Variation and Genotypic Stability of Picea mariana (Mill.) B.S.P. in Newfoundland, Canada

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Summary

This paper presents results of a ten-year black spruce (*Picea mariana* (Mill.) B. S. P.) provenance study in Newfoundland, Canada. The data on ten-year height, height growth in the field up to ten year age and in the tenth year and diameter at 0.3 m were studied together with evaluation of genotypic stability and productive quality of the provenances. Provenances were significant sources of variation at four locations, where intra-provenance variation was small and vice versa at the other three locations.

Height growth in the field showed weak east-west and north-south trends in the mainland and Newfoundland-Labrador provenances respectively. Greater height growth of the fast-growing provenances was not dependent only on the growth in the nursery but was retained in the field also.

Provenances in the fourth quartile had relatively low genotypic stability, which would make choice of suitable provenances difficult if precise information about the environment of the planting site is not available. However, recommendations have been made for planting sites resembling the test locations and for sites whose environmental conditions are not known or do not resemble those of the test locations.

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

Résumé

Sont présentés les résultats après dix ans d'une étude de provenances de l'épinette noire (*Picea mariana* (Mill.) B. S. P.) à Terre-Neuve, au Canada. Les données sur la hauteur à dix ans, l'accroissement en hauteur sur le terrain jusqu'à dix ans et au cours de la dixième année et le diamètre à 0,3 ont été analysées ainsi que la stabilité génotypique et la productivité des provenances. Les provenances ont été des sources importantes de variation à quatre emplacements, où la variation intraprovenance était faible, et c'était le contraire aux trois autres emplacements.

Les provenances de la partie continentale et de la région de Terre-Neuve et du Labrador ont montré une variation de l'accroissement en hauteur dans la direction est-ouest et nord-sud respectivement. L'accroissement supérieur des provenances à croissance rapide n'était pas dû uniquement à la croissance en pépinière, mais était maintenu sur le terrain.

Les provenances classées dans le quatrième quart ont montré une stabilité génotypique relativement faible, rendant le choix des provenances appropriées difficile quand on ne possède pas d'informations précises sur le milieu de plantation. Toutefois, des recommandations sont formulées pour les emplacements ressemblant à ceux de l'étude, ainsi que pour les emplacements dont on ne connaît pas les conditions et ceux qui ne ressemblent pas aux emplacements de l'étude.

Zusammenfassung

In der vorliegenden Arbeit wird über die Ergebnisse aus einem zehnjährigen Herkunftsversuch mit Schwarzfichte (*Picea mariana* (Mill.) B. S. P.) in Neufundland (Kanada) berichtet. An Hand der Höhe von zehn Jahren wurden das Gesamthöhenwachstum über 10 Jahre hinweg und dasjenige im Verlauf des 10. Jahres sowie der Durchmesser in 0,3 m Höhe der Provenienzen untersucht, ebenso im Hinblick auf deren genetische Stabilität und Ertragsfähigkeit. Auf vier Versuchsflächen gab es zwischen den Provenienzen signifikante Herkunftsunterschiede, wobei die Variationsbreite innerhalb der Herkünfte nur gering war. Letztere war auf den übrigen 3 Versuchsflächen groß.

Bei den Herkünften vom kanadischen Festland zeigte das Höhenwachstum auf der Freifläche einen schwachen Ost-West-Klin, bei den Herkünften von Neufundland-Labrador einen schwachen Nord-Süd-Klin. Das stärkere Höhenwachstum der schnellwüchsigen Herkünfte war nicht nur die Folge eines schnelleren Wachstums in der Baumschule, sondern auch im Freiland.

Die Herkünfte des vierten Quartils zeigten eine verhältnismäßig geringe genotypische Stabilität — ein Umstand, der bei der Wahl geeigneter Herkünfte Schwierigkeiten bereiten könnte, wenn keine genauen Angaben über die Umweltbedingungen des vorgesehenen Pflanzgebietes vorliegen. Zur Lösung solcher Probleme dienen Vorschläge zur Bepflanzung von Standorten, die den Versuchsparzellen ähnlich sind, sowie von Standorten, deren Umweltbedingungen nicht bekannt oder anders als an den Versuchsstandorten sind.

Table 1. — Locations of black spruce provenances.

Provenance	Geographic Location			Forest section*
	Lat. (°N)	Long. (°W)	Alt. (m)	
1	51.48	55.00	15	B.32 - Forest Tundra
2	51.05	56.77	61	B.29 - Northern Peninsula
3	50.87	56.12	15	"
4	50.57	57.27	61	"
5	50.40	56.47	32	"
6	50.10	56.17	152	"
7	49.45	56.47	61	"
8	49.42	57.75	107	"
9	49.23	57.28	122	B.28b - Corner Brook
10	49.05	58.20	91	"
11	48.80	58.07	183	"
13	48.57	58.92	30	"
14	48.60	58.68	61	"
15	48.57	58.18	46	"
16	47.90	59.05	61	"
17	49.18	56.10	183	B.28a - Grand Falls
18	48.83	56.48	183	"
19	48.45	57.00	305	"
20	49.02	55.43	61	"
21	49.37	54.42	30	"
22	48.70	55.18	152	"
23	48.67	55.23	122	"
24	48.70	54.45	91	"
25	48.40	54.21	61	"
26	47.92	54.25	15	B.30 - Avalon
27	47.02	55.23	91	"
28	47.22	53.87	61	"
29	47.50	52.86	152	"
30	51.70	56.68	30	B.12 - Hamilton and Eagle Valleys
31	53.42	60.38	3	"
32	45.30	62.40		A.5b - East Atlantic Shore
33	45.97	77.42	160	L.4b - Algonquin - Pontiac
34	46.42	62.45	23	A.8 - Prince Edward Island
36	46.33	63.33	34	"
37	46.02	60.35	76	A.2 - Upper Miramichi Tobique
39	45.70	66.53	15	"
42	49.42	75.83	396	L.4a - Laurentian
43	46.90	71.50	610	"
44	48.57	58.18	305	B.28b - Corner Brook

* Rowe 1972.

