Literature Cited

Ando, T.: Ecological studies on stand density control in even-aged pure stand. Bull. For. & For. Prod. Res. Inst. No. **210**, 1—153, (1968). —— Drew, T. J. and Flewelling, J. W.: Some recent Japanese Theories of yield-density relationships and their application to Monterey pine plantations. For. Sci. **23**, 517—534, (1977). —— Drew, T. J. and Flewelling, J. W.: Stand density management: an alternative approach and its application to Douglas-fir plantations. For. Sci. **25**, 518—532, (1979). —— Dutrow, G. and Row, C.: Measuring financial gains from genetically superior trees. U. S. Department of Agriculture, Forest Service, Res. Paper SO-132, 11p., (1976). —— Falconer, D. S.: Introduction to quantitative genetics. Ronald Press, New York. 365p, (1960). —— Forest Agency: A stand density control diagram on HINOKI in Kyushu area. Japanese Forest Technical Association, Tokyo. 6p. plus one plate, (1982). —— Forest Agency and For. & For. Prod. Res. Inst.: Yield table on HINOKI in Kyushu area. Research note on yield tables No. **19**. Forest Agency and Kumamoto Forest regional office, Kumamoto. 49p, (1962). —— Franklin, E. C.: Model relating levels of genetic variance to stand development of four American conifers. Silvae Genetica **28** (5—6), 207—212, (1979). —— Kira, T., Ogawa, H. and Sakazaki, N.: Intraspecific competition among higher plants. I. Competition-yield-density interrelationship in regularly dispersed populations. Jour. Inst. Polytch., Osaka City Univ. D, **4**, 1—16, (1953). —— Lambeth, C. and van Buijtenen, J. P., Duke, S. D. and McCullough, R. B.: Early selection is effective in 20-year-old genetic tests of loblolly pine. Silvae Genetica **32** (5—6), 210—215, (1983). —— Manabe, A.: Studies on the construction forecast and stumpage appraisal systems for Todomatu (*Abies sachalinensis*). Bull. For. and For. Prod. Res. Inst. No. **317**, 1—65, (1982). —— Osborne, J. G. and Schumacher: The construction of of normal-yield table and stand tables for even-aged timber stands. Jour. Agric. Res. **51**, 547—564, (1935). —— Searle, S. R.: Linear models. John Wiley and Sons, New York. 532p, (1971). —— Tadaki, Y.: Effect of thinning on stem volume yield studied with competition density effect — On the case of *Pinus densiflora* —. Bull. For. and For. Prod. Res. Inst. No. **166**, 1—22, (1964). —— Talbert, J. T.: One generation of loblolly pine tree improvement: Results and Challenges. Proc. 18th Can. Tree Imp. Assoc. Meeting, Duncan, B. C. 15pp, (1981). —— Toda, R.: Studies on the genetic variance in *Cryptomeria*. Bull. For. and For. Prod. Res. Inst. No. 132, 1—46, (1961). —— Warren, L. N. and Wells, O. O.: Site index models for height growth of planted loblolly pine (*Pinus taeda* L.) seed sources. In: Proc. 16th Southern For. Tree Improvement Conference, 86—96, (1981). —— Yahata, H. H., Miyazima, H. and Nogami, K.: Studies on genetic variance in Hinoki (II). Trans. 26th Annu. Mtg., Jap. For. Soc. of Kyushu, 157—158, (1973).

Genetic Variation in Red Spruce (Picea rubens Sarg.)

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Summary

The paper discusses the nature, magnitude and trends of variation in red spruce (*Picea rubens* (Sarg.)) on the basis of twenty-year results of growth, phenology and crown form and recommends provenances most suitable for Newfoundland. Provenances are a significant source of variation in characters of growth, phenology and crown form, except branch angle. Inter- and intra-provenance variation is significant in all characters and is clinal with geographic coordinates. Characters of crown form appear to be closely associated with growth characters. Intra-provenance variation in all characters is partly due to introgression with black spruce (*Picea mariana* (Mill.) B. S. P.). Putative natural hybrids from the lowlands of New Brunswick have shown positive heterosis at the test site rather than the negative heterosis in artificial hybrids, reported earlier.

Red spruce is potentially promising for Newfoundland. The provenances in the top quartile are from the lowlands of New Brunswick and Nova Scotia. Family selection from superior provenances is advocated for best genetic gains. Early selection of superior provenances at ten-year age is possible in red spruce.

Key words: Red spruce; *Picea rubens* Sarg.; Provenance study; Variation; Phenology; Growth; Crown form; Clinal variation.

Résumé

La nature, l'ampleur et les tendances des variations de la croissance, de la phénologie et de la forme de la cime de l'épinette rouge (*Picea rubens*) sont examinées à partir des résultats de vingt années, et les provenances les mieux adaptées à Terre-Neuve sont recommandées Les provenances sont une source importante de variation pour les caractères de croissance, de phénologie et de forme de la cime, sauf pour l'angel des branches. La variation inter provenance et intraprovenance est importante pour tous les caractères et est clinale suivant les coordannées géographiques. Les caractères de forme de la cime semblent étroitement associés à ceux de croissance. La variation intraprovenance pour tous les caractères est due en partie à l'introgression avec l'épinette noire (*Picea mariana* Mill. B.S.P.). Des hybrides supposés naturels des basses-terres du Nouveau-Brunswick ont démonstré une hétérosis positive dans du lieu d'expérience et non l'hétérosis négative des hybrides artificiels dont il a été fait état.

