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Phenotypic stability and delineation of black spruce breeding zones in Quebec

Jean Beaulieu, Armand Corriveau, and Gaétan Daoust

Information Report LAU-X-85E

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RÉSUMÉ

L'analyse des relevés d'observations phénotypiques effectués en 1985 dans quatre répétitions d'un essai de provenances pan-domanial d'épinette noire au Québec permet de faire ressortir les quelques conclusions qui suivent.

Il existe une relation positive entre la croissance en pépinière et celle en milieu forestier, une fois le choc de transplantation passé. Le patron de la variation de l'accroissement périodique en hauteur de l'épinette noire entre 10 et 16 ans après l'ensemencement est de type clinal, bien que variable d'un site forestier à l'autre. Seize ans après l'ensemencement, la part de la variation en hauteur attribuable à l'origine des semences représente entre 5 et 17 % de la variation totale selon le site étudié. On peut espérer un gain par la sélection de provenances supérieures et leur déplacement est possible. Une selection pour l'ensemble du territoire à reboiser basée uniquement sur ces résultats n'est toutefois pas réalisable. En effet, il existe une interaction provenances-milieux. Bien qu'il soit possible d'identifier des provenances relativement stables, il est proposé de subdiviser le territoire en zones d'amélioration plus restreintes. Cinq zones ont été délimitées sur la base

ABSTRACT

Once transplanting shock was overcome, a positive relationship existed between growth in the nursery and growth in the forest environment. The periodic height-growth variation pattern of black spruce, *Picea mariana* [Mill.] B.S.P., between 10 and 16 years from seed is clinal, although its strength varies from one forest site to another. Sixteen years from seed, height variation attributable to seed origin represents 5 to 17 percent of the total variation, depending upon the site studied. Gains may be expected from the selection of superior provenances and, after selection, these provenances may be relocated. However, due to provenance x environment interaction, selection for the entire area to be reforested cannot be based solely on those provenances having shown the best mean potential on the test sites as a whole. Although it is possible to identify relatively stable provenances, we have proposed subdividing the area into smaller breeding zones. Five zones were delineated based on provenance test results and on existing ecological regions. In addition, 5 superior provenance regions were identified. Finally, more than 20 provenances were proposed for individual breeding zones with at least one des résultats de l'essai de provenances et sur celle des régions écologiques existantes. De plus, cinq régions de provenances supérieures ont été identifiées. Finalement, au-delà d'une vingtaine de provenances ont été proposées pour chacune des zones d'amélioration renfermant au moins une répétition de l'essai de provenances. Il en résulterait des gains de 12 à 14 % par rapport à la hauteur moyenne de toutes les provenances.

provenance test repetition. These would result in gains of 12 to 14 percent in mean provenance height.

These conclusions were drawn from the analysis of phenotypic observation surveys conducted in 1985 in four repetitions of a range-wide black spruce test in Quebec.

INTRODUCTION

An ever increasing world demand for a variety of forest products, serious problems of natural regeneration brought about by modern harvesting methods, and the desire to maintain Canada's market share have led our forest managers to support vast reforestation programs involving many commercial species. East of the Rockies black spruce (*Picea mariana* [Mill.] B.S.P.) is unquestionably favored due mainly to its use by the pulp and paper industry. The structural qualities of its wood--its long fibre and relatively high density-- make it one of the most popular species for construction and pulp and paper manufacture (Besley 1959). Because black spruce is relatively unaffected by insects and disease, the protection costs involved in any reforestation program should be lower than with other tree species.

The natural distribution range of black spruce covers most of Canada and several American border states. It is the dominant species of eastern Canada's boreal forest. Its continent-wide distribution (Figure 1) bears witness to the species' ability to adapt to a wide variety of climatic and edaphic conditions (Hosie 1972). In general, black spruce grows in pure stands on poorly drained, cold, surface soil where competition is weak (Linteau 1955; Lafond 1966). A species covering such a vast territory is able to show evidence of high genetic variability due to the varying genotypic stabilities and adaptive capacities of its populations (Khalil 1984). Genetic variability results from such processes as natural selection, migration, random genetic drift, and genetic recombination. In the case of wide-ranging species experiencing variations in photoperiod and length of the growing season (Morgenstern 1975) as well as temperature ranges, natural selection and migration are definitely major factors. They generate general clinal-type variation patterns for certain specific characteristics (Morgenstern et al. 1986). For example, clinal variation patterns have been found in black spruce for germination rate, survival rate, phenology, juvenile growth, and species hardiness (Morgenstern 1969b; Dietrichson 1969; Corriveau 1981; Fowler and Park 1982). In addition, other genetic forces, such as random genetic drift, inbreeding, and interspecific introgression, may be more active under particular climatic and edaphic conditions, thereby effectively rupturing the clinal variation patterns and creating ecotypical ones (Khalil 1981; Morgenstern 1978). Developing effective breeding strategies

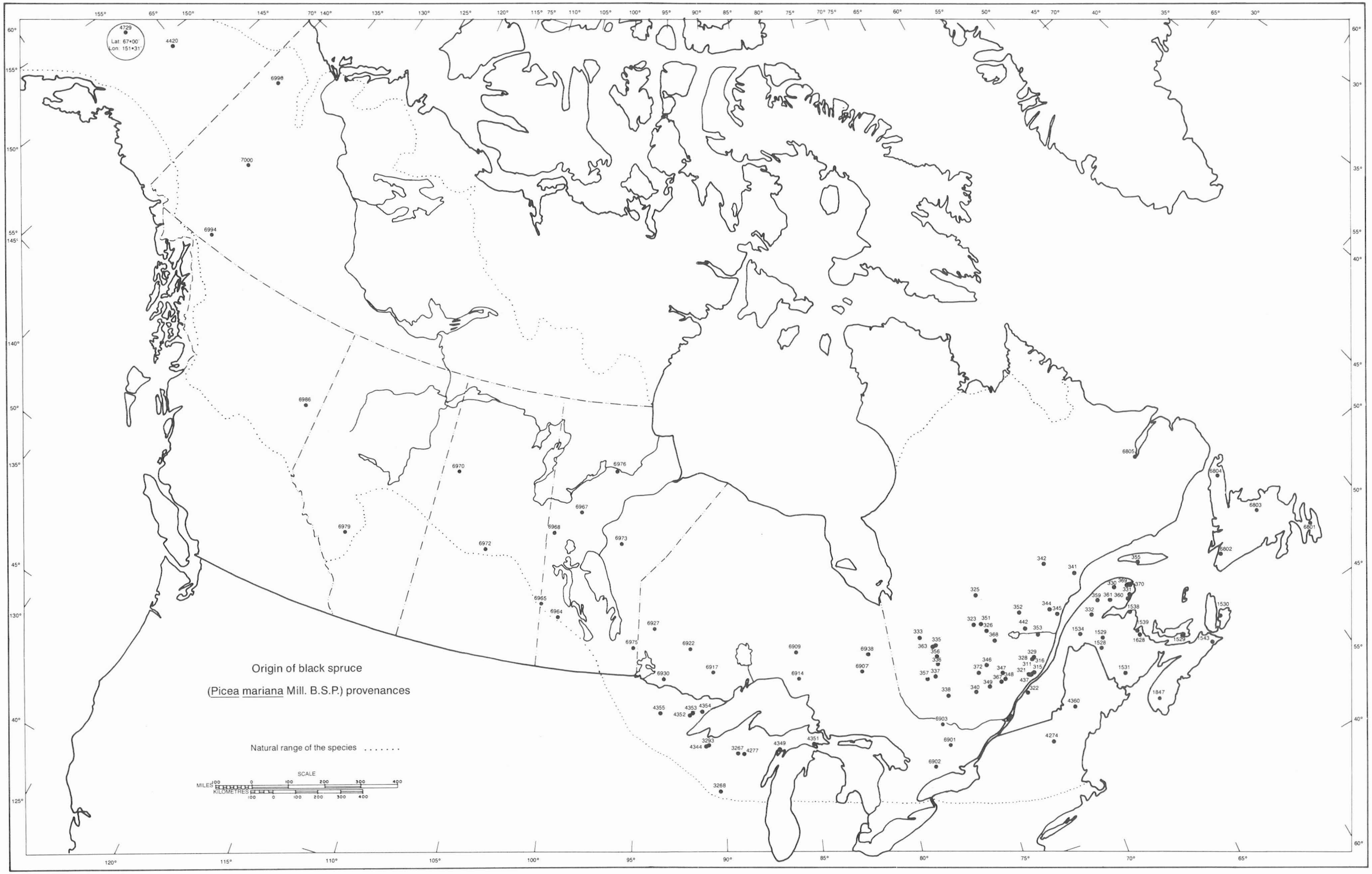

Figure 1. Black spruce natural range and origin of the provenances tested.

as a corollary to reforestation programs is possible only if the genetic variability patterns are known (Fowler and Park 1982). Diverging variation patterns indicate that range-wide studies are necessary if the best provenances are to be selected for a given tree breeding program, since limited regional studies are insufficient for obtaining a global picture of species variability (Morgenstern and Kokocinski 1976). However, in forest environments these patterns seems to become attenuated with time (Boyle 1985) and can even change completely following transplanting shock (Corriveau 1981). The objectives of this study are to identify black spruce height-growth variation patterns in Quebec, to determine whether these patterns are constant over time, to verify whether provenance x environment interaction exists, and where applicable, to establish distinct breeding zones and identify superior genetic provenances or provenance regions for them.

MATERIALS AND METHODS

Provenance origins

Petawawa National Forestry Institute coordinated range-wide testing of black spruce provenances which began in 1967. Because of the overwhelming amount of work involved, numerous logging companies and forest research organizations in Canada and in the Great Lake States cooperated in seed gathering, organizing test repetitions, follow-up in various areas, in data gathering, analysis, and interpretation. From 1967 to 1970, more than 200 populations, 60 in Quebec (Selkirk 1974), were sampled over the entire black spruce natural range. Seed subsamples from individual provenances were distributed to all participating organizations. Each provenance was composed of seeds collected from 7 to 10 trees in the same stand. Seeding was carried out in regional nurseries and seedlings were planted beginning in 1973 in about 30 test sites spread out over the area likely to be reforested with black spruce. In the spring of 1970, the 100 provenances to be tested in Quebec were seeded at the Valcartier Experimental Forest Station nursery. Of these, 45 were from Quebec, 11 from Ontario, 15 from the Maritimes, 13 from the northern United States, and 16 from central Canada, British Columbia, and Alaska (Figure 1, Table 1). Planting was carried out using a randomized complete six-block design, with subdivisions for early observation and the eventual transfer of seedlings to six forest test sites.

