Changes in Heritability Estimates with Age and Site in White Spruce, Picea glauca (Moench) Voss

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(Received 18th June 1984)

Abstract

Ninety-two white spruce, *Picea glauca* (Moench) Voss, progenies from Lake States and southeastern Ontario stands were tested in the Lake States Ontario. The performance of the Ontario progenies on a single site in the Lake States was compared to performance on three Ottawa Valley sites. Of 61 Lake States progenies, 55 were common to two sites, 39 were common to three sites and 20 were common to the three Lake States sites and a single Ottawa Valley site. Measurements in the Lake States included heights in the nursery and at 9 and 15 years from seed in the field. Canadian measurements were from young field tests.

Heritabilities were determined for the 9- and 15-year old trees for individual tests and in a combined analysis of the three Lake Sites tests. Simple correlation was used to compare development in the nursery with 9- and 15-year heights at the sites in the Lake States. Simple correlation was also used to compare growth in the Lake States with growth in Ontario.

Heritabilities were generally higher than those published earlier for white spruce. They:

(1) Were largest on the least productive of the three test sites in the Lake States.
(2) Increased markedly between age 9 and age 15 measurements.
(3) Were biased upwards because the progenies represented a variety climatic origins.
(4) Decreased when the confounding climatic effects were taken into consideration in the analysis. After removal of the bias they remained comparable to or somewhat greater than published values.
(5) Showed no identifiable systematic trends among the test environments and the heritabilities of progenies grouped on the basis of climatic origins.

Age-to-age- correlations were high particularly among the age 9 - age 15 measurements, but also among the measurements in the nursery and in the field. The site-site correlations were also high; even the correlations between measurements in the Lake States and in the Canadian test were significant in many instances. However, compared to climatic origins which were quite stable over the three sites, family performance was not consistent.

The results are discussed as they relate to (1) progeny test design, (2) age of selection, and (3) development of a white spruce breeding system.

Key words: height growth, selection, breeding, climatic effects.

Zusammenfassung

92 Nachkommenschaften von *Picea glauca* (Moench) Voss aus Saatgut von Standorten in den Lake States und aus dem südöstlichen Ontario wurden in den Lake States Ontario getestet. Die Leistung der Ontario-Nachkommenschaften eines einzelnen Standortes in den Lake States wurde mit der Leistung auf drei Tal-Standorten in Ottawa verglichen.

Von 61 Lake States-Nachkommenschaften waren 55 auf 2 Standorten, 39 auf 3 Lake-Standorten und 20 auf 3 Lake-Standorten und einem Talstandort in Ottawa vertreten.

In den Lake States wurden die Höhe in der Baumschule und nach 9 bzw. 15 Jahren die Höhe auf der Versuchsfläche gemessen. In Kanada wurden jüngere Versuchsflächen gemessen.

Für die 9 bzw. 15 Jahre alten Bäume wurden die Heritabilitäten in Individual-Tests und kombinierten Analysen der 3 Lake States-Versuchsflächen ermittelt. Es wurden einfache Korrelationen durchgeführt, um die Entwicklung in der Baumschule mit der Höhenentwicklung im Alter 9 und 15 der Lake States-Standorte zu vergleichen, ebenso, um das Wachstum in den Lake States mit demjenigen in Ontario zu vergleichen. Die Heritabilitäten waren generell höher als solche aus früheren Veröffentlichungen über *Picea glauca.*

Die Heritabilitäten waren:

1) am größten auf dem am wenigsten produktiven der drei Teststandorte in den Lake States,
2) deutlich signifikant zwischen den Messungen im Alter 9 und 15,
3) positiv beeinflußt, weil die Nachkommenschaften verschiedene klimatische Herkünfte repräsentierten,
4) nahmen ab, wenn die verwirrenden klimatischen Einflüsse mit in die Betrachtung der Analysen einbezogen wurden. Nach der Beseitigung des Überhanges blieben sie vergleichbar mit oder etwas größer als die veröffentlichten Werte.
5) Es zeigten sich keine identifizierbaren systematischen Trends zwischen den Test-Standorten und den Heritabilitäten der Nachkommenschaften, die nach ihrer klimatischen Herkunft in Gruppen eingeteilt wurden.

Korrelationen zwischen den Altersstufen waren hoch, besonders zwischen Meßwerten im Alter 9 und 15, aber auch zwischen denjenigen in der Baumschule und auf der Versuchsfläche. Korrelationen zwischen den Standorten waren ebenfalls hoch, besonders die Korrelationen zwischen den Meßwerten in den Lake States, wobei diese im kanadischen Test in vielen Fällen signifikant waren. Jedoch im Vergleich zum Herkunfts-Klima, welches über die drei Standorte hinweg ziemlich stabil war, war die Leistung der Familien nicht beständig.

Die Resultate werden im Zusammenhang mit 1) dem Nachkommenschaftstest-Design, 2) dem Alter der Selektion und 3) der Entwicklung einer *Picea glauca* Züchtungsstrategie diskutiert.

Introduction

Published results have thrown considerable light on the genetic parameters for white spruce progenies, but information is not sufficient to determine the best age at which to make selections in progeny tests or for the development of multi-generation breeding systems.

Jeffers (1969) correlated (r = .81) the annual growth rate of parent trees from the three Lake States with the total height of 28 progenies at age 4. His conclusion supported the "general feasibility of phenotypic selection in white spruce."

