

# Genetic Variation in Juvenile Growth and Phenology in a White Spruce Provenance-Progeny Test

By P. LI<sup>1</sup>), J. BEAULIEU<sup>2</sup>), A. CORRIVEAU<sup>2</sup>\*) and J. BOUSQUET<sup>1</sup>)

(Received 15th September 1992)

## Summary

We investigated the distribution of genetic variation among and within provenances, the extent of genetic control in growth and bud phenology traits and potential of early testing of height growth for 285 open-pollinated families from 57 provenances of white spruce (*Picea glauca*) from Quebec and Ontario. Provenances and families within provenances showed significant genetic variation in seedling growth, 1-year branch number, 3-year budset and 8-year height, but not in 3-year budburst. On average, provenance variance was as large as family-within-provenance variance. Individual heritabilities for all traits were generally low (range 0.08 to 0.19) and family heritabilities were higher (range 0.17 to 0.45). In 3-year-old seedlings, height growth was positively correlated with budset, indicating that selection for greater 3-year height would delay budset. Nonsignificant family-within-provenance-by-site interaction variance and high genetic correlations in 8-year height among test sites suggest that families were stable across environments. If the best 20% of families were selected and mated in a seed orchard, predicted genetic gain for 8-year height would be 8%. Strong genetic correlations between 8-year height and seedling heights indicate that 8-year height could be predicted reliably from seedling heights.

**Key words:** Genetic variation, growth and phenology, provenances, variance components, white spruce.

## Introduction

White spruce (*Picea glauca* MOENCH) Voss.) has a continuous distribution in North America, ranging westward from Newfoundland and Labrador across the continent to northern Alaska and the Northwest Territories, and southward from the northern tree line to the southern limit in the Lake States, New York and Maine (FOWELLS, 1965; HOSIE, 1979). However, some outlying populations are found in South Dakota, northern Montana and Wyoming. This species grows in a variety of climatic and soil conditions with an elevation range from sea level to approximately 1500 m. White spruce is used for lumber, pulpwood, and other wood products and is a main reforestation species in Canada and the northeastern United States. The current annual plantation program in Quebec requires 45 million seedlings. Thus, tree improvement research and breeding activities for this species have been intensive during the past 30 years (NIENSTAEDT and TEICH, 1972).

White spruce provenances differ significantly in growth, phenology, wood density, allozyme frequency, and morphological and physiological traits (NIENSTAEDT and TEICH, 1972; KHALIL, 1986; BEAULIEU and CORRIVEAU, 1985; CORRIVEAU et al., 1987; FURNIER et al., 1991). Field tests in the northeastern United States and Canada have shown that provenances from southeastern Ontario and the St. Lawrence Valley of Quebec have good growth and adaptability (NIENSTAEDT and TEICH, 1972). These provenances have been recommended for use in reforestation and breeding programmes in the Lake States region of the United States (NIENSTAEDT and KANG, 1987), Quebec, the Maritime provinces and Newfoundland (Comité d'amélioration génétique des arbres forestiers du Québec, 1983; KHALIL, 1985b; FOWLER, 1987).

To better assess the potential for selection of families within provenances, the extent of genetic control of economic and adaptive traits must be determined. Past studies have shown genetic variation among white spruce families and a great potential for selection and breeding (DHIR, 1976; MOHN et al., 1975; YING and MORGENSTERN, 1979; KHALIL, 1985a; MERRIL and MOHN, 1985; NIENSTAEDT, 1985; NIENSTAEDT and RIEMENSCHNEIDER, 1985). These earlier studies, however, are restricted to families from the Lake States Region of the United States and to a few families from southern Ontario and Newfoundland. Thus, it is of interest to estimate genetic parameters from other geographical areas such as Quebec and Ontario. Although several studies have examined the inheritance of budburst timing (WILKINSON, 1977; POLLARD and YING, 1979b; O'REILLY and PARKER, 1982; NIENSTAEDT, 1985), none have dealt with the extent of genetic control of budset timing in white spruce.

In this study, we investigated genetic variation in juvenile growth and phenology for 285 families from 57 white spruce provenances from Quebec and Ontario. 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 and bud phenology traits, and (3), to estimate genetic gains and evaluate potential of early testing for 8-year height.

