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# GENETIC VARIATION IN JUVENILE GROWTH OF *PINUS STROBUS* IN REPLICATED QUEBEC PROVENANCE-PROGENY TESTS

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## ABSTRACT

Patterns of genetic variation among and within provenances were investigated for growth traits in *Pinus strobus* L. Sixty-seven provenances represented by 266 families were tested in this study. Four-year height was measured in the nursery as 10-year height was in three tests established in Quebec. Significant differences among provenances and families within provenances were disclosed. In the nursery, provenance variation was twice that of families while both were about the same for 10-year height. While provenance-by-site interaction was significant, suggesting that provenance ranks changed across the test sites, ranks of families within provenances seemed to be stable as supported by the nonsignificant family-within-provenance-by-site interaction and the high genetic correlation coefficients. Estimates of heritabilities were moderate for 4-year height but decreased later in the field. Genetic progress in height could be obtained from selection and breeding, and indirect selection for 10-year height from 4-year height could be considered. Culling of the worst families in the nursery could successfully decrease the costs of field testing without significant loss of potential genetic gain.

**Key words:** *Pinus strobus*, additive variance, breeding, genetic correlation, height growth, heritability

## INTRODUCTION

Eastern white pine (*Pinus strobus* L.) is the largest and formerly the most valuable tree of northeastern America (LITTLE 1986). The wealth of the pine forest reached its peak just prior to 1900 and has diminished steadily ever since (AIRD 1985). Its natural range still extends from Newfoundland in the northeast, westward to Lake Superior, south from western Ontario into the Lake States and then back east to New England. It also extends into the Appalachian Mountains southward into Georgia. But due to massive harvesting, forest fires and pest damage, the dimensions and value of white pine logs have decreased considerably. Today, white pine generally reaches a maximum height of 30 to 35 m and 1 m in diameter. It grows on a variety of soil conditions ranging from xeric sandy soils or rocky ridges to hydric swamps, but reaches its greatest size on a fertile loamy particle-size soil class (FARRAR 1995). Its wood is in great demand for construction, furniture and cabinetwork.

The area covered by white pine forests has shrunk considerably compared with that existing at the end of the last century. This is especially true for the St. Lawrence Lowlands ecoregion in Quebec, Canada (Ecological Stratification Working Group 1995) where small stands and isolated trees are sparsely distributed, mostly on soils poorly suited to agriculture (BEAULIEU & SIMON 1994). Even though white pine has a high economic value, it has not, in the last half of this century, occupied the place it should have in reforestation programs. This can be explained by the significant damage caused by two major pests killing the leader or the tree itself: white pine weevil (*Pissodes strobi* Peck) and white pine blister rust (*Cronartium ribicola* J.C. Fish.). Recent research showed that it was possible to keep this damage at acceptable levels using appropriate forest management practices (MARTINEAU 1984) and by breeding for resistance (KRIEBEL 1983). As a result, interest in white pine is increasing as indicated by higher production in the nurseries and the setting up of breeding programs and seed orchards.

Study of the genetic variation in white pine began as early as the 1930's (HEIMBURGER 1958, PAULEY *et al.* 1955, WRIGHT 1970). Results have been reported at the provenance level for, among other traits, seed germination (FOWLER & DWIGHT 1964, GRABER 1965, MERGEN 1963), survival (SLUDER & DORMAN 1971), monoterpene content (GILMORE & JOKELA 1977), frost tolerance in needles (MARONEK & FLINT 1974), wood characteristics (LEE 1974) and growth traits (FOWLER & HEIMBURGER 1969, FUNK 1979, FUNK & JOKELA 1979, KING & NIENSTEADT 1969, GENYS 1987, SLUDER & DORMAN 1971). These provenance trials, however, included very few provenances from Quebec and Ontario, so knowledge of the genetic variation of white pine colonizing that area was very weak. The development of synthetic varieties by selecting and crossing superior genotypes will make it possible to increase the quality and the productivity of white pine plantations. However, to assess the potential of family as well as individual selection, the extent of genetic control on adaptive and economic traits must first be estimated. Past studies have shown that for many traits, heritabilities are high enough to predict moderate to high genetic gains from selection (DESBORDES & THOR 1979, KRIEBEL 1978, THOR 1974, ADAMS & JOLY 1977, OLSON *et al.* 1980).

Based on these results and on the need to have better knowledge of the genetic variation in adaptive and economic traits of eastern white pine, a breeding program was initiated in the 1970's in Quebec (CORRIVEAU & LAMONTAGNE 1977). As a first step, a series of provenance-progeny tests were established to constitute a sufficient genetic base for the selection of the material for the first breeding generation. In this study, we investigated genetic variation in juvenile growth of eastern white pine in eastern Canada and the United States. Our objectives were: (1) to examine the distribution of genetic variation among and within provenances, (2) to determine the extent of genetic control for growth traits, and (3) to estimate genetic gains and evaluate the potential of early testing for 10-year height.

