All-Range Black Spruce Provenance Study in Newfoundland: Performance and Genotypic Stability of Provenances

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Summary

The paper presents ten year results of a three-location all range black spruce provenance study in Newfoundland, conducted in six-replicated triple lattice design experiments. The data, collected in 1980 on 1979 and 1980 heights, 1980 diameter at 0.3 m, height growth in the 1974—80 period and in 1980 were analysed with analyses of variance by and over locations, Bonferroni t-tests, step-wise regression analyses and evaluation of the provenances for productive quality and genotypic stability, using height growth in the 1974—80 period as the criterion.

Lattice design proved significantly effective in removing intra-replication variation and in improving efficiency compared with the randomized complete block design. High intra-provenance variation was noticed, indicating heterogeneity of the provenances and the possibility of obtaining enhanced genetic gains by intensive family selections within superior provenances.

Most of the provenances in the fourth quartile belong to the region between latitudes 45°—49° N and longitudes 60°—84° W. Variation in the performance of provenances among locations was detected in arrays and confirmed and quantified by analyses of variance over locations. Initial height growth in nursery, six-year growth in field and total growth are significantly correlated with each other. Superior provenances have relatively low genotypic stability, which appears to be due to their high heterozygosity. Eight promising provenances have been tentatively identified by a combined evaluation of the productive quality and genotypic stability of all provenances. These are: MS. 1531, S.6905, MS. 1528, MS. 1533, S.6927, 370, S.6911 and 353.

Key words: Black spruce, *Picea mariana*, Provenance experiments, Productive quality, Genotypic stability.

Résumé

Le présent article donne les résultats, après dix ans, d'une étude de provenance effectuée dans trois emplacements de Terre-Neuve et portant sur toute l'aire d'extension de l'épinette noire. L'expérience a été faite selon un plan en treillis triple, à 6 répétitions.

On a obtenu en 1980 des données sur la hauteur en 1979 et en 1980, le diamètre à 0,3 m en 1980, la croissance en hauteur de 1974 à 1980 et en 1980 et on les a analysées par des études de variance par emplacement et entre les emplacements, des tests du t de Bonferroni, des régressions pas à pas et une évaluation de la qualité de production et de la stabilité génotypique des provenances avec comme critère la croissance en hauteur entre 1974 et 1980.

Le plan d'expérience en treillis s'est révélé efficace pour la suppression des variations entre les répétitions et supérieur au plan d'expériences en blocs complets aléatoires. On a noté une forte variabilité chez une même provenance signe d'une grande hétérogénéité des provenances et la possibilité d'obtenir une amélioration génétique par une sélection intensive des familles dans les provenances supérieures.

La plupart des provenances du quatrième quartile appartiennent à la région située du 45° au 49° de latitude nord et du 60° au 84° de longitude ouest. On a décelé dans les tableaux une variation, entre les emplacements, dans la performance des provenances; elle a été confirmée et quantifiée à l'aide d'analyses de variance entre les emplacements. La croissance en hauteur initiale en pépinière, la croissance sur le terrain pendant six ans et la croissance totale sont significativement corrélées entre elles. Les provenances supérieures ont une stabilité génotypique relativement faible, ce qui semble être dû à leur caractère fortement hétérozygote. Huit provenances prometteuses ont été déterminées grâce à l'évaluation combinée de la qualité de production et de la stabilité génotypique de toutes les provenances: MS.1531, S.6905, MS.1528, MS,1533, S.6927, 370, S.6911 et 353.

Zusammenfassung

In der Arbeit werden die Ergebnisse der ersten 10 Jahre eines Provenienzversuches mit Herkünften von *Picea mariana* aus dem gesamten natürlichen Verbreitungsgebiet in Neufundland auf drei verschiedenen Standorten als Dreisatzgitter mit sechs Wiederholungen dargestellt. Die Meßdaten, die 1980 aufgenommen wurden, waren folgende: die Höhe in den Jahren 1979 und 1980, der Durchmesser in 0,3 m Höhe im Jahre 1980, das Höhenwachstum im Zeitraum von 1974 bis 1980 und im Jahr 1980 selbst. Diese wurden mittels Varianzanalyse innerhalb und zwischen den Standorten, Bonferroni t-Test, stufenweiser Regressionsanalysen und Schätzungen der Provenienzen für Produktionsqualität und genotypische Stabilität ausgewertet, wobei das Höhenwachstum in der Zeit von 1974—1980 als Maßstab benutzt wurde.

Durch die Gitteranordnung wurde im Vergleich zum vollständigen randomisierten Blockversuch die Variation innerhalb der Wiederholungen signifikant verringert und die Effizienz erhöht. Es wurden beachtliche Unterschiede innerhalb der Herkünfte beobachtet, die als Hinweis auf die Heterogenität der Provenienzen und auf die Möglichkeit durch intensive Familienselektion innerhalb überlegener Herkünfte, erhöhte genetische Gewinne zu erzielen, dienen.

Die meisten der Herkünfte aus der vierten Wiederholung stammen aus dem Gebiet zwischen 45° und 49° nördlicher Breite und 60° und 84° westlicher Länge. Die Variation im Höhenwachstum der Provenienzen folgte einem geordneten Schema und wurde durch Varianzanalysen zwischen Standorten bestätigt und quantifiziert. Die Anfangshöhe in der Baumschule, die Höhe nach 6 Jahren im Freiland und die Gesamthöhe sind signifikant miteinander korreliert. Die überlegenen Provenienzen hatten eine relativ geringe genotypische Stabilität, die ihrem hohen Heterozygotiegrad angemessen schien. Acht Herkünfte mit erfolgversprechenden Merkmalen wurden versuchsmäßig durch eine kombinierte Schätzung der produktiven Qualität und der genotypischen Stabilität aller Provenienzen identifiziert. Die-

