White spruce growth to age 44 in a provenance test at the Petawawa Research Forest

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ABSTRACT

Twenty-five provenances of white spruce were planted in 1963 in 144-tree plots and three replications as part of a provenance test series for eastern Canada. The experiment was well maintained and thinned to 50% of its original stocking in 1986 (age 26 years from seed). Measurements at age 44 were subjected to analyses of variance and correlation and compared with height and survival at age 15. The results demonstrated that at age 15, identification of the best provenances is ineffective because of changes in rank and the late expression of survival differences. At age 44, significant differences among provenances were observed for survival, mean height, diameter, basal area, and volume. The greatest volume was produced by a provenance from Cushing in the Ottawa Valley in Quebec, 287 m³ per ha, which was 11% greater than the volume of the local provenance, Chalk River, Ontario. When ranked on the basis of survival and volume, the best eight provenances included five from Quebec, and one each from New Brunswick, Ontario, and Wisconsin. The experiment shows that at the appropriate stage in a selection program, large plots can yield significant results, which has important implications for the design of experiments.

Key words: provenance tests, jack pine, experimental design, growth and yield

RÉSUMÉ

Vingt-cinq provenances d'épinette blanche ont été plantées en 1963 dans 144 parcelles suivant une triple répétition en tant qu'éléments d'une série de test de provenance dans l'est du Canada. Le site expérimental a été bien entretenu et éclairci à 50% de son niveau original de tiges par hectare en 1986 (à 26 ans à partir de la semence). Les mesures effectuées à l'âge de 44 ans ont été soumises à des analyses de variance et de corrélation et comparées avec la hauteur et la survie à l'âge de 15 ans. Les résultats démontrent qu'à l'âge de 15 ans, l'identification des meilleures provenances est inefficace par suite des changements de rangs et de l'expression tardive des différences de survie. À l'âge de 44 ans, des différences significatives entre les provenances ont été observées au niveau de la survie, de la hauteur moyenne, du diamètre, de la surface terrière et du volume. Le plus important volume a été produit par une provenance issue de Cushing dans la Vallée de l'Outaouais au Québec, soit 287 m³ par ha, ce qui était supérieur de 11% au volume de la provenance locale, Chalk River en Ontario. Une fois classées selon la survie et le volume, les huit meilleures provenances comprenaient cinq du Québec et une chacune pour le Nouveau-Brunswick, l'Ontario et le Wisconsin. L'essai démontre qu'au moment approprié d'un programme de sélection, les grandes parcelles peuvent démontrer des résultats significatifs ce qui entraînent des implications importantes au niveau de la conception des essais.

Mots clés : tests de provenance, pin gris, design expérimental, croissance et rendement

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Introduction

Studies of geographic variation in forest trees have covered a broad field of activities ranging from fundamental biosystematic and genecological research to more applied seed source or provenance studies. Biosystematics and genecology are usually explored in short-term experiments conducted in controlled environments such as greenhouses and nurseries by observing juvenile characteristics and phenology. In experiments with a hierarchical structure including populations (stands grouped by regions), subpopulations (stands within regions), and families of half-sibs (progenies of individual trees), genetic variances can be obtained in a very efficient manner from hundreds of seedlots in a relatively small area, and the responses related to climate and other factors of the place of seed origin. The results lend themselves to develop seed zones and rules for seed transfer (Morgenstern 1969, Beaulieu *et al.* 2004, Rehfeldt 2004).

In contrast, provenance studies designed to meet the needs of plantation silviculture (often constituting the second phase in a research program), require field tests with larger areas, more financial resources, and longer time periods before significant results appear. Such studies can be justified on the basis of information obtained on long-term adaptation and survival, resistance to climatic extremes and insects and diseases, wood quality, and volume production per unit area. The general rule is that half a rotation period must elapse before reliable results can be obtained (Schober 1961). It has been shown that often long-term survival is a critical factor and can disqualify early results because of minor differences in adaptation such as inadequate synchronization of the tested populations' seasonal development with the climate of the test area, which gradually accumulate over time and become very significant at the end (Silen 1978, Oleksyn and Giertych 1984). However, the design of such long-term experiments is critical (Cochrane and Cox 1957, Loo-Dinkins 1992).

Experiment 194-D-1 at the Petawawa Research Forest is a 4.6-ha white spruce (*Picea glauca* (Moench) Voss) test plantation, part of a provenance experiment designed by the late Mark Holst in 1958. It is part of a series of six tests, which were arranged in a transect across the province of Ontario from Fort Frances in the northwest to Owen Sound in the south, and planted in 1963 (Holst 1958). Although the location, layout and maintenance of this series with very large plots proved to be difficult, and most of the tests have only been measured once (Teich *et al.* 1975), the Petawawa test is in good condition and is contributing valuable data as will be shown in this paper.

