Tree size, biomass, and volume growth of twelve 34-year-old Ontario jack pine provenances

S. MAGNUSSEN[1]
Royal Veterinary and Agricultural University, Copenhagen, Denmark DK 1870
V. G. SMITH
Faculty of Forestry, University of Toronto, Ont., Canada M5S 1A1
AND
C. W. YEATMAN
Petawawa National Forestry Institute, Chalk River, Ont., Canada K0J 1J0

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Tree size and aboveground biomass in twelve 34-year-old Ontario jack pine (*Pinus banksiana* Lamb.) provenances growing at Petawawa National Forestry Institute (Chalk River, Ontario) was negatively correlated with latitude of origin. The best provenance exceeded the local provenance in tree height and diameter by approximately 10%. The pattern of geographical variation was stable over time, making general and sound predictions of provenance growth based on juvenile performance feasible. Persistent differences among some geographically close provenances indicated the potential for genetic improvement by selecting the best populations within site regions. The results demonstrated have important implications for jack pine breeding and improvement strategies at the provenance level. The provenance averages of aboveground ovendry weight per tree ranged from 44 to 79 kg. The aboveground tree biomass was distributed as follows in seven analyzed provenances: stem wood, 78%; stem bark, 8%; branch wood, 8%; needles, 5%; cones, 1%. Variation in average stemwood mass among provenances was less than the variation in average stem volume because of a strong negative correlation on a single tree basis between stem volume and stem wood density. The mean annual volume and biomass accretion per hectare in the best provenances averaged 10 m^3 and 4 t, respectively. Total stem volume production per hectare varied exponentially with tree height. Mean annual stem volume increment of the best provenances exceeded that of the slowest growing provenances by 22–40%.

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Chez 12 provenances de pins gris (*Pinus banksiana* Lamb.) de 34 ans, cultivées à l'Institut forestier national de Petawawa (Chalk River, Ontario), les dimensions et la biomasse aérienne des arbres étaient en relation inverse de la latitude d'origine. La hauteur et le diamètre des sujets de la meilleure provenance dépassaient de 10% ceux des sujets de la provenance locale. Les écarts liés à la géographie sont restés stables dans le temps, ci qui permet de prédire fidèlement et de façon générale la croissance selon la provenance en se fondant sur la performance des jeunes arbres. Les écarts durables entre certaines provenances géographiquement rapprochées montrent la possibilité d'une amélioration génétique par sélection des meilleures populations à l'intérieur de stations dans des régions. Les résultats constatés ont des conséquences importantes sur les stratégies d'amélioration générale et génétique du pin gris, à l'échelle de la provenance. En moyenne, la biomasse aérienne anhydre des arbres variait, selon la provenance, entre 44 et 79 kg. Chez sept provenances analysées, la biomasse aérienne se répartissait comme suit: bois de fût, 78%, écorce de fût, 8%; bois de branches, 8%; aiguilles, 5%; cônes, 1%. L'écart de la masse moyenne du bois de fût, entre les provenances, était inférieur à l'écart du volume moyen du fût, à cause de la corrélation fortement négative, pour un arbre donné, entre le volume du fût et la masse volumique du bois de fût. L'accroissement annuel moyen du volume et de la biomasse chez les meilleures provenances s'élevait à 10 m^3/ha et à 4 t/ha, respectivement. La production totale du volume des fûts, à l'hectare, variait exponentiellement selon la hauteur des arbres. Chez les meilleures provenances, l'accroissement annuel moyen du fût dépassait de 22 à 40% celui des provenances à croissance lente.

Introduction

Jack pine (*Pinus banksiana* Lamb.) is an important pulp and timber species in Canada and the Lake States (Bickerstaff *et al.* 1981; Rudolph 1984), where it frequently grows in extensive even-aged stands of fire origin (Alban 1982; Cayford *et al.* 1967). The rapid juvenile growth on sites that require a minimum of preparation and tending has given jack pine a preferred status in the reforestation programs of Ontario and Québec (Couture 1984; Heikurinen 1984; Moore 1984). Natural regeneration is encouraged where possible following clear felling, but planting or direct seeding is frequently required to ensure satisfactory stocking.

High quality seed is a prerequisite to the success of jack pine regeneration programs (Carlisle and Teich 1975). Provenance trials initiated at the Petawawa National Forestry Institute were designed to quantify geographic patterns of genetic variation in jack pine and to guide selection of improved seed sources for reforestration in specified regions of Canada.