Results from the four oldest white spruce progeny tests in North America were reported by HOLST and TEICH (1969) and YING and MORGENSTERN (1979) for 8 to 11 and 22-year-old trees. Progeny variation in height was significant in all four tests while the trees were young, but at age 22 one test failed to demonstrate family differences. The authors suggested that this stemmed from site differences which became manifest after age 16. Diameter growth differences were less pronounced, reaching statistical significance in only one of the four tests. Genotype × environment interaction was not significant. This is not surprising because the tests were in close (10 km) proximity (climates were similar, although there were some soil differences) (YING and MORGENSTERN 1979). Heritabilities varied among the four tests and with age. At age 8 to 11 heritabilities ranged from .15 to .35 for height; at age 22 they were very similar (.15 to .32) with the exception of the uneven site mentioned above. There the heritability estimate dropped from .35 at age 11 to .01 at age 22. The much lower estimates for diameters (DBH) at age 22 ranged from .05 to .10.

Comparison of progenies of taller (4.6 percent) narrow-crown trees with smaller broad-crown trees, detected no differences between the two groups, and it was concluded that phenotypic selection based on total height with no age consideration was ineffective. In view of the low heritabilities the authors suggested large-scale, open-pollinated progeny tests as the initial step in the first generation of a breeding program.

That was the approach taken in a cooperative effort in Minnesota (MOHN *et al.* 1976). The progeny test involved 239 progenies from six northern climatic zones (RUDOLF 1956) in Minnesota. In the intermediate climate at the test site the progenies from the mildest zone performed best. The estimated heritability of .27 at age 9 increased to .35 at age 12 (narrow sense, individual tree basis). Height growth gains of 15 to 20 percent were predicted if 90 percent of the slower growing trees were rogued. Selection at an early age was considered a possibility because correlation was high between 9th- and 12th-year heights ($r = .9$).

One test specifically designed to compare stand, family, and test site effects on white spruce progenies (DHIR 1976) involved six parent trees in each of seven stands with three test sites. The stands were located within 80 km (50 miles) of one another; stand differences in progeny performance could not be demonstrated, and the performance of individual families was inconsistent from site to site and correlations were low or nonsignificant. Heritabilities were also low: $h^2 = .10$ on an individual tree basis and $h^2 = .39$ on a family basis. Gain in height growth was estimated at 11 percent from selection of the best tree in each plot of the top five families.

These reports provide no information on site- and age-related changes in heritabilities and no information on possible changes in heritabilities related to the climate at the source of the progeny parents. Our report is an effort to further elucidate these and other questions through the evaluation and analysis of Lake States progeny tests established on three sites in the region. One test included some of the Ontario progenies discussed by DHIR (1976), and some of the Lake States progenies were tested in the Ottawa Valley, Ontario. Nursery results and the results with these additional materials are also discussed briefly.

Materials and Methods

Between 1956 and 1964 seed was collected from 64 white spruce trees selected in the Lake States. *Table 1* summarizes the origins by counties across northern Minnesota, northern and northcentral Wisconsin and the Upper Peninsula of Michigan. Several agencies were involved in the selections, and selection methods and criteria varied; some trees were selected after intense search and detailed comparison with nearby trees, some were selected for unique branching and needle characteristics and some were picked at random to represent the local white spruce population. The varied selection methods could have introduced a bias in the sample. However, with the exception of 11 selection from Menominee County, Wisconsin, the selections were made in natural, unevenaged mixed stands under conditions where phenotypic selection for vigor is the least effective. In Menominee County, both dominant and intermediate trees were sampled. Overall, the selection methods probably introduced minimal bias. Trees varied in age from 33 years to an estimated 150 years at time of selection.

The selections were scattered over six of the 28 climatic zones identified in the Lake States by RUDOLF (1956). The zones are characterized as follows:

Zone	Degree Days above 10°C (50°F)	Ranges of ave. January Temp. °C (°F)	No. of progenies
3d	9,000 - 10,000	-11.1 - - 8.9 (12 - 16)	16
3c	9,000 - 10,000	-13.3 - -11.1 (8 - 12)	1/
4e	8,000 - 9,000	- 8.9 - - 6.9 (16 - 20)	2/
4d	8,000 - 9,000	-11.1 - - 8.9 (12 - 16)	22
4c	8,000 - 9,000	-13.3 - -11.1 (8 - 12)	13
4b	8,000 - 9,000	-15.6 - -13.3 (4 - 8)	7
4a	8,000 - 9,000	-17.8 - -15.6 (0 - 4)	
5b	7,000 - 8,000	-15.6 - -13.3 (4 - 8)	3

1/ Test site - Lake Tomahawk, WI.
2/ Test site - Moran, MI. Test site at Wabeno, WI is in zone 3d.

In addition to material from the Lake States families, 31 families representing five stands in the Ottawa River Valley, Ontario were included in one test: Six trees each from Westmeath and Cormac Townships; six trees each from two stands on the Petawawa Forest Experiment Station; and seven trees from a stand in Pine Valley in Bromley Township. None of the Canadian parents were plus trees.

Seed from the Lake States was sown in the nursery at Rhinelander in the spring of 1965. Seedlings were transplanted by machine in the fall of 1966 and lifted as 2-2 stock. The Ontario material was raised in the nursery at the Petawawa Forest Experiment Station.

