Conclusions

The results of this study point to: (i) moderate broad sense heritability values for tree heights and diameters (ii) moderately high broad sense heritability values for branch length and branch angle (iii) significant clonal variation in analysed traits (iv) possibility of between 11% and 15% genetic gain in individual selection within a half-sib family and subsequent clonal development.

Key words: Clonal Selection, Genetic gain, Pinus grijfithii McCLELLAND X Pinus *strobus* L.

Zusammenfassung

Acht Pfropfklone einer Kreuzungs-Nachkommenschaft (Halbgeschwister-Familie) von Pinus grijjithii McCLELLAND X Pinus strobus L. wurden im Alter 14 auf Gesamthöhe, Brusthöhendurchmesser (∅ in 1,3 m Höhe) und Verzweigung hin untersucht. Zwischen den Klonen wurden in diesen Merkmalen beträchtliche signifikante Unterschiede gefunden. Diese betrugen bis zu 52% bei der Gesamthöhe, 109% beim Brusthöhendurchmesser und rechnerisch 546% beim Volumen. Bei der Zweiglänge und beim Astwinkel gab es Unterschiede bis zu 61% bzw. 37%. Der in dieser Halbgeschwister-Familie durch die Selektion von Einzelbäumen und deren vegetative Vermehrung mögliche genetische Gewinn wird auf 11% bis 15% geschätzt.

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Genetic Variation in Black Spruce (Picea mariana (Mill.) B.S.P) in Newfoundland

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(Received March / July 1975)

Introduction

Though conifers constitute 87 percent of the merchantable volume on the Island and 99 percent in Labrador (ANON. 1973), there are only two commercially important local species, balsam fir (Abies balsamea (L.) MILL.) and black spruce (Picea mariana (MILL.) B.S.P.). The high susceptibility of balsam fir to major insect pests reduces the possible benefits from its genetic irnprovement. Black spruce is relatively free from insect pests and diseases, is adaptable to a wide variety of edaphic and climatic conditions, and is a choice species for pulp on account of its long fibres and high wood density (BESLEY 1959, BASHAM and MORAWSKI 1964, LADELL 1971). Consequently, black spruce is the most important species in the recently started program of reforestation in the Province which aims at an annual planting of approximately 2,000 hectares. Genetic improvement of black spruce is, therefore, both important and urgent.

A provenance trial, using Newfoundland and mainland provenances, started in 1968, is one of several studies on the genetic improvement of black spruce currently in progress at the Newfoundland Forest Research Centre of the Canadian Forestry Service. Results of the first phase of this study have been reported elsewhere (KHALIL 1973). These results show the performance of the provenances in Newfoundland. The data were further analysed to determine the degree and pattern of variation of important characters in the black spruce populations of insular Newfoundland. This paper presents the results.

Review of Literature

Black spruce is the characteristic species of the Boreal Forest Region of Canada and also occurs in several other forest regions (ROWE 1972). It forms a continuous belt from the Newfoundland and Labrador coasts westward to the Rocky Mountains and between latitude 40° N in the north-central and north-eastern United States and 65° N in the Yukon Territory and Alaska (FOWELLS 1965). Consequently, the species is expected to exhibit large phenotypic as well as genotypic variation as a result of its micro-evolution under such widely different environmental conditions.

Precise definitions of clinal and ecotypic variations are necessary for understanding the discussion that follows. "A cline is a gradual change in the phenotypic characters of a population" while "an ecotype is a race (within a species) genetically adapted to a certain environment" (KING 1972). Clinal variation is defined as a gradual change in the phenotypic expression of a character (HUXLEY 1938) and results from natural selection under gradually changing environmental conditions, notably photoperiod and temperature, within the range of the species. On the other hand ecotypic variation exhibits itself in the form of discrete populations within a species, resulting from selection pressures of discrete environmental influences, such as soils and local climates (STERN 1964), or in non-adaptive fashion by migration from different refugia (BOUVAREL 1959), random drift in small populations (WRIGHT and BULL 1963) and inbreeding (MAYR 1963).

VAARTAJA (1959) first suggested the existence of photoperiodic ecotypes in black spruce as an indirect mechanism in the adaptation of the various populations to various seasonally changing climatic conditions. However, MORGENSTERN (1969 a, b) reported clinal variation in the black spruce from the Wisconsin — Ontario — Manitoba — Northwest Territories regions with most samples being from Ontario and the Northwest Territories. Thirteen juvenile characters were studied, six of which related to germination and survival and seven to morphology and phenology. This apparent contradiction with Vaartaja's results can be explained by the fact that Morgenstern's results are based on seed from 24 populations between latitudes 42° N and 60° N along a north — south transect, while Vaartaja's results include only four samples taken from isolated populations between the same latitudes, from areas so far apart as the Northwest Territories, Labrador, Wisconsin and Pennsylvania. So Vaartaja's ecotypes are really four isolated populations of two clines, one in the Northwest Territories — Wisconsin transect and the other in the Labrador — Pennsylvania transect. Thus the two results support rather than contradict each other and both indicate the existence of clinal variation in black spruce in central Canada — north-central United States.

MORGENSTERN (1973) has also shown that the narrow-sense individual tree heritability (WRIGHT 1962, p. 327, *FORMULA* 61) of four-year height in five black spruce populations within 48 km radius of the Petawawa Forest Experiment Station in Ontario is 17 percent. Using his data I have found that the narrow-sense heritability (WRIGHT 1962, p. 327, *FORMULA* 62) of the same populations for four-year height is 62—76 percent and 64—90 percent when grown on wet and dry sites respectively. This shows appreciable intra-provenance genetic variation in the species.