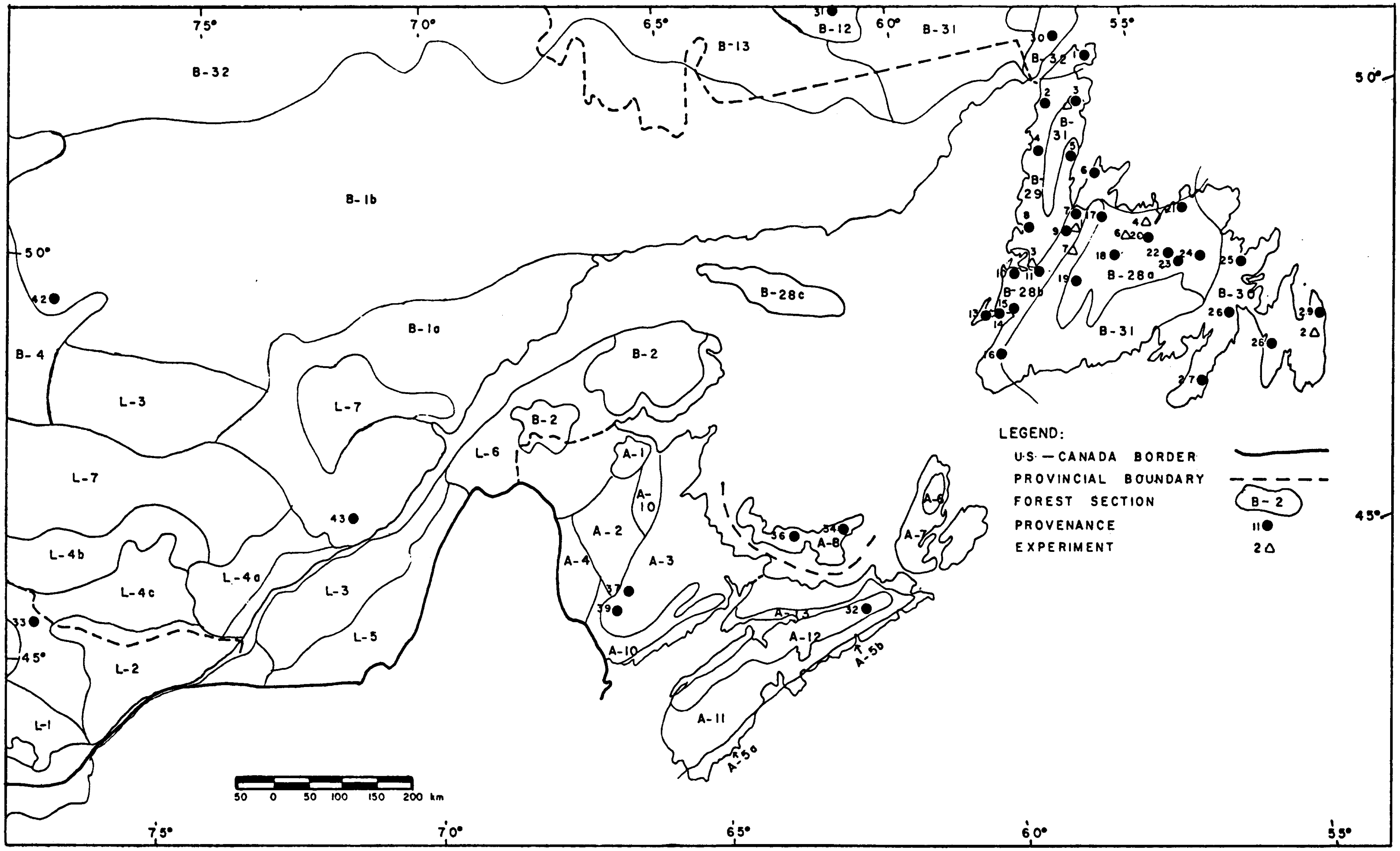

Fig. 1. — Location of black spruce provenances.

Introduction

Black spruce (*Picea mariana* (Mill.) B. S. P.) is one of the most valuable coniferous species of northern North America on account of its abundance over a vast geographic range (Fowells 1965), ease of management and excellent pulping qualities, (Basham and Morawski 1964; Bendtsen 1974; Besley 1959; Ladell 1971). It is the most important local species in the Newfoundland-Labrador region, where it constitutes the largest component of the reforestation program. The species is expected to be genetically very variable with high potential for genetic improvement. Consequently, a study was initiated at the Newfoundland Forest Research Centre in 1968 to determine the nature, magnitude and patterns of genetic variation and to identify superior provenances. Early results of this study have been published (Khalil 1973, 1975; Khalil and Douglas 1979). This paper presents the results of field experiments following ten year growth.

Materials and Methods

Provenances and Planting Materials

Open-pollinated seeds were obtained from 39 provenances in 11 forest sections (Rowe 1972), 31 in the Newfoundland-Labrador region (lat. 47°—55° N, long. 52°—61° W), and eight in eastern mainland Canada (lat. 45°—49° N; long. 62°—78° W) (*Table 1, Fig. 1).* The sample in each area consisted of a minimum of seven dominant and codominant trees, spaced 30 m apart to minimize consanguinity. Seeds were extracted according to Khalil (1975) and bulked by provenance, using equal quantities from each tree. The sites of seed origin on the mainland experience harsher climate than insular Newfoundland, where the field experiments are located (Anon. 1977, 1977a; Hemmerick and Kendall 1972; Ouellet and Sherk 1967; Rowe 1972).

Nursery sowings were made at Pasadena in western Newfoundland (lat. 49.00° N. long. 57.58° W) in two parts, in May 1968 and May 1970 respectively. Seven field experiments were established at Big Falls (lat. 49.27° N, long. 57.15° W), Cochrane Pond (lat. 47.47° N, long. 52.90° W), Little George's Lake (lat. 48.93° N, long. 58.00° W), New Bay Pond (lat. 49.08° N, long. 55 62° W), Roddickton (lat. 50.83° N, long. 56.17° W), Sandy Brook (lat. 48.92° N, long. 55.88° W) and South Brook (lat. 48.95° N, long. 57.60° W).