L'épinette rouge semble une espèce prometteuse pour Terre-Neuve Les meilleures provenances dans le quartile supérieur proviennent des basses-terres du Nouveau-Brunswick et de la Nouvelle-Écosse. La sélection de familles des provenances supérieures est recommandée pour obtenir les meilleurs gains génétiques Une sélection précoce des provenances supérieures à dix ans est possible dans le cas de l'épinette rouge.

Zusammenfassung

Das Manuskript diskutiert die Natur, den Umfang und die Trends der Variation bei *Picea rubens* (Sarg.) auf der Basis der Wachstumsergebnisse, der Phänologie und Kronenform und empfiehlt die geeignetsten Herkünfte für Neufundland. Abgesehen vom Astwinkel sind die Herkünfte eine signifikante Variationsursache bei den Merkmalen Wachstum, Phänologie und Kronenform. Die Variation zwischen den Herkünften sowie innerhalb der Herkünfte ist bei allen Merkmalen signifikant und erweist sich in Bezug auf die geographischen Koordinaten als klinal. Die Merkmale der Kronenform scheinen am engsten mit den Wachstumsmerkmalen gekoppelt zu sein. Die Variation innerhalb der Provenienzen ist bei allen Merkmalen zum Teil der Introgression mit *Picea mariana* (Mill.) B. S P. zuzuschreiben. Vermeintliche natürliche Hybriden aus dem

Table 1. — List of provenances.

Prov. No.	Location	Latitude (°N)	Longitude (°W)	Altitude (m)	Forest* section/Forest cover type
1.	Napadogan, York County, New Brunswick	46.40°	66.98°	260–275	A.2 - Upper Miramichi-Tobique
2.	Great Salmon River, Saint John County, New Brunswick	45.42°	65.42°	105–275	A.9 - Fundy Coast
3.	Timber Lake, Lunenburg County, Nova Scotia	44.68°	64.15°	75–120	A.11 - Atlantic Uplands
4.	Sisters Brook, York County, New Brunswick	46.62°	66.67°	230	A.2 - Upper Miramichi-Tobique
5.	Scott's Bay, King's County, Nova Scotia	45.30°	64.40°	0–150	A.9 - Fundy Coast
6.	Corberrie, Digby County, Nova Scotia	44.17°	65.92°	45–60	A.11 - Atlantic Uplands
7.	Waverley, Halifax County, Nova Scotia	44.78°	63.58°	30–75	A.11 - Atlantic Uplands
8.	Headwaters, East Sheet Harbour River, Nova Scotia	45.22°	62.73°	185	A.11 - Atlantic Uplands
9.	Hart's Lake, Colchester County, Nova Scotia	45.57°	63.52°	275–305	A.3 - Eastern Lowlands
10.	Economy River, Colchester County, Nova Scotia	45.48°	63.93°	185	A.13 - Cobiquid
11.	Canaan Mountain, West Virginia, U.S.A.	39.08°	79.50°	670–915	Eastern spruce - fir
12.	Monongahela National Forest, West Virginia, U.S.A.	38.67°	79.62°	1 145–1 250	Eastern spruce - fir
13.	New River Watershed, Charlotte County, New Brunswick	45.22°	66.55°	60–90	A.9 - Fundy Coast
14.	Upper Blackville, New Brunswick	46.65°	65.85°	60	A.3 - Eastern Lowlands
15.	Rocky Brook, York County, New Brunswick	46.63°	66.62°	245–305	A.2 - Upper Miramichi-Tobique
16.	Acadia Forestry Station, Fredericton, New Brunswick	46.02°	66.25°	60	A.3 - Eastern Lowlands
17.	Boyne Road, Sunbury County, New Brunswick	45.55°	66.52°	45	A.3 - Eastern Lowlands
18.	Lakelands, Cumberland County, Nova Scotia	45.47°	64.33°	30	A.12 - Central Lowlands
19.	Chezzetcook, Nova Scotia	44.75°	63.23°	30	A.11 - Atlantic Uplands
20.	South Paradise, Annapolis County, Nova Scotia	44.85°	65.20°	105	A.12 - Central Lowlands
21.	Blanchard, Pictou County, Nova Scotia	45.47°	62.45°	215	A.13 - Cobiquid
22.	Snare Lake, Colchester County, Nova Scotia	45.58°	63.48°	335	A.3 - Eastern Lowlands
23.	West of Five Mile Lake, Hant's County, Nova Scotia	44.85°	64.00°	150	A.11 - Atlantic Uplands
24.	Crooked Creek, Albert County, New Brunswick	45.82°	65.80°	275	A.9 - Fundy Coast
25.	West of Great Salmon River, Saint John County, New Brunswick	45.42°	65.43°	185	A.9 - Fundy Coast
26.	Penobscot Forest Experiment Station, Maine, U.S.A.	44.87°	68.63°	45	Eastern spruce - fir
27.	Evans Brook, Annapolis County, Nova Scotia	44.70°	65.35°	185	A.12 - Central Lowlands
28.	Little Black River, Maine, U.S.A.	47.22°	69.23°	215–365	Eastern spruce - fir
29.	Nictaux West, Annapolis County, Nova Scotia	44.92°	65.10°	15–30	A.12 - Central Lowlands
30.	Mush-a-mush and Spondo Lakes, Lunenburg County, Nova Scotia	44.53°	64.48°	90–120	A.11 - Atlantic Uplands

*) Eyre (1980); Rowe (1972).

Flachland von New Brunswick zeigten auf dem Versuchsstandort positive Heterosis, vielmehr als die negative Heterosis bei künstlichen Hybriden, über die früher berichtet wurde. *Picea rubens* ist in Neufundland recht vielversprechend. Die im Spitzenbereich liegenden Herkünfte stammen aus dem Flachland von New Brunswick und Nova Scotia. Von einer Familienselektion bei den überlegenen Herkünften kann ein optimaler genetischer Gewinn erwartet werden. Eine Frühselektion auf überlegene Provenienzen ist bei *Picea rubens* im Alter 10 möglich.

