Height Growth of Interprovenance Crosses in White Spruce, Picea glauca (Moench) Voss

By C. C. YING

Canadian Forestry Service
Petawawa Forest Experiment Station
Chalk River, Ontario, KOJ 1JO

(Received July / November 1978)

Abstract

Crosses were made in a 12-year-old white spruce provenance test plantation of trees from the Boreal and Great Lakes-St. Lawrence Forest Regions, by removing male flowers and allowing them to interpollinate with local Petawawa Forest Experiment Station sources. Progenies of 62 hybrid families of 20 provenances were compared with 3 local X local families and with progeny of open-pollinated origins. At age 10 years, survival of provenance hybrids and controls was 80 and 81% respectively.

The total heights of the provenance crosses were from 5% to 30% greater than the controls, but heights of the local X local crosses were equal to those of the controls. Two families were almost 50% taller than the controls; and 4 out of the 62 hybrid families were slightly smaller than the control. Genetic differentiation (gene frequency difference) among provenances and reduced inbreeding are postulated as reasons for the heterotic response. It is suggested that the control of inbreeding in white spruce breeding is important.

Key words: ***Picea glauca,*** Interprovenance cross, height growth.

Résumé

Des croisements on été opérés dans une plantation experimentale de provenances d'Épinette blanche de 12 années situee dans les Regions forestières Boreale et des Grands lacs et du Saint-Laurent, en retirant les fleurs mâles et en permettant une pollinisation croisée avec des provenances locales à la Forêt experimentale de Petawawa. Les descendances de 62 familles hybrides de 20 provenances ont été comparées avec des familles locale X locale et avec des descendances maternelles résultant de pollinisations libres. À l'âge de 10 ans, la survie était respectivement de 80 et 81% pour les hybrides ainsi obtenus et les temoins.

Les hauteurs totales des croisements de provenances étaient de 5% a 30% supérieures a celles des témoins, mais les hauteurs des hybrides local X local etaient egales a celles des temoins. Deux familles étaient presque 50% plus hautes que les temoins; et 4 des 62 familles hybrides étaient legerement plus petites que les temoins. La différenciation génétique (difference de fréquence des gênes) parmi les provenances et l'hybridation intraspecifique sont supposées justifier la réponse hétorotique observée. I1 est suggéré que le contrôle de l'autofécondation est important dans les croisements d'Épinette blanche.

Zusammenfassung

Ein 12jähriger Versuch mit *Picea glauca* Herkünften der Region des St. Lorenz und der Großen Seen gab Gelegenheit zur Herstellung von Provenienzhybriden in Chalk River, Ontario. Die männlichen Blüten wurden entfernt und die Bäume dann durch örtlichen Pollen von natürlichen Beständen in der Umgebung frei bestäubt. Samen von insgesamt 62 Hybridfamilien und 20 Herkünften wurden ausgesät und die Nachkommen in einem Feldversuch ausgepflanzt. Zum Vergleich dienten 3 Familien aus der in demselben Versuch entstandenen Kreuzung einer Herkunft aus Chalk River (örtliche X örtliche Kreuzung) sowie Nachkommen einer natürlichen Population aus der nahen Umgebung.

Im Alter von 10 Jahren überlebten 80% der Provenienzhybriden und 81% der Bäume der Vergleichspopulationen. Die meisten Provenienzhybriden waren um 5—30% höher als die Vergleichspopulationen, aber die örtlichen Kreuzungen und Nachkommen des natürlichen Bestandes waren gleich hoch. Zwei Familien der Hybriden waren fast 50% höher als die Vergleichspopulationen, und nur 4 der 62 Hybridfamilien waren etwas niedriger. Wahrscheinlich können Unterschiede in der Genhäufigkeit zwischen Provenienzen und Verminderung der Inzucht die Heterosis erklären. Es wird festgestellt. daß Inzuchtkontrolle bei dieser Baumart wichtig ist.