Materials and Methods

During the winter of 1953–54 plans were made for a comprehensive white spruce provenance experiment that sampled the Great Lakes – St. Lawrence Forest Region (Rowe 1959). The Woodlands Section of the Canadian Pulp and Paper Association was contacted and promised support, and the provincial forest services of Ontario and Quebec, the U.S. Forest Service, and the University of Toronto also cooperated (Holst 1958). Seed collections were made in 75 natural stands primarily in 1956, a good seed year. The seed was divided into three parts, a western series with 25 provenances to be grown in Ontario, an eastern series with 25 provenances for Quebec,

New Brunswick and Newfoundland, and a combined series with 49 provenances for Ontario, Quebec and New Brunswick (Holst 1958, Corriveau and Boudoux 1971, Teich 1973). In this report only the Petawawa test plantation of the western series can be discussed (Exp. 194-D-1) because results from the other tests are not available and most have been abandoned. The 25 seedlots with their places of origin and latitudes and longitudes are given in Table 1 and a map of their origins in Fig. 1.

The seed was sown in the Petawawa tree breeding nursery in the spring of 1959, seedlings transplanted two years later in the nursery, and the resulting 2-2 stock outplanted in the spring of 1963. The test area is a former hardwood site with a fairly deep acidic till soil of medium fertility and level topography. The experimental design consisted of square plots with 12 rows of 12 trees each planted at 1.8 × 1.8 m spacing in a 5 × 5 balanced lattice square with three replications. In this design, rows and columns of the basic plan are randomized so that neighbourhoods of the same provenances are more often avoided than in randomized-block experiments, making the experiment more efficient (Cochrane and Cox 1957). Plots were separated by single division rows, and two surround rows formed the outside border, again all trees planted at 1.8-m spacing. These large (0.04 ha) plots were adopted to meet the requirements for long-term observation and determination of volume differences. Although very unusual in dimension in comparison with many other experiments, they approximately agreed with an expert's recommendation to use plots of 0.05 ha with conifers for a test period of 35 to 40 years in northern climates (Schober 1961).

Table 1. Provenance origin by seedlot number

Seedlot No.	Location	Province or State	Lat. N.	Long. W
2438	Cobourg	Ontario	44.1	78.0
2445	Cushing	Québec	45.6	74.5
2447	Grandes-Piles	Québec	46.7	73.1
2454	Lac Baskatong	Québec	47.0	75.6
2458	Bissett Creek South	Ontario	46.2	78.1
2462	Lac McNally	Québec	46.5	76.5
2463	Notre-Dame-du-Laus	Québec	46.0	75.4
2464	Chalk River	Ontario	45.9	77.4
2466	Manitoulin Island	Ontario	45.8	82.9
2467	Miller Lake	Ontario	45.0	81.3
2472	Price	Québec	48.2	67.8
2473	Edmundston	New Brunswick	47.4	68.2
2477	Ashley Mines	Ontario	48.0	81.0
2480	Kakabeka Falls	Ontario	48.5	89.5
2483	Pagwachuan Lake	Ontario	49.7	86.1
2484	Lac Mitchinamecus	Québec	47.4	75.1
2486	Swastika	Ontario	48.1	80.1
2491	Valcartier	Québec	46.9	71.5
2570	Chequamegon Nat. For.	Wisconsin	46.8	91.0
2571	Grand Rapids	Minnesota	47.5	94.0
2572	Huron Nat. For.	Michigan	44.5	83.7
2601	Cook County	Minnesota	47.7	90.1
2602	Luce County	Michigan	46.7	85.3
2603	Marquette County	Michigan	46.1	87.6
2604	Rivière Shipshaw	Québec	48.7	71.1

Fig. 1. Provenance origin in eastern Canada and the Lake States of USA (map courtesy of Dr. W.H. Parker).

The plantation grew well and was maintained by removal of competing vegetation. The first assessments were made in 1968 (age 10 years from seed) and 1973 (age 15) including total height and survival % (Teich 1973, Teich *et al.* 1975). As part of the western series, results from this experiment were also reported by Murray and Skeates (1985), and by Morgenstern and Copis (1999). In 1986 (age 26), every second tree in each row was removed by diagonal thinning, leaving 72 trees per plot if all had survived.