Provenance trials generally show a pattern of clinal variation in growth, hardiness, and susceptibility to diseases in jack pine that reflects the migratory history of the species and genetic adaptation to environmental conditions (photoperiod, seasonal temperatures, moisture, etc.) at the site of origin (Hunt and Sickle 1984; Jeffers and Jensen 1980; King 1981; Rudolph and

[1]Present address: Petawawa National Forestry Institute, Chalk River, Ont., Canada K0J 1J0.
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TABLE 1. Ontario jack pine provenances trial at the Petawawa National Forestry Institute (planted in 1954; expt. 40)

Seed origin	Latitude (N)	Longitude (W)	Growing degree-days (no.)[a]	Forest section[b]	Snow damage, 1963 + 1967 (% of trees)
Kabitotikwia Lake	49°40′	89°11′	2200	B10	4.3
Stevens	49°33′	85°50′	1850	B8	10.0
Connaught[c]	48°38′	80°56′	2000	B4	3.2
Goldie	48°35′	89°50′	2300	L11,B11	4.3
Timmins[c]	48°28′	81°20′	2050	B4,B7	13.9
Hardwick	48°10′	90°05′	2500	L11	12.5
Swastika[c]	48°07′	80°06′	2200	L8,B7	5.8
Algoma	46°38′	83°00′	2800	L4e	30.9
Petawawa[c]	46°00′	77°28′	3000	L4c	12.8
Barry's Bay[c]	45°25′	77°30′	2700	L4c	24.8
Angus[c,d]	(44°19′)	(79°53′)	—	—	47.9
St. Williams[c,d]	(42°50′)	(80°30′)	—	—	5.3

[a]Above 5.6°C (Chapman and Brown 1966).
[b]Rowe 1959.
[c]Provenances selected for biomass assessment.
[d]Seed collected in plantations of unknown origin.

Yeatman 1982; Skeates 1979; Steiner 1979; Yeatman 1974). A strong genetic control of branching habit and stem form has also been noted (Kremer and Larson 1982; Polk 1974; Rudolph and Yeatman 1982; Yeatman 1976). In summary, provenance trials expose the risks associated with provenance transfer across latitudinal−climatic gradients owing to winter damage, reduced growth, and increased susceptibility to disease (Hunt and Sickle 1984; Jeffers and Jensen 1980; King 1981; Yeatman 1976).

Selection of superior seed sources relies mainly upon phenotypic traits of the parent trees and upon juvenile growth rates, survival, and hardiness of the offspring (Yeatman 1984). The persistence of desirable traits throughout the rotation period is therefore crucial to the success of tree improvement programs. Evidently, even small genetically controlled differences in biomass allocation to different tree parts can become decisive factors in determining size and worth of actual yield when accumulated over an entire rotation period (Cannell and Last 1976). In considering these aspects, the present study focuses on the following questions. Can future growth in jack pine provenances be predicted in the juvenile stage and are patterns of geographical variation stable over time? Moreover, do trees of provenances differ in biomass production and biomass allocation to bole wood, stem bark, branches, needles, and cones?

For our study we chose an Ontario jack pine provenance trial at the Petawawa National Forestry Institute (Chalk River, Ontario). Earlier results from this study have been published by Yeatman (1974) and Holst and Yeatman (1961).

Materials and methods

Material

Data were collected in August 1984 in a field test of 12 Ontario jack pine provenances at the Petawawa National Forestry Institute. The trial was established in 1954 with 1+2 transplants (spacing, 1.2 m × 1.2 m) in four blocks of twelve 100-tree plots separated by a single row of jack pine from one seed lot (Hardwick). The soil is a variable podsolic fine sand of moderate fertility. The provenances (Table 1) were obtained from the Ontario Government Tree Seed Plant, Angus, Ontario. Details of seed origin other than place name of origin are unknown. The seed lots were samples of larger bulk collections. Two seed lots (Angus and St. Williams) were collected in southern Ontario from plantations of unknown seed origin. One plot was planted with two provenances (Kabitotikwia Lake and Petawawa) in a 1:1 ratio. The geographic location of the provenances is shown in Fig. 1.

Provenance assessments by the Petawawa National Forestry Institute were completed in 1957, 1958, 1960, 1961, 1969, and 1979 (Yeatman 1974). Additional information on an earlier nursery trial was published by Holst and Yeatman (1961). A low thinning of the plantation was carried out in 1969 and again in 1979. The thinning in 1969 removed 32% of all stems (including snow damaged trees), leaving an average of 57 trees per plot (approx. spacing, 1.6 × 1.6 m). The thinning in 1979 reduced the average plot stem number to 30 (48% of all stems thinned), leaving the trees at an average spacing of 2.2 × 2.2 m.

