

Patterns of adaptive genetic variation in eastern white pine (*Pinus strobus*) from Quebec

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Abstract: Genetic structure and patterns of genetic variation among provenances for eastern white pine (*Pinus strobus* L.) in Quebec were examined by a provenance–progeny test. A sample of 66 provenances of eastern white pine from Quebec and adjacent Ontario was tested, with each provenance composed of one to eight separate families (a total of 159 families). Data were collected on total seedling heights at different ages up to 4 years, 4-year branch number, and 3-year bud burst and bud set. Analysis of variance showed significant differences in each trait among provenances and among families within provenances, with one exception. Variance due to provenances was on average twice that due to families within provenances. All traits were intercorrelated at the provenance level. Two principal components summarized 77% of the total variation for all traits. Regressions of different traits on geographical variables accounted for 16% to 62% of provenance variation and disclosed complex patterns of genetic variation among provenances. Provenances from the southeastern part of the sampling area were taller and burst and set terminal buds later than the northwestern ones. The regression models were tested using 10-year height and survival from three field tests, which gave mixed results. We used the models describing patterns of provenance variation to guide seed transfer and delineated two provisional breeding zones for eastern white pine in Quebec.

Résumé : La structure génétique des populations de pin blanc (*Pinus strobus* L.) au Québec de même que les patrons de variation existant entre les provenances ont été examinés à l'aide d'un test de provenances/descendances. Un échantillon de 66 provenances de pin blanc localisées au Québec et près de sa frontière ouest en Ontario ont été testées, chaque provenance étant représentée par un nombre inégal de familles variant de un à huit (pour un total de 159 familles). Des données ont été recueillies sur les semis à plusieurs reprises, soit : la hauteur totale à différents âges depuis l'ensemencement jusqu'à 4 ans, le nombre de branches à l'âge de 4 ans, et les dates de débourrement et d'aoûtement à l'âge de 3 ans. L'analyse de variance a permis de faire ressortir la présence de différences significatives entre les provenances et entre les familles à l'intérieur des provenances et ce pour tous les caractères étudiés à l'exception d'un. La variance due aux provenances était en moyenne deux fois plus élevée que celle due aux familles à l'intérieur des provenances. Tous les caractères étaient interreliés au niveau des provenances. Deux composantes principales ont permis d'expliquer 77% de la variance totale observée chez l'ensemble des caractères. Les régressions des divers caractères en fonction des variables géographiques ont, pour leur part, expliqué de 16% à 62% de la variation au niveau des provenances et ont fait ressortir des patrons de variation génétique complexes entre les provenances. Les provenances du sud-est de la région échantillonnée étaient constituées d'arbres plus grands, et le débourrement et l'aoûtement de leurs bourgeons étaient plus tardifs que ceux des arbres plus petits des provenances du nord-ouest. Les modèles de régression ont été testés à l'aide de données empiriques de trois tests pour lesquels la hauteur à 10 ans et le taux de survie étaient disponibles; les résultats se sont avérés non consistants. Nous avons utilisé les modèles décrivant les patrons de variation au niveau des provenances pour établir des lignes directrices quant au déplacement des semences et pour délimiter provisoirement deux zones d'amélioration génétique du pin blanc au Québec.

Introduction

Known patterns of genetic variation among populations of forest trees are useful in gene resource management to provide guidelines for seed transfer in reforestation, to delineate breeding zones, and for gene conservation programs (Rehfeldt 1991). Regression models have been developed to describe patterns of genetic variation among populations (e.g., Campbell 1986; Rehfeldt 1989, 1991). The adequacy of these models must be tested by examining residuals and testing lack of fit (Neter et al. 1983). More importantly, predictive values of

such models must be compared with empirical data from independent data sets, which has been done for only a few species (Rehfeldt 1989, 1991, 1995; Xie and Ying 1995; Li et al. 1997).