Introduction

Wide use of red spruce (*Picea rubens* SARG.) for lumber and pulpwood makes it a very useful species of northeastern North Amerika (MULLINS and MCKNIGHT, 1981). Red spruce is an important component of the Acadian forest region of Canada (ROWE, 1972) and the adjoining forest cover types of the United States (EYRE, 1980) It has a continous distribution in the area bounded by latitudes 43°—48°N and longitudes 60°—75° W and occurs as isolated stands southwards to 35° N latitude and westwards to 85° W longitude (FOWELLS, 1965). The varriable climate of this area, resulting mainly from physiography and maritime influences and introgression with black spruce (*Picea mariana* (MILL.) B. S. P.), have affected its micro-evolution. These influences are expected to produce much genetic variation. Study of the nature, magnitude and trends of this variation is essential for planning a rational strategy for genetic improvement of the species. One such study was initiated at the Newfoundland Forest Research Centre of the Canadian Forestry Service in 1964 in cooperation with the Maritimes Forest Research Centre, Fredericton, New Brunswick. Preliminary results of this study have been published (KHALIL, 1974, 1981). This paper presents the full synthesis of twenty-year results.

Material and Methods

The Provenances

Bulked seed were obtained from 26 Canadian and four United States provenances, located between latitudees 38.67° and 47.22° N and longitudes **62.45°** and 79.62° W, in six forest sections of the Acadian forest region in Canada (ROWE, 1972) and Eastern spruce - fir forest cover type in U.S.A. (EYRE, 1980) (*Table 1, Fig. 1*).

The two known sources of genetic variation in these populations are natural selection, due to climatic variation, and introgression with black spruce. Climatic variation in this region is produced by the existence of two main climatic

