nursery experiment 1955[2] m
Barry's Bay	9.5 a[3]	3.9 bc	3.3 b	2.09 b	1.21 abc
Algoma	9.4 a	4.0 b	3.3 b	2.11 b	1.01 ef
Angus	9.4 ab	4.3 a	3.6 a	2.37 a	1.29 a
Hardwick	9.3 ab	3.9 bcd	3.2 b	2.04 b	1.11 cde
Petawawa	9.3 ab	3.7 cde	3.1 bc	1.98 bc	1.23 ab
Timmins	9.3 ab	3.9 bcd	3.3 b	2.04 bc	1.05 ef
Goldie	9.2 abc	3.7 cde	3.1 bc	1.93 bcd	1.02 ef
Connaught	9.0 bcd	3.6 de	3.0 cd	1.87 cd	1.07 def
Swastika	8.8 cde	3.5 ef	2.9 de	1.77 de	1.16 bcd
Kabitotikwia L.	8.8 de	3.7 cde	3.1 bc	1.94 bc	1.02 ef
St. Williams	8.5 ef	3.5 ef	3.0 cd	1.88 cd	1.11 cde
Stevens	8.4 f	3.3 f	2.7 e	1.67 e	0.98 f
F-ratio	8.9***	10.4***	10.5***	9.5***	7.8***
100 r^2%[4]		71%***	67%***	63%***	18% n.s.

[1]Based on means of 10 dominant trees per plot.
[2]Based on means of all trees in a plot.
[3]Duncan's range test: means followed by a common letter do not differ at the 5% level.
[4]Coefficient of determination on 1969 height and significance of regression.
***, significant at the 1% level; n.s., not significant.

Snow Damage in a Provenance Plantation - Exp. No. 40

Severe snow damage occurred in the field test during the winters of 1963-64 and 1967-68. Trees were uprooted, bent, or broken under heavy loads of wet snow or ice glaze or both. Young jack pine stands with closed canopy are particularly prone to damage of this nature (Kienholz 1941, Roe and Stoeckler 1950, Cayford and Haig 1961). Out of 4,247 living trees in the test, 38 (0.9%) were damaged before 1963 and 80 (1.9%) during the winter of 1963-64; 522 additional trees (12.3%) were injured in the winter of 1967-68. Snow damage over all years is summarized by provenance in Table 4 and may be compared with the data for tree height (Table 3). Clearly an association exists between growth rate and snow damage. The three tallest provenances suffered considerably more snow damage than the plantation average and there was a strong tendency for damage to fewer trees among the shorter provenances.

TABLE 3. HEIGHT, DIAMETER (b.h.o.b.) AND VOLUME MEANS OF 19-YEAR-OLD (1969) JACK PINE OF 12 ONTARIO PROVENANCES GROWN AT PETAWAWA FOREST EXPERIMENT STATION (EXP. NO. 40)

Tree means are based on measurements of 10 dominant trees per 100-tree plot.

Seed origin	Height m	Diameter cm	Volume[1] cu m/100
Barry's Bay	9.5 a[2]	9.1 a	30.2 a
Algoma	9.4 a	8.9 abc	28.4 ab
Angus	9.4 ab	8.9 ab	28.6 a
Hardwick	9.3 ab	8.7 abcd	27.0 abc
Petawawa	9.3 ab	8.8 abcd	27.4 abc
Timmins	9.3 ab	8.5 abcde	25.9 abcd
Goldie	9.2 abc	8.6 abcde	26.3 abcd
Connaught	9.0 bcd	8.3 bcde	24.1 bcde
Swastika	8.8 cde	8.1 de	22.4 de
Kabitotikwia L.	8.8 de	8.2 cde	23.7 cde
St. Williams	8.5 ef	8.1 e	21.4 e
Stevens	8.4 f	8.1 de	21.6 e
F-ratio	8.9***	3.2***	4.6***

[1]Calculated after Honer (1967).
[2]Duncan's range test: means followed by a common letter do not differ at the 5% level.
***, significant at the 1% level.

The close initial spacing of 4 feet undoubtedly contributed to the susceptibility of the plantation to damage from snow accumulation on the tree canopy.

A number of root systems were excavated of both damaged and stable trees in the experiment and of two naturally regenerated trees growing in the open in a similar soil. An uneven lateral distribution of supporting roots was common to the tilted trees. This was a result of severe root-pruning of the larger transplants at the time of planting, which led to the development of unbalanced root systems. There was no evidence of inherent differences among provenances in genesis or form of their root systems. In addition to tilted trees, the Angus and Algoma provenances had significantly more trees with trunks bent, in many cases owing to the weight of the crowns of tilted trees leaning against them. Algoma was the only provenance with a significantly high number of broken stems; it also grew slowly in the nursery (Table 2) and hence required only moderate root-pruning before being planted. These observations indicate that susceptibility of vigorous jack pine to snow damage can be reduced by avoiding severe root-pruning and close spacing in plantations.

TABLE 4. PERCENTAGE OF TREES DAMAGED BY HEAVY SNOW, 1961-68, FOR 12 ONTARIO PROVENANCES GROWING AT PETAWAWA FOREST EXPERIMENT STATION (EXP. NO. 40)

Seed origin	Snow damage %
Barry's Bay	24.8 a[1]
Algoma	30.9 a
Angus	47.9 a
Hardwick	12.5 b
Petawawa	12.8 b
Timmins	13.9 b
Goldie	4.3 c
Connaught	3.2 c
Swastika	5.8 c
Kabitotikwia L.	4.3 c
St. Williams	5.3 c
Stevens	10.0 b
Mean	15.1

[1]Letters indicate significance (P = .01) relative to the general mean on the basis of the χ^2 test of frequencies: a, high; b, no difference; c, low.

Ontario and Quebec - Exp. No. 82

The locations of nine Ontario and Quebec provenances planted at Petawawa Forest Experiment Station in 1957 are listed in Table 5 and illustrated in Fig. 1. Four-year-old transplants (2-2) were planted at 4 x 4 feet in 100-tree plots with three replications. The Barry's Bay and Petawawa seed lots are common to the earlier test of Ontario provenances.

Early survival was relatively poor owing to the excessive size of the transplants. In 1961 the average stocking was 68% with a range from 35% to 87% within plots. Only the Grand'Mere and St. Zenon provenances exceeded 80% survival over all replications (Table 6). By 1969, 8% of the 1,839 surviving plot trees had been damaged by snow, mostly during the winter of 1967-68, heavier losses occurring typically within the faster-growing provenances (Tables 6 and 7).

Tree height and diameter were measured at 17 years of age (Table 6), before the experiment was thinned to remove snow-damaged and suppressed trees. Differences in height, diameter, and tree volume were detected, but only mean tree height was related to climate (growing degree-days) of seed origin. After adjustment of mean tree volume for the effect of plot-stocking by covariance, 53% of variation among provenances was accounted for by

TABLE 5. FIVE ONTARIO AND FOUR QUEBEC JACK PINE PROVENANCES PLANTED AT PETAWAWA FOREST EXPERIMENT STATION IN 1957 (EXP. NO. 82)

Seed origin	Location Lat. N Deg	Min	Long. W Deg	Min	Forest section[1]	Growing deg-days[2] number
Barry's Bay, Ont.	46	30	77	40	L4c	2,700
Kenora, Ont.	49	47	94	30	L11	2,750
Douglas, Ont.	46	30	76	56	L2	3,100
Petawawa, Ont.	45	58	77	23	L4c	3,000
Chapeau, Que.	45	55	77	04	L2	3,100
Vermilion Bay, Ont.	49	51	93	22	L11/B14	2,650
Grand'Mere, Que.	46	36	72	36	L4a	2,750
St. Zenon, Que.	46	34	73	47	L4a/B7	2,500
Senneterre, Que.	48	25	77	15	B4	2,100

[1]Rowe 1959.
[2]Chapman and Brown 1966.

