the first year take effect. YING and BAGLEY (1976) noted prevalence of a dense crown with small, short branches in northern and western provenances, but more of a spreading crown with long, large branches in eastern provenances.

In addition, height and diameter growth in *P. deltoides* are subject to large genotype × environment interactions (MOHN and RANDALL, 1973) so that ecotypic variation observed under experimental conditions may not readily extrapolate to the plantation environment. Knowledge of the existence of a population with the genetic potential for superior early height growth, however, should be of interest to tree breeders trying to produce improved phenotypes. Further exploratory work is necessary to delineate the boundaries of the observed population response and nature of selective pressures involved as well as factors influencing extrapolation of first year experimental results to older plantations.

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Literature Cited

CANNELL, M. G. R., and WILLETT, S. C.: Shoot growth phenology, dry matter distribution and root:shoot ratios of provenances of *Populus trichocarpa, Picea sitchensis*, and *Pinus contorta* growing in Scotland. Silvae Genetica 25 (2): 49—59 (1976). — DREW, A. P., and FERRELL, W. K.: Morphological acclimation to light intensity in Douglas-fir seedlings. Can. J. Bot. 55: 2033—2042 (1977). — DREW, A. P., and LEDIG, F. T.: Unpublished data (1975). — ELDRIDGE, K. G., ROUTE, A. R., and TURNBULL, J. W.: Provenance variation in the growth pattern of *Populus deltoides*. Austral. Forest Res. 5: 45—50 (1972). — FOWELLS, H. A.: Eastern cottonwood *(Populus deltoides* BARTR. var. *deltoides)*. In: Silvics of forest trees of the United States. U.S.D.A. Handbook 271 (1965). — FURUKAWA, A.: Photosynthesis and respiration in Poplar plant. Journal of the Japanese Forestry Society 54 (3): 80—84 (1972). — HUXLEY, J. S.: Constant differential growth-ratios and their significance. Nature 114: 895—896 (1924). — JOKELA, J. J.: Marssonina leaf spot and rust on eastern cottonwood. Plant Disease Reporter. 60 (12): 1020—1024 (1976). — JOKELA, J. J., and MOHN, C.: Geographic variation in eastern cottonwood. In: Proceedings of International Poplar Commission Cottonwood Symposium. Greenville, Mississippi. In press (1977). — KASKUREWICZ, A., and FOGG, P. J.: Growing seasons of cottonwood and sycamore as related to geographic and environmental factors. Ecology 48: 785—793 (1977). — LEDIG, F. T., and PERRY, T. O.: Physiological genetics of the shoot-root ratio. Pages 39—43. In: Proc. Soc. Amer. Foresters. Detroit, Michigan (1965). — LEDIG, F. T.: A growth model for tree seedlings based on the rate of photosynthesis and the distribution of photosynthate. Photosynthetica 4: 263—275 (1969). — LEDIG, F. T., BORMANN, F. T., and WENGER, K. P.: The distribution of dry matter growth between shoot and roots in loblolly pine. Bot. Gaz. 131: 349—359 (1970). — MARCET, E.: Über die geographische Variabilität blattmorphologischer Merkmale bei *Populus deltoides* BARTR. Silvae Genetica 10: 161—172 (1961). — MOHN, C. A., and RANDALL, W. K.: Interaction of cottonwood clones with site and planting year. Can. J. For. Res. 3: 329—332 (1973). — PAULEY, S. S., and PERRY, T. O.: Ecotypic variation of the photoperiodic response in *Populus*. Jour. Arnold Arboretum 35: 167—188 (1954). — PROMNITZ, L. C.: 1975. A photosynthate allocation model for tree growth. Photosynthetica 9: 1—15 (1975). — ROCKWOOD, D. L.: Variation within eastern cottonwood along the course of the Mississippi River. M. S. Thesis, Univ. of Illinois. 50 pp. (1968). — SEKAWIN, M.: More on the correlation between speed of water loss and rooting of Poplar cuttings. Cellulosa e Carta 25 (1): 3—11 (1974). — WILCOX, J. R., and FARMER, Jr., R. E.: Variation and inheritance of juvenile characters of eastern cottonwood. Silvae Genetica 16: 162—165 (1967). — YING, C. C.: Genetic variation in eastern cottonwood *(Populus deltoides* BARTR.) Neb. Agr. Exp. Sta. Prog. Rep. No. 1, 148 pp. (1974). — YING, C. C., and BAGLEY, W. T.: Genetic variation of eastern cottonwood in an eastern Nebraska provenance study. Silvae Genetica 25, 2: 67—73 (1976).