Eastern white pine (*Pinus strobus* L.) grows in southeastern Canada and the eastern United States, and is one of the most valuable trees (Wendel and Smith 1990). The species is genetically variable in growth (e.g., Wright 1970; Funk 1979), resistance to white pine weevil (*Pissodes strobi* Peck) (Wright 1970), wood density (Lee 1974) and allozymes (Beaulieu and Simon 1994). The southernmost provenances were found to have superior growth as compared with northern ones at nurseries or at southern planting sites (Genys 1968; Wright 1976). At the northern planting sites, they are no longer superior; instead, provenances located 2° to 7° latitude south of the planting site have good performances (Fowler and Heimburger 1969; King and Nienstaedt 1969; Garrett et al. 1973; Genys 1987). One of the factors that could explain the decrease in growth of the southernmost provenances at northern planting sites is their low cold hardiness (Garrett et al. 1973; Maronek

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

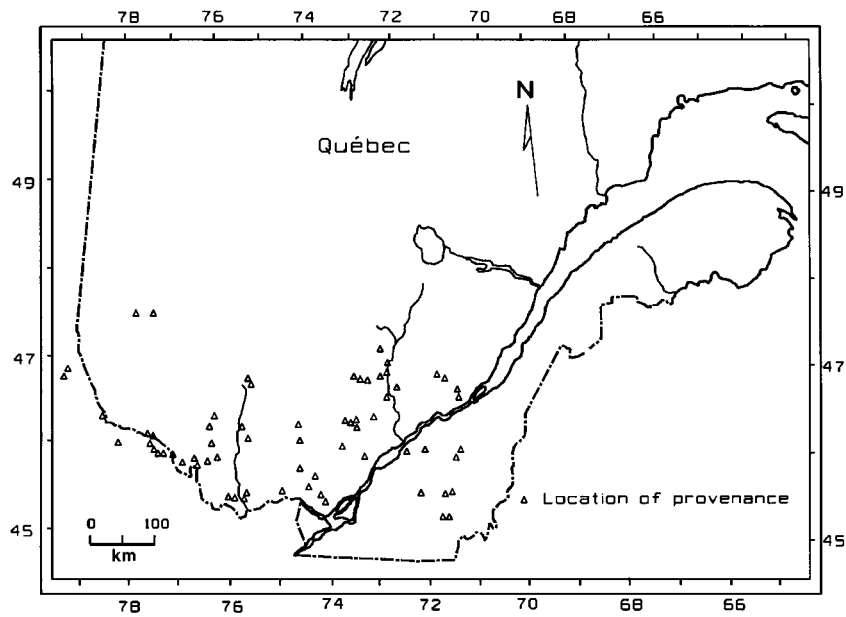


Table 1. Form of analyses of variance for white pine provenance–progeny test.

Source of variation	df	Expected mean squares [†]
Blocks	5	$\sigma_e^2 + 158\sigma_b^2$
Provenances	65	$\sigma_e^2 + 6\sigma_{f(p)}^2 + 14.276\sigma_p^2$
Families(provenances)	93	$\sigma_e^2 + 6\sigma_{f(p)}^2$
Plot error	790	σ_e^2

[†] σ_b^2 , variance of block effect; σ_p^2 , variance of provenance effect; $\sigma_{f(p)}^2$, variance of family within provenance effect; and σ_e^2 , variance of plot effect.

and Flint 1974). A range-wide study of eastern white pine, including more than 100 provenances, was established during the 1960s (Genys 1968, 1987), but it included only 15 provenances from Canada. Therefore, the regional patterns of provenance variation for eastern white pine in Canada are not obvious from that range-wide provenance study.

A regional provenance–progeny test was initiated in Quebec in the 1980s. Data were collected on growth and phenology traits in greenhouse, nursery, and field tests. This study aims to provide more information on patterns of variation for eastern white pine in eastern Canada and to provide materials for selections in the first-generation breeding. We sampled 66 provenances of eastern white pine from Quebec and adjacent Ontario. The objectives of this study were (1) to examine the genetic structure of eastern white pine in Quebec, (2) to determine patterns of provenance variation, (3) to test the validity of the predictions on the adaptability of transferred provenances from regression models describing patterns of provenance variation by using indicators of short-term adaptability from three field provenance tests, and (4) to provide provisional guidelines for seed transfer and for delineating breeding zones for eastern white pine in Quebec. Provenance and population are terms used interchangeably in this paper.

