

Genetic structure and patterns of genetic variation among populations in eastern white spruce (*Picea glauca*)

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Abstract: Known patterns of genetic variation among provenances are useful in gene resource management such as guiding seed transfer and delineating breeding zones. The objectives of this study were (1) to determine the genetic structure of white spruce (*Picea glauca* (Moench) Voss) from Quebec and southeastern Ontario, (2) to develop models describing patterns of genetic variation among provenances and their relationships with environmental variation, (3) to test the validity of the models by using independent data sets, and (4) to guide seed transfer and to delineate provisional breeding zones for white spruce in Quebec. A sample of 63 provenances was used in this study, with each provenance composed of one to five separate families (a total of 263 families). Data were collected on seedling heights at various ages, 1-year branch number, and 3-year bud burst and bud set. Significant differences were found for each trait among provenances and among families within provenances. Provenances and families within provenances accounted for similar amounts of the genetic variability. All traits were moderately to strongly intercorrelated at the provenance level. Two principal components composed 87% of the total variation for all traits. Regression models explained between 19% and 65% (an average of 47%) of provenance variation and showed that patterns of provenance variation followed mainly a south–north cline and to a lesser extent a west–east cline. The regression models were tested using data from seven field tests, which showed that the models performed fairly well in predicting relative risk of seed transfer. White spruce provenances could be transferred long distances with small relative risk. We delineated two provisional breeding zones for white spruce in Quebec from the models describing patterns of genetic variation among provenances.

Résumé : La connaissance des patrons de variation génétique existant entre les provenances permet une meilleure gestion des ressources génétiques tel le déplacement des semences et la délimitation de zones d'amélioration. Les objectifs de cette étude étaient (1) déterminer la structure génétique des populations d'épinette blanche (*Picea glauca* (Moench) Voss) du Québec et du sud-est de l'Ontario, (2) développer des modèles de régression pour représenter les patrons de variation génétique entre les provenances et leur relation avec les conditions variables au niveau environnemental, (3) tester la validité des modèles de régression en utilisant des jeux de données indépendants et (4) établir des lignes directrices pour le déplacement des semences et délimiter de façon provisoire des zones d'amélioration génétique pour l'épinette blanche au Québec. Un échantillon de 63 provenances a été utilisé dans cette étude, chaque provenance étant représentée par 1 à 5 familles (pour un total de 263 familles). Des données de hauteur à différents âges, du nombre de branches à 1 an et des dates de débourrement et d'aoûtement à 3 ans ont été recueillies sur les semis. Des différences significatives ont été trouvées pour chaque caractère étudié entre les provenances et entre les familles à l'intérieur des provenances. Les provenances et les familles étaient sensiblement responsables du même pourcentage de variabilité génétique. Tous les caractères étudiés étaient modérément à fortement corrélés au niveau des provenances. Deux composantes principales ont permis d'expliquer 87% de la variation totale présente chez l'ensemble des caractères. Des modèles de régression ont permis d'expliquer entre 19% et 65% (47% en moyenne) de la variation inter-provenances, et de montrer que les patrons de variation des provenances suivaient principalement un cline sud–nord et à un moindre degré un cline ouest–est. Les modèles de régression développés ont été testés à l'aide de données provenant de sept tests génécologiques : il en est résulté que les modèles semblaient généralement fiables pour prédire le risque relatif découlant du déplacement des semences. Les provenances d'épinette blanche pourraient être déplacées sur de longues distances avec un risque relativement faible. Nous avons provisoirement délimité deux zones d'amélioration génétique pour l'épinette blanche au Québec à partir des modèles décrivant les patrons de variation génétique existant entre les provenances étudiées.

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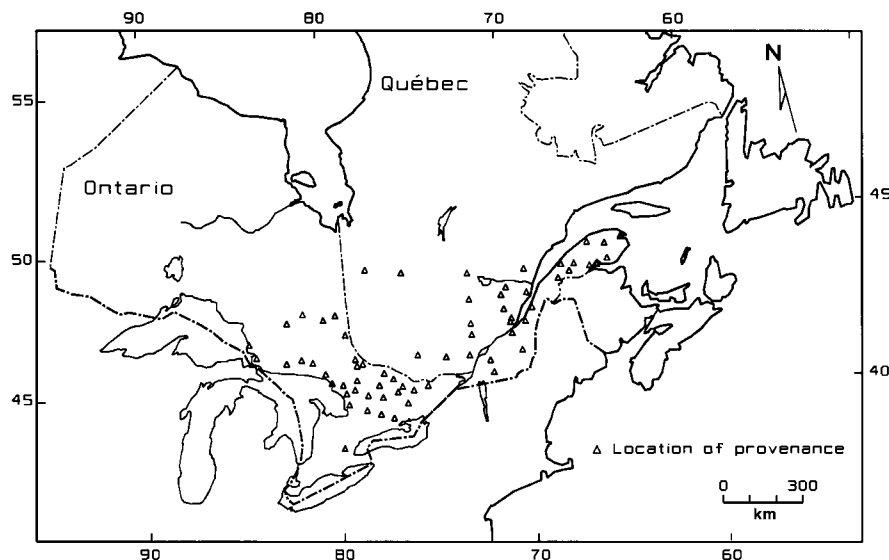
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Introduction

White spruce (*Picea glauca* (Moench) Voss) has a transcontinental range in North America, occurring from Newfoundland westward across the continent to northern Alaska and the Northwest Territories, and southward from the northern tree line to its southern limit in southern British Columbia eastward to northeastern Maine, with scattered populations found in South Dakota, northern Montana, and Wyoming (Nienstaedt and Zasada 1990). Its elevation range is from sea level to

Fig. 1. Geographical locations of provenances used in developing models describing patterns of provenance variation.