Introduction

The practical value of provenance hybridization in tree improvement has been a source of controversy. Some tree breeders stress the benefits of heterosis and combination of desirable characteristics of the parent populations through hybridization. Others are more cautious and argue that native populations have evolved through many generations of natural selection, and have developed a balanced system of well integrated gene complexes which provides for maximum fitness. They content that hybridization will destroy this balance and may reduce ability to withstand environmental stress.

Research with provenance hybridization in tree breeding is a recent event and published information deals mostly with juvenile growth. Response to inter-provenance hybridization seems to vary from species to species. For instance, red pine *(Pinus resinosa* AIT.) shows little difference hetween inter- and intra-provenance crosses (HOLST and FOWLER 1973). NILSSON (1973) reported that Norway spruce *(Picea abies* (L.) KARST) provenance crosses exhibited greater heterotic response than Scotch pine *(Pinus sylvestris* L.). Black spruce *(Picea mariana* (MILL.) B.S.P.) provenance hybrids were, on average, 48 percent taller than the controls when 10 months old, but declined to 15 percent taller at age 5 (MORGENSTERN 1973). Hybrids appear to be favored in some habitats (NILSSON 1973, WOESSNER 1972, REHFELDT 1977). In Douglas-fir *(Pseudotsuga menziesii* (MIRB.) FRANCO), crosses with provenances from the Pacific south and west coast had better growth than crosses with local or northern provenances (ORR-EWING 1966).

The purpose of this paper is to report the height growth of white spruce provenance crosses in a field test at Petawawa Forest Experiment Station (PFES) and to evaluate the role of provenance hybridization in practical tree improvement on the basis of this material.

Materials and Methods

A white spruce provenance study, intended for short-term intensive observation, was established at PFES nursery in 1956 with 2-0 seedlinns. Twenty-five provenances from the Boreal and Great Lakes-St. Lawrence Forest Regions were tested. The experiment was designed and installed as a 5 X 5 balanced lattice with 6 replications of 25-tree plots spaced 0.3 X 0.3 m. Height of the trees was last measured in 1960 at age 6.

Table 1. — The origin of the provenances used as ovulate parents and number of hybrid families in each inter-provenance cross included in the test.

Prov. of female parents (PFES code)	Origin[1]	No. of Seed trees[2]	Lat. N.	Long. W.	No. of hybrid families
1947	Maple Leaf, Ont.	10	45°15'	77°50'	2
1948	Algonquin Park, Ont.	15	45°33'	78°40'	1
1949	Carnarvon, Ont.	5	45°04'	78°42'	4
1950	Sand Lake, Ont.	8	45°38'	79°10'	5
1951	Sundridge, Ont.	6	45°45'	79°25'	4
1953	Dane, Ont.	8	48°03'	80°01'	2
1955	Maniwaki, Que.	15	46°25'	76°04'	1
1956	L'Annonciation, Que.	10	46°25'	75°03'	6
1958	Harrington Forest Farm, Que.	6	45°50'	74°40'	2
1959	St. Zenon, Que.	--	46°35'	73°50'	6
1961	St. Maurice R., Que.	10	46°50'	72°46'	11
1963	Dalhousie Twp., Ont.	7	45°00'	76°30'	2
1964	Hungerford Twp., Ont.	8	44°30'	77°20'	6
1965	Richmond Twp., Ont.	4	44°20'	77°00'	1
1967	Rama Twp., Ont.	10	44°41'	79°18'	1
1968	Essa Twp., Ont.	9	44°18'	79°50'	2
1970	Holland Twp., Ont.	7	44°25'	80°50'	3
1971	Trois Pistoles, Que.	--	48°08'	69°10'	1
1972	Kapuskasing, Ont.	--	49°25'	82°26'	1
1976	PFES, Ont.	20	46°00'	77°27'	3
1979	Erin, Ont.	--	43°45'	80°05'	1
Control (6091)	PFES, Ont.	20	46°00'	77°25'	

[1]) Ont. = Ontario; Que. = Quebec; R. = River; Twp. = Township.
[2]) Number of seed trees used at original provenance collection site.

