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Heritability of juvenile characters of white spruce (*Picea glauca* (Moench.) Voss.) in central Newfoundland, Canada

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Summary. The paper presents results of a growth chamber progeny test of selected phenotypically superior trees from two white spruce (*Picea glauca* (Moench.) Voss.) populations in central Newfoundland, Canada. On the basis of heritability of 11 juvenile characters the superior trees have been demonstrated to be suitable as a base population for continued advanced generation breeding. Family selection would produce good genetic gains in the first generation but these can be enhanced considerably by selection of best individuals within the best families for clonal propagation in the second generation or propagation by seed in the second and subsequent generations.

Key words: White spruce – *Picea glauca* – Heritability – Genetic gains

Introduction

A study has been in progress at the Newfoundland Forest Research Centre since 1971 on twice white (*Picea glauca* (Moench.) Voss.) populations in the Exploits Valley in central Newfoundland, Canada, some results of which have already been published (Khalil 1974, 1975, 1978, 1981). The presence of large intra-family variation in nursery experiments has shown that the phenotypic superiority of "plus" trees could be attributed to the possibility of their greater heterozygosity than that of the "ordinary" trees, indicating greater out-breeding of the former than the latter.

Though most cone characters were found to be under strong genotypic control only seed weight was significantly correlated with fast growth and could be used for identification of "plus" trees. As the annual height growth was found to be positively correlated with seed weight up to four year age and was not a mere carryover of the initial superiority, resulting from the possible favourable effect of the endosperm, seed weight was recommended for inclusion among the criteria for selection of "plus" trees. This recommendation is further justified by the retention of fast juvenile growth up to at least 18 years of age (Nienstaedt 1981).

Though heritability of "plus" trees is lower than that of "ordinary" trees at both locations, selections from "plus" trees have been demonstrated to result in higher expected genetic gains than those from "ordinary" trees for various selection differentials due to initial superiority of "plus" over "ordinary" trees (Khalil 1981).

Subsequent research has been focused on ascertaining the existence of enough genetic variability among "plus" trees to serve as the base population for continued advanced generation breeding. Progency tests of these trees were conducted in a growth chamber with maximum environmental homogeneity to minimize the influence of environmental factors on heritability. The results of this study are presented in the present paper.

Materials and methods

The experiment

Wind-pollinated seeds were collected in September 1975 from the five "plus" trees in each population (Frenchman's Pond and Lake Douglas) which were used in the previous studies. A growth chamber experiment was established on April 30, 1976 in the randomized complete block design with five replications and 25-seed square experimental units (family plots). Spacing of seeds was 6 × 6 cm. The planting medium was 1 : 1 peat : perlite mixture by volume, with dolomite limestone added at 10 g kg^{-1} of dry peat. The experiment was maintained in an 18-h photoperiod at 21 °C and 70% relative humidity. The seedlings were fertilized weekly with a 10-52-10

N-P-K fertilizer for two weeks and a 20-20-20 fertilizer for the remaining period, using one tablespoon fertilizer with five litre water each time. They were watered twice weekly. Some seed of each tree was sown separately the same day and placed in the some growth chamber under the environmental conditions of the experiment. Ungerminated seeds in the experiment were replaced with these seedlings after completion of germination and counting of the germinated seed so as to avoid bias resulting from unequal spacing in experimental units.

The data

The following characters were measured in each experimental unit:

1. Number of seeds germinated by June 1, 1976 by which time germination was complete.
2. Cotyledon numbers
3. Hypocotyl length (cm)

On July 30, 1976 three months after sowing; sample size 10 seedlings

4. Seedling length (cm)
5. Shoot length (cm)
6. Root length (cm)
7. Seedling oven-dry weight (g)
8. Shoot oven-dry weight (g)
9. Root oven-dry weight (g)
10. Shoot/root ratio (length)
11. Shoot/root ratio (oven-dry weight)

