STAND, FAMILY, AND SITE EFFECTS IN UPPER OTTAWA VALLEY WHITE SPRUCE[1]

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ABSTRACT.--Forty-nine open-pollinated white spruce progenies from eight Upper Ottawa Valley white spruce stands were tested at three sites located within 10 miles of each other. Statistical analyses were limited to 42 families--6 from each of 7 of the stands. Performance was site dependent with nearly a two-fold difference between the best and the poorest. Differences due to stands were not important. The best family was 28 percent taller than the family mean height, but performance was not consistent from site to site in spite of a nonsignificant family-site interaction term. This probably was due to limitations imposed by the statistical design. Heritability estimates for heights were h (individual tree heritability) = 0.10; h_2^2 (family heritability = 0.39. Genetic gain in 10 year height through one cycle of simple mass selection was estimated to be 8.6 percent; establishing a clonal orchard with the best trees (4 percent selection intensity) from the best families (10 percent selection intensity) in the test boosts the estimated gain to 11 percent. The genetic parameters determined in this study are compared with previously published data.

White spruce (Picea glauca (Moench) Voss) provenances, have been shown to differ widely in growth and survival in field tests covering a broad spectrum of test sites in Canada and the United States (Nienstaedt 1969, Teich 1973). Among the provenances tested, the Beachburg source from the Upper Ottawa Valley performed consistently well in all field tests and showed the best height growth in most tests. These findings generated interest in the Upper Ottawa Valley white spruce populations and more intensive studies of these populations were initiated by the Petawawa Forest Experiment Station (P.F.E.S.).

The objective of the study reported here was to evaluate the significance of variation among and within white spruce stands of the

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Upper Ottawa Valley. Ten-year height growth and survival (6 years after planting) were studied at three test sites. Heritability of height growth was determined and expected genetic improvement in this trait through selection and breeding examined.

MATERIAL AND METHODS

Open-pollinated seeds were collected from 4 to seven trees in eight stands. A total of 49 seedlots (open-pollinated families) was obtained.

Seedlings of the 49 families were raised in the P.F.E.S. nursery and outplanted as 2-2 stock in spring 1969 at 3 sites identified as D-1, D-2, and D-3. The test sites were located within a distance of 10 miles of each other in Head Township, Renfrew County, but varied markedly in their productivity and previous vegetation (fig. 1). Site D-1 was a cutover hardwood stand where young unmerchantable trees remained in the overstory after planting. Its soil was stony with a well developed humus layer. Sites D-2 and D-3 were abandoned farms with a heavy sod overlying a loamy sand.

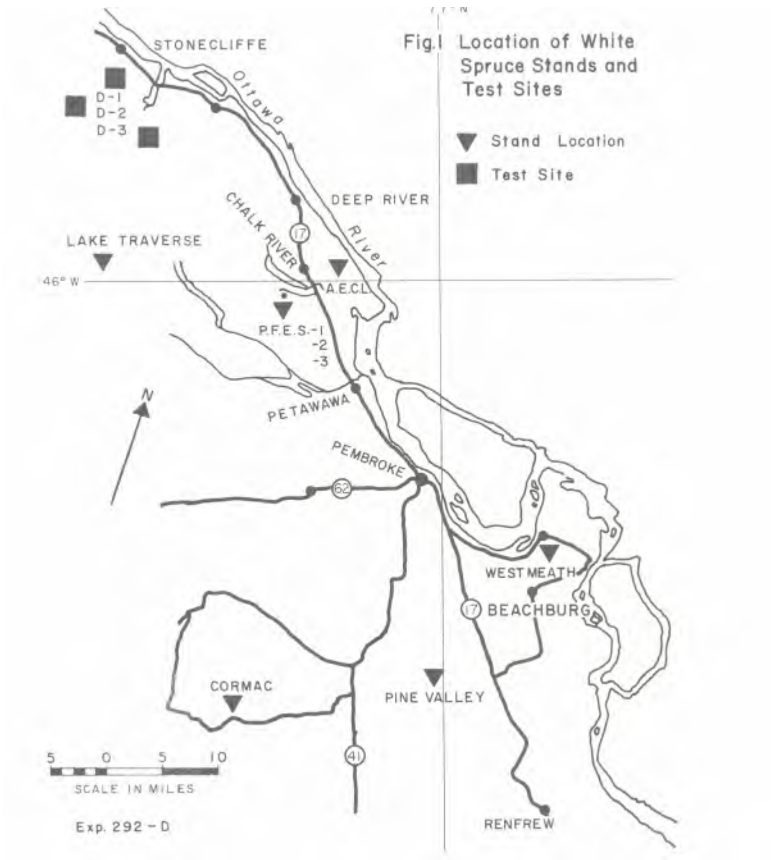

Figure 1.--Location of white spruce stands and test sites.