Materials and methods

Materials and measurements

A sample of 66 provenances from Quebec and adjacent Ontario was used in this study (Fig. 1), which was representative of the current distribution of eastern white pine in the sampling area. The sampled provenances have a mean latitude of 46.22°N (range 45.35°–47.68°N), a mean longitude of 74.68°W (71.23°–79.22°W), and a mean elevation of 197 m (15–366 m). A provenance was represented by one to eight open-pollinated families (totalling 159 families) whose identities were kept separate. Two to eight families were sampled for 32 provenances, while the remaining 34 provenances were represented by one family.

In 1982, seeds were sown in a greenhouse and 1-year-old seedlings were transplanted in a nursery and grown there for 3 years. The experimental design was a randomized complete block design with six blocks, and each family was represented by four seedlings in each block. The following traits were measured: hypocotyledon length; 13-week height; 3-year height, bud burst, and bud set; and 4-year height and branch number. Bud burst was scored once every 2 days and bud set, once a week. Bud burst was defined as the date when green appears on the central terminal bud, and bud set as the date when brown bud scales are visible and terminal and lateral buds are well differentiated.

Statistical analysis

Statistical analysis follows that described in Li et al. (1997). Analysis of variance was conducted to test the significance of variation among and 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 and all effects were assumed to be random. In this paper, statistical significance refers to 5% probability unless otherwise stated. Genetic correlations among traits applicable to the provenance level (Campbell 1986; Campbell and Sugano 1987) were estimated from provenance variance and covariance components. We used this correlation matrix in principal component analysis to extract significant principal components (i.e., whose eigenvalues are greater than one) (Chatfield and Collins 1980). Principal component scores were then calculated for each family from the family mean values of individual traits, and they were also used as input in analysis of variance.

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	$\sigma_{f(p)}^2$	σ_e^2	Total
HTHYP	2.6 (0.8–3.4)	0.1081** (37.73)	0.0572** (19.97)	0.1212 (42.30)	0.2865
HT13W	4.5 (1.0–6.4)	0.06004** (57.67)	0.1028** (9.87)	0.3379 (32.46)	1.0411
HT3YR	27.1 (19.2–33.5)	3.5463** (22.00)	1.6065** (9.96)	10.9691 (68.04)	16.1219
BB3YR	131.3 (130.3–132.6)	0.1480** (14.93)	0.0480 [‡] (4.84)	0.7955 (80.23)	0.9915
BS3YR	230.7 (220.7–235.8)	3.6099** (7.78)	4.1694** (8.99)	38.6192 (83.23)	46.3985
HT4YR	53.3 (38.6–62.4)	12.2991** (20.00)	5.6902** (9.25)	43.5107 (70.75)	61.5000
NBR4YR	5.9 (4.2–6.8)	0.0475** (3.97)	0.0000 [§] (0.00)	1.1500 (96.03)	1.1675
PC1	142.5 (130.9–149.2)	9.4655** (58.93)	6.5981 (41.07)	—	16.0636
PC2	185.9 (178.9–190.0)	2.7229** (31.65)	5.8814 (68.35)	—	8.6043

[†]Characters used in this study were abbreviated as follows: HTHYP, length of hypocotyledon; HT13W, 13-week height; HT3YR, 3-year height; BB3YR, Julian days to date of bud burst; BS3YR, Julian days to date of bud set; HT4YR, 4-year height; NBR4YR, number of branches in the fourth growing season; PC1, first principal component; and PC2, second principal component. A copy of provenance means is available from the corresponding author.

[‡] p -value = 0.025.

[§] p -value = 0.631.