On May 31, 1977, 13 months after sowing; sample size eight seedlings

Statistical and genetical analyses

Germinative capacity was calculated for each experimental unit. Mean values by families were calculated for each character. Analyses of variance with sampling were conducted for all characters, using the mixed mathematical model (Equation 1).

$$Y_{ijkm} = \mu + \beta_i + \gamma_j + \tau_{jk} + \varepsilon_{ijk} + \delta_{ijkm}\,, \tag{1}$$

where Y_{ijkm} = Measurement of a variable on seeding m of tree k, in population j in replication i

μ = Overall mean

β_i = Replication effect, random (i = 1, ..., 5)

γ_j = Population effect, fixed (j = 1, 2)

τ_{jk} = Effect of tree k in population j, random (k = 1, ..., 5)

ε_{ijk} = Experimental error component, random

δ_{ijkm} = Sampling error component, random (m = 1, ..., n = sample size).

The analysis of variance for germinative capacity was performed without arcsin $(Y)^{1/2}$ transformation because most observations were between 30 and 70% (Steele and Torrie 1980, p 236). The Expected degrees of freedom and Mean Squares are shown in Table 1. As $\sigma^2_{\tau_1} \neq \sigma^2_{\tau_2}$ in all the analyses the expected Mean Squares for Populations and Trees within Populations had an additional component, $rn/2\,(\sigma^2_{\tau_1} + \sigma^2_{\tau_2})$ (Douglas 1983). Hence, to test the significance of the Mean Squares for Populations [M.S. (P) + M.S. (E.E.)] had to be divided by [M.S. (T/P_1) + M.S. (T/P_2)] (Steel and Torrie 1980, p 357).

Table 1. Expected mean squares and degrees of freedom

Source of variation	Germination percent			Other characters		
	Expected mean squares	Degrees of freedom		Expected mean squares	Degrees of freedom	
		Expected	Actual		Expected	Actual
Replications	$\sigma^2_\varepsilon + p\,t\,\sigma^2_r$	r − 1	4	$\sigma^2 + n\,\sigma^2_\varepsilon + r\,p\,n \sum_{i=1}^{5} R_i/(r-1)$	r − 1	4
Populations	$\sigma^2_\varepsilon + \frac{t}{2}(\sigma^2_{\tau_1} + \sigma^2_{\tau_2}) + t\,r \sum_{j=1}^{2} \gamma^2_j$	p − 1	1	$\sigma^2 + n\,\sigma^2_\varepsilon + \frac{rn}{2}(\sigma^2_{\tau_1} + \sigma^2_{\tau_2}) + r\,t\,n \sum_{j=1}^{2} \gamma^2_j$	p − 1	1
Trees/Populations	$\sigma^2_\varepsilon + \frac{t}{2}(\sigma^2_{\tau_1} + \sigma^2_{\tau_2})$	(t − 1) p	8	$\sigma^2 + n\,\sigma^2_\varepsilon + \frac{rn}{2}(\sigma^2_{\tau_1} + \sigma^2_{\tau_2})$	(t − 1) p	8
Trees/Population 1	$\sigma^2_\varepsilon + r\,\sigma^2_{\tau_1}$	$(t_1 - 1)$	4	$\sigma^2 + n\,\sigma^2_\varepsilon + r\,n\,\sigma^2_{\tau_1}$	$(t_1 - 1)$	4
Trees/Population 2	$\sigma^2_\varepsilon + r\,\sigma^2_{\tau_2}$	$(t_2 - 1)$	4	$\sigma^2 + n\,\sigma^2_\varepsilon + r\,n\,\sigma^2_{\tau_2}$	$(t_2 - 1)$	4
Experimental error	σ^2_ε	(t−1)(r−1)	36	$\sigma^2 + n\,\sigma^2_\varepsilon$	(t−1)(r−1)	36
Sampling error		–	–	σ^2	prt(n−1)	450 (350)
Total		prt−1	49		prtn−1	499 (399)