1500 m. The species grows under a variety of conditions, including extreme climates and soils.

Given its wide ecological amplitude, white spruce is expected to harbour large amounts of genetic variation. Based on monoterpene compositions, Wilkinson et al. (1971) divided the species into two major groups, a western group and an eastern group along the 95°W longitude boundary between Manitoba and Ontario. However, a range-wide study revealed no relationships between allozyme variation and geographic origins of populations (Furnier et al. 1991). In the western group, introgressive hybridization of white spruce with Sitka spruce (*Picea sitchensis* (Bong.) Carrière) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) plays an important role in shaping patterns of genetic variation among populations (Roche 1969; Yeh and Arnott 1986; Sutton et al. 1994 and references therein). In range-wide provenance tests conducted in northeastern North America, western populations were outperformed by eastern populations (e.g., Nienstaedt 1968; Furnier et al. 1991).

Introgressive hybridization is not important in the eastern group of white spruce, with only one report of a natural hybrid between white and black spruce (*Picea mariana* (Mill.) BSP) in Minnesota (Riemenschneider and Mohn 1975). Patterns of provenance variation seem complex for the eastern white spruce. Provenances from southeastern Ontario and western Quebec (approximately 45–46°N and 75–80°W) are shown to have good growth and adaptability in the northeastern United States and Canada (Nienstaedt 1968; Nienstaedt and Teich 1972). There appears to be a trend for growth to decrease westward and eastward as well as northward and southward from this eastern Ontario – western Quebec area of provenances that perform well (Nienstaedt and Teich 1972; Teich et al. 1975; Tebbets 1981; Radsliff et al. 1983; Murray and Skeates 1984). This probably explains why only weak latitudinal and longitudinal clines were observed for eastern white spruce in growth and wood density (Corriveau and Boudoux 1971; Khalil 1985b, 1986; Beaulieu and Corriveau 1985; Corriveau et al. 1987; Hall 1986). Ecotypic variation also exists for eastern white spruce as provenances from limestone soils differ from

those from granitic soils (Teich and Holst 1974). In addition, white spruce populations from relatively small geographical areas do not show significant differentiation in allozyme frequencies (Cheliak et al. 1988), in wood density, growth, and phenology traits (Dhir 1976; Pollard and Ying 1979a, 1979b; Khalil 1985a; Corriveau et al. 1991). These results suggest that variation among eastern white spruce populations does not follow microgeographical gradients.

These early provenance studies revealed broad patterns of genetic variation among populations, but they were limited in provenance sampling. In 1971, a comprehensive cooperative study of white spruce was initiated in Canada to determine the range-wide and regional patterns of provenance variation as well as to provide a basis for selections in the first-generation breeding population from intensive sampling of provenances within regions (Ying 1979). This paper reports results from this type of regional provenance test established in Quebec. The objectives of this study were (1) to examine the genetic structure of white spruce from Quebec and southeastern Ontario, (2) to determine patterns of provenance variation, (3) to test models describing patterns of provenance variation by using seven independent data sets, and (4) to provide seed transfer guidelines and to delineate breeding zones for white spruce in Quebec. Provenance and population are terms used interchangeably in this paper.

Materials and methods

Materials

Materials used in this study were 63 provenances from Quebec and southeastern Ontario (Fig. 1). The sampled provenances have an even elevational distribution in terms of latitude and longitude, with a mean latitude of 46.75°N (range 43.73°–49.35°N), a mean longitude of 75.18°W (64.25°–84.75°W), and a mean elevation of 236 m (15–460 m). Each provenance was represented by one to five open-pollinated families whose identities were retained, totaling 263 families. Eight provenances were represented by one family, two by two families, four by three families, six by four families, and 43 by five families.

Fig. 2. Patterns of genetic variation among provenances predicted by the regression model for the first principal component at a constant elevation (250 m) with two adjacent contour lines separated by a relative risk of 0.30.