## MATERIALS AND METHODS

### Materials

The provenance-progeny test was established by using 266 families belonging to 67 provenances that were either seedlots sampled in the province of Quebec between 1976 and 1982 or seedlots obtained from collaborators elsewhere in Canada and in the United States. Hence, all the provenances represented a range-wide sample of the eastern white pine natural populations, ranging 10° 52' in latitude (37° 58' to 48° 50' N) and 29° 16' in longitude (64° 41' to 95° 57' W).

### Test designs and measurements

In March 1984, seeds from open-pollinated families were stratified and sown in Hillson-type Spencer-Lemaire rootrainers in a plastic greenhouse at the Laurentian Forestry Centre in Sainte-Foy, Quebec. The growing medium was a commercial mixture called Vitamix. Seedlings were irrigated and fertilizers were diluted in water and applied based on the operational regime for this greenhouse. Temperatures were maintained whenever possible at 20°C during the night and 22° to 26 °C during the day depending on the sunlight intensity. During the germination stage, the daily photoperiod was extended to 16 h with incandescent light. From June 30, seedlings were grown under natural photoperiod. The experimental design was a randomized complete block with 20 blocks, with each family represented by a four-seedling row plot.

Seedlings were taken to the nursery site located at the Valcartier Forest Experiment Station (Table 1, Fig. 1) in August 1984 to overwinter with the containers in exactly the same position as in the greenhouse. Seedlings were transplanted in June 1985 using the same experimental design. Seedlings were spaced 15 cm apart within a row with 30 cm between rows. They were grown there for 3 more years. For all seedlings in a subset of six blocks, 4-year height was measured at the end of the 1987 growing season.

In spring 1988, the 4-year-old seedlings were planted in three test sites (Table 1, Fig. 1). Soils in the test sites were homogeneous with one to three soil series generally belonging to the Orthic Humo-Ferric Podzol sub-group (LAMONTAGNE 1990a, 1990b, 1990c). The three test sites were located in an intermediate white pine blister rust infection hazard zone, that is, one in which between 5 and 15% of the trees are generally affected by that pest (LAVALLÉE 1986). They were representative of old logged areas found in Quebec, which have mainly been regenerated by *Populus tremuloides* Michx., *Populus grandidentata* Michx., *Betula papyrifera* Marsh. and *Acer rubra* L. Three-meter-wide strips were cleared for planting the seedlings. These cut-strips were in a north-south direction to allow the seedlings full light exposure at midday. A 5-m-wide uncut strip was left between two adjacent cleared strips for providing side shade to limit white pine weevil attacks (STIELL & BERRY 1985). Seedlings were planted in two rows with 2 m x 2 m spacing within 3-m-wide cut-strips. The experimental design was a randomized complete block, with each family randomly assigned within each block and represented by a four-tree row plot. Seven blocks were established in the first two tests while the last one was made of six blocks. Six growing years after planting, the 10-year total height of each living tree was measured in all three sites.

### Analyses

The first analyses aimed at disclosing the significance of family as well as provenance variances and estimating variance components based on a random model (Table 2). The model is for a split-plot design although