Table 1. Origin of the 100 black spruce provenances included in range-wide testing in Quebec

No.	Provenance	N. Lat. (° ')	W. Long. (° ')	Alt. (m)	Forest section (Rowe 1972)
S.311	Valcartier I, Quebec	45 56	71 31	245	L.4a
S.315	Rivière aux Pins, Quebec	46 57	71 35	200	L.4a
S.316	Valcartier II, Quebec	46 55	71 31	185	L.4a
S.321	Perthuis, Quebec	46 56	72 06	275	L.3
S.322	Blandford, Arthabaska	46 16	72 02	90	L.3
S.323	Parc Chibougamau, Roberval	49 33	74 10	410	B.1b
S.325	Parc Mistassini, Abitibi-Est	50 27	73 38	365	B.1b
S.326	Parc Chibougamau, Lac-Saint-Jean	49 02	73 27	380	B.1b
S.328	Parc des Laurentides, Montmorency	47 30	71 19	765	B.1a
S.329	Parc des Laurentides, Charlevoix	47 52	71 12	810	B.1a
S.330	Murdochville, Gaspé-Nord	48 55	65 25	610	B.2
S.331	Chandler, Gaspé-Est	48 24	64 53	120	B.2
S.332	Causapscal, Matapédia	48 30	67 07	245	L.6
S.333	Matagami, Abitibi-Est	49 37	77 45	270	B.4
S.335	Lebel-sur-Quévillon, Abitibi-Est	49 07	76 57	305	B.4
S.336	Senneterre, Abitibi-Est	48 22	76 57	365	B.3
S.337	Louvicourt, Abitibi-Est	47 55	77 21	355	B.7
S.338	Parc de la Vérendrye, Pontiac	47 05	76 33	360	B.7
S.340	Mont Saint-Michel, Labelle	46 52	75 11	335	L.4b
S.341	Port-Cartier, Saguenay	50 08	67 09	145	B.1a
S.342	Manicouagan 5, Saguenay	50 40	68 46	430	B.1b
S.344	Labrieville, Saguenay	49 09	69 23	505	B.1a
S.345	Forestville, Saguenay	48 56	69 08	120	B.1a
S.346	Manouane, Laviolette	47 48	74 07	460	B.7
S.347	Rivière-aux-Rats, Laviolette	47 18	73 06	360	B.7
S.348	Lower Mattawin, Saint-Maurice	46 55	73 26	300	B.7
S.349	Saint-Michel des Saints, Berthier	46 50	74 25	520	B.7

Table 1. (continued)

No.	Provenance	N. Lat. (° ')	W. Long. (° ')	Alt. (m)	Forest section (Rowe 1972)
S.351	Normandin (Nicauba), Roberbal	49 26	73 59	410	B.1b
S.352	Péribonka, Roberval	49 36	71 18	185	B.1b
S.353	Mars Ha! Ha!, Chicoutimi	48 12	70 56	245	L.7
S.355	Ile d'Anticosti	49 38	63 22	185	B.28c
S.356	Lac Parent, Augier, Abitibi-Est	48 36	76 41	440	B.3
S.357	Lac Decelles, Pelissier, Abitibi-Est	47 47	77 45	335	B.7
S.359	Gravier, Gravier, Bonaventure	48 34	66 26	275	B.2
S.360	Port Daniel, Daniel, Bonaventure	48 15	64 55	170	L.6
S.361	Cascapédia, Marcil, Bonaventure	48 29	65 51	185	B.2
S.363	Fraser, Fraser, Abitibi-Est	49 10	77 14	295	B.4
S.367	Lac Pimbina, Saint-Maurice	46 55	76 30	305	B.7
S.368	Lac Élaine, Roberval	48 30	73 20	550	B.1a
S.369	Water Creek, Gaspé-Sud	48 53	64 39	185	B.2
S.370	Cap-des-Rosiers, Gaspé-Sud	48 51	64 15	15	B.2
S.372	Lac Doré, Maskinongé	47 30	74 45	490	B.7
S.437	Duchesnay, Portneuf	46 52	71 39	185	L.3
S.442	Chûte-aux-Galets, Chicoutimi	48 37	71 04	185	L.7
S.1329	Garfield, Queens, Prince Edward Island	46 03	62 51	30	A.8
S.1528	Stuart Plains Rd., Victoria, N.B.	46 50	67 10	170	A.10
S.1529	William's Brook, Restigouche, N.B.	47 29	66 52	440	A.3
S.1530	Pengal Rd., Cape Breton, N.S.	45 56	60 10	60	A.7
S.1531	C.F.B. Gagetown, Sunbury, N.B.	45 35	66 29	90	A.3
S.1534	N. First Lake, Madawaska, Green R., N.B.	47 42	68 19	245	B.2
S.1538	N. Caraquet River, Gloucester, N.B.	47 45	65 07	15	A.3
S.1539	Tweedie Stream, Northumberland, N.B.	46 49	65 09	60	A.3
S.1543	Guysborough Shore, N.S.	45 23	61 22	45	A.7
S.1628	Black River North Arm., Kent, N.B.	46 53	65 05	30	A.9
S.1847	Southwestern, N.S.	44 10	65 45	105	A.52

Table 1. (continued)

No.	Provenance	N. Lat. (° ')	W. Long. (° ')	Alt. (m)	Forest section (Rowe 1972)
S.3267	Forest Co. II, Wisconsin	45 44	89 03	460	
S.3268	Mather, Jackson Co., Wisconsin	44 13	90 22	305	
S.3293	Ashland Co., Wisconsin	46 09	90 47	610	
S.4274	Grafton Co., Grafton, New Hampshire	44 15	71 38	405	
S.4277	Forest Co. I, Wisconsin	45 44	88 59	305	
S.4344	Hayward, Sawyer Co., Wisconsin	46 07	90 56	460	
S.4349	Delta Co., Michigan	45 59	86 51	155	
S.4351	Mackinac Co., Michigan	46 03	84 47	155	
S.4352	St.Louis Co., Minnesota	47 31	91 58	305	
S.4353	Isabella, Lake Co., Minnesota	47 42	91 18	305	
S.4354	Tofte, Cook Co., Minnesota	47 37	90 52	155	
S.4355	Itaska Co., Minnesota	47 32	93 43	490	
S.4360	Penobscot County, Maine	45 10	70 00	245	
S.4420	Bonanza I Stream, Alaska	64 44	148 19	340	
S.4729	Bettles Field, Alaska	67 00	151 31	275	
S.6801	Holyrood, Newfoundland	47 20	53 07	90	B.30
S.6802	Jeffrey's, Newfoundland	48 13	58 55	60	B.28b
S.6803	Bishops Falls, Newfoundland	49 01	55 26	60	B.28a
S.6804	Roddickton, Newfoundland	50 54	56 06	55	B.28b
S.6805	Goose Bay, Labrador, Newfoundland	53 25	60 23	5	B.12
S.6901	Bancroft, Hastings, Ontario	45 10	77 10	350	L.4c
S.6902	Apsley, Haliburton, Ontario	44 50	78 05	340	L.4d
S.6903	Chalk River, Renfrew, Ontario	45 58	77 25	160	L.4b
S.6907	Timmins, Ogden, Ontario	48 32	81 25	305	B.4
S.6909	R. Otasawian, Kihlir, Ontario	49 45	85 05	215	B.8
S.6914	White River, Hunt, Ontario	48 38	85 20	375	B.8
S.6917	Ipsala, Ontario	49 00	90 27	475	B.11
S.6922	Tour, Sioux, Ontario	50 15	91 40	400	B.11

Table 1. (concluded)

No.	Provenance	N. Lat. (° ')	W. Long. (° ')	Alt. (m)	Forest section (Rowe 1972)
S.6927	Minaki, Ontario	50 50	94 17	335	L.11
S.6930	Rainy Lake, Ontario	48 48	93 40	365	L.11
S.6938	Cochrane, Ontario	49 21	80 45	275	B.4
S.6964	Pulp River, Manitoba	51 48	100 12	275	B.16
S.6965	Hart Mountain, Manitoba	52 29	101 26	795	B.15
S.6967	Point Lake, Manitoba	55 30	94 40	210	B.21
S.6968	Cranberry Portage, Manitoba	54 35	101 00	315	B.15
S.6970	Peter Lake, Saskatchewan	56 03	108 42	435	B.20
S.6972	Nisbet Prov. Forest, Saskatchewan	53 14	105 46	460	B.17
S.6973	N.W. Angle Forest Reserve, Manitoba	49 17	96 18	350	L.12
S.6975	Whiteshell Prov. Park, Manitoba	50 04	95 27	335	B.14
S.6976	Gauer Lake, Manitoba	57 00	97 52	259	B.27
S.6979	Rocky Mtn, House II, Alberta	52 22	115 15	1070	B.19a
S.6986	Fort St.John III, British Columbia	56 37	121 28	855	B.19a
S.6994	Marsh Lake, Yukon Territory	60 32	134 27	670	B.26b
S.6998	Johnson Stream, Yukon Territory	67 15	138 20	765	B.33
S.7000	Mayo, Yukon Territory	64 34	135 55	505	B.26c

Test site selection

Six forest or agro-forest sites representative of the Quebec black spruce reforestation range were selected for provenance testing (Figure 2). They were chosen for their location so as to include a variety of pedoclimatic conditions likely to be encountered in the reforestation areas (Tables 2 and 3). In the summer of 1973, each test site was treated according to the specific conditions prevailing on it. Forest-site logging debris were either burned or windrowed with a raking blade mounted on a bulldozer, whereas abandoned farm sites were raked with a forest harrow.