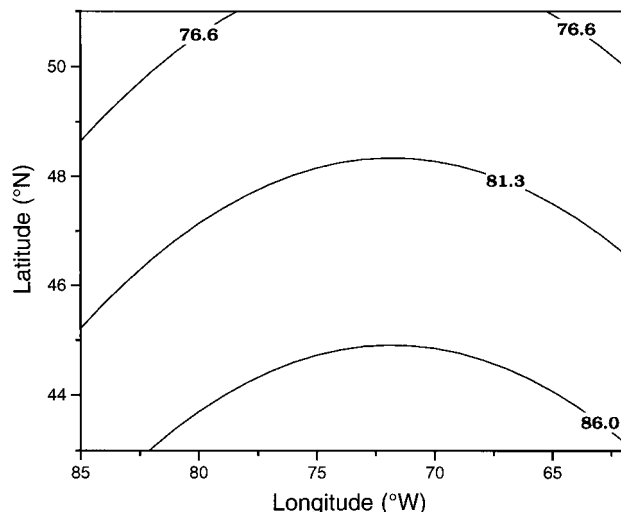


Table 1. Form of analyses of variance for the white spruce provenance–progeny tests.

Source of variation	df [†]	Expected mean square [‡]
Blocks	$b-1$	$\sigma_e^2 + 262\sigma_b^2$
Provenances	62	$\sigma_e^2 + b\sigma_{\bar{r}(p)}^2 + 4.17b\sigma_p^2$
Families (provenances)	200	$\sigma_e^2 + b\sigma_{\bar{r}(p)}^2$
Plot error	$262(b-1)$	σ_e^2

[†] Number of blocks (b) varied for different sets of traits: 10 blocks for 17-week height and 1-year branch number and height, 8 blocks for 2- and 3-year heights, and 5 blocks for 3-year bud burst and bud set.

[‡] σ_b^2 , variance of block effects; σ_p^2 , variance of provenance effects; $\sigma_{\bar{r}(p)}^2$, variance of family within provenance effects; σ_e^2 , variance of plot effects; and b , number of blocks.

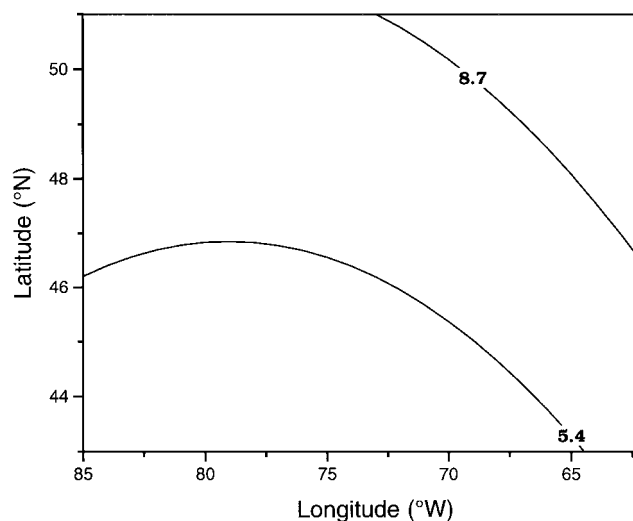
Experimental methods

In 1980, seeds were sown in a greenhouse and 1-year-old seedlings were transferred to a nursery and grown there for 2 years. The following traits describing both growth potential and vegetative cycle were measured: 17-week height, 1-year height and branch number, 2- and 3-year heights, and dates of bud burst and bud set in the third growing season. Details on the experimental design and measurements are described elsewhere (Li et al. 1993).

Statistical analysis

The first step in data analysis was to conduct analysis of variance to determine whether traits varied significantly among provenances and families within provenances and to partition total genetic variation into provenance and family-within-provenance components according to the model outlined in Table 1. Plot means were used as input, and all effects were assumed random. Statistical significance refers to 5% probability in this paper unless otherwise stated. The second step in analysis was to estimate provenance covariance components among traits and use them as well as provenance variance components to estimate genetic correlations among traits applicable to the provenance level (Campbell 1986). With this correlation matrix as input, we applied principal component analysis to extract a new set with fewer independent variables (principal components), which are linear functions of all traits in the correlation matrix. Principal components

Fig. 3. Patterns of genetic variation among provenances predicted by the regression model for the second principal component at a constant elevation (250 m) with two adjacent contour lines separated by a relative risk of 0.30.



with eigenvalues greater than one were retained for further analyses (Chatfield and Collins 1980). Principal component scores were calculated for each family from family mean values of individual traits and were subjected to analysis of variance.

Multiple regression models were built to describe patterns of genetic variation among populations by regressing principal component scores as well as individual traits with environmental indices, in our case, latitude, longitude, and elevation of the origin of provenances and their quadratic terms. Because the second-order ones are generally highly correlated with the first-order terms (i.e., multicollinearity exists), we used, as independent variables, the deviations of the original variables (latitude, longitude, and elevation) from their respective means to substantially reduce multicollinearity, as suggested by Neter et al. (1983). We also used these transformed variables to avoid computational difficulties resulting from a high degree of multicollinearity (Neter et al. 1983). The best regression model was selected using a backward elimination procedure with a significance level of 0.10 for the variables to stay in the model. Given that 55 provenances were composed of two to five families, lack of fit of the selected equation could be tested by using families as repeats (Neter et al. 1983). To visualize patterns of provenance variation revealed by the regression models, contour plots were made by mapping principal component scores with geographical location variables. First, we calculated from the regression models principal component scores for populations within the sampling area, with each pair of populations separated by 0.5° of latitude and 0.5° of longitude at different elevations. We presented the results in a two-dimensional surface (latitude and longitude) only for the 250 m elevation, given that the average elevation for our provenance samples was 236 m. We then plotted the predicted principal component scores (Figs. 2 and 3) as contours with two adjacent contours separated by a value corresponding to a relative risk of 0.30 (Campbell 1986). The relative risk measures the area of the mismatch between the distributions of genotypes for two provenances with the same additive genetic variance, but different means. The additive genetic variance was calculated as three times the family-within-provenance variance component in order to take into account inbreeding and relatedness among neighbouring trees (Coles and Fowler 1976; Campbell 1986). The additive genetic variance was assumed to be the same for all provenances (Westfall 1992). This value of relative risk (0.30) was used in previous studies (Campbell 1986; Campbell et al. 1989).