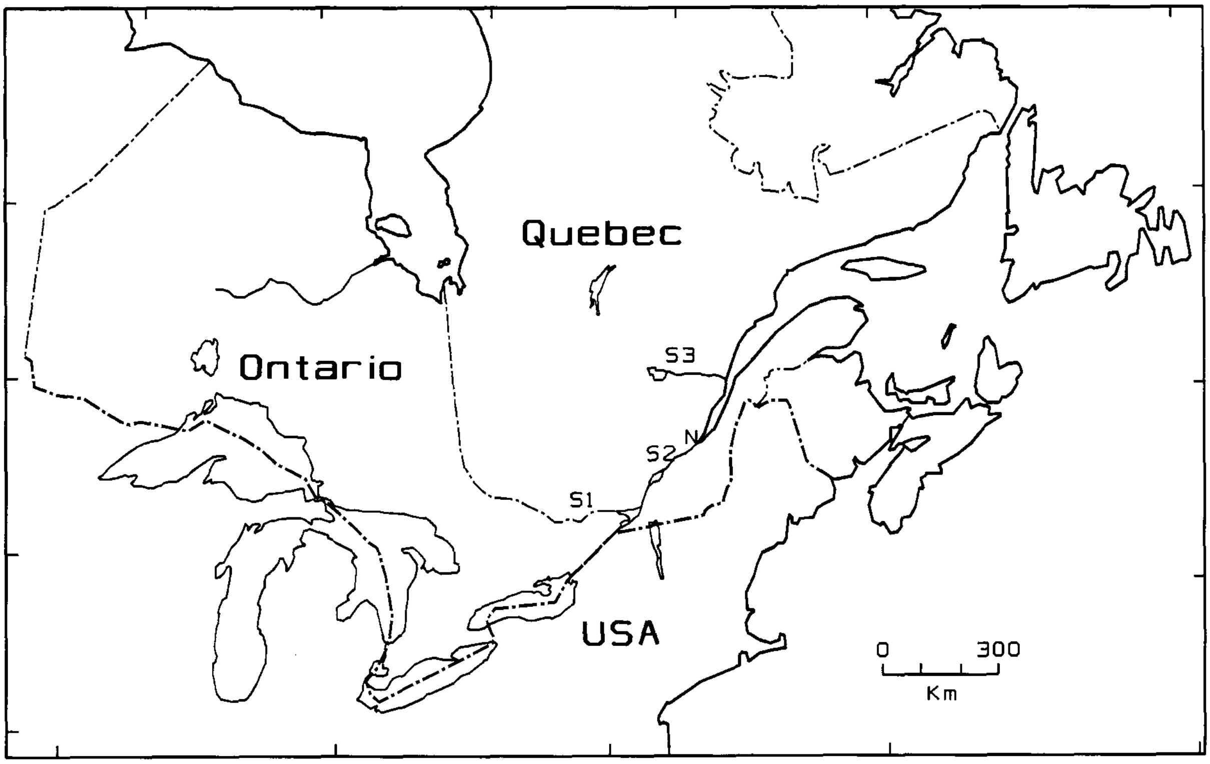

**Figure 1** Natural range of eastern white pine and provenance-progeny test location (N = nursery, S1 = Notre-Dame-du-Laus; S2 = Grand-Mère, S3 = Notre-Dame-du-Rosaire

in this study the families were randomized within the blocks instead of being randomized within a contiguous provenance whole plot within the blocks. The layout is however analoguous to that of a noncontiguous plot (LIBBY & COCKERHAM 1980). Analyses of variance for 4-year height in nursery and for 10-year height in each field site used the same model after excluding any component related to the site factor and setting s equal to 1. Ten-year heights of common families across the three sites were analyzed using the same random model presented in Table 2. Because of large data sets, statistical analyses for any combination of sites were done on a plot mean basis, with within-plot variances and covariances estimated from pooled plot values. Provenance means were compared using the Waller-Duncan T test for unplanned comparisons.

Families used in this study were considered as half-sibs and additive genetic variance was then estimated as four times the family-within-provenance variance (FALCONER 1981). To determine the degree of genetic control for each trait in combined field tests, individual and family narrow-sense heritabilities were obtained using the following equations for individuals [1] and families [2]:

$$h_i^2 = 4\sigma^2_{F(P)} / (\sigma^2_{F(P)} + \sigma^2_{F(P)S} + \sigma^2_E + \sigma^2_w) \qquad [1]$$

$$h_F^2 = \sigma^2_{F(P)}/(\sigma^2_{F(P)} + (\sigma^2_{F(P)S}/s) + (\sigma^2_E/sb) + \sigma^2_w/sbk) \qquad [2]$$

The meaning of each term is presented in Table 2. To estimate heritabilities for traits measured in the nursery or in each individual test, the same formulae were used except for the terms related to site component that were deleted and for s being set to 1. Approximate standard deviations of heritabilities were calculated following Dickerson's method (DIETERS *et al.* 1995).

The family stability of 10-year height across the three sites was first evaluated by testing the significance of family-within-provenance-by-site interaction (Table 2), and then by calculating the genetic correlations between sites (BURDON 1977). The coefficients ($r_A$) between sites were estimated using the formula:

$$r_A = cov_{F(P)xy} / \sqrt{(\sigma^2_{F(P)x} * \sigma^2_{F(P)y})} \qquad [3]$$

where $cov_{F(P)xy}$ is the family-within-provenance covariance in 10-year height between the pair of sites noted by *x* and *y*, and $\sigma^2_{F(P)x}$ and $\sigma^2_{F(P)y}$ respectively stand for sites x and y in the family-within-provenance variances. The family-within-provenance variance was obtained for each site using the model presented in Table 2 in