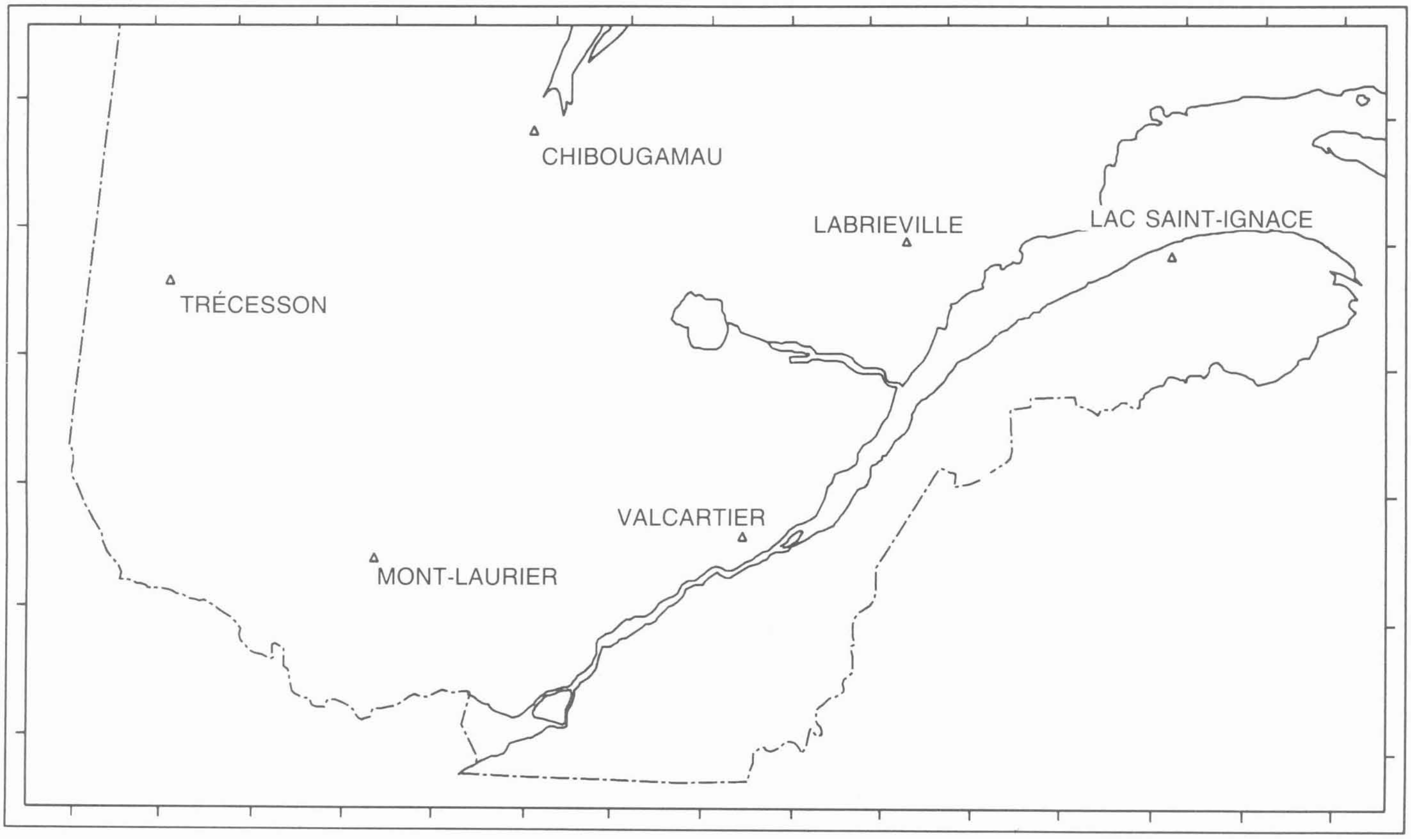

Figure 2. Location of black spruce provenance test sites in Quebec.

Table 2. Test site ecological characteristics

Site	Ecological region (Thibault and Hotte 1985)	Bioclimax	Surface deposit
Mont-Laurier, Gatineau County, Sicotte Township	Maple/yellow birch/ basswood stand	Cool, Continental	Fluvio-glacial sand and sandy granite till
Lac Saint-Ignace, Matane County, Tourelle Township	Fir/white birch stand	Cold, wet	Loamy, schistous till with drift boulders
Chibougamau, Abitibi-Est County, Richardson Township	Black spruce stand associated with mosses	Very cold, continental, dry	Thin granite till and sand
Valcartier, Portneuf County	Maple/yellow birch stand	Cool, continental, wet	Alluvial sand
Labrieville, Saguenay County, Virot Township	Black spruce stand associated with mosses	Very cold, continental, wet	Sandy granite till
Trécesson, Abitibi-Est County, Villemontel Township	Fir/white birch stand	Very cold, continental, dry	Clay and lacustrine sand

Table 3. Test site geographic and climatic characteristics

Site	Altitude m	North latitude	West longitude	Temperature: June July August Mean °C	Temperature: Absolute minimum °C	Total annual precipitation cm	Number of frost-free damp (days)
Mont-Laurier	244-351	46°36'	75°48'	17.0	-44.4	91	80-100
Lac Saint-Ignace	457-655	49°00'	66°20'	14.9	-42.2	99	100-120
Chibougamau	411	50°03'	74°10'	14.4	-49.3	81	80
Valcartier	152	46°52'	71°32'	15.4	-41.7	117	120-140
Labrieville	457-533	49°12'	69°33'	13.2	-43.8	97	80-90
Trécesson	305-366	48°40'	78°30'	15.0	-48.9	99	80-100

Test designs

Provenances were planted on individual sites using a randomized complete 6-block design with 16-tree (4 x 4) square plots. In 1974, seedlings were planted, with 3.05 x 2.45 m between each, at Mont-Laurier, Lac Saint- Ignace, and Chibougamau. The other three repetitions at Valcartier, Labrieville, and Trécesson were established in 1975 with 2.45 x 2.45 m between the trees. These rather large spacings were required for machine maintenance of the sites.

Phenotypic observation surveys

At the end of the first growing season, 10 seedlings per provenance and per block were randomly chosen, permanently identified, and then they were measured annually until they were transferred to forest environments. Data were gathered for *a posteriori* assessment of the effectiveness of early selection on this species. Preliminary interpretation of the data has been completed using an initial measurement taken 5 years after planting (Corriveau 1981). In the fall of 1979, survival, height growth, damage, and deformation due to insects and other environmental factors were noted in order to verify whether variation patterns observed a few years earlier in the nursery had been maintained and to measure the impact of planting in forest environments on these same patterns. In 1985, or 16 years from seed, new phenotypic surveys were carried out in four of the six sites with a view to conducting the same type of study at a more advanced age, and to verify the existence of provenance x environment interactions affecting the growth that could be used to delineate breeding zones and select the provenances that performed best in each zone.

Statistical analyses

Given an uncommonly high mortality rate of the Labrieville and Trécesson sites due to unfavorable pedoclimatic conditions and drought at the time of planting, only four of the six sites are included in our analyses. Pearson correlation and stepwise multiple regression analyses were used to study periodic height-growth genetic variation patterns in nursery and forest environments. Survival and height growth analyses of variance 16 years from seed were also performed for each site using the following formulas:

$$Y_{ij} = \mu + p_i + R_j + e_{ij} \qquad (1)$$

where

$Y_{ji} = \sin^{-1} \sqrt{P_{ij}}$ (Steel and Torrie 1980)

p_{ij} = proportion of living trees 16 years from seed from ith provenance and jth block

μ = overall mean

p_i = effect of ith provenance

R_j = effect of jth block

e_{ij} = within-plot error

$$Y_{ijk} = \mu + p_i + R_j + PR_{ij} + e_{k(ij)} \quad (2)$$

where

Y_{ijk} = height of kth tree of ith provenance in jth block

μ = average height

p_i = effect of ith provenance

R_j = effect of jth block

PR_{ij} = effect of ith provenance x jth block interaction

$e_{k(ij)}$ = within-plot error

An overall location analysis of variance of height growth 16 years from seed was performed using the following formula:

$$Y_{ijklm} = \mu + S_i + P_j + R_{k(i)} + SP_{ij} + PR_{jk(i)} + e_{m(ijk)} \quad (3)$$

where

Y_{ijklm} = height of mth tree of jth provenance of kth block in ith site

μ = average height

S_i = effect of ith site

P_j = effect of jth provenance

$R_{k(i)}$ = effect of kth block in ith site

SP_{ij} = effect of ith site x jth provenance interaction

$PR_{jk(i)}$ = effect of jth provenance x kth block interaction in ith site

$e_{m(ijk)}$ = within-plot error

Due to a high mortality rate in two blocks at Valcartier and Lac Saint-Ignace, four blocks per site were included in the overall location analysis of variance in order to improve provenance and site comparison.

Ecovalences (Wricke 1962; Morgenstern and Teich 1969) were calculated to determine the contribution of individual provenances to provenance x environment interaction and to assess their phenotypic stability. A provenance contributing little to environmental interaction, yet whose performance is roughly equal to the mean overall provenance performance, is considered capable of adapting to a wide range of ecological regions. Such a provenance is said to have a high ecovalence. If a forest geneticist decides against dividing the reforestaton territory into small breeding zones, a group of provenances with high ecovalences may be used as the genetic base for developing synthetic varieties; however, the gain will be less.

Type II genetic correlations, established between the characteristics of provenances on different sites, were used to delineate breeding zones (Burdon 1977). This method was applied first to tree family tests (Fox and Rosielle 1982), and then extended to provenance trials by comparing provenance yield to a synthetic or populational genotype yield (Wellendorf et al. 1986).

Genetic correlation coefficients are obtained as follows:

$$R_{gxy} = r_{xy}/h_x \cdot h_y$$

where

r_{xy} = Pearson correlation coefficient for group means in xth and yth sites

h_x = square root of provenances' mean heritability in xth site

h_y = square root of provenances' mean heritability in yth site

and

$h^2_x = V_G/V_G + V_E$ = provenances' mean heritability in xth site

where

V_G = genetic variance between provenances' means

V_E = environmental variance between provenances' means

A cluster analysis (Varclus *in* SAS 1985) was performed on the genetic correlation matrix thus obtained to regroup the test locations and establish breeding zones.

Except for partitioning the variation among the individual sites, only the 67 provenances in the 4 blocks of the 4 sites selected were included in the analyses.

RESULTS AND DISCUSSION

Temporal growth variation

Corriveau (1981) indicated that black spruce provenances with high growth rates in the favorable climatic and edaphic conditions found in nurseries were outstripped by the slower growing sources in the first years after transplanting. Moreover, he emphasized that this negative relationship was most marked on those sites with the most adverse conditions, attributing this phenomenon to the more severe transplanting shock suffered by larger provenances. Pollard and Logan (1974) showed that some seedlings are able to start new foliar primordia during the growing season; consequently, some provenances show a certain superiority early on. However, this advantage tends to disappear after a few years of growth (Jablanczy 1971), when only predetermined growth is evident. Provenances showing early superiority would then be outstripped by slower developing provenances.

A combination of older material, transplanting shock, and difficulties encountered after planting at sites whose pedoclimatic conditions were harsher than nurseries, led Corriveau (1981) to conclude that the relationship between growth in the nursery and periodic growth between the 5th and 10th year in the forest environment was not significant enough to enable effective nursery selection of the best provenances. He recommended waiting for the results of subsequent observations before definitively rejecting early selection. Nienstaedt (1984) reached the same conclusion for provenances planted in the Great Lakes States. Fowler and Park (1982), on the other hand, indicated that provenance performance in Maritime nurseries is closely related to their height 5 years after planting. The phenotypic observation survey done in 1985, 16 years from seed, allows us to verify whether the conclusions drawn from observations made 5 years after planting hold true.