Methods

Stem diameters of 10 randomly selected trees in each plot were measured with steel calipers at a point 1.3 m above ground level; heights of five of these were measured with a Suunto clinometer.

Aboveground tree biomass was determined on a sample of six trees from each of seven randomly chosen provenances. Of these six trees, two were dominant, two were codominant, and two were intermediate. Trees were selected from the two blocks with the least variation in plot stem numbers.

The field procedures applied to each felled tree, cut at ground level, consisted of the following. (*i*) Recordings of tree height and length of live crown. (*ii*) Determination of an average live crown radius in the upper, middle, and lower thirds of the crown and removal of all living branches from the stem. (*iii*) Recording total fresh weight of foliage plus live branches back to the stem in each of the three crown sections (upper, middle, and lower). Approximately one-third of the crown fresh weight from each crown section was then sampled and reweighed for dry matter determination. (*iv*) Recording stem diameter and cutting of stem disks at tree heights of 0, 0.5, 1.3, and 2.0 m above ground level and for every 2 m thereafter.

In the laboratory, needle-bearing twigs, cones, and branches were dried separately to constant weight in forced-air ovens at 72°C (twigs and needles) and 102°C (branches and cones). Subsequent weighing was done to the nearest 1 g. The weight of foliage and twig wood in the dried twig samples was calculated using an average weight ratio of these components determined from one to five subsamples per crown section.

Wood density of one sanded wood wedge cut from each stem disk was determined by the water immersion method (Smith 1954). The size of the wood wedges ranged from 1 to 50 cm^3. Stem wood density was calculated as a weighted average of the disk densities, the weighting factor being the inside-bark volume of the represented stem

