Correlations of height growth and heritabilities at different ages in white spruce

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Summary

In 1953 parent trees in natural stands of white spruce (*Picea glauca* [Moench] Voss) were measured and their progenies from open pollination established in four experiments in 1958. The objective of the study was to evaluate selection methods, calculate heritabilities, and investigate juvenile-adult correlations. This paper updates earlier results published in 1969.

Measurements in 1975 indicated that there was considerable variation among progenies in height growth, but progenies of taller, narrow-crowned parents were not significantly taller than progenies of shorter, broad-crowned parents. Therefore, in natural stands, phenotypic selection for height growth on the basis of simple comparisons is considered to be ineffective, but could be more promising for crown and branch characters. In the progenies, the heritability of height growth of the two pairs of experiments after combined analysis was 0.15 and 0.18 respectively. Estimates based on measurement at age 8 were slightly higher. Correlations between heights at ages 8 and 22 were high. Early selection of superior progenies appears to be feasible.

Key words: Picea glauca, progeny test, phenotypic selection.

Sommaire

On a mesuré, en 1953 des arbres-mères dans des peuplements naturels d'Epinette blanche (*Picea glauca* (Moench) Voss) et leurs descendants par pollinisation libre établis en quatre expériences en 1958. Le but d'une telle étude était d'évaluer les méthodes de sélection, de mesurer l'héritabilité et d'enquêter sur les corrélations juvéniles-adultes. Ce document remet à jour des résultats antérieurs publiés en 1969.

Des mesurages en 1975 ont indiqué une variation considérable parmi les descendants quant à la croissance en hauteur, mais des descendants des arbres de taille supérieure à cimes étroites n'étaient pas significativement plus grands que ceux issus de parents plus courts à cimes larges. Donc, en peuplements naturels, la sélection phénotypique en vue de la croissance en hauteur sur la base de comparaisons simples est considérée comme inefficace, mais pourrait s'avérer plus prometteuse quant aux caractères propres à la cime et aux branches. Chez les descendants, l'héritabilité reliée à la croissance en hauteur des deux paires d'expériences, après une analyse multiple, était de 0.15 et de 0.18 respectivement. Les estimations fondées sur un mesurage à l'âge de 8 ans se sont avérées légèrement plus élevées. Les corrélations entre les hauteurs aux âges de 8 ans et de 22 ans étaient élevées. Une sélection hâtive de descendants supérieurs semble réalisable.

Mots-clés: Picea glauca, test de descendance, sélection phénotypique.

Zusammenfassung

Im Jahr 1953 wurden Messungen von frei abgeblühten Bäumen in Naturbeständen von *Picea glauca* durchgeführt, ihre Samen geerntet, und 1958 4 Versuche mit ihren Nachkommen angelegt. Ziel der Versuche war Selektionsmethoden, Heritabilitäten, und Korrelationen zwischen Messungen verschiedenen Alters zu erforschen. Nach einer ersten Mitteilung im Jahre 1969 werden hier die Ergebnisse neuer Messungen von 1975 beschrieben.

Obwohl eine beträchtliche Variation zwischen Nachkommenschaften festgestellt wurde, waren Unterschiede zwischen Nachkommen schmalkroniger, höherer Bäume einerseits und breitkronigen, niedrigeren Bäumen andererseits statistisch nicht gesichert. Aus diesem Grunde sind Selektionsmethoden in Naturbeständen, die auf einfachen phänotypischen Vergleichen der Höhe beruhen, wahrscheinlich nicht wirksam; für Kronen- und Stammerkmale mag dies nicht gelten. Die Heritabilität des Höhenwachstums im Alter 22 betrug für die 2 Versuchspaare 0.15 und 0.18; im Alter 8 war sie etwas größer. Korrelationen der Höhe zwischen Nachkommenschaften im Alter 8 und 22 waren stark. Eine frühe Auslese der wüchsigsten Nachkommen unter Versuchsbedingungen wird für möglich gehalten.

