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Heritability Estimates in Ontario White Spruce

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Introduction

Successful breeding requires a genetically variable population and an effective method of selecting genetically superior individuals. The purpose of this study was to assess the genetic variability of white spruce (Picea glauca [MOENCH] VOSS) within a limited area of Ontario and to compare the effectiveness of two selection methods.

The progenies of individual, open-pollinated trees in existing experiments used in this study provided immediate, cheap and reasonably valid information for heritability calculations (fractions of the observed variation transmissible to the next generation). Heritabilities of various characteristics based on four individual white spruce single-tree progeny tests ase discussed. Compromises in the satisfaction of theoretical requirements (notably the deviation from random mating observed by SQUILLACE and BENGSTON, 1961) were well worth accepting.

HATTEMER (1963) listed numerous studies of progenies of open-pollinated trees in species other than white spruce. **A** search of the literature yielded no references dealing with heritability of height growth in white spruce. To provide some background information on a related species we will discuss the most relevant literature on Norway spruce (Picea abies [L.] KARST).

In Sweden SYLVEN (1910) selfed five Norway spruce and established a field test with four of the inbred progenies and open-pollinated controls. These were measured in 1937. The inbred seedlings had a high mortality and only half the height of the controls (LANGLET, 1940). From 1940 to 1960 the Swedes established many tests of open-pollinated progenies of Norway spruce (ANDERSSON, 1947 and 1962; KIELLANDER, 1953). NILSSON (1958a) investigated four of these located in central Sweden and found considerable differences among progenies. NILSSON (1958b) also compared 140 plus trees in natural stands across Sweden in relation to dominant comparison trees in the same stands. The relationship between volume of parent and height of offspring was negligible. He did note, however, that there was a good correlation between the height/diameter quotient of mother trees and progeny height at 10 to 13 years of age. The best third of the mother trees had a quotient 14 percent above average and progeny with a 5 percent faster growth rate. He concluded that the best tree to select was one with superior height and average diameter.

ROHMEDER (1961) reported on a Norway spruce test started in 1936 with 59 progenies of dominant, codominant and

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"mildly suppressed" trees in a 58-year-old stand in Forstamt Eichstätt-West. At age 20 the progenies of the three different crown classes were similar in volume. Selection on the basis of tree volume would not have provided any genetic gain.

Statistical Procedures

Seedlings derived from open-pollinated trees were planted in progeny trials. Heritability of height after eight and eleven seasons of growth was calculated by components of variance and by regression of progeny on mother trees.

The equations used for calculation of heritabilities in this paper are:

(1) Family heritability:

$$h^2_{fa} = \frac{2\sigma^2_f}{\frac{\sigma^2_e}{r} + 2\sigma^2_f} \qquad \text{(Formula 61 — Wright, 1962)}^{2)}$$

Single tree heritability (h^2):

$$h^2_{fa} = \frac{n r_G h^2 + (1-r_G)h^2}{1 + (n-1) r_G h^2} \qquad \text{(Formula 62 — Wright, 1962)}^{2)}$$

where σ^2_f = variance due to female
σ^2_e = error variance
r = number of replications
r_G = genetic correlations among family members
n = number of individuals per family
h^2_{fa} = heritability on a family basis
h^2 = heritability on a single tree basis

(2) (a) $b_{y.x} = \frac{\Sigma xy}{\Sigma x^2}$ (Lush, 1940)

(b) $r_{y.x.} = \frac{\Sigma xy}{\sqrt{\Sigma x^2 . \Sigma y^2}}$ (Lush, 1940; Frey and Horner, 1957)

where $b_{y.x}$ = regression of offspring on parents
$r_{y.x}$ = correlation of offspring on parents
Σxy = corrected sums of squares for crossproducts of progeny and parents
Σx^2 = corrected sums of squares for parents
Σy^2 = corrected sums of squares for progeny

Regression coefficients, b, or correlations, r, were doubled to calculate heritability because data from only one parent in each instance were known and the male gametes were assumed to be random.

Heritability of Heights and Crown Form by Regression of Progeny on Mother Trees and by Variance Components (Experiment No. 91—A)

Materials and Methods

Nine white spruce stands in Ontario were sampled: one stand each at Maple Leaf, Sundridge and Carnarvon; two stands at Sandy Lake; and four stands along Highway 60 in Algonquin Park. In each stand two trees, one slender-crowned plus-tree type and one broad-crowned control were selected to represent a random sample of phenotypically superior trees. The two trees were comparable in that they grew on similar sites and were of similar age, but the slender ones were 4.6 percent higher. For parent-progeny correlations, measurements were made of height and of breast-height diameter (D. B. H.) and expressed as a ratio of broad-crowned tree to slender tree so that the effect on progenies of within-site parental differences could be evaluated.