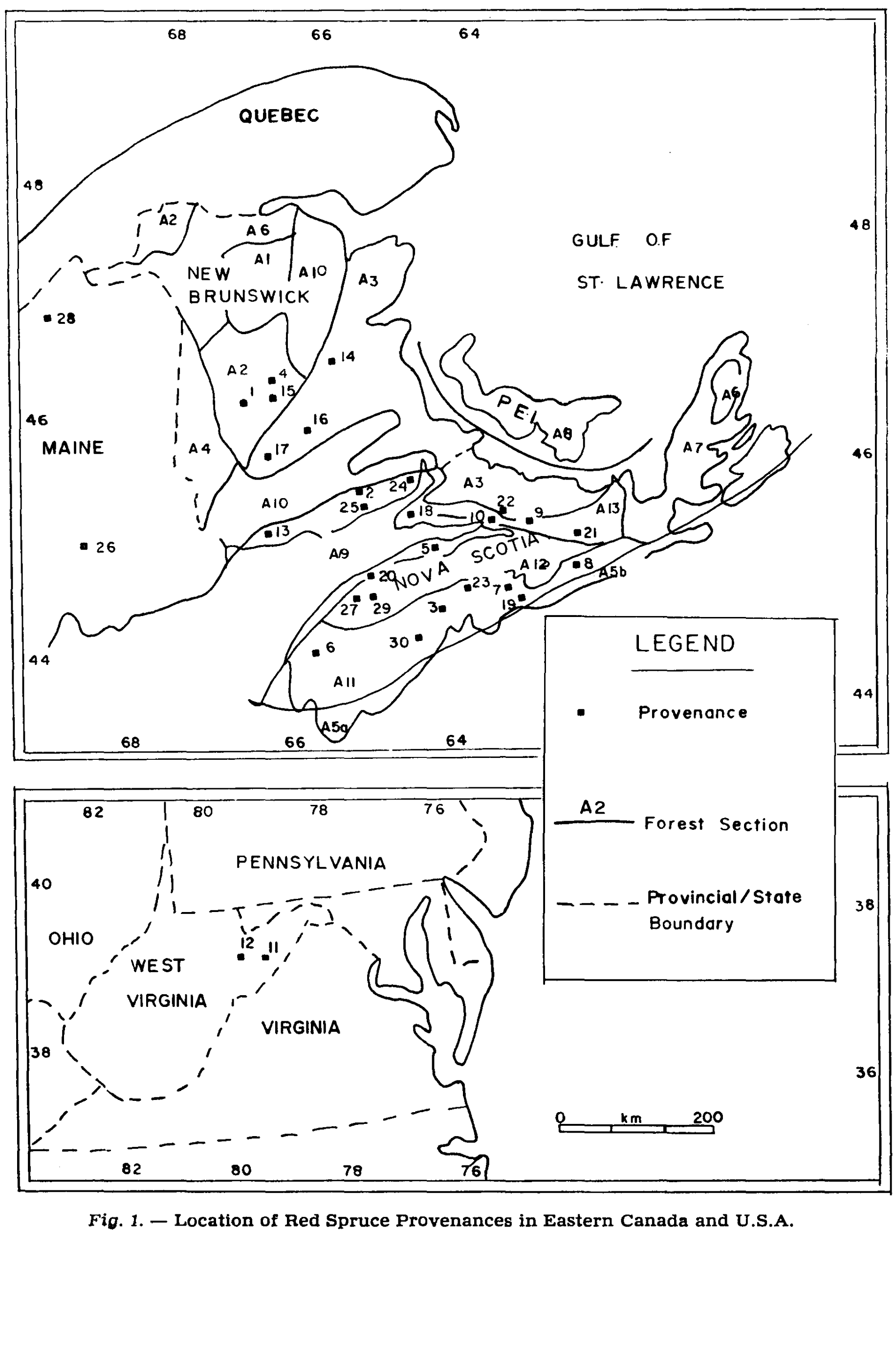

Fig. 1. — **Location of Red Spruce Provenances in Eastern Canada and U.S.A.**

zones and their numerous local variations. These are continental and maritime climates (HUSCKE, 1959), both of which have been effectively sampled. The areas of continental climate are represented by 10 provenances from inland New Brunswick in Canada and from Maine and West Virginia in U.S.A. The climate and vegetation are strongly influenced by abrupt physiographic changes, exerting considerable influence on movement and interaction of continental and maritime air masses. The areas of maritime climate are represented by 20 provenances from Nova Scotia and coastal New Brunswick (ANONYMOUS. 1960; HAWBOLDT and BULMER, 1958; LOUCKS, 1962 and PUTNAM, 1965).

Interspecific hybridization with black spruce is known since long (HEIMBURGER, 1939) and its extent and effects have been well documented. Introgression between red and black spruce is extensive wherever the two species are sympatric. All populations in central New Brunswick and its lowlands are introgressed (MORGENSTERN and FARRAR, 1964). Lowlands, gentle slopes and flat uplands form a continuum between the characteristic habitats, permitting extensive contact between the two species (MANLEY, 1971, 1972). Ecological barriers (MORGENSTERN and FARRAR, 1964) and possibly negative heterosis observed in artificial hybrids (MANLEY and LEDIG, 1979) appear to be the only impediments to hybridization, resulting in the existence of pure forms of these species in addition to hybrids. Variation in height is more closely related to the degree of introgression than to geographic coordinates and precipitation at the source of provenances. The provenances of natural hybrids with the strongest black spruce influence are the best (MORGENSTERN *et al.*, 1981).

The Experiment

The experiment was established in spring 1964 in the North Pond area in east-central Newfoundland (lat. 48.67°N, long. 54.57°W, elevation 107 m) on flat terrain with excessively-drained stony-sandy loam soil of land capability class 5^{F}_{M} (ANONYMOUS, 1972; McCORMACK, 1970). The test site, which formerly supported a mixed balsam fir (*Abies balsamea* (L.) MILL.) — black spruce —white birch (*Betula papyrifera* MARSH.) stand, was clearcut in 1958 and accidentally burnt in 1961, leaving a partially burnt humus layer 5—8 cm deep. It was nutrient poor due to fire and excessive leaching, but the remaining vegetation offered little competition for the remaining nutrients. The experimental area has less favourable growth conditions than the region of seed origin in mean number of frost-free days, mean number of growing days, mean and maximum temperatures, average rainfall in the May-September period and the number of degree-days above 5.6° C (CHAPMAN and BROWN, 1966; ROWE, 1972).

The planting stock comprised 2 + 2 seedlings raised at the Maritimes Forest Research Centre, Fredericton, New Brunswick (lat. 46.77°N, long. 66.25°W). A ten-replicated randomized complete block design was used, with four-seedling square plots and seedlings spaced 1.8 × 1.8 m.

The Data

Measurements were made on all existing trees in each plot in fall 1979 at the age of 20 years from seed. Survival counts were made in each plot and the measurements comprised height, diameter at 0.6 m, and number of branches, crown width and branch angle in the 15th year whorl. The last two measurements were made in duplicate at right angles to each other. Height growth during the 1969—1979 period was calculated from the 1972 measurements.

The Statistical and Genetical Analyses

Analyses of variance

These were performed for all characters except survival which was 98.8% and did not warrant any statistical analyses. Plot means were used to estimate missing values among the four trees in each plot. In case of crown width and branch angle, the second measurements were used to estimate a single missing measurement. Where both measurements were missing the plot means for the remaining tree measurements in the plot were used. The mixed mathematical model, with sampling and sub-sampling, was adopted, using provenances as fixed effects and replications, sampling and sub-sampling as random effects. The equation in STEEL and TORRIE 1980, p. 219 was used with addition of the sub-sampling error term "s_{ijkl}" for crown diameter and branch angle. In the absence of certainty about the existence of replications × provenances interaction, this procedure was considered safe because of the conservative nature of the F-tests in the analyses of variance and the BONFERRONI t-tests. Coefficients of intraclass correlation and determination were calculated to estimate intra-provenance variation.

Bonferroni t-tests for pairwise and general contrasts

These tests were performed according to DOUGLAS (1979) for all characters to make all possible pairwise comparisons between provenances and between their meaningful geographic groups as follows:

New Brunswick: Nova Scotia
Within New Brunswick, Lowlands: Uplands
Within New Brunswick, Lowlands: Coastal areas
Within Bay of Fundy coastal areas, Northern: Southern coast
Within Nova Scotia, Coastal: Inland areas
Within Inland Nova Scotia, Forest Sections A.11: A.12 and A.12: A.13

Equation (1) was used. If the value of the contrast C*) was less than the test statistic B, the null hypothesis H_0: $C = 0$, H_A: $C \neq 0$ was not rejected.

$$B = t_{p,n,f} \left[EEMS \left(\sum_{i=1}^{m} \frac{c_i^2}{r_i} \right) \right]^{\frac{1}{2}} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (1)$$

where B = Value of the test statistic with which the value of each contrast (C)* is compared

*$C = \Sigma c_i \bar{x}_i$, where $\bar{x}_i$ is the mean value of provenance i and c is a constant, such that $\Sigma c_i = 0$.

$t_{p,n,f}$ = Tabulated value of t for an overall probability of p, for n contrasts and f experimental error degrees of freedom.