Table 1. — Summary of Lake States progeny origins.

State & County	Latitude °N	No. of parent trees
MINNESOTA		
Koochiching	48°20' - 48°30'	3
Cook	47°50'	3
Beltrami	47°34' - 47°35'	2
Itasca	45°30'	2
WISCONSIN		
Ashland	46°05'	9
Bayfield	46°20'	2
Florence	45°45'	1
Forest	45°30' - 45°48'	6
Oconto	45°22'	1
Menominee	44°53	11
MICHIGAN		
Alger	46°30'	5
Marquette	46°25' - 46°30'	10
Ontonagon	46°25'	1
Gogebic	46°15'	5

N = 61

Table 2. — Test site description and summary of site preparation, planting, and plantation maintenance.

	Lake Tomahawk, Wisconsin	Wabeno, Wisconsin	Moran, Michigan
Site:	Cleared and cropped, hardwood site in medium-heavy sod.	Cleared and cropped, hardwood site in heavy sod.	Cleared and cropped, hardwood site in light to medium sod.
Soil:	Padus sandy loam.	Predominantly Padus sandy loam.	Variable, Onaway loam and Eastlake and Menominee medium sand.
Site Prep.	60 cm (2') strips treated with Amazine in late summer 1968.	60 cm (2') spots hand-sprayed with Amazine a few weeks prior to fall 1968 planting.	No site preparation.
Planting:	Hand-planted with planting bar May 5 and 7, 1969. 2.4 x 2.4m (8' x 8') spacing.	Hand-planted with shovels in dug holes Sept. 30 - Oct. 4, 1968. 2.4 x 2.4m (8' x 8') spacing.	Hand-planted with shovels in dug holes Sept. 16-18, 1968. 2.4 x 2.4m (8' x 8') spacing.
Maintenance:	Fertilized with 10-10-10 July 1969. Mowed annually for several years.	Mowed July 1969. Hand-sprayed with Amazine around plants August 1969. Fertilized with 10-10-10 summer 1970.	Fertilized with 10-10-10 July 1969.
Remarks:		Nov. 1969 mortality estimated at 15%. Surviving plants golden yellow. Amazine damage suspected.	

Of the 64 families from the Lake States, 61 produced enough seedlings for testing in the field and were established near Rhinelander at Lake Tomahawk, Wisconsin; 39 of the families were also established at Wabeno, 45 miles southeast of Rhinelander, Wisconsin and Moran, Michigan about 22 miles northwest of St. Ignace. An additional 16 of the families were included in the Michigan planting, which involved a total of 55 families. The 31 Ontario families were planted only at Lake Tomahawk, Wisconsin.

Seedlings from 20 Lake States families were shipped to the Petawawa Forest Experiment Station and established in a single test with 10-tree row plots and four replications.

The Lake States site descriptions, site preparations, planting methods, and maintenance procedures are summarized in *Table 2*. All three sites were of a type being replanted to white spruce at the time. The Lake Tomahawk site was a large, open area prone to spring frosts in late May and June. Late spring frosts are less likely at Wabeno and Moran.

A randomized complete block design was used for both nursery and field tests. There were four replications in the nursery, where a "plot" was 10 trees randomly picked from the adjacent rows representing a seed source. In the field tests there were four-tree row plots and 10 replications.

Several characteristics were measured in the nursery and in the Lake Tomahawk planting, but only total heights are reported. They were measured in the 2nd, 3rd and 4th year in the nursery, and in 1973 and 1979 in the field when the trees had completed 9 and 15 years of growth from seed.

Analysis of Data

The objectives of the statistical analyses were:

1. To determine and compare heritabilities of trees at 9 and 15 years from seed at three sites.
2. To analyze the influence of geographic origin on heritabilities at three sites.
3. To determine genotype $\times$ environment interaction among the three sites.
4. To determine age-to-age correlations for nursery heights at ages 2, 3, and 4 and for field heights at ages 9 and 15 years from seed.

Analyses of variance were run for the three individual sites and a combined analysis was done for the 39 progenies common to all three sites.

The model for all analyses of individual locations was:

$X_{ijk} = \mu + F_i + R_j + FR_{ij} + E_{ijk}$,

where:

X_{ijk} = observation of k^{th} within plot tree of i^{th} family in j^{th} replication,

μ = experiment mean,

F_i = effect of i^{th} family,

R_j = effect of j^{th} replication,

FR_{ij} = effect of interaction of i^{th} family and j^{th} replication, and

E_{ijk} = effect of k^{th} plot tree.

In addition, terms were added to separate variance due to progenies into variance due to climatic origins and that due to progenies within climatic origins *(Table 3)*.

Simple correlation was used to compare nursery performance with growth in the field and to compare progenies from southeastern Ontario growing in the more extreme continental climate in the Lake States with those growing in their native habitats. Since differences in the design of the nursery test and the tests in Ontario preclude a direct comparison with heritabilities in Wisconsin and Michigan, these analyses are not presented here.

Results

Survival and Heights - ANOVA'S

Survival and development have been excellent in all three plantings. Survival was lowest at Lake Tomahawk (93 percent in 1979), where mound-building ants have killed many trees. Statistically, survival was significantly higher at both Moran and Wabeno--96.8 and 96.6 percent, respectively, in 1979, but the difference is of no biological importance.