TABLE 6. MEAN TREE HEIGHT, DIAMETER (b.h.o.b.), VOLUME AND SURVIVAL BEFORE THINNING OF NINE ONTARIO AND QUEBEC JACK PINE PROVENANCES AT 17 YEARS OF AGE, PETAWAWA FOREST EXPERIMENT STATION (EXP. NO. 82)

Seed origin	Height m	Diameter cm	Volume cu m/100	Stocking %	Adjusted[1] volume cu m/100
Barry's Bay, Ont.	7.86 a[2]	7.90 a	19.0 a	67.7	19.0 a
Kenora, Ont.	7.80 ab	7.90 a	18.9 a	55.0	17.8 ab
Douglas, Ont.	7.75 ab	8.07 a	19.5 a	65.0	19.3 a
Petawawa, Ont.	7.74 ab	7.97 a	19.1 a	56.7	18.2 a
Chapeau, Que.	7.72 ab	7.83 a	18.4 a	64.0	18.0 ab
Vermilion Bay, Ont.	7.50 bc	7.30 b	15.6 b	75.0	16.1 c
Grand'Mere, Que.	7.47 bc	6.93 b	14.0 b	83.0	15.2 c
St. Zenon, Que.	7.46 bc	7.27 b	15.3 b	81.7	16.5 bc
Senneterre, Que.	7.28 c	7.30 b	15.2 b	65.0	14.9 c
F-ratio	3.6**	5.9***	7.7***	2.0 n.s.	8.0***
100 r^2%[3]	55%*	37% n.s.	42% n.s.	8% n.s.	53%*

[1]Volume adjusted for plot stocking (survival), 1969, by covariance.
[2]Duncan's range test: means followed by a common letter do not differ at the 5% level of significance.
[3]Coefficient of determination on the number of growing degree-days and significance of regression.
***, significant at the 1% level; **, 2.5%; *, 5%; n.s. not significant.

TABLE 7. PERCENTAGE OF TREES DAMAGED BY SNOW FOR NINE ONTARIO AND QUEBEC PROVENANCES GROWN FOR 17 YEARS AT PETAWAWA FOREST EXPERIMENT STATION (EXP. NO. 82)

Seed origin	%
Barry's Bay, Ont.	11.8
Kenora, Ont.	13.3
Douglas, Ont.	8.7
Petawawa, Ont.	6.5
Chapeau, Que.	15.1
Vermilion Bay, Ont.	9.3
Grand'Mere, Que.	4.4
St. Zenon, Que.	3.7
Senneterre, Que.	4.6
Mean	8.3

growing degree-days. The adjusted volume of the provenance in first rank (Douglas) exceeded the poorest (Senneterre) by 30% and the local provenance (Petawawa) by 6%. The mean tree volume of the Barry's Bay provenance again exceeded that of Petawawa, but the difference was 4% in contrast to 10% observed in the earlier experiment (No. 40).

In addition to raising the averages of tree dimensions, removal of damaged and suppressed trees slightly increased the differences among provenances (Table 8 cf. Table 6). The mean tree volume (adjusted for stocking) of Douglas provenance exceeded that of Senneterre by 31% and that of Petawawa by 8%. On the same basis, Barry's Bay exceeded Petawawa by 6% (Table 8). The difference between Douglas and Senneterre in total volume over all plots of the remaining trees was only 3% owing to the larger number of snow-damaged trees removed from plots of the Douglas provenance.

The results of this test of nine Ontario and Quebec provenances support those of the earlier independent experiment with 12 Ontario seed sources. At Petawawa, provenances from areas with long, warm growing seasons similar to the area of the planting site grew better than seed sources from the boreal forest. Although neither of these tests alone revealed statistically significant differences in mean height and volume among the top-ranking provenances at ages 17 and 19 years, the Petawawa provenance grew consistently less (4% to 10%) than the Barry's Bay source, which was top rank and some 40 miles distant in the same climatic region. Sampling and testing of populations within climatic regions can be expected to reveal stands of outstanding genetic potential for wood production.

TABLE 8. STOCKING, MEAN TREE HEIGHT, DIAMETER (b.h.o.b.), AND VOLUME OF NINE ONTARIO AND QUEBEC PROVENANCES AFTER THINNING, 1969 (EXP. NO. 82)

Seed origin	Stocking %	Height m	Diameter cm	Volume cu m/100	Adjusted[1] volume cu m/100
Barry's Bay, Ont.	46.0	8.29 a[2]	8.66 a	20.0 a	19.9 a
Kenora, Ont.	36.7	8.14 ab	8.40 a	19.7 a	18.6 ab
Douglas, Ont.	44.7	8.16 ab	8.76 a	20.5 a	20.3 a
Petawawa, Ont.	43.3	8.03 abc	8.46 a	19.8 a	18.8 ab
Chapeau, Que.	40.3	8.11 ab	8.40 a	19.3 a	18.9 a
Vermilion Bay, Ont.	49.3	7.84 bcd	7.80 b	16.2 b	16.8 cd
Grand'Mere, Que.	57.3	7.71 cd	7.50 b	14.4 b	15.6 cd
St. Zenon, Que.	53.7	7.86 bcd	7.86 b	16.1 b	17.2 bc
Senneterre, Que.	57.0	7.60 d	7.76 b	15.8 b	15.5 d
F-ratio		5.0**	6.9***	8.9***	10.0***

[1]Volume adjusted for plot-stocking before thinning, 1969, by covariance.
[2]Duncan's range test: means followed by a common letter do not differ at the 5% level of significance.
***, significant at the 1% level; **, 2.5%.

Lake States - Exp. No. 125

Seedlings of 16 Lake States provenances supplied by the Institute of Forest Genetics, Rhinelander, Wisconsin, were planted at Petawawa in 1955 (Morgenstern and Teich 1969). Analysis of 1961 height growth data demonstrated significant ($P < .05$) differences among provenances, but range tests indicated only moderate geographic separation, in which two sources from Lower Michigan were significantly taller than three of four from Upper Michigan (Morgenstern, E.K., 1964. File Report, Exp. No. 125). Morgenstern and Teich (1969) compared the growth of the 16 provenances at 12 years of age in 11 Lake States experiments and at Petawawa Forest Experiment Station. Large genotype-environment interactions (stability values) were characteristic of both northern and southern seed sources, a function of the distance that provenances were planted from their origin. Northern provenances moved south grew better than in their native habitats, but not as well as local provenances. Southern provenances moved north by 1 to 2° latitude in many instances were taller than the local stock.

Differences among the same provenances in resistance to injury from insects and diseases have been reported from the Lake States tests (King and Nienstaedt 1965, King 1971). The differences were not evident at all locations and the relation between seed origin and pest resistance was found to be random. Height-growth ranking of the seed sources was little affected by the presence of heavy pest infestations.