In this paper we report on results obtained in 2002 when the trees were 44 years old, and also use some of the 15-year results for comparison purposes. The 2002 measurements and survival counts were made on a maximum of the inner core 50 trees per plot (i.e., 1500 trees if extrapolated to a per-hectare basis). The following characteristics were assessed: survival percent, mean height, dominant height (the average height of the 20 trees per plot with the largest diameter), diameter at breast height (DBH) of all trees, basal area (BA) in square meters per hectare (ha), and wood volume in cubic meters per ha.

Heights were measured using a Criterion 400 Survey Laser instrument (manufactured by Laser Technology Inc.) on about half the trees in each plot, which were randomly

selected by diameter classes. Using these data, a separate height-diameter equation was calculated for each plot to estimate the height of the remaining trees based on the following variation of the Bertalanffy equation (Pinaar and Turnbull 1973):

$$[1] \quad ht = 1.3 + \beta_o \cdot (1 - e^{-\beta_1 \cdot DBH})^{\beta_2}$$

where β_o , β_1 , and β_2 are parameters to be estimated. Volumes were then estimated from equation 14 of Honer *et al.* (1983).

The statistical analyses included analyses of variance and correlation analyses. The analyses of variance at age 44 were based on plot means and included survival, mean height, diameter, basal area, and volume. We assumed a random model and used the randomized complete-block analysis (Steel and Torrie 1960). For survival, percentages were transformed by arcsin from Table A.10 of Steel and Torrie (1960) to meet the requirements of a normal distribution. The correlations were computed from a table of overall means.

The final procedure was the identification of the eight best provenances. From an inspection of the volumes calculated, one top provenance was recognized followed by a cluster of

Table 2. Provenance means over all replications for eight characteristics

Seed Lot No.	Age 15		Age 44					
	Survival %	Height cm	Survival %	Av. height m	Dom. height m	DBH cm	BA m ² /ha	Volume m ³ /ha
2438	88	335	77	15.2	16.8	18.8	34.6	240.1
2445	88	301	78	15.8	17.3	19.7	40.1	287.3
2447	86	324	81	15.3	16.8	18.6	37.4	261.4
2454	89	315	77	15.0	16.8	19.0	35.9	248.9
2458	92	309	81	14.6	16.2	18.2	34.7	231.0
2462	83	269	79	15.3	16.8	18.9	36.9	256.8
2463	86	341	78	15.3	16.9	19.3	37.5	263.2
2464	88	306	78	16.0	17.6	18.9	36.0	259.1
2466	94	306	79	13.9	15.6	17.8	31.8	207.5
2467	81	283	73	14.1	15.3	18.5	30.2	195.7
2472	86	269	78	14.4	15.9	18.8	36.0	238.1
2473	90	301	80	15.0	16.4	19.0	38.2	259.2
2477	96	266	75	15.4	17.3	18.5	31.8	224.0
2480	85	257	79	14.1	15.9	18.0	32.9	216.7
2483	89	237	79	13.5	15.1	17.6	31.2	196.3
2484	83	280	76	14.5	15.9	18.7	33.1	220.4
2486	83	321	76	15.4	17.0	18.8	33.8	237.3
2491	92	269	80	14.7	16.4	18.9	37.4	254.0
2570	77	280	80	15.5	17.4	18.8	36.5	259.0
2571	83	298	75	15.2	16.8	18.6	32.3	224.1
2572	75	283	72	14.7	16.0	19.0	31.3	208.6
2601	75	280	76	13.8	15.5	17.5	29.2	189.1
2602	86	295	73	13.7	14.8	18.9	31.8	201.4
2603	90	251	75	14.2	15.7	19.0	33.6	221.7
2604	82	237	75	14.2	15.5	18.5	31.7	206.3
Mean	86	289	77	14.8	16.3	18.7	34.2	232.3

Table 3. Mean squares (M.S.) and F-values (F) from the analyses of variance at age 44^a

Source		Survival		Mean height		Diameter		Basal area		Volume	
		M.S.	F	M.S.	F	M.S.	F	M.S.	F	M.S.	F
Provenances	d.f. = 24	52.45	1.76*	2.05	5.54**	1.71	2.48**	37.88	4.91**	2816	3.09**
Blocks	d.f. = 2	7.16	0.24	3.16	8.54**	0.90	1.30	11.71	1.52	664	0.73
Errors	d.f. = 48	29.86		0.37		0.69		7.72		910	

^aSignificance levels: *, 5%; **, 1% and higher.**Table 4. Pearson correlation coefficients among seven characteristics at ages 15 and 44, and latitude of origin^a**