The South Brook experiment was planted with 5 + 0 stock in August-September 1972, using linear plots and the rest in May-June 1974 with 2 + 2 stock, using square plots. Six-replicated randomized complete blocks with four-tree plots and a spacing of 1.8 × 1.8 m between trees were used in each experiment. Due to insufficient planting stock of some provenances different number of provenances were planted at different locations with 15 provenances common to all locations *(Table 5).* The growth conditions at these locations are very similar to those at Pasadena except Roddickton which has a harsher climate.

Data and Analyses

Measurements were made in fall 1979, comprising heights of all surviving trees corresponding to falls 1972, 1977, 1978 and 1979 at South Brook and those corresponding to falls 1973, 1978 and 1979 at other locations. Diameters at 0.3 m were also measured. Values of height growth from outplanting to ten year age and in the tenth year were calculated.

Analyses of variance by locations were performed on height at ten year age, height growth from outplanting to ten year age and in the tenth year and on diameter at 0.3 m in the tenth year. The mixed model with sampling, assuming no interaction was used (Steel and Torrie 1980, p. 219) with provenances as fixed and replications, experimental and sampling errors as random effects. In the absence of certainty about existence of replications × provenances interaction this procedure was safe because of the conservative nature of the F-tests in the analyses of variance and t-tests in the Bonferroni tests. Balanced analyses of variance were conducted for all locations except South Brook, after estimating the few missing values according to Yates (1933). Unbalanced analyses of variance were conducted for South Brook due to high and unequal mortality in plots. In this case the estimate of a character for the kth provenance mean would be $\hat{P}_k + \hat{\mu}$ (estimated effects of the kth provenance and overall mean respectively). These were the mean values for provenances over replications used for conducting the Bonferroni t-tests for this location. Intraclass correlation coefficients were calculated for each of the above characters as a measure of intra-provenance homogeneity.

Analyses of variance over locations were conducted for the 15 provenances common to all locations to determine their overall performance in insular Newfoundland and to quantify the locations × provenances interaction, indicated by differences in the performance of provenances at different locations. The South Brook experiment was excluded due to high mortality and unbalanced analyses of variance for this location referred to above. The associated mathematical model was mixed, with locations, provenances and their interactions as fixed effects and replications within locations and error as random effects *(Equation 1).*

$$Y_{ijkt} = \mu + L_i + P_k + R_{ij} + (LP)_{ik} + E_{ijk} + D_{ijkt} \quad \ldots\ldots\ldots\ldots \quad (1)$$

where Y_{ijkt} = Response variable of the tth tree in 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).

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

$(LP)_{ik}$ = Effect of location x provenance interaction (fixed).

E_{ijk} = Experimental error component (random) (Error b).

D_{ijkt} = Sampling error (random)(Error C).

Bonferroni t-tests were performed according to Douglas (1979) for height growth in the field up to ten years of age to make all possible pair-wise comparisons between provenances and between specific meaningful zones, viz. mainland Canada, Ontario-Quebec, Maritime Provinces, Newfoundland-Labrador and forest sections within the last named. *Equation* (2) was used. If the value of the contrast C was less than the test criterion B, the null hypothesis $H_0 : C = 0, H_a : C \neq 0$ was not rejected. This character was selected for the Bonferroni t-tests as it was considered to be the best indicator of the response of provenances to the environmental conditions at various locations.

$$B = t_{p,n,f} \left[\text{EEMS} \left(\sum_{i=1}^{m} \frac{c_j^2}{r_j} \right) \right]^{1/2} \quad \ldots\ldots\ldots\ldots \quad (2)$$

where B = Value of the test statistic with which the value of each constant (C)* is compared.

$t_{p,n,f}$ = Tabulated value of t for an overall probability of p, for n contrasts and f experimental error degrees of freedom.

EEMS = Experimental Error Mean Squares in the analyses of variance.

r_j = Number of observations per experimental unit

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*$C = \Sigma c_j \bar{x}_j$, where $\bar{x}_j$ is the mean value of provenance j and c_j is constant, such that $\Sigma c_j = 0$.

Stepwise regression analyses were performed according to DRAPER and SMITH (1981), using ten year height as the dependent variable, taking each location's mean values separately, as well as the over locations means. The first analysis used latitude, longitude and altitude at the seed sources as indipendent variables to determine geographic trends in variation and to corroborate or modify the BONFERRONI t-tests results. In the second analysis, height at the time of outplanting, height growth in the field up to age ten and in the tenth year were used as independent variables to evaluate the relative role of initial growth in the nursery and subsequent growth in the field on total height growth as a method of early identification of fast growing provenances. This analysis was done over locations, using mean values over locations, and regression passing through the origin. Due to a small number of provenances from a large area in the mainland, the mainland provenances were excluded.

The high percentage and statistical significance of variation due to locations × provenances interaction in the over-locations analyses of variance and the differences in ranking at different locations indicated the need for evaluating the provenances for genotypic stability and productive quality. The 15 provenances common to the six locations were so evaluated. Height growth in the field was used as the criterion because it completely reflected the response of provenances to the environments of the test locations.

Genotypic stability was determined by the methods of TAI (1971) and WRICKE (1962). Productive quality was determined by calculating the Provenance Quality Index (PQI) for each provenance (SEGARAN 1979). In TAI's method, the linear response of the genotype of the provenance i (α_i) and the deviation of the linear response (λ_i) were calculated. As perfectly stable provenances ($\alpha = -1$, $\lambda = 1$) do not exist those with average genotypic stability ($-1 \leqslant \alpha_i \leqslant 0$, $0 \leqslant \lambda_i \leqslant 1$) were selected. WRICKE's (1962) ecovalence was calculated according to his method. Ecovalence is a measure of the genotype × environment interaction and is the quantitative expression of the ecological adaptation of the individual genotypes to the environmental conditions under investigation. The smaller the contribution of the genotype to this interaction the smaller is its ecovalence and the greater is the advantage of a broad ecological range in which the genotype would be stable. Provenance Quality Index (PQI), which is the quotient of the provenance effects and environmental effects, was obtained from *Equation* (3) after SEGARAN (1979).

$$PQI = \frac{P_i}{E_j} = \frac{[\bar{X}_{i.} - \bar{X}_{..}]}{\Sigma \left| (\bar{X}_{.j} - \bar{X}_{..}) \right| \div \ell} \quad \ldots\ldots\ldots (3)$$

where PQI = Provenance Quality Index.