Introduction

Information about genetic variability and effectiveness of phenotypic selection is essential for the development of a tree breeding program. Such information should be gathered as early as possible but at the same time it is necessary to avoid drawing final conclusions until the role of age effects is clear (Namkoong *et al.* 1972). Four open-pollinated white spruce progeny tests designed to obtain this information were established at the Petawawa Forest Experiment Station (PFES) in 1958. These are probably the oldest white spruce progeny tests established in North America. Early results published by Holst and Teich (1969) indicated a significant effect of stands and parent trees on height growth. At age of 11 years, the taller, narrow-crowned parent trees produced progeny significantly taller than the smaller broad-crowned parent trees in one of these tests. However, this conclusion was based only on measurements of the "healthy" trees in each plot. Subsequently heights and diameters (DBH) of the plantations were measured in 1975 when the trees were 22 years old. This paper discusses the new results and compares them with those reported earlier.

Materials and Methods

Progeny origin and establishment procedures have been described in detail in the early report (Holst and Teich 1969) and are summarized in *Table 1.*

The second measurements were made in the autumn of 1975 and recorded on a single-tree basis. Variance analyses were based on plot means and on a separate estimate of within-plot variance. Exp. 91-A was analyzed as split-plot with crown types considered as fixed effect (*Table 2*). The 11-year height of this test was re-analyzed on the basis of whole plots. Variance analyses of the other three tests followed the standard procedures of their respective designs (*Table 1*). Combined analyses for Exp. 91-A and 91-B and for Exp. 92-A and 92-B using common seedlots were performed to estimate the magnitude of family-planting site interaction.

Table 1. — Summary of experiments.

Exp. No.	Seed Origin	Test Design	Test Site
91-A	9 stands within radius of 160 km from PFES; seed collected from 2 trees in each with similar sites, one narrow-crowned, taller tree, and one broad-crowned tree (average 4.6% smaller).	Split-plot, with stands as whole plots, crown type as subplots; 4 replications with 50 trees per subplot, spacing 1.8 x 1.8 m.	Glacial till, formerly occupied by birch, red maple and aspen. Geology as given in Map 1132A. Soil seasonally dry.
91-B	8 narrow-crowned trees from sample in Exp. 91-A.	Randomized complete blocks, 4 replications, 50 trees per plot; spacing 1.2 x 1.2 m.	Delta sands with high water table in the northern part of the experiment (Blocks III and IV). Soil fresh.
92-A	16 randomly selected trees growing at PFES.	4 x 4 balanced lattice square, 5 replications, 49 trees per plot; spacing 1.2 x 1.2 m.	Glacial till, near Exp. 91-A.
92-B	10 trees of the same group included in Exp. 92-A.	Randomized complete blocks, 4 replications, 50 trees per plot, spacing 1.2 x 1.2 m.	Glacial till, near Exp. 91-A.

Table 2. — Form of variance analyses for height and DBH. Crown form considered fixed effect.

Exp. No.	Source	DF	Expected Mean Squares
91-A	Replications	3	
	Stand(s)	8	$\sigma^2_{w/k} + \sigma^2_p + 2\sigma^2_{rs} + 8\sigma^2_s$
	Error (a)	24	$\sigma^2_{w/k} + \sigma^2_p + 2\sigma^2_{rs}$
	Crown form (c)	1	$\sigma^2_{w/k} + \sigma^2_p + 4\sigma^2_{sc} + 36\Theta^2$
	S X C	8	$\sigma^2_{w/k} + \sigma^2_p + 4\sigma^2_{sc}$
	Error (b)	27	$\sigma^2_{w/k} + \sigma^2_p$

Between-age correlation in height growth was calculated by using a covariance analysis technique that partitions sums of products into components for replicates, families, and plot error (Steel and Torrie 1960, p. 317). Error correlation calculated by this method is the correlation of the residuals after the over-all effects of replicates and families have been removed, whereas the correlations of replicates and families are the same as those of simple cross-products. A Z-test was applied after transforming the correlation coefficients (γ) to a Z-value, (Steel and Torrie 1960, p. 190), to determine the heterogeneity of the correlation coefficients of family means and the residuals. Within-plot correlation for individual trees was found from each fourth plot, plots having been randomly selected.