Table 2. Overall means with provenance ranges in parentheses and variance components for each trait (percentage of the total in parentheses).

Trait [†]	Mean (cm)	σ_p^2	$\sigma_{(p)}^2$	σ_e^2	Total
HT17W	10.4 (8.9–11.7)	0.1881** (4.42)	0.2750** (6.47)	3.7899 (89.11)	4.2530
HT1YR	17.3 (14.1–19.8)	0.9211** (5.86)	0.4793** (3.05)	14.3174 (91.09)	15.7178
NBR1YR	14.3 (11.9–17.0)	0.4537** (3.41)	0.7444** (5.59)	12.1242 (91.00)	13.3223
HT2YR	25.5 (23.0–29.1)	0.6578** (3.83)	0.4988 [‡] (2.91)	15.9990 (93.26)	17.1556
HT3YR	39.1 (34.2–46.9)	2.5667** (9.96)	1.7728** (6.88)	21.4248 (83.16)	25.7643
BB3YR	142.8 (141.6–144.3)	0.1957** (7.56)	0.2427** (9.37)	2.1519 (83.07)	2.5903
BS3YR	232.6 (221.1–245.9)	18.2505** (11.82)	16.2190** (10.51)	119.8911 (77.67)	154.3606
PC1	83.0 (72.5–92.1)	9.8282** (44.23)	12.3901 (55.77)	—	22.2183
PC2	6.1 (1.1–10.8)	2.5892** (28.37)	6.5386 (71.63)	—	9.1278

[†]Traits used in this study were abbreviated as follows: HT17W, total height at 17 weeks; HT1YR, total height at 1 year; NBR1YR, number of branches at 1 year; HT2YR, total height at second year; HT3YR, total height at third year; BB3YR, Julian days to date of bud burst; BS3YR, Julian days to date of bud set; PC1, first principal component; and PC2, second principal component. A copy of provenance means is available from the corresponding author.

[‡]P-value = 0.0143.

**Statistical significance at 1% probability level.

Besides describing patterns of provenance variation, regression models for principal component scores could also be used to predict relative risks in transfer of provenances within the sampling area under several assumptions, the most important one being that the local population is optimal (Campbell 1986). Testing the validity of the predicted relative risks (or adaptability) of transferred provenances at planting sites requires the assessment of adaptability of transferred provenances in long-term field provenance tests. In the genetic testing program of white spruce in Quebec, field tests containing the provenances used in developing regression models and other provenances were established. We used height and survival as indicators of adaptability from seven field tests to validate the predicted relative risks of our regression models (Table 6). These seven test sites and the 39 to 63 provenances in these tests were chosen because they were located within the sampling area used for developing models describing patterns of genetic variation (in terms of latitudinal, longitudinal, and elevational range) (Table 6). These provenances were also represented by one to five open-pollinated families. Height and survival rate were recorded at 17 years from seed in two tests (E560A2 and E560A3), while 13-year height and survival rate were available for the other five tests. The validation of regression models proceeded in three steps for each site. First, the scores for first and second principal components (PC1 and PC2, respectively) (see Results) were predicted by using the regression equations for the transferred provenances and for the local provenance at the test site (i.e., indigenous white spruce population). Second, by assuming equal additive genetic variance for all populations, relative risk in seed transfer could be estimated by a mismatch index, which is the area of mismatch between the normal curves for the genotypic distribution of the transferred provenance and the local provenance at the test site (Campbell 1986; Westfall 1992). Because two principal components were extracted, we calculated the

combined risk of seed transfer (CR) as $CR = R_1 + R_2 - R_1R_2$, where R_1 and R_2 are the risks associated with PC1 and PC2 (Campbell 1986). The third step was the use of a correlation analysis to assess the degree of relationship between short-term adaptability of transferred provenances (height and survival) and relative risk of seed transfer for all provenances in the data sets.

Results

Partitioning of total genetic variability

Analysis of variance showed significant differences among provenances and families within provenances for all traits (Table 2). On average, 6.7% of the total variance was attributed to provenances, 6.4% was attributed to families within provenances, while the remaining 86.9% of variation was attributed to plot differences, which include both within-family genetic variance and environmental variance. For 3-year bud burst, the provenance variance was smaller than the family-within-provenance variance, while 3-year bud set had a larger provenance variance than family-within-provenance variance. For PC1, family variance was slightly higher than provenance variance, while for PC2 provenance variance accounted for only 28% of the total variance.