P_i = Provenance effects of provenance i.

E_j = Environmental effects of location j.

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

$\bar{X}_{.j}$ = Mean of environment j over all provenances.

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

ℓ = Number of locations.

Results

Results of measurements of ten year heights and diameters at 0.3 m are summarized in *Table 2*.

Table 2. — Summary of black spruce height and diameter measurements after ten years of growth.

Location	Height at 10 year age (cm)			Diameter at 0.3 m at 10 year age (cm)			Number of provenances
	Mean	S.D. ±	Range	Mean	S.D. ±	Range	
Big Falls	108.2	13.5	88.5–145.4	1.57	0.20	1.28–2.10	20
Cochrane Pond	87.8	6.1	75.3–97.2	1.37	0.18	0.98–1.62	15
Little George's Lake	109.5	14.3	70.2–132.5	1.62	0.22	0.94–1.95	26
New Bay Pond	57.8	4.8	50.0–69.2	0.82	0.09	0.69–1.04	18
Roddickton	77.0	5.7	66.1–88.7	1.03	0.19	0.88–1.21	36
Sandy Brook	60.4	8.0	43.7–84.3	0.87	0.17	0.47–1.27	37
South Brook	109.9	9.7	88.3–127.9	Data not available.			

Analyses of Variance by Locations

Results are summarized in *Table 3*. Excluding South Brook due to unbalanced analyses of variance, the proportion of variation increased successively from replications through provenances, and experimental error to sampling error at all locations (0.08—10.69%; 4.61—21.25%; 23.89—43.07% and 37.07—65.86% respectively). The level of significance of replications with respect to the different characters varies. Provenances are a significant source of variation in all characters at three locations, Big Falls, Little George's Lake and Sandy Brook, in two characters at South Brook and only in one character at Cochrane Pond. They are nonsignificant for all characters at New Bay Pond and Roddickton. Experimental error is significant for all characters at all locations except for height growth in the tenth year at Cochrane Pond and South Brook.

Analyses of Variance Over Locations

Results are summarized in *Table 4*, which also shows the appropriate error term for testing significance of each source of variation. The important result of these analyses is the high proportion and significance of the locations × provenances interaction for all characters.

BONFERRONI-T-Tests

Table 5 presents these results. They show differences in the performance of provenances at different locations. The locations in the decreasing order of the suitability for these provenances are Little George's Lake, Big Falls, South Brook, Cochrane Pond, Roddickton, New Bay Pond and Sandy Brook.

Regression Analyses

Ten year height had significant regression on geographic coordinates at seed origin only at three locations, Little George's Lake, Sandy Brook and South Brook *(Table 6)*. The order of appearance of independent variables indicates their relative importance in influencing expression of the character and this varies with location. The regression of ten year height on periodic heights is represented by *Equation* (4).

Genotypic Stability and Productive Quality of Provenances

Table 7 presents the results of these analyses. On the basis of TAI's method nine provenances (3, 4, 6, 10, 16, 19, 24, 26 and 43) have average genotypic stability. With two exceptions, provenances 24 and 43, they are acceptable under WRICKE's method also. However, these provenances do not rank high in growth and have average or below average Provenance Quality Indices.

Table 3. — Summary of analyses of variance by locations.

Location	Character	F-Values for Sources of Variation: Replications	Provenances	Experimental error	Sampling error	Coef. of intraclass correlation
Big Falls	Height at 10 year age	3.55***(5)	2.80***(19)	2.04***(95)	(316)	0.7444
	Height growth in field up to 10 year age	4.42***(5)	2.91***(19)	1.99***(95)	(316)	0.7500
	Height growth in 10th year	2.44* (5)	1.98***(19)	2.14***(95)	(316)	0.6232
	Diameter at 0.3 m	6.84***(5)	2.05***(19)	2.09***(95)	(316)	0.6351
Cochrane Pond	Height at 10 year age	0.96^{NS} (5)	0.99^{NS} (14)	2.04***(69)	(235)	0.0000
	Height growth in field up to 10 year age	1.08^{NS} (5)	0.86^{NS} (14)	2.11***(69)	(234)	0.0000
	Height growth in 10th year	1.36^{NS} (5)	1.66^{NS} (14)	1.24^{NS} (69)	(235)	0.3138
	Diameter at 0.3 m	4.45***(5)	2.04* (14)	1.83***(69)	(235)	0.5254
Little George's Lake	Height at 10 year age	2.28^{NS} (5)	2.78***(25)	2.54***(125)	(308)	0.8250
	Height growth in field up to 10 year age	2.46* (5)	2.77***(25)	2.43***(125)	(306)	0.8173
	Height growth in 10th year	2.07^{NS} (5)	1.78* (25)	2.48***(125)	(308)	0.6676
	Diameter at 0.3 m	1.41^{NS} (5)	1.68* (25)	2.65***(125)	(308)	0.6540
New Bay Pond	Height at 10 year age	2.65* (5)	1.42^{NS} (17)	2.28***(84)	(234)	0.4029
	Height growth in field up to 10 year age	2.13^{NS} (5)	1.44^{NS} (17)	2.20***(84)	(233)	0.4087
	Height growth in 10th year	3.50** (5)	1.10^{NS} (17)	1.64***(84)	(234)	0.1028
	Diameter at 0.3 m	2.17^{NS} (5)	1.15^{NS} (17)	2.05***(84)	(234)	0.1764
Roddickton	Height at 10 year age	1.46^{NS} (5)	1.19^{NS} (35)	1.52***(175)	(618)	0.2909
	Height growth in field up to 10 year age	1.68^{NS} (5)	1.12^{NS} (35)	1.55***(175)	(615)	0.2115
	Height growth in 10th year	1.00^{NS} (5)	1.21^{NS} (35)	1.23***(175)	(618)	0.2768
	Diameter at 0.3 m	6.28***(5)	0.72^{NS} (35)	1.96***(175)	(618)	0.0000
Sandy Brook	Height at 10 year age	2.49* (5)	2.75***(36)	1.68***(180)	(549)	0.8156
	Height growth in field up to 10 year age	1.79^{NS} (5)	2.68***(36)	1.76***(180)	(549)	0.8168
	Height growth in 10th year	1.11^{NS} (5)	1.77** (36)	2.06***(180)	(549)	0.7035
	Diameter at 0.3 m	5.33***(5)	2.44***(36)	1.44***(180)	(549)	0.7566
South Brook	Height at 10 year age	2.34* (5)	1.39* (38)	1.52***(164)	(272)	0.4826
	Height growth in field up to 10 year age	4.70***(5)	1.32^{NS} (38)	1.47***(164)	(272)	0.4301
	Height growth in 10th year	3.11***(5)	1.83***(38)	0.77^{NS} (164)	(272)	0.5029
	Diameter at 0.3 m	1.21^{NS} (5)	0.86^{NS} (38)	1.65***(164)	(272)	0.0000