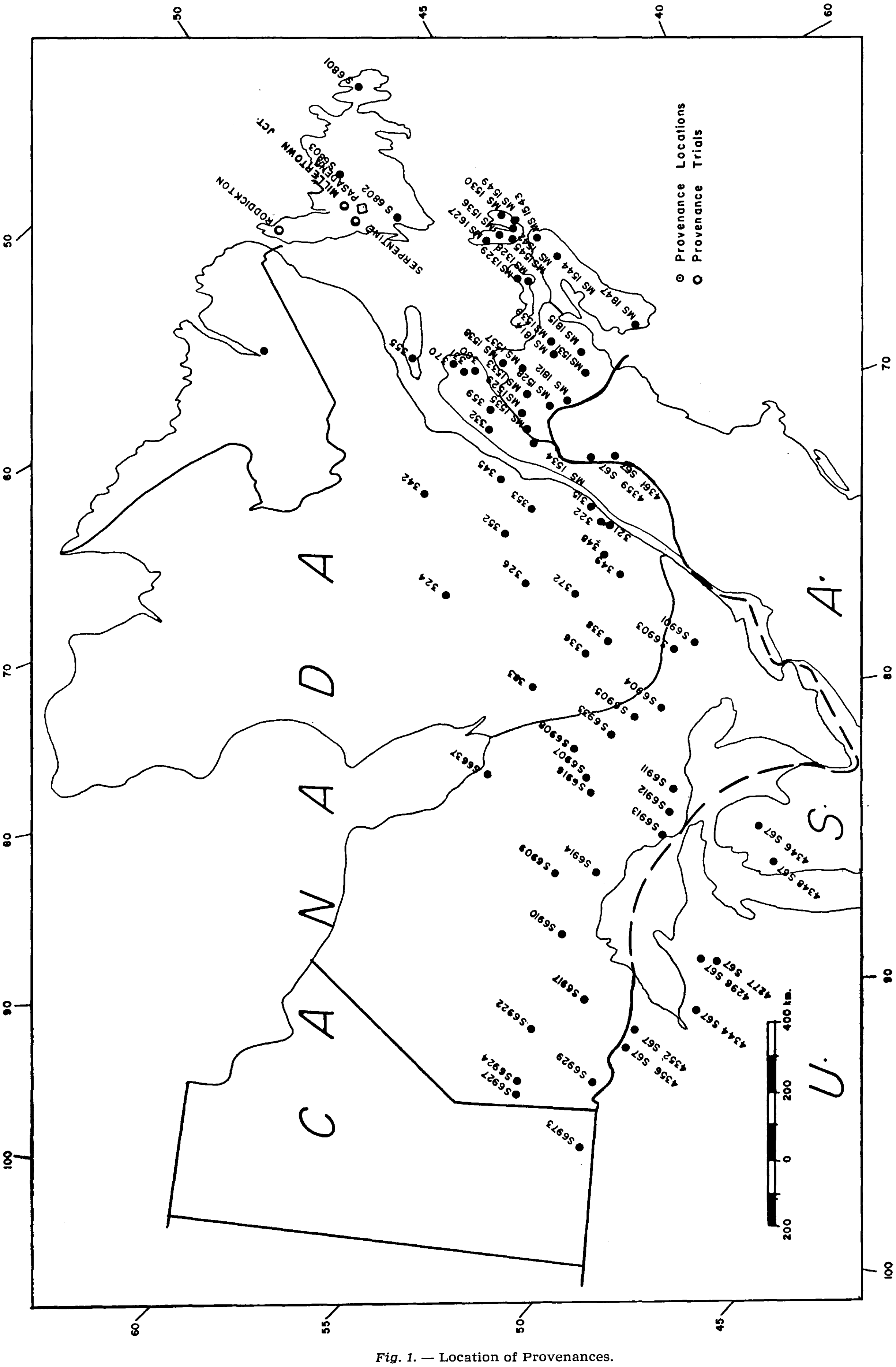

Fig. 1. — Location of Provenances.

se sind: MS. 1531, S. 6905, MS. 1528, MS. 1533, S. 6927, 370, S. 6911 und 353.

Introduction

Black spruce *(Picea mariana* (MILL.) B.S.P.) is one of the most abundant coniferous species of northern North America, is the principal constituent of the boreal forest and covers most of Canada and the United States. Such a widely distributed species has potential for genetic variability, with populations differing in their suitability for various sites and in genotypic stability.

The widespread distribution of black spruce, its relative freedom from diseases and insect pests, adaptability to a wide range of climatic and edaphic conditions and suitability for pulp, due to high wood density and long thin-walled wood fibres, make it economically valuable (BASHAM and MORAWSKI 1964, BENDSTEN 1974, BESLEY 1959 and LADELL 1971). To determine the genetic structure of the species, the Petawawa National Forestry Institute, Chalk River, Ontario, Canada, initiated a 32-location provenance study, based on range-wide sampling. This paper presents the results of three of these experiments located in Newfoundland.

Materials and Methods

THE PROVENANCES

Open-pollinated seed was collected from 202 provenances, and information on the habitat and seed trees was recorded (SELKIRK 1974). Seed was extracted according to the method described earlier (KHALIL 1975). Of these, 109 provenances, located between latitudes 43°—64° N, longitudes 60°—136° W, were initially selected for Newfoundland on the basis of climatic similarity. Plantable nursery stock of only 78 provenances was ultimately available, covering the range between latitudes 44°—54° N, longitudes 52°—100° W *(Fig. 1).*

THE NURSERY

The bulked seed was sown broadcast in June 1971, separated by provenances, in the nursery at Pasadena, Newfoundland (lat. 49°00'N, long. 57°35'W) *(Fig. 1).* Pasadena has an average frost-free period of 96 days (June 10—September 15), an average of 164 days with the mean temperature above 5.6° C (May 5—October 20), 1 100 degree-days above 5.6° C, and mean temperature and rainfall of 12.8° C and 432 mm respectively in the May—September period (ROWE 1972). The site had been prepared earlier in the standard manner described by KHALIL (1975).

THE FIELD EXPERIMENTS

Three field experiments were established in spring 1975 with 2—2 seedlings at Millertown Junction Road (Forest Section B.28a), Serpentine Lake (Forest Section B.28b) and Roddickton (Forest Section B.29) (ROWE 1972) *(Fig. 1).* The sites were good black spruce habitats in recently cutover areas and were topographically as homogeneous as possible.

The Millertown Junction Road and Serpentine Lake experiments had 72 provenances each and Roddickton had 64, with 57 provenances common to the three experiments. Six-replicated triple lattice design was used, being 8 × 9 rectangular lattice in the Millertown Junction Road and Serpentine Lake experiments and 8 ×8 lattice at Roddickton. The six replications represented two repetitions of the basic set of three replications (COCHRAN and COX 1964; FEDERER 1955). Nine-tree square plots, with a spacing of 2 × 2 m were used. The incomplete blocks within replications were arranged across contours so that the plots within them could be aligned along contours to minimize intra-block variation. Two border rows were planted round each experiment.

THE DATA

Four response variables were measured in fall 1980 on each surviving tree in each plot, i.e. 1974 height (Y1), 1979 height (Y2), 1980 height (Y3) and 1980 diameter at 0.3 m (Y4). Height growth in the 1974—80 period and in 1980 were calculated from the above measurements.