Table 3. — Combined analyses of variance for total tree heights of 38 white spruce families growing on three Lake States sites.

	Age 9			Age 15			EMS[1/]
	DF	MS	F	DF	MS	F	
Reps/Locations	27	0.19630	----	27	1.7778	----	
Locations	2	5.14174	98.88**	2	80.3100	171.24**	$\delta^2 + 10\,\delta^2_{FL} + 380\,\delta^2_L$
Families	37	0.31158	5.99**	37	4.4189	9.40**	$\delta^2 + 10\,\delta^2_{FL} + 30\,\delta^2_F$
Origins	3	2.14198	14.27**	3	33.1500	17.63**	$\delta^2 + 10\,\delta^2_{F(O)L} + 10h\,\delta^2_{OL} + 30\,\delta^2_{F(O)} + 30h\,\delta^2_O$
Fam/Origins	34	0.15007	2.82**	34	1.8838	3.93**	$\delta^2 + 10\,\delta^2_{F(O)L} + 30\,\delta^2_{F(O)}$
Families x Locations	74	0.05200	1.90**	74	0.4688	1.54**	$\delta^2 + 10\,\delta^2_{FL}$
Origins x Locations	6	0.03826	0.72 ns	6	0.3667	0.77 ns	$\delta^2 + 10\,\delta^2_{F(O)L} + 10h\,\delta^2_{OL}$
Fam/Origins x Locations	68	0.05321	1.94**	68	0.4772	1.57**	$\delta^2 + 10\,\delta^2_{F(O)L}$
Plot Error	999	0.02738	1.60**	999	0.3049	2.16**	δ^2
Within Plot	3824	0.01715		3228	0.1410		δ^2_w/n *

1/ h = harmonic mean #families/origin
= 8.39

$\delta^2 = \delta^2_w/n + \delta^2_e$

δ^2_w = within plot variance

δ^2_e = plot error variance

n = harmonic mean #trees/plot
= 3.83 in 1973
= 3.76 in 1979

In the combined analysis of 38 of the progenies common to all three plantings, the F values for plantings were F = 98.88** at age 9 and F = 171.24** at age 15 *(Table 3).*

Geographic origin strongly influenced growth on all three sites both at ages 9 and 15. The differences due to origins were highly significant--F = 14.27** and F = 17.63** at ages 9 and 15, respectively.

The progeny × environment interaction was also highly significant at ages 9 and 15 (F = 1.90** and F = 1.54**, respectively) in the combined analyses of all three tests. However, although the interaction effect was significant, it was much less than the main effect of progenies. From *Table 4* the interaction variance components (origins confounded) are found to be only 28 percent and 12 percent of the between family components at ages 9 and 15, respectively. In addition, climatic origins were very stable over locations *(Table 6).* The F tests of the origin × location effect were nonsignificant at both 9 and 15 years--F = 0.72 and F = 0.77 *(Table 3).* When the effect of origin is removed, the family × location interaction is much higher in relation to family effects--80 and 37 percent, respectively *(Table 4).*

Height growth has been best at Lake Tomahawk *(Table 5).* Ranking of the two other sites changed between ages 9 and 15; at age 9 the Moran trees were slightly taller than the Wabeno trees, but by age 15 the Wabeno trees were taller. The mean values and ranges of the 39 progenies common to all three sites did not differ significantly from the values in *Table 5.*

Herbicide damage may explain the initially slower growth at Wabeno. As mentioned in *Table 2,* the trees were fall planted in 1968, and treated with Amazine in

Table 4. — Relative magnitude of variance components from combined analysis of variance of total tree heights at ages 9 and 15 years from seed.

	Age 9				Age 15			
	Origins accounted		Origins confounded		Origins accounted		Origins confounded	
FAM	0.00323	4.0%	0.00865	9.9%	0.0469	6.2%	0.1317	15.6%
FAM x LOC	0.00258	3.2%	0.00246	2.8%	0.0172	2.3%	0.0164	1.9%
PLOT ERROR	0.01023	12.5%	0.01023	11.8%	0.1639	21.6%	0.1639	19.5%
WITHIN PLOT	0.06568	80.3%	0.06568	75.5%	0.5302	69.9%	0.5302	63.0%
	.08172		.08702		.7581		.8422	
h^2	.158		.398		.247		.626	

$$h^2 = \frac{4\ (\text{FAM})}{\text{WITHIN PLOT} + \text{FAM x R/L} + \text{FAM x LOC} + \text{FAM}}$$

Table 5. — Mean heights and ranges at age 9 and 15 at the three test sites.

	Number of progenies	Age 9		Age 15	
		Mean height	Range	Mean height	Range
		meters			
Lake Tomahawk	92	1.14	.89 - 1.43	3.94	3.10 - 4.57
Wabeno	39	.87	.70 - 1.17	3.27	2.33 - 4.31
Moran	55	.97	.73 - 1.19	2.93	1.99 - 3.75

Table 6. — Mean heights at age 9 and 15 for progenies arranged according to climatic origins for three tests.