All-range - Exp. No. 255

Seed was collected from populations of jack pine for the exploration of the nature and extent of genetic variation associated with location of seed source throughout the natural range of the species (Holst 1960, 1962). Variation in growth, form, cold-hardiness and resistance to diseases and insects must be investigated in a range of natural environments to determine productivity in relation to climate, site, and evolutionary history of the species. Seedling studies and physiological and biochemical investigations provide additional insight into the adaptive basis of provenance variation.

In 1962 the first complete sowings were made of 99 provenances (Fig. 2) collected during the previous 5 years by the Canadian Forestry Service and cooperators in Canada and the United States. Complete details of seed collections, distribution of seed and seedlings, and tables of climatic data associated with the areas of seed origin were prepared for cooperators and are available upon request.[1]

At Petawawa, 98 provenances were included in each of two replicated tests - a nursery test sown in 1962 and a field test planted in 1966. Unreplicated plots of 99 provenances were planted for future provenance breeding (Holst 1962, 1964, 1967). Growth and hardiness of 87 provenances were evaluated in a series of tests of seedlings grown in controlled environments, a greenhouse, and nurseries (Yeatman 1966b).

Twenty-nine additional tests, involving varying numbers of provenances, were successfully established during the same period: two nursery tests in Canada and two in the United States; 12 field tests in Canada (Ontario, Quebec, New Brunswick), 11 in the United States, and two in Great Britain. Seed or seedling material was used in five studies in North America dealing with wood anatomy, biochemistry, and nuclear volume in relation to seed source (Durzan and Chalupa 1968, Giertych and Farrar 1962, Kennedy 1969, King 1968, Mergen and Thielges 1967). Seed was distributed to a further 21 cooperators in a number of countries, including Canada, Czechoslovakia, Denmark, Finland, Germany, Great Britain, Holland, New Zealand, and the United States.

Results - Exp. No. 255

Results to date have begun to elucidate patterns of genetic variation in growth, phenology, hardiness, disease resistance, and biochemical composition that are associated with geographic location and climate of seed origin.

[1]Holst, M.J. 1967. All-range pine provenance experiment. Petawawa Forest Exp. Sta. Intern. Rep. PET-PS-6. 144 p.

Seedling Studies in Controlled Environments

Northern provenances grown in controlled environments were more responsive than southern to change in photoperiod in a test of nine provenances ranging from New York State to Saskatchewan (Giertych and Farrar 1962). One hundred and fifteen days from sowing, total dry weight, height, dry weights of foliage and roots, and dry weight per unit of nitrogen content were all positively correlated with number of growing degree-days (base 42°F, 5.6°C) associated with the seed origin. Similar relations of dry weight and shoot length to the growing season of seed origin were found among seedlings of 50 provenances representative of the entire range grown for 3 months in nine controlled environments in combinations of three photoperiods and three temperatures (Yeatman 1964). Discrimination at the 5% level could be made among all but a few of the 50 provenances when response in shoot and root dry weight in the nine environments was subject to multivariate (canonical) analysis. Provenances differed in mean performance and in response to photoperiod, but the effect of temperature contributed little to provenance differentiation. Of a number of climatic variables tested, taken alone and in combination, the number of growing degree-days best accounted for variation in response among seed sources (Yeatman 1965, 1966b).

Seed weight and number of growing degree-days together accounted, with about equal weight, for 76% of variation in seedling size among the same 50 provenances harvested at the cotyledon stage shortly after sowing (Yeatman 1966a). After growing for 3 months in a 15-hour photoperiod and 21°C/13°C day/night temperature, 72% of variation in seedling dry weight among the provenances was accounted for by the two independent variables. By this stage, however, the effect of seed weight was only one-eighth that of growing degree-days and statistically insignificant. Regressions of seedling weight on growing degree-days at seed origin were significantly different east and west of longitude 91°W, running through the western end of Lake Superior, and the association was stronger in the west ($100r^2 = 81\%$) than in the east ($100r^2 = 71\%$) (Yeatman 1966b).

Needle characteristics and shoot length of 60-day-old seedlings sampled from the controlled environment tests of the 50 provenances just outlined were reported by Mergen *et al.* (1967). Racial differences were masked in some environments and expressed in others, and were generally greater in moderate (15-hour) and short (10-hour) photoperiods than in a long (20-hour) photoperiod. Each of the applied environmental variables (photoperiod and temperature) accounted for significant portions of the total variance in number of primary needles (for example), but photoperiod was about 4 times as important as temperature.

A highly significant correlation ($r = 0.85$) was found between seedling dry weight after 4 months in a controlled environment (15-hour photoperiod, 21°C/13°C day/night temperature) and seedling height at 4 years in the Petawawa nursery (latitude 41°N) for 38 provenances extending over the range of jack pine (Yeatman and Holst 1967). Among the faster-growing provenances, coastal and maritime sources generally lost rank and southern continental sources tended to gain rank in the nursery test in relation to growth in the laboratory test.

Nursery Tests - Growth, Hardiness, and Scleroderris Canker

In the nursery tests sown at Petawawa and at Longlac, northern Ontario, tree height at 4 years of age correlated best with daily mean temperature during May, June, and July of the seed origin. At Longlac, frost-hardiness was associated with low summer temperatures at provenance locations (Holst *et al.* 1969, p. 82).

In the fifth growing season, 99% of trees in the Longlac experiment had died or showed symptoms of infection from the fungal disease, scleroderris canker [*Gremmeniella abietina* (Lagerberg) Morelet (*Scleroderris lagerbergii* Gremmen)]. Seven provenances retained more healthy trees than could be attributed to chance alone and appeared to be partially resistant to disease. The three provenances with the highest number of healthy trees originated from the north shore of the St. Lawrence River to central Quebec in the vicinity of 50°N latitude (Teich 1967). Later studies showed that in October the moisture content in needles of trees of southern origin growing at Petawawa was higher than that in trees of northern origin, and that frost and fungal damage at Longlac were correlated with needle moisture content at Petawawa Forest Experiment Station. Infection, however, apparently was not conditional on visible frost damage, since many hardy provenances of northern origin were completely infected by scleroderris canker (Teich 1968). Artificial inoculation of the three Quebec and two Ontario provenances growing at Petawawa substantiated the relative resistance of the Quebec sources (Teich and Smerlis 1969). Confirmation of the scleroderris resistance of selected Quebec populations will be sought by testing progenies of 50 trees from three stands from which seed was collected in 1969 (A.H. Teich, personal communication).

Field Tests - Height at 6 Years of Age

Tree height and current leader length were recorded in 1969 in eight all-range provenance tests planted in Ontario (Table 9). The locations range from the shore of Lake Erie in the south to Red Lake in the northwest. Significant differences occurred in height and increment at all locations, but both plantation mean height and provenance differentiation were greater at the southern locations. These early data are intended primarily as establishment records for comparison with later assessments to be made periodically beginning at 10 years from sowing.

Physiology - Phenology, Wood Properties

A number of studies in controlled environments and nurseries have shown that seasonal rhythm in growth (phenology) is related to latitude and climatic variables of seed origin and is largely the cause of observed variations among provenances in height, dry weight, hardiness, and biochemical composition. Southern provenances respond more slowly to warming temperatures in the spring and form buds later in the growing season than do seedlings of northern origin (Rudolph 1964, Yeatman 1966b, Kennedy 1969, Teich and Holst 1969). Differing rates of maturation were reflected by later development of

TABLE 9. ALL-RANGE JACK PINE PROVENANCE TESTS IN ONTARIO MEASURED AT 6 YEARS FROM SOWING (EXP. NO. 255)

Variance ratios (F) of tree height and 1969 height increment and mean heights of shortest and tallest provenances at each location. These summaries are based on trees with single leaders only (Yeatman 1971).