STATISTICAL ANALYSES

The following statistical analyses were performed on 1979 and 1980 heights, 1980 diameter at 0.3 m and height growth during the period 1974—80 and in 1980.

Analyses of variance by locations

Survival was excellent with only one missing plot each in the Serpentine Lake and Roddickton experiments and none in the Millertown Junction Road area. As the variability in the number of observations within plots and the intra-plot standard deviations for all response variables were low, the analyses of variance planned for these variables were conducted on unweighted plot means. These were done in the lattice as well as in the randomized complete block designs and the efficiency of the former over the latter was culculated, using Canada Department of Agriculture program SO26 (JUI and HOBBS 1981). The mixed mathematical model represented by equation (1) was used.

$$Y_{xijm} = \mu_x + R_{xi} + B_{xj} + P_{xm} + e_{xijm} \quad \cdots\cdots \quad (1)$$

where Y_{xijm} = Response of the mth provenance, in the jth incomplete block in the ith replication in the xth location, where $x = 1$, ----- 3, $i = 1$, ----- 6, $j = 1$, ------ k or $(k + 1)$, $m = k(k + 1)$, or k^2.

μ_x = Overall response at location x.

R_{xi} = Effect of replication i at location x (random).

B_{xj} = Effect of incomplete block j at location x (random).

P_{xm} = Effect of provenance m at location x (fixed).

e_{xijm} = Residual effect at location x (random).

The Incomplete Blocks within Replications (adjusted) line was tested using the Intra-Block Error mean squares as denominator, to determine the effectiveness of the incomplete blocks in reducing the error variance in the experiments. To test for provenances, adjusted for incomplete blocks, the program computed a mean squares value from the adjusted treatment totals and computed an approximate F-test, using average effective error mean squares as the denominator (DOUGLAS and CHOPRA 1982; COCHRAN and COX 1957; FEDERER 1955). The other Error terms used were: component (A) for replications, incomplete blocks for repetitions and replications/repetitions; and Intra-Block Error for the rest. The relative efficiency of the lattice designs was also output by the program, indicating the effectivenes of the incomplete blocks. Coefficients of intra-class correlation were calculated for all characters as a measure of intra-provenance variation.

Analyses of variance over locations

These analyses were performed to determine the role of locations and locations × provenances interactions as sources of variation. Because of the different lattice designs used, it was necessary to treat the experiments as randomized complete blocks as the basis for these analyses of variance. Since Errors (a) and (b) in these analyses were pooled over locations, an estimation of these values for each location was made to determine their homogeneity over locations. As reasonable homogeneity in this respect existed the F-tests over locations, provenances and locations × provenances interactions were considered valid. The associated mathematical model was mixed, represented by equation (2).

$$Y_{ijk} = \mu + L_i + P_k + R_{ij} + (LP)_{ik} + \epsilon_{ijk} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (2)$$

where Y_{ijk} = Response variable of the kth provenance in the jth replication within the ith location

μ = Overall mean

L_i = Effect of location i (fixed)

P_k = Effect of provenance k (fixed)

R_{ij} = Effect of the replication j in the location i (random) (Error a)

$(LP)_{ik}$ = Location x provenance interaction effect (fixed) (Error a)

ϵ_{ijk} = Lowest error component (random) (Error b).

Bonferroni *t-tests within locations*

These tests were performed according to Douglas (1979) after grouping the provenances into 43 geographical cells comprised of 1° latitude and 4° longitude (*Table 1*). This

Table 1. — Latitude-longitude cells.

	Longitudes											
Latitudes	96.01-100.0	92.01-96.00	88.01-92.00	84.01-88.00	80.01-84.00	76.01-80.00	72.01-76.00	68.01-72.00	64.01-68.00	60.01-64.00	56.01-60.00	52.01-56.00
53.01-54.00										6805 (43)		
52.01-53.00												
51.01-52.00					S.6937 (42)		324 (41)					
50.01-51.00		S.6924 S.6927 (40)	S.6922 (39)					342 (38)				
49.01-50.00	S.6973 (37)		S.6917 (36)	S.6909 S.6910 (35)		333 (34)	326 (33)	352 (32)		355 (31)		6803 (30)
48.01-49.00		S.6929 (29)		S.6914 (28)	S.6906 S.6907 S.6908 S.6933 (27)	336 (26)		345 353 (25)	370 331 360 359 332 (24)		6802 (23)	
47.01-48.00		4356.S67 (22)	4352.S67 (21)			338 (20)	372 (19)	MS.1534 (18)	MS.1529 MS.1533 MS.1535 MS.1537 MS.1538 (17)			6801 (16)
46.01-47.00			4344.S67 (15)	S.6913 (14)	S.6911 S.6912 (13)	S.6904 S.6905 (12)	348 322 321 349 (11)	4359.S67 315 (10)	MS.1528 MS.1539 MS.1812 MS.1814 (9)	MS.1536 MS.1542 MS.1549 MS.1627 MS.1328 MS.1329 (8)		
45.01-46.00			4277.S67 4296.S67 (7)			S.6901 S.6903 (6)		4361.S67 (5)	MS.1531 MS.1815 (4)	MS.1530 MS.1543 MS.1544 MS.1545 (3)		
44.01-45.00				4346.S67 4348.S67 (2)					MS.1847 (1)			

The figures in parentheses are the serial number of the cells.

reduced the number of multiple comparisons in the Millertown Junction Road and Serpentine Lake sites from 2 556 each to 804 and 769 respectively and from 2 016 in the Roddickton area to 755. The tests were performed among, as well as within, cells to determine whether the natural range of the species could be divided into homogeneous geographical cells which would be significantly different from each other. These comparisons were made between the provenance means over replications adjusted for the Incomplete Blocks Effects. The effective error mean squares with the degrees of freedom associated with the intra-block error in the analyses of variance tables were used in each case. Equations (3) and (4) were used to make these comparisons.

(i) Comparisons between geographical cells.

$$B = m_2 \sum_{j=1}^{m_1} \bar{Y}_{ij_1} - m_1 \sum_{k=1}^{m_2} \bar{Y}_{ik_2}$$

$$= t_{p,n,f} \left[\left(\frac{\text{Effective Error M.S.}}{6}\right) \sum_{s=1}^{m_1+m_2} c_s^2 \right]^{1/2} \quad \ldots (3)$$

where B = The test statistic

p = Overall probability (0.05, 0.01)

n = Total number of contrasts for the location

f = Intra-block error degrees of freedom for each location

C_s = Coefficient of the sth mean in the comparison

m_1 = Number of means within cell 1

m_2 = Number of means within cell 2.