Table 4 shows the Pearson's product-moment correlation coefficients for the annual growth of black spruce nursery provenances and their periodic height growth between the 10th and 16th year on individual test sites. These correlation coefficients are low to moderate, and all are positive and statistically significant (r=0.25 to r=0.57). Therefore, provenances started to show the same relative potential observed in the nursery. We also observed that the relationship between height growth in the nursery and that measured in forest sites decreases with the harshness of the site's environmental conditions. This correlation is not unrelated to the major changes observed in provenance ranks on these harsher sites (Corriveau 1981). These results also confirm Corriveau's assertion (1981) that the harsher the climate and the poorer the soil in reforestation sites, the less effective early selection will be for rapid growth in outlying nurseries, and the more it will be necessary to test sources in environmental conditions comparable to those found on reforestation sites. The overall location correlation coefficient for the last year of nursery growth and growth from the 10th to the 16th year in the forest environment is 0.71. This figure

Table 4. Pearson correlation coefficients for black spruce juvenile growth and periodic height growth in forest environments

	Nursery 2 years	Nursery 2-3 years	Nursery 3-4 years	Mont-Laurier 10-16 years	Lac Saint-Ignace 10-16 years	Chibougamau 10-16 years	Valcartier 10-16 years	Overall locations 10-16 years
2	1.00	0.51	0.75	0.38	0.40	0.26	0.49	0.53
2-3		1.00	0.72	0.49	0.25	0.32	0.55	0.55
3-4			1.00	0.57	0.43	0.47	0.56	0.71
Mont-Laurier				1.00	0.41	0.58	0.54	0.88
Lac St-Ignace					1.00	0.35	0.25	0.60
Chibougamau						1.00	0.29	0.75
Valcartier							1.00	0.67
Overall locations								1.00

Table 5. Pearson correlation coefficients for black spruce juvenile height growth and the geographic coordinates of provenance origin

	Nursery 2 years	Nursery 2-3 years	Nursery 3-4 years	Mont-Laurier 10-16 years	Lac Saint-Ignace 10-16 years	Chibougamau 10-16 years	Valcartier 10-16 years	Overall locations 10-16 years
Lat.	-0.58	-0.43	-0.57	-0.28	N.S.	-0.25	N.S.	-0.30
Long.	N.S.	0.25	N.S.	0.38	N.S.	0.34	N.S.	0.30
Alt.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.

Table 6. Stepwise multiple regressions in the height growth of black spruce provenances in nurseries and forest environments due to the geographic coordinates of their origin

	R^2	S_e
Nursery 3-4 years		
$Y = 61.10 - 0.96\ X_1 + 0.010\ X_2 - 0.0049\ X_3$	0.44	2.38
Mont-Laurier 10-16 years		
$Y = 370.54 - 4.39\ X_1 + 0.9211\ X_2$	0.22	25.03
Lac Saint-Ignace 10-16 years		
No relation		
Chibougamau 10-16 years		
$Y = 247.27 - 3.07\ X_1 + 0.66\ X_2$	0.17	20.45
Valcartier 10-16 years		
No relation		
All-sites 10-16 years		
$Y = 295.75 - 3.34\ X_1 + 0.80\ X_2 - 0.023\ X_3$	0.22	18.89

where

Y = height growth (cm)
X_1 = north latitude (degrees)
X_2 = west longitude (degrees)
X_3 = altitude (m)

indicates that, in general, early selection would have been feasible. However, individual test site correlation coefficients are lower. In relation to the overall mean, selection of the 10 best nursery provenances 16 years from seed would have netted height gains of 5 to 8 percent, depending on the test site.

Growth variation due to geographic origin

Height growth characteristics observed in the nursery and periodic growth between the 10th and 16th year for all four test sites are related to the geographic coordinates of black spruce provenance origins (Table 5). Provenance height growth is negatively related to origin latitude and positively related to origin longitude. At Mont-Laurier and Chibougamau, a significant relationship was found between the geographic coordinates of black spruce provenance origins and periodic height growth between the 10th and 16th year. However, this relationship was not observed at the other 2 test sites, even though at Valcartier, for example, nursery growth correlated closely with growth from the 5th to the 11th year after planting. The highest mortality rate was, in fact, observed at Valcartier, therefore it is not surprising that provenance growth and the geographic coordinates of provenance origins are unrelated. Although mortality was high for all of the provenances, it did not necessarily affect each provenance in the same way. This in itself is sufficient to mask a significant relationship. Lac Saint-Ignace, the second largest site, also showed a high mortality rate, and no relationship was found there either.

Using regression analysis, we were able to study these same relationships by incorporating the geographic coordinates of provenance origins into a single mathematical formula. Regression figures thus obtained reinforce the conclusions drawn from simple correlations (Table 6). Regression plots show range-wide clinal variation in black spruce juvenile growth. This variation is observed both in the nursery and in periodic growth on test sites. The geographic coordinates of provenance origins account for about 20 percent of the total growth variation in forest environments as opposed to more than 40 percent in the nursery. These results concur with those obtained by others (Morgenstern 1969a; Corriveau 1981; Fowler and Park 1982; Boyle 1985; Morgenstern et al. 1986). In general, then, height growth increases with provenance origin from north to south, east to west, and high to low altitude regions. In the nursery, as on the test sites as a whole, periodic height growth is greater in the provenances from the southwestern portion of the range and lower in those from the northeast. However, this variation pattern is not expressed in the same way on each site. As in the case of simple correlations, significant regression plots were not found at Lac Saint-Ignace or Valcartier, while provenance origin latitude and longitude play an important role at the other 2 sites. In addition, clinal variation has a tendency to decrease with time (as the trees get older), as is shown by the drop from R^2=0.44 to R^2=0.22 in the determination coefficient. This trend was also observed at the Ontario sites (Boyle 1985).

Partition of survival and total height variations

When the proportion of the variation due to provenance origin is high and significant, provenance selection can lead to substantial gains. The proportion of the provenance survival variation attributable to place of origin is not significant, except in the case of the Lac Saint-Ignace site (Table 7). Therefore, the survival factor does not have significant, global influence over the yield obtained through provenance selection based on other characteristics such as growth or productivity. Because of the very close correlation between

Table 7. Analyses of the black spruce survival variance ($\sin^{-1}\sqrt{p}$) 16 years from seed on 4 test sites

	Mont-Laurier				Lac St-Ignace				Chibougamau				Valcartier			
Source of variation	D.F.	M.S.	F	Pr>F	D.F.	M.S.	F	Pr>F	D.F.	M.S.	F	Pr>F	D.F.	M.S.	F	Pr>F
Blocks	5	0.0089	8.68	0.0001	5	0.3752	40.41	0.0001	5	0.1254	26.45	0.0001	5	0.4070	34.09	0.0001
Provenances	84	0.0012	1.16	0.1765	67	0.0139	1.50	0.0140	88	0.0056	1.18	0.1455	88	0.0135	1.13	0.2305
Error	420	0.0010			335	0.0093			440	0.0047			264	0.0119		

Table 8. Analyses of the black spruce provenance height variance 16 years from seed at each of the 4 test sites

Source of variation	Sum of squares	Degrees of freedom	Mean squares	F	PR>F	Variance components	Variance components (%)
			VALCARTIER				
Provenances	220.10	88	2.50	4.00	0.001	0.090	10
Blocks	63.77	3	21.26	34.00	0.001	0.050	5
Prov. x Blocks	357.41	264	1.35	2.17	0.001	0.140	15
Within-plot	1 458.08	2 332	0.63			0.630	70
Total		2 687				0.910	
			MONT-LAURIER				
Provenances	777.41	84	9.25	19.69	0.001	0.104	17
Blocks	43.20	5	8.64	18.38	0.001	0.007	1
Prov. x Blocks	493.98	420	1.18	2.50	0.001	0.050	8
Within-plot	3 344.90	7 116	0.47			0.470	74
Total		7 625				0.631	
			LAC ST-IGNACE				
Provenances	173.56	67	2.59	5.16	0.001	0.045	5
Blocks	452.39	5	90.48	180.24	0.001	0.169	20
Prov. x Blocks	518.69	335	1.55	3.08	0.001	0.134	16
Within-plot	2 139.47	4 262	0.50			0.502	59
Total		4 669				0.850	
			CHIBOUGAMAU				
Provenances	305.97	88	3.48	12.56	0.001	0.050	9
Blocks	819.04	5	163.81	591.20	0.001	0.150	27
Prov. x Blocks	484.28	444	1.09	3.93	0.001	0.070	13
Within-plot	1 883.04	6 796	0.28			0.280	51
Total		7 333				0.550	

growth from the 10th to the 16th year and height at 16 years (r=0.992**), this figure was used in subsequent analyses. As is shown in Table 8, the proportion of tree height variation 16 years from seed due to geographic origin varies from 5 to 17 percent depending upon the site. This source of variation is large enough to warrant selection of the best provenances. The table also shows that the major part of the total variation (50 to 75%), the effect of micro-sites on individual tree growth included, occurs within provenances. Mass selection could therefore help to increase the genetic gain anticipated from initial selection at the provenance level. Variance analysis also shows considerable provenance x block interaction, which is indicative of the effect of micro-sites on provenances. Selection of the best provenances must, therefore, be carried out meticulously to minimize the impact of this interaction.

Provenance x environment interaction and phenotypic stability

Provenance variability and/or rank may vary from one forest environment to the next. When this occurs, a provenance x environment interaction is generated. Because this interaction affects selection effectiveness and expected genetic gains (Kremer 1986), the forest geneticist cannot indiscriminately select those provenances having shown the best mean overall locations potential for the entire reforestation area. Table 9 shows a significant provenance x environment interaction for black spruce.

