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Provenance Hybrids in Jack Pine: 15-Year Results in Eastern Canada

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Summary

Results of height growth, stem form, injury, and branch angle at age 15 (16 in one case) are reported for 26 jack pine provenance hybrids and 16 control provenances on six sites in eastern Canada. Variations in stem form, tree status, and branch angle were comparable in hybrids and provenances, with greater differences among provenances and hybrids than between the two groups. Hybrid height growth adjusted for the effects of damage was, as a rule, intermediate to that of its control provenances; hybrids captured on an average 68% of the difference between control provenances. No hybrid exceeded significantly the best control provenance. Examples of hybrid or provenance tree heights in excess of results obtained with local unimproved seed sources were very rare. A strong genotype × environment interaction of tree height on five sites could be isolated to 11 of the 37 tested entries. These entries had below average rank stability and above average regression coefficients of height versus local height. Hybrids had environmental stability intermediate to that of the control provenances.

Key words: *Pinus banksiana*, provenance, population-hybrids, stem, form, branch angle, height adjustment, genotype × environment interactions, stability analysis.

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Zusammenfassung

Es wird über das Höhenwachstum, die Stammform, Schäden und den Astwinkel im Alter von 15 (in einem Fall 16) Jahren von 26 Hybriden der Bankskiefer und 16 Kontrollprovenienzen, die auf sechs Orten in Ostkanada stocken, berichtet. Die festgestellte Variation bei der Stammform, dem Baumstatus und dem Astwinkel war bei Hybriden und Provenienzen vergleichbar, wobei aber größere Unterschiede zwischen Provenienzen und Hybriden auftraten als zwischen den beiden Gruppen. Nach Adjustierung des Höhenwachstums der Hybriden in bezug auf Schadefekte war dieses in der Regel intermediär zu den Kontrollprovenienzen. Die Hybriden lagen im Durchschnitt bei 68% der Differenz zwischen den Kontrollprovenienzen. Kein Hybrid war der besten Kontrollprovenienz signifikant überlegen. Beispiele, in denen die Höhe von Hybriden oder Provenienzen über der der lokalen, züchterisch nicht bearbeiteten Saatkunft lag, waren sehr selten. Eine starke Genotyp-Umwelt-Interaktion der Baumhöhe auf fünf Standorten konnte überwiegend auf 11 der 37 Versuchsglieder zurückgeführt werden. Diese Versuchsglieder hatten eine unterdurchschnittliche Rangstabilität und einen über dem Durchschnitt liegenden Regressions-Koeffizienten der Höhe gegenüber der lokalen Höhe. Hybriden hatten eine gegenüber den Kontrollprovenienzen intermediäre Umweltstabilität.

Schlagwörter: *Pinus banksiana*, Provenienz, Populationshybriden, Höhe, Stammform, Astwinkel, Höhenadjustierung, Genotyp-Umwelt-Interaktion, Stabilitätsanalyse.

Introduction

Interest in intervarietal or provenance hybrids in forest tree improvement programs is mainly focused on capturing hybrid vigour and combining desirable parental traits. Hybrid vigour, defined here as the deviation from the mid-parent value (KNIGHT, 1973) achieved in agricultural crops (for example CRESS, 1966; MOLL *et al.*, 1965), sparked interest in forest tree hybridization (NILSSON and ANDERSON, 1970; STUBER, 1970). Crosses of parents from different geographic regions produce new genotypes otherwise not found in nature nor achievable by selection (FOWLER, 1978; WOESSNER, 1972; WRIGHT, 1964). In forestry, the possibility of combining fast growth rates in provenances from favourable climates with the "hardiness" (climatic, pest, and diseases) of provenances from more severe environments has been pursued as a means to augment slow tree growth in adverse environments. Attempts to achieve this by creating provenance hybrids has been undertaken within major commercial tree species (KRAUS, 1986; MORGENSTERN, 1973; NIKLES *et al.*, 1987; NILSSON, 1973; REHFELDT, 1977; WOESSNER, 1972; YING and MORGENSTERN, 1982). Ideally, hybridization is also suited to reintroduce genetic variation (NIKLES, 1984; GERHOLD and PARK, 1986) or to combine fast juvenile growth with fast mature growth (EKBERG *et al.*, 1982; WOESSNER, 1972).

Hybrid vigour is a complex genetic phenomenon that results from a wide range and combinations of gene effects. Genetic theory deals generally only with additive and dominant effects although epistatic interactions between gene loci also are known to be manifest (JINKS and JONES, 1958). Obviously gene allelic differences between parents are a prerequisite (FALCONER, 1981), but crossing too distant parents may lead to reduced vigor in offspring due to genetic imbalance (FALCONER, 1981). Hybrid vigour is sometimes considered the reverse of inbreeding depression (JINKS and JONES, 1958; FOWLER, 1978) and is commonly manifest when outcrossing inbred lines (FALCONER, 1981). Although the general combining ability (GCA) is generally much higher than the specific combining ability (SCA) in forestry hybrid-trials (EKBERG *et al.*, 1982; PARK and GERHOLD, 1986; NILSSON and ANDERSON, 1970; SKRØPPA, 1979) the prediction of hybrid vigour has been hampered by complex interactions with age and environment (ZOBEL and TALBERT, 1984).

The value of provenance hybridization is controversial in today's forest tree improvement technology. In spite of the promising potential, results obtained so far have failed to fulfill expectations (FOWLER, 1978). Four reasons are given. First, no general superiority is to be expected from hybrids when compared to the best parent (EKBERG *et al.*, 1982; GERHOLD and PARK, 1986; HOLST and FOWLER, 1973; MORGENSTERN, 1973; NILSSON and ANDERSON, 1970; WOESSNER, 1972; YING, 1978; YING and MORGENSTERN, 1982; ZOBEL and TALBERT, 1984). Second, the occurrence of hybrid vigour is difficult to predict (KNIGHT, 1973; REHFELDT, 1977; WRIGHT, 1964). This is especially so when fast and slow growing provenances occur at random within seed zones (HOLST and FOWLER, 1973). Third, if a cross is made between two populations adapted to different environments, it is likely that the hybrid excels in "hybrid" environments, intermediate or different from those associated with the parental genotypes and in which the species is not favored by nature (FALCONER, 1981;

FOWLER, 1978; MORGENSTERN, 1973; NIKLES, 1987; YING, 1978). Fourth, operational breeding and breeding strategies with intervarietal hybrids are more expensive and more complex than traditional approaches (FOWLER, 1978; STUBER, 1970; WRIGHT, 1964).

Our knowledge today about performance of forest tree provenance hybrids is still fragmentary and results have been almost exclusively obtained in juvenile populations (GERHOLD and PARK, 1986; MORGENSTERN, 1973). In this study we present 15-year results of height growth on six sites in eastern Canada of 26 jack pine provenance hybrids. The results presented here will be supportive in developing the most efficient breeding program for this important commercial species which has shown a strong clinal geographic differentiation of growth, phenology, and hardiness associated with latitude and climate (MORGENSTERN and TEICH, 1969; YEATMAN and MORGENSTERN, 1978). Jack pine with its wide natural range (RUDOLPH and YEATMAN, 1982) is an excellent candidate for wide crosses. Its frequent occurrence in well separated populations with little or no continuity sets the potential for exploration of performance of provenance hybrids (BENZIE, 1977; SKEATES 1979; YEATMAN, 1966; YEATMAN and MORGENSTERN, 1978).

Materials and Methods

Crossing Design

A total of 26 jack pine provenance hybrids are included in this study (Table 1). Controlled pollination crosses were made in 1961 on seven-year old parental trees from 19 provenances growing in the Petawawa National Forestry Institute (PNFI) pine graft arboretum. Further details of the crossing design are given in Table 1. The geographic origin of parental provenances is illustrated in Figure 1 (Id.-no. as in Table 1). Pollen used in individual crosses were pollen mix from 10 trees. Pollination was done on a minimum of five selected trees in each cross. All staminate strobili were removed from the provenance planting prior to pollination. Of the 26 provenance hybrids, 14 were made on open flowers with airborne pollen of the local provenance (Petawawa Plains, Ontario) as pollen donor. All hybrids are considered as wide crosses.