**Table 1 Nursery and field test site location, climatic and soil conditions**

| | Valcartier (Nursery) | Notre-Dame-du-Laus (S1) | Grand-Mère (S2) | Notre-Dame-du-Rosaire (S3) |
|---|---|---|---|---|
| Latitude N | 46° 56' | 46° 00' | 46° 36' | 48° 54' |
| Longitude W | 71° 30' | 75° 33' | 72° 39' | 71° 27' |
| Elevation (m) | 183 | 210 | 110 | 183 |
| Ecozone [a] | Boreal Shield | Boreal Shield | Mixed Wood Plain | Boreal Shield |
| Ecoregion [a] | Southern Laurentians | Southern Laurentians | St. Lawrence Lowlands | Central Laurentians |
| Ecological regions [b] | Maple/yellow birch | Maple/yellow birch | Maple/yellow birch | Balsam fir/yellow birch |
| Ecoclimatic regions [c] | Humid High Cool Temperate | Humid High Cool Temperate | Humid High Cool Temperate | Transitional High Cool Temperate |
| Precipitation [d] (mm) | 800–1,100 | 800–1,100 | 800–1,100 | 900–1,400 |
| Frost-free period [d] (days) | 120 | 120 | 120 | 70–80 |
| Degree-days above 5 °C [e] | 1,400–1,700 | 1,700–1,950 | 1,700–1,950 | 1,100–1,400 |
| Aridity index [c] | 25–75 | 125–175 | 175–225 | 25–75 |
| Soil names [f] (percentage) | St. Raymond (100) | 1) Deligny (60)<br>2) Morin (40) | Ivry (100) | 1) Honfleur (40)<br>2) Ascension (30)<br>3) Milot (30) |
| Deposit [f] | Fluvial | Fluvial | Fluvial | 1,2) Fluvial<br>3) Glacio-fluvial |
| Particle size [f] | Coarse-loamy | Sandy | Sandy | 1) Sandy<br>2) Sandy (10% coarse fragments)<br>3) Sandy-skeletal |
| Subgroup CSSC [f] | O.HFP | 1) GL.HFP<br>2) O.HFP | GL.HFP | 1,2) GL.HFP<br>3) O.HFP |
| Drainage class [f] | Well | 1) Moderately to imperfectly<br>2) Well | Moderately | 1,2) Moderately to imperfectly<br>3) Well to rapidly |

[a] See Ecological Stratification Working Group (1995)
[b] See THIBAULT and HOTTE (1985)
[c] See Groupe de travail sur les écorégions (1989)
[d] See CHAPMAN and BROWN (1966)
[e] See MASSIN (1971)
[f] See LAMONTAGNE (1990a, 1990b, 1990c)
[g] See Agriculture Canada Expert Committee on Soil Survey (1987)

which all terms related to site were discarded. A pooled estimate of covariance over the common provenances in each pair of tests was calculated by adding the sums of cross products between family means for each of these provenances and dividing it by the sum of the degrees of freedom of each individual provenance.

Genetic correlation coefficients between 10- and 4-year heights were also estimated using eq. [3]. $Cov_{F(P)xy}$ was then the family-within-provenance covariance between 10- and 4-year heights, and $\sigma^2_{F(P)x}$ and $\sigma^2_{F(P)y}$ were the family-within-provenances for 10- and 4-year heights, respectively. Family phenotypic correlations

**Table 2 Form of analysis of variance of 10-year height of combined field tests** [a]

| Source of variation | Degrees of freedom [b] | Expected mean squares[c] |
|---|---|---|
| Sites | s–1 | $\sigma^2_w/k + \sigma^2_E + b\sigma^2_{F(P)S} + f\sigma^2_{PB(S)} + bf\sigma^2_{PS} + fp\sigma^2_{B(S)} + bfp\sigma^2_S$ |
| Blocks (Sites) | (b–1)s | $\sigma^2_w/k + \sigma^2_E + f\sigma^2_{PB(S)} + fp\sigma^2_{B(S)}$ |
| Provenances | p–1 | $\sigma^2_w/k + \sigma^2_E + b\sigma^2_{F(P)S} + bs\sigma^2_{F(P)} + f\sigma^2_{PB(S)} + bf\sigma^2_{PS} + bsf\sigma^2_P$ |
| Provenances × Sites | (p–1)(s–1) | $\sigma^2_w/k + \sigma^2_E + b\sigma^2_{F(P)S} + f\sigma^2_{PB(S)} + bf\sigma^2_{PS}$ |
| Provenances × Blocks (Sites) | (p–1)(b–1)s | $\sigma^2_w/k + \sigma^2_E + f\sigma^2_{PB(S)}$ |
| Families (Provenances) | (f–1)p | $\sigma^2_w/k + \sigma^2_E + b\sigma^2_{F(P)S} + bs\sigma^2_{F(P)}$ |
| Families (Provenances) × Sites | (f–1)(s–1)p | $\sigma^2_w/k + \sigma^2_E + b\sigma^2_{F(P)S}$ |
| Plot error | (f–1)(b–1)sp | $\sigma^2_w/k + \sigma^2_E$ |
| Within-plot error | $\sum_{i=1}^{t}(n_i - 1)$ | $\sigma^2_w$ |

[a] The expected values of mean squares were obtained following SEARLE (1971). Covariance components were derived by replacing the mean squares by the cross-products in the equations. Approximate F-tests were used to test the significance of provenance, provenance × site interaction and site effects.