## Material and Methods

### 1. Material

In 1979, 91 white spruce provenances were used to establish a provenance-progeny test in Quebec, either from newly collected seeds in Quebec, or from stored seedlots in the National Tree Seed Bank (Petawawa National Forestry Institute, Chalk River, Ontario). In this study we used only 57 of the 91 provenances because each of these 57 provenances had 5 open-pollinated families, which makes it easier to interpret the results. These provenances represented the originally sampled provenances in Quebec and Ontario well (Fig. 1), ranging 6 degrees in latitude (43°30' to 49°36'), 30 degrees in longitude (64°15' to 94°36') and 15 m to 842 m in elevation.

<sup>1</sup>) Centre de recherche en biologie forestière, Faculté de foresterie et de géomatique, Université Laval, Sainte-Foy, Quebec, Canada G1K 7P4

<sup>2</sup>) Laurentian Forestry Centre, Forestry Canada, Quebec Region, Sainte-Foy, Quebec, Canada G1V 4C7

Corresponding Author: PENG LI, Centre de recherche en biologie forestière, Faculté de foresterie et de géomatique, Université Laval, Sainte-Foy, Quebec, Canada G1K 7P4.

\*) We would like to dedicate this paper to our friend Dr. ARMAND CORRIVEAU, who initiated the work reported herein, but who unfortunately passed away on November 3, 1990, and of whom we keep the best thoughts.

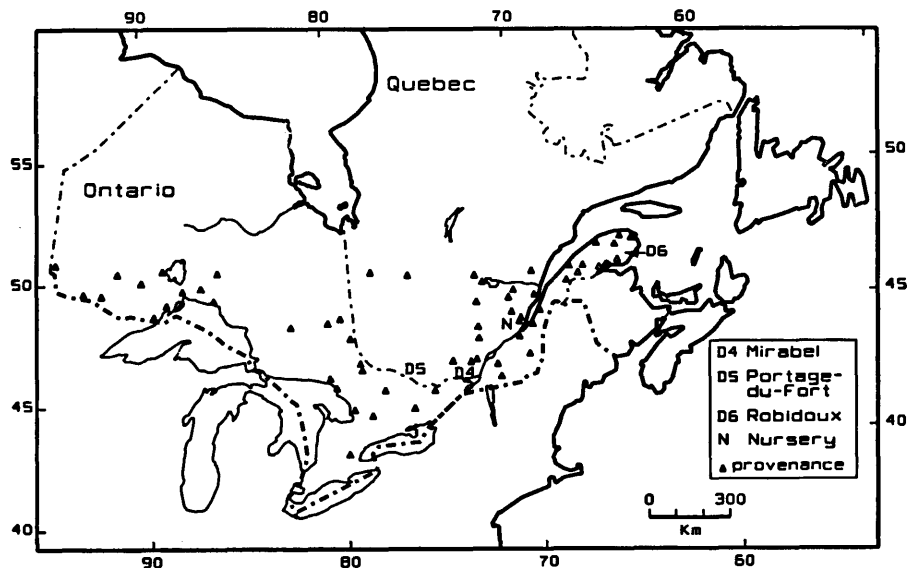


Figure 1. — Geographical locations of the 57 white spruce provenances (Δ) and nursery (N) and field test sites (D) used in this study.

## 2. Test designs and measurements

### Greenhouse phase

In February 1980, stratified seeds were sown in Spencer-Lemaire containers in a greenhouse at the Laurentian Forestry Centre in Sainte-Foy, Quebec. The growing medium was sphagnum peat moss. Seedlings were irrigated and fertilized based on the operational regime for this greenhouse. The thermoperiod was 21°C during the day and 18°C at night, with a 16 h day and 8 h night photoperiod. From June 21, seedlings were grown under natural photoperiod so that they would set buds for overwintering. All seedlings set buds before August 11, 1980. The experiment design was a randomized complete block with 24 blocks. Within a block, each family was represented by a 4-seedling row plot.

The following traits were measured in ten blocks: total height 17 weeks after sowing, and total height and branch number at the end of the first growing season. Given the large number of seedlings, only two randomly selected seedlings were measured within each family plot in the ten blocks.

### Nursery phase

Seedlings were taken to the nursery site (Table 1, Figure 1) to overwinter in late August 1980 and were transplanted in early May 1981, with the experimental design used in the greenhouse maintained in the nursery. The spacing was 15 cm between seedlings within each row and 30 cm between rows. Seedlings were grown for two seasons in the nursery.