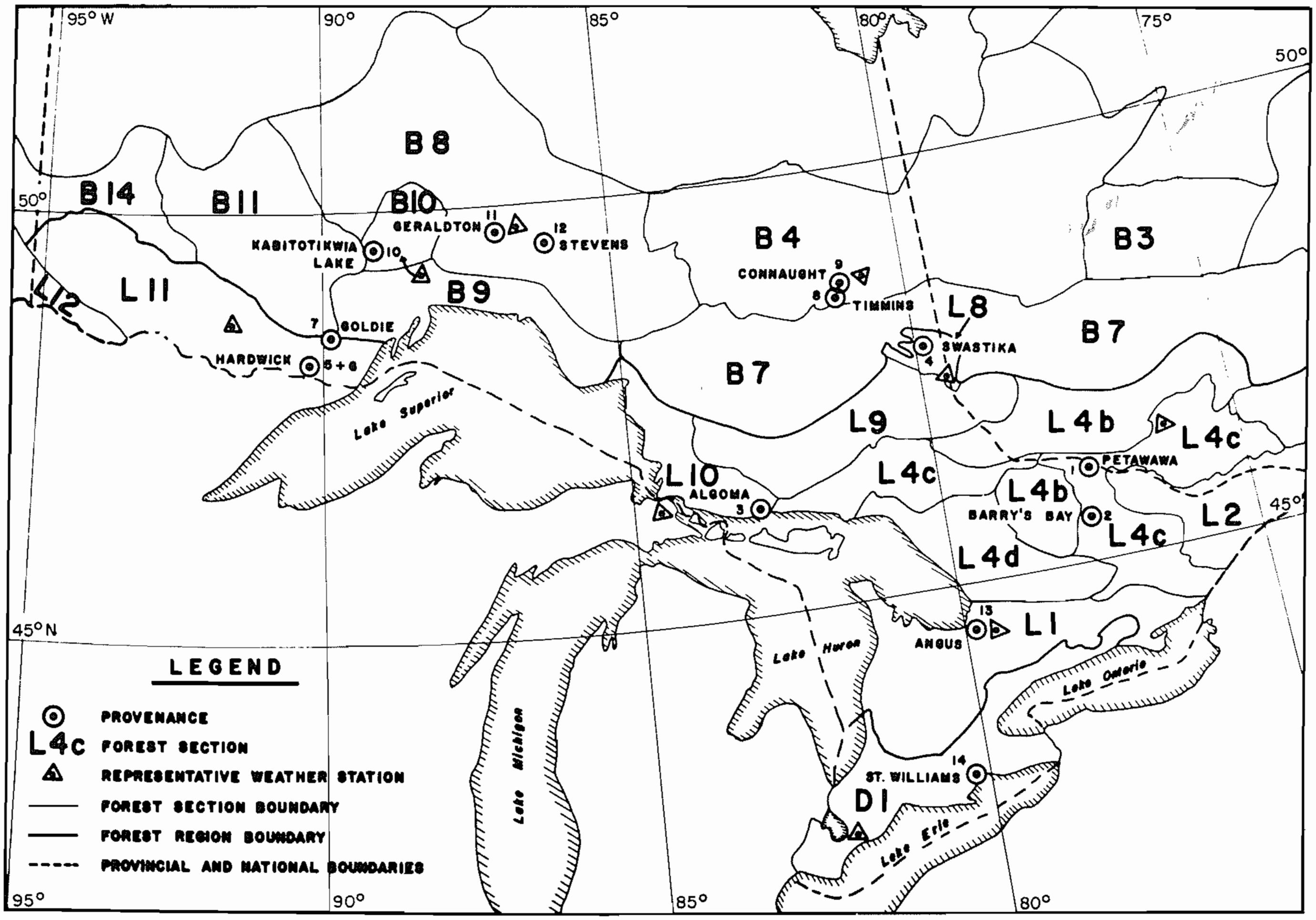

FIG. 1. Geographic location of the Ontario jack pine provenances.

section. Stem volume was calculated by Smalian's formula (Avery and Burkhart 1983).

Errors associated with the methods of measurement are not included in the statistical analyses of the results because they were insignificant when compared with the average within-provenance variance. Statistical significance of the results is indicated as follows: *, $P = 0.05$; **, $P = 0.01$; ***, $P = 0.001$; NS, not significant.

Results

Stem numbers

Provenances varied significantly in numbers of stems remaining at age 34 years (Table 2). The differences among the faster growing provenances arise mainly from the severe snow damage that occurred in the field test during the winters of 1963–1964 and 1967–1968 (cf. Table 1). The taller provenances suffered more from snow breakage than the slower growing provenances (Yeatman 1974). Observations made on excavated root systems indicated that the majority of damaged trees had an unbalanced or eccentric root system. This was a result of severe root pruning of the larger transplants at the time of planting and the close spacing in the plantation (Yeatman 1974). The two thinnings deliberately reduced differences in stem numbers among provenances. In 1984, eight plots had less than 15 trees (average 12) as compared with an average of 30 trees in the remaining 40 plots. Stem numbers per hectare were corrected by excluding these eight plots, thus considerably reducing the variation in stem numbers among provenances (cf. Table 2). These corrected stem numbers are used in the calculations of both volume and biomass per hectare.

Tree height

Mean tree height of the 12 Ontario provenances ranged from 14.7 m in St. Williams to 17.1 m in the Petawawa provenance, differing significantly by 16%. Height growth of three fast- and three slow-growing provenances is shown in Fig. 2. Although differences between the two groups have increased steadily since the establishment of the trial, the separation of provenance mean values has become statistically less well defined with time, particularly among the faster growing seed sources (cf. Yeatman 1974).

The ranking of provenances in terms of height at age 34 years correlated significantly (Spearman's rank correlation coefficient) with the height ranking observed in the nursery, the 1st year in the field, and again with the ranking after 18 years in the field (cf. Fig. 1).

Diameter

Differences in diameter at breast height over bark among provenances were highly significant at 34 years of age, although not as well defined as tree height. The provenance mean quadratic diameters in Table 2 are negatively correlated with latitude and only marginally (nonsignificantly) influenced by differences in stem number per hectare (cf. Table 3). However, the within-provenance correlation between plot stem number and quadratic mean diameter was significant ($\bar{r} = -0.67$**).

TABLE 2. Stem numbers, tree size, and biomass of 12 Ontario jack pine provenances at age 34 years