Test location	Lat. Deg N	Number of provenances	Variance ratio Height F	Variance ratio Increment F	Shortest provenance cm	Tallest provenance cm
Turkey Point	43	81	17.3	20.1	48	150
Petawawa F.E.S.	46	98	11.5	12.2	54	155
Swastika	48	81	7.6	7.7	66	149
Cochrane	50	81	3.9	3.7	46	112
Espanola	47	43	3.6	2.5	52	89
Caramat	50	49	3.6	2.7	55	106
Kakabeka	48	72	3.2	3.4	86	134
Red Lake	51	56	4.9	5.4	60	116

secondary needles, winter coloration, needle sugar content, and cold-hardiness in seedlings of southern origin than in seedlings of northern origin when both were grown in a nursery in Connecticut (Yeatman 1966b). Total ring width, early-wood and late-wood ring width, and delayed cessation of cambial activity were positively correlated with growing degree-days of the seed origin among provenances grown at Petawawa (Kennedy 1969). In a study of 5-year-old seedlings growing in Wisconsin, seed sources from cool eastern and northern climates had the slowest growth rate, shortest tracheids, and highest specific gravity in contrast to southern provenances from the Lake States (King 1968). Differences in photosynthesis among provenances at certain times of the year are correlated with growth (Logan and Pollard 1971).

Biochemistry - Seed, Resin, Nuclear Volume

Durzan and Chalpua (1968) examined the free sugars, amino acids, and soluble proteins of female gametophyte (haploid, n = 12) and embryo (diploid) tissue of jack pine seed representative of populations from across the range of the species. Most chemical components correlated well with climatic factors of seed origin and were more concentrated, on a dry weight basis, in seed of northern than in that of southern origin. Concentrations were markedly higher in embryo than in gametophyte tissue. Arginine, the main nitrogenous storage compound, decreased with increasing mean annual temperature and precipitation at the seed origin. More advanced mobilization of storage compounds during incipient germination (seed maturation) was indicated for seed from warmer climates by greater embryo weight and length and increased amide content of seed. Thus the chemical components reflected the phenotypic state of the seed, which seemed to be preconditioned by the climate of the seed source.

Resin samples from 52 jack pine provenances growing at Petawawa Forest Experiment Station were analyzed in 1967 by Professor G.R. Stairs, New York State College of Forestry at Syracuse University, New York. The results of gas chromatograms indicated little systematic variation among provenances (Holst *et al.* 1969, p. 83).

The nuclear volume of 12 jack pine seed sources, ranging from Nova Scotia to the Northwest Territories, was determined by Mergen and Thielges (1967) and compared with measurement of provenances of Scots pine (*Pinus sylvestris* L.), white spruce (*Picea glauca* (Moench) Voss), and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) from similar latitudinal ranges. Nuclear volume increased with latitude in all species and seemed to present an example of parallel evolution in relation to cold resistance. Nuclei examined in root tips of germinated seed showed that the mean nuclear volume of the pines was greater than that of the spruces, and that jack pine nuclei were larger than those of Scots pine at a given latitude.

Discussion - Migration, Selection, Improvement

The broad patterns of variation in physiological characteristics of jack pine reveal well-defined adaptational gradients (clinal variation) associated with latitude (photoperiod), length of growing season, and summer temperature at the seed origin that suggest caution be exercised in seed movement. These gradients evolved as jack pine migrated from glacial refugia after withdrawal of the ice from the Wisconsin glacial maximum some 17,000 to 19,000 years ago. Yeatman (1967) concluded from published paleobotanical evidence that jack pine survived the Wisconsin glaciation in the Appalachian highlands south of the farthest extent of the ice in eastern North America, from where it migrated north and west during the postglacial period. This view, however, was questioned by Zavarin *et al.* (1969) on the basis of morphological and biochemical evidence of ancient introgression of jack pine in northern Rocky Mountain stands of lodgepole pine and of evidence in northeastern Saskatchewan of introgression of lodgepole pine into jack pine (Argus 1966). Further investigation is required to clarify the questions of glacial survival and postglacial (Wisconsin) migration of jack pine.

Significant variation among provenances within limited areas and from similar climates, particularly to the south and east of the species' range, indicates a high potential for selection among populations within restricted geographic and climatic ranges, e.g. site regions. As soon as they are identified, the better populations will provide an immediate gain in the genetic quality of seed collected for planting and direct seeding within specified regions for which they are suited. Improvement of superior populations will be made through further selection and breeding.

SELECTION AND BREEDING

Growth and Form

When the best wild populations for seed supply have been chosen, further genetic gains may be made by developing strains that combine desirable attributes of selected parental phenotypes. In the decade following 1960, the Petawawa Forest Experiment Station initiated experiments to investigate the heritability of important phenotypic traits of growth and form of local jack pine (Holst 1964, 1967; Holst *et al.* 1969). In 1961 seed was collected from trees rated for stem straightness, branch angle, and cone shape and angle. Two hundred and fifty-five open-pollinated progenies planted in 1964 will be assessed for growth and form characteristics at 10 years of age. Control-pollinated progenies produced in 1964 from parents rated for stem form will provide further estimates of heritability of this character when sufficient time has elapsed for its phenotypic expression. A systematic study of variation and heritability within and among 10 stands from the Upper Ottawa Valley was initiated in 1967. Performance of 100 open-pollinated progenies will be tested at three sites within the area of seed collection. Measurements of seedling height and dry weight at 2 years of age in a replicated nursery test failed to show clear distinctions among the progenies. Significant differences in dry weight were evident among populations and progenies within populations when seedlings were grown for 3 months in growth cabinets. The predictive value of this early test must await the results of the field trials.

Cone Serotiny

Teich (1970) analyzed a number of populations and progenies of jack pine and lodgepole pine for frequency of trees bearing closed cones (serotinous), open cones, or mixed open and closed cones by applying the Hardy-Weinberg law for gene equilibrium in stable populations. Although subject to environmental modification, including tree age, cone serotiny appears to be governed by a single gene with two alleles. Difficulty in making a clear identification of the heterozygote (mixed-cone type) led to inflated and unreliable estimates of inbreeding coefficients. The heritability of cone serotiny will be subjected to further analysis, including parent-progeny correlation, when the current progeny tests planted at Petawawa are sufficiently mature to permit reliable identification of the genotypes.

Interspecific Hybrids

Lodgepole pine is closely related to jack pine, and the interior form (*Pinus contorta* var. *latifolia*) is of particular breeding interest because of its superior stem and branch form and tolerance of moist environments. It is highly susceptible, however, to infection by sweet fern blister rust as shown in the early introductions of this species at Petawawa. New introductions of lodgepole pine from Washington, Oregon, and Utah, natural lodgepole pine x jack pine hybrids from Alberta and from plantations of the two species at Spruce Woods Forest Reserve, Manitoba, and also hybrids produced by controlled pollination were planted at Petawawa and elsewhere in eastern Canada. These were intended as potential sources of breeding material and to test the hybrids directly for cold-hardiness, growth, and disease resistance. At Petawawa the initial survival was high, but within a decade all pure lodgepole pine died from infection with sweet fern blister rust. Ziller (1967) reported: "Serious damage can be anticipated (from sweet fern blister rust) if susceptible pines are planted outside their natural range where telial hosts are common." The rate of infection within the hybrid combinations is high and survival is poor in comparison with jack pine as was also found in the Lake States (Anderson and Anderson 1965). The hybrids show no superiority in growth and, in general, reflect the poorer form of the jack pine component.