		X ₁	X ₂	X ₃	X ₄	X ₅	X ₆	X ₇	X ₈
X ₁	Survival ₁₅	1.00	0.38	-0.05	0.10	0.03	0.29	0.24	0.08
X ₂	Survival ₄₄		1.00	0.11	0.22	-0.13	0.62**	0.54**	0.24
X ₃	Height ₁₅			1.00	0.49*	0.35	0.36	0.43*	-0.48*
X ₄	Height ₄₄				1.00	0.65**	0.67**	0.83**	-0.27
X ₅	DBH ₄₄					1.00	0.69**	0.71**	-0.44*
X ₆	BA ₄₄						1.00	0.97**	-0.14
X ₇	Vol ₄₄							1.00	-0.19
X ₈	Latitude								1.00

^aSignificance levels: *, 5%; **, 1% (23 d.f.)

Table 5. The top eight provenances when ranked at ages 15 and 44 for several characteristics according to a point system.

Age 15		Age 44							
Height		Height		Survival		Volume		Survival & Volume Combined	
Provenance	Points	Provenance	Points	Provenance	Points	Provenance	Points	Provenance	Points
Notre-Dame-du-Laus	1	Chalk River	1	Grandes-Piles	1	Cushing	1	Grandes-Piles	4
Cobourg	2	Cushing	2	Bissett Creek	1	Notre-Dame-du-Laus	2	Cushing	5
Grandes-Piles	3	Chequamegon	3	Edmundston	2	Grandes-Piles	3	Notre-Dame-du-Laus	6
Swastika	4	Ashley Mines	4	Valcartier	2	Chalk River	4	Edmundston	6
Lac Baskatong	5	Swastika	4	Chequamegon	2	Edmundston	4	Chequamegon	8
Bissett Creek	6	Notre-Dame-du-Laus	5	Lac McNally	3	Chequamegon	4	Chalk River	9
Chalk River	7	Grandes -Piles	5	Manitoulin Island	3	Lac McNally	5	Lac McNally	10
Manitoulin Island	7	Lac McNally	5	Kakabeka	3	Valcartier	6	Valcartier	10

seven provenances with minor differences and then a substantial drop in the remainder. As a result, the best eight provenances were identified at every stage and a point system used assigning points 1, 2, 3 to the first-, second-, and third-highest ranking provenances, etc. and the sum of individual points when the ranking was based on the combined value of two characteristics, such as survival and volume.

Results

A summary of results in the form of provenance means over all replications at ages 15 and 44 from seed is given in Table 2. The 15-year data were taken from Tables 5 and 6 of Teich *et al.* (1975). The results of the analysis of variance at age 44 for survival, mean height, diameter, basal area and volume are presented in Table 3. Correlation coefficients for all seven characteristics and latitude of origin are shown in Table 4, and a list of the eight best provenances in Table 5.

General observation

The growth of the plantation reflects a site of intermediate productivity. The local provenance, S.2464, Chalk River, had reached an average height of 16.0 m, dominant height of 17.6 m, basal area of 36.0 m² and volume of 259 m³ (Table 2). It exceeded the plantation average in every characteristic. When compared with figures in a local yield table (Berry 1978), it ranks somewhere between Site Class 18 and 21 where 15 is the lowest and 24 the highest class. In contrast to earlier impressions, this is only an average site and growth was not as rapid as expected on the basis of earlier observations.

Survival

At age 15, mean survival was 86% and there was no significant difference among provenances at the 5% level (Teich *et al.* 1975). By age 44 it had declined only 9% to 77% and the differences had become significant at the 5% level according to the analysis of variance (Table 3). Correlations were significant between age 44 survival and basal area and volume (Table 4).

Height

At age 15, mean height had differed significantly only at the extremely low level of 25% as shown by Teich *et al.* (1975) in their Table 2 but by age 44 had differentiated much and was significant at 0.01% (higher level than shown in Table 3).

Correlations were significant between height at age 15 and height at 44, and between height at 15 and volume, and height at 44 and diameter, basal area, and volume. Correlations between latitude and height were always negative and significant only at age 15 (Table 4).

Diameter

Diameters differed significantly among provenances at the 1% level (Table 3). As expected, they are strongly correlated with basal area and volume (Table 4).

Basal area

Basal area ranged from 29.2 to 40.1 m² per ha (Table 2) and differed significantly among provenances at the 1% level (Table 3).

Volume

Volume ranged from 189 to 287 m³ per ha and differed significantly at the 1% level (Tables 2 and 3). The top ranking provenance, S.2445, Cushing, with 287 m³, exceeded the local, S.2464, Chalk River with 259 m³ by 10.8%.