Provenance	Stem no./ha	No. of plots with less than 15 trees	Corrected stem no./ha[a]	Lorey's height (m)	Quadratic mean DBH (cm)	Absolute form quotient	Average total stem volume (m^3)	Average ovendry above-ground biomass (kg $tree^{-1}$)	Total stem volume (m^3) per ha[b]	Ovendry biomass (t) per ha[b]
Kabitotikwia Lake	(1295)	2	2153	15.5*bc*	13.4*ab*	—	0.144*bcd*	60.2*abc*	310*bc*	130*bc*
Stevens	1648	1	1884	15.2*bc*	12.8*b*	–	0.143*bcde*	60.4*abc*	269*ef*	114*de*
Connaught	2540	—	2540	16.1*abc*	12.5*b*	0.69*b*	0.134*cde*	54.7*abc*	340*ab*	139*b*
Goldie	2035	—	2035	15.2*bc*	12.8*b*	—	0.128*de*	52.3*bc*	260*fg*	106*ef*
Timmins	2105	—	2105	16.5*ab*	13.4*ab*	0.63*c*	0.144*bcd*	58.7*abc*	303*cde*	124*bde*
Hardwick	1830	1	2130	16.4*ab*	13.1*ab*	—	0.138*bcde*	56.7*abc*	294*def*	121*cde*
Swastika	1951	—	1951	17.0*a*	13.3*ab*	0.75*a*	0.169*abc*	68.1*abc*	330*bc*	133*bc*
Algoma	1631	1	1861	16.6*ab*	13.6*ab*	—	0.155*abcd*	63.9*abc*	288*def*	119*cde*
Petawawa	1446	1	1929	17.1*a*	13.5*ab*	0.73*a*	0.167*abc*	66.9*abc*	322*bcd*	129*bcd*
Barry's Bay	2018	—	2018	17.0*a*	14.6*a*	0.70*b*	0.187*a*	78.6*a*	377*a*	159*a*
Angus	1160	1	1300	17.0*a*	14.7*a*	0.69*b*	0.173*ab*	71.3*ab*	225*h*	93*f*
St. Williams	1732	1	2108	14.7*c*	12.0*b*	0.70*b*	0.108*e*	44.4*c*	228*gh*	94*f*
S_x	—	—	—	0.35	0.39	0.03	0.012	5.5	34[c]	16[c]
F-ratio blocks	14.2[d]	—	6.4NS[d]	1.41NS	2.05NS	—	1.22NS	1.19NS	—	—
F-ratio provenances	21.4[d]	—	—	5.72**	4.25**	2.89*	3.70**	2.77**	—	—
Correlation latitude[e]	0.01NS	—	0.32NS	−0.70*	−0.75**	—	−0.77**	−0.76**	−0.54NS	−0.49NS
Correlation growing degree-days[e]	0.37NS	—	−0.40NS	0.61NS	0.60NS	—	0.55NS	0.49NS	0.26NS	0.21NS
$S^2_{provenance}:S^2_{total}$ [f]	—	—	—	0.28	0.21	—	0.18	0.16	—	—

NOTE: Means followed by a common letter do not differ at the 95% probability level (based on the test of studentized range; Snedecor and Cochran 1971). Significance level: *, 5%; **, 1%; ***, 0.1%; NS, nonsignificant.
[a]Excluding plots with less than 15 trees.
[b]Based on corrected stem number.
[c]Least significant difference.
[d]Chi-square values.
[e]Not including Angus and St. Williams.
[f]Variation ratio (see text).

TABLE 3. Analysis of the partial effect of latitude and stem number per hectare on the quadratic mean diameter (10 provenances)

Source of variation	df	SS	MS	F
Latitude and stem number	2	1.87		
Latitude	1	1.68		
Stem number after latitude	1	0.19	0.19	0.19/0.16 = 1.2NS
Stem number	1	0.21		
Latitude after stem number	1	1.66	1.66	1.66/0.16 = 10.4***
Deviation (predicted−observed)	7	1.15	0.16	

NOTE: SS, sum of squares; MS, mean square. Significance levels are indicated as in Table 2.