[b] s = number of sites (3 for combined and 1 for separate analyses); b = number of blocks within each site (6 for the nursery data, 6 for combined analyses of field tests, 7 for sites S1, S2, and 6 for site S3); k = harmonic mean number of seedlings per plot; p = number of provenances; f = number of families within provenance; $n_i$ = number of seedlings within the ith plot; t = total number of plots;

[c] $\sigma^2_w$ = within-plot variance, $\sigma^2_E$ = plot variance, $\sigma^2_{F(P)S}$ = family-within-provenance-by-site interaction variance, $\sigma^2_{F(P)}$ = family-within-provenance variance, $\sigma^2_{PB(S)}$ = provenance-by-block-within-site interaction variance, $\sigma^2_{PS}$ = provenance-by-site interaction variance, $\sigma^2_P$ = provenance variance, $\sigma^2_{B(S)}$ = block-within-site variance, $\sigma^2_S$ = site variance

were then calculated in the same way, but by replacing the family-within-provenance variances with variances of family means:

$$\sigma^2_{\overline{F(P)}} = \sigma^2_{F(P)} + \sigma^2_E/b + \sigma^2_W/bk. \qquad [4]$$

To estimate the accuracy of early selection of families in the nursery for 10-year height, a coefficient of relative efficiency (RE) of early selection was calculated. This coefficient is the ratio of the genetic gain obtained by indirect selection to that from direct selection, that is, the genetic gain for 10-year height with selection based on 4-year height to the genetic gain for 10-year height when selection is based on that character (FALCONER 1981).

## RESULTS

Seedlings averaged 41.2 cm in the nursery (Table 3). Ten-year mean heights were 203.1 cm, 195.5 cm and 154.1 cm in Grand-Mère (S2), Notre-Dame-du-Laus (S1) and Notre-Dame-du-Rosaire (S3), respectively. The average 10-year height over the three tests was 188.4 cm. Survival was good as 87.7%, 93.5% and 85.3% of the transplanted trees were still alive 6 years after planting in tests S1 to S3, respectively. The overall survival was 88.8%. Eastern white pine, a species highly susceptible to blister rust infection, was weakly affected with no more than 1% of trees affected in each test. White pine weevil damage was also at a low level, with less than 1% of the trees having been attacked in Grand-Mère and Notre-Dame-du-Rosaire while the percentage of trees showing damage in Notre-Dame-du-Laus was about 4%.

Provenances differed significantly for all growth traits (Table 3, Table 4). Significant differences among families within provenances in the nursery as well as in each individual site and for combined data over the test sites were also found. Furthermore, significant provenance-by-site interaction for 10-year height was revealed in the combined analysis over the three test sites. Of the total variance observed in the nursery, around 20% was due to provenance differences, 10% to families within provenances, and the remaining 70% to plot and within-plot variation. In the field tests, these figures changed to 4% each, which is attributable to provenances, and to families within provenances, and the remaining 92% to plot variation and variation among trees within plots. Hence, while the percentage of the total variation explained by the provenances was two times that due to families within provenances, it was almost equal in test sites except for Notre-Dame-du-Rosaire. Additive genetic variance within half-sib families ($\frac{3}{4}\sigma^2_A$) accounted on average for 30% of the within-plot variance in the nursery, while it accounted on average for 13% in field tests.

**Table 3 Test mean (cm), variance components (%), and individual ($h^2_i$) and family ($h^2_F$) heritabilities for height in eastern white pine[a)].**

| Trait[b)] | Mean (cm) | Components of variance as % of the total variance ($\sigma^2_T$) | | | | | | | | $h^2_i$ [d)] | $h^2_F$ [d)] |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | $\sigma^2_T$ [c)] | $\sigma^2_P$ | $\sigma^2_{PS}$ | $\sigma^2_{PB(S)}$ | $\sigma^2_{F(P)}$ | $\sigma^2_{F(P)S}$ | $\sigma^2_E$ | $\sigma^2_W$ | | |
| H4YS2 | 41.2 | 127.95 | 20.26** | – | 5.49** | 10.16** | – | 10.00** | 54.09 | 0.547(0.055) | 0.698(0.048) |
| H10YS1 | 195.5 | 2053.32 | 5.53** | – | 1.82* | 4.55** | – | 13.06** | 75.04 | 0.196(0.041) | 0.461(0.104) |
| H10YS2 | 203.1 | 2841.27 | 7.76** | – | 2.02** | 5.88** | – | 15.66** | 68.68 | 0.261(0.046) | 0.533(0.105) |
| H10YS3 | 154.1 | 1508.46 | 5.44** | – | 0.72 | 2.50** | – | 7.90** | 83.43 | 0.107(0.036) | 0.292(0.115) |
| H10YS123 | 188.4 | 2197.50 | 4.35** | 2.97** | 1.67* | 4.26** | 0.67 | 12.13** | 73.95 | 0.187(0.026) | 0.688(0.104) |

[a)] Definitions given in Table 2. **: significant at 0.01 level, *: significant at 0.05 level.