Table 9. Overall locations black spruce height analysis of variance, 16 years from seed

Source of variation	Sum of squares	Degrees of freedom	Mean squares	F	PR>F
Locations	1 495.41	3	498.47	268.7	0.0001
Provenances	570.38	66	8.64	4.7	0.0001
Blocks (locations)	229.87	12	19.16	13.4	0.0001
Prov. x Blocks (locations)	1 130.17	792	1.43	3.1	0.0001
Prov. x Locations	367.38	198	1.86	1.3	0.0001
Within-plot	5 731.65	12 253	0.47		

Table 10. Wricke ecovalences -- total height and rank of black spruce provenances in the 4 Quebec test sites -- 16 years from seed

No.	Name	Contribution to the sum of squares	MONT-LAURIER Height (m)	MONT-LAURIER Rank	LAC ST-IGNACE Height (m)	LAC ST-IGNACE Rank	CHIGOUGAMAU Height (m)	CHIGOUGAMAU Rank	VALCARTIER Height (m)	VALCARTIER Rank
S.6922	Tour, Sioux, Ontario	0.83	3.52	1	2.84	2	2.38	5	3.32	10
S.4360	Penobscot County, Maine	4.97	3.50	2	2.57	23	2.17	24	2.65	75
S.367	Lac Pimbina, Saint-Maurice	16.17	3.49	3	2.36	46	1.89	58	2.85	50
S.6903	Chalk River, Renfrew, Ontario	12.71	3.48	4	2.65	16	2.10	31	3.57	2
S.6927	Minaki, Ontario		3.44	5	2.61	20	2.52	1	3.34	8
S.356	Lac Parent, Augier, Abitibi-Est	6.03	3.43	6	2.57	24	2.08	35	3.54	3
S.1528	Stuart Plains Rd., Victoria, N.B.	4.99	3.38	7	2.28	56	2.40	4	3.39	5
S.4353	Isabella, Lake Co., Minnesota	3.82	3.38	8	2.46	34	2.26	11	3.18	25
S.3267	Forest Co. II, Wisconsin		3.37	9					2.78	60
S.6902	Apsley, Haliburton, Ontario	5.96	3.34	10	2.44	39	1.93	54	3.33	9
S.6930	Rainy Lake, Ontario	4.83	3.31	11	2.24	62	2.27	9	3.24	15
S.357	Lac Decelles, Pelissier, Abitibi-Est	10.30	3.31	12	2.34	50	2.10	33	3.59	1
S.6901	Bancroft, Hastings, Ontario		3.30	13	2.53	27	2.26	13	3.22	20
S.323	Parc Chibougamau, Roberval	12.95	3.30	14	2.54	26	2.16	26	2.47	84
S.333	Matagami, Abitibi-Est	4.33	3.29	15	2.74	8	1.95	51	3.29	12
S.340	Mont Saint-Michel, Labelle	0.27	3.29	16	2.44	38	2.27	10	3.20	22
S.4352	St. Louis Co., Minnesota	11.34	3.29	17	2.03	77	2.04	41	2.85	51
S.6917	Ipsala, Ontario	1.88	3.28	18	2.68	14	2.24	16	3.19	24
S.6907	Timmins, Ogden, Ontario		3.28	19	2.76	6	2.47	2	3.09	33
S.346	Manouane, Laviolette		3.27	20	2.35	48	2.04	43	3.42	4
S.4344	Hayward, Sawyer Co., Wisconsin		3.27	21	2.15	67	2.12	29	2.84	52
S.363	Fraser, Fraser, Abitibi-Est	2.87	3.24	22	2.42	40	2.06	39	2.78	59
S.315	Rivière-aux-Pins, Quebec	7.95	3.23	23	2.25	59	1.87	63	3.16	27
S.6973	N.W. Angle Forest Reserve, Manitoba		3.16	24			2.21	20	2.73	69
S.1538	N. Caraquet River, Gloucester, N.B.	7.94	3.15	25	2.85	1	1.96	47	3.36	7
S.326	Parc Chibougamau, Lac-Saint-Jean	11.52	3.15	26	2.68	15	2.04	42	2.70	71
S.348	Lower Mattawin, Saint-Maurice		3.13	27	2.64	18	2.26	14	2.82	54
S.316	Valcartier II, Quebec	9.90	3.12	28	1.94	81	1.92	56	3.22	19
S.337	Louvicourt, Abitibi-Est	1.74	3.11	29	2.47	33	2.10	34	3.31	11
S.1628	Black River North Arm, Kent, N.B.	0.91	3.11	30	2.36	47	2.19	22	2.89	44
S.1531	C.F.B. Gagetown, Sunbury, N.B.	6.01	3.11	31	2.70	13	2.21	18	2.59	78
S.338	Parc de la Vérendrye, Pontiac	3.23	3.10	32	2.46	36	2.30	7	2.90	42
S.442	Chutes-aux-Galets, Chicoutimi	1.98	3.10	33	2.74	7	2.13	28	3.14	28
S.4351	Mackinac Co., Michigan	3.05	3.08	34	2.33	51	2.10	32	3.23	18

Table 10. (continued)

No.	Name	Contribution to the sum of squares	MONT-LAURIER Height (m)	Rank	LAC ST-IGNACE Height (m)	Rank	CHIBOUGAMAU Height (m)	Rank	VALCARTIER Height (m)	Rank
S.4355	Itaska Co., Minnesota	1.74	3.07	35	2.41	43	2.15	27	2.78	61
S.6938	Cochrane, Ontario	14.24	3.04	36	1.90	83	1.92	55	2.19	97
S.361	Cascapédia, Marcil, Bonaventure	4.30	3.04	37	2.52	32	1.75	73	3.01	36
S.1539	Tweedie Stream Northumberland, N.B.	12.07	3.04	38	2.73	10	1.87	62	3.39	6
S.349	Saint-Michel des Saints, Berthier	0.48	3.04	39	2.52	29	2.12	30	2.76	64
S.6914	White River, Hunt, Ontario	5.16	3.02	40	2.16	66	1.85	65	3.03	35
S.1534	North First Lake, Madawaska, Green R., N.B.	5.54	3.01	41	2.77	4	1.70	79	2.92	41
S.372	Lac Doré, Maskinongé	7.97	3.01	42	2.62	19	2.16	25	2.54	80
S.352	Péribonka, Roberval	2.41	3.00	43	2.73	9	2.07	38	2.86	48
S.347	Rivière-aux-Rats, Laviolette	2.55	2.99	44	2.77	5	2.26	12	3.26	14
S.353	Mars Ha! Ha!, Chicoutimi	1.38	2.98	45	2.60	21	2.01	45	3.04	34
S.1329	Garfield, Queens, Prince Edward Island		2.98	46	2.09	73	2.08	37	3.09	32
S.321	Perthuis, Portneuf	2.27	2.97	47	2.81	3	2.30	8	3.12	30
S.335	Lebel-sur-Quévillon, Abitibi-Est		2.97	48	2.39	45	1.95	49	2.79	57
S.359	Gravier, Gravier, Bonaventure		2.96	49	2.12	70	2.23	17	2.90	43
S.6909	R. Otasawian, Kihlir, Ontario	1.87	2.96	50	2.60	22	1.95	50	2.86	49
S.336	Senneterre, Abitibi-Est		2.96	51	2.07	74	1.95	48	3.16	26
S.322	Blandford, Arthabaska	4.02	2.93	52	2.39	44	1.80	70	2.47	87
S.4354	Tofte, Cook Co., Minnesota	8.44	2.92	53	2.14	68	2.25	15	2.87	47
S.4277	Forest Co. I, Wisconsin	6.65	2.92	54	2.31	55	2.40	3	2.98	37
S.370	Cap des Rosiers, Gaspé-Sud	5.82	2.90	55	2.25	61	1.89	59	3.21	21
S.368	Lac Élaine, Roberval		2.90	56	2.34	49	2.03	44	2.93	40
S.328	Parc des Laurentides, Montmorency		2.84	57	2.32	53	1.86	64	2.78	62
S.360	Port Daniel, Daniel, Bonaventure	1.37	2.83	58	2.19	64	2.05	40	2.74	67
S.369	Water Creek, Gaspé-Sud	1.52	2.83	59	2.14	69	1.67	82	2.66	74
S.1530	Bengal Rd., Cape Breton, N.S.	3.26	2.81	60	2.04	76	1.77	71	2.79	56
S.3293	Ashland Co., Wisconsin	6.71	2.80	61	2.11	71	2.18	23	2.95	38
S.4349	Delta Co., Michigan	4.92	2.79	62	2.70	12	1.99	46	3.14	29
S.6803	Bishops Falls, Newfoundland	6.18	2.75	63	2.65	17	1.74	75	2.94	39
S.3268	Mather, Jackson Co., Wisconsin	7.76	2.75	64	1.98	79	2.08	36	2.87	46
S.332	Causapscal, Matapédia	6.30	2.73	65	2.52	28	2.20	21	2.69	73
S.6801	Holyrood, Newfoundland	3.64	2.68	66	2.31	54	1.49	87	2.81	55
S.6979	Rocky Mtn, House II, Alberta	0.79	2.64	67	1.97	80	1.64	85	2.63	76

Table 10. (concluded)

No.	Name	Contribution to the sum of squares	MONT-LAURIER Height (m)	Rank	LAC ST-IGNACE Height (m)	Rank	CHIBOUGAMAU Height (m)	Rank	VALCARTIER Height (m)	Rank
S.355	Île d'Anticosti	7.62	2.62	68	2.32	52	1.74	74	2.14	98
S.6965	Hart Mountain, Manitoba		2.62	69			1.90	57	2.76	65
S.325	Parc Mistassini, Abitibi-Est	7.00	2.61	70	2.27	57	1.94	52	2.32	94
S.341	Port-Cartier, Saguenay	2.16	2.60	71	2.26	58	1.81	69	2.49	82
S.1847	Southwestern, N.S.		2.59	72	2.41	41			3.11	31
S.342	Manicouagan 5, Saguenay	1.80	2.58	73	2.25	60	1.84	66	2.36	92
S.345	Forestville, Saguenay	6.48	2.57	74	2.52	31	1.71	77	2.72	70
S.1529	William's Brook, Restigouche, N.B.	8.14	2.57	75	2.41	42	2.21	19	2.89	45
S.344	Labrieville, Saguenay	0.96	2.55	76	1.99	78	1.76	72	2.79	58
S.329	Parc des Laurentides, Charlevoix	2.68	2.55	77	2.18	65	1.38	88	2.48	83
S.6968	Portage Cranberry, Manitoba		2.53	78					2.84	53
S.331	Chandler, Gaspé-Est	6.53	2.52	79	2.46	35	1.88	60	2.46	90
S.330	Murdochville, Gaspé-Nord	2.13	2.51	80	2.06	75	1.67	83	2.47	85
S.6802	Jeffrey's, Newfoundland	5.53	2.50	81	2.44	37	1.83	67	2.74	68
S.6967	Lac Point, Manitoba		2.47	82	1.93	82	1.71	76	2.56	79
S.6805	Goose Bay, Labrador, Newfoundland	7.13	2.41	83	2.23	63	1.68	81	2.75	66
S.6804	Roddickton, Newfoundland	12.87	1.98	84	2.09	72	1.69	80	2.33	93
S.437	Duchesnay, Portneuf	8.52	1.97	85	1.62	84	1.01	89	2.36	91
S.1543	Guysborough Shore, N.S.						1.70	78	2.47	86
S.311	Valcartier I, Quebec									
S.351	Normandin (Nicauba), Roberbal				2.56	25	2.31	6	2.46	89
S.4274	Grafton Co., Grafton, New Hamshire								3.23	17
S.4420	Bonanza I Stream, Alaska								1.67	99
S.4729	Bettles Field, Alaska								2.77	63
S.6964	Pulp River, Manitoba				2.52	30	1.93	53	2.61	77
S.6970	Peter Lake, Saskatchewan								3.19	23
S.6972	Nisbet Prov. Forest, Saskatchewan								2.50	81
S.6975	Whiteshell Prov. Park, Manitoba				2.71	11	1.88	61	3.27	13
S.6976	Gauer Lake, Manitoba								2.47	88
S.6986	Fort St. John III, B.C.								2.69	72
S.6994	Marsh Lake, Yukon Territory								2.32	95
S.6998	Johnson Stream, Yukon Territory								3.24	16
S.7000	Mayo, Yukon Territory				1.52	85	1.83	68	2.23	96
	Mean site height		2.97		2.38		1.99		2.90	