An assessment at 6 years of age of jack pine provenances, provenance hybrids and (lodgepole x jack) x jack pine hybrids planted in northern Ontario showed marked variation in hardiness among seed lots. Winter injury was associated with latitude of origin of the parental populations according to a pattern of polygenic inheritance consistent with that found in the Lake States by Rudolph and Nienstaedt (1962). No hybrid combination, either within or between species, was superior in hardiness or height growth at 8 years of age to the best provenance, Baskatong Lake, western Quebec (Yeatman and Holst 1972).

COMPARISONS WITH EXOTIC SPECIES

Early unreplicated plantings of jack pine together with Scots pine, lodgepole pine, Austrian pine (*Pinus nigra* Arnold) and Korean *P. densiflora* Sieb. and Zucc., have demonstrated the growth superiority of jack pine on typically infertile, dry sand jack pine sites at Petawawa Forest Experiment Station. Scots pine is most frequently considered as a possible alternative species to jack pine, but few well-designed experiments have been established that incorporate a wide range of Scots pine provenances with the indigenous provenance of jack pine. Local jack pine was planted with nine Russian provenances of Scots pine in replicated tests at two locations near Swastika, northern Ontario. At 11 years of age and 8 years after planting, jack pine was taller at both locations than the best Scots pine provenances (by 23% and 90%). Jack pine was also superior in survival and had fewer damaged leaders than the Scots pine (Teich and O'Neill 1969). In a test of the same Russian provenances planted near Prince Albert, Saskatchewan, the best Scots pine provenances were taller at 11 years of age than an adjacent plot of jack pine. Survival and growth of both species were poor on this site (Teich and Holst 1970). At Spruce Woods Forest Reserve, Manitoba, the merchantable volume of Scots pine of German origin was 45% more than jack pine at 48 years of age (Bella 1967). Jack pine is not indigenous to either of these prairie locations, both of which are sandy plains of low fertility.

Selected Scots pine provenances are of potential value for planting on particular sites not normally occupied by jack pine, but evidence indicates that the exotic species is inferior to jack pine on typical jack pine sites.

GROWTH ACCELERATION AND FLOWER INDUCTION

The period between seed germination and sexual maturity limits the rate of progress of breeding through successive generations. Two approaches have been taken to reduce this time interval - first, the promotion of rapid early growth by optimization of the environment and, second, the induction of early and abundant flowering by the application of mechanical or chemical treatments.

Photoperiodic Control

Jack pine seedlings increase shoot growth and dry weight in response to long photoperiods (15-20 hours) when grown at normal temperatures (21°C) and with adequate moisture and nutrition. Northern provenances respond relatively more to increasing photoperiod than do seedlings of southern origin. Low temperatures (10°C) inhibit seedling growth at all photoperiods (Yeatman 1966b). Rudolph (1966) found that when a 20-hour photoperiod was applied in a greenhouse during the first year before the seedlings were transplanted to a nursery, more than 50% of the plants bore female strobili in the second year. A long photoperiod gives almost continuous growth for at least a year from germination. Once the seedlings form resting buds and enter a dormancy cycle, response by jack pine to a long photoperiod is more limited (Rudolph T.D., personal communication).

CO_2 Enriched Atmosphere

A threefold enrichment of carbon dioxide in the atmosphere (990 ppm) resulted in a 40% increase in dry weight of 3-week-old seedlings grown at two light intensities (11,800 lux and 30,100 lux) in growth cabinets that maintained a 15-hour photoperiod. A further twofold increase in CO_2 to 1,500 ppm gave no significant advantage. Seedlings grown at the higher light intensity were 69% heavier on the average than seedlings exposed to the lower light intensity. At this age the effects of light and CO_2 were independent (Yeatman 1970). The advantage in dry weight is maintained at 3 months of age by seedlings grown in an enriched atmosphere at the higher light intensity. Seedlings at the lower light intensity were taller and fewer of them had formed buds (Yeatman 1971). Growth of jack pine seedlings and other conifers can be increased substantially by manipulating factors of light, temperature, and CO_2 concentration.

Growth stimulation of jack pine and white spruce seedlings is currently being studied in laboratory and greenhouse experiments to determine optimal levels and cycles of temperature and photoperiod (Pollard and Logan 1971).

Flower Induction

The effects of mechanical injury, applications of nitrogenous fertilizers and spraying with guanine and triiodobenzoic acid (antiauxins) have been tested over a number of years in relation to abundance and type of flowering (Holst 1967, 1971; Holst *et al.* 1969; Cayford *et al.* 1967, p. 197). Root-pruning had no effect on 5- to 7-year-old jack pine saplings. The formation of both female and male flowers was stimulated by branch-girdling, and timing of the treatment was found to be critical. Both positive and negative effects resulted from the application of chemicals, and in most instances male and female flowering were in opposition, an increase in one being accompanied by a decrease in the other. Applications of ammonium nitrate fertilizer from May to early June increased by up to 100% the number of female flowers borne by young jack pine in the following year. Fertilizing later in the growing season was not effective. Comparisons among applications of ammonium nitrate, potassium nitrate, and ammonium sulphate showed stimulation of female flowering to be related to total nitrogen applied. Fertilization, particularly with ammonium sulphate, also increased male flowering in the lower crown. Spraying with antiauxins stimulated both female and male flowering.

GRAFTING

Reciprocal grafts of jack, red, and Scots pine were made in all combinations to test graft compatibility and possible stimulation of growth or of flowering (Holst and Santon 1958). Combinations of jack and red pine failed at an early age. Combinations of jack and Scots pine survived well, and the initial growth of Scots pine scions grafted on jack pine was some 10% more than that of the controls. However, the long-term survival and growth do not indicate any practical advantages to be gained from interspecific grafting with jack pine used as either scion or rootstock.

DISCUSSION

Increased emphasis is being placed on planting and direct seeding of jack pine, for which large quantities of seed are required. The initial work with jack pine at Petawawa Forest Experiment Station dealt with the question of provenance, i.e. the effect of geographic seed source on tree characteristics, particularly on those associated with survival and growth. Studies were undertaken in response to the immediate need for information concerning seed collection and use in Canada and to provide a basis for further selection and breeding of improved populations.

Laboratory, nursery, and field studies at the Petawawa Forest Experiment Station and elsewhere have revealed dominant patterns of clinal (continuous) variation in jack pine across the geographic range of the species.

High correlations of growth with climate at the seed origin have been demonstrated with young seedlings, particularly with those grown in controlled environments, as well as with trees up to 19 years of age growing in plantations. Genetic adaptation has led to population differentiation strongly associated with latitude (photoperiod) and the duration and temperature of the growing season. Northern provenances from areas with long photoperiods during short, cool growing seasons grow significantly more slowly than southern sources when planted in a southern location of relatively short photoperiod and long, warm growing season. Provenances from southern areas grow more rapidly than locally adapted sources at a northern location, but they are liable to suffer winter injury because they mature late in the growing season and do not harden adequately before winter sets in. The use of seed from plantations of unknown origin may result in significant losses of productivity, as has been demonstrated in an early provenance test of Ontario sources planted at Petawawa.