For all seedlings in eight blocks, 2- and 3-year heights were measured at the beginning and at the end of the 1982 growing season respectively. For 3-year-old seedlings in five blocks, bud phenology on the leader shoot was assessed by scoring budburst date (the date when green needles ruptured through scales of the terminal bud) and budset date (the date when the terminal bud separated from the surrounding needles and bud scales turned brown). Four of these five blocks were also measured for 2- and 3-year heights. Budburst was scored twice a week in May and budset once a week from July to October

1982. If multiple flushing occurred, budset date was scored as the date of the final budset. Given the large number of seedlings, budburst and budset were scored on a plot basis, that is, within each family plot the number of seedlings that flushed or set terminal buds on each scoring day was recorded until all four seedlings within each plot had flushed or set buds. This scoring scheme made it possible to score budburst and budset in a single day for all seedlings in the 5 blocks. However, individual seedling identity could not be retained, so that although within-plot variances for budburst and budset dates could be estimated, it was not possible to calculate within-plot covariances between phenology and growth traits in the 4 blocks where both growth and phenology were measured.

From these measurements on 3-year-old seedlings, the following variables were derived: 3-year height increment (difference between 3- and 2-year heights), shoot growth duration (difference between dates of budset and budburst for each family plot), and shoot growth rate (3-year height increment divided by the shoot growth duration).

### Field phase

In spring 1983, the 3-year-old seedlings were transplanted into 3 field test sites (Table 1, Figure 1). These sites were representative of the white spruce reforestation region in Quebec, and were prepared for planting. Spacing was 1.5 m within a row and 2.5 m between rows. Seedlings were watered immediately after planting to ensure a good rate of survival. The experimental design was a randomized complete block, with each family randomly assigned within each block and represented by a 4-tree row plot. Owing to mortality in the nursery, blocks were consolidated so that each plot in field tests would have four trees. As a result, out of the 8 original blocks intended for each field site, only six blocks were established in two sites (D5 and D6) and seven blocks in the third (D4). This consolidation of blocks may introduce a bias in estimating within-plot variance for field height because some plots contained seedlings from different nursery blocks.

Five years after planting, total height (8 years from seed) was measured in all three sites.

Table 1. — Nursery and field test site characteristics.

Test site	Temperature			Elevation	Longitude	Latitude	Average June-Aug. temperature	Total annual precipitation	Number of frost-free days	Ecological region	Climate	Surface deposit
	Average	Absolute Minimum	Absolute Maximum									
Valcartier (Nursery)	46°37'	74°04'	152m	15.4°C	-41.7°C	130cm	120	Maple/yellow birch stand	Cool and wet, continental	Loamy sand		
Mirabel (D4)	45°37'	74°04'	60m	21.6°C	-33.9°C	99cm	125	Maple/Bitternut hickory stand	Warm, continental	Till and clay		
Portage-du-Fort (D5)	45°36'	76°37'	122m	18.7°C	-34.4°C	74cm	125	Balsam fir/Yellow birch stand	Warm and dry continental	Till and loamy sand		
Robidou (D6)	48°12'	65°43'	150m	18.6°C	-40.0°C	92cm	110	Balsam fir/White spruce stand	Warm, maritime	Till		

"Ecological region": according to THIBAUT and HOTTE (1985)

### 3. Data analysis

The first step in data analysis was to examine the significance of family and provenance variances in all

traits and to estimate variance components based on a random model (Table 2). This model is for the split-plot design although in our study families from a provenance were randomized within a block, not randomized within a contiguous whole plot as in the formal split-plot design. However, each provenance could be treated as being represented by a non-contiguous whole plot within a block, analogous to the concept of non-contiguous plot described by LIBBY and COCKERHAN (1980). Eight-year height across the 3 field sites was analyzed using the model in table 2. Analysis of variance for data from greenhouse, nursery and single field site followed the same form, but excluded any terms that included site as a factor and set  $s$  equal to 1. Because of large data sets, statistical analyses were done on a plot mean basis, with within-plot variances and covariances estimated from pooled plot values. Depending on data sets, 0% to 2.5% of the plots were missing. Missing plot values were estimated following YATES (1933) and degrees of freedom for plot error were adjusted accordingly. For the purpose of statistical testing, significance refers to the 0.05 probability level.

To determine the degree of genetic control for each trait, individual and family heritabilities and their standard errors were calculated (NAMKOONG, 1979). Additive genetic variance was estimated as 4 times the family-within-provenance variance. For overall 8-year height, individual heritability was calculated as:

$$(1)$$

$$h^2_I = 4\sigma^2_{F(P)} / (\sigma^2_{F(P)} + \sigma^2_{F(P)S} + \sigma^2_E + \sigma^2_W)$$

and family heritability was calculated as:

$$(2)$$

$$h^2_F = \sigma^2_{F(P)} / (\sigma^2_{F(P)} + \sigma^2_{F(P)S/s} + \sigma^2_E/sb + \sigma^2_W/s^2)$$

where all terms are defined in table 2. In calculating heritabilities for traits in greenhouse, nursery, and single field site, terms that included  $\sigma^2_{F(P)S}$  were deleted in eq. (1) and (2) and  $s$  is equal to 1 in eq. (2).