Genetic correlations

At the provenance level, traits were moderately to strongly intercorrelated (Table 3). Heights and branch number were positively correlated. Provenances with early bud burst and late bud set had greater heights than provenances with late bud

Table 3. Genetic correlations (above the diagonal) among traits for provenances and correlation based on provenance means (below the diagonal).

	HT17W	HT1YR	NBR1YR	HT2YR	HT3YR	BB3YR	BS3YR
HT17W	1.000	0.338	0.302	0.613	0.413	0.150	-0.032
HT1YR	0.415	1.000	0.835	0.775	0.853	-0.590	0.689
NBR1YR	0.339	0.736	1.000	0.549	0.737	-0.747	0.742
HT2YR	0.471	0.568	0.289	1.000	0.841	-0.229	0.380
HT3YR	0.364	0.656	0.418	0.766	1.000	-0.620	0.773
BB3YR	0.051	-0.348	-0.344	-0.178	-0.442	1.000	-0.834
BS3YR	-0.005	0.492	0.460	0.280	0.625	-0.583	1.000

Note: See Table 2 for trait definitions.

Table 4. Principal components (PC) with eigenvector coefficients, eigenvalues, and trait loadings.

Trait	PC1		PC2	
	Loading	Coefficient	Loading	Coefficient
HT17W	0.370	0.174	0.834	0.666
HT1YR	0.930	0.436	0.082	0.066
NBR1YR	0.898	0.422	-0.119	-0.095
HT2YR	0.770	0.361	0.538	0.430
HT3YR	0.948	0.445	0.121	0.097
BB3YR	-0.741	-0.348	0.593	0.473
BS3YR	0.830	0.390	-0.445	-0.355
Eigenvalue	4.538		1.569	
% of total variance	64.8		22.4	

Note: See Table 2 for trait definitions.

burst and early bud set, as indicated by negative genetic correlations between 3-year bud burst and heights and positive genetic correlations between 3-year bud set and heights (Table 3).

Principal component analysis

Principal component analysis extracted two significant principal components, with PC1 accounting for 64.8% of total variation among all traits and PC2 accounting for 22.4% (Table 4). Thus, 87% of the total variation was attributed to the first two components. First-year height and branch number, and 3-year height and bud set, received high loadings in PC1 (Table 4). PC2 had relatively high loadings from 17-week and 2-year heights, and 3-year bud burst.

Multiple regression analysis

Except for 1-year branch number, the selected equations were complex for different traits, involving the original location variables (latitude, longitude, and elevation) as well as their quadratic terms (Table 5). These regression equations on average accounted for 47% (range 19% to 65%) of the total variation among provenances. The regression models accounted for 65% and 59% of the provenance variation for PC1 and PC2, respectively. First-year branch number, 17-week height, and 2-year height were weakly associated with geographical locations of provenances, with less than 39% of provenance variation explained by independent variables. First- and third-year heights, and 3-year bud burst and bud set, were moderately associated with geography, with regression equations accounting for 47% to 64% of total provenance variation (Table 5).

Adequacies of regression models could be examined by the lack of fit statistics in this study, since families from a provenance were kept separate and thus could be used as repeats in testing regression models (Neter et al. 1983). Lack of fit for regression equations was not significant for PC2, 2-year height, 3-year bud burst, and 3-year bud set, but a significant lack of fit was observed for PC1, 17-week height, 1-year height, 1-year branch number, and 3-year height (Table 5). The significant lack of fit might imply that regression models describing the geographical variation of provenances were not adequate. The problem of lack of fit was alleviated somewhat when the cubic terms of the original geographical variables (latitude, longitude, and elevation) were included in regression equations (data not shown). In this case, the ratio of the number of independent observations to the number of independent variables is quite small (63/19), which could lead to overfitting of regression models (Westfall 1992). Thus, we consider the regression equations in Table 5 as the best equations describing patterns of provenance variation in this study.

Patterns of provenance variation are shown, respectively, in Figs. 2 and 3 for PC1 and PC2, and individual traits follow similar patterns. These contour plots indicate that there were moderate south to north clines for the adaptive traits, with southern provenances having higher values for PC1 (e.g., greater heights and late bud set) (Fig. 2). Provenances with the best performances were found in southeastern Ontario and western Quebec. There was a weak west-east cline from these areas eastward. For PC2, northeastern provenances had higher values than the southwestern ones (Fig. 3). For both PCs, areas with homogeneous provenances were large, more than 2° in latitude and several degrees in longitude.

Practical application of regression models

For all seven data sets used for appraising the validity of the regression models developed, provenances differed significantly in height and survival rate except for 13-year survival rate at sites E410D2, E410D5, and E410D6 (results not shown). On average, the relative risk of seed transfer varied from 0.161 at site E560A3 to 0.470 at site E410D4, though some provenances had quite a high relative risk (Table 6). The correlation between relative risk and adaptability as expressed by height was negative at six of the seven test sites, and was moderately high for three southern test sites: E410D4, E410D5, and E560A3 (Table 6). The correlation between relative risk and survival rate used as an indicator of adaptability (at 13 and 17 years old) was negative and weak at five test sites, while it was positive at two test sites (Table 6). Because relative risk measures the proportion of genotypes for the transferred

Table 5. Results of multiple regression analyses.