Considerable amount of work has been done on the genetic and environmental control of phenology in trees. WAREING (1956) indicated a weak correlation of growth initiation and photoperiod in a few species and WITHROW (1959) showed a correlation between photoperiod and cessation of growth and initiation of dormancy. SMITH and KEFFORD (1964) recognize three phases, viz. (1) phasic development of dormancy culminating in a truly dormant state, (2) releasing of dormancy, leading to a transient non-dormant state, and (3) growth initiation in spring leading to a steady development. The alternation of the dormant and the active states is very gradual (KOZLOWSKI 1971). Bud setting and onset of dormancy in the fall and bud-swelling and bursting in spring as a precursor of the year's growth are brought about by complex interaction among several environmental conditions outside and physiological processes within the tree. KOZLOWSKI (1964) showed that bud dormancy is produced, controlled and terminated by the endogenous synthesis and balance between two classes of growth hormones, called "inhibitors" and "promoters". WAREING (1974) has shown that the relationship and control of these two classes of hormones is very complex and insufficiently understood. The synthesis of these classes of hormones appears to be controlled by the environment as well as the genotype of the tree. Low temperatures and short photoperiods produce inhibitors and high temperatures and long photo-periods produce promoters. Edaphic factors, like nutrients and water regime of the substratum, also control the synthesis of these hormones. While the environment initiates, controls and stops the synthesis of these hormones, the genotype of the tree controls the threshold effects of the environmental factors, the exact dose of the hormones produced at different levels of these factors, and the threshold levels of the hormones.

Out of the many environmental factors affecting bud dormancy exposure to low temperatures for varying periods is necessary for most temperate zone woody plants in order to break dormancy and resume normal growth in the following spring (DOORENBOS 1953, SAMISH 1954, ROMBERGER 1963, and SMITH and KEFFORD 1964). The chilling requirements for black spruce are not known but NIENSTAEDT (1967) has shown that such requirements vary between 4—8 weeks with the species and provenances in the genus *Picea*.

Material and Methods

The provenances — Seed was obtained from 29 provenances in insular Newfoundland, all were from within the Boreal Forest Region (ROWE 1972) which covers the Island between latitudes 48° and 52° N and longitudes 52° and 59° W. The provenances were located in five forest sections as shown in *Table 1* and *Fig. 1*.

The climate of insular Newfoundland is strongly influenced by the Labrador and Gaspe currents and also by wind velocity, physiography and summer cloudiness. The complex interaction of these factors produces large variations in meteorological values from year to year as well as during the year and masks the more commonly known latitudinal and longitudinal trends.

The areas sampled were selected for wide north-south and coastal-inland distribution so as to represent the maximum number of climatic and edaphic conditions. Two provenances occur at relatively high elevations and some were obtained from highly calcareous soils. Each stand represented trees of average quality for the locality.

Cone collection — A minimum of seven dominant and co-dominant trees were selected in each stand. They were spaced at least 30 m apart so as to avoid sampling close relatives. Cones were collected and kept separate by trees.

Table 1. — Location of provenances.

Forest section	Provenance	Latitude (°N)	Longitude (°W)	Altitude (m)
B.28a - Grand Falls	17	49°-11'	56°-06'	183
	18	48°-50'	56°-29'	183
	19	48°-27'	57°-00'	305
	20	49°-01'	55°-26'	61
	21	49°-22'	54°-25'	30
	22	48°-42'	55°-11'	152
	23	48°-40'	55°-14'	122
	24	48°-42'	54°-27'	91
	25	48°-24'	54°-13'	61
B.28b - Corner Brook	9	49°-14'	57°-17'	122
	10	49°-03'	58°-12'	91
	11	48°-48'	58°-04'	183
	13	48°-34'	58°-55'	30
	14	48°-36'	58°-41'	61
	15	48°-34'	58°-11'	46
	16	47°-54'	59°-03'	61
	44	48°-34'	58°-11'	305
B.29 - Northern Peninsula	2	51°-03'	56°-46'	61
	3	50°-32'	56°-07'	15
	4	50°-34'	57°-16'	61
	5	50°-24'	56°-28'	32
	6	50°-06'	56°-10'	152
	7	49°-27'	56°-28'	61
	8	49°-25'	57°-45'	107
B.30 - Avalon	26	47°-55'	54°-15'	15
	27	47°-01'	55°-14'	91
	28	47°-13'	53°-53'	61
	29	47°-30'	52°-52'	152
B.32 - Forest-Tundra	1	51°-29'	55°-42'	15