Narrow-sense heritability (h^2) was estamited on a single-tree basis by:

$$h^2 = \frac{4\sigma^2_f}{\sigma^2_f + \sigma^2_p + \sigma^2_w + \sigma^2_s}$$

where σ^2_s = variance due to stand-to-stand differences.

σ^2_f = family variance which accounts for one-fourth of additive variance assuming that progenies are families of half-sibs and epistasis is negligible, and all trees are derived from a single random-mating population.

σ^2_p = variance due to environmental differences among plots within replications.

σ^2_w = variance due to differences among plants within plots.

Family variance (σ^2_f) in Exp. 91-A was obtained by pooling the crown type and stand-crown type interaction together *(Table 2)* considering the two crown types within each stand as random families. The family effect for Exp. 91-B was confounded by that of stand because only one family from each stand was included *(Table 2)*, and thus heritabilities estimated from this and its combined analysis with Exp. 91-B were biased. The amount of bias depends on the magnitude of the stand component (σ^2_s).

The standard errors (S.E.) of variance components were computed using the following equations (Becker 1975):

$$\text{S.E.}(\sigma^2) = \sqrt{\frac{2}{c^2}\left(\sum \frac{V^2_i}{f_i + 2}\right)}$$

where C^2 = coefficient of the component being estimated.

V_i = the ith mean square involved in the estimate of the component (σ^2).

f_i = degrees of freedom of the ith mean square.

Results

General

Survival was very good in all plantations and ranged from 70 to 83%. No significant differences in survival were detected among families, and this was not surprising because all the progenies were either of local origin or from an area with very similar climates. Experimental means and ranges in height and DBH are given in *Table 3*. Differences from test to test reflected mainly influences of soil moisture on height (Exp. 91-B was tallest, 603 cm) and of spacing on diameter (Exp. 91-A, largest DBH, 8.1 cm).

Analysis of Variance

Results of the variance analyses and estimates of variance components are summarized in *Table 4*. The family effect on height growth was statistically significant except in Exp. 91-B. The magnitude of the family components (σ^2_f) at the same age in all experiments was very similar, and the standard errors were approximately half the size of the

Table 3. — Plantation means and ranges in height and diameter.

	Height (cm) at age[1]		Diameter (cm)
Experiment	11 or 8	22	22
91-A	131 117 - 149	520 453 - 569	8.1 7.4 - 8.8
91-B	112 91 - 127	603 565 - 642	7.9 7.3 - 8.7
92-A	68 58 - 79	453 404 - 504	5.8 5.1 - 6.4
92-B	66 51 - 79	481 426 - 543	6.1 5.5 - 7.0

1) First measurement of Exp. 91-A, B was at age 11, and 92-A, B at age 8.

variance components indicating that estimates of σ^2_f are reasonably accurate. The discrepancy observed in Exp. 91-B, as will be seen later, is related to a special site effect.

DBH followed a similar pattern as height growth but the relative magnitude of the family component was smaller (*Table 4*). Diameter growth is more density-dependent. Crown closure in the plantations had begun before measurement. Competition may have affected its genetic expression.

Table 4. — Estimates of variance components (σ^2), narrow-sense heritabilities (h^2) and standard error (*s. e.*) for height and DBH.

