# Variation in Seed Quality and some Juvenile Characters of White Spruce (Picea glauca (Moench) Voss)

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**Abstract**

A range-wide greenhouse experiment was conducted on the variation in seed quality and juvenile characters of white spruce *(Picea glauca* (Moench) Voss.). Provenances as well as trees within provenances are significant sources of variation in all characters. There are north-south trends in seed weight, germinative capacity, hypocotyl length and four-month height, and east-west trends in seed weight, cotyledon numbers and four-month seedling height, showing selection pressures to be the causative agents.

Intra-provenance variation in germinative energy increases with time and is maximum at the time of full germination. This variation is low for germinative capacity and high for juvenile characters. It exists among and within trees and could be partially due to introgression. The earlier finding of the advisability of including seed weight among the criteria for selection of superior provenances and plus trees is supported. Germinative energy and germinative capacity are valid methods for early selection of fast-growing provenances. Fifteen provenances primarily from latitude 48°—50° N appear superior for a combination of characters of seed quality and juvenile growth with good indication that the superiority would be sustained.

*Key words:* Provenance study, Bonferroni t-tests, Selection pressure, Introgression, Correlation analyses.

**Résumé**

Sont présentés les résultats d'une étude en serre de la variation de la qualité des graines et des caractères juvéniles de l'épinette blanche *(Picea glauca* (Moench) Voss) pour toute son aire. Les provenances et les arbre eux-mëmes sont des sources importantes de variation pour tous les caractères. Il y a des tendances nord-sud dans la variation de la masse des graines, de la faculté germinative, de la longueur de l'hypocotyle et de la hauteur à quatre mois et des tendances est-ouest pour la masse des graines, le nombre de cotylédons et la hauteur des semis à quatre mois, indiquant que la pression de sélection est un facteur en cause.

La variation intraprovenance de la vigueur germinative augmente avec l'approche de la germination totale, où elle est maximale. Elle est faible pour la faculté germinative et élevée pour les caractères juvéniles. Cette variation est à la fois inter- et intra-arbre et pourrait être due en partie à l'introgression. La conclusion déjà formulée concernant l'opportunité d'inclure la masse des graines parmi les critères de sélection des provenances supérieurs et des arbres plus est corroborée. La vigueur et la faculté germinatives sont des critères valides de sélection précoce des provenances à croissance rapide. Quinze provenance principalement des latitudes 48°—50° N semblent supérieures pour une combination de caractère se rapportant à la qualité des graines et à la croissance en phase juvénile, et les indications sont bonnes que la supériorité serait maintenue.

**Zusammenfassung**

Die vorliegende Arbeit berichtet über die Ergebnisse von Gewächshausversuchen zur Samenqualität und zu Jugendmerkmalen der Weißfichte *(Picea glauca* (Moench) Voss) mit Samen aus dem gesamten Verbreitungsgebiet dieser Baumart. Bei allen Merkmalen zeigen die Herkünfte, wie auch Bäume innerhalb der Herkünfte signifikante Variationsunterschiede. Es zeigten sich Nord-Süd-Tendenzen bei Samengewicht, Keimfähigkeit, Hypokotyllänge und Höhe nach vier Monaten, Ost-West-Tendenzen beim Samengewicht, bei der Kotyledonenzahl und Höhe der Sämlinge nach vier Monaten; woraus sich auf eine Einwirkung von Selektionsdruck schließen läßt.

Die Variationsbreite für die Keimkraft innerhalb der Herkünfte steigt mit fortschreitender Keimung und erreicht bei voller Auskeimung ihr Maximum. Sie ist gering für das Keimvermögen, jedoch groß für die Jugendmerkmale. Variationen treten sowohl zwischen Bäumen als auch für die einzelnen Bäume auf und könnten teilweise auf Introgression zurückzuführen sein. Aus den Resultaten ist auch ersichtlich, daß im Einklang mit früheren Erkenntnissen das Samengewicht tatsächlich ein gutes Selektionskriterium für überlegene Herkünfte und Plusbäume darstellt. Keimvermögen und Keimkraft sind zuverlässige Entscheidungsparameter bei der Frühselektion schnellwüchsiger Herkünfte. Fünfzehn Herkünfte, die meisten zwischen 48° und 50° nördl. Breite, erwiesen sich hinsichtlich einer Kombination der Merkmale Samenqualität und Jugendwachstum als überlegen, und die Ergebnisse lassen vermuten, daß diese Überlegenheit auch weiterhin beibehalten wird.

## Introduction

High economic value and wide distribution of white spruce *(Picea glauca* (Moench) Voss.), creating potential for large genetic variation, predominantly in the Boreal, Great Lakes - St. Lawrence and Acadian forest regions of Canada and the adjoining forest cover types of the United States (Eyre 1980; Rowe 1972), have prompted intensive genetics research on the species since 1950. Natural selection and introgression have potential for producing genetic variation in the main zone of its distribution; and migration, drift and inbreeding, in the isolated populations.

Two major genetically distinct populations have been distinguished, west and east of longitude 95° W (Nienstaedt and Teich 1972). The western population is complex, with three races of pure white spruce and three introgressed sub-populations. The races are: western, *P. glauca* var. *Albertina* (S. Brown) Sarg. in Alberta, British Columbia, Wyoming and Montana; northwestern. *P. glauca* var. *Porsildii* (Raup.) in Alaska and Yukon; and southeastern, *P. glauca* var. *Densata* Bailey in the Black Hills (Dallimore *et al.* 1966). The introgressed sub-populations are hybrids with Sitka spruce *(P. sitchensis* (Bong.) Carr.), known as *Picea* × *lutzii* Little; Engelmann spruce *(P. engelmannii* Parry et Engelmann); and black spruce *(P. mariana* (Mill.) B. S. P.) (Habeck and Weaver 1969; Hanover and Wilkinson 1970; La Roi and Dugle 1968; Ogilvie and von Rudloff 1968; Roche 1969). There are no races in the eastern population and only one hybrid with black spruce has been recognized,

*Table 1.* — List of provenances and their allocation to geographic cells.