An additional 16 "control" provenances were included to obtain the best available estimate of the parental provenances (Table 1). A direct comparison of hybrids versus parental provenances was generally not possible owing to the lack of seed from identical provenance sources. However, care was taken to ensure that the control provenances were the most appropriate choice with respect to similarity of climatic and edaphic conditions (ROWE, 1972). Control provenances were grown from seed collected in 1958 to 1960 for a range-wide provenance trial (Holst¹), 1967, unpubl.). The geographic origin of control provenances is illustrated in Figure 1 (Id.-no. as in Table 1).

Experiments

Three-year-old seedlings (2-1) were outplanted manually in the spring of 1966 at a 1.8 m × 1.8 m spacing on six sites (Fig. 1). The experimental layout on five sites was that of a completely randomized split-plot design with three replications (blocks). Each plot contained one provenance cross and two control provenances arranged in three five-tree rows. The number of initial plants on each of these sites was 25 (provenance-crosses) × 3 (replicates) ×

¹) "All-range jack pine provenance experiment", Dept. For. and Rural Development. Internal Report PET-PS-6. 144 pp.

Table 1. — Provenance crossing design and control provenances used to obtain parental values.

Id. No.	Maternal provenance	Pollen donor (by provenance Id-no.)														Control provenances (Id-no.)			
		17	18	19	20	21	22	23	24	25	26	27	28	29	30		31	32	33
17	Somerset Co., ME							X								X ²	X ¹	Spencer Lake, ME	(3)
18	Cumberland Co., NS							X									X ¹	Thomson Station, NS	(1)
19	Northumberland Co., NB							X			X ¹						X ¹	Cains River, NB	(5)
20	Danville Tp., PQ							X										Taillon Peninsula, PQ	(4)
21	St. Zenon, PQ							X										St. Louis de France, PQ	(7)
22	Opawica Dist., PQ							X										Downs Lake, PQ	(12)
23	Angus, ON							X										Marl Lake, MI	(8, 10)
24	Petawawa Plains, ON							X										Petawawa Plains, Goulais River, ON	(10)
25	Spanish River, ON							X										Goulais River, ON	(9)
26	Timmins, ON							X										Lac Villebon, PQ	(12)
27	Crawford Co., MI							X										Marl Lake, MI	(11)
28	Vilas Co., WI							X										Nokomis, WI	(11)
29	Marinette Co., WI					X ¹		X ¹										Nokomis, WI	(11)
30	Oneida Co., WI			X ²				X ¹										Nokomis, WI	(13)
31	Becker Co., MN							X ¹	X ¹	X ¹	X ¹						Cass Lake, MN	(14)	
32	Sandilands, MB			X ¹	X ¹			X										Hadashville, MB	(7)
33	Manouan Lake, PQ							X										Downs Lake, PQ	(15)
34	Smith, AB			X ²				X										Lac la Biche	(16)
35	Fort Smith, NT							X										Fort Smith, NT	

1) Not planted at Blackville, NB.
 2) Not planted at Swastika, Clova, and Blackville.
 3) Planted only at Swastika and Clova.

5 (trees per row) × 3 (1 cross + 2 control rows) = 1,125. A double surround row of a local provenance was planted about the perimeter. On the sixth site in Blackville, NB, a completely randomized block design with 11 provenance crosses and 11 control provenances was established with 6 replicates (blocks) of 22 plots. Each plot had 4 × 10 trees (spacing 1.8 m × 1.8 m) of a single provenance or cross. All provenance crosses had Petawawa Plains, ON, as the pollen donor. In the spring of 1967 dead or missing plants were replaced with seedlings held over in the PNFI nursery. Between 100 and 300 seedlings were replaced on each site. Regulation of competing vegetation was repeated in 1968 and 1969.

Measurements

Height in 1973 (age 10) and height and diameter in 1978 (age 15) were measured on five sites; at the Sturgeon Lake site measurements were taken at age 10 and 16. In addition, trees were classified according to status, agent of damage, stem form, and branch angle (Table 2).

Statistical Analyses

1. Tree status, damage, stem form, and branch angle

In order to test whether the proportion of single leader trees, trees without damage, trees with straight stem, or trees with variable branch angle was the same in both hybrids and provenances, we performed statistical tests on the departures from the following log-linear model (cf. BISHOP *et al.*, 1972):

$$[1] \text{Log}_e(P_{ijk}/(1-P_{ijk})) = m_i + a_{ij} + b_{ik} + e_{ijk}, \quad i=1,2,3,4, \quad j=1,2,3, \quad k=0,1$$

where P_{ijk} is the observed proportion of hybrid ($k = 1$) or provenance ($k = 0$) trees with either single leader ($i = 1$), no damage ($i = 2$), straight stem ($i = 3$), or variable branch angle ($i = 4$) in the j th block; m_i is the grand mean of trait i ; the terms a , b , e stand for the effects of blocks, hybrids and errors, respectively. Statistical tests of the hypotheses $H_{01}:m_i = 0$; $H_{02}:a_{i1} = a_{i2} = a_{i3}$; $H_{03}:b_{i0} = b_{i1}$; and $H_{04}:e_{ijk} = 0$ (model fit) were tested against the alternative hypotheses $H_{A1}:m_i \neq 0$, $H_{A2}:a_{ij} \neq a_{ij}'$, for at least one block com-

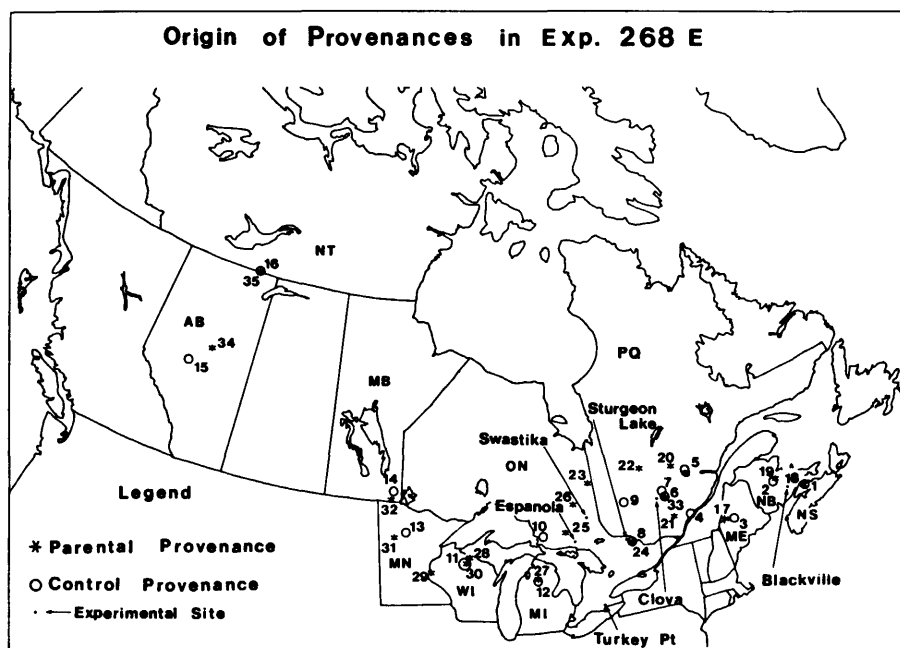


Fig. 1. — Provenance origins and experimental sites.