Ecovalences (Wricke 1962) were calculated to determine each provenance's contribution to the sum of squares of the provenance x environment interaction. The relative stability of individual provenances may thus be ascertained through ecovalences. Table 10 shows that ecovalences vary between 0.27 for the S.340 Mont Saint-Michel provenance in Labelle, Quebec, which presents a good relative stability, and 16.17 for the S.367 Lac Pimbina provenance in Saint-Maurice, Quebec, which has the least stable relative stability. It is the latter provenance, then, which contributes most to the provenance x environment interaction and is very sensitive to differences between sites. These figures show that caution must be exercised in selecting provenances for reforestation of territoires whose pedo-climatic characteristics differ from those on the test sites if optimum yields are to be obtained from plantations.

However, if major difficulties are encountered in biological reforestation material management and the forest manager is willing to accept slightly lower plantation yields, provenances with relative phenotypic stability and higher than average productivity may be planted on a variety of sites. The plasticity and hardiness of the species seem to be conducive to this. If the 15 most productive provenances overall were to be used, there would be a gain of about 11 percent over the mean growth of the tested provenances. Due to the potential difficulty in obtaining sources from outside Quebec, a forest manager might decide to use only the best domestic sources, in which case there would be a 9 percent gain. The forest manager should, however, be aware of the negative impact that such a decision could have on the productivity of certain sites.

Identification of superior provenance regions

Five superior provenance regions were delineated using the 25 best performing provenances in each of the test locations (Figure 3). These regions are defined as follows:

Acadia provenance region [1]

The Acadia provenance region [1], located between long. 65° - 70°W and lat. 45° - 48°N, encompasses all of New Brunswick, part of the state of Maine, and the Lower St. Lawrence region, and is characterized by the presence of red spruce in association with balsam fir, sugar maple, yellow birch, some red pine, white pine, and eastern hemlock. Pure and mixed stands of black spruce, red spruce, and tamarack (Rowe 1972) are also abundant in poorly drained flatlands.

Laurentian provenance region [2]

The southern portion of the Laurentian provenance region [2] corresponds roughly to the Laurentian forest section L.4a (Rowe 1972). It forms a narrow strip located between long. 71 and 75°30W and lat. 46°30 and 47°30'N. Like the Acadia region, it features red spruce in pure stands and in stands introgressed with black spruce (Morgenstern et al. 1981; Brulotte 1984; Morgenstern and Farrar 1964).

Saguenay-Lac-Saint-Jean provenance region [3]

As its name indicates, the Saguenay-Lac-Saint-Jean region [3] encompasses the Saguenay-Lac-Saint-Jean region proper as well as Haute-Mauricie, Chibougamau, and Chicoutimi parks. It is located between lat. 48°N and 49°30'N and long. 70°W and 75°W, and overlaps balsam fir/white birch ranges and the ranges of black spruce in asssociation with mosses (Thibault and Hotte 1985).

Abitibi-Ottawa provenance region [4]

The Abitibi-Ottawa provenance region [4] covers a vast latitudinal range, stretching south-north from Lake Ontario (44°N) to Lac Matagami (50N), and east-west from long. 76° to 80°W. The region features a wide variety of climatic ranges with its maple/basswood stands in the south and its black spruce stands in association with mosses in the north. Provenances from this region are particularly well suited to southern Quebec.

Winnipeg-Superior provenance region [5]

The Winnipeg-Superior provenance region [5] covers a vast territory between long. 90° and 96°W and lat. 47° and 51°N. Balsam fir/black spruce and balsam fir/white birch ranges are found in the northern portion of the region, whereas fir/white pine ranges are found in the south. In each provenance test location, superior results were obtained from some 50 percent of the provenances form this region; the top 25 percent of the results were obtained for northern provenances.

Proposed black spruce breeding zones

Given the vastness of the territory under consideration for black spruce reforestation, we will attempt to subdivide it into smaller breeding zones based on the results obtained from the

Table 11. Matrix of the estimated genetic correlations between black spruce provenance heights on the 4 test locations

	Mont-Laurier	Lac St-Ignace	Chibougamau	Valcartier
Mont-Laurier	1.0000	0.4667	0.8784	1.0000
Lac Saint-Ignace	0.4667	1.0000	0.7624	0.9115
Chibougamau	0.8784	0.7624	1.0000	0.8414
Valcartier	1.0000	0.9115	0.8414	1.0000

provenances tested in individual test sites and on ecological data. A breeding zone is defined as an area with sufficiently homogenous pedoclimatic conditions to be suitable for a specific genetic stock. The origin of this stock is based first on selection of the best performing provenances, although they must also be well adapted to the site, followed by selection and hybridization of the best breeders. By delineating breeding zones, it should be possible to optimize yields from artificially regenerated areas.

To do this, we must begin by calculating genetic correlations between total provenance heights at the individual test sites (Table 11). A cluster analysis (Varclus *in* SAS 1985) is then performed on the matrix obtained from these correlations. This analysis allows us to distinguish three groups: the Mont-Laurier and Valcartier sites, Chibougamau, and Lac Saint-Ignace. The two sites with maple/yellow birch associations are in the same group. The Lac Saint-Ignace site, with its balsam fir/white birch populations, is distinct from the Chibougamau site, with its stands of black spruce in association with mosses (Grandtner 1966; Thibault and Hotte 1985). Additional provenance test locations might have resulted in the creation of more groups and the subdivision of the territory conducive to black spruce reforestation into still smaller breeding zones. Initially, however, the reforestation territory is subdivided into five breeding zones based on provenance test results, pedoclimatic data, and descriptions and maps of southern Quebec's ecological regions (Thibault and Hotte 1985) (Figure 4).

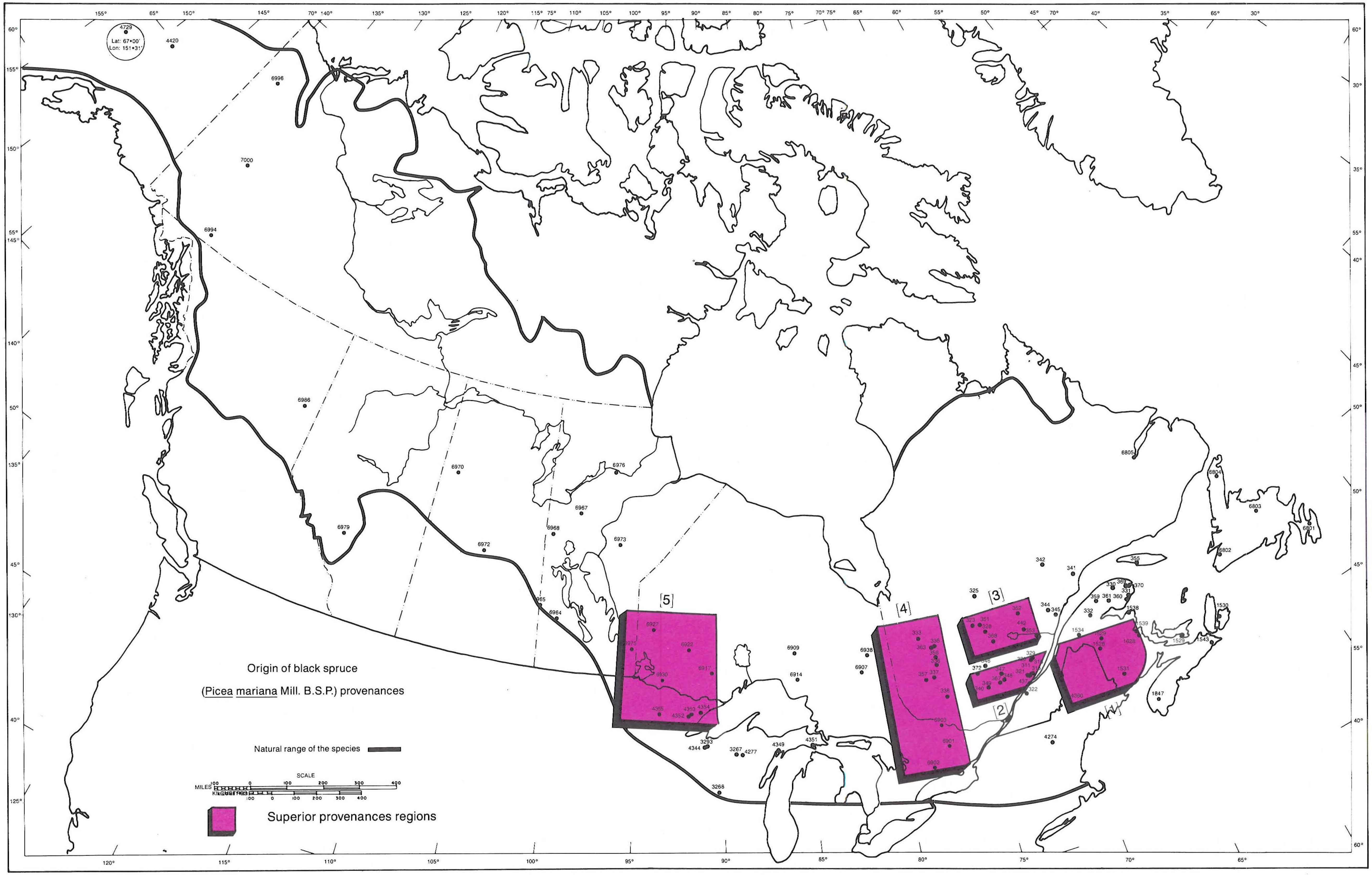

Figure 3. Black spruce provenance region: [1] Acadia Region; [2] Laurentian Region; [3] Saguenay-Lac-Saint-Jean Region; [4] Abitibi-Outaouais Region; [5] Superior Winnipeg Region.