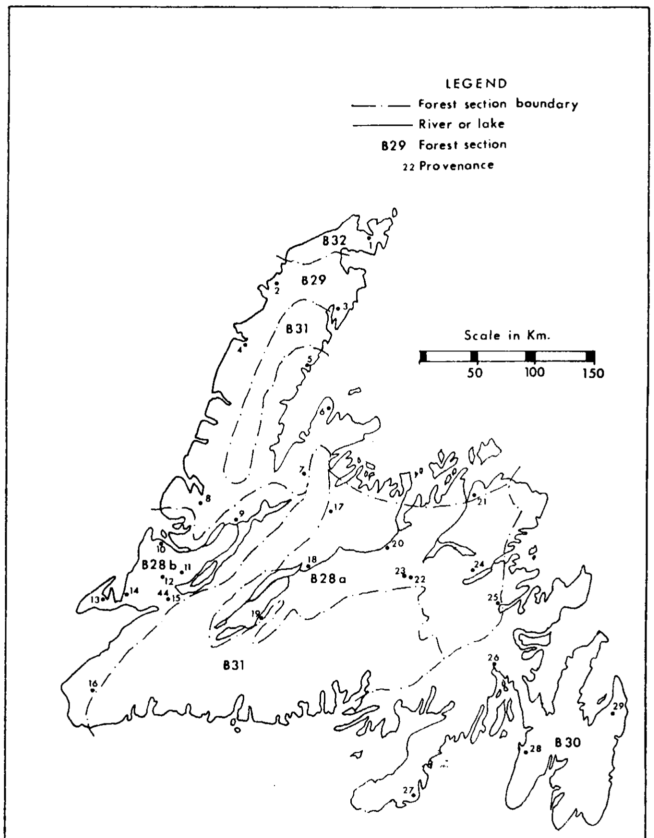

Fig. 1. — **Map of insular Newfoundland showing Forest Sections (after Rowe, 1972) and location of Provenances.**

Total height, breast height diameter and age of each selected tree were determined.

Seed extraction — Seed was extracted by heating the cones for 20 hours in an incubator at 57° C and 30 percent relative humidity. The cones were then shaken and the seed so obtained was dewinged by rubbing in a cloth bag and cleaned by passing through a small fanning mill.

Experimental design — Equal quantities of seed from each of the seven trees of a provenance were bulked and the bulked seed was divided into lots of 100 seeds each. A nursery experiment using a five-replicated complete block design was laid out in the Canadian Forestry Service research nursery at Pasadena in western Newfoundland (latitude 48° 57' N, longitude 57° 35' W) near Deer Lake. Seed beds were prepared in the spring of 1967 by mixing the soil with peat moss to improve texture and to reduce frost heaving. A 6-7-8 commercial fertilizer was applied at the rate of 7.32 kgm/100 m^2. The seed was sown on May 27—29, 1968 in row plots 15—24 cm apart, laid out across the bed. The 100 seeds of each provenance were sown in 12 lines approximately 1.25 m long and about 4 cm apart, using 8 or 9 seeds in each line so as to ensure uniform distribution of seedlings in the row. The seed was covered with about 0.6 cm of fine sand.

The Data Recorded

For parent populations — A random sample of 20 cones was obtained from each tree in each provenance and oven-dried at 105° C. The length and the diameter at the widest point of each cone, and the weight of 1000 oven-dried bulked seeds of each provenance, were determined.

For progenies — The following data were recorded on a sample of eight randomly selected seedlings in each provenance in each replication:

1. Percentage survival of 1 + 0 and 2 + 0 seedlings.
2. Dates of bud burst in the spring of 1970, converted to degree-days above 6° C. This date was set as the date on which green needles were visible on the terminal bud of the leader.
3. Dates of bud set in the fall of 1970. This date was set when well-defined bud was visible at the apex of the leader.
4. Frost damage in the spring of 1970.
5. Height of seedlings in the fall of 1969, 1970 and 1971 and in the spring of 1970 and 1971.
6. Root-collar diameter of seedlings in the fall of 1970 and 1971 and in the spring of 1971.
7. Date of initiation of height growth in the spring of 1970.
8. Height at periodic intervals during the spring and summer of 1970.
9. Date of cessation of height growth in the summer — fall of 1970.
10. Tally for multiple leader production in the summer of 1970.

Data on items 2, 3, 7 and 9 were recorded on every alternate day and those on item 8 once a week.

Statistical analyses — The following statistical analyses were conducted on the data on cone morphology and seed weight of the parent populations:

1. Correlation between cone length and cone diameter for all cones, for cones within provenances and for cones within trees within provenances.
2. Hierarchical analysis of variance of cone length, cone diameter and cone length/cone diameter ratio to determine the proportion of total variance associated with the different levels of sampling.
3. Multiple correlation and regression analyses of cone length, cone diameter and 1000-seed weight with latitude, longitude and altitude of the provenances.

The following analyses were performed on the data collected from progenies:

1. Analyses of variance, based on plot means, together with Student-Newman-Keul's multiple range tests and single degree of freedom comparisons between sets of provenances from tle different forest sections.

2. Determination of intra-class correlations as a measure of the homogeneity of the provenances tested (STEEL and TORRIE 1960, pp. 192—193).
3. Analyses of variance, based on individual tree data for height and for root-collar diameter in the fall of 1971 and for the number of degree-days above 6^0 C from January 1, 1970 to the date of bud bursting, to determine the proportion of the total variance associated with the various sources and to assess the magnitude and statistical significance of the provenances × replications interaction and the intra-provenance variation so as to confirm or modify the results of (2) regarding homogeneity of the provenances tested (STEEL and TORRIE, 1960, pp. 142—146).
4. Matrix of correlations among 1000-seed weights, survival percent in the falls of 1968 and 1969, heights and root-collar diameters each year.
5. Determination of the pattern of annual growth of the leading shoot of each provenance in each replication by solving the best fitting regression equation $Y = a + b \log X$, where Y is the length of the leading shoot at the time of the periodic measurements in the summer of 1970, and X is the number of days from January 1, 1970 to the date of each measurement.
6. Analysis of variance, Student-Newman-Keul's multiple range test and single degree of freedom comparisons between sets of provenances from various forest sections for "a" and "b" in (5) above.