*** Statistically significant (0.005 level).
** Statistically significant (0.01 level).
* Statistically significant (0.05 level).
NS Statistically nonsignificant (0.05 level).
Figures in parentheses are degrees of freedom.

Discussion

Analyses of Variance by Locations

The differences in the levels of significance of replications at different locations indicate differences in the homogeneity of locations. Big Falls is very heterogeneous, while New Bay Pond, Sandy Brook and South Brook are moderately heterogeneous and the remaining test locations are homogeneous. Results show the effectiveness of the randomized complete block design with six replications in detecting and removing inter-replication variation in most locations. However, this does not preclude the possibility of intra-replication variation, though small size of the plots should minimize this variation.

Nonsignificance of F-values for provenances for various characters at some locations does not necessarily indicate lack of interprovenance variation. Nonsignificance could be due to overall unfavourable growth conditions in the experiments resulting in the reduction in the display of the poptential of provenances for growth. At Cochrane Pond the nutrient-poor shallow soil; and at Roddickton the poor soil combined with harsh climate have slowed growth. The dense competing vegetation al all locations, particularly at New Bay Pond and South Brook, reduced growth

Table 4. — Summary of analyses of variance over locations.

Source of variation	Expected mean squares	Degrees of Freedom		Height at 10 yr. age		Height growth in field up to 10 yr. age		Height growth in 10th yr.		Diameter at 0.3 m	
		Expected	Actual	Var. %	F	Var. %	F	Var. %	F	Var. %	F
Locations	$\sigma^2 + T\sigma^2_\varepsilon + TP\sigma^2_R + T\frac{PR\Sigma L^2_i}{L-1}$	(L-1)	5	43.78	81.40***	41.60	71.66***	27.63	58.41***	32.95	29.90***
Replications/locations (Error a)	$\sigma^2 + T\sigma^2_\varepsilon + TP\sigma^2_R$	(R-1)L	30	3.23	2.78***	3.48	2.90***	2.84	2.11***	6.60	4.79***
Provenances	$\sigma^2 + T\sigma^2_\varepsilon + T\frac{RL}{P-1}\Sigma P^2_k$	(P-1)	14	2.01	3.73***	1.95	3.48***	1.78	2.61***	1.08	1.69^{NS}
Locations x provenances interaction	$\sigma^2 + T\sigma^2_\varepsilon + T\frac{R}{(P-1)(L-1)}\Sigma\Sigma(LC)^2_{ik}$	(P-1)(L-1)	70	5.04	1.87***	5.37	1.92***	7.02	2.06***	5.23	1.63***
Provenances/locations	$\sigma^2 + T\frac{R}{P_1-1}\Sigma P^2_{1k}$	(P-1)L	84	7.05	2.18***	7.32	2.18***	8.80	2.15***	6.31	1.64***
Provenances/location 1	$\sigma^2 + T\sigma^2_\varepsilon + TR\sigma^2_{P_1}$	(P_1-1)	14	3.34	6.16***	3.40	6.07***	3.02	4.41***	2.16	3.36***
Provenances/location 2	$\sigma^2 + T\sigma^2_\varepsilon + TR\sigma^2_{P_2}$	(P_2-1)	14	0.58	1.07^{NS}	0.52	0.92^{NS}	0.79	1.15^{NS}	1.57	2.44***
Provenances/location 3	$\sigma^2 + T\sigma^2_\varepsilon + TR\sigma^2_{P_3}$	(P_3-1)	14	1.40	2.58***	1.48	2.64***	2.77	4.04***	0.81	1.26^{NS}
Provenances/location 4	$\sigma^2 + T\sigma^2_\varepsilon + TR\sigma^2_{P_4}$	(P_4-1)	14	0.42	0.77^{NS}	0.45	0.80^{NS}	0.29	0.42^{NS}	0.45	0.70^{NS}
Provenances/location 5	$\sigma^2 + T\sigma^2_\varepsilon + TR\sigma^2_{P_5}$	(P_5-1)	14	0.47	0.86^{NS}	0.49	0.87^{NS}	0.61	0.89^{NS}	0.37	0.58^{NS}
Provenances/location 6	$\sigma^2 + T\sigma^2_\varepsilon + TR\sigma^2_{P_6}$	(P_6-1)	14	0.84	1.57^{NS}	0.98	1.75*	1.32	1.92*	0.95	1.47^{NS}
Provenances x replications/locations (Error b)	$\sigma^2 + T\sigma^2_\varepsilon$	(P-1)(R-1)L	418	16.16	1.71***	16.75	1.71***	20.45	1.60***	19.24	1.74***
Sampling error (Error c)	σ^2	(T-1)PRL	(a) (b) 1316/1320	29.78		30.85		40.28		34.90	
Total			(a) (b) 1853/1857	100.00		100.00		100.00		100.00	

(a) For height in 1973.
(b) For other characters.
*** Statistically significant (0.005 level).
** Statistically significant (0.01 level).
* Statistically significant (0.05 level).
NS Statistically nonsignificant (0.05 level).

and increased inter-plot and intra-plot variation, which increased both the experimental error and sampling error mean squares. The former reduced sensitivity of the F-tests and the latter increased intra-replication variation, which masked interprovenance variation. In these circumstances it would be reasonable to conclude that interprovenance differences exist in all characters at all locations, which call for investigation of the existence and extent of intraprovenance variation.