Figures in parentheses in the last column refer to characters 3 – 11

r, p, t, t_1, t_2 and n are replications, populations, trees within populations, trees within population 1, trees within population 2 and sample size respectively

Narrow sense family and single tree heritabilities were calculated for each character using the variance components method. Due to the nonsignificance of populations as a source of variation in all characters, the ten families were combined for heritability calculations. Due to the difference in the method of analysis of variance used for germinative capacity and other characters, the heritabilities for germinative capacity were calculated according to Wright's Equations 61 and 62 (Wright 1962) and those for other characters were calculated according to Equations (2) and (3). The latter equations are modifications of Wright's equations (Wright 1976, pp 242–243) resulting from one-site nature of the experiment and use of wind-pollinated progenies.

Wind pollinated families are often treated as half-sib families for the sake of simplicity. This may not be strictly true as a wind-pollinated family may contain a mixture of selfs, crosses with related male trees and crosses with unrelated male trees, i.e. selfs, true half-sib and full-sib families. The heritability estimates of wind-pollinated families would be biased downwards or upwards depending upon the proportion of self and full-sib families, respectively. Though it is not possible to estimate the nature and magnitude of this bias the net bias is expected to be usually small due to the simultaneous presence of the above three classes of progenies. However, this bias can be minimized by using an appropriate coefficient instead of 4.0 in Wright's equations (Wright 1976, pp 242–243). For white spruce Coles and Fowler (1976) have shown that germination percent and cotyledon numbers are significantly influenced by the female parent only and the influence of the male parent is nonsignificant. The effect of the female parent on epicotyl length is much higher than that of the male parent. Hence, in this experiment the progenies would have a greater resemblance to full-sib families than to half-sib families and the coefficient of 3.0 used in Equation (3) would be most appropriate.

Standard errors of all heritability estimates were calculated according to Equations (4)–(6) after Wright (1976, pp 244–245), modified on account of one-site nature of the experiment and use of the coefficient 3.0 instead of 4.0 for reasons mentioned above.

Narrow sense family heritability

$$(h^2_{fa}) = \frac{\sigma^2_f}{\sigma_e/NR + \sigma^2_{fr}/R + \sigma^2_f} . \qquad (2)$$

Narrow sense single tree heritability

$$(h^2) = \frac{3\sigma^2_f}{\sigma^2_e + \sigma^2_{fr} + \sigma^2_f} . \qquad (3)$$

Table 2. Heritabilities of characters

Character	Family heritability		Single tree heritability	
	Herit-ability	SE ±	Herit-ability	SE ±
Germination percent	0.9075	0.8598	0.5836	0.0069
Cotyledon numbers	0.3892	0.1347	0.0639	0.0027
Hypocotyl length	0.8429	0.5520	0.5478	0.0109
Seedling length	0.6838	0.4037	0.3924	0.0100
Shoot length	0.6667	0.5011	0.3887	0.0099
Root length	0.8000	0.6495	0.8276	0.0161
Seedling oven-dry weight	0.4524	0.1958	0.1310	0.0049
Shoot oven-dry weight	0.7168	0.3641	0.3378	0.0090
Root oven-dry weight	Negative value		–	–
Shoot/root (length)	0.6942	0.4251	0.4229	0.0105
Shoot/root (oven-dry weight)	0.7560	0.3751	0.3527	0.0093