| Cell | Latitude class (°N) | Longitude class (°W) | Provenances | Cell | Latitude class (°N) | Longitude class (°W) | Provenances |
|---|---|---|---|---|---|---|---|
| 1 | 44.01-46.00 | 60.01-62.00 | 8001 | 29 | 48.01-50.00 | 78.01- 80.00 | 8270 |
| 2 | 44.01-46.00 | 62.01-64.00 | 8207 | 30 | 48.01-50.00 | 80.01- 82.00 | 8044,8170,8643 |
| 3 | 44.01-46.00 | 66.01-68.00 | 8657 | 31 | 48.01-50.00 | 82.01- 84.00 | 8661 |
| 4 | 44.01-46.00 | 72.01-74.00 | 8613 | 32 | 48.01-50.00 | 84.01- 86.00 | 8045,8066 |
| 5 | 44.01-46.00 | 74.01-76.00 | 8209,8612 | 33 | 48.01-50.00 | 86.01- 88.00 | 8644 |
| 6 | 44.01-46.00 | 76.01-78.00 | 8011,8323,8352,8624,8676,8677,8679,8692 | 34 | 48.01-50.00 | 88.01- 90.00 | 8087 |
| 7 | 44.01-46.00 | 78.01-80.00 | 8604,8605,8623,8625 | 35 | 48.01-50.00 | 92.01- 94.00 | 8097 |
| 8 | 44.01-46.00 | 82.01-84.00 | 8629 | 36 | 48.01-50.00 | 94.01- 96.00 | 8098,8128,8129 |
| 9 | 46.01-48.00 | 52.01-54.00 | 8014 | 37 | 48.01-50.00 | 118.01-123.00 | 8232 |
| 10 | 46.01-48.00 | 62.01-64.00 | 8191,8192,8193,8194,8195,8196,8198,8199 8200,8201,8202,8203 | 38 | 50.01-52.00 | 92.01- 94.00 | 8106 |
| | | | | 39 | 50.01-52.00 | 94.01- 96.00 | 8131 |
| 11 | 46.01-48.00 | 64.01-66.00 | 8197 | 40 | 50.01-52.00 | 113.01-118.00 | 8138,8303 |
| 12 | 46.01-48.00 | 66.01-68.00 | 8636 | 41 | 50.01-52.00 | 118.01-123.00 | 8144 |
| 13 | 46.01-48.00 | 68.01-70.00 | 8637 | 42 | 52.01-54.00 | 60.01- 62.00 | 8367,8368 |
| 14 | 46.01-48.00 | 70.01-72.00 | 8245,8615 | 43 | 52.01-54.00 | 98.01-103.00 | 8365 |
| 15 | 46.01-48.00 | 72.01-74.00 | 8243,8244,8277,8614 | 44 | 54.01-56.00 | 113.01-118.00 | 8296,8297,8298,8302,8314 |
| 16 | 46.01-48.00 | 74.01-76.00 | 8274,8616,8619 | 45 | 54.01-56.00 | 118.01-123.00 | 8140,8318,8659 |
| 17 | 46.01-48.00 | 76.01-78.00 | 8002,8610,8620,8669 | 46 | 54.01-56.00 | 123.01-128.00 | 8219 |
| 18 | 46.01-48.00 | 78.01-80.00 | 8004,8621,8640 | 47 | 56.01-58.00 | 92.01- 94.00 | 8652,8653 |
| 19 | 46.01-48.00 | 82.01-84.00 | 8628 | 48 | 56.01-58.00 | 113.01-118.00 | 8315 |
| 20 | 46.01-48.00 | 84.01-86.00 | 8039 | 49 | 56.01-58.00 | 118.01-123.00 | 8224 |
| 21 | 48.01-50.00 | 54.01-56.00 | 8007,8080 | 50 | 58.01-60.00 | 108.01-113.00 | 8311 |
| 22 | 48.01-50.00 | 56.01-58.00 | 8034,8096,8171 | 51 | 60.01-62.00 | 108.01-113.00 | 8147 |
| 23 | 48.01-50.00 | 64.01-66.00 | 8251 | 52 | 60.01-62.00 | 133.01-138.00 | 8280,8651 |
| 24 | 48.01-50.00 | 66.01-68.00 | 8248 | 53 | 60.01-62.00 | 138.01-142.00 | 8284,8285,8287 |
| 25 | 48.01-50.00 | 68.01-70.00 | 8250 | 54 | 62.01-64.00 | 133.01-138.00 | 8290,8291 |
| 26 | 48.01-50.00 | 70.01-72.00 | 8265,8266 | 55 | 62.01-64.00 | 138.01-142.00 | 8289 |
| 27 | 48.01-50.00 | 72.01-74.00 | 8267 | | | | |
| 28 | 48.01-50.00 | 76.01-78.00 | 8268 | | | | |

known as Rosendahl spruce (Riemenschneider and Mohn 1975; von Rudloff and Holst 1968).

A greenhouse study based on a range-wide seed collection was conducted by the Newfoundland Forest Research Centre in 1978 on the magnitude and trends of variation in seed quality and some juvenile characters for identifying the influence of selection and introgression and for early identification of potentially superior provenances. The seeds were obtained from the Petawawa National Forestry Institute of the Canadian Forestry Service. The experiment was conducted in the greenhouse of the Forest Tree Nursery of the Newfoundland Department of Forest Resources and Lands at Wooddale in central Newfoundland.

## Material and Methods

*The Provenances*

The seeds from 110 provenances were used, 72 provenances with bulked seed and 38 with individual tree seed from 130 trees. The region of the seed origin is bounded by latitudes 44°—64° N, longitudes 52°—142° W and covers five forest regions in Canada: Acadian, Boreal, Great Lakes - St. Lawrence, Montaine and Subalpine (Rowe 1972) (*Tab. 1, Fig. 1*). The climate across the species range is varied due to its extent and physiography (Chapman and Brown 1966; Putnam 1965).

*The Experiment*

The experiment was established in a greenhouse at the Wooddale Forest Tree Nursery (latitude 49°09' N, longitude 55°36' W) in a three-replicated randomized complete block design with 25-seed row plots in wooden flats 10 cm deep, occupying a total area of 68 m². The seeds were sown on April 5—7, 1978, 5 cm apart after stratification for 21 days at 2° C. The planting medium consisted of a 2:1 peat:vermiculite mixture by volume, with an initial pH of 3.9 rising to 4.9 at the end of the experiment. The greenhouse was maintained at a temperature of 26.5° C during germination and 22° C thereafter, with a relative humidity of 55—60%, without artificial lighting. Two weeks after germination 2 000 g of 10-52-10 NPK fertilizer were applied, followed by 1 500 g of 20-20-20 fertilizer every two weeks. The experiment was irrigated uniformly with an overhead sprinkler as necessary.