Discussion

It is a well-known principle of genetic and yield studies that favourable environments accelerate growth and differentiation. Consequently, this experiment, on an average site, can be expected to develop greater differences in survival and volume during the next one or two decades. For this reason it should be maintained and protected for some time to come.

A second important principle of provenance research is that statistical tests of significance are not independent of sampling and field testing. In short-term studies, when many provenances can be grown in a small area, clinal variation in phenology and growth in response to natural selection by photoperiod and temperature is commonly observed and confirmed by significant correlations in our northern, widely distributed conifers (Morgenstern 1996). This correlation is strongest with the weekly decline in day length between the longest day, 21 June and the day of the fall equinox, 23 September (Withrow 1959). In contrast, in long-term field experiments with greater environmental confounding influences, this clinal trend is not always detected. In this experiment, particularly, it is therefore not surprising that this trend is only weakly expressed by negative, usually non-significant

correlations with latitude (Table 4). The fact that the south-north distribution of the provenances sampled is relatively narrow may also be involved (Fig. 1).

There is a substantial difference between early and late results. At age 15, height was only correlated at the 5% level with height at 44 and with volume (Table 3). Only four of the eight tallest provenances at age 15 were also among the tallest at age 44 (Table 5). Significant differences in survival were not detected until age 44 (Table 3).

The eight best provenances with greatest survival and volume come primarily from southeastern Quebec and the Ottawa Valley in Quebec and Ontario. Exceptions are Edmundston, New Brunswick, and Chequamegon, Wisconsin, United States. Most of these provenances originated from areas within 1 to 1.5 degrees of latitude from the test site (Tables 1, 2, 5). The excellent performance of Cushing is of special interest because it confirms the existence of vigorous populations in the Ottawa Valley east of the Petawawa Research Forest. Another Ottawa Valley provenance from Beachburg performed very well in several companion experiments of the 194 series (Teich *et al.* 1975), and it was the top performer at the 14 test sites in the Lake States and New Brunswick in a cooperative series initiated by the U.S. Forest Service (Nienstaedt 1969, Nienstaedt and Teich 1972). For this reason the Petawawa National Forestry Institute selected several hundred plus trees in many stands in the area east of Pembroke and established a clonal seed orchard (Murray and Cheliak 1984). Provenances from this area were also included in the new range-wide test series established between 1979 and 1984 (Ying 1980), which has already yielded results to study potential effects of climate change and carbon sequestration (Cherry and Parker 2003).

The two southernmost provenances, Cobourg (lat. 44.1°N) and Huron National Forest (lat. 44.5°N) have not been growing well and are in 10th and 19th position for volume (Table 2). From two tests, one on a granitic (acid) site at Petawawa, and another on a limestone site at Lake Dore 56 km to the south, Teich and Holst (1974) obtained a significant provenance-site interaction, and proposed an ecotype hypothesis. The limestone-origin provenances grow better on the limestone site and the granitic-origin provenances performed better on the granitic site. Cobourg is a limestone-origin provenance. How general this hypothesis applies is not known. In another sample of provenances, Lesser *et al.* (2004) could not confirm the hypothesis.

Another plausible theory is inbreeding: disjunct or isolated small populations mate with close relatives and become less variable and more narrowly adapted. This theory has merit because low levels of inbreeding are not rare in this species (Coles and Fowler 1976), and the Cobourg area stands are definitely small and isolated.

Conclusion

This test has contributed valuable information with respect to provenance origin. The excellent performance of Cushing, Que. is further evidence for the existence of fast-growing populations in the Ottawa Valley.

The history of this experiment contains important lessons with respect to experimental design. Shortly after this experimental series was established across Ontario, difficulties with these large inflexible square plots and blocks became evident during layout and maintenance. At the same time, a very

influential paper (Wright and Freeland 1960) stressed the advantage of many replications and small plots. In consequence, the next white spruce test series was redesigned and smaller plots were adopted. Unfortunately, the cited authors had focussed attention on one test environment only and neglected the fact that each experiment should have at least two test environments in the same region to determine the provenance-environment interaction. In that situation, the error variance (which determines statistical efficiency) is calculated from all replications over all environments, i.e., it is a pooled error. In such a situation, experience has shown that it is usually more efficient to include more environments with fewer replications than vice versa, so that often two or three replications per environment are sufficient (Loo-Dinkins 1992, Morgenstern 1996). In addition, large square plots have advantages because they yield results independent of plot-to-plot competition and allow for calculations on a per-unit area basis and are therefore much more useful for long-term studies than row-plots. It is now important to learn that lesson.

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