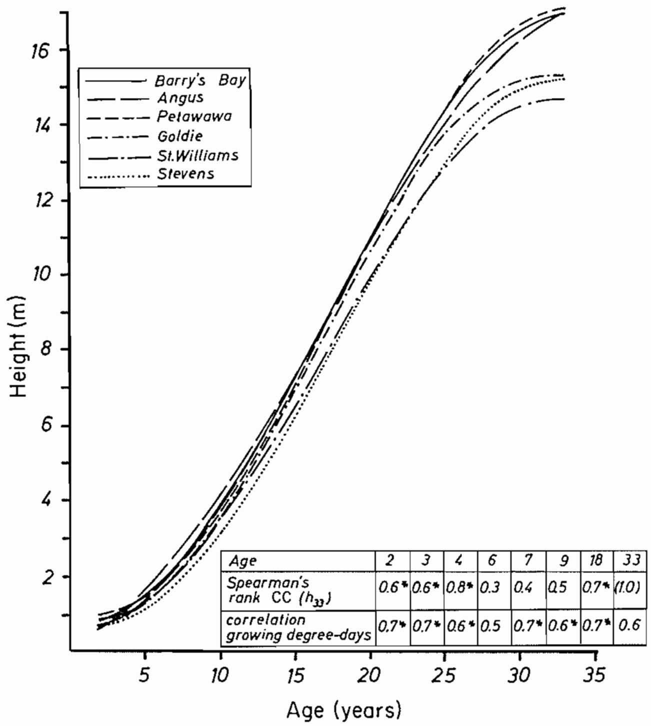

FIG. 2. Tree height growth of three fast- and three slow-growing provenances. Curves depict third degree polynomials derived from regression on eight paired values of height and age. Correlations are based on the 10 provenances with known origin (CC, correlation coefficient).

Stem volume

Stem volumes (V) of all trees with known heights (H) and diameters (DBH) were estimated with the following regression model (SEE, standard error of the estimate):

$$[1]\quad V = 3.8563 \times 10^{-5} \times H^{1.3905} \times \mathrm{DBH}^{1.7411}\ (\mathrm{SEE} = 8\%,\ R^2 = 0.96)$$

The volume equation was derived from the 42 felled trees. A statistical analysis of the regression residuals revealed no differences in the overall fit among the seven sampled provenances ($F_{6,35} = 0.2$NS). A correction factor of 1.003 for negative bias is incorporated in the volume expression (Baskerville 1972; Lee 1982).

Mean tree volume, calculated using the common regression model, varied significantly among provenances (cf. Table 2) and followed a rank order similar to that of tree height and diameter. Mean tree volume of the St. Williams plantation provenance was 42% less than that of Barry's Bay, the top-ranking seed source. The latter exceeded the local Petawawa provenance by 12%, but the difference was not statistically significant. Note that the average stem volume in Angus is 8% less than in Barry's Bay despite almost identical average volume factors of height, diameter, and form quotient. This result can be explained by differences in the covariance of these factors (Cunia and Michelakackis 1983).

Form quotient

The absolute form quotient, calculated as the ratio of stem diameter at half the tree length above breast height to diameter at breast height (1.3 m), varied significantly among provenances (cf. Table 2). The variation in absolute form quotients partly reflects significant differences found in the height−diameter relationship among provenances (not shown). The inclusion of the absolute form quotient in the above stated volume expression brought only an insignificant improvement in the overall fit.

Aboveground biomass

The ovendry aboveground tree biomass (TBM), i.e., dry matter of bole wood, stem bark, and live crown, was estimated for all trees with known height and diameter (i.e., 12 × 20) with the following formula:

$$[2]\quad \mathrm{TBM} = 0.02101 \times H^{1.234} \times \mathrm{DBH}^{1.7308}\ (R^2 = 0.93,\ \mathrm{SEE} = 10\%)$$

The equation was derived from the sample of 42 trees. A statistical analysis of regression residuals revealed no differences in goodness of fit among the seven sampled provenance means ($F_{6,35} = 0.61$NS) or in provenance residual variances ($\chi^2_{[6]} = 3.61$NS).

Provenance averages of aboveground biomass per tree, calculated using the above formula, ranged from 44 kg in the St. Williams provenance to 79 kg in Barry's Bay (cf. Table 2). The differences among the provenances were highly significant but statistically not well defined owing to a considerable standard error of 5.5 kg.

The aboveground biomass was distributed as follows:

	% biomass
Stem	
Bole wood	78
Bark	8
Total	86
Crown	
Branch wood	8
Foliage	5
Cones	1
Total	14

TABLE 4. Wood density, stem volume, and bark characteristics of seven Ontario jack pine provenances

Provenance	V_{ub} (m^3)	Bark (% of stem volume)	Bark thickness at breast height (mm)	Average stem wood density ($kg\ m^{-3}$)	Average stem wood mass (kg)
Connaught	0.122	9.1*b*	2.9*b*	400	49*ab*
Timmins	0.130	9.4*b*	3.4*b*	396	51*ab*
Swastika	0.151	10.7*ab*	3.7*b*	385	58*ab*
Petawawa	0.149	10.6*ab*	4.2*b*	387	58*ab*
Barry's Bay	0.167	10.9*ab*	4.1*b*	373	62*a*
Angus	0.151	12.7*a*	5.5*a*	385	58*ab*
St. Williams	0.097	10.5*ab*	3.1*b*	401	39*b*
S_x	0.011	0.7	0.4	9.5	4.8
$F_{provenance}$	3.42**	2.65**	5.00**	1.13NS	—

NOTE: Means followed by a common letter do not differ at the 95% probability level. Significance levels are as indicated in Table 2.