Planting was done at 1.2 by 1.2 in spacing. Scalping removed competing vegetation within about 20 cm of the planted trees. The experimental design consisted of two replications at each site. Twenty-five tree plots were used at sites D-2 and D-3, but at Site D-1, where lesser survival was anticipated because of stony soil, 40 tree plots were used.

The plantations were generally healthy and showed no serious damage by any pest. The plantation on site D-3, however, had suffered moderate frost damage in early years but appeared to have recovered. Ground competition was considered to be an integral part of the test environment and no attempt was made to control this after the field trials were successfully established.

STATISTICAL ANALYSIS

The data were summarized by standard statistical methods. Standard errors of site and stand means were calculated from the error mean sum of squares of the appropriate analysis of variance (Steel and Torrie 1960).

Analysis of variance for data combined from all the sites was done by using a balanced set of 42 families (6 families each from 7 stands). The analysis of variance format and expectation of the mean sums of squares, assuming a completely random model, are given in table 1. The variance components and their standard errors were determined using procedures described by Hanson (1955). All tests of statistical significance were made at the 5 percent probability level.

Table 1.--Analysis of variance format and expectation of the mean sums of squares

Source of variation	d.f.	E(M.S.S.)[1]
Sites	$\ell-1$	$\frac{\sigma_w^2}{k} + \sigma_e^2 + sf\sigma_{R/L}^2 + rsf\sigma_L^2$
Reps/sites	$\ell(f-1)$	$\frac{\sigma_w^2}{k} + \sigma_e^2 + sf\sigma_{R/L}^2$
Stands	$s-1$	$\frac{\sigma_w^2}{k} + \sigma_e^2 + \ell r\sigma_{F/S}^2 + \ell rf\sigma_S^2$
Families/stands	$s(f-1)$	$\frac{\sigma_w^2}{k} + \sigma_e^2 + \ell r\sigma_{F/S}^2$
Pooled error[2]	$(\ell rsf-sf-\ell r+1)$	$\frac{\sigma_w^2}{k} + \sigma_e^2$
Within plots	$\sum_{i=1}^{\ell rsf}(n_i-1)$	σ_w^2

[1] ℓ = No. of sites, r = No. of reps. in each site, s = No. of stands, f = No. of families per stand, n = No. of plants per plot, k = harmonic mean of number of plants per plot.

[2] Contains sources of variation due to families x sites and families x reps/sites.

RESULTS

The performance of white spruce families was greatly influenced by test sites (table 2). Mean height on the best site (D-1) was nearly twice as much as on the poorest site (D-3). Site D-1 was characterized by a more favorable moisture regime, lack of severe grass competition, and protection from severe frosts. Poor survival on site D-1 was attributed to difficulty in planting among the stones and stumps on this site.

Table 2.--Mean height and survival of the families at three sites

Site	Height (cm) mean ± s.e.	Survival (percent) mean ± s.e.
D-1	151.1 ± 2.2	79.5 ± 1.2
D-2	120.3 ± 1.6	91.8 ± 0.9
D-3	77.3 ± 1.3	93.7 ± 1.0
All sites	116.2 ± 1.0	88.3 ± 0.6

Mean height of the stands ranged from 110.1 cm to 123.6 cm and mean survival from 82.9 percent to 91.2 percent (table 3). Westmeath showed the best performance among the eight stands studied. Its height growth and survival were respectively 6 percent and 3 percent better than the average (table 4). However, its superiority was not consistent on all sites, e.g., on site D-2 Lake Traverse showed the best height and P.F.E.S. -2 showed the best survival.

Table 3.--Mean performance of white spruce stand collections

Stand origin	Families	Height (mean ± s.e.)	Survival (mean ± s.e.)
	No.	cm	Percent
Westmeath	7	123.6 ± 2.7	91.2 ± 1.6
P.F.E.S. -3	6	118.9 ± 2.9	90.3 ± 1.7
Lake Traverse	4	117.1 ± 3.5	87.1 ± 2.1
Pine Valley	7	115.9 ± 2.7	89.6 ± 1.6
A.E.C.L. Reserve	7	115.4 ± 2.7	88.3 ± 1.6
P.F.E.S. -2	6	113.7 ± 2.9	88.5 ± 1.7
Cormac	6	113.4 ± 2.9	82.9 ± 1.7
P.F.E.S. -1	6	110.1 ± 2.9	87.4 ± 1.7

Table 4.--Performance of the best stand and family at each site as percent of the site mean

	Height			Survival			D-1,D-2,D-3 combined	
	D-1	D-2	D-3	D-1	D-2	D-3	Height	Survival
Stand	106	110	112	105	106	105	106	103
Family	128	138	132	118	109	107	128	108

Individual families varied more in height than they did in survival (table 4). Considering all sites, the tallest family was found to be 29 percent taller than the average. Mean height and survival of the families showed significant correlation for site D-2 (r = 0.54) and D-3 (r = 0.46) but not for site D-1 (r = 0.19).