Statistical analyses involving survival percents were conducted after transformation to arcsin $\sqrt{\text{perentage}}$. All statistical analyses were performed after verifying homogeneity of variance by Bartlett's method (SNEDECOR and COCHRAN 1967, pp. 296—298).

Results and Discussion

Parent Populations

The correlation coefficients between cone length and cone diameter are 0.80—0.98 and are statistically significant ($p > 0.99$) for all three levels of sampling. The results of the analysis of variance of the hierarchical sampling for cone length, cone diameter and cone length/cone diameter ratio are summarized in *Table 2*. *Table 3* summarizes the results of multiple correlation and multiple regression analyses of the characters of cone morphology versus geographic factors.

Table 2. — Results of anlysis of variance of characters of cone morphology.

Source of variance	Cone length: Percentage variance	Cone length: F	Cone diameter: Percentage variance	Cone diameter: F	Cone length/cone diameter: Percentage variance	Cone length/cone diameter: F
Provenances	20.17	2.74**	24.31	3.89**	9.27	0.98^{NS}
Trees within provenances	45.76	29.78**	40.60	24.51**	58.61	40.35**
Cones within trees	34.07		35.09		32.12	
TOTAL	100.00		100.00		100.00	

**Statistically significant ($p > 0.99$)
^{NS}Statistically non-significant ($p < 0.95$)

The high correlation between cone length and cone diameter at the three levels of sampling indicates that these characters are controlled by the same factors. As the levels of sampling do not change the magnitude of the coefficient of correlation environment seems to have little control on the characters. They are genetically controlled and are under the influence of pleiotropic genes.

Table 3. — Results of multiple correlation and multiple regression analyses of characters of cone morphology versus geographic factors.

Character	Statistic	Independent variable: Latitude	Longitude	Altitude	Remarks
Cone length	r	0.4143*	-0.5772**	0.4326**	R = 0.6735**
	b	0.0480*	-0.0687**	0.0007^{NS}	R^2 = 0.4536
Cone diameter	r	0.3351^{NS}	-0.5526**	0.2354^{NS}	R = 0.6159**
	b	0.0175^{NS}	-0.0261**	0.0003^{NS}	R^2 = 0.3793
1000-seed weight	r	-0.3214^{NS}	-0.3753^{NS}	0.3539^{NS}	R = 0.5362**
	b	-0.0246^{NS}	0.0143^{NS}	-0.00003^{NS}	R^2 = 0.2876

**Statistically significant ($p > 0.99$)
*Statistically significant ($p > 0.95$)
^{NS}Statistically non-significant ($p < 0.95$)

The results of the analyses of variance show that though provenances are significantly different among themselves in cone length and cone diameter, trees constitute the major part of the variance and are also statistically significant. The relatively small control by the environment over these characters is confirmed by the results of the analysis of variance, which show that in spite of the existence of large environmental differences due to the climatic and edaphic conditions of the 29 provenances, the contribution of provenances to the total variance is small. This. together with the fact that the seed trees were dominant or codominant and were selected from within small and relatively homogeneous sites in each stand provides sufficient assurance to conclude that the contribution of micro-environmental factors like competition, crown size and soil nutrients to the large among-trees within-provenance variance is minimal. The effect of position in the crown was minimized by sampling only the previous year's shoot on the leader. It follows from this that the largest proportion of the variance among cones within trees is due to the genotype of the male and the female parent which appear to have the largest degree of control on cone length and cone diameter in black spruce. This conclusion agrees with similar results for white spruce reported by KHALIL (1974).

Having concluded that cone length and cone diameter in black spruce are mainly under genetic control it is useful to investigate the geographic trends in this genetic control. *Table 3* shows that while cone length is affected by latitude, longitude and altitude, cone diameter is affected by longitude only. This apparent disagreement with the results of the multiple range test, which does not show any geographical trends, is explained by a large error term in the analysis of variance. The existence of a smaller proportion of total variance due to provenances than that due to trees within provenances for all the three characters indicates ecotypic rather than clinal variation in these characters in insular Newfoundland (MORGENSTERN 1969 a). As characters of cone morphology do not determine the adaptability of genotypes, the ecotypic variation cannot be explained by marked and abrupt differences in the climate of insular Newfoundland exercising abruptly changing selection pressures during the micro-evolution of the species on the Island. As will be shown later, characters of phenology and growth are also ecotypically variable in Newfoundland. Hence there appears to be some degree of genotypic correlation between characters of cone morphology and growth in black spruce. There is only a small and statistically non-significant correlation between seed weight and geographical factors.

Progenies

Phenology — The mean dates of bud bursting varied between May 25 and 28, 1970 which was equivalent to 48—56 degree-days above 6° C. The mean daily temperature at Deer Lake during this period varied between 2° C and 12° C (ANON. 1970). The photoperiod for Deer Lake (latitude 48° 47' N) during this time is 15 hours-40 minutes (ANON. 1974). These degree-days, temperatures and photoperiod appear to be the threshold levels for endogenous synthesis of promoters and for initiation of bud bursting.

Similarly, the mean dates for initiation of bud dormancy were September 4 to October 7, 1970, during which time the mean daily temperature at Deer Lake varied between 1° C and 16° C (ANON. 1970). The photoperiod between these dates varies between 11 hours-24 minutes and 13 hours-15 minutes (ANON. 1974). These temperatures and photoperiods appear to be threshold levels for endogenous synthesis of inhibitors and for initiation of bud dormancy.