This distribution was found to be similar in all sampled provenances. A variance test of homogeneity (Snedecor and Cochran 1971) revealed only random fluctuations in dry matter partitioning among provenances.

Volume and biomass per hectare

Stem volume and biomass per hectare varied significantly among provenances, but were only weakly correlated to latitude or length of growing season at the place of origin. The best provenance, Barry's Bay, exceeded the local Petawawa provenance by 17% (statistically significant). The Petawawa provenance ranked third in stem volume per hectare and fifth in biomass accretion.

Wood density

The average ovendry stem wood weight per unit of "green" volume varied on the provenance level from 373 to 401 kg m^{-3} (cf. Table 4). Most of the variation among provenances was attributable to a negative correlation between average stem volume under bark (V_{ub}, cubic metres) and average stem wood density (SWD, kilograms per cubic metre). The relationship found was as follows:

$$[3] \quad SWD = 444.6 - 398 \times V_{ub} \ (R^2 = 0.86^{**})$$

Accordingly, the expected stem wood mass (SWM, kilograms per tree is

$$[4] \quad SWM = 444.6 \times V_{ub} - 398 \times V_{ub}^2$$

This latter function shows a diminishing increase in stem wood mass with increasing stem volume within the range of stem sizes found in this trial. Hence, the best volume producers were also the best producers of wood mass.

The analyses of wood densities also showed a significant between- and within-tree variation ($S_{within} = 34$ kg m^{-3}, $S_{between} = 23$ kg m^{-3}). The within-tree variation was caused mainly by a significant negative gradient in density from the base to the terminal shoot which averaged −5.7 kg m^{-3} m^{-1}. Wood density at breast height ($WD_{1.3}$) correlated strongly with the average stem wood density ($SWD = 0.94 \times WD_{1.3}$, $R^2 = 0.72^{**}$).

Bark thickness

Bark thickness at breast height and bark volume (per cent of total stem volume) were found to vary significantly among provenances (cf. Table 4). In the five sampled provenances with known origin, bark thickness and bark volume percent correlated negatively with latitude ($r < -0.74$). When adjusted for the influence of diameter (under bark), the correlation was slightly stronger ($r \leq -0.77$). The correlations were significant on the 3% level (bark thickness) and 16% level (bark percent), respectively.

Influence of origin on tree size

Latitude of origin explained 50–70% of the variation in average tree size (i.e., height, diameter, and stem volume) and biomass among provenances. This result is based upon the squared values of the correlation coefficients shown in Table 2. The greatest tree size and aboveground biomass were found in provenances from the southernmost regions (i.e., Barry's Bay, Petawawa, and Algoma). The two northernmost provenances, Stevens and Kabitotikwia Lake, performed somewhat better than expected, considering their latitude of origin. The opposite was true of the provenances Goldie and Connaught.

In contrast to latitude, the number of growing degree-days at the place of seed origin explained less than one-third of the variation in provenance averages of tree size and biomass variables (cf. Table 3).

The variance ratio $S^2_{provenance} : S^2_{total}$ (cf. Table 3) was largest in tree height, indicating that this variable reflects genetic differences among provenances better than the other tree size variables.

Stem volume growth

Gross total stem volume production ($\sum I_{v,total}$) per hectare in the provenance trial varied according to the average height of dominant and codominant trees (H). The relationship found was

$$[5] \quad \sum I_{v,total} = 3.524 \times (H - 1.3)^{1.76} \ (SEE = 6.3\%)$$

For the remaining stand (rem), the equation reads as follows:

$$[6] \quad \sum I_{v,rem} = 3.308 \times (H - 1.3)^{1.72} \ (SEE = 8.1\%)$$

These two equations are based upon calculation of plot values of height and total stem volume production in 1961, 1969, 1979, and 1984. Only 35 plots that were considered fully stocked throughout this period were included in the calculations. Excluded were plots with less than 15 trees in 1984, 20 trees in 1979, and 30 trees in 1969. Volumes in 1961 and 1969

TABLE 5. Mean annual stem volume increment (cubic metres per hectare per year) by provenance

Provenance	Growth periods (years) 0–10	10–20	20–30
Barry's Bay	1.6	15.0	15.3
Angus	2.0	16.3	16.4
Petawawa	1.4	14.8	16.0
Goldie	1.4	13.6	10.6
St. Williams	1.2	12.0	11.0
Stevens	1.0	12.2	12.5

were calculated using form-class volume tables (Berry 1981). The remaining volume calculations are based upon Eq. 1. Dead trees removed in thinnings in 1969 and 1979 have been assigned the same average size as the thinned trees.