Table 2. — Tree classifiers used to describe status, damage, stem-form, and branch angle at age 15.

status	damage	stem-form	branch angle
single leader	none	straight	uniform wide, >60°
double leader	rodent	slight bend	variable, 30°-60°
multiple leader	insects	ripples/repeated ripples	uniform acute, <30°
damage on current apic. bud	fungi	wave	
damage on last year's apic. bud	man-made	crooked	
runt	frost		
dying	snow		
dead	cut		
missing	not identified		

parison, $H_{0A3}:b_{j0} \# b_{j1}$ and $H_{A4}:e_{ijk} \# 0$. Chi-square distributed test statistics were derived for each hypothesis by ordinary least squares analysis of model residuals and compared to table values at prescribed significance levels. Significance of site effects were tested with ordinary t-tests.

Statistical assessments of the effect of the tree status, damage, stem form, and branch angle on height growth were carried out with t-tests assuming unequal variances and unequal sample sizes.

2. Data screening for height analyses

Analyses of height were done on reduced data sets. Excluded were: (i) runts, dead and dying trees, (ii) plots with less than six trees at age 15 or 16, (iii) row plots with only one tree left at age 15(16), (iv) extreme outliers. The latter was defined as a row-plot mean value exceeding the mean of the two remaining rows of a given entry by more than three times the population standard deviation. Rows were excluded when a subsequent t_{max} -test was significant at the 0.01% level (SNEDECOR and COCHRAN, 1971, p. 157). The data screening process eliminated between 7% (Sturgeon Lake and Blackville) and 41% (Clova) of the initially planted trees from further analyses. Approximately 60% of the trees included in the height analyses were single leader trees without any apparent damage.

3. Adjustment of observed height to potential height

With only three replicates and five trees per plot the height growth results were confounded by random extraneous effects of tree status and damage. To obtain the best estimate of the growth potential of the test material, it was deemed necessary to adjust tree height for these effects. Adjustments to an undamaged single leader status were done by analysis of covariance (AOCV) with a height index reflecting the combined tree status and appearance as a covariate. The height index was construed in the following manner: First, each combination of tree status and agent was ranked in ascending order of mean height. Second, ranks were converted into fractional ranks by dividing each rank by the number of ranked groups. Henceforth we shall refer to these fractional ranks as height indices. The linear model describing the effect of height index (X) on tree height (Y) was computed by weighted least squares (WLS) regression (DRAPER and SMITH, 1981) with weights proportional to the number of trees in each group and inversely proportional to their standard deviation of tree height. Equation [2] describes the model.

$$[2] Y_{ijk} = \theta + \alpha_i + \delta_j + \bar{\beta}_i \cdot X_{ijk} + \epsilon_{ijk}$$

where Y_{ijk} is the mean height of the k th tree in entry i (a provenance or a hybrid) in block j ; θ is the intercept, α_i is the effect of entry i and δ_j is a block effect; the term $\bar{\beta}_i \cdot X_{ijk}$ denotes the effect of the height index X_{ijk} on tree height. $\bar{\beta}_i$ is the average within block regression coefficient

(slope) of entry i . ϵ_{ijk} is an error term assumed independent and normal distributed with mean zero and common variance σ^2 .

Homogeneity tests of regression coefficients for provenances and hybrids in the linear relationship between observed height and height index, indicated on four sites that it was consistent to use only a single average slope coefficient. In the Swastika data, however, differences among slopes were significant at the 5% level. A separate analysis of provenance regressions disclosed two extreme slopes in the Opawica \times Petawawa and the Sandilands \times Cumberland hybrids. Deleting these two entries in the analysis of covariance decreased the F-value from 1.43* to a non-significant 1.03 n.s. ($df = 35, 735, P(F > F_{obs}) = 0.41$). Owing to the negligible effect of these two hybrids on the overall regression and their minor net height adjustments we decided to ignore these differences in provenance slopes and adjust with only a single regression coefficient. Each tree included in the analyses had subsequently its height adjusted to a height index of 1.0.

4. Estimates of local height

For each test-site, estimates of expected tree height of well adapted local provenances were provided by 3 to 4 provenances growing in a range wide jack pine provenance test (YEATMAN, 1974). This experiment was also established in 1966 and it is adjacent to or within a short distance from the sites of the provenance hybrid study. With its 6 to 9 replications of 6- or 10-tree row-plots this range wide experiment provides reliable and independent estimates of local height that were little influenced by any visual damage. Corrections for local site differences between experiments were done by multiplying the local height estimates obtained in the range wide experiment with an experimentwise height ratio derived from 10 to 15 provenances common in the two experiments. The standard errors of the ensuing local height estimates were computed using Gauss' law of error propagation and data on standard errors of provenance means obtained from the range-wide experiment. Standard errors computed this way varied from 2% in Turkey Point and Swastika to 6% and 7% in Blackville und Clova, respectively.

5. Analysis of adjusted heights

The hypothesis of all provenance and hybrid means on a given site being equal was tested by an F-test based on Yates' weighted squares of means technique (Type III analysis, (MILLIKEN and JOHNSON, 1984)) using weighted row-plot means of adjusted heights. Weights of row-means were proportional to the number of trees in the row and inversely to the variance of row tree heights. The latter was deemed appropriate due to a general lack of variance homogeneity (test: Levene, Box, Bartlett, (MILLIKEN and JOHNSON, 1984)). The assumption of normally distributed height data was reasonable on five sites. A strong violation

($\alpha < 0.01$) of this assumption was only observed in two out of every ten entries.

Population marginal means (MILLIKEN and JOHNSON, 1984) of adjusted tree height were compared against the estimate of local height (cf. section 3). Test of significant departure from this local average was done with student's *t*-test assuming unequal variances and sample sizes equal to the effective number of replicates of each mean value, (degrees of freedom were obtained using Satterthwaite's method (SATTERTHWAITE, 1946)).

6. Comparing hybrid performance with controls

Adjusted height comparisons of hybrids versus controls were done on a plot basis. From each plot two linear contrasts were computed with a subsequent one-way analysis of variance on the resulting estimates. The first contrast calculated as: $H_{\text{hybrid}} - (H_{\text{control1}} + H_{\text{control2}})/2$ is a measure of hybrid deviation from the 'mid-parent' performance. The second contrast: $H_{\text{hybrid}} - \max(H_{\text{control1}}, H_{\text{control2}})$ gives the difference in height between a hybrid and its tallest control parent. Significance of individual contrasts were assessed with a student's *t*-test (assuming unequal variances). In the Blackville trial contrasts were estimated from the overall test results in the usual manner (SNEDECOR and COCHRAN, 1971, p. 269).

A general assessment of hybrid performance was derived from the regression model:

$H_{\text{hybrid}} = H_{\text{min(control)}} + \beta(H_{\text{max(control)}} - H_{\text{min(control)}})$
The model is a modification of the multiple regression analysis approach of hybrid vigor advocated by KNIGHT (1971).

Hence, a β -value above 1.0 indicates a cross value that exceeds both control values, i.e. true heterosis.

7. Genotype by environment analyses

Genotype-environment analyses were performed on a subset of 37 provenances and hybrids common on five sites (excluding Blackville, NB). Two models adopted from FREEMAN and PERKINS (1971) were applied.

I: $Y_{ijk} = \mu + d_i + \epsilon_j + g_{ij} + e_{ijk}$ where
 μ = grand mean over all replicates(k), genotypes (i) and environments (j)

d_i = additive contribution of the *i*th genotype ($i=1,2,\dots,37$)
 ϵ_j = additive environmental contribution of the *j*th environment ($j=1,2,3,4,5$)
 g_{ij} = genotype-environment interaction of the *i*th genotype in the *j*th environment
 e_{ijk} = residual variation contributed by the *k*th replicate ($k=1,2,3$) of the *i*th genotype in the *j*th environment

The second model includes the estimated local height (X_j) as a measure of the environment:

II. $Y_{ij} = \mu + d_i + \bar{\beta}X_j + \epsilon_j + (\beta_i - \bar{\beta})X_j + \delta_{ij}$ where
 $\bar{\beta}$ = the average slope in the regression of $Y_{.j}$ on X_j
 X_j = environmental index as the mean of local heights of site *j*
 ϵ_j = deviation of $Y_{.j}$ from the combined regression line
 β_i = slope of regression Y_{ij} on X_j
 δ_{ij} = deviation of the *i*th line from its linear regression on X_j the *j*th environment less ϵ_j

A maximum number of entries that showed no significant $G \times E$ interaction was found by a "maximum linkage" cluster algorithm (see LIN (1982) and SOKAL and MICHENER (1958) for details²).