*The Data and Statistical Analyses*

The data on the following characters were used:

1 000-seed weight (Yo)

Characters of germinative energy: Days to commencement of germination ($Y_1$); days to 25% ($Y_2$); to 50% ($Y_3$); to 75% ($Y_4$); to full germination ($Y_5$).

Germinative capacity or Germination percent ($Y_6$).

Juvenile characters: Cotyledon numbers ($Y_7$); hypocotyl length ($Y_8$); four-month seedling height ($Y_9$).

The data on 1 000-seed weight were obtained from the Petawawa National Forestry Institute and the rest was collected from the experiment. The percent germination ($Y_2$ to $Y_5$) refers to the percentage of the number of seeds which actually germinated. The following statistical analyses were performed.

*Analyses of Variance* were performed for all characters except 1 000-seed weight with the bulked and individual tree seed provenances combined to estimate inter- and intra-provenance variation. A mixed mathematical model was used, assuming no interaction, with no sampling for characters of germinative energy and germinative capacity ($Y_1$ to $Y_6$) and with sampling for juvenile characters ($Y_7$ to $Y_9$). The equation in Steel and Torrie (1980, p. 219) was used for characters of germinative energy ($Y_1$ to $Y_6$) and with addition of the term $\sigma_{ijkl}$ for effect of seedlings for juvenile characters. Provenances were taken as fixed and replications, trees within provenances and sampling as random effects. Provenances and trees within provenances

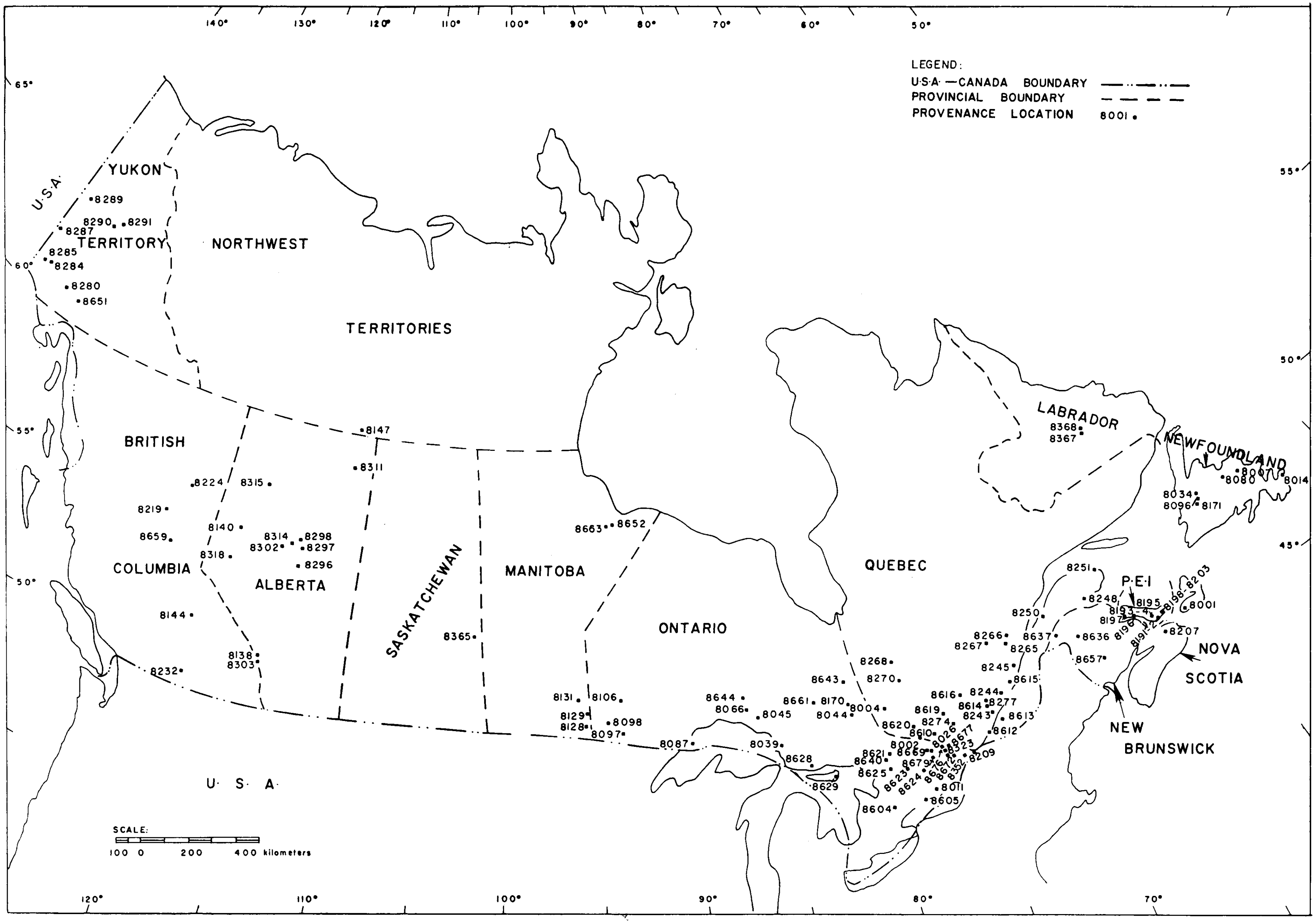


*Figure 1.* — Location of Provenances.

*Table 1A.* — Expected mean squares for different sources of variation.

| Source of variation | Characters of germinative energy and germinative capacity | Juvenile characters |
|---|---|---|
| Replications | $\sigma^2 + (\sum_{i=1}^{p} n_i)\sigma_R^2$ | $\sigma_s^2 + s\sigma^2 + s(\sum_{i=1}^{p} n_i)\sigma_R^2$ |
| Among provenances | $\sigma^2 + rd_w^2 + r \dfrac{\sum_{i=1}^{p} n_I P_I^2 - \dfrac{(\Sigma n_i P_i)^2}{n_i}}{p-1}$ | $\sigma_s^2 + s\sigma^2 + rs\sigma_w^2 + rs \dfrac{(\sum_{i=1}^{p} n_i P_i^2 - \dfrac{(\Sigma n_i P_i)^2}{n.}}{p-1}$ |
| Among trees/ provenances | $\sigma^2 + r\sigma_w^2$ | $\sigma_s^2 + s\sigma^2\ rs_w^2$ |
| Experimental error | $\sigma^2$ | $\sigma_s^2 + s\sigma^2$ |
| Sampling error | | $\sigma_s^2$ |

with zero germination were excluded from the analyses for characters of germinative energy. Coefficients of intraclass nondetermination were calculated to determine the variation at the intra-provenance level. The expected mean squares and the appropriate denominator for each F-test are shown in *Table 1A*.