The significance of experimental error for all characters at all locations emphasizes the intra-provenance variation. Experimental error measures two effects, i. e. variation of the same provenance in the same experimental unit, or replication (σ^2) plus variation of the same provenance in different experimental units, or replications × provenances interaction ($\sigma^2\varepsilon$). Significance of the experimental error mean squares indicates that either one or both of the above components are significant. Though it is not possible to know from this experiment whether the above interaction exists, its possibility cannot be excluded.

Coefficients of intraclass correlation are important. Due to the small plot size the major proportion of intra-plot

Table 5. — Ranking of black spruce provenances and BONFERRONI T-test for height growth in the field up to age of ten years.

Rank	Big Falls Prov.	Big Falls Mean	Cochrane Pond Prov.	Cochrane Pond Mean	Little George's Lake Prov.	Little George's Lake Mean	New Bay Pond Prov.	New Bay Pond Mean	Roddickton Prov.	Roddickton Mean	Sandy Brook Prov.	Sandy Brook Mean	South Brook Prov.	South Brook Mean
1	20	123.5*	24	78.2*	20	114.4*	24	58.9*	20	74.4*	33	69.5*	28	99.7*
2	21	107.3*	13	77.9*	36	113.6*	37	53.9*	23	73.6*	43	66.6*	29	96.3*
3	23	102.1	19	76.1*	44	112.3*	10	53.3*	33	70.4*	24	62.1*	25	92.3
4	28	100.5	10	74.3	25	111.8*	26	52.5	2	68.5*	18	57.9*	14	92.0
5	10	98.1	36	73.3	39	105.4	6	52.1	14	68.4*	29	56.8*	7	91.8
6	37	95.6	16	72.1	37	104.1	4	50.6	15	68.0	15	53.0	44	91.6
7	36	94.7	6	71.7	13	103.4	36	50.2	22,31	67.3	17,44	52.2	27	91.2
8	7	94.6	43	71.3	7	101.3	19	49.2	24	67.2	16	52.1	37	90.1
9	44	94.1	4	68.0	24	99.8	7	48.6	26	66.8	20,25	50.8	13	90.0
10	15	92.3	28	68.0	4	96.9	15	47.4	10	66.5	10	50.7	8	88.0
11	26	91.6	3	67.7	43	95.7	20	47.0	17,39	65.8	23	50.4	36	87.9
12	6	91.3	26	67.6	10	94.8	13,23	46.5	28	65.6	26	49.8	32	86.7
13	43	88.3	20	65.0	16	93.2	28	46.3	13	64.3	14	49.1	22	86.4
14	34	86.4	7	64.6	28	92.4	21	45.4	36	64.0	27	49.0	34	85.9
15	13	84.8	37	59.8	19	92.2	43	44.8	8	63.8	37	48.0	43	85.6
16	4	78.1			21	92.0	3	41.5	7	63.7	32	47.7	13	84.8
17	24	76.5			15	90.7	16	40.7	4	63.5	7,39	47.6	33	83.9
18	16	75.3			23	88.7			43	63.4	3	46.2	10	83.8
19	19	74.1			3	87.9			5	63.3	1	45.6	18,23	83.7
20	3	72.0			26	87.0			19	62.8	21	45.5	42	82.8
21					34	85.5			21	62.6	19	44.9	16	82.7
22					6	84.4			34	61.8	13	44.4	24	81.8
23					18	79.8			3	61.6	36	44.3	39	81.5
24					5	78.0			1,32	59.8	11	44.1	26	81.2
25					8	74.5			18	59.7	31	43.4	2	80.8
26					30	58.1			44	59.4	4	43.3	20	79.5
27									30	58.2	34	43.0	4	79.0
28									25	58.1	8	42.0	19	76.8
29									6	56.8	28	41.3	6	74.1
30									11	56.4	22	41.2	21	73.4
31									37	55.3	6	41.1	15	72.7
32									16	54.2	2	40.6	31	70.7
33									27	53.5	30	40.4	17	70.2
34											5	30.8	1,5	68.7
35													3	68.0
36													1	65.8
37													9	63.7
Mean		91.1		70.4		93.8		48.6		63.4		48.3		80.4
S.D. (±)		12.5		5.2		13.1		4.5		5.0		7.5		14.8

* Provenances above the mean by one standard deviation.
Summary of BONFERRONI t-test (0.05 level):
Big Falls — Provenance 20 > 3, 4, 16, 19, 24.
Cochrane Pond — All differences nonsignificant.
Little George's Lake — Provenances 20, 36 > 30; 25 > 34.
New Bay Pond — All differences nonsignificant.
Roddickton — All differences nonsignificant.
Sandy Brook — Provenance 33 > 2, 5, 6, 22, 28, 30, 43, 29, 24 > 5.
Ontario-Quebec provenances > Maritime provenances.
Labrador-Northern Peninsula provenances < Provenances from the rest of insular Newfoundland.
South Brook — All differences nonsignificant.

variation would be due to genetic differences within provenances. These correlations are high for all characters at Big Falls, Little George's Lake and Sandy Brook, indicating low intra-provenance variation, i. e. high homogeneity within provenances. The low value of this coefficient at Cochrane Pond, New Bay Pond, Roddickton and South Brook is not necessarily an indication of high intra-provenance variation. Low estimates could be due to the adverse growth conditions mentioned earlier. As the first three locations with high values for the coefficient of intraclass correlation have large numbers of provenances, the results can be extended to other locations and it can be safely concluded that provenances have low intra-provenance variation and thus are fairly homogeneous. They could, however, differ among themselves in the degree of homogeneity, which will be discussed later under genotypic stability and productive quality.