As an index of height rank stability over sites we used HÜHN'S S_1 index (HÜHN, 1979):

$$[3] S_{.i} = 2_j \bar{\epsilon}_{ij} / r_{ij} - r_{ij} / n(n-1)$$

i denotes an entry (i. e. provenance or hybrid) and r_{ij} its rank in the *j*th environment ($j = 1, 2, \dots, n$). A high index value indicates an unstable provenance or hybrid.

Results

Tree status

Results of the tree status classification on five sites showed that 52% to 70% were single-leader trees (Table 3). This group encompasses about 80% of all trees free of any observed damaging agent. The proportion of single-leader trees was significantly higher at Swastika than at Black-

²) A Fortran algorithm is available from the senior author upon request.

Table 3. — Relative distribution (%) of trees, by status at age 15.

Tree status	Turkey Point,	Espanola,	Swastika,	Clova,	Blackville,
	ON %	ON %	ON %	PQ %	NB %
Single leader	55.3	51.6	69.7	54.3	59.5
Double leader	4.6	10.2	8.3	4.8	1.7
Multiple leader	11.8	9.2	4.4	5.9	2.9
Damage on current apic. bud.	0.1	10.8	2.7	5.1	1.8
Damage on last years apic. bud.	0.4	2.8	2.0	2.8	1.0
Runt	20.5	1.2	2.0	1.8	4.9
Dying	0.1	0.5	0.0	0.1	0.2
Dead	2.0	0.5	0.8	12.6	2.5
Missing	5.2	13.2	10.1	12.6	25.5

Log-linear model of proportion of single leader trees²:

	df.	Chi-square	Chi-square	Chi-square	Chi-square	Chi-square
Intercept	1	182.97***	140.53***	285.89***	213.56***	730.85***
Blocks	2	18.32***	0.36n.s.	4.40n.s.	21.36***	0.41n.s.
Hybrids vs provenances	1	0.90n.s.	0.92n.s.	5.89*	1.99n.s.	3.36n.s.
Residual	2	0.32n.s.	0.41n.s.	3.35n.s.	1.63n.s.	0.60n.s.

¹) Significance level (α); n.s., non significant ($\alpha > 0.05$); *, $0.05 \leq \alpha < 0.01$; **, $0.01 \leq \alpha < 0.001$; ***, $\alpha \leq 0.001$.

²) excluding dead, missing and dying trees.

Table 4. — Relative distribution (%) of damage by agents at age 15 (excluding runts, dying, dead and missing trees).

Agent	Turkey Point, ON %	Espanola, ON %	Swastika, ON %	Clova, PQ %	Blackville, NB %
None	64.3	39.6	73.0	56.9	76.3
Rodent	0.0	0.2	0.0	0.0	0.0
Insects	5.0	4.1	1.1	4.5	0.1
Fungi	0.0	0.0	0.2	0.0	23.1
Frost	0.0	5.6	1.9	8.3	0.3
Snow	9.1	0.2	0.3	0.6	0.2
Not identified	21.6	50.3	23.5	29.7	16.0

Log-linear model of proportion of damage-free trees:

	df	Chi-square	Chi-square	Chi-square	Chi-square	Chi-square
Intercept	1	129.77***	92.49***	168.89***	159.47***	247.92***
Block	2	37.67***	8.98n.s.	10.79**	25.86***	36.94***
Hybrids vs provenances	1	1.34n.s.	1.86n.s.	9.92**	2.33n.s.	46.40***
Residual	2	1.66n.s.	8.80n.s.	0.61n.s.	4.23n.s.	15.81**

¹⁾ Exclusive runts, dying and dead trees.

ville where, in turn, the proportion was significantly higher than at the remaining three locations. Differences in proportions among sites could not be related to any environmental data. Runts, dying, dead, and missing trees accounted for 13%—33% of the initial number of trees. Factors associated with planting, and plant quality at the time of planting and winter injury (Clova), determined the extent of failed trees. Although individual provenances and hybrids differed by as much as 40% in the number of trees with single-leader, no single pairwise difference was significant at the 5% risk level (test: "Studentized Range Test", (SNEDECOR and COCHRAN, 1971)). Significant differences between provenance and hybrid proportions of single-leader trees were seen in the Swastika data, where hybrids on an average had 5% more trees in the single-leader category than the provenances. Single-leader trees were 3% to 12% taller than trees in any other tree status class, the differences being in most cases, highly significant.

Tree damage

The proportion of damage-free trees was significantly higher in Swastika and Blackville than at the other sites (Table 4). Damaged trees were distributed on all sites in a patchy or clustered fashion and block differences in the proportion of undamaged trees were highly significant on four sites. Provenance hybrids on two sites (Swastika and Blackville) showed significantly higher proportions of undamaged trees (+10%) than found in the control provenances. Reductions in height due to damage varied from 4% to 18% (significant). The proportion of trees with unidentified agents was high on all sites but especially in Espanola (50.3%).

Wet snow caused considerable damage in Turkey Point whereas winter injury (desiccation) was a problem in Espanola and Clova where only the provenances from western Canada and northern Quebec were free of damage (non-significant). Two southern provenances (Nokomis, WI and Marl Lake, MI) were among the most severely damaged by desiccation (10% to 46% of all trees) in Espanola, Swastika, and Clova (non-significant). Widespread infection by sweetfern blister rust (*Cronartium comptoniae* ARTH.) was observed in the Blackville trial.

Stem form

Classification results of stem form (Table 5) showed that 80% to 90% of the trees included in the height analyses

were either straight or had only a slight bend. Inconsistent results were obtained when hybrids were compared with provenances. In Turkey Point the proportion of trees with desirable stem forms (straight or slight bend) was 5% higher in the provenances than in the hybrids (significant). The opposite was true in Clova. Stem form had little effect on height on the three Ontario sites.

Branch angle

The frequency distribution of branch angle categories confirmed that 75% or more of the classified trees were of the variable type (Table 5). A significant influence of branch angle on tree height was observed only in two instances: In Turkey Point, trees with acute angles were 6% taller than variable trees and, in Clova, trees with wide angles were 5% shorter than the variable type. No significant differences emerged when hybrids were compared with provenances.

Height growth

Details of the height indices used to adjust observed tree height to the expected height of single leader and damage-free trees are given in Table 6. It becomes quite clear that identical classifications had quite different effects on height growth on the various sites. The average index was on all sites within 21% from the maximum possible and the effect on overall height growth performance was a modest 0—5% in Ontario and Quebec but a recognizable 9% in New Brunswick.

Adjusting for the effect of tree status and damage on height reduced the within-plot error by 8 to 21% and the plot error term by 3 to 13%. The error terms relevant to the local height estimates were 24% to 48% lower than the pooled experimental error on the Ontario and Quebec sites (Table 7). In Blackville the local height error was 31% higher than the latter owing to a considerable error mean square in the range-wide experiment from which the local height data were derived.

Adjusted height at age 15(16) varied significantly among provenances and hybrids on all six sites (Table 7). The best statistical discrimination among provenances and hybrids as measured by the calculated F-ratio was obtained on the two warmer sites (Turkey Point and Petawawa) which also ranked highest in local heights. The poorest discrimination was obtained in Espanola. A height growth significantly greater than that of local seed sources was

Table 5. — Relative distribution (%) of trees by stem form and branch angle.