These results indicate the apparently non-significant role played by provenances in controlling bud bursting, which appears to be dependent primarily upon environmental factors, particularly the number of degree-days above 6° C or the cumulative effect of temperature. As all seedings were exposed to an overdose of chilling of about 24 weeks the differences among provenances in the requirements of degree-days for break of dormancy in the spring is a good measure of the quantity of heat necessary for producing promoters or for transporting them to the centres of meristematic activity. On the other hand, the wide range of temperatures and photoperiods required for initiation of bud dormancy suggest that provenances play a significant role in the control of this phenomenon.

The results of analyses of variance of the number of degree-days above 6° C to the dates of bud bursting in the spring of 1970 and to the number of days from January 1 to the dates of bud setting, summarized in *Table 4*, throw very valuable light on the genetic control of these phenomena in black spruce. These results show that differences in edaphic factors, reflected by replications, are statistically significant ($p > 0.99$) in controlling bud bursting but not in controlling bud dormancy. This appears to be due to differences in the degree of ground thawing, possibly resulting from differences in the depth of the root systems of seedlings in different replications in addition to differences in the chemical or micro-biological constituents of the soil. Provenances and replications × provenances interactions have statistically significant control ($p > 0.99$) on bud bursting as well as on bud dormancy. This indicates a significant role of the genotype in controlling bud bursting and bud dormancy in black spruce. The high percentage of variance associated with sampling error and the not very high coefficients of intra-class correlation and determination indicate only moderate fraternal resemblance and large intra-provenance variation for both characters.

The multiple range tests do not show any geographical trends among provenances for bud burst or bud dormancy. However, single degree of freedom comparisons show that provenances from forest section B.28a (ROWE 1972) have the highest and those from forest section B.30 the lowest requirements of degree-days above 6° C for bud bursting. The same test shows that the provenances can be grouped into the folllowing five geographic regions, arranged in increasing order of the days from January 1 to the dates of bud dormancy: forest sections B.32, B.29, B.28b, B.30 and B.28a.

The single degree of freedom comparisons also show ecotypic variation in bud dormancy and possibly in bud burst in insular Newfoundland in contrast to clinal variation in these characters in central Canada and north-central United States as reported by MORGENSTERN (1969 a, b). These characters determine the adaptability of the genotype to the environment, and the differences in the patterns of variation are obviously the result of differences in trends in climate. Clinal variation in Central Canada and north-central United States provenances is explained by the continental nature of the climate with continuous latitudinal and altitudinal gradients. Hence, the selection pressures exerted on the black spruce of that region during the micro-evolution of the species had a continuous spatial gradation, resulting in clinal variation. On the other hand, the island of Newfoundland has distinct climatic regions, which approximate to Rowe's forest sections. These distinct climatic regions have exerted differential selection pressures on the species during its micro-evolution on the Island, resulting in ecotypes.

Table 4. — Summary of results of analyses of variance on phenology data.

Source of variance	Bud burst: Percent variance	Bud burst: F	Bud set: Percent variance	Bud set: F
Replications	3	9.55**	2	1.24^NS
Provenances	22	8.00**	10	2.82**
Replications x provenances interaction	11	1.54**	15	1.83**
Sampling error	64		73	
Coefficient of intra-class correlation	0.566		0.618	
Coefficient of intra-class determination	0.321		0.382	

**Statistically significant ($p > 0.99$)
NS Statistically non-significant ($p < 0.95$)

Effect of frost — The mean date of the last spring frost for Deer Lake is June 10 and the mean dates of bud burst have been found to be May 25—28. This indicates the proneness of all provenances to late spring frost damage. The lowest minimum temperature recorded at Deer Lake in spring during the four years of the experiment was —3° C on May 25, 1970 (ANON. 1968—1971). The absence of frost damage during the experiment indicates that low temperatures down to —3° C do not do any damage in spring.

The mean date of the first fall frost at Deer Lake is September 15 and the mean dates of bud setting have been found to be September 4 to October 7. Ranking of the provenances by the mean number of days from January 1 to the dates of bud setting shows that seven provenances set buds before September 15 and 22 after that date. Though this indicates that 22 out of the 29 provenances tested are prone to fall frost damage such damage occurred only once, on September 19, 1969, when the minimum temperature reached —3° C. This appears to be the critical temperature in fall. However, no damage was noticed among the provenances from the Northern and Baie Verte Peninsulas (forest sections B.29 and B.32). The provenances from forest sections B.28b and the western one-third of forest section B.28a had only 12 percent of their seedlings affected, and only 9.8 percent had damaged leaders. The provenances from the eastern half of forest section B.28a and those from forest section B.30 had 28 percent seedlings affected and 15.2 percent had damaged leaders. Production of multiple leaders was the only visible effect of the frost damage. A north-south trend was noticed within the above forest sections in terms of multiple leader production.

Survival — The results of the analysis of variance are summarized in *Table 5*. Provenances constitute a large and statistically significant ($p > 0.99$) percent of the variance in both years, showing that the genotype has a highly significant role in controlling survival. The high statistical significance of the variance among replications in 1968 and the high proportion of the variance associated with the replications × provenances interaction (experimental error) in both years appear to have been caused by differences in soil conditions in the nursery bed in which the five replications were located. These differences were most probably caused by variation in the level of fertilizer used and in other micro-climatic conditions. The effects of these differences diminished in 1969 when the seedlings gained strength and soil conditions ceased to be statistically significant in determining survival.