Exp. No.	Traits	Age (years)	$\sigma^2_f \pm s.e.$	F-ratio[1] (families)	$\sigma^2_p \pm s.e.$	$\sigma^2_w \pm s.e.$	h^2
91-A	Height	11	42 ± 25	3.44**	42 ± 18	986 ± 27	0.15
		22	973 ± 490	6.70**	367 ± 180	10515 ± 303	0.32
	DBH	22	0.08 ± 0.06	2.35*	0.10 ± 0.06	4.09 ± 0.13	0.07
91-B	Height	11	102 ± 58	6.06**	58 ± 25	989 ± 33	0.35
		22	69 ± 469	1.08NS	2720 ± 661	17975 ± 704	0.01
	DBH	22	-0.04 ± 0.12	0.86NS	0.82 ± 0.29	6.06 ± 0.26	--
Comb.[2]	Height	11	49 ± 32	4.33**	93 ± 25	962 ± 29	0.18
		22	475 ± 353	3.12*	1388 ± 382	10472 ± 443	0.15
	DBH	22	0.07 ± 0.05	1.93NS	0.46 ± 0.13	5.46 ± 0.17	0.05
92-A	Height	8	27 ± 13	4.13**	35 ± 11	413 ± 10	0.23
		22	639 ± 303	3.97**	766 ± 286	12703 ± 343	0.18
	DBH	22	0.08 ± 0.06	2.00NS	0.27 ± 0.13	4.02 ± 0.11	0.07
92-B	Height	8	49 ± 27	4.50**	44 ± 15	531 ± 18	0.31
		22	956 ± 707	2.46*	2061 ± 685	19938 ± 735	0.17
	DBH	22	0.16 ± 0.13	2.21NS	0.35 ± 0.14	6.14 ± 0.23	0.10
Comb.[2]	Height	8	24 ± 13	4.64**	48 ± 10	458 ± 10	0.18
		22	325 ± 257	2.20*	1899 ± 340	18571 ± 468	0.06
	DBH	22	0.05 ± 0.05	1.83 NS	0.41 ± 0.10	4.94 ± 0.12	0.04

1) Significance levels: NS, not significant; *, 5%; **, 1%.

2) Since family-planting site interaction was not significant, mean squares for the interaction and plot error were pooled to test and estimate the family component.

No genotype-environment interaction was found in the combined analyses. This was not surprising because the climatic conditions for the four tests, which are only about 10 km apart, are similar although the soil in Exp. 91-B differs from soils in the other experiments (*Table 1*).

The split-plot (Exp. 91-A) and lattice square (Exp. 92-A) designs considerably reduced plot error variances (σ^2_p) (*Table 4*). In the former, σ^2_p was reduced to half the size after removal of the main-plot error variance. The relative precision of the lattice-square over the randomized-block design was 145 and 118% respectively for height and DBH at age 22. But there were few changes in ranks of family means before and after adjustment.

Without exception, variation within plots (within family) contributed the largest variance components in all four experiments, accounting for over 70% of total variation (*Table 4*). Both genetic and environmental factors contribute to this variance, but in segregating families, a sizeable genetic component can be expected.

In Exp. 91-A, variance analyses revealed no difference between crown types in height growth, but the effects of stands and stand-crown type interactions were highly significant (F = 3.40 and 3.87 for stand and stand-crown type interaction respectively at age 11 and 4.87 and 7.52 at age 22, all significant at 1% level). At age 22 the mean heights of progenies from narrow- and broad-crowned parent trees were 519 and 521 cm. Results of 11-year height reported by Holst and Teich (1969) differed from those reported here because only „healthy" trees were included in their analyses. Discerning „healthy" from „unhealthy" trees is subjective and bias can be introduced. Many „unhealthy" trees excluded from their analysis now grow vigorously.

In Exp. 91-B, results at the two ages differed. The effect of family on height was highly significant at age 11, but diminished at age 22 (*Table 4*). The height of this plantation had been measured again in 1969 when the trees were 16 years old. The results were essentially the same as at age 11. Family effects were highly significant (F = 4.92, significant at 1% level) and the correlation of family means between ages 11 and 16 was 0.95. The drastic change in growth pattern that occurred after age 16 appears to be related to the high water table in parts of the test site. Presumably tree growth was affected after the root system reached the water level and root development became restricted. The height ranking of replicates was reversed as shown in the negative correlation of replicate effect (*Table 5*). Trees in the tallest replicate at ages 11 and 16 became the shortest at age 22.

Table 5. — Correlation of height growth between age 22 and 11 (Exp. 91-A, 91-B) or age 8 (Exp. 92-A, 92-B) estimated by covariance analyses.