Trait	R^2	Lack of fit (p) [†]	Intercept	LT	LN	EL	LT ²	LN ²	EL ²	LT×LN	LT×EL	LN×EL
HT17W	0.19	0.0015	10.3049	—	0.0480	—	—	—	—	-0.0207	0.0010	—
HT1YR	0.47	0.0023	17.3585	-0.2352	0.0575	-0.0038	0.0842	-0.0102	—	—	0.0012	—
NBR1YR	0.19	0.0061	14.3176	-0.2705	—	-0.0014	—	—	—	—	—	—
HT2YR	0.39	0.0763	25.2745	-0.4084	—	—	—	—	—	—	0.0041	0.0011
HT3YR	0.60	0.0287	39.2770	-0.8047	—	—	—	-0.0226	2.4×10^{-5}	-0.0800	0.0070	0.0017
BB3YR	0.53	0.2676	142.7989	0.2612	—	0.0010	0.0670	—	—	0.0305	-0.0008	—
BS3YR	0.64	0.2818	234.0056	-2.2818	-0.4259	-0.0128	—	-0.0500	—	—	0.0103	—
PC1	0.64	0.0069	83.6412	-1.4529	—	-0.0116	—	-0.0246	—	—	0.0060	—
PC2	0.59	0.2036	5.5251	0.6853	0.1661	0.0063	—	0.0124	—	—	—	0.0009

Note: Independent variables included in a model are indicated by their regression coefficients. LT, latitude (degrees); LN, longitude (degrees); EL, elevation (m). Their deviations from their respective means were used in regression analysis. See Table 2 for trait definitions.

[†]Probability of lack of fit for the regression.

provenance that does not overlap with genotypes for the native population at the plantation site, the correlation between relative risk and indicators of adaptability (e.g., height and survival) of transferred provenances is expected to be negative. This prediction was borne out in 11 of 14 instances (Table 6).

Discussion

This and earlier studies (Li et al. 1993) show that provenances and families within provenances accounted for similar amounts of genetic variability for growth and phenology traits. For white spruce from the U.S. Lake States (Minnesota, Wisconsin, and Michigan) (Nienstaedt and Riemenschneider 1985) and Ontario, Quebec, and Maine (Tebbetts 1981), a higher proportion of genetic variation (63% to 75%) was due to differences among provenances. For black spruce from each of three site regions in Ontario, the variance due to families within provenances was larger than or about equal to that for provenances (Boyle 1986). When provenance sampling is restricted to a relatively small area in the eastern part of white spruce distribution (from about 2000 to 60 000 km²), no significant differences are detected among provenances for many traits (Dhir 1976; Pollard and Ying 1979a, 1979b; Khalil 1985b; Corriveau et al. 1991). This pattern of variation is in contrast with those observed in the Pacific Northwest for coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) (Campbell 1979, 1986), Sitka spruce (Campbell et al. 1989), sugar pine (*Pinus lambertiana* Dougl.) (Campbell and Sugano 1987), and ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) (Sorensen and Weber 1994), where provenances from relatively small areas differ significantly and account for a substantial amount of genetic variation. For each of three regions of interior lodgepole pine (*Pinus contorta* ssp. *latifolia* Engelm. ex S. Wats.) in British Columbia of a sampling area comparable in size to our white spruce study, variance due to populations is five to eight times that due to families within populations (Xie and Ying 1995). This indicates that white spruce provenances in most of the eastern distribution are moderately differentiated despite the species' wide ecological amplitude. Thus, natural selection appears in the Pacific Northwest to more strongly promote microadaptation of populations to their environments than in eastern Canada because of the greater amount of environmental heterogeneity in the Pacific

Northwest. Alternatively, because insufficient time has passed (no more than 8000 to 9000 years) since the retreat of the continental ice sheet and recolonization of the land by white spruce (Davis 1981), natural selection may not yet have led to microadaptation for white spruce in eastern Canada.

To assess important environmental factors in shaping patterns of genetic variation among provenances, it is preferable to use climatic variables as independent variables in regression analyses (e.g., Parker et al. 1994). Instead, we used geographical locations as surrogates to index environmental variables that might shape patterns of genetic variation in white spruce in the sampled area because climatic stations are sparse and not close to the populations sampled in most cases. Past experience shows that geographical locations might be adequate in indexing climatic conditions of the provenance origins in conifers (e.g., Joyce 1988; Rehfeldt 1989, 1991, 1994, 1995). Despite that in this study we used the deviations of latitude, longitude, and elevation from their respective means in regression analyses to reduce the multicollinearity (Neter et al. 1983), a significant lack of fit was found for five of the nine equations (Table 5). This indicates that potentially important environmental variables such as aspect, slope, and soil types may not be included in the regression models, which were shown in previous studies of other species to be important determinants in shaping patterns of provenance variability (e.g., Campbell 1986). In white spruce, soil types were shown to be important in causing genetic differentiation among populations, as the limestone soil ecotype of white spruce has been reported (Teich and Holst 1974). These variables were not available for this study and therefore their contribution to the regression equations could not be examined.