Table 3. Mean values of characters by families

Character	Family mean									
	Family 1	Family 2	Family 3	Family 4	Family 5	Family 6	Family 7	Family 8	Family 9	Family 10
1. Germination percent	67.2	72.0	75.2	76.0	65.6	70.4	76.8	67.2	32.8	57.2
2. Cotyledon numbers	6.44	6.40	6.36	6.40	6.44	6.20	6.18	6.72	6.24	6.32
3. Hyocotyl length (cm)	2.34	2.22	2.32	2.29	2.43	2.18	2.20	2.72	2.25	2.09
4. Seedling length (cm)	21.46	20.71	18.98	19.53	22.75	21.92	20.01	19.68	21.30	21.47
5. Shoot length (cm)	13.64	12.55	10.91	11.26	14.18	13.26	11.88	11.81	13.01	12.65
6. Root length (cm)	7.83	8.14	8.08	8.26	8.68	8.14	8.04	7.87	8.31	8.82
7. Seedling O.D.W.[a] (g)	2.98	2.77	2.16	2.41	2.90	2.43	2.18	3.31	2.41	2.46
8. Shoot O.D.W.[a] (g)	1.86	1.79	1.21	1.33	1.75	1.33	1.36	1.41	1.41	1.43
9. Root O.D.W.[a] (g)	1.12	0.97	0.95	1.08	1.15	1.09	0.84	0.90	1.00	1.00
10. Shoot/root ratio (length)	1.77	1.56	1.35	1.38	1.64	1.63	1.49	1.51	1.58	1.45
11. Shoot/root ratio (O.D.W.[a])	1.79	1.97	1.42	1.37	1.57	1.35	1.83	1.63	1.61	1.55

[a] O.D.W. = Oven-dry weight

Table 4. Summary of analyses of variance

Source of variation	Germination %		Cotyledon nos.		Hypocotyl length		Seedling length	
	Var. %	F	Var. %	F	Var. %	F	Var. %	F
Replications	3.07	0.75 ^{NS}	1.57	1.16 ^{NS}	0.75	0.49 ^{NS}	11.98	4.99***
Populations	11.90	1.08 ^{NS}	0.25	0.66 ^{NS}	0.09	0.17 ^{NS}	0.07	0.27 ^{NS}
Trees/Populations	48.27	5.91***	3.59	1.32 ^{NS}	11.42	3.69***	10.01	2.08 ^{NS}
Trees/Population 1	3.12	0.76 ^{NS}	0.08	0.06 ^{NS}	1.01	0.65 ^{NS}	7.06	2.94*
Trees/Population 2	45.15	11.05***	3.51	2.58 ^{NS}	10.41	6.73***	2.95	1.25 ^{NS}
Experimental error	36.76		12.24	1.86***	13.93	2.36***	21.63	3.73***
Sampling error			82.35		73.81		56.31	
Total	100.00		100.00		100.00		100.00	

*** Statistically significant (0.005 level); * Statistically significant (0.05 level); ^{NS} Statistically nonsignificant (0.05 level)

Standard error of family heritability

$$s_{h^2_{fn}} = \frac{(1-h^2/3)\,(1+NR\,h^2/3)}{[NR\,(F-1)/2]^{1/2}}. \qquad (4)$$

Standard deviation of single tree heritability:

$$\sigma_{h^2} = \frac{(1-h^2/3)\,[1+(NR-1)\,h^2/3]}{[(NR/2)\,(NR-1)\,(F-1)]^{1/2}}. \qquad (5)$$

Standard error of mean single tree heritability of NR trees

$$= s_{h^2} = \frac{\sigma_{h^2}}{(NR)^{1/2}}, \qquad (6)$$

where σ_f^2 = Variance component for mother trees (Table 1)

$$= \frac{\text{M.S. Trees} - \text{M.S. Experimental Error}}{NR}$$

σ_{fr}^2 = Variance component for mother trees within replications

$$= \frac{\text{M.S. (Mother trees} \times \text{Replications)} - \text{M.S. Sampling error}}{N}$$

σ_e^2 = Sampling error
N = Sample size
R = Number of replications
F = Number of mother trees.