P = Number of means compared

EEMS = Experimental Error Mean Squares in the analyses of variance

r_i = Number of observations

Regression analyses

Step-wise regression analyses were performed on the 1979 data and the 1972 phenology data to estimate the influence of geographic coordinates at the origin of the provenances on the expression of these characters under the conditions of the test site and to establish geographic trends in them. Mean value of the character was used as the dependent variable and latitude, longitude and altitude at the origin of the provenances as independent variables (DRAPER and SMITH, 1981, Equation 5.0.1).

Table 2. — Summary of analyses of variance.

Source of variation	Expected mean squares	Expected degrees of freedom	Characters with sampling									Characters with sub-sampling					
			Height			Diameter			No. of branches			Crown width			Branch angle		
			D.F.	Var. %	F	D.F.	Var. %	F	D.F.	Var. %	F	D.F.	Var. %	F	D.F.	Var. %	F
Replications (R)	$\sigma_d^2 + t\sigma_e^2 + tp\sigma_r^2$	r-1	9	5.11	5.63***	9	3.31	3.65***	9	3.48	4.06***						
Provenances (P)	$\sigma_d^2 + t\sigma_e^2 + tr\Sigma P_j^2/(p-1)$	p-1	29	9.83	3.36***	29	9.05	3.11***	29	5.40	1.95***						
Experimental error (R x P)	$\sigma_d^2 + t\sigma_e^2$	(r-1)(p-1)	261	26.31	1.52***	261	26.23	1.44***	261	24.87	1.25***						
Sampling error (T/RP)	σ_d^2	rp(t-1)	884	58.75		883	61.42		862	66.25							
Total		rpt-1	1 183	100.00		1 182	100.00		1 162	100.00							
Coefficient of intraclass correlation				0.6313			0.6043			0.4086							
Coefficient of intraclass determination				0.3985			0.3652			0.1670							
Replications (R)	$\sigma_s^2 + m\sigma_d^2 + mt\sigma_e^2 + mtp\sigma_r^2$	r-1										9	8.41	10.39***	9	3.46	5.000***
Provenances (P)	$\sigma_s^2 + m\sigma_d^2 + mt\sigma_e^2 + mtr\Sigma P_j^2/(p-1)$	p-1										29	7.42	2.84***	29	3.06	1.37NS
Experimental error	$\sigma_s^2 + m\sigma_d^2 + mt\sigma_e^2$	(r-1)(p-1)										261	23.48	1.64***	261	20.08	1.27***
Sampling error (T/RP)	$\sigma_s^2 + m\sigma_d^2$	rp(t-1)										863	47.29	4.67***	859	52.17	3.29***
Sub-sampling error (M/TRP)	σ_s^2	rpt(m-1)										1 143	13.40		1 151	21.23	
Total		rptm-1										2 305	100.00		2 309	100.00	
Coefficient of intraclass correlation													0.4006			0.1187	
Coefficient of intraclass determination													0.1605			0.0141	

Note — The deviations in degrees of freedom from the expected values are due to missing observations.
***) — Statistically significant (0.005 level).
NS — Statistically non-significant (0.05 level).

Simple regression analyses were done with the 1979 height as the dependent variable and the 1969 and 1972 heights as independent variables to estimate the influence of the latter on total height. Simple regression analysis was also performed with growth during the 1969—79 period as the dependent variable and 1969 height as the independent variable to estimate the influence of the pre-1969 growth on subsequent growth.

Results and Discussion

Analyses of Variance

Table 2 summarizes these results. The high significance of replications indicates adequacy of the size and design of the experiment for detecting and removing the unwanted variation due to environmental differences within the experiment and improving the credibility of the F-tests for provenances. The inter-replications variation appears to have been caused by differential effects of the 1961 fire on soil nutrients in the different replications and differential recovery from it. The significance of experimental error for all characters throws light on replications × provenances interaction and intra-provenance variation. Experimental error measures two effects, i. e. variation of the same provenance in the same plot or replication (σ^2) plus variation of the same provenance in different plots or replications × provenances interaction (σ^2_ε). Significance of the experimental mean squares indicates that either one or both of the above components are significant. Though it is not possible to know from this experiment whether the above interaction exists its possibility cannot be excluded. However, consideration of variation due to sampling error is helpful in understanding the variation of the same provenance in the same plot or replication (σ^2). These values are high (47.29—66.25 percent). This variation is the sum of the variations due to intra-provenance genetic differences and intra-plot environmental differences. Minimization of the latter by the small size and square shape of the plot suggests that most of this variation is due to intra-aovenance genetic differences. This inference is further supported by the low values of the coefficients of intraclass determination for all characters, particularly those of crown form. These results also suggest that most of the variation in experimental error is intra-plot variation and only a small proportion is due to the replications × provenances interaction. However, whether this interaction is significant or not, the F-tests for provenances are statistically valid (Steel and Torrie, 1980, p. 219).

Comparison of the distribution of variation in height in 1969 and 1979 is interesting (*Table 3*). The variation due to replications increased while that due to the replications × provenances interaction and sampling error decreased slightly, indicating a possible reduction of nutrient differences between replications caused by differential recovery from the 1961 fire. The decrease in variation due to provenances and sampling error is small, indicating lack of significant change in inter- and intra-provenance variation.

Bonferroni T-Tests for Pairwise and General Contrasts

Bonferroni t-tests show significant differences among provenances (0.05 and 0.01 level) in all characters, including branch angle, for which provenances are a nonsignificant source of variation. Provenance 5 has larger branch angles than provenances 8 and 23. The results for the remaining characters are summarized in *Table 4*. Contrasts among groups show significant differences only in growth and crown width between three forest sections in New Brunswick. Lowland provenances (forest section A.3) are faster growing than coastal ones (forest section A.9) and have larger crowns than coastal and upland provenances (forest sections A.9 and A.2 respectively).