Performance of individual families was generally inconsistent from site to site and the family ranks fluctuated considerably. This is illustrated by simple correlation coefficients of family means on different sites (table 5); correlations based on family ranks were very similar. Out of the 49 families studied, only 7 showed above average height growth on all test sites.

Table 5.--Simple correlation coefficients of family height and survival means among test sites

		D-2	D-3
D-1	Height	0.11	0.01
	Survival	0.02	0.16
D-2	Height	--	0.31*
	Survival	--	0.29*

* Significant at $p < 0.05$

The error mean squares of the analyses of variance were derived by pooling families x sites and families x replications in sites sums of squares because families-sites interactions were negligible for both height and survival (respective F-ratios 0.95 and 0.90) (table 6). Sites, replications in sites, and families in stands were significant sources contributing to the variability of height growth but percent survival was significantly influenced by sites and reps in sites only (table 6) .

Table 6.--Mean squares in the analyses of variance and corresponding variance components and their standard errors

Source of variation	d.f.	M.S.S.		Variance components		
		Height	Survival	Component estimated	Height	Survival
Sites	2	113,354 1/	5,713 1/	σ^2_L	1281.5±1350.6	60.1±68.3
Reps/sites	3	5,711 1/	668 1/	$\sigma^2_{R/L}$	128.8± 111.0	13.4±13.0
Stands	6	686	273	σ^2_S	5.8± 11.5	4.1± 4.5
Families/stands	35	479 1/	125	$\sigma^2_{F/S}$	35.6± 19.7	4.0± 5.2
Pooled error	205	295	101	σ^2_e 2/	250.3± 29.2	100.7± 8.3
Within plots (k=25.08)	7,609	1,128	--	σ^2_W	1,128.3 18.3	--

1/ Significant at $p<0.05$

2/ For survival, variance component estimated is $\frac{\sigma^2_W}{k} + \sigma^2_e$.

Estimates of narrow sense heritability of tree height for individual plants (h^2_1) and family means (h^2_2) reference units were constructed from the variance components listed in table 6 (Comstock and Robinson 1948, Dudley and Moll 1969). It was assumed that the members of individual families were true half-sibs.

h^2_1 (individual tree heritability)

$$= \frac{\sigma_A^2}{\sigma_p^2} = \frac{142.4}{1,420.0} = 0.10$$

h^2_2 (family heritability)[3]

$$= \frac{\sigma_{A'}^2}{\sigma^2_{\bar{p}}} = \frac{35.6}{90.6} = 0.39$$

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[3] The correct numerator for computing family heritability can be either $\sigma_{A'}^2$, as used in the case illustrated above, or $2\,\sigma_{A'}^2$ depending upon the type of selection to be practiced (Dudley and Moll 1969).

Where[4]

$$\sigma_A^2 = 4\ \sigma_{F/S}^2$$ (additive genetic variance of individual trees)

$$\sigma_p^2 = \sigma_w^2 + \sigma_e^2 + \sigma_{F/S}^2 + \sigma_S^2$$ (phenotypic variance of individual trees)

$$\sigma_{A'}^2 = \sigma_{F/S}^2$$ (additive genetic variance of half-sib families)

$$\sigma_{\bar{p}}^2 = \frac{\sigma_w^2}{\ell rk} + \frac{\sigma_e^2}{\ell r} + \sigma_{F/S}^2 + \sigma_S^2$$ (phenotypic variance of half-sib families)

Heritability of survival percentage was not calculated because the effects of families in stands for this trait were not significant. Because stand origin effects were also nonsignificant, it can be assumed that variability in the surviving ability of the families was purely environmental in origin,

DISCUSSION

Genetic differences in 10-year height of local white spruce in the Upper Ottawa Valley were primarily due to mother trees as shown by the performance of their progenies. Differences attributable to stand origin were not important, which suggests a lack of genetic differentiation among local white spruce populations. Similar findings were reported by Yeatman (197S) for early height growth of the Ottawa Valley jack pine progenies. Substantial variation among open-pollinated progenies of white spruce was reported in earlier studies by Hoist and Teich (1969) and Jeffers (1969). These workers, however, sampled material from wider geographic areas and tested it at only one location.