Abitibi breeding zone (A)

The Abitibi breeding zone (A) (Figure 3) covers a vast territory to the north of the Ottawa Valley-Laurentian zone (D) and to the west of the High Laurentian and Gaspé plateaus (C) and Saguenay-Appalachian (E) zones. Black spruce and jack pine, *Pinus banksiana* Lamb., are both abundant in mixed stands in the sandy plains of this region due to frequent forest fires. Pure black spruce stands predominate on the clayed soils left by the Objibway glacial lake, whereas jack pine thrives on dry sites. Balsam fir, *Abies balsamea* (L.) Mill., in association with white spruce *Picea glauca* (Moench) Voss, and white birch, *Betula papyrifera* Marsh., is particularly abundant in the southern portion of this zone. Mixed trembling aspen, *Populus tremuloides* Michx., balsam poplar, *Populus balsamifera* L., white birch/white spruce/balsam fir stands cover upland tills and lakeshores and riverside alluvia. The zone lies on Precambrian volcanic rock, granite, gneiss, and sediments partially covered by glacial and fluvioglacial drifts transformed by lacustrine materials. Humoferric podzols have developed on shallow tills, fluvial terraces, and glacial outwash; gray luvisols on limestone clays and modified tills; and gleysols on flat, poorly drained ground (Rowe 1972). Breeding zone A covers the balsam fir/white birch ranges (8) and the ranges of black spruce in association with mosses (12), where aridity indexes vary from 50 to 150 and the growing season ranges from 1 000 to 1 200 degree-days (Thibault and Hotte 1985).

Lower North Shore breeding zone (B)

Breeding zone B borders on the Gulf of St. Lawrence and on zones D and C to the west and southwest respectively. Black spruce can be found on its peaty lowlands, well-drained uplands drift and rock, sites with humoferric podzols, and peaty gleysolic soils in narrow swamps. Balsam fir and white spruce are rare here. Ferro-humic podzols form on richer tills generally colonized by balsam fir (Rowe 1972). This zone covers mainly the range of black spruce in association with fir and mosses (11) and some fir/black spruce ecological regions. The climate here is cold and wet, aridity indexes are less than 100 and the growing season is shorter than 1 000 degree-days (Thibault and Hotte 1985).

High Laurentian and Gaspé plateaus breeding zone (C)

Breeding zone C includes the Gaspé Peninsula and Laurentian uplands, which surround the Lac-Saint-Jean plain and the Saguenay region bottomlands and mountains. Balsam fir is dominant on the sides of the Laurentian hills and on wet, well-drained ecological sites, while black spruce is predominant on upland sites with thin soil layers and on poorly drained land. The entire Laurentian portion of this zone lies on Precambrian crystalline rock. Soils from ferro-humic and humo-ferric podzol subgroups form on the surface drift. Shallow peats and deep peats characterize dwarf-shrub uplands and moss-bog lowlands, respectively (Rowe 1972). Aside from pure fir and black spruce stands, mixed balsam fir/spruce with eastern white cedar, *Thuya occidentalis*, L., and white birch stands are the main tree associations found on the Gaspé plateau-like highlands, which is composed of sedimentary rock. Thin humo-ferric podzol profiles are found in its well-drained areas, while acid peat is found in poorly drained areas. The climate here is cold and wet with a 50-100 aridity index and the number of degree-days vary between 890 and 1 220, according to the ecological region. The zone covers balsam fir/white birch (8) and balsam fir/black spruce (9) ranges (Thibault and Hotte 1985). Climatic conditions in this zone are more conducive to forest growth than on the Lower North Shore (B) due to less intense cold and a longer growing season. Because this zone lies on two types of parent rock, one solution would be to split it in half, assigning specific genetic stocks to each half based on additional testing.

Ottawa Valley-Laurentian breeding zone (D)

Breeding zone D extends from the Ottawa River to the uplands on the eastern border of the Laurentides Park and roughly from lat. 46° to 48°N. It also includes the mountainous Eastern Townships region, largely populated by red spruce, *Picea rubens* Sarg., associated with intolerant hardwoods, and by white spruce, balsam fir, eastern white pine, *Pinus strobus* L., and eastern hemlock, *Tsuga canadensis* (L.) Carr. Mixed forests of balsam fir, black spruce, and white birch are found in the northern portion of this zone. Scattered white spruce and trembling aspen also grow here. White pine and red pine *Pinus resinosa* Ait., are predominant on rocky peaks, while jack pine is predominant on sand terraces. Black spruce and tamarack, *Larix laricina* (Du Roi) K. Koch, cover vast surfaces of wet organic soil. The bedrock is composed of Precambrian granitic volcanic and sedimentary rock. Humo-ferric podzols are the most common soils. The southern part of the zone is predominantly hardwood with white pine, red pine, and red spruce. The main species are sugar maple, *Acer saccharum* Marsh., yellow birch, *Betula alleghaniensis* Britton,

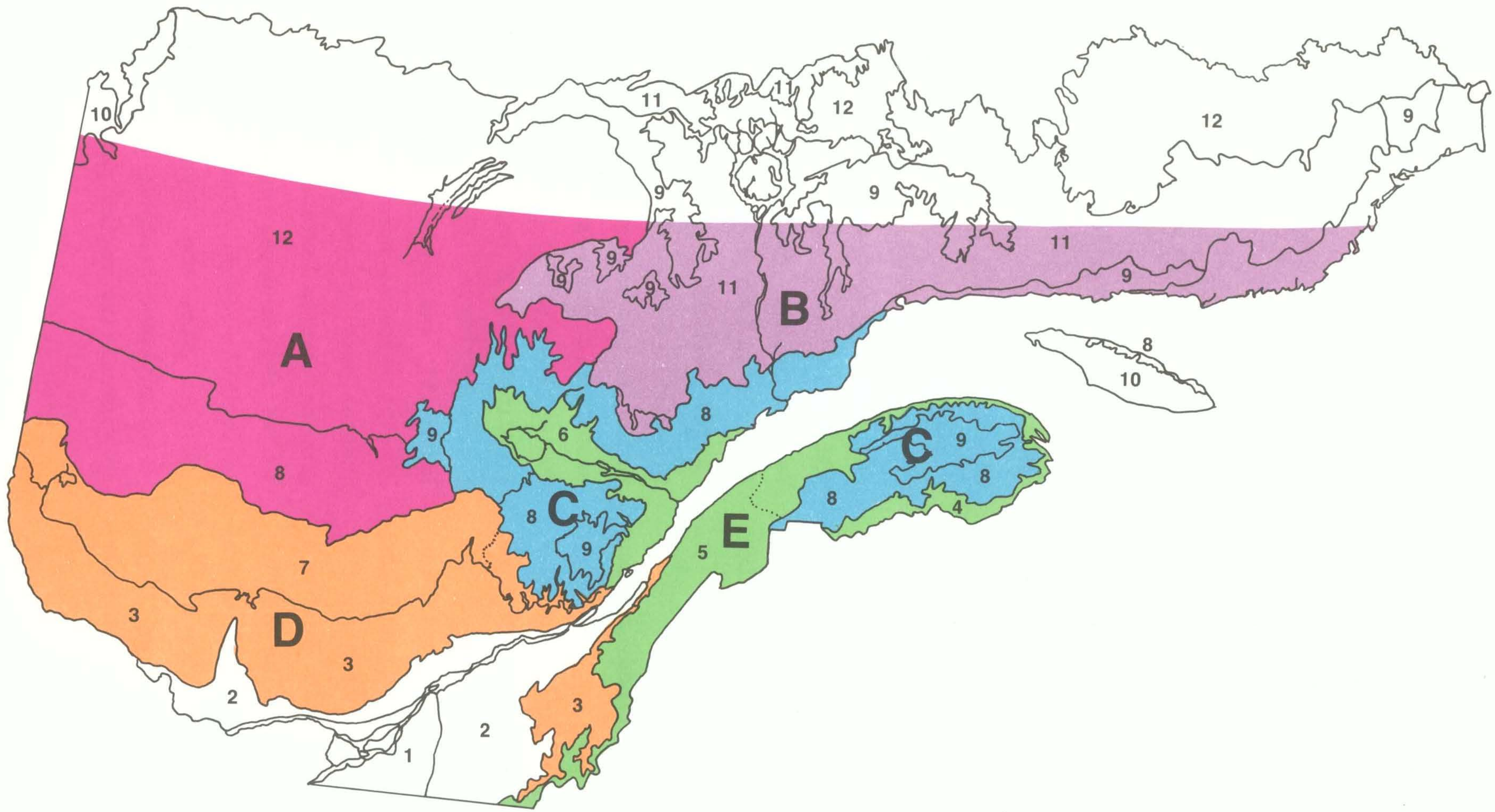

Figure 4. Proposed black spruce breeding zones in Quebec: A to E, breeding zones of black spruce; 1 to 12, ecological regions (Thibault and Hotte 1985)

and red maple *Acer rubrum* L. White spruce is scattered throughout, while black spruce grows on poorly drained uplands and in swamps. The bedrock, composed of Precambrian gneisses, granites, and schists, is covered with shallow layer of till and fluvioglacial deposits. Sand terraces, silt flats, and vast wetlands are also found here. Dystric brunisols and humo-ferric podzols have formed from the surface materials (Rowe 1972). This breeding zone covers the balsam fir/yellow birch (5), maple/yellow birch (3), and yellow birch/fir (7) ranges. Aridity indexes vary from 75 to 255 and the growing season from 1 220 to 1 330 degree-days in the north, and from 1 220 to 1 660 degree-days in the south (Thibault and Hotte 1985).