Progenies were tested in a split-plot design, with stands as main plots and single-tree progenies (crown form of parent) as subplots. There were 50 trees per plot and four replications. The test was established with 2-2 seedlings in the spring of 1958 and was measured in the autumn of 1964. Plant height, length of the last two internodes of the leader, the longest branch in the second whorl, the percent of trees with more than one leader, and stem damage were recorded. In the analysis only the healthy trees were used for the first three characters while all the living trees were used for the fourth. The analyses of this experiment are presented in *Tables 1, 2 and 3.*

Results

Progenies from different stands differed in height ($p = .05$). Progenies from slender tall trees were taller than progenies from broad trees by 4 percent ($p = .05$), indicating that even moderately intensive selection for slender, tall plus trees was effective. When branch length was put in relation to growth rate by dividing the branch length of the second whorl by the length of the last two internodes, a low ratio indicated a slender crown. In this experiment the ratios were significantly different ($p = .05$) for the progenies from broad- vs. slender-crowned parents. The progenies of broad-crowned parents had a ratio that was 2 percent higher than those from slender-crowned parents. There were no significant differences among stands in this ratio. The percent of trees with more than one leader was significant for stands ($p = .01$), but not within stands. Branch length alone did not show any significant differences — either by parental form or by stand.

In a second method of analysis, the form of parents and the relationship of the two trees in the same stand were ignored to allow analysis as a randomized blocks design. This was necessary for heritability calculations by the variance-component method. Bias caused by this unorthodox procedure was expected to be negligible, and the expectation was justified by results from more conventional procedures in the other three experiments.

Among progenies there were significant differences in height ($p = .01$), plants with more than one leader ($p = .001$), and branch length/leader length ratio ($p = .10$). Branch-length variation was not significant even at $p = .10$. Heritabilities calculated from these analyses are presented in *Table 2.*

The narrow-sense heritabilities on a family and single-tree basis among progenies were respectively: plants with more than one leader, 85 and 13.0 percent; height, 75 and 9.8 percent; branch length/leader length ratio, 57 and 4.5 percent; and branch length, 0.

By the regression of progeny on mother trees the heritability of plant height was 6 percent (2b) by regression and 12 percent (2r) by correlation. A comparison of diameter at breast height of the mother trees with progeny height indicated heritabilities of 8 percent (2b) by regression and 22 percent (2r) by correlation. Regression and correlation values are listed in *Table 3.*

Because of the low number of degrees of freedom, no correlation or regression values were significant at the conventional levels of probability, but these values nevertheless most likely indicate true biological relationships.

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[2] Prof. J. W. Wright in a personal communication has stated that these formulae are controversial.

Table 1. — Analysis of variance of 11-year-old white spruce progenies from 18 open-pollinated single trees with broad or slender crowns, in a split-plot design. Experiment No. 91—A.

		Branch vs. leader length		Branch length		Height		Percent with multiple leaders	
Source	D. F.	M. S.	F	M. S.	F	M. S.	F	M. S.	F
Stand	8	9.69	0.63	6.09	1.66	312	3.15*	265	7.95**
Error (a)	24	15.36		3.37		99		33	
Crown form	1	29.52	5.54*	1.90	0.59	523	6.30*	0	—
Crown form × stand	8	10.09	1.89	5.52	1.72	96	1.16	45	1.06
Error (b)	27	5.33		3.20		83		43	

* Significant at the 0.05 level of probability.
** Significant at the 0.01 level of probability

Table 2. — Analysis of variance and heritability estimates of 11-year-old white spruce progenies from 18 open-pollinated single trees with broad and slender crowns in a split-plot design. Heritability estimates were calculated from components of variance. Experiment No. 91—A.

	Source	D. F.	M. S.	F	Heritability Percent	
					Families	Single trees
Height	Families	17	222	2.52**	75	9.8
	Error	51	88			
Branch length/ leader length	Families	17	5.58	1.66	57	4.5
	Error	51	3.36			
Branch length	Families	17	9.84	0.98	0	0
	Error	51	10.00			
Percent with more than one leader	Families	17	146	3.80***	85	13.0
	Error	51	38			

** Significant at the 0.01 level of probability.
*** Significant at the 0.001 level of probability.

We believe, however, that correlations involving branch length were predominantly due to chance, because in the analysis of variance branch length was not significantly different ($p = .10$) among progenies, even though there were a considerable number of degrees of freedom in the numerator and denominator of the F ratio.

The negative correlation of parent D. B.H. with progeny height is so small as to be of no consequence, and this is consistent with the results of Nilsson (1958 b). However, since the relationship between height and diameter is a result of a large number of factors — such as age, stand density and site — not considered in our experiments, our results are not conclusive.