Analyses of Variance Over Locations

The significance of provenances within individual locations agrees with that shown by the analyses of variance by locations *(Table 3)*, except for Little George's Lake and

Table 6. — Summary of step-wise regression analyses.

Location	Regression equation	R	Simple Correlation Coefficient of Y with X_1	X_2	X_3
Little George's Lake (Error d.f. = 17)	$Y = 416.8830 - 6.4177X_1^{*} + 0.0089X_2^{NS} + 0.0923X_2^{NS}$	0.4918^{*}	-0.4890^{*}	-0.0409^{NS}	0.1603^{NS}
Sandy Brook (Error d.f. = 24)	$Y = 166.1960 - 2.1411X_1^{*} + 0.0080X_3^{NS} - 0.0406X_2^{NS}$	0.5087^{*}	-0.4696^{**}	-0.1895^{NS}	0.2389^{NS}
South Brook (Error d.f. = 28)	$Y = 425.2000 - 6.4587X_1^{**} + 0.5742X_2^{NS} + 0.0103X_3^{NS}$	0.6225^{**}	-0.5733^{**}	-0.2029^{NS}	0.2265^{NS}

Y = Height at 10 year age.
X_1 = Latitude at seed origin.
X_2 = Longitude at seed origin.
X_3 = Altitude at seed origin.
** Statistically significant (0.01 level).
* Statistically significant (0.05 level).
NS Statistically nonsignificant (0.05 level).

Sandy Brook. This is due to the large differences in the number of provenances included in these two locations in the two analyses. While the analyses of variance by locations are based on 27 and 36 provenances at Little George's Lake and Sandy Brook, respectively, the over locations analyses have only 15 provenances at these locations.

The high significance of the locations × provenances interaction emphasizes the need to examine the relative performance of provenances at various locations and to assess their genotypic stability in different environments.

BONFERRONI T-Tests

Differences in ranking of the same provenance at different locations indicate the need for caution in selecting superior provenances *(Table 5)*. Assessment of genotypic stability is necessary before making a decision in this respect

Though pair-wise comparisons between provenances show significant differences no geographic trends can be detected *(Table 5)*. Contrasts between geographic zones show that at Sandy Brook the Ontario-Quebec provenances are faster growing than those from the Maritime Provinces and the Labrador-Northern Peninsula provenances are slower growing than those from the rest of insular Newfoundland. The latter difference has been shown to be due to the slower rate of growth of the northern provenances compared with the southern ones in the Newfoundland-Labrador region (KHALIL 1975).

Regression Analyses

These analyses further elucidated geographic trends in variation. Out of the geographic coordinates at the seed sources only latitude is a significant source of variation, with negative influence, indicating decrease in growth in provenances from south to north. These results confirm those from BONFERRONI t-tests.

Equation 4 shows that when all periodic height growth measurements are considered together, the ten year height is influenced by the initial growth in the nursery as well as the growth from outplanting to age ten, with the former exerting a larger influence than the latter. These results are supported by highly significant coefficients of simple correlations of ten-year height with height at the time of outplanting (R = 0.9981***), growth from outplanting to ten-year age (R = 0.9997***), and growth in the tenth year (R = 0.9979***). Thus, the superior height growth of the fast growing provenances is not a mere carryover of the fast growth in the nursery. Such provenances maintain superior growth in subsequent years also. These results agree with those reported earlier from another study on black spruce (KHALIL 1984).

$$Y = 0.9613X_2^{***} + 1.2414X_1^{***} - 0.0887X_3^{NS} \quad (4)$$

(R = 0.9999***)

where Y = 10 year height.
X_1 = Height at the time of outplanting.
X_2 = Height growth from outplanting to 10 year age.
X_3 = Height growth in 10th year.

Genotypic Stability and Productive Quality of Provenance

These results may be used for selection of suitable provenances. The ideal approach should be to select suitable provenances by a combination of productive quality and genotypic stability so as to obtain provenances with fast growth and at least average stability over a wide range of environments. Suitable provenances should be selected successively for a positive and high pre-selected provenance quality index and good genotypic stability by one or both of the above methods.

Selection can be made on this basis from the provenances listed in *Table 7*, limiting the initial selection to the seven provenances with positive Provenance Quality Index (PQI). Four of them have WRICKE's ecovalence equal to or less than the mean (264.24), i. e. 7, 10, 13 and 36. Only provenance 10 qualifies on the basis of TAI's method. As only preliminary results are currently available, this method, which restricts us to only one provenance is not safe. In these circumstances two options are suggested.

In the first option the initial selection should be restricted to the seven provenances which are fastest growing on

*** Statistically significant (0.001 level).

Table 7. — Genotypic stability and productive quality of black spruce provenances for height growth during the period 1973—79.

Rank	Provenances	Mean ht. growth 1973–79 (cm)	TAI's α	TAI's λ	WRICKE's Ecovalence	PQI
1	20	79.2	0.1321	1.7034	1 083.23	0.5950
2	24	73.8	-0.0842	0.6512	417.53	0.2568
3	36	73.3	0.0772	0.3547	244.39	0.2255
4	10	73.0	-0.0052	0.1234	68.49	0.2067
5	43	71.7	-0.0429	0.4188	313.69	0.1253
6	13	70.2	0.0277	0.2403	139.11	0.0313
7	7	70.1	0.0300	0.1286	78.40	0.0251
8	37	69.5	0.0337	0.4975	284.35	-0.0125
9	26	69.2	-0.0440	0.2326	144.31	-0.0313
10	28	69.0	0.0347	0.3874	224.01	-0.0438
11	4	66.7	-0.0186	0.1958	111.10	-0.1879
12	19	66.5	-0.0436	0.4170	246.03	-0.2004
13	6	66.3	-0.0219	0.3787	213.34	-0.2129
14	16	64.6	-0.0277	0.4015	222.04	-0.3194
15	3	62.8	-0.0325	0.2983	173.53	-0.4321

the basis of mean height over locations and have positive PQI. From this list, provenances should be selected with at least average genotypic stability. This would identify provenances which are fast growing and potentially best suited for the environmental conditions represented by the test locations used. This method is recommended if the environmental conditions at the planting site are known and resemble those of the test locations used in this study.