Zone of origin	Number of progenies	Moran Zone 4e		Lake Tomahawk Zone 3c		Wabeno Zone 3d	
		Age 9	Age 15	Age 9	Age 15	Age 9	Age 15
		meters					
Ontario	31	--	--	1.21	4.18	--	--
3d	10	1.10	3.45	1.24	4.25	.98	3.78
4d	13	.92	2.70	1.03	3.64	.81	3.04
4c	10	.94	2.73	1.07	3.70	.88	3.25
4b	4	.86	2.53	1.04	3.66	.81	2.95
4a	1	1.07	3.05	1.27	4.15	.96	3.21
5b	1	.85	2.55	1.07	3.72	.78	2.78

July 1969. Establishment notes indicate that the hand application of herbicide damaged many plants.

On all sites, seed from the mildest climate (3d) produced the most vigorous seedlings. Seed from colder origins (4b, 4c and 4d) produced less vigorous seedlings with mean heights similar to each other *(Table 6)*. The number of progenies representing the two coldest zones (4a and 5a) was too limited to permit any conclusion--one progeny (4a) was combined with those from the next mildest zone (4b), and another (5b) was not included in the combined analyses of all three tests. The 31 progenies from Ontario are among the fastest growing at Lake Tomahawk. Their mean heights at ages 9 and 15 do not differ significantly from the heights of the 10 Lake States progenies from the mildest zone (3d) *(Table 6)*.

Heritabilities

With origins confounded heritabilities in the three individual tests were high, ranging from .43 to .62 at age 9. In 1979 at age 15 they had increased, ranging from .63 to .98 *(Table 7)*. Heritabilites were highest at Moran, Michigan, where the growing season is cooler than at the other two sites (8,000—9,000 degree days versus 9,000—10,000), but where January temperatures are probably somewhat milder (-6.7^0 to -8.9^0 C versus -8.9^0 to -13.3^0 C). Based on the 1979 height measurements, Moran is the least productive of the three sites *(Table 5)*. When estimates were made for only the 38 progenies common to all three plantations, they did not differ greatly from those involving all the progenies.

Combined analyses of the sources common to the three tests showed a remarkable increase in heritability from age 9 ($h^2 = .40$) to age 15 ($h^2 = .63$) for progenies with origins confounded *(Table 7)*.

Sorting the progenies on the basis of climatic origin and estimating the heritabilities separately for the individual groups generally resulted in lower estimates. In the combined analysis the heritabilities for progenies within origins across the three sites were reduced from $h^2 = .40$ (origins confounded) to $h^2 = .16$ at age 9 and from $h^2 = .63$ to $h^2 = .25$ at age 15 *(Table 4)*.

The heritability estimates for progenies within origins at each of the three sites are shown in *Table 8*. With the exception of values for age 9 at Moran, estimates are lower than those that confound family and origin effects. The magnitude of change, however, showed no clear trends that could be related to the difference between the climates at progeny origins and the climate at the tests site. Nevertheless, it is interesting to note that progenies originating in climates that most closely resemble the test environmen tend to have the largest heritabilities--4d progenies at Moran (4e); 3d at Wabeno (3d); and 3d at Lake Tomahawk (3e). At Lake Tomahawk the five progenies from the

Table 7. — Heritabilities (h^2 individual) of height growth at three test sites (origins confounded).

	Number of progenies	Age 9	Age 15
	ALL PROGENIES AT INDIVIDUAL SITES		
Lake Tomahawk	92	.44	.63
Wabeno	39	.43	.84
Moran	55	.62	.98
	38 PROGENIES COMMON TO ALL SITES		
Lake Tomahawk	38	.40	.63
Wabeno	38	.43	.84
Moran	33	.65	(1.15)1/

1/ This value can perhaps be explained on the basis that the random mating assumption was invalid. If the families contain a large number of full-sibs then the estimate of additive-genetic variance ($4\sigma^2$) would be biased upward.

Table 8. — Combined analysis of heritabilities for 38 progenies common to three test sites (separate estimates developed for progenies grouped on the basis of the climatic zone in which they originated).

Zone of origin	Number of progenies	Moran Zone 4e Age 9	Moran Zone 4e Age 15	Lake Tomahawk Zone 3c Age 9	Lake Tomahawk Zone 3c Age 15	Wabeno Zone 3d Age 9	Wabeno Zone 3d Age 15
All	38	.65	(1.15[1])	.38	.64	.43	.84
3d	10	.16	.47	.24	.21	.40	.82
4d	13	.84	.75	.15	.30	.23	.45
4c	10	.38	.50	.00	.33	.25	.21
4a,b	5	.78	.89	.44	.52	.20	.56

1/ This value can perhaps be explained on the basis that the random mating assumption was invalid.

Table 9. — Simple correlation coefficients among heights of 55 progenies growing in the nursery and at Moran and Lake Tomahawk in the Lake States.

	1	2	3	4	5	6
1. Moran, age 9						
2. Lake Tomahawk, age 9	.725					
3. Moran, age 15	.943	.727				
4. Lake Tomahawk, age 15	.756	.930	.809			
5. Nursery, age 2	.619	.530	.603	.503		
6. Nursery, age 3	.675	.494	.642	.490	.795	
7. Nursery, age 4	.640	.519	.608	.513	.673	.937

Significance level, d.f. 53 p=.05, r=.266; p=.01, r= .345

combined zones 4a and 4b did in fact have a larger heritability, but because the sample is so small the estimates are the least reliable of those shown in *Table 8*.