Table 3. — Comparison of analyses of variance for height in 1969 and 1979.

Source of variation	Deg. of freedom 1969	Deg. of freedom 1979	Height 1969 Var %	Height 1969 F	Height 1979 Var %	Height 1979 F
Replications	9	9	1.28	1.34^{NS}	5.11	5.63***
Provenances	29	29	10.11	3.29***	9.83	3.36***
Experimental error (Replications x provenances interaction)	261	261	27.69	1.57***	26.31	1.52***
Sampling error (within plot variation)	900	884	60.92		58.75	
Total	1 199	1 183	100.00		100.00	
Coefficient of intraclass correlation			0.6239		0.6313	
Coefficient of intraclass determination			0.3893		0.3985	

*** — Statistically significant (0.005 level).
NS — Statistically nonsignificant (0.05 level).

The mean, average maximum and average minimum heights at 20 years from seed are 177.7 cm, 233.6 cm and 142.5 cm respectively, though heights up to 387 cm have been achieved. This growth on an exceptionally impoverished site, where the climate is also less favourable than in the natural range of red spruce, compares favourably with the average height of 305 cm in open stands on medium sites in northeastern United States (Fowells, 1965). Direct comparison with the major local species, black spruce, is not possible, due to absence of the latter in this experiment. However, black spruce provenances from Newfoundland have attained 10-year heights of 43.7—145.4 cm depending upon provenance and test site in the Province, while red spruce provenances in this experiment attained mean heights of 52.6—88.0 cm at the same age (Khalil, 1974, 1981a). These results demonstrate the potential of red spruce for planting in the boreal regions of Newfoundland.

The 20-year results of growth and crown form can be used to identify superior provenances. *Table 4* shows ranking and significance of provenances on the basis of Bonferroni t-test for the four characters for which provenances are a significant source of variation. As height and diameter are the more important criteria they have been examined in detail. On the basis of height six of the eight provenances in the fourth quartile (14, 16, 17, 18, 20, 30) were also in the same quartile in 1972 and 1969 (3, 14, 16, 17, 20, 30) (Khalil, 1974). One provenance (29) ranked ninth and thirteenth in 1972 and 1969 respectively. Thus, these provenances have been genetically stable during the study period. They are among the top 10 on the basis of diameter in 1979. Hence, on the basis of growth these eight provenances can be accepted as suitable for Newfoundland. Seven of them are in the third and second quartile in terms of number of branches and are superior in that respect also. However, they are among the top 11 for crown width, which shows their unsuitability. Crown width appears to be closely and positively associated with growth and the drawback is unavoidable. As large crown width does not reduce the value of superior provenances for pulping it can be ignored for Newfoundland. Thus, these eight provenances belonging to forest sections A.3, A.11 and A.12

Table 4. — Summary of BONFERRONI t-tests.

Rank	Height: Prov.	Height: Mean (cm)	Height: Significant differences	Diameter at 0.6 m: Prov.	Diameter at 0.6 m: Mean (cm)	Diameter at 0.6 m: Significant differences	No. of branches in 15th whorl: Prov.	No. of branches in 15th whorl: Mean (cm)	No. of branches in 15th whorl: Significant differences	Crown diameter at 15th whorl: Prov.	Crown diameter at 15th whorl: Mean (cm)	Crown diameter at 15th whorl: Significant differences
1	14	233.6	a	14	3.69	abc	28	4.45	a	14	50.8	a
2	17	215.0	ab	30	3.48	abc	1	4.43	a	17	43.7	ab
3	30	213.4	abc	17	3.36	abc	8	4.40	a	16	43.2	abc
4	16	203.4	abc	16	3.30	abc	15	4.40	a	30	42.8	abcd
5	20	202.6	abc	20	3.14	abc	26	4.35	a	28	42.6	abcd
6	29	195.9	abc	28	3.10	abc	23	4.33	a	20	42.2	abcd
7	18	195.1	abc	15	3.10	abc	29	4.33	a	29	40.0	abcd
8	3	193.6	abc	29	3.05	abc	6	4.30	a	18	39.3	abcd
9	15	192.4	abc	18	3.05	abc	17	4.30	a	13	39.3	abcd
10	28	192.2	abc	3	3.01	abc	16	4.28	a	19	38.4	bcd
11	13	182.4	abc	13	2.97	abc	20	4.28	a	3	38.3	bcd
12	1	179.2	abc	12	2.83	abc	27	4.25	a	1	38.1	bcd
13	5	177.4	abc	1	2.81	abc	14	4.23	a	6	37.5	bcd
14	12	176.2	abc	27	2.80	abc	30	4.18	a	15	37.2	bcd
15	27	174.9	abc	2	2.79	abc	18	4.13	a	11	37.1	bcd
16	4	174.5	abc	21	2.70	abc	9	4.10	a	12	36.9	bcd
17	19	173.5	abc	4	2.68	abc	13	4.08	a	26	36.9	bcd
18	9	172.7	abc	6	2.67	abc	19	4.05	a	23	36.8	bcd
19	6	172.1	abc	5	2.65	abc	3	4.05	a	4	36.6	bcd
20	2	169.7	abc	19	2.63	abc	4	3.98	a	8	36.2	bcd
21	26	166.4	abc	9	2.62	abc	5	3.95	a	21	36.0	bcd
22	21	166.0	abc	24	2.54	abc	11	3.95	a	2	35.9	bcd
23	23	162.2	bc	23	2.39	abc	2	3.88	a	9	34.8	bcd
24	7	158.1	bc	26	2.37	abc	22	3.85	a	27	34.7	bcd
25	24	157.7	bc	7	2.30	bc	24	3.85	a	22	33.7	bcd
26	22	151.3	bc	22	2.27	bc	7	3.80	a	24	33.2	bcd
27	25	147.8	bc	8	2.26	bc	21	3.80	a	5	32.7	cd
28	10	146.7	c	11	2.16	bc	12	3.63	a	25	31.7	cd
29	8	143.9		25	2.09	c	25	3.60	b	7	31.0	
30	11	142.5		10	2.02		10	3.58	b	10	30.4	
Mean		177.7			2.77			4.09			37.6	
S.D.		± 22.6			± 0.41			± 0.26			± 4.3	

Note: Provenances marked by the same letter are nonsignificantly different from each other (0.05 level).