Careful selection of seed source from natural populations on a climatic basis is the first and essential step in the collection of seed for artificial regeneration of jack pine.

There remains substantial variation around the broad climatic trends in inherent productivity. When geographically separated, populations from similar climates or within a single ecological region often show marked differences in growth and pest resistance. To date no physiological or ecological basis has been found for identifying genetically superior populations from a restricted geoclimatic range. Growth in the nursery could not be used to predict differences in field performance of climatically associated populations tested at Petawawa. Well-planned and properly conducted field trials are essential to identify the best seed sources, and initially a broad base of many populations must be considered for selection from a given climatic region.

Early gains in productivity of from 5% to 10% can be expected when use is made of the better populations from within defined geoclimatic regions for mass seed production.

Important differences in susceptibility to insect and disease attack associated with seed origin have been reported in the Lake States. Resistance to scleroderris canker, a lethal disease of jack pine seedlings, was found in a number of provenances from eastern Quebec growing at a nursery in northern Ontario. The value of these populations for breeding for disease resistance or direct use is being investigated further.

Further genetic gain will be realized by developing improved jack pine strains from parents selected, tested, and proven for their breeding value. The research objective at Petawawa is to investigate the basis for selection and tree improvement. Climatic adaptability remains the primary criterion for improved stock, which must therefore be developed for specific regions. Recent experiments are designed to provide estimates of variation and heritability of growth rate within and among local populations as a basis for calculating the intensity, and hence the cost, of selection needed and the gain to be expected. Crown and stem form show wide phenotypic variation in jack pine and markedly affect wood quality and yield. During the past decade open- and control-pollinated progeny tests were planted at Petawawa for estimating heritabilities of these characteristics. Genetic parameters derived from these experiments can be expected to have broad application in the breeding of jack pine in Canada.

Hybrids between tree species or between provenances within a species offer interesting possibilities for combining desirable traits or broadening the adaptive base of selected strains. Jack pine provenance hybrids and hybrids with lodgepole pine have been planted together with natural populations and parental species at a number of locations in eastern Canada. Analysis of data from 6-year-old trees planted in northern Ontario showed that winter-hardiness and growth rate of jack pine hybrids were intermediate between those of the parental genotypes. In this boreal environment the hybrids were at a disadvantage in comparison with a natural population originating from a climate similar to that of the planting area.

Both lodgepole pine and its hybrids with jack pine are highly susceptible to sweet fern blister rust in those parts of eastern Canada where the alternate hosts, sweet fern (*Comptonia peregrina* (L.) Coult.) and sweet gale (*Myrica gale* L.), are commonly found. Extreme caution should be exercised in the introduction of lodgepole pine provenances or hybrids into areas of indigenous jack pine. Frost-hardy provenances and hybrids of lodgepole pine will survive long enough to flower heavily, producing pollen and seed that in succeeding generations will increase the overall rust susceptibility of the native jack pine in which the disease is endemic.

FUTURE GENETIC RESEARCH AND DEVELOPMENT

The provenance and progeny tests established at Petawawa and elsewhere in Canada will be a continuing source of new information on the genetic improvement of jack pine. Many of these tests are young, and time is required for adequate expression of genetic components of variation affecting survival, growth, and genotype-environment interaction. Trees must grow to sufficient size and maturity before morphological characteristics of stem and branch form and cone type can be evaluated effectively. Measurement, analysis, and interpretation of established experiments must receive first priority at Petawawa during the next decade.

A systematic study of provenance hybridization was initiated in 1971 in cooperation with the Institute of Forest Genetics (Rhinelander, Wisconsin) of the U.S. Forest Service, North Central Forest Experiment Station. Cooperators will carry out controlled pollinations among selected provenances from the range-wide collections growing at Petawawa and in the Lake States. Seed will be exchanged and seedlings raised to be outplanted at a number of locations in Canada and the United States ranging from the eastern seaboard to Alberta. The establishment phase from pollination to outplanting will require from 5 to 7 years, depending on the abundance of flowering in the provenance material. This study will provide basic information on the general and specific combining ability of jack pine populations and will constitute a source of new genetic combinations for testing, selection, and breeding.

Differences in growth and form are obvious among open-grown jack pine trees, but variation among dominant trees tends to be obscured in typically even-aged stands with closed canopy. Rudolph (1964) presented evidence that late-season shoot growth is under genetic control and recommended that seed collection be avoided from trees subject to lammas growth or prolepsis that results in characteristic and undesirable forms of branching. Further information is needed concerning the recognition, heritability, and silvicultural significance of phenotypic characteristics of individual trees before reliable prescriptions can be formulated for selection of plus-trees for tree improvement. Some guidance will be obtained from progeny tests already initiated. A pilot study will be undertaken to determine the feasibility of plus-tree selection in local jack pine stands. To test the silvicultural significance of stem and crown form, grafted clones of trees rated for extremes of these characteristics will be produced and planted at different spacing in blocks of single phenotypes and in mixture. This material will also provide estimates of broad sense heritability of these factors. Narrow sense heritabilities and breeding values of the plus trees will be estimated from open-pollinated progenies. After genetic evaluation, the plantations may be converted to breeding orchards for seed for second- and third-generation seedling seed orchards.

On a broader scale, research and management must work together now to discover the better seed sources for immediate seed requirements. Canadian forest services have adopted rules for seed collection and identification and conservative seed transfer (Wang and Sziklai 1969) that ensure the avoidance of serious losses in productivity due to incorrect provenance. Within these guidelines, designation of selected jack pine stands for mass seed collection and integration of testing of such collections with operational reforestation will permit early identification of the better seed sources, with consequent gains in productivity. Research workers can be called upon to design suitable stand tests and assist in their evaluation.

Normal designs for seed-production areas or seed orchards are not appropriate for jack pine because of its serotinous cones, which cannot be harvested in quantity from mature standing trees without severe damage to the cone-bearing branches. Removal of several whorls of two or more cones each leaves the branch mechanically weak and liable to breakage and winter desiccation. Jack pine, however, has the advantage that a number of years' seed production is stored on the tree and cones are harvested most efficiently and economically from the crowns of felled trees. Thus stands reserved and managed for seed production, whether of natural origin or established as seedling seed orchards, should be large enough to permit periodic felling for cone collection as required. The areas involved (excluding genetic buffer zones) will be calculated on the basis of expected seed requirements and the length of the normal rotation from regeneration to harvest. Early cone collections from young seed-orchard plantations can be made economically from standing trees without excessive damage to the crowns.

Precise seed origin should be known and recorded for every acre planted or seeded in Canada. With time, accurate records of reforestation will provide unique opportunities for detailed analyses of productivity in both silvicultural and genetic terms. Policies should be adopted to avoid uncontrolled introductions into any forest area of populations of unknown or unsuitable origin and to ensure perpetuation of the selected and representative genetic resources (gene pools). Regeneration of a stand designated for seed production should be restricted to planting or seeding with seed of the same origin. In this way gene pools of selected populations, logically distributed geographically and climatically, will remain essentially intact within the environments in which they have evolved and to which they are uniquely adapted. With suitable management, the best of these protected genetic resources will provide early and continuing supplies of superior seed at minimal cost and in quantities required for extensive reforestation.