Saguenay-Appalachian breeding zone (E)

Breeding zone E includes such diverse regions as the Appalachians, the Lower St. Lawrence, the shores of the Gaspé Peninsula, the Lac-Saint-Jean plain, the Saguenay bottomlands, and the narrow strip on the north shore of the St. Lawrence between Baie Saint-Paul and Forestville. The south shore of the St. Lawrence is home to a predominantly white spruce softwood forest, but white birch, eastern white cedar, tamarack, and trembling aspen also grow here. White spruce and balsam fir are also found in inland valleys. Hill tops are populated by maple sugar, beech, *Fagus grandifolia* Ehrh., and yellow birch. Black spruce and tamarack are found only in bottomlands and areas typified by peat bogs. Although hardwoods are found in sheltered areas, the forest around the Saguenay-Lac-Saint-Jean basin is essentially boreal. Here, jack pine stands are predominant on sandy areas, while black spruce, white spruce, balsam fir, white birch, and trembling aspen are common on other sites. In this region, the parent rock is basically granite-gneiss. Lowlands are covered with layers of clay and marine sand, while the other areas feature glacial drifts and alluvia. The Appalachian bedrock is made up of ancient layers having metamorphosed in some places. Soils derived from glacial materials are composed of rough-textured humo-ferric podzols, which, along with humic gleysols, are common (Rowe 1972). Breeding zone E encompasses the balsam fir/white birch (6), balsam fir/yellow birch (5), and maple/yellow birch ranges. Precipitation is abundant here. Aridity indexes vary between 50 and 175, and the growing season extends from 1 000 to 1 390 degree-days, depending upon the ecological region (Thibault and Hotte 1985). Like the High Laurentian and Gaspé plateaus breeding zone, this area, in view of its varied parent rock, could be subdivided into smaller zones based on additional studies.

Recommended superior provenances by breeding zone

Superior provenances and superior provenance regions were recommended only for those breeding zones having yielded reliable results in black spruce provenance testing. No recommendation has been made for the Saguenay-Appalachian location site and delineation was based solely on ecological considerations. Provenances have not been recommended for the Lower North Shore zone (B), since the Labrieville test results were not sufficiently reliable for the provenances to be judged adequately. All provenances from superior provenance regions were considered first and ultimately will be selected as long as they belong to the dominant group.

Isolated provenances were retained only if the anticipated gain is at least equivalent to the gain expected from superior provenance regions.

Abitibi breeding zone (A)

Provenance selection for this zone is based on the Chibougamau test site. The most promising provenance regions are Winnipeg-Superior [5] and Abitibi-Ottawa Valley [4]. In addition, the yield from two isolated provenances was exceptional. The mean of the selected provenances in the following list is 14 percent higher than the mean of the provenances tested.

	Mean (m)	Gain (%)
Winnipeg-Superior provenance region [5]	2.30	16
S.4353 Isabella, Lake Co., Min.		
S.4354 Tofte, Cook Co., Min.		
S.4355 Itaska Co., Min.		
S.6917 Ipsala, Ont.		
S.6922 Tour Sioux, Ont.		
S.6927 Minaki, Ont.		
S.6930 Rainy Lake, Ont.		

	Mean (m)	Gain (%)
Abitibi-Ottawa Valley provenance region [4]	2.28	15
S.338 Parc de la Vérendrye, Pontiac, Que.		
S.6901 Bancroft, Hastings, Ont.		
Acadia provenance region [1]	2.23	12
S.332 Causapscal, Matapédia, Que.		
S.1528 Stuart Plains Rd., Victoria, N.B.		
S.1529 William's Brook, Restigouche, N.B.		
S.1531 C.F.B. Gagetown, Sunbury, N.B.		
S.1628 Black River North Arm, Kent, N.B.		
S.4360 Penobscot Co., Maine		
Laurentian provenance region [2]	2.23	12
S.321 Perthuis, Portneuf, Que.		
S.340 Mont St-Michel, Labelle, Que.		
S.347 Rivière-aux-rats, Laviolette, Que.		
S.348 Lower Mattawin, Saint-Maurice, Que.		
S.349 Saint-Michel des Saints, Berthier, Que.		
S.372 Lac Doré, Maskinongé, Que.		
Saguenay-Lac-Saint-Jean provenance region [3]	2.20	11
S.323 Parc Chibougamau, Roberval, Que.		
S.351 Normandin, Roberval, Que.		
S.442 Chûte-aux-Galets, Chicoutimi, Que.		
Other provenances	2.44	23
S.4277 Forest Co. I, Wis.		
S.6907 Timmins, Ogden, Ont.		

High Laurentian and Gaspé plateaus breeding zone (C)

Provenance selection was based on the Lac Saint-Ignace black spruce provenance test. Two highly superior provenance regions -- Acadia [1] and Winnipeg-Superior [5] -- emerged. Productivity at the S.6907 Timmins, Ogden, Ont. provenance was 16 percent higher than the mean. The following is the list of superior provenances.

On the average, these provenance are superior by 12 percent to the overall provenances tested at Lac Saint-Ignace.

	Mean (m)	Gain (%)
Acadia provenance region [1]	2.72	14
S.1531 C.F.B. Gagetown, Sunbury, N.B.		
S.1534 North First Lake, Madawaska, N.B.		
S.1538 North Caraquet River, Gloucester, N.B.		
S.1539 Tweedie Stream, Northumberland, N.B.		
S.4360 Penobscot Co., Maine		
Winnipeg-Superior provenance region [5]	2.71	14
S.6917 Ipsala, Ont.		
S.6922 Tour Sioux, Ont.		
S.6927 Minaki, Ont.		
S.6975 Whiteshell Prov. Park, Man.		
Laurentian provenance region [2]	2.67	12
S.321 Perthuis, Portneuf, Que.		
S.347 Rivière-aux-Rats, Laviolette, Que.		
S.348 Lower Mattawin, Saint-Maurice, Que.		
S.349 Saint-Michel des Saints, Berthier, Que.		
S.372 Lac Doré, Maskinongé, Que.		

	Mean (m)	gain (%)
Saguenay-Lac-Saint-Jean provenance region [3]	2.64	11
S.323 Parc Chibougamau, Roberval, Que.		
S.326 Parc Chibougamau, Lac-Saint-Jean, Que.		
S.351 Normandin, Roberval, Que.		
S.352 Péribonka, Roberval, Que.		
S.353 Mars Ha! Ha!, Chicoutimi, Que.		
S.442 Chûte-aux-Galets, Chicoutimi, Que.		
Abitibi-Ottawa Valley provenance region [4]	2.62	10
S.333 Matagami, Abitibi-Est, Que.		
S.356 Lac Parent, Abitibi-Est, Que.		
S.6901 Bancroft, Hastings, Ont.		
S.6903 Chalk River, Renfrew, Ont.		
Other provenances	2.76	16
S.6907 Timmins, Ogden, Ont.		

Ottawa Valley-Laurentian breeding zone (D)

The Valcartier and Mont-Laurier sites were classed in the same breeding zone following cluster analysis of the between-site genetic correlation matrix. Provenance selection was therefore based on the mean provenance performance at these two sites. In 3 of the 5 superior provenance regions, the yield of some provenances was greater than that of the overall selected provenance yield. Provenances from the Saguenay-Lac-Saint-Jean region are not suitable for the Ottawa Valley-Laurentian breeding zone (D). The following is the list of selected provenances 13 percent superior to the overall provenance mean.

	Mean (m)	Gain (%)
Abitibi-Ottawa Valley provenance region [4]	3.36	16
S.333 Matagami, Abitibi-Est, Que.		
S.337 Louvicourt, Abitibi-Est, Que.		
S.356 Lac Parent, Abitibi-Est, Que.		
S.357 Lac Decelles, Abitibi-Est, Que.		
S.6901 Bancroft, Hastings, Ont.		
S.6902 Apsley, Haliberton, Ont.		
S.6903 Chalk River, Renfrew, Ont.		
Winnipeg-Superior provenance region [5]	3.31	14
S.4353 Isabella, Lake Co., Maine		
S.6917 Ipsala, Ont.		
S.6922 Tour Sioux, Ont.		
S.6927 Minaki, Ont.		
S.6930 Rainy Lake, Ont.		
S.6975 Whiteshell Provincial Park, Man.		
Acadia provenance region [1]	3.29	13
S.1528 Stuart Plains Rd., Victoria, N.B.		
S.1538 North Caraquet River, Gloucester, N.B.		
S.1539 Tweedie Stream, Northumberland, N.B.		
Laurentian provenance region [2]	3.21	13
S.315 Rivière aux Pins, Quebec City, Que.		
S.316 Valcartier II, Quebec City, Que.		
S.340 Mont Saint-Michel, Labelle, Que.		
S.346 Manouane, Laviolette, Que.		
S.347 Rivière-aux-Rats, Laviolette, Que.		
S.367 Lac Pimbina, Saint-Maurice, Que.		

Other provenances	Mean (m)	Gain (%)
S.6907 Timmins, Ogden, Ont.	3.19	10

CONCLUSIONS

This study has shown that a positive, significant relationship existed between the annual growth of black spruce provenances in the nursery and their height growth between the 10th and 16th years in the forest environment, indicating that the relative superiority shown by provenances in the nursery is maintained on the test sites. This positive relationship shows that early selection would have been possible. However, given the low gains that would have been obtained, it cannot be claimed that early selection would have been effective or that it would have resulted in acceleration of the black spruce breeding program. It remains to be seen whether over the next few years an even more positive relationship develops. Only then would it be possible to consider selection at a very young age. A weak clinal variation pattern in growth during the 10th and 16th year as a function of provenance's geographic origin was also shown to exist. Provenances from the southwestern portion of the black spruce distribution range tend to perform better than those from the northeast. This clinal variation pattern implies that seeds may be relocated in the same manner and that their yield may be predicted with some degree of confidence. The pattern is, however, attenuated with time.

Distribution of the survival variation among individual test sites as a function of the sources revealed by the test design indicates that the percentage attributable to the provenances is insignificant, with the exception of the Lac Saint-Ignace site. This is not surprising considering the vast territory covered by black spruce and, consequently, its capacity to adapt to diverse pedoclimatic conditions. Moreover, depending upon the test site chosen, provenance origin accounts for 5 to 17 percent of the total height variation 16 years from seed. This means that provenance selection would net significant genetic gains. Mass selection of the provenances chosen should also be carried out to optimize gains. By regrouping the data from the four sites, a provenance x environment interaction was shown to exist. This interaction appreciably affects the genetic gains that can be expected from a selection. Despite the advantageous relative phenotypic stability of some provenances, we preferred subdividing Quebec territory into smaller breeding zones due to the vastness of the reforestation range. Five zones were delineated based on ecological data and black spruce provenance test results. These zones vary in size and were named after the administrative regions they encompass: Abitibi, Lower North Shore, High Laurentian and Gaspé plateaus, Ottawa Valley Laurentian, and Saguenay-Appalachian. Five superior provenance regions were also identified: Acadia, Laurentian, Saguenay-Lac-Saint-Jean, Abitibi-Ottawa Valley and Winnipeg-Superior. More than 20 superior provenances were recommended with a view to developing a breeding program for each zone in which at least one provenance test site is located. On the average, these provenances were superior by 14, 12, and 13 percent to the provenances tested overall in the Abitibi (A), High Laurentian, and Gaspé plateaus (C), and Ottawa Valley-Laurentian (D) breeding zones.

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