One source of error for our regression models might be the sampling design in this study. An average of 4.2 families represented a provenance, so the provenance mean might be inaccurately estimated. However, 19% to 65% (mean 47%) of provenance variation was accounted for by the regression equations. These values are comparable to those obtained for other conifers in eastern North America, for which each provenance was represented by seeds bulked from at least 10 trees. In black spruce from northwestern Ontario, 10% to 57% of the among-provenance variation could be explained by regression models (Parker et al. 1994). In another study including black spruce provenances east of 100°W, regression accounted for

Table 6. Application of the regression model.

Site [†]	No. of provenances	Height (m) [‡] §	Survival rate [‡] §	Relative risk [‡] §	Correlation between relative risk and	
					height [¶]	survival rate [¶]
E410D2	61	2.09 (1.60–2.31)	0.82 (0.67–0.91)	0.238 (0.029–0.513)	–0.31 (0.016)	–0.12 (0.340)
E410D3	61	2.02 (1.63–2.36)	0.86 (0.71–0.94)	0.226 (0.028–0.533)	–0.11 (0.397)	–0.16 (0.218)
E410D4	63	2.74 (2.33–3.46)	0.84 (0.69–1.00)	0.466 (0.044–0.796)	–0.61 (<0.001)	–0.08 (0.518)
E410D5	63	2.72 (2.05–3.36)	0.91 (0.80–1.00)	0.398 (0.016–0.754)	–0.50 (<0.001)	0.20 (0.122)
E410D6	63	2.67 (2.40–3.13)	0.82 (0.68–0.91)	0.181 (0.012–0.754)	0.27 (0.034)	–0.36 (0.004)
E560A2	45	2.80 (1.73–3.32)	0.83 (0.65–0.91)	0.201 (0.019–0.545)	–0.33 (0.028)	–0.33 (0.031)
E560A3	40	2.57 (2.10–3.17)	0.77 (0.69–0.86)	0.285 (0.015–0.540)	–0.60 (<0.001)	0.018 (0.911)

[†]Locations of test sites were as follows: E410D2 (47°30'N, 69°03'W, elev. 270 m), E410D3 (48°30'N, 72°13'W, elev. 200 m), E410D4 (45°37'N, 74°04'W, elev. 60 m), E410D5 (45°36'N, 76°37'W, elev. 122 m), E410D6 (48°12'N, 65°43'W, elev. 150 m), E560A2 (48°21'N, 72°13'W, elev. 323 m), and E560A3 (46°31'N, 73°13'W, elev. 223 m). Data for sites E410D2 to E410D6 were based on 13-year-old trees, while data for sites E560A2 and E560A3 were based on 17-year-old trees.

[‡]Range in parentheses.

§A copy of provenance means is available from the corresponding author.

||Mean relative risk of seed transfer as calculated from the mismatch index.

¶Probability is given in parentheses.

40% to 72% of variation among populations (Stahl and Persson 1992). In eastern larch (*Larix laricina* (Du Roi) K. Koch), 74% of variation in frost hardiness among populations could be explained by a regression model (Joyce 1988). The unaccounted-for portion of the among-provenance variation for white spruce could be caused by the omission of important environmental variables in the regression models as discussed earlier, or alternatively by factors such as migration, genetic drift, or past natural history.

Patterns of genetic variation among white spruce provenances from Quebec and Ontario are complex and follow geographical gradients. In our study, white spruce in the sampled area had a strong latitudinal component and a weak longitudinal one (Figs. 2 and 3). How do these patterns of among-provenance variation compare with those of earlier studies for white spruce based on less intensive provenance sampling? Two aspects of our findings conform to earlier results. First, our models indicate that provenances from southeastern Ontario and southwestern Quebec have the highest growth potential (Fig. 2). This result confirms the earlier reports that populations from these areas show good growth and adaptation over a wide range of conditions (Nienstaedt 1968; Corriveau and Boudoux 1971; Nienstaedt and Teich 1972). Genetic materials from these areas have been incorporated into several breeding populations in the United States and Canada (Fowler 1986; Nienstaedt and Kang 1987; Beaulieu 1994). Second, our contour plots indicate that areas with similar predicted principal component scores are large, spanning about 2° in latitude and several degrees in longitude (Fig. 2). This finding agrees with earlier results indicating that populations from a relatively small geographic area do not show significant differences in common environment studies (Dhir 1976; Pollard and Ying

1979a, 1979b; Khalil 1985b; Cheliak et al. 1988; Corriveau et al. 1991). It is difficult to compare patterns of variation of white spruce with those of other conifers in northeastern North America because limited information is available. In black spruce, a moderate to strong latitudinal cline was found for many traits in both range-wide (Morgenstern 1978; Park and Fowler 1988; Beaulieu et al. 1989) and regional studies (Stahl and Persson 1992; Parker et al. 1994).