Since height and diameter of mother trees are both components of volume, it is not unreasonable to calculate "heritabilities" on the progeny heights relative to parent diameter. This, however, may not be justified for crown form and branch length. Be that as it may, in order to have comparable values we have chosen to express these relationships in a similar manner as progeny heights. Thus the family heritabilities of branch length/leader length ratios of the progenies when related to mother tree height were 30 percent (2b) and 80 percent (2r); when the ratio was related to mother tree diameter at breast height, heritabilities were 18 percent (2b) and 92 percent (2r). When progeny branch length was related to mother tree height, heritabilities were 8 percent (2b) and 2 percent (2r); when branch length was related to mother tree diameter at breast height, heritabilities were 12 percent (2b) and 34 percent (2r).

Table 3. — Correlation (r) and regression (b) of 11-year-old progenies on their open-pollinated trees. Experiment No. 91—A.

Mother tree	Progeny	Height	Branch length/ leader length	Branch length
Height	b	0.03	0.15	0.04
	r	0.06	0.40	0.01
D.B.H.	b	—0.04	0.09	0.06
	r	—0.11	0.46	0.17

Heritability of Height among Progenies of Slender-Crowned Trees by the Variance Component Method (Experiment No. 91—B)

Materials and Methods

Eight white spruce trees of slender-crowned type from Ontario were progeny-tested by open-pollinated seed, in 50-plant plots in four randomized blocks with 4' × 4' spacing, at the Petawawa Forest Experiment Station. The trees were sampled from Maple Leaf, Algonquin Park, Carnarvon, Sandy Lake, Sundridge and the Nipissing Game Reserve, and were similar to the slender trees of Experiment No. 91-A. In the spring of 1958, 2-2 seedlings were planted on a somewhat frosty site. Surround rows about each plot were planted with seedlings of the Maple Leaf provenance.

Heights were measured in the autumn of 1964 on 11-year-old trees. The analyses of progeny heights and progeny heights relative to surround rows are presented in *Table 4.*

Results

In the past we had found that evaluating plots relative to surround rows removed extraneous site variation and reduced experimental error. In this instance the procedure did not improve the experiment. Family heritability of height growth was 91 percent, 16 percent higher than in

Table 4. — Analysis of variance and heritability estimates of height of 11-year-old progenies (in a randomized block design) of eight slender-crowned open-pollinated white spruce trees. Experiment No. 91—B.

	Source	D. F.	M. S.	F	Heritability Percent	
					Families	Single trees
Plot data	Families	7	497	6.06***	91	18.1
	Error	21	82			
Plot data relative to surround rows	Families	7	630	4.44**	87	13.7
	Error	21	142			

** Significant at the 0.01 level of probability.
*** Significant at the 0.001 level of probability.

Experiment 91-A. As the experimental errors in the two experiments were similar, the difference in heritability was due to greater genetic variance in Experiment 91-B, which was probably due to sampling procedure for parents.

Increase in Heritability by a Lattice Square Design (Experiment No. 92—A)

Materials and Methods

Sixteen random trees were sampled from the white spruce population at the Petawawa Forest Experiment Station, and their open-pollinated progenies were tested in a 4 × 4 balanced lattice square with 49-plant plots and five replications. The 2-2 seedlings were planted in 1958 and measured in 1961 as eight-year-old trees.

Results

As demonstrated in *Table 5*, the lattice square analysis increased family heritability of height from 80 percent (randomized blocks analysis) to 86 percent by reducing the error. However, the five best progenies, both before and after adjustment for rows and columns, were identical; therefore the lattice advantage was only of academic interest.

Heritability of Height and Stem Form (Experiment No. 92—B)

Materials and Methods

Ten plus trees from the Petawawa Forest Experiment Station were progeny-tested by open-pollinated seed. In 1958, 2-2 seedlings were planted in a randomized blocks design with 4' × 4' spacing, 50 trees per plot and four replications. In 1961 the eight-year-old trees were measured.

Results

Variance analysis of height and multiple-leader percentage are presented in *Table 6*. Estimates of family heritability were 87 percent for height and 68 percent for multiple leaders.

Discussion

Genetic advance in a selection program is governed by three factors — additive genetic variance in the population, heritability, and selection intensity. The first may be enhanced by the introduction of exotic germ plasm. The second may be increased by refined techniques of evaluating potential parents in the wild and by increased precision of progeny tests. The third has a practical limit after which the law of diminishing returns restricts further intensity of selection.

To have a 50 percent chance of finding one phenotype 3.8 standard deviations above the population mean in one character, it would be necessary to examine 10,000 trees. Any desired selection intensity beyond this is impractical. The problem is compounded because the tree breeder cannot afford to ignore such economic factors as resistance to disease and insects, and branch form. If only three characters are being selected for with equal intensity, the selection differential cannot be much greater than one standard deviation. Under these circumstances, characters with low heritabilities have little possibility of major improvement.