Stem form (SF)	Turkey Point, ON %	Espanola, ON %	Swastika, ON %	Clova, PQ %	
Straight	20.5	0.2	15.0	7.4	
Slight bend	65.6	83.5	64.2	80.6	
Ripples	4.5	5.7	5.4	6.2	
Wave	8.0	6.7	9.6	4.1	
Extreme wave	1.4	4.0	5.9	7.7	
Branch angle (BA)					
Wide (>60°)	15.4	0.3	5.2	15.8	
Variable (30-60°)	74.6	99.1	79.0	83.9	
Acute (<30°)	10.0	0.6	15.8	0.3	
Log-linear model of proportion of straight plus slightly bent trees:					
	df	Chi-square	Chi-square	Chi-square	Chi-square
Intercept	1	406.62***	384.94***	335.53***	361.94***
Blocks	2	0.80n.s.	27.81***	4.03n.s.	2.74n.s.
Hybrids vs. Provenances	1	5.86*	3.57n.s.	0.03n.s.	5.61n.s.
Residuals	2	2.72n.s.	1.43n.s.	0.18n.s.	4.48n.s.
Log-linear model of proportion of trees with variable branch angle:					
	df	Chi-square	Chi-square	Chi-square	Chi-square
Intercept	1	552.79***	247.31**	538.94***	257.66**
Blocks	2	34.12***	4.35n.s.	12.41*	122.14***
Hybrids vs. Provenances	1	0.87n.s.	0.26n.s.	0.07n.s.	1.40n.s.
Residuals	2	2.31n.s.	0.50n.s.	3.51n.s.	4.32n.s.

only observed in one provenance and in five hybrids. Of these six observations (all with above average survival), five were found in Blackville and one in Espanola (Somerset Co. × Petawawa Plains).

A wide selection of provenances and hybrids were within a 10% limit of the local height estimate on each site. Inferior growth was, as expected, observed in high latitude provenances from Lac la Biche in Alberta and Fort Smith in the North West Territories. Provenances from Quebec and the Maritimes were slow growing at Turkey Point, whereas provenances from the Maritimes and Maine were slow growing in the Sturgeon Lake Plains trial. A comparison of within plot variances and plot to plot variances of tree height did not reveal any significant differences between provenances and hybrids ($\alpha > 0.34$).

A significant positive height difference between a hybrid and the average of both controls was observed in 10 cases. Although these differences were rather inconsistent over

sites, the fact that five were crosses with Smith (Alberta) suggested that the slow growth of this high latitude provenance may effectively be modified in hybrids with this provenance when grown in eastern Canada.

Correlation and regression analyses revealed clearly the nature of hybrid performance (Table 8). Tree height of the hybrid was positively correlated to the height of the control provenances. When heights of hybrids were significantly less than the local height it was, as a rule, associated with parallel results in one or both of the controls. Regression analysis indicated that the hybrids on four sites yielded, on the average, significantly more than the mid-value of of the controls (i.e. $b > 0.5$) but also significantly less than the better control (i.e. $b < 1.0$). Regression coefficients calculated from the Ontario and Quebec sites were almost identical (test: multivariate-t-method; result: $t_{\max} = 1.60 < t_{0.05, 5, 293} = 2.03$). Hybrid height growth expectations on these five sites can thus be expressed as:

Table 6. — Above: Height indices of trees of varying status and damage. Below: Results of weighted least squares (WLS) regression of height index on tree height (cf. model in equation [2]).

Tree status, damage	Turkey Point	Espanola	Swastika	Clova	Blackville
single leader, no damage	1.00	1.00	1.00	1.00	1.00
single leader, frost	-	.90	.75	.80	.99
double leader, unknown	.71	.55	.81	.73	.67
single leader, fungi	-	-	.31	-	.80
multiple leader, unknown	.57	.65	.63	.67	.73
single leader, unknown	.86	.70	.44	.33	.60
apic. bud damage, unknown	.93	.60	.56	.87	.27
single leader, snow damage	.64	.05	.19	.40	.87
single leader, insects	.36	.75	.38	.60	-
last years apic. bud damage, unknown	.50	.30	.88	.47	.40
double leader, insects	.14	.85	.69	.13	-
multiple leader, fungi	-	-	-	-	.47
multiple leader, snow damage	.43	-	-	-	-
last years apic. bud damage, insects	-	.25	.50	-	.27
double leader, snow damage	.29	.45	-	-	-
multiple leader, insects	.21	.50	.06	.53	.20
apic. bud damage, rodents	-	.20	-	-	-
Average index	.85	.79	.91	.79	.84
WLS - estimates:					
intercept (θ)	4.90	3.24	5.05	2.73	1.90
slope (β)	1.36**	0.90**	1.22**	0.77**	2.00**
standard error of β	0.01	0.06	0.01	0.01	0.01
correlation coefficient (height, index)	0.95	0.94	0.98	0.90	0.98

Table 7. — Relative heights at age 15 (16) of provenances and hybrids. + = significant positive deviation from local mean, - = significant negative deviation from local mean, * = significant positive deviation from mid-control value.

	Turkey Point, ON	Sturgeon Lake Plains, ON	Espanola, ON	Swastika, ON	Clova, PQ	Blackville, NB
Local height estimate (= 100), (s.e. %)	6.6 m (2.4%)	8.2 m (2.7%)	4.1 m (4.1%)	6.5 m (2.0%)	3.5 m (7.1%)	3.5 m (6.4%)
CONTROLS						
Thomson Station, NS	91	90	91	89-	93	96
Cains River, NB	93-	91-	95	93-	94	95
Spencer Lake, ME	97	90	101	96	89	96
St. Louis de France, PQ	92	97	96	97	121	-
Tailon Peninsula, PQ	85-	95	90	94	101	96
Downs Lake, PQ	78-	89-	96	95	105	104
Petawawa Plains, ON	99	100	96	96	94	-
Lac Villebon, PQ	89	97	110	97	95	-
Goulais River, ON	89-	98	97	98	100	117
Nokomis, WI	103	101	95	98	103	110
Marl Lake, MI	102	96	93	92-	84	112+
Cass Lake, MN	98	103	105	98	86	-
Hadashville, MB	99	97	89-	98	101	98
Lac la Biche, AB	74-	79-	92	79-	88	74-
Fort Smith, NT	60-	69-	84-	77-	70-	66-
Hybrids						
Somerset Co., ME x Petawawa Plains, ON	102	96	112+	95	106	112
Cumberland Co., NS x Petawawa Plains, ON	99	101	86-	99	*115	120+
Northumberland Co., NB x Petawawa Plains, ON	94	93	102	95	96	100
Manouan Lake, PQ x Petawawa Plains, ON	*93	96	93	95	108	118+
Opawica Dist., PQ x Petawawa Plains, ON	90	99	102	93	111	113
Damville Tp., PQ x Petawawa Plains, ON	87-	97	95	95	99	106
Spanish River, ON x Petawawa Plains, ON	87-	96	97	100	104	118+
Crawford Co., MI x Petawawa Plains, ON	101	103	89-	100	91	103
Vitas Co., WI x Petawawa Plains, ON	98	100	86-	104	98	-
Oneida Co., WI x Petawawa Plains, ON	101	105	104	103	105	-
Sandilands, MB x Petawawa Plains, ON	92	101	86-	95	103	117+
Smith, AB x Petawawa Plains, ON	85-	93	90	*97	94	*109
Becker Co., MN x Petawawa Plains, ON	100	105	100	100	92	-
Fort Smith, NT x Petawawa Plains, ON	79-	82-	85-	89-	91	92
Somerset Co., ME x Smith, AB	*93	90-	*110	90-	99	-
Somerset Co., ME x Sandilands, MB	103	103	91	95	-	-
Cumberland Co., NS x Fort Smith, NT	*82-	89-	84-	88-	88	-
Northumberland Co., NB x Smith, AB	82-	86-	97	87-	102	-
Northumberland Co., NB x Crawford Co., MI	95	103	99	95	98	-
Sandilands, MB x Cumberland Co., NS	96	95	88-	92-	88	-
Sandilands, MB, x Northumberland Co., NB	99	94	93	98	107	-
Smith, AB x Cumberland Co., NS	*93	90-	91	-	-	-
Becker Co., MN x Angus, ON	103	93	104	92	69	-
Becker Co., MN x Timmins, ON	98	105	109	97	76	-
Marinette Co., WI x St. Zenon, PQ	102	97	*105	98	119	-
Oneida Co., WI x Northumberland Co., NB	-	-	-	101	101	-