	Exp. No.			
Components	91-A	91-B	92-A	92-B
Replicates	.26	-.78	.78	.84
Families	.62	.60	.69	.94
Plot errors	.61	.22	.67	.78
Within-plot	.72	.77	.77	.76

Heritability

The estimated narrow-sense heritabilities (h^2) for height growth vary from age to age and from test to test *(Table 4)*. Some of these inconsistencies are explainable. The adverse site effect in Exp. 91-B just mentioned, which reduced the range of family means at age 22, obviously accounted for the drastic decrease of heritability from age 11 to 22. The low within-plot variation (σ^2_w) in Exp. 91-A, which resulted from wider spacing in this test *(Table 1)*, partially accounted for the higher heritability at age 22. Inadequate sampling also likely causes the inconsistency. However, even in a well-defined maize population, with sample sizes ranging from 256 to 400 families (Gardner 1977), large discrepancies were found. There are additional weaknesses when estimating genetic parameters from open-pollinated families (Squillage 1974). Nevertheless, the heritability averaged over the three tests, (Exp. 91-A, 92-A and 92-B) was 0.23 for both ages, which is well within the range of published reports on heritability of this species (Mohn *et. al* 1976, Dhir 1976).

Correlation

The correlation coefficients, relating heights at age 22, 11, and 8, are positive for all components with the exeption of the replicate effect in Exp. 91-B *(Table 5)*. Family correlations varied from plantation to plantation. The ranking at ages 8 and 22 remained virtually unchanged in Exp. 92-B. Changes in other experiments were minor, mostly within the range of 1 to 3. Generally, family performance at age 11 or 8 was a good indication of performance at age 22.

With the exception of Exp. 91-B, correlation coefficients between the deviations in plot means (after effects of replicates and families had been removed) were not significantly different from family means at early and late ages, indicating the homogeneity of between- and within-family correlations. Low plot correlation in Exp. 91-B *(Table 4)* was obviously caused by the environmental effects mentioned earlier. Within-plot correlations were high and uniform among tests. If family selection is made at a juvenile stage, individual-tree differences should be taken into consideration.

Discussion and Conclusion

The lack of differences among progenies of selected narrow-crown and random parent trees is not surprising since the parent trees were selected for total height and crown form, without taking age into account. In view of the low narrow-sense heritability of height growth, such simple comparisons cannot be expected to make phenotypic selection effective. Khalil (1975) reported no difference in germination, survival and first-year height between selected plus trees and ordinary trees from two white spruce stands in Newfoundland. Similar results were found in black spruce *(Picea mariana* [Mill.] B.S.P.) (Morgenstern 1974).

Results from this study clearly indicate that genetic variation is substantial, and that it will respond to selection. In Canada, phenotypic selection in white spruce usually begins in natural, uneven aged stands since plantations are not available. In these circumstances, selection efficiency is low unless carried out using very refined methods (Teich 1975). Family selection, which is theoretically more effective than mass selection when heritability is low (Falconer 1960), should be considered as an alternative. In the first generation of breeding, selection of open-pollinated families is generally preferred over selection after controlled pollination because open-pollinated seed is cheap and easy to obtain (Wright 1976). A large open-pollinated progeny test involving hundreds of families is not difficult to establish, and selection intensity can be substantial. Combined family and individual-tree selection is then a practical possibility which should give a higher genetic gain than family selection alone. Snyder (1969) reported that gain from selection of open-pollinated families was almost three times that of phenotypic selection in the forest.

Genetic gain per unit time can further be improved if juvenile selection is feasible. Results reported from pine species generally suggest that selection can be made at about age 10 when the effects of seed size, nursery culture, and planting shock have largely disappeared (Squillace and Gansel 1974, Steinhff 1974). Squillace and Gansel (1974) further suggested to use stepwise selection to increase efficiency. Selection is made with relatively low intensity at the beginning and increased progressively as the trees get old. The result of this study show that selection for height at age 22 could have been made at about age 10 with relatively small errors. Judged in this manner, early selection in white spruce is feasible. King *et al.* (1965) and Teich and Khalil (1973) had come to the same conclusion in this species. Johnsson (1964) stated that the test period should include one-third of the rotation, which would amount to about 20 years in white spruce. Our results indicate that this period might be shorter.

In this paper so far crown and branch form have been given little consideration although they are also important in a white spruce selection program. Their heritability is probably high and well formed plus trees could be identified fairly rapidly in natural stands (Shelbourne 1969). Following plus-tree selection, open-pollinated progeny testing to find the fastest growing families and individuals would then constitute the second stage in a comprehensive selection program (Teich 1975).