Site had a dominating influence on performance of the families but family-site interactions were statistically nonsignificant. Absence of family-site interaction usually implies a good agreement in the ranking of families on different sites, but this was not true for the results of this study. This was largely due to inconsistency in the performance of families among replications on individual sites. It was, therefore, felt that the experimental design used in this study provided a poor control of site heterogeneity. Smaller plots and three or more replications per site would have increased the efficiency of the tests.

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[4] See tables 1 and 6 for definition of variance components and subscripts.

The single tree heritability value of 0.10 for 10-year height, reported here, is similar to a value of 0.145 obtained by Yeatman (1975) for 6-year height in the Ottawa Valley jack pine in a similar experimental design and reference environment. Heritability values for 8- and 11-year heights of Ontario white spruce ranged from 0.06 to 0.18 on an individual tree basis and from 0.75 to 0.91 on a family basis, in the studies reported by Holst and Teich (1969). However, the procedure used by these authors for computing heritability differs from the one used in the present study so the results are not comparable.[5]

Heritability values should always be interpreted with caution because such values are applicable only to the defined base population, reference selection unit, and reference test environment (Hanson 1963,Dudley and Moll 1969). Furthermore, heritability estimates obtained from genetic parameters estimated by open-pollinated progeny tests, assuming families to be true half-sibs, are expected to be biased and tend to be inflated (Namkoong 1966, Squillace 1974).

Genetic parameters estimated in this study can be used to derive the expected genetic gain through selection and breeding (Namkoong et al. 1966, Shelbourne 1969). Genetic gain in 10-year height of the Upper Ottawa Valley white spruce through one cycle of simple mass selection was estimated to be 8.6 percent. This is an appreciable gain and particularly noteworthy in view of the poor heritability of this trait reported by this study. Genetic gain resulting from the seed produced in a clonal seed orchard, established with scions collected from the tallest tree in each plot (4 percent selection intensity) of the top five families (10 percent selection intensity), was estimated to be 11 percent.

The heritability of early height found in this study is less than the value of this parameter suggested by white spruce progeny tests in the Lake States (Jeffers 1969, Mohn et al., these proceedings). As pointed out earlier, experimental plantations used by this study suffered several shortcomings and it is likely that field experiments emphasizing better design and more uniform treatment of experimental units will show higher heritability for this trait of local white spruce in the Upper Ottawa Valley.

SUMMARY AND CONCLUSIONS

1. Open-pollinated progenies of the Upper Ottawa Valley white spruce stands (provenances) were studied for early height growth and field survival at three test sites.

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[5] Method used by Holst and Teich (1969) in their heritability calculations does not take into account "within plot" variance. This method is appropriate for one-way classification experiments but not for multi-way classification experiments. Also for family heritability calculations they used $2\sigma_A^2$ in the numerator. The formulae used by Holst and Teich (1969), give the following values with my data: single tree heritability = 0.06; family heritability = 0.63.

2. The stands showed similar performance indicating lack of genetic differentiation among them for the traits studied. It appears that the superior white spruce sources of Beachburg and Douglas identified in earlier provenance tests are part of a larger population that extends beyond the original collection area of these sources. Further studies with more intensive sampling of stands and better field design are needed to delineate the boundaries of this population complex.

3. Site had a dominating influence on progeny performance, which was very inconsistent from site to site.

4. Substantial variation was found for height growth among families but their ability to survive in the field was primarily determined by the site factors.

5. Heritability of individual plant height was low (0.10) but appreciable genetic gain (8.6 percent) was expected to result from one cycle of simple mass selection at 1 percent selection intensity. Overall benefits resulting from white spruce breeding in the Upper Ottawa Valley, using multistage and multitrait selection procedures, can be expected to be larger than the 8.6 percent gain reported for simple mass selection.

ACKNOWLEDGMENT

The author is grateful to Mr. M. J. Holst for initiating this study and for many helpful discussions. The field experiments were established in cooperation with the Ontario Ministry of Natural Resources. Thanks are due Mr. P. Viidik for establishment and maintenance of the plantations, and Mr. T. Pickett for excellent technical assistance. The author is indebted to Dr. E. K. Morgenstern and Dr. C. W. Yeatman for advice and guidance. This research was supported by National Research Council Canada through a Postdoctoral Fellowship award to the author.

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