CONCLUSIONS

1. Tree improvement, including short- and long-term goals, must be conducted on a regional basis for jack pine, for which pronounced clinal patterns of growth are evident over broad ecogeographic ranges.

2. In the absence of contrary experimental evidence, seed for direct seeding and planting should be of local origin if risk of substantial loss in productivity is to be avoided.

3. Important differences in growth and pest susceptibility have been found among populations originating from a single region or ecological zone. Gains up to 10% can be expected if populations within regions are systematically sampled and tested and if seed collection is limited to the better sources as soon as they can be identified, i.e. after 10 to 20 years of testing.

4. Well-stocked stands on good-quality sites should be designated for seed collection within ecological zones. Since many years' seed production is stored on the branches, felling successive portions of a stand yields cones in quantities and at times as needed. Strict attention should be given to labelling and retaining seed-source identification from cone collection to field establishment by direct seeding or planting.

5. The genetic integrity of a designated seed-collection area should be maintained by regenerating after felling with seed from that area, and with no other. This will ensure the genetic quality of the population for future seed collection. Gene pools of the better populations may in this way be protected indefinitely.

6. Additional gains will be realized in seedling seed orchards. Such intensive improvement of jack pine must be directed toward the economically most favorable circumstances with respect to site quality, quantity, and location.

7. There is no evidence that exotic pine species such as Scots pine or lodgepole pine are more productive of wood than jack pine on typical jack pine sites of eastern Canada. On the contrary, because of their high

susceptibility to sweet fern blister rust and capacity to degrade future generations of jack pine through dispersal of pollen, lodgepole pine and its hybrids with jack pine should not be planted or sown.

8. Genetic research in jack pine must continue to capitalize on the research investment made to date, much of which has yet to reach maturity, and also intensify investigations of heritability and breeding values. Strategically planned clonal and progeny tests will provide information essential for prediction of gains, calculation of costs and benefits, and determination of appropriate breeding systems for the production of improved growing stock in future generations.

REFERENCES

Anderson, N.A., and R.L. Anderson. 1965. The susceptibility of jack pine and lodgepole pine and their hybrids to sweetfern rust and eastern gall rust. U.S. Forest Serv. Res. Note LS-56. 4 p.

Argus, G.W. 1966. Botanical investigations in northeastern Saskatchewan: the subarctic Patterson-Hasbala Lakes region. Can. Field Natur. 80:119-143.

Bella, I.E. 1967. Development of jack pine and Scots pine in the Spruce Woods Forest Reserve, Manitoba. Can. Dep. Forest. Rural Develop., Forest. Br. Publication 1171. 13 p.

Carlisle, A. 1970. Tree improvement programs and their role in Canadian forestry. Forest. Chron. 46:439-444.

Cayford, J.H., and A. Bickerstaff. 1968. Man-made forests in Canada. Can. Dep. Fish. Forest., Forest. Br. Publication 1240. 68 p.

Cayford, J.H., Z. Chrosciewicz, and H.P. Sims. 1967. A review of silvicultural research in jack pine. Can. Dep. Forest. Rural Develop., Forest. Br. Publication 1173. 255 p.

Cayford, J.H., and R.A. Haig. 1961. Glaze damage in forest stands in southeastern Manitoba. Can. Dep. Forest., Forest Res. Br. Tech. Note 102. 16 p.

Chapman, L.J., and D.M. Brown. 1966. The climates of Canada for agriculture. Can. Dep. Forest. Rural Develop., ARDA. The Can. Land Inventory, Rep. 3. 24 p., 24 fig., 1 table.

Critchfield, W.B., and E.L. Little. 1966. Geographic distribution of the pines of the world. U.S. Forest Serv. Misc. Publication 991. 97 p.

Durzan, D.J., and V. Chalupa. 1968. Free sugars, amino acids, and soluble proteins in the embryo and female gametophyte of jack pine as related to climate at the seed source. Can. J. Bot. 46:417-428.

Giertych, M.M., and J.L. Farrar. 1962. A provenance study of jack pine seedlings. Silvae Genet. 11:111-114.

Hall, John. 1970. Site preparation in Ontario. Forest. Chron. 46:445-447.

Holst, M.J. 1960. Forest tree breeding and genetics at the Petawawa Forest Experiment Station. Biennial report, April 1, 1958, to March 31, 1960. Proc. Seventh Meeting Comm. Forest Tree Breeding Can. Part II: K-1 - K-27. Can. Dep. Forest., Forest Res. Br.

Holst, M.J. 1962. Forest tree breeding and genetics at the Petawawa Forest Experiment Station. Biennial report, April 1, 1960, to March 31, 1962. Proc. Eighth Meeting Comm. Forest Tree Breeding Can. Part II: M-1 - M-25. Can. Dep. Forest., Forest Res. Br.

Holst, M.J. 1964. Forest tree breeding and genetics at the Petawawa Forest Experiment Station. Biennial report, April 1, 1962, to March 31, 1964. Proc. Ninth Meeting Comm. Forest Tree Breeding Can. Part II: 63-107. Can. Dep. Forest., Forest Res. Br.

Holst, M.J. 1967. Forest tree breeding and genetics at the Petawawa Forest Experiment Station. Proc. Tenth Meeting Comm. Forest Tree Breeding Can. Part 2:57-84. Can. Dep. Forest. Rural Develop., Forest. Br.

Holst, M.J. 1971. The stimulation of flowering in spruce and pine. Proc. Twelfth Meeting Comm. Forest Tree Breeding Can. Part 2:125-128. Can. Dep. Fish. Forest., Can. Forest. Serv.

Holst, M.J., E.K. Morgenstern, A.H. Teich, and C.W. Yeatman. 1969. Forest tree breeding and genetics at the Petawawa Forest Experiment Station. Proc. Eleventh Meeting Comm. Forest Tree Breeding Can. Part 2:77-100. Can. Dep. Fish. Forest., Forest. Br.

Holst, M.J., and J.B. Santon. 1958. Interspecific grafting of hard pines. Proc. Sixth Meeting Comm. Forest Tree Breeding Can. Part II:R-13 - R-14. Can. Dep. Northern Aff. Nat. Resources, Forest. Br., Forest Res. Div.

Holst, M.J., and C.W. Yeatman. 1961. A provenance study in *Pinus banksiana* Lamb. Pages 1612-1616 *in* Recent advances in botany, vol. II. Univ. Toronto Press, Toronto.

Honer, T.G. 1967. Standard volume tables and merchantable conversion factors for the commercial tree species of central and eastern Canada. Can. Dep. Forest. Rural Develop., Forest. Br., Forest Manage. Res. Serv. Inst. Inform. Rep. FMR-X-5. 21 p. and appendices.

Kennedy, R.W. 1969. Wood formation in jack pine seedlings of various provenances. Proc. Eleventh Meeting Comm. Forest Tree Breeding Can. Part 2: 101-110. Can. Dep. Fish. Forest., Forest Br.

Kienholz, R. 1941. Jack pine in Connecticut damaged by sleet storm. J. Forest. 39:874-875.

King, J.P. 1968. Seed source variation in tracheid length and specific gravity of five-year-old jack pine seedlings. Proc. Eighth Lake States Forest Tree Impr. Conf., U.S. Forest Serv. Res. Pap. NC-23:5-9.

King, J.P. 1971. Pest susceptibility variation in Lake States jack pine seed sources. U.S. Forest Serv. Res. Pap. NC-53. 10 p.