(ii) Comparisons within geographic cells.

$$B = \bar{Y}_{ij} - \bar{Y}_{ik}$$

$$= t_{p,n,f} \left[2 \frac{\text{(Effective Error M.S.)}}{6} \right]^{1/2} \quad \ldots\ldots\ldots\ldots\ldots\ldots (4)$$

where the symbols have the same meanings as in equation (3).

Step-wise regression analyses by locations

These analyses were performed to evaluate the relative role of the initial growth in the nursery and the subsequent growth in the field in determining the total growth. Height in 1980 was used as the dependent variable and height in 1974, growth in the 1974—80 period and growth in 1980 as the independent variables (Draper and Smith 1966). In each case the values averaged over replications were used.

Genotypic stability and productive quality

The high percentage and statistical significance of variation due to Locations × Provenances Interaction in the over-locations analyses of variance indicated the need for evaluating the provenances for genotypic stability and productive quality. The 57 provenances common to the three test sites were evaluated. As height growth in the 1974—80 period completely reflected the response of the provenances to the environments of the test sites, it was used as the criterion for this test. Genotypic stability was determined by the methods of Tai (1971) and Wricke (1962). Productive quality was measured by calculating the Provenance Quality Index (PQI) for each provenance according to Segaran (1979).

In Tai method (Tai 1971) the linear response of the genotype of the provenance i (α_i) and the deviation from the linear response (λ_i) were calculated according to equations (5) and (6) respectively. As perfectly stable provenances ($\alpha_i = -1$, $\lambda_i = 1$) do not exist those with average genotypic stability ($-1 \leq \alpha_i \leq 0$; $0 \leq \lambda_i \leq 1$) were selected. Wricke's ecovalance was calculated from equation (7). Provenance Quality Index, which is the quotient of the provenance effects and environmental effects was obtained from equation (8).

$$\alpha_i = \frac{\Sigma[(\ell_j)\ (g\ell_{ij})] \,/\, (\ell-1)}{(MSL = MSB) \,/\, pr} \quad \ldots\ldots\ldots\ldots\ldots\ldots (5)$$

$$\lambda_i = \frac{(\Sigma[(g\ell)^2_{ij} \,/\, (\ell-1)]) - \alpha_i \Sigma[(\ell_j)\ (g\ell)_{ij}] \,/\, (\ell-1)}{[(P-1)\ MSE] \,/\, pr} \quad \ldots\ldots (6)$$

where ℓ_j = Location effect = $\bar{X}_{.j} - \bar{X}_{..}$

$(g\ell)_{ij}$ = Genotype x environment interaction

$X_{ij} - \bar{X}_{i.} - \bar{X}_{.j} + \bar{X}_{..}$

ℓ = Number of locations

MSL = Mean squares due to locations

MSB = Mean squares due to replications

p = Number of provenances

r = Number of replications within locations

MSE = Mean squares due to error

$$E = \Sigma(g\ell)^2_{ij} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (7)$$

where E = Ecovalence

$(g\ell)_{ij}$ = Genotype x environment interaction

$= X_{ij} - \bar{X}_{i.} - \bar{X}_{.j} + \bar{X}_{..}$

$$P_i = \bar{X}_{i.} - \bar{X}_{..} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (8)$$

P_i = Provenance effects of provenance i

$\bar{X}_{i.}$ = Mean of provenance i over all environments

$\bar{X}_{..}$ = Overall mean

$$E_j = \frac{\Sigma\ |(\bar{X}_{.j} - \bar{X}_{..})|}{\ell} \quad \ldots\ldots\ldots\ldots\ldots\ldots (9)$$

$$PQI = \frac{P_i}{E_j} = \frac{[\bar{X}_{i.} - \bar{X}_{..}]}{\Sigma|(\bar{X}_{.j} - \bar{X}_{..})| + \ell} \quad \ldots\ldots\ldots\ldots\ldots (10)$$

Results and Discussion

ANALYSES OF VARIANCE BY LOCATIONS

The results, summarized in *Table 2*, are important for demonstrating the efficiency of the design and layout of the experiments in identifying and removing the variation due to environmental effects and improving the sensitivity of the experiments. Replications are significant sources of variation in all response variable at all locations. This not only indicates the sensitiveness of black spruce to micro-environmental differences within the experiments but also demonstrates the effectiveness of the design in removing the variation due to such effects from total variation. Incomplete blocks within replications (adjusted) are significant in the Millertown Junction Road and Roddickton areas, showing the effectiveness of the lattice design in improving sensitivity of the experiments compared with the randomized complete block design. Efficiency computations showed such improvement to be 2—5% for the various response variables. More improvement in efficiency is expected in subsequent measurements when inter-provenance differences are expected to be enhanced. Both components (A) and (B) of the incomplete blocks within replications are nonsignificant for all response variables in the Serpentine Lake area, which is to be expected. In the Millertown Junction Road area both components are signifi-

Table 2. — Summary of analyses of variance by locations.