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Patterns of variation in bud-burst timing among populations in several Pinus species

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Summary

Intraspecific variation in bud-burst timing was studied in range-wide provenance tests of eight north-temperate *Pinus* species: *P. banksiana* Lamb., *the P. flexilis* James - *P. strobiformis* Engelm. complex, *P. nigra* Arnold, *P. ponderosa* Laws., *P. resinosa* Ait., *P. strobus* L., *P. sylvestris* L., and *P. virginiana* Mill. Only in *P. resinosa* were differences among populations statistically non significant In all others, variation followed strong geographic patterns, as shown by the fact that regressions of population means in each species on polynomial functions of latitude and longitude of origin accounted for 69 to 88 percent of total variation.

Variation patterns were similar in all species when interpreted in general terms of the effects of latitude and proximity to oceans on climate. Populations from northern and continental regions were earlier to burst bud than populations from southern and coastal regions. The tendency for populations in the direction of coasts to burst bud late for their latitudes occurred farther inland on west sides of continents, where prevailing winds move from the ocean to the continent. Furthermore, this tendency was strongest in Europe, where prevailing winds are unimpeded by major north-south mountain ranges. Most of the pronounced departures from major trends were consistent with more local climatic anomalies caused by factors other than latitude or proximity to oceans.

There was a close correspondence between variation patterns in all species (except *P. resinosa)* and January mean temperature isotherms over the species' ranges. Similarly, consistently high correlations in all species were obtained between bud-burst timing and January through March mean temperatures measured near population origins, but not between bud-burst timing and spring and summer temperatures or variables related to spring frosts. Similarities among the species in their variation patterns presumably indicate similarity in adaptive response to environmental gradients. Other species in other genera have variation patterns in budburst timing that differ from those observed here in minor or major respects. This is to be expected, since closely related species should adapt to environmental gradients in manners more similar than distantly related species.

Key words: phenology, adaptive variation, provenance testing trend surface analysis, Pinus banksiana, P. flexilis, P. nigra, P. ponderosa, P. resinosa, P. strobus, P. strobiformis, P. sylvestris, P. virginiana.

Zusammenfassung

In weitgestreuten Provenienversuchen wurde an 8 Kiefernarten der nördlich gemäßigten Zone die intraspezifische Variation im zeitlichen Austriebsverhalten untersucht. Es handelte sich dabei um: *P. banksiana* Lamb., den *P. flexilis* James-*P. strobiformis* Engelm. Komplex, *P. nigra* Arnold, *P. ponderosa* Laws., *P. resinosa* Ait., *P. strobus* L., *P. sylvestris* L., und *P. virginiana* Mill. Nur bei *P. resinosa* waren die Unterschiede zwischen den Populationen statistisch nicht signifikant. Bei allen anderen Arten war eine große geographische Variation festzustellen, was durch die Tatsache belegt wird, daß in jeder Art die Regression auf polynome Funktionen von georgraphischer Länge und Breite der Herkunft mit 69—88 % der Gesamtvariation zu erklären waren.

Durch den Einfluß von Breitengrad und Meeresnähe auf das Klima waren die Variationsmuster bei allen Arten ähnlich. Populationen aus nördlichen und kontinentalen Regionen trieben früher aus, als Populationen aus südlichen und Küstengebieten. Die Tendenz der küstennahen Populationen zum späten Knospenaufbruch setzt sich weiter ins Binnenland, bis in westliche Teile des Kontinents fort, da sich die vorherrschenden Winde vom Meer her auf den Kontinent zubewegen. Am deutlichsten wird diese Tendenz in Europa, wo die Winde durch keine größeren, in Nord-Süd-Richtung verlaufenden Gebirge aufgehalten werden. Die meisten der wichtigen Abweichungen von diesen Trends gehen mit lokalen klimatischen Anomalien einher, werden also durch andere Faktoren als geographische Breite oder Meeresnähe verursacht.

Bei allen Arten (außer bei *P. resinosa)* besteht eine enge Verbindung zwischen dem Variationsmuster und den Ja-

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