Early growth of some progenies from two phenotypically superior white spruce provenances in Central Newfoundland

II. Heritability and genetic gain

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Summary

The nursery phase of the study started in 1971 to verify the genetic superiority of phenotypically superior trees of white spruce *(Picea glauca* (MOENCH) VOSS) from two locations in central Newfoundland, Canada, was completed in 1975. Although statistically significant differences in four-year growth between the two locations were detected there were no such differences between the progenies of "plus" and "ordinary" trees at either location. The superiority of "plus" trees over "ordinary" trees may be due to more outbreeding in the former than in the latter class of trees. Heritability studies show the possibility of more genetic gain by selection from "plus" trees than that from "ordinary" trees. Establishment of a seed orchard of "plus" trees from each location is recommended.

Sommaire

L'étape de l'étude en pépinière amorcée en 1971 pour vérifier la supériorité génétique d'Épinettes blanches *(Picea glauca* [MOENCH] VOSS) phénotypiquement supérieures et provenant de deux endroits du centre de Terre-Neuve, Canada, fut complétée en 1975. Bien que des différences statistiquement significatives entre les deux endroits fussent décelées pour une période de croissance de 4 ans, il n'y a pas eu de telles différences entre les deux descendances d'arbres «plus» et «ordinaires» à l'un ou l'autre endroit. La supériorité des arbres «plus» sur les arbres «ordinaires» est peut-être due à un croisement libre plus intense chez le premier groupe que chez le second. Des études sur l'héritabilité démontrent la possibilité d'une meilleure amélioration génétique par la sélection d'arbres «plus» que par celle d'arbres «ordinaires». On recommande l'établissement d'un verger à graines d'arbres «plus» provenant des deux endroits.

Zusammenfassung

Die Untersuchung von Nachkommenschaften von phaenotypisch überlegenen Einzelbäumen (Plusbäumen) und zugleich nach forstwirtschaftlichen Maßstäben phaenotypisch geringer zu beurteilenden Bäumen aus zwei Herkünften von *Picea glauca* (MOENCH) VOSS im mittleren Neufundland (Kanada) erbrachte signifikante Unterschiede wohl zwischen den beiden Herkünften, jedoch nicht zwischen den Plusbaum-Nachkommenschaften und denjenigen der übrigen Bäume der jeweiligen Bestände. Auf Grund von Heritabilitätsstudien erscheinen aber dem Autor Züchtungsfortschritte eher möglich, wenn sog. Plusbäume ausgewählt und damit Samenplantagen begründet werden.

Key words: Genetic gain, genetic superiority, heritability, inbreeding, outbreeding, *Picea glauca* (MOENCH) VOSS, white spruce.

Introduction

Identification of superior provenances of white spruce (*Picea glauca* (MOENCH) VOSS) and verification of their genetic superiority are important components of the research on the genetic improvement of the species in Newfoundland. One such study was started at the Newfoundland Forest Research Centre in the fall of 1971 to verify the genetic superiority of selected phenotypically superior trees of white spruce located in two small and isolated stands in the Exploits River Valley in central Newfoundland. Preliminary results on the nursery phase of this study, comprising germination percent, survival and two-year height growth have been published (KHALIL 1975), which indicate that the mean phenotypic values of the progenies of the phenotypically superior trees were not significantly superior to those of the progenies of the phenotypically average trees. Phenotypic differences between the two provenances of trees partially appeared to be caused by genetic drift and micro-climatic differences influencing natural selection. The phenotypic differences between the individual mother trees appeared to result from differential inbreeding, partly due to the nature of the species and partly to the small size and isolated existence of the stands.

The nursery phase of the study was completed in the fall of 1975 and the results of the subsequent measurements in 1974 and 1975 are reported in this paper. The data were collected and analysed to verify or modify the previous results and to evaluate the stands for genetic superiority for establishing seed orchards.