**Statistical significance at 1% probability level.

We built multiple regression models to describe patterns of provenance variation by using latitude, longitude, and elevation and their quadratic terms as independent variables and principal component scores as well as individual traits as dependent variables. Deviations of the original variables (latitude, longitude, and elevation) from their respective means were used to reduce the multicollinearity between the first- and second-order terms for any original variable (Neter et al. 1983). Backward elimination was used with a significant level of 0.10 for variables to remain in the model to choose the best regression model. Given that 32 provenances were composed of two to eight families, lack of fit for 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 latitude and longitude at a fixed elevation (Figs. 2 and 3, see Li et al. 1997 for details). The chosen fixed elevation was 200 m, given that the average elevation for our provenance sample was 197 m. The predicted principal component scores were plotted as contours with two adjacent contours separated by a value that corresponds to a relative risk of 0.30 (Campbell 1986). The additive genetic variance was assumed to be the same for all provenances (Westfall 1992) and was calculated as three times the family-within-provenance variance component in order to take into account inbreeding and relatedness among neighbouring trees (Campbell 1986).

Three field provenance–progeny tests were used to check whether the regression models give biologically sound predictions of risk in seed source transfer (Table 6). These three test sites and the 56 to 66 provenances from these tests were chosen because they were located within the sampling area of provenances used for developing models describing patterns of provenance variation. Some of these

provenances were represented by 1 to 10 open-pollinated families, while others were bulked seed lots from at least 10 parent trees. Seedlings were spaced 2 × 2 m apart and planted between two adjacent 3 to 5 m wide hardwood bands in one row at the centre of each 2-m clear-cut strip at one site (E60011), and in two rows within each 3-m clear-cut strip with a seedling row 0.5 m away from the hardwood band at the two other sites. The experimental design for the three sites was a randomized complete block design with six or seven blocks and with a family represented by a four-tree row plot or a bulked seed lot by two four-tree row plots in each block. Height and survival rate were recorded at 10 years from seed. The testing of the validity of the model predictions proceeded in three steps, as detailed in Li et al. (1997).

Results

Genetic variability and genetic correlations

Significant differences were found among provenances and families within provenances for all traits except for the 4-year branch number (Table 2). For seedling heights (HTHYP, HT13W, HT3YR, and HT4YR), variance due to provenances was more than twice that due to families within provenances. For 3-year bud burst, provenance variance was three times the family-within-provenance variance, while both variance components were about equal for 3-year bud set. The first principal component (PC1) had greater provenance variance than family-within-provenance variance, but the reverse was true for the second principal component (PC2).

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

	HTHYP	HT13W	HT3YR	BB3YR	BS3YR	HT4YR	NBR4YR
HTHYP	1.000	0.921	0.625	0.348	0.227	0.655	0.370
HT13W	0.915	1.000	0.868	0.532	0.248	0.840	0.454
HT3YR	0.550	0.684	1.000	0.827	0.465	0.930	0.372
BB3YR	0.255	0.352	0.526	1.000	0.286	0.886	0.293
BS3YR	0.089	0.116	0.206	0.057	1.000	0.557	-0.053
HT4YR	0.573	0.691	0.908	0.541	0.219	1.000	0.409
NBR4YR	0.339	0.386	0.358	0.118	-0.185	0.333	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
HTHYP	0.763	0.371	-0.283	-0.302
HT13W	0.901	0.438	-0.232	-0.247
HT3YR	0.936	0.455	0.110	0.117
BB3YR	-0.776	-0.377	0.186	0.199
BS3YR	0.459	0.223	-0.674	-0.720
HT4YR	0.960	0.466	0.155	0.166
NBR4YR	0.480	0.233	-0.585	-0.625
Eigenvalue	4.233		1.141	
% of total variation	60.5		16.3	

Note: See Table 2 for trait definitions.

Heights at different ages were moderately to strongly inter-correlated at the provenance level (Table 3). Provenances with late bud burst and late bud set had greater heights than provenances with early bud burst and early bud set, as indicated by positive genetic correlations of 3-year bud burst and bud set with heights.