Rehfeldt (1989, 1991) pointed out that the validity of models developed for describing provenance variation should be tested in order for such models to guide seed transfer and to delineate breeding zones. The concept of relative risk proposed by Campbell (1986) establishes a framework for comparing predicted values from models describing patterns of provenance variation and actual data. This approach requires sampling as many populations as possible, with some populations represented by one parent tree and others by more than one parent tree (Campbell 1986; Westfall 1992). As pointed out earlier, this sampling scheme could lead to inaccurate estimates of provenance means for regression analyses. But it allows for tests of adequacies of regression models by testing the lack of fit component. Also, it allows for the estimation of within-population additive variance, and with this estimate relative seed transfer risk could be predicted and thus evaluated directly by comparing the predicted relative risk with adaptability of field-tested provenances. The assumption that all populations have the same additive genetic variance may not be correct. However, testing the homogeneity of the additive genetic variance among populations requires sampling large numbers of families, which is not generally the case in the majority of studies (Westfall 1992). The assumption of the optimality of the local population provides a basis for predicting

relative risk of seed transfer, but may not be valid (Namkoong 1969). However, without extensive long-term field testing it is not possible to predict which nonlocal provenances will show good adaptability. Another approach to model validation is to relate predicted values from the regression equations to field performances of an independent population sample at different sites (Rehfeldt 1991, 1995) or the same site (Xie and Ying 1995). The first method may be confounded by provenance by site interaction effects. If seedlings are raised under favourable conditions and used for developing regression models, one would expect a positive correlation between predicted values and actual performances at good sites and at earlier ages, but a negative or no correlation at harsh sites. The decrease of correlation between predicted and actual performances with age for ponderosa pine supports the first expectation (Rehfeldt 1991). For both approaches, field tests must be established and evaluated on a long-term basis for testing the validity of the regression models describing patterns of genetic variation.

Our regression models for patterns of provenance variation were applied and tested using seven independent data sets. Although short-term adaptability of transferred provenances as expressed by their height and survival were not strongly correlated with relative risks estimated from the models, the negative correlation observed in most instances between the adaptability and relative risk was to be expected, that is, the greater the relative risk, the worse the transferred provenances will perform (e.g., lower height and reduced survival). At the three southern test sites, the correlation between relative risk and height as an indicator of adaptability was moderate, indicating a good performance of the regression models in estimating relative risks of transferred provenances. There are at least four reasons why we did not observe a strong correlation between relative risk and adaptability of transferred provenances. First, Campbell (1986) emphasized the importance of characterizing genotypes of families well by raising seedlings in different test environments so that traits related to different aspects of adaptation could be expressed and evaluated. In our study, although traits representing adaptability (growth and vegetative cycle (phenology)) were evaluated, they were assessed only in one favourable test environment located in southern Quebec. Thus, the nursery environmental conditions are more similar to the southern test sites than to the northern ones. This may explain why our regression models performed better for relating relative risk of seed transfer and provenance adaptability at the three southern test sites than at the northern ones. Second, the plant material used for practical application of the models was relatively young (13 and 17 years from seed) and the seven test sites are not very harsh, though representative of the average site for reforestation of white spruce in Quebec. At less harsh test sites, the manifestation of the detrimental effects of seed transfer might be gradual. The timing may depend on the occurrence of extreme climatic events and (or) on the accumulation of minor damage resulting from slight mismatches between growth cycles of transferred provenances with seasonal climatic cycles (Adams and Campbell 1982). Finally, some important environmental factors might not be included in the regression models as discussed earlier. This could lead to inaccurate estimation of predicted principal component scores for native and transferred populations, and consequently the predicted relative risks would not be accurately estimated.

Known patterns of variation among populations are useful in gene resource management (Rehfeldt 1991). For example, the patterns of variation among provenances elucidated by this study could be used in guiding seed transfer for reforestation and delineating breeding zones for Quebec. Since the 1970s, seed transfer guidelines in Quebec have been mainly based on ecological regions with a few modifications for administrative purposes. There are a dozen seed zones in Quebec for white spruce and other conifers. The regression models developed could help forest managers devise guidelines for seed transfer. These models suggest that white spruce seed could be transferred long distances with small risks: 2° to 3° in latitude from south to north and several degrees in longitude from west to east. The good growth and adaptability of southeastern Ontario provenances at several sites in Quebec support this (Corriveau and Boudoux 1971; Beaulieu 1994). Reforestation for white spruce in Quebec is concentrated south of 50°N, white spruce populations are not strongly differentiated in large geographic areas, and financial resources are limited for breeding activities and maintenance of many breeding populations. We thus recommend that at present two breeding zones be used in Quebec with demarcation roughly at 47°N, one in the south corresponding to the maple vegetation zone and the other in the north corresponding to the balsam fir – yellow birch (*Abies balsamea* (L.) Mill. – *Betula alleghaniensis* Brit.) vegetation zone. Given that our provenance samples were from elevations lower than 460 m and typical in elevation range of reforestation sites, we do not feel that elevational zoning is important for delineating breeding zones for white spruce in Quebec. As more results become available from progeny tests, the two breeding zones could be merged or further divided.

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