(lowlands of New Brunswick and Nova Scotia) can be accepted to be most suitable for Newfoundland. However, in view of large intra-provenance variation and lack of information about heritability of height, family selection should be exercised instead of mass selection for attaining maximum genetic gain.

Regression Analyses

Table 5 presents the regression equations for growth, crown form in 1979 and phenological characters in 1972, with geographic coordinates of the sites of seed origin. All regression equations are significant and show that a high proportion of variation is due to these independent variables. The order of appearence of the independent variables in these equations, which is the same as that in the computer output, shows their relative importance in influencing expression of the character.

Table 5. — Regression equations showing relationship of characters with geographic coordinates of the sites of seed origin.

Character	Regression equation	R
Height	$Y = -308.8800 + 4.7309X_1^{NS} + 4.3266X_2^{*} - 0.0609X_3^{*}$	0.5067**
Diameter at 0.6 m	$Y = -6.4302 + 0.0994X_1^{NS} + 0.0739X_2^{*} - 0.0008X_3^{NS}$	0.4424*
Number of branches	$Y = -1.8118 + 0.0595X_1^{NS} + 0.0512X_2^{*} - 0.0008X_3^{*}$	0.5639***
Crown width	$Y = -71.6782 + 1.0774X_2^{**} + 0.9029X_1^{NS} - 0.0127X_3^{*}$	0.5435**
Branch angle	$Y = 113.6470 + 0.0761X_2^{NS} - 0.0055X_1^{NS} - 0.0035X_3^{NS}$	0.4008*
Days from May 31 to bud bursting	$Y = 36.3703 - 0.3355X_1^{NS} + 0.0012X_3^{NS} + 0.0388X_2^{NS}$	0.6229***
Days from May 31 to bud setting	$Y = 162.6130 - 1.0400X_1^{NS} - 0.1058X_2^{NS} - 0.0086X_3^{NS}$	0.5021**

*** — Statistically significant (0.005 level).
** — Statistically significant (0.01 level).
* — Statistically significant (0.05 level).
NS — Statistically nonsignificant (0.05 level).
Y — Character
X_1, X_2, X_3 — Latitude, longitude and altitude respectively of the locations of provenances.

Characters of growth and phenology, which have been subject to selection pressure during micro-evolution of the species, have exhibited trends in variation. The east-west trends in height and diameter, indicated by BONFERRONI tests are confirmed by regression equations, which show significant positive partial regression coefficients of these variables with longitude. Clinal variation with altitude is also indicated for height, which emphasizes the part played by physiography in influencing micro-evolution of the species by indirectly influencing the environment in the manner indicated earlier. However, in view of the findings of MORGENSTERN *et al.* (1981) these trends may not be entirely due to the selection pressures created by the environment, and may be partially the consequence of genotypic variation caused by introgression. MANLEY's hypothesis of the existence of an introgression continuum from coastal through lowland to upland populations in New Brunswick (MANLEY, 1971, 1972) finds support in the above results, which may be responsible for the significant differences in growth. It is also interesting that in the changed environment of the test site, the natural hybrids from the lowlands have shown positive rather than the negative heterosis recognized in artificial hybridization (MANLEY and LEDIG, 1979).

Similarly, contrasts among groups show some north-south trend in bud bursting and bud setting dates (KHALIL, 1974). Regression equations show latitude to have the largest influence on these characters and support the results of the contrasts among groups.

The results of regression analyses of characters of crown form, which were not subject to selection pressure during micro-evolution, are interesting. Contrasts among groups are nonsignificant for number of branches and branch angle thus showing lack of trends. Those for crown width show mild east-west trends in New Brunswick. However,

Table 6. — Regression analysis of periodic growth.

Character	Regression equation	R
1979 Height: (Y) 1969 height (X)	$Y = 24.4040 + 2.2612X$	0.8297***
1979 height: (Y) 1972 height (X)	$Y = -4.5535 + 1.6391X$	0.9166***
1969–1979 growth: (Y) 1969 height (X)	$Y = 24.7387 + 1.2526X$	0.6448***

***) — Statistically significant (0.005 level).

regression equations show longitude to have the most important partial regression coefficient with these characters, followed by altitude and latitude. The trend in this respect is the same as that for height. As these characters of crown form are not influenced by selection pressure, their variation cannot be considered to have resulted from environmental variation caused by geographic coordinates. The trend of variation in these characters only shows their significant association with height growth.

Table 6 presents simple regression equations of relationship of 1979 height with the 1969 and 1972 heights. They show that the height at 20-year age is not only positively and significantly correlated with the 10- and 13-year heights but growth during the last 10 years has also a positive and significant correlation with the previous 10-year height. Such correlation indicates the possibility of early selection of superior red spruce provenances on the basis of juvenile growth.