[b)] H4YS2 is 4-year height average of seedlings transferred to site S2. H10YS1, H10YS2, H10YS3 are 10-year height averages for sites S1, S2, S3 respectively. H10YS123 is 10-year height average over the three tests.

[c)] $\sigma^2_T = \sigma^2_P + \sigma^2_{PS} + \sigma^2_{PB(S)} + \sigma^2_{F(P)} + \sigma^2_{F(P)S} + \sigma^2_E + \sigma^2_W$

[d)] Numbers in parentheses are standard deviations obtained by Dickerson's approximation (DIETERS *et al.* 1995).

**Table 4 Multiple comparisons of means[a] for height growth of eastern white pine provenances**

| Provenance | Latitude (° ') | Longitude (° ') | Average height (cm) [b] | |
|---|---|---|---|---|
| Little River, Vermont | 44 29 | 73 06 | 215.9 | a |
| Niagara, Ontario | 43 10 | 79 20 | 205.8 | ab |
| New Hampshire | 42 55 | 71 20 | 205.0 | bc |
| Fryeburg-Has, Maine | 44 00 | 70 58 | 200.3 | bcd |
| Oconto River, Minnesota | 47 40 | 91 30 | 200.1 | bcde |
| Cewaygo Co., Michigan | 43 25 | 85 48 | 199.8 | bcde |
| Minden, Ontario | 44 55 | 78 45 | 198.7 | bcdef |
| Lac Balsam, Québec | 46 15 | 76 54 | 195.0 | cdefg |
| Howard City, Michigan | 43 15 | 85 30 | 194.7 | cdefgh |
| Wells-Goodwin, Maine | 43 10 | 70 50 | 192.7 | defghi |
| Baie Downey, Québec | 46 03 | 77 15 | 192.5 | defghij |
| Petawawa, Ontario | 45 59 | 77 23 | 192.5 | defghij |
| Lac Kipawa, Québec | 47 03 | 78 57 | 191.6 | defghijk |
| Kipawa, Québec | 46 46 | 79 01 | 191.0 | defghijkl |
| Rivière aux rats, Québec | 47 16 | 72 58 | 190.8 | defghijklm |
| Eldee, Ontario | 46 37 | 79 05 | 190.6 | defghijklm |
| Waldob. Totman, Maine | 44 05 | 69 22 | 190.5 | defghijklm |
| Lachute, Québec | 45 43 | 74 17 | 190.2 | defghijklm |
| Ishpening, Québec | 46 20 | 87 41 | 189.9 | defghijklm |
| Espanola, Ontario | 46 15 | 81 46 | 189.8 | efghijklmn |
| Tabaret, Québec | 46 56 | 79 15 | 189.8 | efghijklmn |
| Deux-Rivières, Québec | 46 16 | 78 18 | 189.2 | fghijklmno |
| Chequameg N.F.Tr., Michigan | 46 01 | 91 28 | 189.0 | fghijklmnop |
| Three Lakes, Wisconsin | 45 52 | 89 05 | 188.1 | ghijklmnopq |
| Lincoln Co. Tree, Wisconsin | 45 11 | 88 44 | 187.9 | ghijklmnopq |
| Lac Danford, Québec | 45 56 | 76 09 | 187.5 | ghijklmnopqr |
| Lac des Araignées, Québec | 45 27 | 70 47 | 187.3 | ghijklmnopqr |
| Lac Stoke, Québec | 45 32 | 7148 | 186.9 | ghijklmnopqr |
| Buena Vista, Minnesota | 46 55 | 9410 | 186.9 | ghijklmnopqr |
| Rivière Schyan, Québec | 46 13 | 77 12 | 186.2 | ghijklmnopqrs |
| Ville-Marie, Québec | 47 20 | 79 26 | 186.1 | ghijklmnopqrs |
| Rivière de l'Aigle,Québec | 46 21 | 76 10 | 185.6 | ghijklmnopqrs |
| Jemseg, New Brunswick | 45 50 | 66 00 | 184.8 | ghijklmnopqrst |