In all cases except $Y_4$ to $Y_7$ the experimental error mean squares for individual tree seed provenances did not estimate the same quantity as the experimental error mean squares for bulked seed provenances. The experimental error mean squares for individual tree seed provenances estimate the conceptual variation associated with a single tree; i. e., the variation in response of a single tree, should the experiment be repeated an infinite number of times. The experimental error mean squares for bulked seed provenances contain in addition to the above, a component due to the variation among trees within provenances. The denominator used for the F-tests of these characters is the weighted average of the above two mean squares and is upward biased, reducing sensitivity of the F-tests.

Contrast between geographic cells

$$C = m_2 \sum_{i=1}^{m_1} \bar{y}_{1i} - m_1 \sum_{j=1}^{m_2} \bar{y}_{2j} \quad \ldots\ldots (1)$$

where $m_1$, $m_2$ = Number of provenances in cells 1 and 2; respectively

$\bar{y}_{1i}$ = Mean of provenance $i$ in cell 1.

$\bar{y}_{2j}$ = Mean of provenance $j$ in cell 2.

Contrast within geographic cells

$$C = \bar{y}_i - \bar{y}_j \quad \ldots\ldots (2)$$

where $\bar{y}_i$ and $\bar{y}_j$ are means of provenances i and j respectively.

Test statistic B for comparison between geographic cells for $Y_1$-$Y_3$ and $Y_8$-$Y_9$.

$$B = t_{p,n,f} \left[ \frac{\sum_{k=1}^{m_1+m_2} c_k^2 \text{ (Expt'l. error MS)}_k}{s_k} \right]^{1/2} \quad \ldots\ldots (3)$$

where (Expt'l. error M.S.)$_k$ = Expt'l. error M.S. appropriate to the $K^{th}$ mean, be it a bulked or individual tree seedlot.

$c_k$ = coefficient of $k^{th}$ mean in the contrast; f was taken to be 250, a weightd average based on the frequency of bulked and individual tree seedlots.

$s_k$ = Number of observations for $\bar{y}_k$; 3 replications with < 10 seedlings in each.

Test statistic B for comparison within geographic cells where the populations are both either bulked or from individual trees

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

where $t_{p,n,f}$, = Tabulated value of t for an over-all probability of p = 0.05 for n contrasts and f Experimental Error degrees of freedom

$s_i$ = Number of observations in the ith. population

$s_j$ = number of observations in the jth. population

Test statistic B for comparison between geographic cells for $Y_4$ to $Y_7$.

$$B = t_{p,n,f,} \left[ \text{Expt'l. error M.S. } \frac{\sum_{k=1}^{m_1+m_2} c_k^2}{s_k} \right]^{1/2} \quad \ldots\ldots (5)$$

where the symbols have the same meaning as in Equation 5

and n = 1676 for $Y_4$ and $Y_5$

n = 2057 for $Y_6$

f = 358 for $Y_4$ and $Y_5$

f = 402 for $Y_6$

Comparison within geographic cells where one population is bulked and one is an individual tree population.

$$B = t_{p,n,f} \left[ \frac{\text{Expt'l Error M.S. (bulked)}}{s_i} + \frac{\text{Expt'l Error M.S. (Indiv. Tree)}}{s_j} \right]^{1/2} \quad \ldots\ldots (6)$$

where $s_i$ = no. of obs. for bulked population.

$s_j$ = no of obs. for individual tree population.

Bonferroni *T-Tests* were performed according to Douglas (1979) to study geographic trends in variation and to select superior provenances. The provenances were grouped into 55 geographic cells with varying numbers of provenances. The cells comprised 2⁰ latitudinal classes and 2⁰ and 5⁰ longitudinal classes east and west of 98⁰ W longitude respectively. This grouping reduced the multiple comparisons from 320 301 to 1 676 and 1 744 for character of germinative energy and germinative capacity ($Y_1$ to $Y_6$) and juvenile characters ($Y_7$ to $Y_9$) respectively. The tests were performed between pairs of cells as well as within cells to determine geographic trends in variation and estimate the degree of homogeneity within cells. Provenance means over replications were used for both comparisons.

Contrasts (C) were calculated according to *Equations* (1) and *(2)* and their significance was determined by calculating the test criterion (B) according to *Equations (3) to (6)*. If the value of the contrast (C) was less than the test criterion (B) the null hypothesis $H_0$:C = 0, $H_A$:C ≠ 0 was not rejected. The test criterion (B) was calculated from the

*Table 2.* — Summary of analyses of variance.

| Source of variation | Characters of germinative energy: Degrees of freedom | F-values $Y_1$ | $Y_2$ | $Y_3$ | $Y_4$ | $Y_5$ | Germinative capacity: Degrees of freedom | F-values $Y_6$ | Juvenile characters: Degrees of freedom | F-values $Y_7$ | $Y_8$ | $Y_9$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Replications | 2 | $83.94^{***}$ | $28.70^{**}$ | $7.11^{***}$ | $6.16^{***}$ | $12.21^{***}$ | 2 | $13.10^{***}$ | 2 | $14.29^{***}$ | $298.64^{***}$ | $19.32^{***}$ |
| Populations | 179 | | | | | | 201 | | 182 | | | |
| Among Provenances | 90 | $3.14^{***}$ | $2.24^{***}$ | $1.79^{***}$ | $1.38^{*}$ | $1.23^{NS}$ | 109 | $5.34^{***}$ | 91 | $2.01^{***}$ | $3.38^{***}$ | $8.09^{***}$ |
| Among Trees/Provenances | 89 | $1.74^{***}$ | $1.85^{***}$ | $2.14^{***}$ | $1.88^{***}$ | $1.36^{*}$ | 92 | $5.57^{***}$ | 91 | $1.30^{*}$ | $0.97^{NS}$ | $1.87^{***}$ |
| Experimental error | 358 | | | | | | 402 | | 364 | $3.91^{***}$ | $5.94^{***}$ | $6.57^{***}$ |
| Sampling error | | | | | | | | | 4 507 | | | |
| Total | 539 | | | | | | 605 | | 5 055 | | | |
| Coefficient of intraclass non-determination | | 0.9611 | 0.9508 | 0.9247 | 0.9484 | 0.9882 | | 0.6358 | | 0.7729 | 0.9874 | 0.4736 |
| Coefficient of intraclass non-determination for individual tree seed provenances | | 0.9200 | 0.9225 | 0.8982 | 0.9233 | 0.9853 | | 0.6558 | | 0.7729 | 0.8523 | 0.9615 |

*** - Statistically significant (0.005 level)
** - Statistically significant (0.01 level)
* - Statistically significant (0.05 level)
NS - Statistically nonsignificant (0.05 level)

$Y_1$ - Days to commencement of germination
$Y_2$ - Days to 25% germination
$Y_3$ - Days to 50% germination
$Y_4$ - Days to 75% germination
$Y_5$ - Days to full germination

$Y_6$ - Germinative capacity
$Y_7$ - Cotyledon numbers
$Y_8$ - Hypocotyl length
$Y_9$ - Four-month seedling height

same experimental error mean squares as were used in the analysis of variance of the character concerned.