Source of variation	Degrees of freedom: Expected	Degrees of freedom: Value	Height in 1979: Var. %	Height in 1979: F*	Height in 1980: Var. %	Height in 1980: F*	Diameter: Var. %	Diameter: F*	Height growth (1974–80): Var. %	Height growth (1974–80): F*	Height growth (1980): Var. %	Height growth (1980): F*
Location 1 – Millertown Junction Road												
Replications	$(r-1)$	5	5.2	3.08 (0.01)	6.4	3.80 (0.01)	7.7	4.41 (0.005)	6.8	4.07 (0.005)	7.9	4.54 (0.005)
Repetitions	$(p-1)$	1	0.6	1.75 (<0.10)	0.4	1.17 (<0.10)	1.5	4.40 (0.05)	0.1	0.16 (<0.10)	0.1	0.17 (<0.10)
Replications/Repeat.	$p(n-1)$	4	4.5	3.41 (0.025)	6.0	0.29 (<0.10)	6.2	4.41 (0.005)	6.7	5.04 (0.005)	7.8	5.63 (0.005)
Provenances	(k^2+k-1)	71	22.0	1.56 (0.005)	21.2	1.52 (0.01)	20.1	1.46 (0.05)	20.2	1.44 (0.05)	19.7	1.38 (0.05)
Incomplete blocks within replications (adj.)	(rk)	48	15.8	1.78 (0.01)	16.1	1.83 (0.005)	16.7	1.92 (0.005)	16.1	1.81 (0.005)	16.5	1.89 (0.005)
Component A	$nk(p-1)$	24	8.3	1.86 (0.01)	8.0	1.82 (0.005)	8.6	1.98 (0.005)	7.9	1.77 (0.025)	7.3	1.67 (0.025)
Component B	nk	24	7.5	1.70 (0.025)	8.1	1.83 (0.005)	8.1	1.86 (0.005)	8.2	1.85 (0.01)	9.2	2.10 (0.005)
Intra-block error	$(r-1)(k^2-1)-k$	307	57.0		56.3		55.5		56.9		55.9	
Total	(rk^2+rk-1)	431	100.0		100.0		100.0		100.0		100.0	
Location 2 – Serpentine Lake												
Replications	$(r-1)$	5	3.1	2.84 (0.025)	4.4	3.86 (0.005)	8.6	8.17 (0.005)	5.2	5.13 (0.005)	7.3	6.27 (0.005)
Repetitions	$(p-1)$	1	0.3	1.51 (<0.10)	0.8	3.35 (0.10)	0.3	1.51 (<0.10)	1.5	7.14 (0.025)	1.9	8.08 (0.01)
Replications/Repeat.	$p(n-1)$	4	2.8	3.17 (0.025)	3.6	3.98 (0.025)	8.3	9.84 (0.005)	3.7	4.63 (0.005)	5.4	5.81 (0.005)
Provenances	(k^2+k-1)	71	33.0	2.59 (0.005)	32.1	2.53 (0.005)	25.3	1.91 (0.005)	32.8	2.64 (0.005)	25.3	1.88 (0.005)
Incomplete blocks within replications (adj.)	(rk)	48	10.6	1.26 (<0.10)	10.9	1.33 (<0.10)	10.2	1.16 (<0.10)	9.7	1.18 (<0.10)	11.2	1.27 (0.10)
Component A	$nk(p-1)$	24	4.8	1.15 (<0.10)	4.8	1.17 (<0.10)	5.1	1.17 (<0.10)	4.4	1.07 (<0.10)	4.7	1.08 (<0.10)
Component B	nk	24	5.8	1.38 (0.10)	6.1	1.48 (0.10)	5.1	1.15 (<0.10)	5.3	1.29 (<0.10)	6.5	1.46 (0.10)
Intra-block error	$(r-1)(k^2-1)-k$	307	53.3		52.6		55.9		52.3		56.2	
Total	(rk^2+rk-1)	431	100.0		100.0		100.0		100.0		100.0	
Location 3 – Roddickton												
Replications	$(r-1)$	5	9.2	5.62 (0.005)	11.4	6.96 (0.005)	15.4	7.99 (0.005)	15.7	9.41 (0.005)	15.3	9.09 (0.005)
Repetitions	$(p-1)$	1	0.1	0.23 (<0.10)	0.1	0.11 (<0.10)	0.1	0.11 (<0.10)	0.1	0.34 (<0.10)	0.1	0.04 (<0.10)
Replications/Repeat.	$p(n-1)$	4	9.1	6.96 (0.01)	11.3	8.61 (0.005)	15.3	9.96 (0.005)	15.6	11.68 (0.005)	15.2	11.36 (0.005)
Provenances	(k^2-1)	63	20.4	1.51 (0.005)	19.5	1.46 (0.025)	15.7	1.25 (0.10)	15.7	1.19 (<0.10)	18.8	1.49 (0.01)
Incomplete blocks within replications (adj.)	$r(k-1)$	42	13.8	1.57 (0.05)	13.7	1.61 (0.01)	16.2	1.99 (0.005)	14.0	1.66 (0.025)	14.1	1.76 (0.005)
Component A	$n(p-1)(k-1)$	21	9.7	2.23 (0.005)	9.2	2.14 (0.005)	10.9	2.67 (0.005)	8.7	2.07 (0.005)	8.8	2.21 (0.005)
Component B	$n(k-1)$	21	4.1	0.92 (<0.10)	4.5	1.07 (<0.10)	5.3	0.55 (<0.10)	5.3	1.26 (<0.10)	5.3	1.31 (<0.10)
Intra-block error	$(k-1)(rk-k-1)$	272	56.6		55.4		52.7		54.6		51.8	
Total	(rk^2-2)	382	100.0		100.0		100.0		100.0		100.0	

Note (1): * The figures in parentheses indicate the level of significance of F values; r = No. of complete blocks; n = No. of arrangements, p = No. of repetitions of the n arrangements; k = No. of treatments in an incomplete block.
(2): The F-test was approximate using the average effective error mean squares as the denominator (Cochran and Cox, 1957).

cant, while in the Roddickton area component (A) effects are significant but component (B) effects are not. Significance of component (A) shows the significance of the interaction between confounded effects and replications. The significance of component (B) shows that the differences represented by the comparisons between the groups of treatments in replications in which they are unconfounded with the same treatments in the replications in which the group comparisons are confounded with incomplete block differences are significant.

The coefficients of intraclass correlation *(Table 3)* are low, which indicates high intra-provenance variation in all response variables studied. This shows heterogeneity of the provenances and indicates good opportunity for genetic gains by intensive family selection.

Table 3. — Coefficients of intraclass correlation.

Response variable	Millertown Junction Road	Serpentine Lake	Roddickton
Height in 1979	0.0786	0.2086	0.0709
Height in 1980	0.0720	0.2021	0.0635
Diameter at 0.3 m in 1980	0.0608	0.1320	0.0218
Height growth in the 1974-80 period	0.0600	0.2154	0.0226
Height growth in 1980	0.0561	0.1279	0.0645

Table 4, which lists the provenances in the fourth quartile with respect to the five response variables, shows the performance of these provenances at the three locations and their variation between locations. On the basis of 10-year height the provenances in the fourth quartile occupy 17 geographic cells of *Table 1.* However, most of them lie between latitudes 45°—49° N and longitudes 60°—84° W.

ANALYSES OF VARIANCE OVER LOCATIONS

The results of these analyses are summarized in *Table 5,* which also shows the appropriate error terms for testing the significance of each source of variation. Though all sources of variation are significant at various levels the significance of locations and Locations × Provenances Interaction is important in that it confirms and quantifies the preliminary indications of *Tables 2* and *4.*

BONFERRONI T-TESTS

The purpose of dividing the zone of natural distribution of provenances into expected homogeneous geographic cells was achieved. Of the 17 cells with multiple provenances, only cell 24 had two provenances (331 and 359) significantly different from each other at the 0.01 or 0.05 levels for all response variables in the Millertown Junction Road area. Significant differences between cells at the 0.01 or 0.05 level could not be detected for any response variable at any location. Failure to detect such differences in the pair-wise combinations tested does not rule out the possibility of their existence. The failure could be due to the dense competing vegetation which increased the intra-block error mean squares on account of differential densities of the competing vegetation among as well as within plots. As this mean squares was used as the effective error term in the calculation of the test criteria, the sensitivity of the test was reduced. Also, other cell combinations may show the between-cell differences.