Principal component analysis

When estimating correlations between many traits simultaneously, the errors can be compounded so that the probability of obtaining a matrix whose eigenvalues are not all positive (matrix not positive definite) is very high (Hill and Thompson 1978). This leads to some linear combinations of the variables with negative variance, which is theoretically impossible. Further, it is well known that eigenvalues of a sample correlation matrix are biased relative to their expectations. The larger eigenvalues are biased upwards; the smaller ones downwards. However, their mean remains unbiased. This suggests that the eigenvalues could be compressed together without altering their mean and leave the corresponding eigenvectors unchanged (Hayes and Hill 1981).

In the present study, the genetic correlation matrix was not positive definite (Chatfield and Collins 1980), as the eigenvalue for the seventh eigenvector was negative (-0.051). A good review of approaches for refining the correlation estimates and obtaining an admissible matrix (i.e., no eigenvalue is negative) was given by Hodge and White (1992). One solution to the problem of inadmissibility is to drop some variables, but it was not obvious which variable could be dropped given

that no correlations were greater than one. In addition, by doing so, information could be lost. Instead we decided to use the bending approach (Hayes and Hill 1981; Hodge and White 1992). The bending principle deals with the inadmissibility by multiplying the genetic correlation matrix by a factor of $1 - \gamma$, which causes a shrinkage of the eigenvalues towards their mean of one. Hayes and Hill (1981) showed for a specific case that the eigenvalues of estimated genetic correlation matrices were typically too spread out when compared with the eigenvalues of the true matrices and that the bending procedure was improving the precision of the estimates. We chose a γ that gave us the smallest shrinkage of the eigenvalues, while producing an admissible correlation matrix. A γ of 0.05 (i.e., all genetic correlations were reduced by 5%) resulted in an admissible system of correlations. The bending approach was superior to that of dropping some variables because it used all original variables and did not give eigenvalues that were less than zero.

The use of the modified correlation matrix resolved two significant principal components, with PC1 accounting for 60.5% of the total variation for all traits and PC2 for 16.3% (Table 4). Thus, 77% of the total variation was attributed to the first two PCs. Five traits (HTHYP, HT13W, HT3YR, BB3YR, and HT4YR) received high loadings in PC1 (Table 4). PC2 obtained high loadings from 3-year bud set and 4-year branch number.

Multiple regression analysis

Multiple regression analysis revealed that latitude and longitude were main determinants of patterns of provenance variation in eastern white pine, as regression coefficients were zero or small for terms involving elevation (Table 5). Regression equations for individual traits accounted for 16% to 56% (average of 36%) of the total variation among provenances. Three traits (HTHYP, BS3YR, and NBR4YR) were weakly associated with the geography, as the proportion of the total variation explained by regression equations was between 16% and 29%, while the other four traits (HT13W, HT3YR, BB3YR, and HT4YR) were moderately related to the geography, with 38% to 56% of the total variation explained by regression equations. The amount of provenance variation accounted for by the regression equation was moderate: 62% for PC1 and 41% for PC2.

A significant lack of fit was found for all but two of the nine regression equations (BS3YR and PC2) (Table 5). This might imply that regression models did not take into account other important environmental variables. The inclusion of the cubic terms in the deviations of the original variables (latitude, longitude,

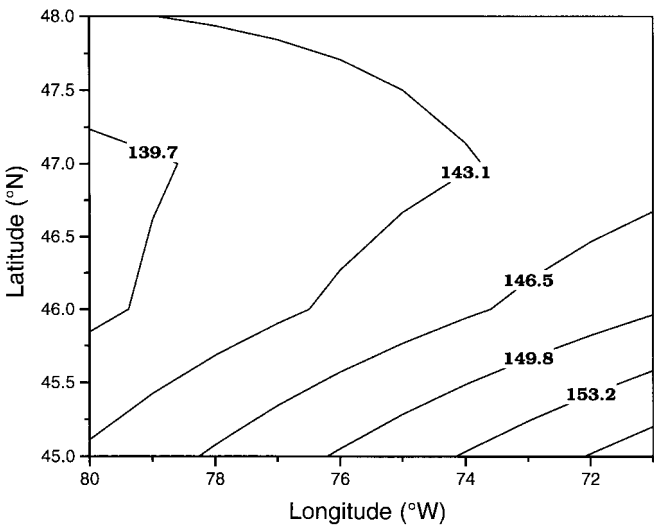
Table 5. Results of multiple regression analyses.