Correlations

No trends in genotype × environment interactions stand out. The coefficients for simple correlation among heights of the 39 progenies common to the three sites are all highly significant. At age 9 they ranged from r = .484 (Wabeno-Lake Tomahawk) to r = .728 (Moran-Lake Tomahawk). The coefficients were essentially unchanged when they were computed on the basis of the 55 families common to the Moran and Lake Tomahawk plantings. They did increase between age 9 and age 15, as shown in *Table 9* for the 55 progenies common to Moran and Lake Tomahawk. The growth potential on the three sites was quite different, as indicated by the means in *Table 5,* but the correlations suggest considerable stability regardless of site quality. However, as already mentioned family and origin variances in the analyses *(Table 3)* indicate that the stability of the origins--as opposed to the families--must be the primary source of the highly significant correlations.

Age-to-age correlations based on progeny means were very high in the field plantings. For all 55 progenies it was r = .943** at Moran and r = .930** at Lake Tomahawk *(Table 9).* Separate values were computed for the 39 progenies common to all three plantings. The values were very similar to the values in *Table 9,* so they are not in the Table; the correlation was lowest for Wabeno (r = 915** d.f. 37) and highest for Moran (r = .951** d.f. 37). Nursery heights were available for 1966, 1967, and 1968 when the plants were 2, 3, and 4 years old, respectively. The correlations between these heights and the heights of 55 progenies at Moran, Michigan and Lake Tomahawk, Wisconsin were all highly significant *(Table 9).* The coefficients ranged from .490 to .675; the highest values were between the nursery heights and the heights at Moran, Michigan.

As mentioned earlier, 31 Ontario progenies developed very well at Lake Tomahawk. Heights at age 10 were available from three sites in the Ottawa River Valley about 45 miles northwest of Pembroke, Ontario. The correlation among the three Canadian sites ranged from .048 to .177 and never attained statistical significance. The correlations between the heights of the trees in Canada and age 9 and 15 heights at Lake Tomahawk were also low. Nevertheless r = .358* for the correlation between the development on the best site in Canada and the 9-year heights at Lake Tomahawk was significant at the .05 percent level (d.f. 29) *(Table 10).* For the measurements at age 15, the value dropped to .337 and was no longer significant.

In contrast, the correlations were much higher for the 20 Lake States progenies common to a test in the Ottawa River Valley and the three Lake States tests. Correlations between 12-year heights in Ontario and 9- und 15-year heights in the Lake States ranged from r = .394 n.s. to r = .679**. Using the heights at age 15, the values were .509**, .547*, and .679** for Lake Tomahawk, Moran, and Wabeno data, respectively.

Discussion

Tree growth ih the three tests has been comparable to that in white spruce plantations growing on high quality sites elsewhere in Wisconsin (Wilde *et al.* 1965). Heritability estimates in this study for individual tests are high compared with other published estimates. Indeed, the range of 0.63 to .98 for 15 year heights *(Table 7)* for the three plantings based on all progenies is higher than any published figures for the species. This is explained in part by uniform raising of the planting stock, and planting on

Table 10. — Simple correlation of height growth of 31 Ontario progenies growing at Lake Tomahawk, Wisconsin and on three sites in the Ottawa River Valley, Ontario.

	1	2	3	4
1. Lake Tomahawk, age 9				
2. Lake Tomahawk, age 15	.898**			
3. Ontario D-1, age 10	.358*	.337		
4. Ontario D-2, age 10	.110	.134	.091	
5. Ontario D-3, age 10	.130	.113	.048	.177

Significance Level, d. f. 29, p=.05, r=.355; p=.01, r=.456

old fields where past cultivation has tended to reduce variation over the site. The experimental design--four-tree plots with 10 replications--undoubtedly also contributed. DHIR (1976), for example, used 25- or 40-tree plots with two replications, and the studies reported on by HOLST and TEICH (1969) and YING and MORGENSTERN (1979) were 49-or 50-tree plots with four or five replications. In tests for early evaluation of progenies and selection, small plots with many replications are clearly advantageous (BRIDGWATER *et al.* 1983). However, using old previously cultivated fields can only be recommended if old fields make up the majority of planting sites.

The values also are biased upward due to provenance variation. Heritabilities computed for progenies grouped by climatic zone are indeed lower *(Table 8)*. However, even after these adjustements, the heritabilities published here are as large or larger than single-test site estimates published by others (MOHN *et al.* 1976; FOWLER and COLES 1977; YING and MORGENSTERN 1979).

Somewhat surprisingly, there were no clear trends in heritability related to climatic origin and to quality of test site. Higher heritabilities observed on the poorer Moran site are not in agreement with the common recommendation that progeny tests should be established on the best sites, where the trees can achieve their full growth potential (WRIGHT 1976).

The progeny groups originating in the climate most closely resembling the test site climate may tend to have the largest heritabilities. This is particularly suggested by the 1979 Wabeno and Moran data, but not by the data from Lake Tomahawk. Explanations are not obvious. One could postulate that the progenies from climates similar to that of the test sites would grow faster, would express growth differentials more clearly, and would therefore have the largest heritabilities. However, this is not borne out by the results. A single origin, 3d, is the fastest growing on all three sites, yet does not have the highest heritabilities. If anything, the tendency is for faster growing groups to have lower heritabilities. The correlation of heritabilities and height growth is negative for both the 1973 and the 1979 measurements, and the value ($r = -.511$) for the 1979 heights approaches significance (d.f. 10, $p = .10$, $r = .497$).