Table 4. — Array of provenances in the fourth quartile.

Height in 1979		Height in 1980		Ht. growth 1974-80		Ht. growth 1980		Diameter	
Prov.	Ht. (cm)	Prov.	Ht. (cm)	Prov.	Ht. (cm)	Prov.	Ht. (cm)	Prov.	Diam. (cm)
				Millertown Junction Road					
359	71.0**	359	95.9**	359	80.1**	359	24.8**	359	1.45**
S.6924	68.3**	MS.1329	89.0**	MS.1329	75.2**	370	22.2**	MS.1329	1.29**
MS.1329	67.1**	S.6924	88.1**	S.6924	72.6**	MS.1329	21.8**	4361.S67	1.27**
4361.S67	66.6**	4361.S67	85.8**	4361.S67	72.0**	4346.S67	21.5*	370	1.27**
S.6903	63.8*	370	84.5*	370	71.6**	6802	21.0*	MS.1536	1.16*
370	63.1*	S.6903	82.7*	MS.1528	69.3*	MS.1528	20.4*	MS.1812	1.14*
S.6905	62.1*	MS.1528	82.5*	4346.S67	68.3*	MS.1530	20.1*	S.6924	1.12*
MS.1528	62.1*	S.6905	80.7*	MS.1531	67.9*	326	20.1*	S.6903	1.12*
349	60.5*	349	80.2*	MS.1812	67.7*	MS.1536	19.9*	355	1.11*
MS.1531	60.3*	4346.S67	80.1*	S.6903	66.7*	S.6924	19.9*	MS.1530	1.09*
S.6910	59.9	MS.1531	79.4*	MS.1536	65.9*	MS.1812	19.7*	332	1.08*
S.6917	59.8	S.6910	78.8	4296.S67	65.8*	349	19.7*	4352.S67	1.08
4352.S67	59.4	MS.1529	78.6	S.6905	65.6	MS.1529	19.6*	MS.1529	1.06
333	59.3	MS.1812	78.5	4348.S67	65.6	S.6912	19.4*	349	1.06
S.6973	59.2	MS.1536	78.4	349	65.3	MS.1328	19.3	345	1.06
S.6911	59.1	MS.1530	77.8	S.6907	65.1	353	19.3	333	1.05
S.6914	59.1	MS.1328	77.7	S.6910	65.0	4361.S67	19.2	4296.S67	1.05
MS.1529	59.1	353	77.6	333	64.0	MS.1531	19.0	S.6905	1.04
				Serpentine Lake					
S.6905	105.2**	MS.1531	130.5*	MS.1815	118.9**	MS.1539	28.7**	MS.1544	2.10**
MS.1531	103.7**	S.6905	130.3*	MS.1545	118.5**	MS.1545	28.3**	332	2.01**
MS.1815	103.1**	MS.1815	128.5*	S.6905	117.8**	MS.1537	27.0**	MS.1538	2.00**
S.6903	102.1**	MS.1545	127.8*	MS.1531	117.5**	MS.1531	26.8**	4361.S67	1.97*
322	101.5**	MS.1329	126.3*	MS.1329	116.9**	6803	26.5**	321	1.96*
MS.1329	101.1**	322	126.3*	MS.1539	116.6**	332	26.2**	MS.1537	1.96*
321	100.5*	S.6903	125.8*	322	115.5**	MS.1538	26.2*	MS.1545	1.96*
MS.1544	100.4**	352	125.3*	352	115.3**	359	25.8*	S.6903	1.95*
352	99.8*	MS.1544	124.1*	MS.1528	114.6**	MS.1815	25.6*	MS.1814	1.95*
MS.1545	99.4*	359	123.8*	S.6903	113.1*	352	25.5*	359	1.94*
MS.1814	98.9*	MS.1528	123.6*	359	112.1*	6802	25.4*	MS.1549	1.91*
353	98.6*	321	123.5*	321	111.6*	MS.1528	25.3*	345	1.91*
S.6917	98.4*	MS.1539	123.4*	MS.1544	111.2*	349	25.3*	MS.1329	1.90*
MS.1528	98.3*	353	123.4*	353	111.1*	MS.1329	25.3*	MS.1533	1.89*
359	98.0*	MS.1814	123.3*	MS.1814	110.7*	S.6903	25.3*	353	1.86*
S.6927	97.9*	MS.1537	122.5*	MS.1537	110.4*	S.6905	25.1*	MS.1539	1.86*
S.6911	97.8*	S.6911	122.2*	S.6911	110.2*	353	24.9*	MS.1812	1.85*
MS.1533	96.1*	S.6927	121.4*	MS.1533	110.1*	322	24.6*	360	1.84*
				Roddickton					
MS.1531	71.4**	MS.1531	95.3**	MS.1531	75.2**	MS.1531	25.4**	MS.1531	1.29**
S.6910	70.8**	S.6910	92.8**	S.6910	71.0**	MS.1328	22.1**	S.6910	1.21**
S.6927	70.4**	S.6927	92.0**	S.6927	69.3**	S.6910	22.0**	S.6927	1.17*
S.6905	67.6**	S.6905	88.3**	MS.1533	68.5***	MS.1528	21.5**	MS.1533	1.16*
S.6911	66.1*	MS.1533	86.6*	S.6905	66.7**	S.6927	21.4*	S.6904	1.13*
MS.1533	65.3*	MS.1328	85.7*	MS.1328	64.6*	MS.1533	21.4*	353	1.13*
S.6904	64.8*	S.6911	85.3*	326	64.3*	370	21.1*	338	1.11*
353	64.7*	353	84.6*	352	64.1*	6803	20.8*	MS.1328	1.11*
S.6907	64.4*	326	84.5*	S.6911	64.0*	S.6905	20.7*	332	1.10*
326	63.9*	S.6904	84.4*	S.6904	63.6	326	20.6*	321	1.09
MS.1329	63.9*	352	83.4	353	63.1	MS.1534	20.6*	370	1.09
372	63.8*	S.6907	83.2	MS.1528	62.8	S.6914	20.4	MS.1329	1.09
MS.1328	63.7*	4296.S67	82.6	332	62.7	332	20.3	372	1.08
352	63.4	MS.1329	82.1	S.6914	62.6	331	20.2	MS.1538	1.08
4296.S67	63.2	370	82.1	370	62.6	MS.1529	20.2	315	1.07
322	63.0	MS.1528	82.0	6802	62.0	MS.1539	20.2	326	1.07

* Provenances one standard deviation above the mean

** Provenances two standard deviations above the mean

Note — The values in columns 2, 4, 6, 8 and 10 are adjusted provenance means

Table 5. — Summary of analyses of variance over locations.