Material and Methods

Two stands were selected for study in 1971 in the Frenchman's Pond and Lake Douglas areas respectively, which were about 80 km apart. Both stands are second growth, even-aged and of natural origin, resulting from the clearfelling of 1942—45. Trees were designated as "ordinary" (mean height = $\bar{X} \pm 1\sigma$)*), "plus" (mean height $> \bar{X} + 1\sigma$)*) and "minus" (mean height $< \bar{X} - 1\sigma$)*) trees on the basis of height. The stand structure of the Frenchman's Pond area, obtained from a sample tally in August 1976 is presented in *Table 1*.

Open-pollinated single tree seed was collected from five "plus" and five "ordinary" trees in each stand. The experiment was laid out in the five-replicated randomized complete block design in the Canadian Forestry Service Research Nursery at Pasadena in western Newfoundland (lat. 49° 00' N, long. 57° 35' W) in June 1972. Ten randomly selected, or all available half-sib seedlings (if less than 10) in each experimental unit were measured for heights in October 1974 and for heights and root-collar diameters in

*) $\bar{X}$ = Mean height of stand.
σ = Standard deviation.

Table 1. — Stand structure of the Frenchman's Pond area.

Class	% of trees	Height (m)		Diameter at 1.3 m (cm)	
		Mean	Range	Mean	Range
"Plus" ($\bar{X}$ + 1σ and over)	13	13.41	> 12.28	21.5	> 16.8
"Ordinary" ($\bar{X} \pm 1\sigma$)	72	10.54	8.42 - 12.28	16.3	9.7 - 25.8
"Minus" ($\bar{X}$ - 1σ and under)	15	7.13	< 8.42	9.7	< 6.7

Table 2. — Expected values of mean squares and the error term used in analysis of variance.

Source of variation	Degrees of freedom	Expected mean squares
Replications	r-1	$\sigma^2 + st\ \Sigma\ \beta_j^2\ /\ (r-1)$
Treatments	t-1	$\sigma^2 + sr\ \Sigma\ \tau_i^2\ /\ (t-1)$
Replications x treatment interaction	(r-1) (t-1)	$\sigma^2 + s\ {}_{i.}\Sigma_j (\tau\beta)^2_{ij}\ /\ (r-1)\ (t-1)$
Residual (within progenies differences)	rt (s-1)	σ^2

October 1975. The statistical and genetical analyses comprised (1) analysis of variance with multiple and unequal number of observations in each experimental unit (STEEL and TORRIE 1960), (2) SCHEFFE's S-tests for multiple comparisons between all trees and contrasts between provenances and between the "plus" and "ordinary" trees in each provenance, and (3) narrow sense single tree heritability of height in 1975, using WRIGHT's formulae 61 and 62 (WRIGHT 1962). Fixed model with interaction and sampling (STEEL and TORRIE 1960) was used for statistical analyses.. *Table 2* shows the expected values of mean squares of the various sources of variation and the error term used in the analysis of variance.

SCHEFFE's S-test, though less sensitive than the other commonly used range tests and the single degree of freedom comparisons, was used on account of unequal number of observations in each experimental unit, which made it advisable to be conservative.

Results and Discussion

Table 3 summarizes the results of analyses of variance. These results show that although mother trees are a statistically significant source of variation in all the three characters, the largest percentage of the variation is due to the residual effect, or the differences within the progenies of individual mother trees. These half-sib progenies are highly variable. It is not possible to rank mother trees on the basis of SCHEFFE's S-test. *Table 4* shows that the only statistically significant differences revealed by this test are those between Frenchman's Pond and Lake Douglas areas for heights and diameters at 1.30 m in 1975. The high proportion of variance due to within progenies differences and the low sensitivity of the SCHEFFE's S-test are at least partially responsible for failure to detect statistically significant differences between the progenies of the "plus" and "ordinary" trees at either location. However, such differences cannot be completely ruled out. Field tests currently in progress will provide further data.

COLES and FOWLER (1976) have shown that 35 percent of the pollinations in white spruce within a radius of 100 m produce putative relatives. Beyond 100 m the crosses produce a much lower percentage of relatives. As the stands are small and some trees are isolated the large within progenies differences could be attributed to the variable degree of inbreeding among the seedlings from each mother tree.

Table 3. — Summary of analyses of variance.