*The following regression and correlation analyses* were performed to determine geographic trends in variation and to establish correlations between selected characters:

1. Step-wise multiple regression and correlation analyses of each character with geographic coordinates at the origin of the provenances, using characters as dependent and geographic coordinates as independent variables.
2. Simple regression and correlation analyses of each character with 1 000-seed weight as the independent variable.
3. Simple regression and correlation analyses of germinative capacity and juvenile characters with characters of germinative energy, using the former as the dependent and the latter as the independent variables.

## Results and Discussion

### *Analyses of Variance*

The analyses of variance results are summarized in *Table 2.* Significance of replications as a source of variation in all characters indicates the adequacy of the design and size of the experiment for detection and removal of this unwanted source of variation.

Significance of the variation among provenances for all characters except number of days to full germination and that of the trees among provenances for all characters except hypocotyl length needs further examination. In the case of the provenances the assumption that the trees within provenances mean squares derived from individual tree seed provenances case only, is also the appropriate error term for the bulked seed provenances produces a slight upward bias in the error term and makes the F-test conservative. The conservative nature of the F-test, explained earlier, makes it safe to accept the significance of provenances and trees among provenances for all characters.

The high significance of experimental error for juvenile characters further elucidates the nature of intra-provenance variation. Experimental error measures the variation of the same provenance in the same replication ($\sigma_s^2$) and the variation of the same provenance in different replications or replications × provenances interaction ($\sigma^2$). Significance of experimental error mean squares shows that one of the above components is substantially large. Both these components result from a combination of intra- and inter-replication environmental differences and intra-provenance genetic differences. The former two sources of variation have been minimized by the nature of the experiment, leaving intra-provenance genetic differences as the major source of variation. Hence, intra-provenance variation is mainly responsible for the significance of experimental error.

The above conclusion is supported and extended to the characters of germinative energy and germination capacity by the high values of the coefficients of intraclass non-determination calculated from these analyses of variance and from the analyses of variance for individual tree seed provenances *(Table 2).* The high values for the former statistic show the existence of large intra-provenance variation and those for the latter statistic show that most of this variation is intra-tree which indicates the existence of considerable influence of introgression, migration, drift and differential inbreeding on all characters.

Thus, in addition to the large inter-provenance variation caused by natural selection there is genotypic variation resulting from introgression and variable degrees of inbreeding and outbreeding.

### Bonferroni *T-Tests*

The mean values and ranking of geographic cells for all characters are shown in *Table 3.* There are only a few significant differences in number of days to commencement of germination ($Y_1$), number of days to 25% and 50% ger-

*Table 3.* — Summary of Ranking and Bonferroni t-test among geographic cells.