Source of variation		Expected mean squares	Degrees of freedom Expected	Degrees of freedom Value	Height in 1979 Var. %	Height in 1979 F	Height in 1980 Var. %	Height in 1980 F	Diameter Var. %	Diameter F	Height growth (1974–80) Var. %	Height growth (1974–80) F	Height growth (1980) Var. %	Height growth (1980) F
Locations	(L)	$\sigma^2 + P\sigma_R^2 + \frac{PR\Sigma L_i^2}{L-1}$	L-1	2	59.8	222.92 (0.005)	53.1	133.71 (0.005)	47.7	75.09 (0.005)	61.8	163.32 (0.005)	16.3	17.10 (0.005)
Provenances	(P)	$\sigma^2 + \frac{RL}{P-1} \Sigma P_k^2$	P-1	56	6.5	4.25 (0.005)	6.9	3.36 (0.005)	5.3	2.20 (0.005)	5.1	3.03 (0.005)	9.5	2.47 (0.005)
Locations x provenances interaction	(LXP)	$\sigma^2 + \frac{R}{(P-1)(L-1)} \Sigma\Sigma (LC)_{ik}^2$	(L-1)(P-1)	112	5.1	3.64 (0.005)	5.9	1.42 (0.005)	6.4	1.35 (0.01)	5.1	1.50 (0.005)	9.4	1.22 (0.05)
Replications within locations (Error a)	(R/L)	$\sigma^2 + P\sigma_R^2$	(R-1)L	15	2.0	1.44 (0.005)	3.0	5.37 (0.005)	4.8	7.45 (0.005)	2.8	6.30 (0.005)	7.1	6.94 (0.005)
Provenances x replications within locations (Error b)	(PR/L)	σ^2	(P-1)(R-1)L	840	26.6		31.1		35.8		25.2		57.7	
Total				1 025	100.0		100.0		100.0		100.0		100.0	

The figures in parentheses indicate the level of significance of the F values.

STEP-WISE REGRESSIONS ANALYSES

The results (*Tables 6* and *7*) indicate that total height growth at 10-year age is highly correlated separately with each of the single independent variables tested. Height growth in the field during the 1974—80 period is very significantly correlated with the height in the nursery but the growth of the year 1980 is not significantly correlated. The 10-year height growth is determined jointly by the 1974—80 growth and the initial growth in the nursery, with the former making the greater contribution. The contribution of the growth in 1980 is statistically nonsignificant in each location. This shows that the superior height growth of the fast-growing provenances is not a mere carry-over of the fast growth in the nursery. Such provenances exhibit superior growth in the field also.

Table 6. — Correlation matrix.

Variable	Millertown Junction Road X_1	Millertown Junction Road X_2	Millertown Junction Road X_3	Serpentine Lake X_1	Serpentine Lake X_2	Serpentine Lake X_3	Roddickton X_1	Roddickton X_2	Roddickton X_3
X_2	0.43**			0.39**			0.26*		
X_3	0.27*	0.90**		0.19^{NS}	0.85**		0.08^{NS}	0.89**	
Y	0.55**	0.98**	0.87**	0.47**	0.99**	0.83**	0.58**	0.94**	0.78**
	R = 0.9688			R = 0.9874			R = 0.9962		

X_1 = Height in 1974; X_2 = Height growth in the 1974—80 period; X_3 = Height growth in 1980, Y = Total height in 1980.
** = Statistically significant (0.01 level).
* = Statistically significant (0.05 level).
NS = Statistically nonsignificant (0.05 level).

Table 7. — Summary of step-wise regression analyses.

Location	Regression equation	F	Order of entry of X
Millertown Junction Road	$Y = 1.0770 + 0.9661X_1 + 0.9635X_2 + 0.0777X_3$	$b_2 = 29.59$*** $b_1 = 11.98$*** $b_3 = 0.90^{NS}$	X_2, X_1, X_3
Serpentine Lake	$Y = 0.5185 + 0.9622X_1 + 1.0402X_2 + 0.0796X_3$	$b_2 = 32.25$*** $b_1 = 7.08$*** $b_3 = 0.73^{NS}$	X_2, X_1, X_3
Roddickton	$Y = -0.7784 + 1.0104X_1 + 0.9899X_2 + 0.0104X_3$	$b_2 = 42.72$*** $b_1 = 40.73$*** $b_3 = 0.17^{NS}$	X_2, X_1, X_3

*** = Statistically significant (0.01 level).

GENOTYPIC STABILITY AND PRODUCTIVE QUALITY

Table 8 presents the results of these analyses. On the basis of TAI method 18 provenances have average genotypic stability. These are 370, MS.1328, S.6907, 6802, S.6904, 4296.S67, MS.1529, 349, S.6912, 345, 4352.S67, 315, 355, 342, 4356.S67, 324, 6801 and MS.1627. With one exception (4296.S67) they are also acceptable under WRICKE's method. However, these provenances do not rank high in performance and have average or below average Provenance Quality Indices. The low genotypic stability of the provenances in the top quartile agrees with the results of TAI (1971) and SEGARAN (1979). This is further supported by MITTON *et al.* (1981) who found that in aspen (*Populus tremuloides* MICHX.) heterozygosity is associated with high mean growth and high growth variability. They have also collected considerable theoretical and empirical evidence to suggest that heterozygosity is associated with morphological variation in many species. These results suggest high heterozygosity in these provenances which makes them fast growing but susceptible to high degree of deviation from the linear effect of the genotype × environment interaction, especially in environments different from those in their native habitats.

In these circumstances the rational approach should be to select suitable provenances by a combination of productive quality and genotypic stability so as to obtain those which are superior in performance as well as have at least average stability over a wide range of environments. This is particularly important when the genotype × environment interaction is significant. Suitable provenances should be selected successively for a positive and high preselected Provenance Quality Index and genotypic stability by one or both of the above methods.