Table 5. — Summary of results of analysis of variance of survival data.

Source of variance	Survival in 1968 Percent variance	F	Survival in 1969 Percent variance	F
Replications	8	6.18**	3	1.95^{NS}
Provenances	41	3.23**	38	2.58**
Experimental error	51		59	

**Statistically significant ($p > 0.99$)
^{NS}Statistically non-significant ($p < 0.95$)

The coefficients of intra-class correlation for survival in 1968 and 1969 were 0.310 ($r^2 = 0.096$) and 0.240 ($r^2 = 0.057$) respectively which shows low fraternal resemblance and consequently high intra-provenance variation. High intra-replication and high intra-provenance variations have resulted in high proportions of the variance being associated with their interaction or experimental error. These results agree with Morgenstern's results reported earlier (MORGENSTERN 1973).

Geographical trends in variation in survival are weak. The multiple range tests do not show any such trends. The single degree of freedom comparisons between Rowe's forest sections show that in 1968 forest section B.32 was significantly lower than all others ($p > 0.95$), which were not significantly different from each other ($p < 0.95$). This continued in 1969 but in that year forest section B.30 became superior to all others ($p > 0.99$).

The coefficients of correlation of 1000-seed weight with survival in 1968 and 1969 were 0.486 ($t = 3.38^{**}$, $r^2 = 0.236$) and 0.596 ($t = 4.51^{**}$, $r^2 = 0.355$) respectively. The coefficient of correlation between survival in 1968 and 1969 is 0.885 ($t = 11.53^{**}$, $r^2 = 0.783$). This shows that seed weight is statistically significant ($p > 0.99$) in determining survival in the first two years and that survival in the first year is statistically significant ($p > 0.99$) in determining survival in the second year.

Height growth — Results of analyses of variance based on plot means are summarized in *Table 6*. Provenances have consistently contributed the largest proportion of variance which has been statistically significant ($p > 0.99$) throughout the duration of the experiment.

Though the multiple range tests do not show consistent geographical trends on the basis of individual provenances, grouping of the provenances into Rowe's forest sections brings out differences between them. The provenances from forest section B.32 were significantly slower growing than the ones from other forest sections ($p > 0.99$) until spring 1970. Further differentiation developed among forest sections later and by 1971 the provenances from forest sections B.28a, B.28b and B.30, i.e. from central, eastern and southern areas of the Island, had grown faster than those from forest sections B.29 and B.32 on the Northern Peninsula ($p > 0.99$). This is explained by the earlier bud setting dates of the Northern Peninsula provenances resulting in a shorter growing period for them than for the provenances from other forest sections. These results indicate ecotypic rather than clinal variation in four-year height growth in black spruce in Newfoundland. This also is in contrast with the results of MORGENSTERN (1969 b) which show clinal variation in juvenile growth in black spruce of central Canada and north central United States.

Having established that variation in juvenile height growth is under strong genetic influence, which, in turn, shows ecotypic variation, further analyses were conducted to study the nature of the variation within provenances.

Table 7 shows the distribution of variances among the various sources. This analysis shows that sampling error contributes the highest proportion of variance. The very low proportions of the variance attributable to replications and to the replications × provenances interaction indicate high intra-provenance variation, which in turn increases the variance due to sampling error. *Table 6* shows relatively low coefficients of intra-class correlation and determination, indicating low fraternal resemblance and high intra-provenance variation in juvenile height growth. The two results support each other. The variation in juvenile height growth is similar to that in characters of cone morphology, discussed earlier.

Table 6.- Summary of results of analyses of variance of height.

Statistic	Fall 1969 % variance	F	Spring 1970 % variance	F	Fall 1970 % variance	F	Spring 1971 % variance	F	Fall 1971 % variance	F
Variance due to replications	6	6.32**	4	4.84**	1	1.19^{NS}	1	1.16^{NS}	1	1.42^{NS}
Variance due to provenances	55	5.66**	62	7.42**	54	4.74**	57	5.35**	66	8.13**
Variance due to experimental error	39		34		45		42		33	
TOTAL	100		100		100		100		100	
Coefficient of intra-class correlation	0.483		0.545		0.428		0.466		0.585	
Coefficient of intra-class determination	0.233		0.297		0.184		0.217		0.346	

**Statistically significant ($p > 0.99$)
^{NS}Statistically non significant

Table 7. — Distribution of variances in height among the various sources.

Source of variance	Percentage	F
Replications	1	1.38^{NS}
Provenances	32	8.00**
Replications x provenances interaction	16	2.78**
Sampling error	51	
TOTAL	100	

**Statistically significant (p > 0.99)
*Statistically significant (p > 0.95)
NS Statistically non-significant (p < 0.95)

The results of correlation analyses of height growth are summarized in *Table 8*. These results show the presence of a statistically significant (p > 0.99), positive correlation between 1000-seed weight and height growth. There is a similar correlation between survival and height growth and between height growth in consecutive years. These results, combined with those of survival discussed earlier, show that provenances with heavier seed have better survival and faster juvenile height growth than those with lighter seed. This indicates that seed weight, survival and height growth in black spruce are at least partially controlled by pleiotropic genes.

Table 8. — Summary of results of correlation analyses of height growth.