| Rank | 1 000-seed weight (g) | | Days to commencement of germination (Y) | | Days to 25% germination ($Y_2$) | | Days to 50% germination ($Y_3$) | | Days to 75% germination ($Y_4$) | | Days to full germination ($Y_5$) | | Germinative capacity ($Y_6$) | | Number of cotyledons ($Y_7$) | | Hypocotyl length (cm) ($Y_8$) | | Seedling height at four month age (cm) ($Y_9$) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Cell | Mean | Cell | Mean | Cell | Mean | Cell | Mean | Cell | Mean | Cell | Mean | Cell | Mean | Cell | Mean | Cell | Mean | Cell | Mean |
| 1 | 22 | 3.157** | 1,21,22,37, 39,41,49 | 11.00* | 37,41 | 11.00* | 37 | 11.33** | 37 | 14.00** | 29,51 | 17.00** | 54 | 88.27* | 2 | 6.86** | 5 | 1.99* | 41 | 7.79* |
| 2 | 9 | 2.970* | 54 | 11.13* | 1,39,55 | 11.33* | 41,55 | 12.00* | 55 | 14.67* | 13,47 | 17.33* | 32 | 82.17* | 1 | 6.73* | 39 | 1.97* | 37 | 7.50* |
| 3 | 55 | 2.967* | 29,45 | 11.17 | 22,49 | 11.67* | 1 | 12.33* | 54 | 14.95* | 18,22 | 17.56* | 22 | 81.78* | 49 | 6.63* | 27 | 1.95* | 39 | 7.13* |
| 4 | 23 | 2.769* | 32 | 11.21 | 54 | 11.79* | 22 | 12.67* | 22,27,39, 41,47,49 | 15.00* | 39,50 | 17.67* | 55 | 80.00* | 21 | 6.57* | 1 | 1.91* | 22 | 7.05* |
| 5 | 10 | 2.731* | 35,52 | 11.22 | 27,29 | 11.83 | 56 | 12.93* | 32 | 15.05* | 30 | 17.88* | 36 | 79.33* | 7 | 6.56* | 29 | 1.88* | 46 | 6.83* |
| 6 | 27 | 2.696* | 30 | 11.27 | 52 | 11.89 | 49 | 13.00 | 30 | 15.16* | 1,5,7 | 18.00 | 11,28 | 78.67* | 51 | 6.52* | 10,28 | 1.87 | 5 | 6.78* |
| 7 | 5 | 2.683* | 36 | 11.31 | 8,21 | 12.00 | 27,39 | 13.33 | 36 | 15.47 | 40 | 18.13 | 21 | 78.00* | 39 | 6.50 | 26,38 | 1.86 | 27 | 6.74 |
| 8 | 21 | 2.680* | 27,28,31, 46,55 | 11.33 | 30 | 12.09 | 36 | 13.39 | 27,45,53 | 15.50 | 37 | 18.33 | 29 | 77.00* | 22 | 6.45 | 47 | 1.85 | 21 | 6.61 |
| 9 | 1 | 2.660* | 34 | 11.53 | 32 | 12.16 | 30 | 13.41 | 1,8,11, 46,51 | 15.67 | 54 | 18.35 | 39 | 74.00* | 23 | 6.42 | 21 | 1.84 | 36 | 6.51 |
| 10 | 29 | 2.630 | 42 | 11.57 | 36 | 12.19 | 32 | 13.54 | 26 | 15.73 | 45 | 18.50 | 35 | 71.56 | 36 | 6.41 | 22,36 | 1.83 | 30 | 6.46 |
| 11 | 19 | 2.600 | 8,11,16 | 11.67 | 42 | 12.22 | 53 | 13.60 | 14 | 15.75 | 14,43 | 18.67 | 42 | 71.45 | 37 | 6.40 | 6,7,9 | 1.82 | 26 | 6.28 |
| 12 | 15 | 2.543 | 53 | 11.69 | 11,20,46 | 12.33 | 11,29,52 | 13.67 | 16 | 15.84 | 32 | 18.80 | 37 | 70.67 | 24 | 6.38 | 2,16 | 1.81 | 20 | 6.15 |
| 13 | 51 | 2.530 | 10,20 | 11.83 | 53 | 12.55 | 42 | 13.70 | 15 | 15.96 | 17 | 18.92 | 53 | 70.31 | 45 | 6.35 | 11,30,32, 45 | 1.78 | 29 | 6.13 |
| 14 | 26 | 2.498 | 26 | 11.95 | 16 | 12.56 | 47,51 | 14.00 | 13,21,29 | 16.00 | 53 | 18.98 | 1,27 | 68.00 | 15,27 | 6.34 | 18 | 1.77 | 32 | 6.09 |
| 15 | 24 | 2.484 | 5,14,50 | 12.00 | 45,51 | 12.67 | 20 | 14.08 | 52 | 16.11 | 16,20,44, 46,55 | 19.00 | 38 | 66.67 | 10,44 | 6.32 | 14 | 1.76 | 9 | 6.01 |
| 16 | 38 | 2.474 | 15 | 12.02 | 15,34 | 12.73 | 21,45 | 14.17 | 42 | 16.14 | 6 | 19.20 | 20 | 65.83 | 5,8 | 6.30 | 41 | 1.75 | 8 | 5.96 |
| 17 | 39 | 2.460 | 24 | 12.20 | 10 | 12.86 | 15 | 14.19 | 10 | 16.22 | 15 | 19.21 | 26 | 62.89 | 34 | 6.28 | 17,23,35 | 1.74 | 1 | 5.95 |
| 18 | 7 | 2.436 | 6 | 12.24 | 35 | 12.89 | 16 | 14.28 | 17 | 16.25 | 26 | 19.22 | 8 | 62.67 | 38,46,55 | 6.27 | 24,44 | 1.73 | 13 | 5.91 |
| 19 | 20 | 2.421 | 51 | 12.33 | 5,14,47 | 13.00 | 8,14,26 | 14.33 | 34 | 16.27 | 24,34 | 19.27 | 10 | 60.89 | 14 | 6.26 | 15 | 1.70 | 6 | 5.88 |
| 20 | 50 | 2.412 | 38 | 12.67 | 26 | 13.06 | 34 | 14.40 | 5,31,35 | 16.33 | 10,11,23, 31,41,49,52 | 19.33 | 34 | 60.00 | 26 | 6.24 | 55 | 1.69 | 10,16 | 5.86 |
| 21 | 28 | 2.313 | 17 | 12.75 | 28 | 13.17 | 10 | 14.44 | 7 | 16.34 | 21 | 19.50 | 30 | 57.41 | 29,50 | 6.19 | 51 | 1.68 | 49 | 5.80 |
| 22 | 44 | 2.294 | 23 | 12.78 | 17 | 13.25 | 35 | 14.56 | 6,18 | 16.41 | 42 | 19.52 | 6 | 56.72 | 42 | 6.18 | 49 | 1.67 | 14 | 5.78 |
| 23 | 43 | 2.258 | 47 | 13.00 | 6 | 13.44 | 17 | 14.58 | 20 | 16.50 | 9 | 19.67 | 46 | 56.67 | 9,11 | 6.17 | 4,20,42 | 1.64 | 35 | 5.77 |
| 24 | 53 | 2.257 | 25 | 13.07 | 24 | 13.53 | 23 | 14.67 | 40 | 16.59 | 36 | 19.86 | 49 | 50.67 | 18 | 6.16 | 34,46 | 1.63 | 23 | 5.67 |
| 25 | 18 | 2.252 | 40 | 13.21 | 23 | 13.56 | 6 | 14.87 | 28,38,50 | 16.67 | 27 | 20.17 | 41 | 49.33 | 6,13 | 6.14 | 31 | 1.61 | 24,42 | 5.63 |
| 26 | 34 | 2.242 | 13 | 13.33 | 40 | 13.63 | 24 | 14.93 | 43 | 17.11 | 25 | 20.20 | 9 | 48.33 | 30 | 6.12 | 54 | 1.58 | 38 | 5.44 |
| 27 | 8 | 2.226 | 18 | 13.63 | 13,31,38 | 13.67 | 5,28,31 | 15.00 | 24 | 16.80 | 8,38 | 20.33 | 25 | 43.20 | 16,17,28 | 6.10 | 50 | 1.56 | 45 | 5.38 |
| 28 | 48 | 2.210 | 7 | 14.17 | 18 | 14.22 | 18 | 15.03 | 23,44 | 17.00 | 28 | 20.50 | 5 | 42.00 | 53 | 6.08 | 25 | 1.55 | 34 | 5.34 |
| 29 | 11 | 2.198 | 44 | 14.44 | 50 | 14.33 | 40 | 15.17 | 25 | 17.33 | 35 | 20.67 | 13,31 | 41.33 | 25,35 | 6.07 | 8 | 1.54 | 11,17 | 5.30 |
| 30 | 30 | 2.185 | 9 | 15.00 | 25 | 14.40 | 13,38,44 | 15.33 | 9 | 18.00 | | | 24 | 41.07 | 40 | 6.05 | 52 | 1.53 | 2 | 5.16 |
| 31 | 45 | 2.183 | 43 | 16.33 | 44 | 14.78 | 25 | 15.60 | | | | | 15 | 40.74 | 20,52 | 6.03 | 37 | 1.43 | 7 | 5.14 |
| 32 | 6 | 2.164 | | | 7 | 14.84 | 7,9,50 | 15.67 | | | | | 18 | 39.00 | 41 | 5.97 | 40 | 1.42 | 44 | 5.13 |
| 33 | 12 | 2.162 | | | 9 | 16.00 | 44 | 15.78 | | | | | 23 | 38.67 | 32 | 5.88 | 13 | 1.40 | 28 | 5.05 |
| 34 | 36 | 2.160 | | | 43 | 16.33 | 43 | 17.00 | | | | | 51 | 36.00 | 4 | 5.86 | 53 | 1.38 | 25 | 5.00 |
| 35 | 52 | 2.120 | | | | | | | | | | | 14 | 34.33 | 31 | 5.83 | | | 31 | 4.99 |
| 36 | 16 | 2.102 | | | | | | | | | | | 16 | 34.22 | 54 | 5.77 | | | 18 | 4.92 |
| 37 | 41 | 2.094 | | | | | | | | | | | 17 | 34.17 | 47 | 5.71 | | | 40 | 4.84 |
| 38 | 40 | 2.087 | | | | | | | | | | | 52 | 33.34 | | | | | 13 | 4.81 |
| 39 | 2 | 2.080 | | | | | | | | | | | 45 | 31.55 | | | | | 47 | 4.08 |
| 40 | 54 | 2.076 | | | | | | | | | | | 40 | 22.00 | | | | | 51 | 3.95 |
| 41 | 4 | 2.060 | | | | | | | | | | | 50 | 21.33 | | | | | 4 | 3.75 |
| 42 | 49 | 2.004 | | | | | | | | | | | 7 | 15.33 | | | | | 50 | 3.67 |
| 43 | 17 | 2.000 | | | | | | | | | | | 44 | 11.07 | | | | | 55 | 3.47 |
| 44 | 14 | 1.989 | | | | | | | | | | | 6 | 10.67 | | | | | 52 | 2.47 |
| 45 | 35 | 1.965 | | | | | | | | | | | 47 | 10.00 | | | | | 54 | 2.36 |
| 46 | 25 | 1.898 | | | | | | | | | | | 3,43 | 6.67 | | | | | 53 | 1.62 |
| 47 | 46 | 1.844 | | | | | | | | | | | 2 | 4.00 | | | | | | |
| 48 | 37 | 1.758 | | | | | | | | | | | 33 | 2.67 | | | | | | |
| 49 | 13 | 1.754 | | | | | | | | | | | 19,48 | 1.33 | | | | | | |
| 50 | 31 | 1.716 | | | | | | | | | | | 12 | 0.00 | | | | | | |
| 51 | 33 | 1.468 | | | | | | | | | | | | | | | | | | |
| 52 | 3 | 1.206 | | | | | | | | | | | | | | | | | | |
| 53 | 47 | 1.023 | | | | | | | | | | | | | | | | | | |
| 54 | | | | | | | | | | | | | | | | | | | | |
| 55 | | | | | | | | | | | | | | | | | | | | |
| Mean | | 2.252 | | 12.42 | | 13.06 | | 14.15 | | 16.03 | | 18.96 | | 47.28 | | 6.25 | | 1.71 | | 5.44 |
| Standard deviation | | ±0.405 | | ±1.27 | | ±1.24 | | ±1.17 | | ±0.84 | | ±0.97 | | ±25.50 | | ±0.27 | | ±0.17 | | ±1.31 |