Selection should be made on this basis from the provenances listed in *Table 8*, limiting the initial selection to the top quartile. All the 14 provenances in this quartile have positive Provenance Quality Indices. Eight of them have WRICKE's ecovalence of equal to or less than the mean, i.e. 95 in this study. These provenances are MS.1531, S.6905,

Table 8. — Genotypic stability and productive quality of provenances for height growth during the period 1974—80.

Rank	Provenance	Mean growth 1974-80 (cm)	Tai's α	Tai's λ	Wricke's ecovalence	PQI
1	MS.1531	86.9	0.0958	0.3665	34.21	0.7286
2	S.6905	83.4	0.2312	-0.0027	62.33	0.5411
3	MS.1329	83.3	0.1969	2.4629	203.13	0.5357
4	359	83.1	0.0307	4.2415	272.85	0.5250
5	MS.1528	82.2	0.1557	0.3757	52.41	0.4768
6	MS.1533	80.6	0.0535	0.1780	14.75	0.3911
7	S.6927	79.4	0.0939	0.7583	58.89	0.3268
8	MS.1815	79.3	0.4167	-0.0163	202.02	0.3214
8	370	79.3	-0.1309	0.1564	63.62	0.3214
9	S.6911	78.9	0.1199	0.0090	17.39	0.3000
10	352	78.7	0.3089	0.3484	133.89	0.2893
11	353	78.1	0.1802	0.0854	43.45	0.2571
12	S.6910	77.9	-0.2912	0.2460	114.91	0.2464
13	MS.1538	77.3	0.1357	0.1671	32.24	0.2143
14	S.6903	77.0	0.2870	1.9682	222.43	0.1982
15	MS.1328	76.8	-0.1101	-0.0007	14.13	0.1875
16	332	76.7	0.1130	0.0580	18.65	0.1821
17	MS.1539	76.6	0.4305	0.0890	222.41	0.1768
18	MS.1545	76.3	0.5117	0.0296	308.09	0.1607
18	322	76.3	0.4044	0.2228	205.53	0.1607
19	MS.1814	75.8	0.2480	0.0015	72.02	0.1339
20	321	75.6	0.2876	0.0087	97.28	0.1232
21	S.6907	74.7	-0.2017	0.0926	53.52	0.0750
22	6802	74.5	-0.0393	0.0177	2.94	0.0643
23	S.6904	74.4	-0.1145	0.0617	19.28	0.0589
24	S.6917	74.2	0.2357	0.4564	94.22	0.0482
25	4296.S67	73.6	-0.2917	0.1553	109.46	0.0161
26	MS.1537	73.5	0.3215	0.0832	126.19	0.0107
27	MS.1535	73.0	0.1913	0.2091	56.18	-0.0161
28	MS.1529	72.7	-0.2764	0.0295	90.05	-0.0321
28	326	72.7	-0.3482	0.0006	141.74	-0.0321
28	349	72.7	-0.1227	0.8186	70.05	-0.0321
29	348	72.6	0.2131	-0.0044	52.83	-0.0375
30	S.6912	72.0	-0.0385	0.0109	2.43	-0.0696
31	345	71.9	-0.0303	0.0340	3.25	-0.0750
31	4352.S67	71.9	-0.1133	0.1473	24.41	-0.0750
32	315	71.8	-0.0389	0.0857	7.26	-0.0804
33	360	71.0	0.1699	0.3200	54.26	-0.1232
34	4277.S67	70.7	0.0256	0.1658	11.39	-0.1393
35	333	70.4	-0.3196	0.3393	141.05	-0.1554
36	MS.1542	69.9	0.0013	0.0039	0.25	-0.1821
36	4344.S67	69.9	-0.3942	0.0137	182.61	-0.1821
37	MS.1530	69.7	-0.2876	0.5429	131.33	-0.1929
38	336	68.7	0.0571	1.0822	73.15	-0.2464
39	MS.1536	68.6	-0.5497	0.4168	380.03	-0.2518
40	S.6909	68.2	-0.5084	0.1718	310.21	-0.2732
40	355	68.2	-0.2359	-0.0043	64.81	-0.2732
41	331	67.3	0.0693	1.3952	95.01	-0.3214
42	342	67.2	-0.0484	0.9134	61.26	-0.3268
43	4345.S67	66.0	-0.0842	0.0359	10.59	-0.3911
44	338	65.9	-0.1824	1.0966	109.15	-0.3964
45	372	65.8	0.1408	0.9672	85.15	-0.4018
46	MS.1543	65.2	0.0608	0.5641	40.46	-0.4339
47	324	63.2	-0.2066	0.0847	55.33	-0.5411
48	6801	62.7	-0.2159	0.6518	96.65	-0.5679
49	MS.1627	62.2	-0.1707	0.0753	38.89	0.5946
50	6805	62.1	-0.3276	0.0390	128.01	-0.6000

MS. 1528, MS. 1533, S.6927, 370, S.6911 and 353. Only two of these qualify on the basis of Tai method, viz. 370 and 6910. As only the first results at the age of six years after planting are available, it is advisable to use the more liberal Wricke's method and select the eight provenances which qualify under that method. These provenances have high productive quality and would be reasonably stable in the habitats represented by the three test locations.

Conclusions

The important conclusions available to date are listed below:

1. The use of lattice design has significantly improved the sensitivity of these experiments, compared with the randomized complete block designs even at the early stage of six years in the field. Such sensitivity is particularly important in conducting the Bonferroni t-tests.
2. There is high intra-provenance variation at each location in all the variables studied, suggesting intra-provenance heterogeneity and heterozygosity and providing opportunity for good genetic gains by intensive family selections in superior provenances.
3. Most of the provenances in the fourth quartile at each location belong to the region between latitudes 45°—49° N and longitudes 60°—84° W. There is considerable variation between test sites in the performance of these provenances which has been confirmed and quantified by the analyses of variance over locations.
4. Total height growth has highly significant simple correlation with the initial growth in the nursery, subsequent growth in the field and growth in the last year. However, when the above independent variables are considered together only the initial growth in the nursery and the subsequent growth in the field are significant. The latter is more important than the former, which shows that the provenances which are fast growing in the nursery maintain their superiority in the field.
5. The top quartile provenances have relatively low genotypic stability. This seems to be due to their high heterozygosity which exposes them to a high level of deviation from the linear effect of the location × provenance interaction.
6. Using a combination of Provenance Quality Indices and Wricke's ecovalence, the eight most promising provenances are: MS.1531, S.6905, MS.1528, MS.1533, S.6927, 370, S.6911 and 353.

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