Source of variation	1974 D.F.	1974 Height Percent variance	1974 Height F	1975 D.F.	1975 Height Percent variance	1975 Height F	1975 Root-collar diameter Percent variance	1975 Root-collar diameter F
Replications	4	1.8	2.56*	4	3.8	6.99***	3.8	6.45***
Mother trees	16	12.2	4.77***	16	16.8	7.56***	12.5	5.30***
Replications x mother trees interaction	42	12.0	1.79***	42	14.2	2.43***	15.0	2.42***
Residual (within progenies differences)	470	74.0		466	65.2		68.7	
Total	537	100.0		533	100.0		100.0	

*Statistically significant (P > 0.95).

***Statistically significant (P ≥ 0.995).

Table 4. — Summary of SCHEFFE's S-test.

Variable	Contrast	Contrast estimate	Critical value (0.05 level)	Critical value (0.01 level)
Height in 1974	Frenchman's Pond vs Lake Douglas	1.2635 NS	1.5924	1.7575
	Frenchman's Pond - "Plus" vs "Ordinary" trees	0.7311 NS	1.5951	1.7605
	Lake Douglas - "Plus" vs "Ordinary" trees	0.4805 NS	2.8032	3.0940
Height in 1975	Frenchman's Pond vs Lake Douglas	4.3999**	3.4402	3.7907
	Frenchman's Pond - "Plus" vs "Ordinary" trees	1.3495 NS	3.3783	3.7286
	Lake Douglas - "Plus" vs "Ordinary" trees	0.0409 NS	6.0246	6.6494
Root-collar diameter in 1975	Frenchman's Pond vs Lake Douglas	0.1379**	0.1164	0.1285
	Frenchman's Pond - "Plus" vs "Ordinary" trees	0.0324 NS	0.1143	0.1262
	Lake Douglas - "Plus" vs "Ordinary" trees	0.0068 NS	0.2039	0.2250

NS Statistically non-significant (P < 0.95).

**Statistically significant (P > 0.99).

The results of this experiment and the findings of COLES and FOWLER (1976) support the earlier hypothesis that the genetic superiority of the "plus" trees over "ordinary" trees may be due to a greater degree of outbreeding in the former than in the latter class of trees (KHALIL 1975). Work to verify this hypothesis is in progress.

Notwithstanding the absence of conclusive evidence of the genetic superiority of "plus" over "ordinary" trees, heritability studies indicate the relative degree of potential genetic gains expected from family and mass selection in these classes of trees. Narrow sense family and single-tree heritability of "plus" and "ordinary" trees for four-year height are listed below:

Table 5 shows the expected genetic gains from family and mass selection of "plus" as well as "ordinary" trees with different selection differentials. Measurements of parent trees show that the "plus" trees in the Frenchman's Pond and Lake Douglas areas (mean heights 13.41 m and 12.80 m respectively) are 27. 2 and 25.5 percent superior to "ordinary" trees in the respective areas (mean heights 10.54 m and 10.21 m respectively). Thus, "plus" trees have already undergone one stage of severe phenotypic selection, reducing them to 13 percent of the stand, while the "ordinary" trees have not undergone such selection. For this reason there is a definite, though small, advantage of family as well as mass selection among the "plus" trees, compared with similar selection among the "ordinary" trees. In view of the high heritability it is also advantageous to select superior individuals, superior families or superior individuals in superior families in the nursery for use in seed orchards. Further gains can be obtained in the second generation by control pollination among superior individuals.

Table 5. — Expected genetic gains for total height with different selection differentials.

Selection differential %	Frenchman's Pond area "Plus" trees Family	Frenchman's Pond area "Plus" trees Mass	Frenchman's Pond area "Ordinary" trees Family	Frenchman's Pond area "Ordinary" trees Mass	Lake Douglas area "Plus" trees Family	Lake Douglas area "Plus" trees Mass	Lake Douglas area "Ordinary" trees Family	Lake Douglas area "Ordinary" trees Mass
5	2.45	1.62	4.14	3.54	1.25	0.49	2.21	1.73
10	4.90	3.24	8.29	7.08	2.49	0.98	4.42	3.46
20	9.79	6.48	16.57	14.15	4.98	1.97	8.84	6.91
30	14.69	9.73	24.86	21.23	7.47	2.95	13.26	10.37
40	19.58	12.97	33.15	28.31	9.96	3.94	17.68	13.82
50	24.48	16.21	41.44	35.38	12.46	4.92	22.10	17.28