Secondly, the initial selection should be made on the basis of a value for WRICKE's ecovalence equal to or less than the mean value (264.24). Out of the 11 provenances selected, viz., 3, 4, 6, 7, 10, 13, 16, 19, 26, 28 and 36, seven (3, 4, 6, 10, 16, 19 and 26) qualify under TAI's method. This method would identify provenances which may not be the fastest in growth but would be genotypically stable, and it would be suitable for situations in which environmental conditions at the planting site are not known or do not resemble those at any of the test locations used in the study.

Conclusions

The following conclusions are supported by this study.

1. There are east-west trends in height growth of *Picea mariana* in the mainland provenances and north-south trends in the Newfoundland-Labrador ones.
2. Though fast growing provenances in the nursery also have fast total growth the latter is not a mere carry-over of the former. Such provenances maintain fast growth in the field also.
3. Differences in ranking of the same provenances at various test locations and highly significant locations × provenances interaction indicate the need for caution in selection of superior provenances.
4. Two options are suggested for selection of superior provenances. First, the initial selection should consist of provenances with positive Provenance Quality Index followed by screening for at least average genotypic stability. This method would identify provenances which are fast growing and best suited for the environments represented by the test locations; it is recommended if the environmental conditions at the planting site are known and resemble those at any of the test locations. In the second option, the initial selection would consist of provenances whose ecovalence is less than or equal to the mean of the study. The second selection would comprise provenances out of the above with at least average genotypic stability under TAI's method. This method would identify provenances which may not be the fastest in growth but would be genetically stable, and is suitable for situations in which the environmental conditions at the planting site are not known or do no resemble those at the test locations.

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Literature Cited

ANON.: Degree-days 1941—1970, Quebec. Fish. and Environ., Can. Atm. Environ., June 1977 (1977). — ANON.: Degree-days 1941—1970. Atlantic Provinces. Fish. and Environ., Can. Atm. Environ., June 1977 (1977a). — BASHAM, J. T. and MORAWSKI, J. R.: Cull studies, the defects and associated basidiomycete fungi in the heartwood of living trees in the forests of Ontario. Dep. Forests. Publ. 1072, 69 pp. (1964). — BENDSTEN, B. A.: Specific gravity and mechanical properties of black, red and white spruce and balsam fir. U. S. Dep. Agr., Forest Serv., Res. Pap. F. P. L. 237, 28 pp. (1974). — BESLEY, L.: Relationship between wood fibre properties and paper quality. Pulp and Pap. Res. Inst. Can., Res. Pap. 156, 19 pp. (1959). — DOUGLAS, A. W.: On levels of significance. Data Anal. and Syst. Br., Comput. and App. Statist. Dir., Environ. Can., Ottawa, Output No. 3: 36—49 (1979). — DRAPER, N. R., and SMITH, H.: Applied regression analyses. Second Edition. John Wiley & Sons Inc., New York. xiv + 709 pp. (1981). — FOWELLS, H. A.: Silvics of the forest trees of the United States. U. S. Dep. Agri., Forest Serv., Agri. Handbook No. 271, vi + 762 pp. (1965). — HEMMERICK, G. M. and KENDALL, G. P.: Frost data 1941—1970. Environ. Can., Can. Atm. Environ., Rep. CLI 5—72 (1972). — KHALIL, M. A. K.: Results of a four-year nursery provenance experiment on black spruce in Newfoundland. Environ. Can., Forest Serv., Inform. Rep. N-X-99, viii + 76 pp. (1973). — KHALIL, M. A. K.: Genetic variation in black spruce (*Picea mariana* (MILL.) B. S. P.) in Newfoundland. Silv. Genet. 24 (4): 88—96 (1975). — KHALIL, M. A. K.: All-range black spruce provenance study in Newfoundland: Performance and genotypic stability of provenances. Silv. Genet. 33 (2—3) 63—71 (1984). — KHALIL, M. A. K. and DOUGLAS, A. W.: Correlation of height growth in black spruce with site factors of the provenances. Silv. Genet. 28 (4): 122—124 (1979). — LADELL, J. L.: Variation outward and some internal correlations in the wood of black spruce (*Picea mariana* (MILL.) B. S. P.). Ont. Res. Found., Sheridan Park, Ont., Can., Occas. Publ., 34 pp. (1971). — OUELLET, C. E. and SHERK, L. C.: Map of plant hardiness zones in Canada. Can. Dep. Agri. (1967). — ROWE, J. S.: Forest regions of Canada. Dep. Environ., Can. Forest Serv., Publ. No. 1300, x + 172 pp. + 1 map (1972). — SEGARAN, S.: Comparative genotypic stability parameters in provenance selection as applied to twenty local provenances of black sprurce (*Picea mariana* (MILL.) B. S. P.). Man. Dep. Mines, Nat. Res. and Environ., Tree Imp. and Forest Genet., 65 pp. (1979). — STEEL, G. R. D. and TORRIE, J. H.: Principles and procedures of statistics: A biometrical approach. McGraw-Hill Book Co., Inc., New York. xxi + 633 pp. (1980). — TAI, G. C. C.: Genotypic stability and its application to potato regional trials. Crop. Sci. 11: 184—190 (1971). — WRICKE, G.: Über eine Methode zur Erfassung der ökologischen Streubreite in Feldversuchen. A. Pflanzenzucht. 47: 92—96 (1962). — YATES, F.: The analysis of replicated experiments when the field results are incomplete. Emp. J. Exp. Agri. 1: 129—142 (1933).