Trait	R^2	Lack of fit [†]	Intercept	LT	LN	EL	LT ²	LN ²	EL ²	LT×LN	LT×EL	LN×EL
HTHYP	0.29	<0.0001	2.5861	-0.1585	0.0910	—	0.4068	-0.0146	1.4×10^{-5}	—	-0.0033	-0.0006
HT13W	0.38	<0.0001	4.4237	-0.5768	0.1833	—	0.6972	—	—	-0.0948	—	—
HT3YR	0.46	0.0029	27.9063	-0.8155	0.6514	—	—	-0.0936	—	—	—	-0.0025
BB3YR	0.44	0.0118	131.2933	-0.5090	0.0686	—	—	—	—	-0.0650	—	0.0007
BS3YR	0.26	0.1107	230.9069	-2.0331	0.3826	—	—	—	—	—	—	—
HT4YR	0.56	0.0303	53.3040	-3.2636	1.2531	—	2.2556	—	—	-0.5804	—	-0.0051
NBR4YR	0.16	0.0262	5.9433	-0.1673	—	—	—	—	-1.3×10^{-5}	-0.0757	0.0033	—
PC1	0.62	0.0043	142.4596	-3.2285	1.0783	—	2.1899	—	—	-0.4748	—	-0.0038
PC2	0.41	0.1459	186.0847	-1.8790	0.4371	—	—	—	—	—	—	—

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 the mean were used in regression analysis. See Table 2 for trait definitions.

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

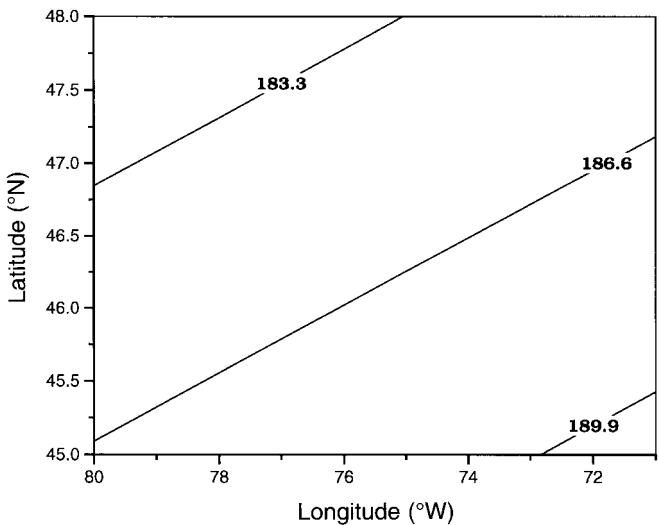
Fig. 2. Patterns of genetic variation among provenances predicted by the regression model for the first principal component at a constant elevation (200 m) with two adjacent contour lines separated by a relative risk of 0.30.



and elevation) somewhat alleviated the problem of lack of fit (results not shown). However, the ratio of the number of independent observations to the number of independent variables is quite small (66/19), which could lead to overfitting of regression models (Westfall 1992). Furthermore, it is not easy to biologically interpret the cubic terms in a regression model. Thus, we consider that the equations in Table 5 are the best ones for this study.

Patterns of provenance variation are shown in Figs. 2 and 3, respectively, for PC1 and PC2, and individual traits follow similar patterns. PC1 shows a complex pattern of genetic variation (Fig. 2). Provenances with high PC1 scores were from the southeastern part of the sampling area, while provenances

Fig. 3. Patterns of genetic variation among provenances predicted by the regression model for the second principal component at a constant elevation (200 m) with two adjacent contour lines separated by a relative risk of 0.30.



with low PC1 scores were located in the west-central part of the sampling area. This indicates that the southeastern provenances have greater seedling heights and late bud burst. The PC2 follows a different pattern of variation, with southeastern provenances having higher PC2 scores and northwestern provenances, lower PC2 scores (Fig. 3). This implies that southeastern provenances set buds later and have more 4-year branches than northwestern provenances. For PC1, genetic differentiation among provenances was sharper in the southeastern sampling area than in the northwestern one (Fig. 2), while for PC2, areas with similar PC2 scores are quite large, spanning nearly 2° in latitude and several degrees in longitude (Fig. 3).