Plotted values of height and total stem volume production indicated that the formulae shown above apply equally well in all provenances. Variations among provenances in stem volume growth can therefore be assessed directly from provenance differences in height growth.

The mean annual volume increment (remaining stand) of three fast- and three slow-growing provenances are listed in Table 5.

Table 5 shows considerable differences among the fast- and slow-growing provenances. The mean annual increment of the three fastest growing provenances exceeded that of the slowest growing provenances by 22% in the age interval from 10 to 20 years and by 40% during the following decade. These values represent, of course, an ideal situation of fully stocked stands. However, they emphasize the great variation in production potential among provenances.

Discussion

Tree size in the 10 provenances from natural stands at the age of 34 years was significantly related to latitude of origin, which accounted for approximately 50–70% of the variation in tree height, quadratic mean diameter at breast height, and stem volume. The number of growing degree-days above 5.6°C at origin, in contrast, explained only 14–37% of the variation in tree size variables.

A comparison of the results presented herein with those obtained at earlier stages (Holst and Yeatman 1961; Yeatman 1974) shows that the influence of geographic origin on tree size has been more or less constant since the beginning of this provenance trial. Hence, juvenile growth is a reliable indicator of tree size and geographical variation in provenances of jack pine nearing economical maturity. These results do not necessarily apply to families within provenances.

Contrary to the prevalent trend in the provenance trial towards a negative correlation between tree size and latitude of origin, persistent significant differences among some geographically close provenances indicated a high potential for selection among populations within site regions (Jeffers and Jensen 1980; Skeates 1979; Yeatman 1974).

The growth performance of trees of unknown origin cannot be predicted. From the accumulated growth records it seems probable that seed for trees in the St. Williams plantation was collected in a boreal location with a cool climate (Yeatman 1974). Seeds for the Angus plantation were most likely collected in a southerly location with a relatively warm climate.

The marked variation in provenance averages of aboveground biomass per tree reflected provenance differences in tree height as well as diameter. Zavitkovski *et al.* (1981) came to a similar conclusion in a jack pine provenance trial in the Lake States, in which they were able to predict provenance aboveground biomass from diameter at breast height alone.

Equations predicting jack pine biomass from tree height and diameter are available in great numbers (e.g., Alemdag 1983; Ker 1980; Ouellet 1983; Singh 1984; Stanek and State 1978); however, without the incorporation of age, site, and stand factors, these equations apply only to the locality from which they are derived (Ouellet 1983; Zavitkovski *et al.* 1981).

The allocation of only 14% of the aboveground biomass to the crown seems to be a typical feature found in many medium-aged jack pine stands in Canada and the Lake States (Alban and Laidly 1982; Alemdag 1983; Doucet *et al.* 1976; Hegyi 1972; Ker 1980; Singh 1982, 1984). Silvicultural treatments may, of course, drastically effect the expression of this inherent characteristic (Adams 1928; Albrektson 1980; Morrison 1973).

The mean annual accretion of approximately 10 m^3 stem volume and 4 t aboveground dry matter per hectare demonstrates clearly the great production potential of superior jack pine provenances (Cannell 1982; Peterson *et al.* 1983; Smith 1982). Conversely, the large differences between provenances indicate the near catastrophic losses that can result from planting ill-adapted provenances (Jeffers and Jensen 1980; King 1981; Yeatman 1976).

Jack pine stem wood density is usually found to range from 370 to 490 kg m^{-3} (Alemdag 1984; Panshin and Zeeuw 1980). The values obtained in this study lie in the lower half of this range. Both the considerable within- and between-tree variations in wood density are common findings in most species (Alemdag 1984; Panshin and Zeeuw 1980). In summary, our biomass findings showed no difference between jack pine provenances in biomass allocation to foliage, branches, cones, stem, and bark. Furthermore, it was established that differences in biomass production can be deduced from tree height and diameter alone. Stem wood mass showed less variation among provenances than volume growth owing to the combined effect of a genetic control of bark thickness and a negative correlation between stem wood density and stem volume.

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