**Table 4** (continued)

| Provenance | Latitude (° ') | Longitude (° ') | Average height (cm) [b] | |
|---|---|---|---|---|
| Lac Usborne, Québec | 46 15 | 76 40 | 184.8 | ghijklmnopqrst |
| Rivière Noire, Québec | 46 01 | 76 52 | 184.8 | hijklmnopqrst |
| Hiles, Wisconsin | 45 44 | 89 00 | 184.3 | hijklmnopqrstu |
| Lac Ward, Québec | 46 23 | 76 38 | 184.1 | ijklmnopqrstu |
| Rivière Poussière, Québec | 46 22 | 77 40 | 184.1 | ijklmnopqrstu |
| Joliette, Québec | 46 03 | 73 27 | 183.6 | ijklmnopqrstuv |
| Lac Piscotosin, Québec | 46 53 | 75 38 | 183.1 | ijklmnopqrstuv |
| Lac Bryson, Québec | 46 24 | 76 58 | 182.2 | jklmnopqrstuv |
| White Earth, Minnesota | 47 19 | 95 57 | 182.1 | jklmnopqrstuv |
| Nicolet N. For., Wisconsin | 45 18 | 88 31 | 181.3 | klmnopqrstuvw |
| Rawdon, Québec | 46 04 | 73 45 | 181.2 | klmnopqrstuvw |
| Cass Lake, Minnesota | 47 50 | 94 75 | 180.9 | lmnopqrstuvw |
| PA Clone, Pennsylvania | 40 00 | 75 00 | 180.7 | lmnopqrstuvw |
| Mont-Tremblant, Québec | 46 13 | 74 36 | 180.4 | mnopqrstuvwx |
| Iron County, Michigan | 46 05 | 88 38 | 180.3 | mnopqrstuvwx |
| Chippawa N.F.Tr., Minnesota | 47 05 | 94 35 | 179.4 | nopqrstuvwxy |
| St-Adolphe, Québec | 45 58 | 74 20 | 179.1 | opqrstuvwxy |
| Nicolet For. Tree, Wisconsin | 45 08 | 89 06 | 178.7 | opqrstuvwxy |
| Chippawa N.F.Tr., Minnesota | 47 03 | 93 55 | 178.5 | pqrstuvwxy |
| G. Wash. S.F.Tr., Minnesota | 47 30 | 93 25 | 178.3 | qrstuvwxy |
| Montebello, Québec | 45 40 | 74 58 | 177.3 | rstuvwxy |
| G. Wash. S.F.Tr., Minnesota | 47 20 | 93 30 | 176.3 | stuvwxy |
| Lac Emery, Québec | 46 53 | 73 14 | 176.2 | tuvwxy |
| St-Damien-de-Br., Québec | 46 18 | 73 33 | 174.4 | tuvwxy |
| Lac St-Joseph, Québec | 46 51 | 71 38 | 174.2 | uvwxy |
| Falls Mills, West Virginia | 38 47 | 80 33 | 173.3 | vwxyz |
| Sherbrooke, Québec | 45 21 | 71 53 | 170.9 | wxyz |
| Lac du Castor Noir, Québec | 46 55 | 73 02 | 170.0 | xyza |
| Parc de la Mauricie, Québec | 46 36 | 72 54 | 169.5 | yza |
| T.P. 22, Rge 11, Ontario | 46 54 | 83 48 | 163.1 | zab |
| Baie Gaspé sud, Québec | 48 52 | 64 41 | 160.3 | abc |
| Rivière York, Québec | 48 50 | 64 42 | 159.8 | abc |
| Superior N.F.Tr., Minnesota | 47 36 | 91 21 | 159.0 | bc |
| Borden Twp, Ontario | 47 53 | 83 10 | 151.6 | c |

[a] Waller-Duncan T test: K-ratio = 100; df = 3034; MSE = 792.5; F = 12.2; critical value of T = 1.81
[b] Means with the same letter are not significantly different

**Table 5 Genetic correlations ($r_A$) in 10-year height across the field test sites.**

| | Notre-Dame-du-Laus (S1) | Grand-Mère (S2) |
|---|---|---|
| Notre-Dame-du-Rosaire (S3) | 0.955 | 0.991 |
| Grand-Mère (S2) | 1.036 | – |

Heritabilities at the individual level were moderate for 4-year height and low for 10-year height (Table 3). On the other hand, estimates at the family level were moderate to high. Furthermore, the precision of these estimates was good. Genetic correlations ($r_A$) of 10-year height across the three test sites were high, indicating that ranking of families within provenances was quite similar in those sites (Table 5). At Grand-Mère, genetic correlation between 4-year height in the nursery and 10-year height was strong and positive ($r_A$ = 0.86 and the estimate of family phenotypic correlation was lower ($r_P$ = 0.66).

## DISCUSSION

Six years after planting, the average height ranged from 154.1 cm in Notre-Dame-du-Rosaire to 203.1 cm in Grand-Mère. Best results were obtained in the southeast site (S2) on a fertile coarse-loamy particle-size Gleyed Humo-Ferric Podzol soil development. The test is located along the St. Maurice River in the region having the highest heat sum (Table 1). The slowest height growth was as expected observed in the northernmost site where the climatic conditions are less favorable (S3).