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 [¶]
E600I1	66	1.33 (0.83–1.59)	0.75 (0.54–0.92)	0.336 (0.037–0.737)	–0.03 (0.793)	0.07 (0.587)
E600II1	57	1.95 (1.68–2.17)	0.81 (0.63–0.93)	0.240 (0.016–0.628)	–0.34 (0.010)	0.06 (0.642)
E600II2	56	1.99 (1.70–2.32)	0.87 (0.73–1.00)	0.389 (0.039–0.725)	0.33 (0.012)	–0.06 (0.645)

[†]Locations of test sites were as follows: E600I1 (45°58'N, 76°04'W, elev. 244 m), E600II1 (45°00'N, 75°33'W, elev. 210 m), and E600II2 (46°36'N, 72°39'W, elev. 110 m).

[‡]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.

Practical application of regression models

The relative risk of seed transfer averaged from 0.240 for site E600II1 to 0.389 for site E600II2 (Table 6). The correlation between relative risk and 10-year height was negative at site E600II1 and positive at site E600II2, but close to zero at site E600I1. The correlation between relative risk and 10-year survival rate was nearly zero at the three sites (Table 6). Because relative risk measures the proportion of genotypes for the transferred provenance that does not overlap with genotypes for the native population at the test site, the correlation between relative risk and performances (e.g., height and survival) of transferred provenances is expected to be negative. This prediction was borne out in only three of six instances (Table 6).

Discussion

This study showed that on average, variance due to provenances (23%) in growth and phenology traits was twice that due to families within provenances (9%) (Table 2). In eastern white pine from Tennessee, North Carolina, and Georgia (from an area of 2° lat. × 2° long.), provenance variance was about 3× that of family variance for growth traits (desBordes and Thor 1979). In contrast, an allozyme study of eastern white pine in Quebec shows that populations are weakly differentiated, as only 2% of the total variability is due to population differences (Beaulieu and Simon 1994). On the other hand, for white spruce (*Picea glauca* (Moench) Voss) from a much larger geographic area (Quebec and southeastern Ontario), provenances and families within provenances accounted for a similar amount of genetic variability in growth and phenology traits (Li et al. 1993, 1997). For black spruce (*Picea mariana* (Mill.) BSP) from each of three site regions in Ontario (each region covering an area a bit smaller than eastern white pine in this study), variance due to provenances is smaller than or equal to that due to families within provenance (Boyle 1986). Thus, the genetic structure of eastern white pine is different from those of white and black spruce in eastern Canada; it has a greater population differentiation for growth and phenology traits. The reasons for these different genetic structures are not clear, but it is to be noted that eastern white pine is a temperate species, while white and black spruce are boreal species. More comparative studies are needed to test whether boreal species have less genetic differentiation among populations than temperate species. However, western white pine (*Pinus monticola*

Dougl. ex D. Don) shows a contrasting pattern of genetic variation compared with eastern white pine: little genetic differentiation among populations, but abundant within-population variation in growth and phenology traits in most of its natural range (Rehfeldt et al. 1984 and references therein).

Regression models accounted for 16% to 62% (mean 40%) of provenance variation in eastern white pine, which is comparable to those obtained for other conifers in eastern Canada (Joyce 1988; Stahl and Persson 1992; Parker et al. 1994; Li et al. 1997). Patterns of genetic variation among eastern white pine provenances from Quebec follow complex geographical gradients (Figs. 2 and 3). Comparisons of our results with previous studies of eastern white pine are difficult because only five provenances from our sampling area were included in the range-wide study (Genys 1968, 1987). If we compare means of 2-year height for these five populations (Genys 1968) with our predicted scores for PC1, our models were good at predicting their relative performances (results not shown).