(Expected genetic gains %; Selections: Family / Mass)

	Frenchman's Pond Area "Plus" trees	Frenchman's Pond Area "Ordinary" trees	Lake Douglas Area "Plus" trees	Lake Douglas Area "Ordinary" trees
Family heritability	0.490	0.829	0.249	0.442
Single-tree heritability	0.324	0.708	0.098	0.346

Conclusions

(1) The hypothesis of the genetic superiority of "plus" trees over "ordinary" trees being due to more outbreeding in the former than in the latter is further supported. (2) Family as well as mass selection out of the "plus" trees is more advantageous than similar selection out of the "ordinary" trees for specified selection differentials. (3) Establishment of seed orchards of "plus" trees and control pollination among phenotypically superior trees in the second generation is indicated as a possible step to increase genetic gain.

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References

COLES, J. F., and FOWLER, D. P.: Inbreeding in neighbouring trees in two white spruce populations. Silvae Genetica 25 (1): 29—34 (1976). — KHALIL, M. A. K.: Early growth of progenies from some phenotypically superior white spruce provenances in central Newfoundland. Silvae Genetica 24 (5-6): 160—163 (1975). — STEEL, R. G. D., and TORRIE, J. H.: Principles and procedures of statistics. McGraw-Hill Book Co. Inc., New York, 481 pp. (1960). — WRIGHT, J. W.: Genetics of forest tree improvement. FAO Forestry and Forest Products Studies No. 16, Food and Agriculture Organization of the United Nations. — ROME, S. P. A.: Arti Grafiche Panetto & Petrelli — Spoleto — Roma. 399 pp. (1962).

Estimating parent effects in full-sib progeny tests following use of an irregular mating design

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Summary

In an irregular mating design, a particular female might produce good progeny because it was mated with good males rather than because of her own genetic quality. To overcome that difficulty, direct comparisons are made among families sharing pairs of parents. The general combining ability of a parent then is the average difference between that parent and all parents in the test.

Key words: Unbalance incomplete design, family effect, intrablock information.

Zusammenfassung

In einem unvollständigen Kreuzungsplan bestehen Fehlermöglichkeiten bei der Schätzung der „Allgemeinen Kombinationseignung (AKE). Beispielsweise kann ein Mutterbaum von nur geringer genetischer Qualität eine gute Nachkommenschaft hervorbringen, wenn er mit einem guten Vaterbaum gekreuzt wird. Zur Problemlösung wird eine mathematische Auswertungsmethode dargestellt.

Introduction

Full-sib progeny tests can provide information on specific combining ability as well as general combining ability. Data on general combining ability are obtained by calculating the effects due to female parents and to male parents. Differences among family means due to the particular combination between male and female parents rather than to general male or female effects are considered to constitute specific combining ability.

Effects due to female or male parents are calculated easily for a diallel experiment in which every female is crossed with every other tree in all possible combinations. They are also easily calculated for experiments following NC State Design II, where each female is crossed with the same three or four males. In either case the effect due to a particular female (or male) parent is calculated by considering the average performance of the offspring of that female (or male) parent in all combinations because every female was crossed with the same set of males.

Either by design or by accident, it is not always true that each female is crossed with the same set of males. Usually each female is crossed with a different set of males, or a given set of males might be crossed with one set of females and another set of males crossed with another set of females. In that case, a particular female might produce good progeny because it was mated with good males rather than because of its own genetic quality. If so, it could be regarded as having high general combining ability even though it was really below average genetically.

The present method was devised to overcome that difficulty. Briefly, the method involves a series of comparisons among families sharing pairs of parents.

Table 1. — Height of control- pollinated offspring resulting from crossing male parents A through I with female parents R through Z.

Male Parent	Female Parent R	S	T	U	V	W	X	Y	Z
	-------height in arbitrary units----------								
A	4	--	16	20	25	--	--	--	--
B	--	15	19	--	31	35	--	--	--
C	--	--	26	--	34	--	45	--	--
D	--	--	--	35	41	46	49	54	--
E	--	--	--	--	44	50	56	60	65
F	--	--	--	--	--	54	61	66	69
G	34	41	--	--	--	--	64	70	76
H	41	--	49	--	--	--	--	75	--
I	46	49	--	60	--	--	--	--	85

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