King, J.P., and H. Nienstaedt. 1965. Variation in needle cast susceptibility among 29 jack pine seed sources. Silvae Genet. 14:194-198.

Logan, K.T., and D.F.W. Pollard. 1971. Physiological growth parameters for tree selection. Proc. Twelfth Meeting Comm. Forest Tree Breeding Can. Part 2:131. Can. Dep. Fish. Forest., Can. Forest. Serv.

Mergen, F., and B.A. Thielges. 1967. Intraspecific variation in nuclear volume in four conifers. Evolution 21:720-724.

Mergen, F., J. Worrall, and G.M. Furnival. 1967. Genotype-environment interactions in 50 sources of jack pine seedlings. XIV IUFRO Congr., München. Sect. 22:459-466.

Morgenstern, E.K., and A.H. Teich. 1969. Phenotypic stability of height growth of jack pine provenances. Can. J. Genet. Cytol. 11:110-117.

Pollard, D.F.W., and K.T. Logan. 1971. Mechanisms of seedling growth in improved environments. Proc. Twelfth Meeting Comm. Forest Tree Breeding Can. Part 2:129. Can. Dep. Fish. Forest., Can. Forest. Serv.

Roe, E.I. 1963. Seed stored in cones of some jack pine stands, northern Minnesota. U.S. Forest Serv. Res. Pap. LS-1. 14 p.

Roe, E.I., and J.H. Stoeckler. 1950. Thinning over-dense jack pine seedling stands in the Lake States. J. Forest. 48:861-865.

Rowe, J.S. 1959. Forest regions of Canada. Can. Dep. Northern Aff. Nat. Resources, Forest. Br. Bull. 123. 71 p. and map.

Rudolf, P.O. 1958. Silvical characteristics of jack pine (*Pinus banksiana* Lamb.). U.S. Forest Serv., Lake States Forest Exp. Sta. Pap. 61. 31 p.

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

Rudolph, T.D. 1966. Stimulation of earlier flowering and seed production in jack pine seedlings through greenhouse and nursery culture. U.S. Forest Serv. Res. Pap. NC-6:80-83.

Rudolph, T.D., and H. Nienstaedt. 1962. Polygenic inheritance of resistance to winter injury in jack pine - lodgepole pine hybrids. J. Forest. 60:138-139.

Rudolph, T.D., W.J. Libby, and S.S. Pauley. 1957. Jack pine variation and distribution in Minnesota. Univ. Minn. Sch. Forest., Minn. Forest. Notes 58. 2 p.

Schoenike, R.E. 1962. Natural variation in jack pine (*Pinus banksiana* Lamb.). Ph.D. Thesis, Univ. Minn. 211 p.

Scott, J.D. 1970. Direct seeding in Ontario. Forest. Chron. 46:453-457.

Teich, A.H. 1967. Resistance of jack pine to *Scleroderris lagerbergii* Gremmen. Can. Dep. Forest. Rural Develop., Bi-mon. Res. Notes 23:5.

Teich, A.H. 1968. Foliar moisture content as a criterion for resistance to frost and scleroderris canker in jack pine. Can. Dep. Forest. Rural Develop., Bi-mon. Res. Notes 24:3

Teich, A.H. 1970. Cone serotiny and inbreeding in natural populations of *Pinus banksiana* and *Pinus contorta*. Can. J. Bot. 48:1805-1809.

Teich, A.H., and M.J. Holst. 1969. Breeding for height growth of *Pinus banksiana* Lamb. Second World Consultation Forest Tree Breeding, Washington (FAO, Rome, 1970). Sect. II, FO-FTB-69-2/9. 7 p.

Teich, A.H., and M.J. Holst. 1970. Early survival and growth of *Pinus sylvestris* L. in Canada. Forest. Chron. 46:325-328.

Teich, A.H., and K.J. O'Neill. 1969. Growth of Russian Scots pine versus local jack pine in northern Ontario. Can. Dep. Fish. Forest., Bi-mon. Res. Notes 25:47-48.

Teich, A.H., and E. Smerlis. 1969. Jack pine resistance to *Scleroderris lagerbergii*. Can. Dep. Fish. Forest., Bi-mon. Res. Notes 25:47.

Wang, B.S.P., and O. Sziklai. 1969. A review of forest tree seed certification. Forest Chron. 45:378-395.

Yeatman, C.W. 1964. Genetic variation in seedlings of jack pine provenances grown in controlled environments. Progress report. Proc. Ninth Meeting Comm. Forest Tree Breeding Can. Part II:135-140. Can. Dep. Forest.

Yeatman, C.W. 1965. Provenance discrimination of jack pine seedlings grown in controlled environments. Abstract, Can. J. Genet. Cytol. 7:359.

Yeatman, C.W. 1966a. Germinant size of jack pine in relation to seed size and geographic origin. Joint Proc. Second Genet. Workshop, Soc. Amer. Forest., and Seventh Lake States Forest Tree Impr. Conf. U.S. Forest Serv. Res. Pap. NC-6:28-36.

Yeatman, C.W. 1966b. Geographic variation in jack pine (*Pinus banksiana* Lamb.) seedlings. Ph.D. Thesis. Yale Univ., New Haven, Conn. 231 p.

Yeatman, C.W. 1967. Biogeography of jack pine. Can. J. Bot. 45:2201-2211.

Yeatman, C.W. 1970. CO_2 enriched air increased growth of conifer seedlings. Forest Chron. 46:229-230.

Yeatman, C.W. 1971. Genetics of jack pine, seedling response to CO_2 and pollination studies, Petawawa, 1968-70. Proc. Twelfth Meeting Comm. Forest Tree Breeding Can. Part 2:101-105. Can. Dep. Fish. Forest., Can. Forest. Serv.

Yeatman, C.W., and M.J. Holst. 1967. Correlations between controlled-environment and nursery-grown seedlings of jack pine provenances. Proc. 14th Northeastern Forest Tree Impr. Conf.:24-29.

Yeatman, C.W., and M.J. Holst. 1972. Hardiness of jack pine hybrids and provenances in the boreal forest. Forest. Chron. 48:30-31.

Yeatman, C.W., and A.H. Teich. 1969. Genetics and breeding of jack and lodgepole pines in Canada. Forest Chron. 45:428-433.

Zavarin, E., W.B. Critchfield, and K. Snajberk. 1969. Turpentine composition of *Pinus contorta* x *Pinus banksiana* hybrids and hybrid derivatives. Can. J. Bot. 47:1443-1453.

Ziller, W.G. 1967. Sweetfern blister rust *Cronartium comptoniae* Arth. Pages 181-183 *in* A.G. Davidson and R.M. Prentice, eds. Important forest insects and diseases of mutual concern to Canada, the United States and Mexico. Can. Dep. Forest. Rural Develop., Ottawa.

ACKNOWLEDGMENT

Much of the material reported upon and many of the conclusions reached in this paper are directly due to the outstanding pioneering work of Mark Holst in assembling seed and establishing plantations of jack pine when this species was considered little better than a weed. I, and all who are concerned with the seeding and planting of jack pine in Canada, owe a lasting debt of gratitude to Mark for his energy, persistance, and originality.

I also wish to thank my colleagues at the Petawawa Forest Experiment Station, and Dr. A. Carlisle in particular, for the sound advice they gave during the preparation of this paper.