Geographical gradients are sharper for eastern white pine than for white spruce, especially in the southeastern part of the sampling area (see Li et al. 1997). Also, for eastern white pine, the best provenances are located in the southeastern part of the sampling area and the worst ones are in the northwest, while for white spruce the best provenances are from southeastern Ontario and southwestern Quebec (Nienstaedt 1968; Li et al. 1997). The latter difference may reflect a different history of species evolution, or it may be a sampling effect: the sampling area for eastern white pine was smaller (45.35–47.68°N, 71.23–79.22°W) than that for white spruce (43.73–49.35°N, 64.25–84.75°W), so that better southeastern Ontario populations were not included in our study. In fact, two southeastern Ontario provenances were among the best in the range-wide study of eastern white pine (Genys 1987). Interestingly, the southeastern populations performed better in our study than the northwestern ones, although the latter have greater allozyme variability (Beaulieu and Simon 1994). In coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), the best performing provenances are those with the highest genetic variability at allozyme loci (Li and Adams 1989).

Results were mixed for relating the relative risk of provenance transfer predicted by our regression models and the indicators of short-term adaptability in the three field provenance–progeny tests (Table 6). In contrast, for a study of white spruce from Quebec and Ontario, the model validation

led to expected results in most instances (Li et al. 1997). In addition to possible inadequacies in characterizing genotypes of families, regression models, and estimation of provenance means (Li et al. 1997), three other factors may have led to the weak validation of our regression models. First, the field tests used to model practical applications were younger (10 years from seed) than the white spruce tests (13 or 17 years from seed), so that time since planting was too short for the manifestation of provenance differences in adaptability. Given the younger age of field tests, the effect of transplanting shock for bare-root seedlings since planting (4 years from seed) might still have been present and have masked population differences if it had greater adverse effects on faster growing provenances than slow-growing ones, with the former losing a greater proportion of their roots when extracted from the nursery. Second, the planting method may have contributed to mixed results. Hence, eastern white pine in the field tests was planted within clear-cut strips between hardwood bands to alleviate damage from white pine weevils. Thus, trees were grown under protected and possibly under more heterogeneous conditions, as the differences among provenances might not have manifested themselves yet. Third, damage from biotic or abiotic factors could partially explain the failure to obtain the expected results from the regression models at two sites: at site E600I1, hare browsing severely affected 16% of trees, 35% of trees lost buds on their terminal leaders as a result of browsing and unknown reasons, and 10% of trees were damaged by blister rust, while at site E600II2, 27% of trees lost buds on the terminal leaders. At these two sites, hare browsing, terminal bud abortion, and blister rust interfered with normal growth of trees and thus may have masked the population differences in height as an indicator of adaptability. In contrast, at site E600III1, where little damage occurred and where the hardwood canopy is more open than at the two other sites, we found the expected negative correlation, albeit small, between 10-year height and relative risk. However, analyses after the exclusion of damaged trees improved only marginally the correlations of relative risk with height and survival at the two other sites (results not shown).

The patterns of variation among provenances disclosed from this study could be tentatively used in guiding seed transfer for reforestation and delineating breeding zones for breeding. Because population differentiation was sharper in the southeastern part of the sampling area than in the northwestern one, provenances could be transferred at longer distances in the northwest than in the southeast. Given that reforestation efforts for eastern white pine in Quebec are concentrated south of 47°N, that because of financial restrictions we cannot afford to maintain numerous breeding populations, and that white pine populations show strong differentiation between the southeastern and northwestern parts of the sampling area, we recommend, for the present, two breeding zones corresponding to these two regions in Quebec. Elevational zoning is not essential for delineating breeding zones in the sampling area because elevation is not an important determinant in shaping patterns of provenance variation. As eastern white pine also grows outside our sampling area (i.e., in eastern Quebec along the Appalachian mountains), studies are needed to determine whether other zones are to be delineated for breeding in Quebec. In conclusion, given that our sampling of eastern white pine did not cover the whole range in Quebec and that our field

tests are still young, it would be prudent to gather more information from these tests in the future and to wait for results of new studies in order to make sound recommendations on seed transfer and on the delineation of breeding zones.

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