Weighted least squares analysis of variance:

F-test (H_0 : all means are equal) F =	20.77***	14.77**	3.05**	7.59**	11.15**	7.31**
Degrees of freedom (f, f ₁)	(39,120)	(39,177)	(39,169)	(38,167)	(38,153)	(21,89)
Experimental mean in m and in % of local tree height	6.1 (92%)	7.8 (95%)	3.9 (95%)	6.1 (95%)	3.47 (97%)	3.6 (103%)
Pooled standard error in m and in % of exp. mean	.28 (4.6%)	.30 (3.8%)	.21 (5.4%)	.22 (3.6%)	.32 (9.3%)	.12 (4.9%)

$H_{\text{hybrid}} = H_{\text{min(control)}} + 0.68 (H_{\text{max(control)}} - H_{\text{min(control)}})$
 i.e. 68% of the height differences between the two controls was captured in the provenance hybrid (standard error = 5.5%). A low coefficient of 0.26 obtained in Blackville is a consequence of the good performance of the Goulais River provenance which was used as one of the controls in all the hybrids in Blackville.

Height growth performance at age 10 (1973) paralleled in relative terms the growth at age 15, owing to a strong correlation between the two sets of results. The average

correlation of provenance and hybrid mean heights on the two occasions was 0.91** (s.e. = 0.07) with an average within entry correlation of 0.72** (s.e. = 0.01). Correlation coefficients calculated for provenances were in all instances not significantly different from those of the hybrids.

Genotype-environment interaction analyses

Site to site correlations of provenance and hybrid heights varied from weak to strong as shown in Table 9. The strong correlations ($r > 0.8$) between site 1 and 2, 2 and 4, 2 and 8, and 4 and 8 indicated little $G \times E$ interactions

Table 8. — Summary statistics of height growth performance of provenance crosses.

	Turkey Point, ON	Sturgeon Lake Plains, ON	Espanola, ON	Swastika, ON	Clova, PQ	Blackville, NB
Partial correlation ¹ between plot mean heights of hybrids and one control provenance	.614** (46)	.413** (66)	.052n.s. (64)	.329** (61)	.328* (52)	.715** (7)
Regression coefficient β (s.e. (β))	.75 (.06)	.68 (.07)	.57 (.09)	.69 (.07)	.73 (.11)	.26 (.08)
model: $H_{\text{hybrid}} = H_{\text{min}}(\text{control}) + \beta(H_{\text{max}}(\text{control}) - H_{\text{min}}(\text{control}))$						
F-tests:						
$H_0: \beta = 0.5$ vs. $H_A: \beta \neq 0.5$	20.11** ($<.01$)	5.84* (.02)	0.57n.s. (.45)	7.36** ($<.01$)	4.52* (.04)	9.84** (.01)
$H_0: \beta = 1.0$ vs. $H_A: \beta \neq 1.0$	21.18** ($<.01$)	19.26** ($<.01$)	23.30** ($<.01$)	20.38** ($<.01$)	6.47* (0.01)	93.16** ($<.01$)

1) Adjusted for the effect of the second control provenance.

2) PEARSON correlation coefficient based on one parent only.

among these four sites. Height growth in Espanola and Clova was, with the exception of a highly significant correlation between Clova and Blackville, poorly correlated to the performance on any other site. The low correlations

Table 9. — PEARSON correlations among sites of provenance and hybrid means heights.

Site	2	3	4	5	8
1) Turkey Point, ON	.80**	.36*	.72**	.22**	.67**
2) Sturgeon Lake Plains, ON		.29	.86**	.34*	.87**
3) Espanola, ON			.22	.09	.31
4) Swastika, ON				.48**	.83**
5) Clova, PQ					.77**
8) Blackville, NB					

were generally caused by a systematic shift in ranking between northern and southern provenances and associated hybrids.

A joint regression analysis of variance with 37 entries at five sites (Ontario and Quebec) is presented in Table 10. Highly significant effects of G, E, and the $G \times E$ interactions were found. An analysis with local height as covariate supported the contention that $G \times E$ interactions to a large extent were caused by differences of slopes (β_i) in the regressions of height versus local height. When compared against a theoretical slope value of 1.00, which indicates a stable entry, ten of the slopes were found to be significantly below this threshold value (Table 11). No significant differences were detected in pairwise comparisons between slopes of hybrids and the mean of their controls. The correlation coefficients between the two sets of slopes was 0.83. Similar results were obtained by comparing rank stabilities (S_1 in Table 11).

The statistical significance of the $G \times E$ interactions was associated with 11 entries with either a low rank stability (a high S_1 index), a high β_i value or both (cf. Table 11). Hence, the ecological amplitude for these entries is narrower in comparison to the remaining entries. Three provenances, from Alberta, Minnesota, and the North-West Territories, and six crosses associated with these provenances, were a major source of the $G \times E$ interactions.

Taken over five sites, two hybrids, Petawawa Plains, ON \times Oneida Co., WI, and Marinette Co., WI \times St. Zenon, PQ, surpassed the average local height by 8 to 10% (significant). Both had a high rank stability combined with an overall high average rank. Only two of the 37 listed mean heights in Table 11 were significantly lower than the combined average local mean height. Both cases included a provenance parent from the far Northwest.

Height growth of entries was predominant site specific. A regression model of provenance height versus a linear combination of local height and geographic variables (latitude, longitude, growing degree days) confirmed

Table 10. — Genotype-environment interaction analysis of variance of 38 entries common on five sites in Ontario and Quebec (cf. text for underlying model).

Source of variation	d.f.	M.S.	F-test	F-value
provenances and hybrids (G)	36	16313	MS_G/MS_{GE}	5.9**
environments (E)	4	399	MS_E/MS_{GE}	1280.4**
combined regression (B)	1	1399	MS_B/MS_{BE}	21.5**
residual (ϵ_j), (RE)	3	65		
interaction (G \times E)	144	2751	$MS_{G \times E}/MSE$	2.1**
heterogeneity of regr. (BG)	36	6303	MS_{BG}/MSE	4.9**
residual (ϵ_{ij}), (RBG)	108	1566	MS_{RBG}/MSE	1.2n.s.
error between replicates	302	1286		

Table 11. — Mean height (adjusted), rank, rank stability, and regression slopes (β). Mean heights and regression slopes followed by a + or a - are significantly above (+) or significantly below (-) the local estimate (based on t-tests).