Heritabilities clearly increased with age. This common relationship (NAMKOONG and CONKLE 1976) has not previously been clearly demonstrated for white spruce. YING and MORGENSTERN (1979) found increased heritability for height from age 8 to age 22 in only one of four tests they discussed, and in the study by MOHN *et al.* (1976), h^2 increased only from a value of .27 at age 9 to .35 at age 12. FOWLER and COLES (1977) considered $h^2 = .52$ for 2-year nursery heights unrealistically high and expected it to drop in field tests. Considering these Lake State tests their estimate may not be out of line, and although transplanting to the field may result in an initial drop, the heritability estimate would be expected to increase during the early years of the test. Later, after crown closure, heritabilities can be expected to level off and begin to decline. When this will happen undoubtedly will depend on management and growth at the individual tests sites (NAMKOONG and CONKLE 1976).

DHIR (1976) determined heritability estimates for Ottawa River Valley white spruce progenies, including the 31 progenies in the Lake Tomahawk test. The $h^2 = .10$ value he determined is less than half the value ($h^2 = .222$) for the same trees in Wisconsin. As DHIR concluded, smaller plots and more replications undoubtedly would have improved the efficiency of his test.

The highly significant correlations among mean progeny heights at the three sites and the nonsignificant origin $\times$ location interaction *(Table 3)* might seem to indicate that broadly adapted genotypes should be the goal with white spruce. The results also suggest that seed zones and breeding zones may be of lesser importance in the Lake States than in many other regions. However, the large main effect progeny variance and the highly significant progeny $\times$ location interaction make it clear that broadly adapted genotypes will not be a biologically sound approach to white spruce breeding. The instability of the families on the three sites agrees with the inconsistent performance of families in DHIR's (1976) study. In his study the stands essentially represented a single region in the Ottawa Region--a single origin as defined in this study. The stand effect was nonsignificant in DHIR's study.

The origin stability and the high heritabilities could lead to rapid loss of genetic diversity in a multi-generation breeding program. The original 39 progenies common to all three test sites represent six climatic origins and 15 stands--six in Minnesota, three in Wisconsin and six in the Upper Peninsula of Michigan. Even very mild family selection would greatly reduce this representation. Selecting the 15 best families on the basis of the 1979 heights would reduce representation of climatic origins to four, three, and four, and stand representation to seven, four and six stands in the Moran, Wabeno, and Lake Tomahawk tests, repectively. Selection of the same intensity using the 1979 measurements--20 families of 55--would reduce the original seven climatic origins and 22 stands represented at the Moran and Lake Tomahawk tests to four and five climatic origins and nine and 10 stands, respectively. In the larger Lake Tomahawk test, the effect of selecting 34 families--i.e., the same intensity--would be disproportionally greater; only nine of the original 29 stands and four of the eight original climatic origins would be represented in the selected population.

Simple mass selection that would convert the Lake Tomahawk test to a seed orchard would leave 64 of the original 92 progenies represented if all but the 200 tallest (5.4 percent) of the original trees were cut. Selection of the 25 tallest trees for further breeding would include only 18 progenies from seven stands--three from the Lake States and four from the Ottawa River Valley--and only four climatic regions would be represented.

MOHN *et al.* 1976 suggested that early selection in white spruce is a possibility. Our results support that conclusion at least to age 15. Considering the high correlation between nursery performance and height at 15 years, mild selection at age 4 in the nursery would definitely increase the efficiency of testing. Of the 200 tallest trees at Lake Tomahawk, 102 were from Lake States progenies; seven of these trees from six families would have been eliminated with 30 percent roguing in the nursery--an insignificant loss considering the great cost reduction in progeny testing.

Much has been written about the superiority of the Ottawa River Valley white spruce provenance (NIENSTAEDT 1969; NIENSTAEDT and TEICH 1972; STELLRECHT *et al.* 1974; DHIR 1976; FOWLER and COLES 1977). This study clearly demonstrates the excellent performance of the provenance at Lake Tomahawk, Wisconsin, where 22 (65 percent) of the best 34 families were from the Ottawa River Valley. However, equally good white spruce genotypes--the best family at Lake Tomahawk is from Wisconsin--can be selected from Lake States provenances.

Conclusions

In properly designed tests white spruce combines large genetic differences in growth potential with high heritability estimates. Therefore, the potential for improvement is great. However, the results suggest that multi-generation white spruce breeding systems must be designed conservatively, with adequate safeguards for genetic diversity.

In this study family variance was high and progeny × environment interaction, although statistically significant, showed no clear trends; thus, family performance was inconsistent. At the same time, origins were stable. Lacking other detailed information on the responses of Lake States provenances to the region's climates, it is not possible to develop breeding zones in the region for white spruce on the basis of our results. Neither is it clear that breeding for broadly adapted genotypes is biologically sound. Thus, the initial approach to development of a breeding system for white spruce in the Lake States must be conservative. A large number of progenies should be tested on many sites with the objective of identifying breeding zones while at the same time advancing the breeding population one generation.

Maintaining genetic diversity while achieving optimum gain from generation to generation can best be achieved if short-term and long-term breeding are separate but coordinated efforts; mass production of improved seed for reforestation should be a third distinct effort.