To obtain a conservative estimate of potential genetic gain in height, we calculated the expected and actual genetic

Table 5. — Analysis of variance and heritability estimates of height of eight-year-old progenies in a balanced lattice square and as randomized blocks from 16 open-pollinated white spruce mother trees of local origin. Experiment No. 92—A.

	Source	D. F.	E. M. S.	M. S.	F	Heritablity Percent	
						Families	Single trees
Randomized blocks analysis	Families	15	$\sigma_e^2 + 5\sigma_f^2$	166	2.95**	80	6.3
	Error	60	σ_e^2	56			
Lattice square analysis	Families	15	$\sigma_e^2 + 5\sigma_f^2$	180	4.13***	86	9.8
	Error	30	σ_e^2	44			

** Significant at the 0.01 level of probability.
*** Significant at the 0.001 level of probability.

Table 6. — Analysis of variance and heritability estimates of height and multiple leaders of eight-year-old progenies (in a randomized blocks design) from 10 open-pollinated white spruce trees of local origin. Experiment No. 92—B.

	Source	D. F.	M. S.	F	Heritability Percent	
					Families	Single trees
Height	Families	9	250	4.50**	87	13.3
	Error	27	56			
Percent with more than one leader	Families	9	99	1.89	68	4.6
	Error	27	52			

** Significant at the 0.01 level of probability.

gains for our first example (Experiment No. 91-A). If all parents whose heights were above the mean of the population had been selected, there would have been a selection differential of 12 percent of the population mean. With a heritability of 9 percent (mean of regression and correlation heritabilities) the expected response is:

$$R = i \times \sigma_p \times h^2 \qquad \text{(Formula 11.3 — Falconer, 1960)}$$

where R = expected response to selection
i = selection intensity in standard deviations
σ_p = phenotypic standard deviation
h^2 = heritability

$R = .75 \times 32 \times .09 = 2.16$ units, or 2.23 percent of the population mean (as the population mean corresponds to 96.9 units). The expected response to selection for open-pollinated progenies is, therefore, $\frac{2.23}{2} = 1.11$ percent. This is identical to the actual response, which was 1 percent.

Response prediction based only on progeny-test data for the same experiment was:

$$R = i \times h \times \sigma_A \qquad \text{(Formula 11.4 — Falconer, 1960)}$$

where σ_A is the standard deviation of additive genetic effects, $2\sigma_f^2$.

$R = .75 \times .865 \times 8.18 = 5.31$ units, or 4.02 percent of the population mean, which was 132 units.

The expected height response could easily be increased by increasing the selection intensity. If 10 percent of the individuals were selected by each of the two methods, the expected response by the two methods would be respectively 5.33 percent and 9.65 percent of the population mean.

After several generations of selection the additive genetic variance, and therefore heritability, should, theoretically, be reduced. Experience in other crops, however, indicates only slight reductions. Moreover, with the rate of generation turnover in tree-breeding, the reduction in genetic variability is not a serious problem.

There are three approaches to the achievement of genetic advance in tree-breeding. The first applies where plus-tree selection is so efficient that selections do not have to be tested individually; the second, where plus-tree selection is so ineffective that testing could be of random trees; and the third, where plus-tree selection is effective but where testing is required to confirm the value of selected trees and to provide material for continuing improvement.

Our data for white spruce indicate that plus-tree selection is both effective and relatively cheap, compared with progeny tests. Nevertheless, the two methods complement each other, and we suggest that plus-tree selection followed by progeny-testing is more effective than either method by itself.

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Summary

We studied individual slender- and broad-crowned white spruce trees for their ability to produce fast-growing, single-leadered progeny by open pollination. Slender-crowned plus trees (which were 4 percent taller than the broad-crowned control trees) produced progeny 4 percent taller than the progeny of broad-crowned trees. Stands also differed in the height of their progeny; the best were 18 percent taller than the worst. Leader number varied significantly among progeny of different stands but not between progeny of parents from the same stands. Progeny branch length was random, with the result that there was no parent-progeny correlation in this trait.

Heritabilities of height and leader number were calculated by parent-progeny regression and by variance component analysis. Parent-progeny regression resulted in a heritability of 9 percent for height, indicating that plus-tree selection could be effective. Variance component analysis resulted in single tree heritability of 11 ± 3 percent for height and 9 ± 4 percent for leader number. On a family basis, these heritabilities were as high as 91 and 85 percent. A lattice square analysis increased heritability relative to a randomized block analysis.

The positive correlation of parent height with progeny height indicated that only plus trees should be progeny-tested in a programme for the improvement of growth rate in white spruce.

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