In 1965 when trees were 12 years old, 23 of the 25 provenances flowered. Hybridization with the local provenance was accomplished in the simplest way by removing male flowers from the plantation trees and allowing them to be pollinated by local white spruce. Seed was harvested from 125 open-pollinated parent tres. Open-pollinated seeds collected from a local stand were bulked to serve as a control. Information about origins of parent provenances is given in *Table 1.*

Seed was sown at PFES nursery in the fall of 1966. Hybrid families were randomly distributed in the nursery beds without replication. A field test was established at PFES in the spring of 1971 using 2—2 stock. Only 65 families from 21 provenances, including 3 local × local families, produced enough seedlings for a replicated test. Heights were measured before lifting. The number of hybrid families in each provenance varied from 1 to 11 *(Table 1).*

The soil of the testing site is a loamy sand derived from glacial till. A compact-family-block (split-plot) design was used with provenance crosses assigned to main plots and families to sub-plots. The sizes of the main-plots were unequal because of the varying numbers of hybrid families produced in each provenance. The experiment had 5 replications of 5-tree plots spaced 1.8 × 1.8 m. Seventy-five control plots, 15 in each replication, were included. The plantation was measured in 1976 after 5 growing seasons. Height increments of the last two years were also recorded.

Analysis of variance was performed according to procedures for the compact-family-block design with unequal size of main-plots and on the basis of sub-plot means. The main-plot data were first analyzed as randomized complete block with unequal number of units per treatment. Individual main-plots were then analyzed separately and pooled to form sub-plots (families within provenances variation). The control plots were inclued in the main-plot analysis *(Table 2).* This is pertinent because they were bulked progenies and were included primarily for comparison with provenance crosses. The main-plot variation was further subdivided into 3 components: among provenance crosses; provenance crosses vs. controls and local × local; and controls vs. local × local *(Table 2).*

Correlations among nursery height, total height, height increment, and height of parent provenances were compared on the basis of both family and provenance means.

Results

Survival of provenance hybrids averaged 80% and controls averaged 81%. Trees of provenance crosses were from 5 to 30% taller and averaged 17% taller than trees of local controls *(Figure 1).* The difference was highly significant *(Table 2).* Trees originating from local × local were the same mean height as trees of controls (131.1 vs. 130.7 cm) *(Figure 1, Table 2)* indicating that they represent the same general population. The difference in total height among provenance crosses was also significant *(Table 2).* With the exception of the cross with trees from Erin, it seems that crosses with parent provenances from the extreme north, south and east did not perform as well as others *(Figure 1).*

There was considerable variation in total height among hybrid families within provenance crosses *(Table 2).* For example, the 11 families from the provenance 1961 *(Table 1)* ranked from first to fifty-eighth among the 65 families.

Average increments of trees of all provenance crosses, excluding local × local, were 32 and 25 cm versus 26 and 21 cm for the controls during the 1975 and 1976 growing seasons, respectively. The provenance hybrids grew 19.5 percent more in height over the two seasons than the controls.

Table 2. — Variance analyses of height growth.

		Height increment				Total height	
		age 9		age 10		age 10	
Source of variation	DF	MS	F[1]	MS	F[1]	MS	F[1]
Replications	4	62	1.13 NS	144	3.06 *	1561	1.80 NS
Provenance crosses	19	76	1.37 NS	64	1.36 NS	1498	1.74 *
Provenance crosses vs. control and local x local	1		35.42 ***	817	17.26 ***	35252	40.98 ***
Control vs. local x local	1	26	0.46 NS	34	0.71 NS	1	0.00 NS
Error a	84	55		47		860	
Families/Prov. crosses	44	68	1.60 *	33	1.08 NS	1029	1.88 **
Error b	246	42		30		548	

[1]) Significance of F-values: NS = not significant; *, **, *** = significant at 5%, 1%, and 0.1% level of probability, respectively.