** - Cells two standard deviations above or below the mean.

* - Cells one standard deviation above or below the mean.

NOTE - In each "cells" column the cells underlined are significantly different from cells 9 and 43 (0.05 level).

mination ($Y_2$ and $Y_3$ respectively) and seedling height ($Y_9$). However, considerable significant differences between pairs of geographic cells exist in germinative capacity ($Y_6$) as shown below:

| Cell | Significantly different from cells (0.05 level) |
|---|---|
| 1 | 2, 4, 19, 33, 43, 48, 50 |
| 2 | 8, 9, 11, 21, 22, 28, 29, 37-39, 41, 46, 49 |
| 4 | 8, 11, 22, 37-39, 46 |
| 8 | 19, 33, 43, 48, 50 |
| 9 | 19, 22, 33, 43, 48 |
| 11 | 12, 19, 33, 43, 48, 50, 51 |
| 12, 13, 19 | 21, 22, 28, 29, 37-39, 41, 46, 49 |
| 21 | 33, 43, 48 |
| 22 | 31, 33, 41, 43, 47-51 |
| 28 | 33, 43, 48 |
| 29 | 33, 48 |
| 33 | 37-39, 41, 46, 49 |
| 37, 38, 40 | 43, 48, 50 |
| 41 | 43, 48 |
| 43 | 46, 49 |
| 46 | 48 |
| 48 | 49 |

Lack of significant differences between geographic cells shows that in spite of significant inter-provenances differences the species cannot be divided into significantly different geographic areas, except for germinative capacity and four-month seedling height. Such differences are random and do not show any geographic trends, indicating a relatively minor role of natural selection and a major role of introgression, migration, drift and differential inbreeding on these characters. Significant differences within geographic cells exist mostly in germinative capacity (*Table 4*). The cells are fairly homogeneous and their formation has achieved the object of the experiment. The results of Bonferroni t-tests support the conclusions derived from the analyses of variance.

*Table 4.* — Number of significant pair-wise differences within cells.

| Cell No. | Response variable $Y_1$ | $Y_2$ | $Y_3$ | $Y_4$ | $Y_5$ | $Y_6$ | $Y_9$ |
|---|---|---|---|---|---|---|---|
| 5 | | | | | | 1 | |
| 6 | | | | | | 31 | |
| 7 | 1 | | | | | | |
| 10 | 11 | 5 | | | | 15 | |
| 14 | | | | | | 4 | |
| 15 | 4 | 1 | | | | 20 | |
| 16 | | | | | | 4 | |
| 18 | | | | | | 6 | |
| 20 | | | | | | 4 | |
| 24 | | | | | | 2 | 1 |
| 26 | | | | | | | |
| 30 | | | | | | 8 | |
| 34 | | | | | | 2 | |
| 42 | | | | 2 | | 14 | |
| 45 | | | | | | 1 | |
| 52 | | | | | | 2 | |
| 53 | | | 1 | | | 9 | |
| 54 | | | | | | 9 | |

$Y_1$ - Days to commencement of germination.
$Y_2$ - Days to 25% germination.
$Y_3$ - Days to 50% germination.
$Y_4$ - Days to 75% germination.
$Y_5$ - Days to full germination.
$Y_6$ - Germinative capacity.
$Y_9$ - Four-month seedling height.