Character		Height in Fall 1969	Spring 1970	Fall 1970	Spring 1971	Fall 1971
1000-seed weight	r	0.583	0.614	0.637	0.555	0.572
	t	4.37**	4.73**	5.03**	4.06**	7.21**
Survival in 1968	r	0.323	0.243	0.599	0.425	0.378
	t	2.08**	1.53^{NS}	4.56**	2.86**	2.48**
Survival in 1969	r	0.521	0.484	0.644	0.590	0.527
	t	3.72**	3.36**	5.12**	4.44**	3.78**
Height in fall 1969	r	-	-	0.916	0.896	0.893
	t	-	-	13.90**	12.28**	12.17**
Height in spring 1970	r	-	-	0.927	0.864	0.890
	t	-	-	15.01**	10.43**	11.87**
Height in fall 1970	r	-	-	-	0.946	0.936
	t	-	-	-	17.77**	16.16**
Height in spring 1971	r	-	-	-	-	0.949
	t	-	-	-	-	18.31**

**Statistically significant (p > 0.99)
NS Statistically non-significant (p < 0.95)

Patterns of height growth of the leading shoot — A regression equation of the general form Y = a + b log X (where Y is the length of the leading shoot at each measurement and X is the number of days from May 31 to the days of periodic measurements) was found to give the best fit for the data among all common curve forms. The results of the analyses of variance of constants *a* and *b* and of the number of days from May 31 to the dates of cessation of height growth are summarized in *Table 9*.

The value of the constant *a* indirectly indicates the date of commencement of height growth, and that of constant *b* directly indicates the rate of height growth.

Though the contribution of environment, represented by replications, is low it is statistically significant (p > 0.99) for all three characters. The statistical significance of this contribution is apparently due to minor differences in nutrient levels among replications. The effects of such differences on the commencement and cessation of growth have been reported earlier by KOZLOWSKI (1964). The above analyses indicate the existence of such effects in case of black spruce also.

Table 9. — Summary of results of analyses of variance of the parameters of growth in 1970.

Statistic	a: % variance	a: F	b: % variance	b: F	No. of days to cessation of growth: % variance	F
Variance due to replications	5	4.00**	4	2.90**	3	3.54**
Variance due to provenances	53	4.91**	38	2.65**	68	9.23**
Variance due to experimental error	42		57		29	
TOTAL	100		100		100	
Coefficient of intra-class correlation	0.439		0.249		0.622	
Coefficient of intra-class determination	0.193		0.618		0.387	

**Statistically significant (p > 0.99)

The contribution of provenances to the total variance is very high and statistically significant (p > 0.99) for all three characters. It is the lowest for constant *b*, higher for constant *a* and highest for the number of days from May 31 to the cessation of height growth. Inter-provenance differences for these variables follow the same order.

Though the multiple range tests do not show any consistent pattern of variation in these characters, grouping of the provenances into Rowe's forest sections and single degree of freedom comparisons between them show interesting results. All the five forest sections of insular Newfoundland are significantly different from each other in terms of constant *a*. Provenances from forest section B.29 are the earliest to commerce growth, followed by those from forest sections B.28b, B.32, B.28a and B.30 *ad seriatim.*

As regards constant *b*, forest sections B.28a and B.30 both have significantly higher values than forest sections B.28b, B.29 and B.32 (p > 0.99). The provenances from the former two forest sections grow faster than those of the latter three.

The provenances can be divided into three groups in terms of the number of days from May 31 to cessation of growth. These are: forest sections B.29 and B.32 with the earliest cessation of height growth, B.28b which is intermediate and forest sections B.28a and B.30 which are the latest.

The values of the coefficients of intra-class correlation and determination, which indicate the degree of intra-provenance variation, are the lowest for constant *b*, higher for constant *a* and highest for the number of days from May 31 to the cessation of height growth.

These results show that the variation in these characters in ecotypic in the black spruce of Newfoundland and that there is high intra-provenane variation for constant *a* and for the number of days from May 31 to cessation of height growth. Ecotypic variation in these characters is due to the differential selection pressures exerted by widely different climatic conditions prevailing in the various forest sections during the micro-evolution of black spruce on the Island.

Root-collar diameter — Results of analysis of variance of plot means are summarized in *Table 10*.

As in the case of height growth, discussed earlier, prove-

Table 10. — Summary of results of analysis of variance of root-collar diameter in 1970 and 1971.

Statistic	Fall 1970 % variance	Fall 1970 F	Spring 1971 % variance	Spring 1971 F	Fall 1971 % variance	Fall 1971 F
Replications	1	0.40^{NS}	9	8.69**	4	3.44**
Provenances	53	4.68**	50	4.98**	54	5.09**
Experimental error	46		41		42	
TOTAL	100		100		100	
Coefficient of intra-class correlation	0.424		0.443		0.443	
Coefficient of intra-class determination	0.180		0.196		0.197	

**Statistically significant ($p > 0.99$)
NSStatistically non-significant ($p < 0.95$)

nances provide the largest source of variance, which has been statistically significant ($p > 0.99$) throughout the duration of the experiment. This indicates strong genetic control of this character.

The multiple range tests do not show consistent geographical trends on the basis of individual provenances. However, grouping of provenances into Rowe's forest sections and single-degree of freedom comparisons between forest sections gave useful results. The five forest sections of the Island are significantly different from each other ($p > 0.99$), with the root-collar diameter growth increasing from the northern to the southern forest sections. These results indicate ecotypic rather than clinal variation in four-year root-collar diameter growth in the black spruce of Newfoundland.