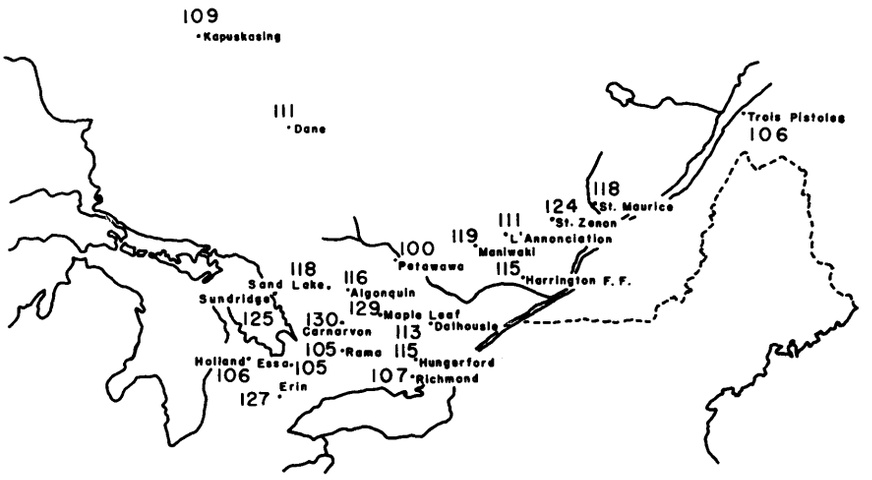

Figure 1. — Mean height of provenance crosses at age 10 expressed as percent of the control (= 130.7 cm) in a one direction interprovenance hybridization with local PFES white spruce as male parent. Standard error for differences between any two means is 9.9 cm (= 8% of the control).

The difference was highly significant *(Table 2)*. Average nursery height of provenance hybrids, at age 4, was 17 percent taller than controls (35 vs. 30 cm).

The frequency distribution of mean tree height of hybrid families grew almost 50 percent more than those in the coned in *Table 3*. Trees in only 4 of the 62 hybrid families were shorter or equal to those in the controls. Trees of two families grew almost 50 percent more than those in the controls indicating the potential of further improvement of height growth through selection.

Total tree height at age 10 was significantly correlated with height in the nursery and height increments based on family and provenance means *(Table 4)*. Correlations with parent tree height and mean height of parent provenances at age 6 in the nursery provenance test was low but positive *(Table 4)*. However, the correlation coefficients were 0 when based on the parent heights at age 4.

Discussion

Superiority of provenance hybrids became evident in the nursery and was maintained in the field test. A logical question to ask is why progenies of interprovenance crosses grow faster than trees of open-pollinated local controls and progenies of local × local (intra-provenance crosses). One is tempted to interpret it as heterosis. Heterosis in the classical sense (deviation of hybrid from mid-parent) cannot be estimated because only male parent provenances were included in the test. Local PFES white spruce, being tested in a number of provenance trials in Ontario, was one of the fast growing sources (Teich *et al.* 1975). The local provenance was also the second tallest at age 6 in the nursery trial where this hybridization was done. So the results would not be expected to change even if female parent provenances had been included and comparisons been based on mid-parent.

Also, maternal effect cannot be estiamted in this study because no reciprocal crosses were made. Morgenstern (1974) found that the maternal effect was mainly associated with germination characteristics and was negligible with respect to height growth in black spruce. Influence of seed weight usually disappears in a few years. The maternal effect is probably not an important component with height growth in white spruce.

There is experimental evidence in maize that crosses between lines or varieties of diverse origins exhibit greater heterotic response than that of similar origins (Lonnquist and Gardner 1961, Moll *et al.* 1962). Theoretical explanations as to the type of gene actions responsible for heterotic response of a diverse cross are still far from satisfactory. It is generally believed that a gene frequency difference between parent populations is required for the expression of hybrid heterosis. If the populations crossed do not differ in the frequency of the gene loci there will be no heterosis no matter whether a partial dominant, dominant or overdominant genic model is assumed (Falconer 1960, Cress 1966).