For short-term breeding a small number of the fastest growing trees should be selected and bred; the goal should be to optimize gain. Since provenance hybridization of white spruce may result in heterosis (Ying 1978), it would be desirable to select the parents from diverse provenances adapted to the potential planting sites.

A large, genetically diverse breeding population will be required for the multi-generation long-term breeding program. The selections for a Lake States program should favor Ontario selections from the Ottawa Valley and Lake States selections from the milder climatic zones within the white spruce range. Some selections from other areas should also be included to increase the likelihood of heterosis resulting from provenance hybridization.

In the Lake States, large numbers of progenies and clones are being tested and should be used for establishment of a multi-generation breeding program. Elsewhere, where new programs are being initiated, it would probably be worthwhile to start with more families than the number scheduled to make up the breeding population and to rogue at a very early age. The risk of losing the best genotypes as a result of errors in such early selection is small and probably offset by the opportunity to test a greater number of diverse genotypes.

Selection of parents for subsequent generations can probably also be done at an early age in field tests. In the Lake States white spruce is grown primarily for fiber, and future management undoubtedly will emphasize intensively managemend plantations. In that situation, selection sometime between ages 9 and 15 probably will be feasible, but additional research will be needed to determine optimum age. On the other hand, selections may have to be delayed in test situations where establishment and early maintenance is poor, particularly when "check" (the prolonged period of quiescence after planting) is pronounced, or under long-rotation management.

Literature Cited

Bridgwater, F. E., J. T. Talbert and D. L. Rockwood: Field design of genetic tests of forest trees. In: Progeny Testing of Forest Trees. Proceedings of Workshop on Progeny Testing, June 15—16, 1982; Auburn, Alabama. Southern Cooperative Series Bulletin No. 275. Dept. Agri. Communications, Texas A & M Univ. College Station, Texas 77843. 68 p. (1983). — Dhir, N. K.: Stand, family, and site effects in Upper Ottawa Valley white spruce. In: Proceedings 12th Lake States Forest Tree Improvement Conference. August 18—22, 1975. Petawawa Forest Experiment Station, Chalk River Ontario. USDA Forest Service North Central Forest Experiment Station, General Tech. Report NC-26. 98—107 (1976). — Fowler, D. P. and J. F. Coles: Seedling seed orchards of Ottawa Valley white spruce for the Maritimes. Maritimes Forest Research Center, Fredericton, New Brunswick. Information Report M-X-73. Canadian Forestry Service Department of Fisheries and the Environment. 46 p. (1977). — Holst, M. J. and A. H. Teich: Heritability estimates in Ontario white spruce. Silvae Genetica **18**: 23—27 (1969). — Jeffers, R. M.: Parent-Progeny growth correlations in white spruce. In: C. W. Yeatman, editor: Proceedings of the 11th meeting of the committee on forest tree breeding in Canada. Part 2 Reports, Papers, and Abstracts. MacDonald College Quebec, Aug. 8—10th, 1968. Forestry Branch Department of Fisheries and Forestry of Canada, Ottawa. 213—221 (1969). — Mohn, C. A., D. E. Riemenschneider, W. Cromell and L. C. Peterson: A white spruce progeny test--seedling seed orchard: 12th Year Progress Report. In: Proceedings 12th Lake States Forest Tree Improvement Conference. Aug. 18—22. 1975. Petawawa Forest Experiment Station, Chalk River Ontario. USDA Forest Service North Central Forest Experiment Station, General Tech. Report NC-26. 98—107 (1976). — Namkoong, G. and M. T. Conkle: Time trends in genetic control of height growth in ponderosa pine. Forest Science **22**: 2—12 (1976). — Nienstaedt, H.: White spruce seed source variation and adaptation to 14 planting sites in northeastern United States and Canada. In: C. W. Yeatman, editor: Proceedings of the 11th meeting of the committee on forest breeding in Canada. Part 2 Reports, Papers, and Abstracts. MacDonald College, Quebec, Aug. 8—10th, 1968. Forestry Branch Department of Fisheries and Forestry of Canada, Ottawa. 183—194 (1969). — Nienstaedt, H. and A. Teich: Genetics of white spruce. USDA Forest Service Res. Pap. WO-15. 24 p. (1972). — Rudolf, P. O.: A basis for forest tree seed collection zones in the Lake States. In: Proceedings The Minnesota Academy of Science **24**: 21—28 (1956). — Stellrecht, J. W., C. A. Mohn, and W. Cromell: Productivity of white spruce seed sources in a Minnesota test planting. Univ. of Minn., Minn. For. Res. Notes No. 251, 4 p. (1974). — Wilde, S. A., J. G. Iyer, Ch. Tanzer, W. L. Trautman and K. G. Watterston: Growth of Wisconsin coniferous plantations in relation to soils. Univ. Wisconsin, Madison. Research Bulletin 262. 81 p. (1965). — Wright, J. W.: Introduction to forest genetics. Academic Press. 463 p. (1976). — Ying, C. C.: Height growth of inter-provenance crosses in white spruce, *Picea glauca* (Moench) Voss. Silvae Genetica **27**: 226—229 (1978). — Ying, C. C. and E. K. Morgenstern: Correlations of height growth and heritabilities at different ages in white spruce. Silvae Genetica **28**: 181—185 (1979).