	Mean height (m)	GXE-interaction	Mean rank m (ties + high)	Rank stab. index S ₁	β_1
Controls					
Thomson Station, NS	5.2		26	4.8	.82-
Cains River, NB	5.4		22	6.0	.89
Spencer Lake, ME	5.5		19	11.4	.93
St. Louis de France, PQ	5.7		9	10.8	.98
Taillon Peninsula, PQ	5.3		22	8.2	.88
Downs Lake, PQ	(5.2)	*	22	15.0	.82-
Petawawa Plains, ON	5.6		14	8.6	1.01
Lac Villebon, PQ	5.2		13	11.6	.76-
Goulais River, ON	5.7		13	8.6	.98
Nokomis, WI	5.8		7	7.0	1.05
Hari Lake, MI	(5.5)	*	20	15.2	1.02
Cass Lake, MN	(5.7)	*	11	14.2	.95
Hadashville, MB	5.6		14	8.6	1.01
Lac la Biche, AB	(4.6)	*	32	6.2	.63-
Fort Smith, NT	(4.1)	*	38	0.6	.56-
Hybrids					
Somerset Co., ME x Petawawa Plains, ON	5.8		8	12.2	.93
Cumberland Co., NS x Petawawa Plains, ON	5.8		9	12.8	.93
Northumberland Co., NB x Petawawa Plains, ON	5.5		17	8.6	.86-
Manouan Lake, PQ x Petawawa Plains, ON	5.6		16	9.4	.97
Opawica Dist., PQ x Petawawa Plains, ON	5.7		13	12.8	.91
Damville Tp., PQ x Petawawa Plains, ON	5.4		18	6.0	.91
Spanish River, ON x Petawawa Plains, ON	5.5		13	13.0	.97
Crawford Co., MI x Petawawa Plains, ON	(5.7)	*	13	16.2	1.09
Vilas Co., WI x Petawawa Plains, ON	(5.7)	*	13	15.6	1.07
Oneida Co., WI x Petawawa Plains, ON	6.0		2	3.2	1.02
Sandilands, MB x Petawawa Plains, ON	5.5		17	13.8	1.01
Smith, AB x Petawawa Plains, ON	5.3		22	8.4	.91
Becker Co., MN x Petawawa Plains, ON	(5.7)	*	11	16.2	1.02
Fort Smith, NT x Petawawa Plains, ON	4.5-		32	3.6	.84-
Somerset Co., ME x Smith, AB	(5.5)	*	19	14.6	.73-
Cumberland Co., NS x Fort Smith, NT	5.0-		33	2.4	.74-
Northumberland Co., NB x Smith, AB	(5.1)	*	24	14.6	.72-
Northumberland Co., NB x Crawford Co., MI	5.7		12	8.4	.97
Sandilands, MB x Cumberland Co., NB	5.3		13	8.2	.94
Becker Co., MN x Angus, ON	(5.4)	*	19	20.4	.98
Becker Co., MN x Timmins, ON	(5.7)	*	12	16.8	1.00
Marquette Co., WI x St. Zenon, PQ	5.9+		5	7.8	.95
Average	5.4			10.4	1.02
Local estimate	5.4				1.00

¹⁾ Significant G × E interaction.

this. Overall local height explained 85% of the observed phenotypic height variation among provenances. In comparison, the best linear combinations of geographic variables explained no more than 14%. This was considered insufficient for any modelling purposes.

Among the geographic variables only latitude (LAT) and the number of growing degree days (GDD) at the place of parental origin correlated significantly with height growth at each of the six test sites. However, with the exception of the southernmost experimental site (Turkey Point), these correlations became non-significant when contributions from provenances and hybrids from Alberta or the Northwest Territories were discounted. Only Turkey Point (latitude 49° N) fell outside the 45° to 50° latitudinal limits of the remaining test sites and the majority of provenances involved.

Discussion

Design and analyses

Evaluation of the present study raised several problems of general concern. First, it must be stressed that the sites and provenances included in this study are too few and too geographically imbalanced to warrant a detailed description of seed source variation or to give seed source recommendations. Information of this kind is available from jack pine provenance trials (MORGENSTERN and TEICH, 1969; HUNT and VAN SICKLE, 1984; TEICH and HOLST, 1969; JEFFERS and JENSEN, 1980; KING, 1971; SKEATES, 1979; YEATMAN,

1974). The provenances in this study served entirely as controls or check-lots for the tested hybrids.

Hybrids resulting from crosses between geographically distinct provenances as seed parents and pollen mix of trees from other defined provenances can be expected to provide valuable genecological information when planted over a range of test environments. Interprovenance hybrid variances (genetic) are expected to be greater than variances within provenances (NILSSON, 1973). The high ratio of general to specific combining ability in many conifers supports this contention (EKBERG *et al.*, 1982; GERHOLD and PARK, 1986; SKRØPPA, 1979). A complication arises when hybrids from controlled pollinations are compared to open pollinated offsprings from natural stands, owing to a level of inbreeding in the latter due to high relatedness and gene exchange among neighbours in natural populations (FOWLER, 1978; MORGENSTERN, 1973; NILSSON, 1973).

Field designs such as those in Ontario and Quebec are not suitable for long term observations. They were chosen as adequate compromises for a preliminary testing of provenance hybrids. On favorable sites, intra-specific competition will bias results soon after crown closure (MAGNUSSEN and YEATMAN, 1987). On adverse sites, as in Espanola and Clova, the environmental conditions and the rise over time of the number of damaged trees interact with the genetic entries and may drastically increase the error variance or even render analysis meaningless (JEFFERS and

JENSEN, 1980; KNIGHT, 1973). Fortunately, it appears that juvenile trials in jack pine yield quite reliable indicators of later performance at a more mature stage (JEFFERS and JENSEN, 1980; MAGNUSSEN *et al.*, 1985; MAGNUSSEN and YEATMAN, 1986). Our recommendation, therefore, is to make final assessments in this type of field design at an age between eight and 10 in favorable environments, but to delay evaluation in adverse sites in order to await growth differentiations of practical importance.

Average yield per unit area is a combined estimate of growth potential and the risk of injury or loss of a given "genotype" grown in a specific environment (KING, 1971). When based on a large sample, this estimate is of practical value, as it reflects the yield that one would expect normally. However, with small samples, environmental disturbances may seriously confound the results, inasmuch as these disturbances frequently occur in patches scattered over the entire trial. The trials reported here fall in the latter category and an adjustment of the height data to potential height (single leader/no damage) was considered appropriate, although it limits the practical application of the results. In this study the covariance approach was facilitated by the absence of provenance or cross effects in the covariate and also by the fact that the number of trees observed in the various coding categories was unrelated to the height prior to damage.

Estimates of yield of local unimproved seed sources at each study site simplified the statistical analysis to a basic hypothesis of whether any of the tested entries exceeded the local sources or not. Positive results would then require more specific hypotheses. The more traditional approach has been to make all possible comparisons among the tested entries.

The alternative breakdown of the $G \times E$ sum of squares into clusters of test entries with and without significant $G \times E$ interactions (LIN, 1982) greatly simplifies interpretations of two-way tables with interactions. This is especially so, when, as in this study, almost three quarters of the test entries showed no interaction.

Performance of entries

The fact that no provenance or hybrid significantly outperformed the local unimproved seed sources, when tested on five sites, strongly suggests that genetic yield improvement is most likely to succeed with selection and breeding of locally well-adapted material within well defined breeding zones (SKEATES, 1979; YEATMAN and MORGENSTERN, 1978). Results obtained in Blackville, NB, suggests that the Goulais River, ON, provenance and hybrids with Sturgeon Lake Plains, ON, on this site may have found an optimal niche in the Eastern Lowlands.

The large number of geographically unrelated entries without significant genotype \times environment interactions suggest that, together with the generally significantly positive site to site correlations, future breeding zones can safely be quite large, at least in the southern and milder regions within the range of jack pine. A similar conclusion was reached in a Lake States provenance trial (JEFFERS and JENSEN, 1980). These observations do not, however, diminish the considerable risk of planting poorly adapted "genotypes", as illustrated in considerable rank changes of entries among the five sites. Also, the small sample sizes made statistical analysis of damage too insensitive to screen provenances and crosses with respect to their site specific fitness.