Natural white spruce in eastern Canada seldom grows in large pure stands. It usually grows in groups of various sizes mixed with other conifers and hardwoods. Gene flow between stands would thus be restricted; and differentiation in gene frequency among stands through genetic drift and inbreeding would be expected.

The increased growth of the hybrids was probably due to reduced inbreeding. Coles and Fowler (1976) found that neighboring trees in natural white spruce stands were

Table 3. — Frequency distribution of height classes of hybrid families at age 10 expressed as percent of the control (= 130.7 cm).

	%					
Height Class	90–100	101–110	111–120	121–130	131–140	141–150
No. of families	4	12	21	16	7	2

Table 4. — Correlation coefficients[1]) showing relationship between height of provenance crosses at age 10 and nursery height at age 4, height of parent trees and parent provenances at age 6 and height increments at age 9 and 10.

Level of means	Nursery height	Height of parents	Height increment at age 9	10
Family	.63 **	0.26 *	.75 **	.54 **
Provenance	.55 **	.17 NS	.66 **	.56 **

[1]) Significant levels: NS = not significant; *, ** = significant at 5% and 1% level, respectively.

highly related. The coefficients of relationship in the two stands investigated by them were estimated to be 0.23 and 0.30, i.e., equivalent to half-sibs. Inbreeding is almost universally harmful. One of its consequences is the increase in homozygosity with greater accumulation of recessive alleles which tend to be deleterious (FALCONER 1960, CROW 1948). Crossing between unrelated provenances will produce progenies in which many of the deleterious genes would be rendered ineffective by dominant alleles from one parent provenance and would result in improved hybrid performance. The results of this study support the suggestion that a substantial portion of the improved growth of progenies from the seed orchard over progenies of wind-pollinated seed from natural stands may result from reduced inbreeding rather than genetic superiority of the parents (COLES and FOWLER 1976).

The greater height growth of provenance hybrids of white spruce compared with trees grown from seed from a general collection in the local stand appears to be much higher than has been found for a number of other conifers (NILSSON 1973, WOESSNER 1972, REHFELDT 1976, ORR-EWING 1966). Crosses in most studies of other conifers, however, involved parent provenances from a much wider geographic area than in this one. As a result of some earlier studies in maize, it is widely believed that heterosis increases with increased genetic divergence of parent populations. More recent studies, however, have shown that heterosis increases with increased genetic diversity within a rather limited range of divergence and decreases beyond that (MOLL *et al.* 1965). All the provenances involved in this study are from a relatively limited geographic range, but even within this limited range the growth of the widest crosses was relatively poor *(Figure 1)*. Crosses between extremely distant provenances may cause genic imbalance in the hybrid populations and may not be beneficial (FALCONER 1960).

Results of this study indicate that substantial improvement in height growth can be achieved by a reduction of inbreeding combined with selection. This could be achieved rapidly through combined progeny-provenance tests and sedling seed orchards developed on a regional basis, e.g. the ecological regions described by HILLS (1961). Only the trees of the best families from the best stands would be retained to cross with each other for final seed production.