Conclusions

The important conclusions are summarized below:

1. The size and design of the experiment are adequate for maximizing the credibility of F-tests for all sources of variation.
2. Provenances are a significant source of variation in all characters except branch angle. However, significant differences between specific provenances exist in all characters including branch angle.
3. The characters of growth and phenology have exhibited geographic variation with longitude and altitude for height, with longitude for diameter and with latitude for bud bursting and bud setting dates, indicating the influence of natural selection on these characters.
4. The characters of crown, which were not influenced by natural selection, also show trends with longitude, altitude, and latitude, in decreasing order, indicating close association of these characters with growth characters.
5. The trends in variation may not be entirely due to environmental variation but may be partially due to introgression with black spruce. The hypothesis of the existence of an introgression continuum from coastal to upland populations is supported.
6. Red and black spruce natural hybrids from the lowlands of New Brunswick have shown positive heterosis at the test site rather than the negative heterosis exhibited by artificial hybrids reported earlier.
7. The provenances tested have considerable intra-provenance genetic variation, possibly due to introgression with black spruce.
8. Red spruce is a potentially useful exotic for Newfoundland for sites with mild maritime climate. The most suitable provenances are 3, 14, 16, 17, 18, 20, 29 and 30 from forest sections A.3, A.11 and A.12. Family selection from these provenances is indicated in preference to mass selection.
9. Early identification of superior provenances at 10-year age is possible in red spruce.

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Literature Cited

Anonymous: The climate of Canada. Meteorol. Br., Air Serv., Dep. Transp., Toronto, Ontario, 74 pp, (1960). —— Anonymous: Land capability for forestry, Gander Lake 2D. Dep. Environ., Lands Dir., Ottawa, 1 map, (1972). —— Douglas, A. W.: On levels of significance. Environ. Can., Comput. and Appl. Statist. Dir., Data Anal. and Syst. Br., Output No. 3: 36—49, (1979). —— Chapman, L. J. and Brown, D. M.: The climates of Canada for agriculture. The Can. Land Invent. Rep. No. 3, Dep. Forest. and Rural Develop., Can. vi and 24 pp., (1966). —— Draper, N. R. and Smith, H.: Applied regression analysis. John Wiley and Sons Inc., New York. xiv and 407 pp., (1966). —— Eyre, E. H. (Ed.): Forest cover types of the United States and Canada. Soc. Amer. Forest. vi and 148 pp. and 1 map, (1980). —— Fowells, H. A.: Silvics of forest trees of the United States. U.S. Dep. Agric., Forest Serv., Agric. Handbook No. No. 271 vi and 762 pp., (1965). —— Hawboldt, L. S. and Bulmer, R. M.: The forest resources of Nova Scotia. Dep. Lands and Forest, Prov. Nova Scotia. 171 pp., (1958). —— Heimburger, C.C.: Notes on red spruce. Sorest. Chron. 15: 226—227, (1939). —— Huschke, R. E. (Ed.): Glossary of meteorology. Amer. Meteorol. Soc. Boston, Massachusetts, viii and 638 pp., (1959). —— Khalil, M. A. K.: Preliminary results of a red spruce (*Picea rubens* Sarg.) provenance experiment in Newfoundland. Environ. Can., Forest. Serv., Inform. Rep. N-X-117, 45 pp., (1974). —— Khalil, M. A. K.: Twenty year results of the red spruce provenance study in Newfoundland. Environ. Can., Can. Forest. Serv., Inform. Rep. N-X-191, vi and 26 pp., (1981). —— Khalil, M. A. K.: Ten year results of regional black spruce provenance study in Newfoundland. Environ. Can., Can. Forest. Serv., Inform. Rep. N-X-200, 43 pp., (1981a). —— Loucks, D. C.: A forest classification for the Maritime Provinces. Proc. Nova Scotia Inst. Sci. 25 (2): 86—167, (1962). —— McCormack, R. J.: Land capability classification for forestry. Dep. Reg. Econ. Exp., Can. Land Invent. Rep. No. 4, 2nd. Ed. 72 pp., (1970). —— Manley, S. A. M.: Identification of red, black and hybrid spruces. Dep. Environ., Can. Forest Serv., Publ. No. 1301, 14 pp., (1971). —— Manley, S. A. M.: The occurrence of hybrid swarms of red and black spruces in central New Brunswick. Can. J. Forest. Res. 2 (4): 381—397, (1972). —— Manley, S. A. M. and Ledig, F. T.: Photosynthesis in black and red spruce and their hybrid derivatives. Ecological isolation and hybrid adaptive inferiority. Can. J. Bot. 57: 305—314, (1979). —— Morgenstern, E. K. and Farrar, J. L.: Introgressive hybridization in red spruce and black spruce. Tech. Rep. Fac. Forest. Univ. Toronto, No. 4, 46 pp., (1966). —— Morgenstern, E. K., Corriveau, A. G. and Fowler, D. P.: A provenance test of red spruce in nine environments in eastern Canada. Can. J. Foreset Res. 11 (1): 124—131, (1981). —— Mullins, E. J. and McKnight, T. S. (Ed.): Canadian woods: Their properties and uses. Univ. Toronto Press, Third Ed. xviii and 389 pp., (1981). —— Putnam, D. F.: Canadian regions. A geography of Canada. J. M. Dent and Sons (Canada) Ltd., Toronto. Seventh Ed., 601 pp., (1965). —— Rowe, J. S.: Forest regions of Canada. Environ. Can., Can. Foreset. Serv. Publ. 1300. x and 172 pp. and 1 map, (1972). —— Steel, R. G. D. and Torrie, J. H.: Principles and procedures of statistics. A biometrical approach. McGraw-Hill Book Co., New York. xxi and 633 pp., (1980).