Provenances and families accounted for the same percentage of variance in the field, as shown by the results of the combined analysis. However, provenances explained a greater percentage of total variation than families in the nursery (20% vs 10%), with the latter being a tendency already reported for growth traits (KRIEBEL 1983). Analysis of data from two 10-year open-pollinated progeny tests showed that the proportion of total variance in height due to differences among the 13 southeastern provenances represented by those families was about three times that due to families within the provenances (DESBORDES & THOR 1979). Ratio of provenance over family variation was then about the same as those reported for each of the two sites 5 years earlier (THOR 1974). However, percentages of total variance explained by both sources in the combined analysis of 10-year height was about twice that of 5-year height. On the other hand, OLSON *et al.* (1980) showed that for specific gravity, equivalent proportions of total variation were explained by family and provenance for 10-year-old white pine trees from other southern Appalachian sources.

Results of the present study also suggest that the level of population differentiation is higher for growth traits than for allozyme markers, for which 98% of total variation was found to be within populations (BEAULIEU & SIMON 1994). Furthermore, white pine seems to be different from white spruce (*Picea glauca* [Moench] Voss) in the sense that for the latter species, percentages of variation due to provenances and families within provenances were reported to be about the same in the nursery as in field tests (LI *et al.* 1993). The nursery used for that white spruce study was the one used for the present study, and the test sites for both species were located in meridional Quebec. Thus, one could suggest that differences in patterns of genetic variation might also be due to differences in the size of the area sampled, since the white spruce study was regional while that of white pine was range-wide, with sampled sources of the latter species being adapted to a much larger range of ecological conditions. However, analysis of a white spruce subsample including only provenances from Quebec showed results similar to those based on all provenances (LI *et al.* unpublished). On the other hand, white spruce tests were established in open fields while white pine tests were in cut-strips within pioneer species stands. Thus, for white pine, field test conditions with side protection from uncut-strips of trees were fairly different from those in the nursery and they could have acted as a buffer against the manifestation of provenance differences.

For all height growth traits, the within-plot variance component accounted for the largest percentage of the total variation, ranging from 54% to 83%. This result is in agreement with observations reported in earlier studies (ADAMS & JOLY 1977, DESBORDES & THOR 1979, KRIEBEL *et al.* 1972, KRIEBEL *et al.* 1974, THOR 1974). On the other hand, the plot variance component accounted for about the same percentage of the total variation, that is about 8-16%, as compared with the earlier studies, even though trees were planted in cut-strips within a young forest stand in the present study. We expected that heterogeneity in light conditions would cause more variation among plots than when a test is established in full light. Since white pine is a moderately shade-tolerant species (LOGAN 1966), effects of such heterogeneity might have been buffered. Estimates of narrow-sense heritabilities were moderate at 4 years of age but decreased in field tests for 10-year height. They were slightly lower than those already reported by other authors (ADAMS & JOLY 1977, DESBORDES & THOR 1979, KRIEBEL 1978, KRIEBEL *et al.* 1974) and this might be related to the type of plantation used in the present study, which could have prevented families from expressing their full potential.

The absence of significant family-within-provenance-by-site interaction in the combined analysis indicates that ranks of families across the sites are quite stable. A nonsignificant location-by-family-within-stands was also reported for 10-year height of open-pollinated families from Tennessee, North Carolina and Georgia provenances (DESBORDES & THOR 1974). The genetic correlations between each pair of tests in the present study were very high. This is another indication of stability of family ranks across the sites. However, considering the vastness of the Quebec territory, it might be safer to delineate more than one breeding zone as suggested by LI *et al.* (1996). Moreover, results from more than three sites would be necessary for making sound decisions on the constitution of the breeding populations.

The high genetic correlation between 4-year height in the nursery and 10-year height at Grand-Mère (S2) suggests that an indirect selection made in the nursery for 10-year height could be successful. Relative efficiency of early family selection for 10-year height in Grand-Mère was estimated to be 99% ($RE = r_A \,.\, h_{F\,(H4YS2)} / h_{F\,(H10YS2)} = 0.86 \times [0.698^{1/2} / 0.533^{1/2}]$). This indicates that culling the worst families based on 4-year height in the nursery would be efficient and make it possible to limit the number of families included in the field tests and reduce the cost of such testing.

Even though the narrow-sense heritabilities reported in the present study are low to moderate, it does not mean that genetic progress cannot be made by selection and breeding of superior material. Indeed, from the selection of the top 10% of families within an average white pine population, one could expect a genetic gain of 14.1 cm (7.5%) in 10-year height. However, a long-term follow-up study is needed because the trees are still too young for extrapolating the expected gains calculated to the rotation age with some confidence, and because the strength of juvenile-mature correlation is not known.

## CONCLUSIONS

The results presented here for height growth have shown that lots of variation exists in this trait in eastern white pine. Much of this variation is located within families and provenances. Significant differences among provenances and among families within provenances were disclosed. Furthermore, estimates of heritability were moderate to high at the family level, suggesting that selection of the best families and breeding work would make it possible to genetically improve this species. Selection of the best families could also be done at an early stage.

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