Literature Cited

COLES, J. F., and FOWLER, D. P.: Inbreeding in neighbouring trees in two white spruce populations. Silvae Genet. 25: 29—34 (1976). — CRESS, C. E.: Heterosis of the hybrid related to gene frequency differences between two populations. Genetics 53: 269—274 (1966). — CROW, J. F.: Alternative hypotheses of hybrid vigor. Genetics 33: 477— 487 (1948). — FALCONER, D. S.: Introduction to quantitative genetics. Ronald Press Co., New York. 365 pp. (1960). — HILLS, G. A.: The ecological basis for land use planning. Ont. Dept. Lands and Forests, Res. Br. Rep. 46. 204 pp. (1961). — HOLST, M. J., and FOWLER, D. P.: Selfing and provenance hybridization in red pine. Proc. Fourteenth Meet. Can. Tree Improv. Assoc., Pt. 2. pp. 39—50 (1973). — LONNQUIST, J. H., and GARDNER, C. O.: Heterosis in intervarietal crosses in maize and its implication in breeding procedures. Crop Sci. 1: 179—183 (1961). — MOLL, R. H., SALHUANA, W. S., and ROBINSON, H. F.: Heterosis and genetic diversity in variety crosses of maize. Crop Sci. 2: 197—198 (1962). — MOLL, R. H., LONNQUIST, J. H., VELEZ FORTUNO, J., and JOHNSON, E. C.: The relationship of heterosis and genetic divergence in maize. Genetics 52: 139—144 (1965). — MORGENSTERN, E. K.: Early results of provenance hybridization in black spruce. Proc. Fourteenth Meet. Can. Tree Improv. Assoc., Pt. 2. pp. 27—37 (1973). — MORGENSTERN, E. K.: A diallel cross in black spruce. *Picea mariana* (MILL.) B.S.P. Silvae Genet. 23: 67—70 (1974). — NILSSON, B.: Recent results of interprovenance crosses in Sweden and the implications of breeding. Proc. Fourteenth Meet. Can. Tree Improv. Assoc., Pt. 2. pp. 3—14 (1973). — ORR-EWING, A. L.: Inter- and intraspecific crossing in Douglas-fir. Silvae Genet. 15: 121—126 (1966). — REHELDT, G. E.: Growth and cold hardiness of intravarietal hybrids of Douglas-fir. Theor. Appl. Genetic. 50: 3—15 (1977). — ROWE, J. S.: Forest Regions of Canada. Depart. of Environment, Can. Forest. Serv. Pub. No. 1300., 172 pp. (1972). — TEICH, A. H., SKEATES, D. A., and MORGENSTERN, E. K.: Performance of white spruce provenances in Ontario. Can. Forest. Serv. and Ont. Ministry of Nat. Resources Special Joint Report No. 1. 31 pp. (1975). — WOESSNER, R. A.: Crossing among loblolly pines indigenous to different areas as a means of genetic improvement. Silvae Genet. 21: 35—39 (1972).

Provenance Study of Douglas-fir in the Pacific Northwest Region

III. Field Performance at Age Twenty Years

By K. K. CHING and P. N. HINZ[1])

Professor and Visiting Associate Professor
School of Forestry, Oregon State University

(Received September / November 1978)

Summary

Height growth and DBH of 20-year-old trees from 14 seed sources of Douglas-fir were assessed and analyzed in 10 outplanting areas located on the west side of the Cascade Range in the Pacific Northwest. Differences in traits measured from trees of various provenances were statistically significant at $P < 0.01$. The analysis indicated a significant interaction between seed sources and the outplanting locations. Almost all of this interaction is because of provenance G, originated from Shelton, Washington. Future research of similar genetic studies should be designed to separate the experimental and genetic influences among provenances.

Key words: Douglas-fir, provenance, genotype-environment interaction.

Zusammenfassung

Höhenwachstum und Brusthöhendurchmesser von 20 Jahre alten Douglasien, die 14 verschiedene Herkünfte repräsentieren, wurden auf zehn Versuchsflächen auf der Westseite der Kaskaden im Pazifischen Nordwesten erhoben und ausgewertet. Unterschiede zwischen den untersuchten Eigenschaften der Bäume der verschiedenen Provenienzen waren statistisch hoch signifikant mit $P < 0.01$. Die Analyse machte eine signifikante Interaktion zwischen Herkünf-

[1]) Dr. HINZ is on leave from the Department of Statistics, Iowa State University, Ames. This is paper 1282, For. Res. Lab., Oregon State Univ., Corvallis.