Having established strong ecotypically distributed genetic control on root-collar diameter growth, further analyses of variance of single-tree data for root-collar diameter in the fall of 1971 were conducted to study the nature of variation within provenances. The results of this analysis are summarized in *Table 11*.

Table 11. — Summary results of analysis of variance of root-collar diameter by single trees.

Source of variance	% variance	F
Replications	1	3.70**
Provenances	17	4.84**
Replications × provenances interaction	14	1.84**
Sampling error	68	
TOTAL	100	

** Statistically significant ($p > 0.99$).

These results show that sampling error is the largest source of variance. The low proportions of variance associated with replications and replications × provenances interaction indicate high intra-provenance variation which increases the variance due to sampling error. The low values for coefficients of intra-class correlation and determination shown in *Table 10* indicate low fraternal resemblance and high intra-provenance variation in juvenile root-collar diameter growth. The variation in juvenile root-collar diameter growth follows the same pattern as height growth.

Table 12 summarizes the results of important correlation analyses of root-collar diameter. These positive and statistically significant ($p > 0.99$) correlations show that provenances with heavy seed and high survival at the age of 1- and 2-years also have faster root-collar diameter growth and *vice versa*.

Table 12. — Results of correlation analyses of root-collar diameter.

Character		Root-collar diameter in Fall 1970	Spring 1971	Fall 1971
1000-seed weight	r	0.658	0.550	0.579
	t	5.32**	4.00**	4.31**
Survival in fall 1968	r	0.395	0.364	0.390
	t	2.62**	2.38**	2.57*
Survival in fall 1969	r	0.588	0.577	0.577
	t	4.42**	4.30**	4.30**

*Statistically significant ($p > 0.95$)
**Statistically significant ($p > 0.99$)

Summary

A provenance study of black spruce, based on 29 Newfoundland provenances was started in 1968. The experiment was established in a nursery at Pasadena, in western Newfoundland in a five-replicated randomized complete block design using open-pollinated bulked seed with 100-seed plots. A sample of eight randomly selected seedlings was obtained from each plot. This paper reports the results of a four-year study of the degree and nature of variation in Newfoundland populations.

Length and diameter of 20 randomly selected oven-dried cones from each tree, and weight of bulked seed from each provenance, were determined. Data on phenology, survival and growth of seedlings were collected. The data were analysed by means of (1) analyses of variance, (2) Student-Newman-Keul's multiple range tests, (3) single degree of freedom comparisons, and (4) correlation and regression analyses.

Variation in cone-length, cone diameter and seed-weight is ecotypic, with some indication of an indirect correlation of cone length and cone diameter with height growth. Cone-length and cone diameter are mutually correlated and are under strong genetic control.

Initiation and release of bud dormancy are under strong genetic control with large intra-provenance variation in both cases. Variation in these characters is ecotypic. The threshold levels of climatic factors for initiation of bud dormancy are temperatures of 1°—6° C and a photoperiod of 11.5—13.25 hours, and those for release of bud dormancy are 48—56 degree-days above 6° C, mean daily temperatures of 2—12° C and a photoperiod of 15.67 hours. Soil conditions affect release but not initiation of bud dormancy.

Though soil and microclimate have statistically significant effects on 1-year survival, both 1- and 2-year survival are under strong genetic control and are mutually correlated. Intra-provenance and intra-replication variances as well as replications × provenances interactions are high. Survival in both years is positively correlated with seed weight and only weakly correlated with latitude, longitude and altitude.

Height and root-collar diameter are under strong genetic control. Variation in both characters is ecotypic, with a statistically significant contribution from provenances, trees within provenances and replications × provenances interaction. There is a strong positive correlation between seed weight and growth and between growth in subsequent years. Seed weight, survival and growth appear to be under control of pleiotropic genes.

Commencement, cessation and rate of annual height growth are under strong genetic and weak environmental control. The genetic control and intra-provenance variation are largest in terms of cessation, weaker on com-

mencement and weakest on rate of annual growth. Variation in all three characters is ecotypic.

Key words: Black spruce; *Picea mariana* (MILL.) B.S.P.; Genetic variation; Provenance trials; Genetic parameters; Heritability; Phenology.

Zusammenfassung

Im Jahre 1968 wurde ein Herkunftstest mit Absaaten aus 29 neufundländischen Provenienzen der Schwarzfichte (*Picea mariana* (MILL.) B.S.P. eingeleitet. Der Versuch wurde in einer Baumschule in Pasadena, West Neufundland, in 5 Wiederholungen in randomisierten vollständigen Blocks angelegt. Dabei gelangten Portionen von je 100 Samen aus der von jeweils 7 frei abgeblühten Bäumen einer Herkunft geernteten Saatgutmenge pro Wiederholung zur Aussaat, nachdem zuvor noch die Zapfen jeder Herkunft auf Durchmesser, Länge und Gewicht untersucht worden waren. Die Untersuchung der Zapfen ergab eine signifikante Beziehung zwischen Zapfenlänge und Zapfendurchmesser, wobei sich diese Merkmale zugleich als ökotypisch und genetisch kontrolliert herausstellten. Die Untersuchung der Nachkommenschaften auf Überlebensprozent, Austreibetermin, Spätfrostschäden, Pflanzenhöhe, Wurzelhalsdurchmesser sowie Beginn und Verlauf des Höhenwachstums in der Vegetationsperiode ergab insbesondere, daß die Pflanzenhöhe und der Wurzelhalsdurchmesser als streng genetisch kontrolliert anzusehen sind.

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