With 85% of all variation explained by the local height, little was left for geographical variables of provenance origin (see also MORGENSTERN and TEICH, 1969; MORGENSTERN, 1978). The significant correlations between tree height and latitude or GDD were in most cases the result of two entries well to the north and in colder climates than the test locations. With the exception of the two Alberta provenances, the remainder span a narrow latitudinal range of only five degrees (45° to 50° N), but a wide longitudinal range (64° to 95° W). Only at the southernmost test site at Turkey Point, Ont., beyond the five-degree latitudinal range of sampling, was growth linearly related to latitude and GDD. Recent results have shown growth of provenances from a limited geographic (environmental) range to be correlated strongly with levels of foliage density (MAGNUSSEN *et al.*, 1986).

Our results are not supportive of the observation in juvenile material of a better than local height growth in provenances that have been moved 1° to 2° (lat.) north of the place of origin (KING, 1966, 1971; MORGENSTERN and TEICH, 1969). This pattern is related to the earlier growth cessation of more northern sources when grown in shorter photoperiods and longer growing seasons than in their places of origin (TEICH and HOLST, 1969; RIEMENSCHNEIDER, 1983; YEATMAN, 1974). The inability to provide support is not due to experimental insensitivity. With a standard error less than 5% of the experimental mean in five of six trials we were indeed able to discriminate effectively among seed sources and crosses on a scale of practical significance.

A principal reason for testing genotypes in a wide range of environments is to estimate their stability (FREEMAN, 1973). Most provenances and hybrids tested had a height regression coefficient (β) of almost 1.0 when regressed on local height, i.e. high stability over these test environments. The results thus indicate a desirable broad environmental adaptation among midrange provenances rather than a narrow one attuned to either mild ($\beta > 1$) or boreal ($\beta < 1$) environments (FINLAY and WILKINSON, 1963; KNIGHT, 1970; SKRØPPA, 1984; OWINO and ZOBEL, 1977). By using LIN's (1982) clustering approach we were, furthermore, provided with $G \times E$ interaction threshold values for the stability parameters (rank and slope).

It was confirmed that hybrids as a rule were intermediate to their "parents" in height, stem, and crown characters (FOWLER, 1978; HOLST and FOWLER, 1973; KNIGHT, 1973; NILSSON and ANDERSON, 1970; YING, 1978). Although the hybrids captured an average of 68% of the height difference between two "parents" the practical value of this relative gain is limited as it amounts to no more than a 2% to 5% superiority over the mid-"parent" value. For jack pine, a species with virtually no inbreeding (CHELIAK *et al.*, 1985; SNYDER *et al.*, 1985), the negative effect of natural inbreeding is likely to be of the same magnitude. The presumption of hybrids having less fitness than either parent (FOWLER, 1978; FALCONER, 1981; MORGENSTERN, 1973) could not be confirmed in this study. With intermediate environmental stability in provenance hybrids one expects hybrids to better than their parents on diversified sites (NILSSON, 1973; NILSSON *et al.*, 1973; REHFELDT, 1977; WOESSNER, 1972). It is assumed that the higher environmental buffering in hybrids is associated with a higher degree of heterozygosity (FALCONER, 1981; KNIGHT, 1973; WRIGHT 1964). This can be expected to be more evident in subsequent generations derived from the F_1 hybrids.

The occurrence of two very promising hybrids confirms the potential of hybridization to combine desirable traits,

but it also affirmed that such results are few compared to the numerous exploratory matings involved. The low expectation of a substantial gain using hybrids has direct bearing to seed orchards designed to produce hybrids (EKBERG *et al.*, 1982; KLEIN, 1986). Their value may be highest as a source of new gene combinations in advanced generations with a threatening narrow genetic base (ZOBEL and TALBERT, 1984).

A key to success in the future use of hybrids will be the degree to which vegetative propagation is applied in mass production of outstanding genotypes, in order to capitalize on the expensive breeding efforts. A renewed interest in increasing the genetic buffering of our tree species has been spurred by the recent symptoms of forest decline in Europe and North America (GOVINDARAJU and DANCİK, 1986; GREGORIUS *et al.*, 1985; OWINO and ZOBEL, 1977). Inter-population intraspecific hybridization may prove useful in this context.

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The G-banded Karyotype of *Pinus resinosa* Ait.

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Summary

Characterization of the individual chromosomes of *Pinus resinosa* ($2n = 24$) by means of G- and Q-banding techniques is presented. This is the first report of a G-banded karyotype in a plant species and reasons for lack of previous success are discussed. The similarity of the banding patterns and secondary constrictions in apparently non-homologous chromosomes indicates that polyploidy may have played a role in the evolution of *Pinus*.

Key words: *Pinus resinosa*, G-banding, Q-banding.

Zusammenfassung

Durch G- und Q-Bandmuster werden einzelne Chromosomen bei *Pinus resinosa* ($2n = 24$) charakterisiert. Dies ist der erste Bericht über die Anwendung von G-Banden zur Charakterisierung des Karyotypes bei Pflanzen. Gründe für frühere Mißerfolge werden diskutiert. Die Ähnlichkeit der Bandmuster und sekundäre Einschnürungen in offensichtlich nicht-homologen Chromosomen zeigen, daß möglicherweise Polyploidie eine Rolle bei der Evolution von *Pinus* gespielt hat.

Introduction

Identification of individual chromosomes of plants belonging to the genus *Pinus* has not been possible on the basis of such morphological characteristics as size and arm ratio since most of the chromosomes are metacentrics of similar size. In addition there exists a remarkable degree of similarity of chromosome morphology between species of the genus *Pinus*, whose members possess $2n = 24$ chromosomes (SAYLOR, 1964). Since *Pinus* is well represented by fossils over 100 million years old (FLORIN, 1963) the genus provides an opportunity to study unusually slow evolution.

Karyotype comparisons between *Pinus* species with conventional stains have been previously limited by the lack of identifying characteristics for individual chromosomes. Similar problems in human cytology have been solved by the use of fluorochromes and G- and C-banding. In this report G- and Q-banding have been used to identify the individual chromosomes of *Pinus resinosa* AIT. As far as

this author is aware, this is the first plant in which clear G-banding has been demonstrated (DREWRY, 1982).

Materials and Methods

Seeds of red pine *Pinus resinosa* were germinated following stratification. When the primary roots were 1 to 2 cm long, the seeds were placed overnight on filter paper moistened with a 1% solution of colchicine. Root tips were fixed in 3:1 ($C_2H_5OH:CH_3COOH$). The fixed roots were refrigerated (4°C) until they were made into slides 1 to 7 days later.

The fixed roots were rinsed in 45% acetic acid and squashed in the same solution. The coverslips were removed with dry ice.

For Q-banding the slides were briefly air-dried and then stained in 0.5% Atebrin (Gurr) (quinacrine HCL) solution for 5 to 10 minutes. The preparations were passed through a flame and rinsed in water. Coverslips were mounted with 40% sucrose solution. Thereafter the slides were kept on a hot plate at 45 to 60°C until banded (15 to 60 minutes).

For G-banding squashed root tips were air-dried at room temperature and then kept at 45 to 60°C for 1 to 12 hours. Thereafter the slides were treated with trypsin solution (Gibco: Trypsin-EDTA 10X 5.0 ml, Hanks BBS 4.5 ml, H_2O 40.5 ml) at room temperature for 20 to 40 minutes. Staining was accomplished in a filtered Giemsa solution (1 part Gurr's R66 Giemsa to 3 parts buffer from Gurr's buffer tablets adjusted to pH 7.9 with sodium bicarbonate). After 3 to 6 minutes in the stain the slides were briefly rinsed in a pH 6.8 buffer solution (Gurr's buffer tablets). As mounting medium Permount was used. Complete banded metaphase spreads were obtained for both G and Q-banded (Fig. 1) chromosomes. Individual examples from each pair of chromosomes were selected from G- and Q-banded partial metaphase spreads and assembled for Figure 2. Since the two arms of many of the chromosomes are of similar size, the arm with a secondary constriction is up in the karyotype.

Results

The significance of the various types of bands is far from clear even in human chromosomes for which these

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