Results and discussion

The results are presented in Tables 2–4. The heritability estimates have been obtained with minimum bias as explained earlier. The negative value of the heritability of root oven-dry weight is interesting. This negative value has arisen from the negative value of the variance component due to female trees (σ_f^2), which is the variance component of level 2 of a 3-level hierarchial analysis of variance. Leone and Nelson (1966) and Searle (1971) state that such negative variance components, which are estimated indirectly, are not only experimentally possible but quite likely. Searle (1971) states that the appearance of a negative estimate from the analysis of variance method does not depend upon any implied distributional assumptions. Of the six alternative methods of dealing with negative estimates of variance components dealt with by Searle (1971) it is best to regard it as evidence that the true value of the component is zero. As this component is the sole member of the numerator in the equations for both family and single tree heritabilities it is not possible to use it as zero or with a negative value. Another explanation is also possible. Many positive values near zero will provide negative estimates more than half the time in repeated experiments and the average of such values will be zero. This particular sampling may be one of the negative values. Hence, the only valid conclusion can be that the family and single tree heritabilities of root oven-dry weight are so low as to approach zero.

Both family and single tree heritabilities are high ($\geqq 0.4$) for most characters (Table 2) indicating the suitability of "plus" trees as base population for breeding. Since the between family differences are small for most characters (Table 3) statistical significance is achieved for Trees within Populations in only five of 11 characters (Table 4). Trees within Populations, i.e. between wind-pollinated families, are significant for more characters in the Frenchman's Pond area than in the Lake Douglas area. This indicates the need for family selection within both populations, particularly for important growth characters like seedling length, shoot length and root length. High values for family heritabilities of all characters support the above inference. Nonsignificance of Replications as sources of variation and the high proportion of variation due to Sampling Error indicate high intra-family genetic variation, which is also indicated by high single tree heritabilities for all important characters.

Conclusions

Heritability estimates have been made with insignificant bias on the basis of which "plus" trees appear

Table 4 (continued)

Shoot length		Root length		Seedling O.D.W.[a]		Shoot O.D.W.[a]		Root O.D.W.[a]		Shoot/root (length)		Shoot/root (O.D.W.)[a]	
Var. %	F	Var. %	F	Var. %	F	Var. %	F	Var. %	F	Var. %	F	Var. %	F
19.86	8.43***	24.35	10.72***	4.08	1.94$^{\mathrm{NS}}$	5.87	3.25*	2.41	1.08$^{\mathrm{NS}}$	30.45	15.47***	7.88	5.12***
0.00	0.00$^{\mathrm{NS}}$	0.06	0.17$^{\mathrm{NS}}$	2.34	1.93$^{\mathrm{NS}}$	2.32	1.35$^{\mathrm{NS}}$	1.08	1.69$^{\mathrm{NS}}$	0.01	0.24$^{\mathrm{NS}}$	0.05	0.22$^{\mathrm{NS}}$
9.41	2.00$^{\mathrm{NS}}$	14.90	3.28**	5.93	1.41$^{\mathrm{NS}}$	8.18	2.27*	3.87	0.86$^{\mathrm{NS}}$	8.40	2.13$^{\mathrm{NS}}$	7.85	2.55*
7.77	3.30*	6.32	2.78*	5.34	2.54$^{\mathrm{NS}}$	8.02	4.45***	1.76	0.78$^{\mathrm{NS}}$	7.17	3.64*	5.37	3.49*
1.64	0.70$^{\mathrm{NS}}$	8.58	3.78*	0.59	0.28$^{\mathrm{NS}}$	0.16	0.09$^{\mathrm{NS}}$	2.11	0.94$^{\mathrm{NS}}$	1.23	0.63$^{\mathrm{NS}}$	2.48	1.61$^{\mathrm{NS}}$
21.21	2.40***	20.44	4.94***	18.89	2.67***	16.24	2.34***	20.16	2.70***	17.72	3.97***	13.85	1.91***
49.52		40.25		68.76		67.39		72.48		43.42		70.37	
100.00		100.00		100.00		100.00		100.00		100.00		100.00	

[a] O.D.W. = Oven-dry weight

suitable as the base population for breeding. Good genetic gains can be expected from family selection and these can be enhanced by selection of best individuals within the progenies of best families.

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