Though the results do not show any geographic trends they can be used for selection of geographic cells with superior provenances for specific characters or their combinations. Cells 1, 21, 22, 27, 29, 32, 36, 37 and 39 are in the fourth quartile for eight to ten characters. In view of high heritability of germinative capacity and juvenile seedling height in white spruce (KHALIL 1978) and significant correlations of seed weight with juvenile height growth (vide infra) which is maintained up to 18 years of age (KHALIL 1981; NIENSTAEDT 1981), there is a good indication that the provenances in these cells are superior in seed quality as well as height growth. Cells 1, 27, 29, 37 and 39 have only one provenance each and cells 21, 22, 32 and 36 are homogenous in all characters (*Table 4*). This supports the reliability of the provenances in these cells for superiority. The fifteen superior provenances in these cells are 8001, 8007, 8034, 8045, 8066, 8080, 8096, 8098, 8128, 8129, 8131, 8171, 8232, 8267 and 8270.

*Regression Analyses*

Results of regression analyses are represented by 16 regression equations which are available with the author. Geographic trends are shown in seed weight, germinative capacity, cotyledon numbers, hypocotyl length and four-month seedling height as shown below:

| Character | Latitude | Longitude | Altitude |
|---|---|---|---|
| 1 000 seed weight | Positive***) | Negative*** | NS |
| Germinative capacity | Positive*) | NS | NS |
| Cotyledon numbers | NS | Negative*) | NS |
| Hypocotyl length | Negative*** | NS | Negative**) |
| Four-month seedling height | Negative*** | Negative*) | NS |

***) — Statistically significant (0.005 level).
**) — Statistically significant (0.01 level).
*) — Statistically significant (0.05 level).
NS — Statistically nonsignificant (0.05 level).

Regarding correlation of characters among themselves germinative capacity and juvenile characters are significantly and positively correlated with seed weight at various levels. Germinative capacity is negatively correlated with characters of germinative energy at the 0.005 level except with the number of days to full germination with which the correlation is significant at the 0.05 level. Seedling height is negatively correlated with number of days to 25% germination at the 0.05 level.

The detection of geographic trends by regression analyses and the failure of BONFERRONI t-tests to do so is due to a difference in approach. While BONFERRONI t-tests compare the means of appropriate response variables as influenced by gross effects of the environments, the regression analyses show the influence of the individual components of the environment. The latter comparatively more detailed analyses identify the components which have significant effects. The results show that all characters except those of germinative energy, have been influenced to some extent by natural selection, resulting from climatic differences produced by geographic coordinates.

The correlation with seedling height is specially important. The present results, based on range-wide sampling, confirm those based on a restricted sample reported by KHALIL (191). This, together with the fact that provenances with fast juvenile growth rates maintain this superiority until later development stages (KHALIL 1981; NIENSTAEDT 1981) confirms the earlier conclusion that in white spruce seed weight can be included among the criteria for selection of plus trees and fast growing provenances.

Provenances with high germinative energy also have high germinative capacity. The nature of this relationship is important. It is logarithmic linear for the number of days to commencement of germination and to 25% germination; linear for the number of days to 50 % and 75% germination; and cubic for number of days to full germination. This will also facilitate early detection of provenances with high germinative capacity. Alternatively, provenances should be selected for the easily measurable character of germinative capacity; provenances with high germinative capacity would also have high germinative energy. The significant correlation of seedling height with the number of days to 25% germination is helpful in identifying fast growing provenances.

## Conclusions

The important conclusions of this range-wide study of white spruce are:

1. The three-replicated randomized complete block design is adequate for detection and removal of environmental variation and improvement of F-tests for other sources of variation in a greenhouse experiment.
2. The populations studied have been influenced by selection pressures, creating significant inter-provenance variation and by introgression and differential inbreed-

ing and outbreeding causing intra-provenance variation in all characters except germinative energy.

3. Trends in inter-provenance variation and selection pressures on many characters have been demonstrated by regression analyses but not by BONFERRONI t-tests. South to north trends are shown in seed weight, germinative capacity, hypocotyl length, and seedling height; and east-west trends in seed weight, cotyledon numbers and seedling height.
4. Germinative capacity and juvenile characters are significantly and positively correlated with seed weight. This confirms the earlier finding that in white spruce seed weight can be included among the criteria for selection of plus trees and superior provenances.
5. Provenances with high germinative energy also have high germinative capacity and fast juvenile growth.
6. The fifteen promising provenances are 8001, 8007, 8034, 8045, 8066, 8080, 8096, 8098, 8128, 8129, 8131, 8171, 8232, 8267 and 8270.

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# Mapped genetic variation of Douglas-fir to guide seed transfer in southwest Oregon

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### Summary

A procedure is illustrated for using mapped genetic variation in indigenous species to develop provisional seed transfer rules and seed zones. Genotypic values for 13 traits of 135 parent trees from 80 locations furnished data for Douglas-fir in a region about 110 × 130 km in southwest Oregon. Genotypic values were estimated from open-pollinated progeny grown in two nursery beds. The data were reduced to manageable dimensions by principal component analysis. The genetic correlation matrix at the seed-source level was used as input for the analysis. Two principal components accounted for about 96 percent of the total family and seed-source variation in all traits. Factor scores derived from principal components exhibited strong gradients with location variables: elevation, latitude, distance from the ocean, slope, and sun exposure as affected by shade of adjacent mountains. Seed transfer rules and a procedure for calculating relative risk indicated that risks were largest when seed was transferred either east-west along the southern boundary or north-south along the western boundary of the region. These gradients in risk coincide with the steepest precipitation and temperature gradients within the region.

Advantages, disadvantages, and potential sources of error in the procedure are discussed. In spite of the limitations of genetic mapping, the conclusion is that for genetically heterogenous species in mountainous regions, genetic mapping is a prerequisite to directly estimating transfer effects by long-term tests.

*Key words:* Genetic variation, seed source, seed zones, provenance, Douglas-fir, *Pseudotsuga menziesii*, southwest Oregon.

### Zusammenfassung

Es wird ein Verfahren beschrieben, um die bei einheimischen Arten bereits kartographisch festgehaltene genetische Variation zu benutzen und daraus vorläufige Saatgut-Transfer-Vorschriften und Saatguterntezonen zu ent-