To assess the extent of association between traits for the greenhouse and nursery data, genetic correlations and their standard errors were calculated (BECKER, 1984). In addition, family phenotypic correlations were calculated using the following equation:

$$r_P = \frac{COV_{F(P)12}}{\sqrt{\sigma^2_{F(P)1} \times \sigma^2_{F(P)2}}} \quad (3)$$

where  $COV_{F(P)12}$  is covariance of family mean between traits 1 and 2,  $\sigma^2_{F(P)1}$  and  $\sigma^2_{F(P)2}$  are variances of family means for traits 1 and 2 respectively. Variance of family mean was estimated as  $\sigma^2_{F(P)} + \sigma^2_E/b + \sigma^2_W/bk$  and covariance of family mean was calculated in the same fashion by replacing variances with covariances.

The family stability of 8-year height across the three sites was first evaluated by testing the significance of family-within-provenance-by-site interaction variance (Table 2) and then by estimating genetic correlations for 8-year height between pairs of sites (BURDON, 1977). The genetic correlation ( $r_A$ ) between sites was estimated as:

$$r_A = \frac{COV_{F(P)xy}}{\sqrt{\sigma^2_{F(P)x} \times \sigma^2_{F(P)y}}} \quad (4)$$

Table 2. — Form of analyses of variance of 8-year height in field tests<sup>a</sup>.

Source of variation	Degrees <sup>b</sup> of freedom	Expected mean square <sup>c</sup>
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)p	$\sigma^2_w/k + \sigma^2_E + f\sigma^2_{PB}(S) + fp\sigma^2_B(S)$
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 x 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 x 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) x 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	$\sum_{i=1}^t (n_i - 1)$	$\sigma^2_w$

<sup>a</sup>) The expected values of mean squares were derived following SEARLE (1971, pp. 393 to 394). Replace expected mean squares with expected mean cross-products for estimating covariance components. Tests for the effects of provenance, provenance x site interaction and site effects were conducted by constructing approximate F-test (SEARLE, 1971).

<sup>b</sup>) s = number of sites (3 for combined analyses and 1 for all separate analyses)

b = number of blocks within each site (10 for the greenhouse data, 8 for 3-year growth data, 6 for combined analyses of fields tests, 7 for site D4 and 6 for sites D5 and D6)

p = number of provenances (57)

f = number of families within each provenance (5)

n<sub>i</sub> = number of seedlings within the i<sup>th</sup> plot

t = total number of plots

<sup>c</sup>) k = harmonic mean number of seedlings per plot (2 for the greenhouse data, 3.86 for 3-year growth data, 3.81 for phenology data, 3.32 for combined analyses of field tests, 3.1 for site D4, 3.39 for site D5 and 3.32 for site D6)

$\sigma^2_w$  = 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

in table 2 excluding all terms that include site as a factor. Given that families were from 57 provenances, a pooled estimate of covariance over the 57 provenances was calculated by adding the sums of cross products between family means in 8-year height for each provenance and

Table 3. — Test mean ( $\bar{X}$ ), variance components, and individual ( $h^2_I$ ) and family ( $h^2_P$ ) heritabilities (with standard errors in parentheses) for growth and phenology traits<sup>a)</sup>.

Trait <sup>b)</sup>	$\bar{X}$	$\sigma^2_{TC}$	$\sigma^2_P$	$\sigma^2_{PS}$	$\sigma^2_{PB(S)}$	$\sigma^2_{F(P)}$	$\sigma^2_{F(P)S}$	$\sigma^2_E$	$\sigma^2_W$	$h^2_I$	$h^2_T$	Components of variance as % of the total variance ( $\sigma^2_T$ )							
												$\sigma^2_P$	$\sigma^2_{PS}$	$\sigma^2_{PB(S)}$	$\sigma^2_{F(P)}$	$\sigma^2_{F(P)S}$	$\sigma^2_E$	$\sigma^2_W$	$h^2_I$
H17WK	10.5	6.92	3.7**	-	0.0 <sup>d</sup>	4.5**	-	34.9**	56.9	0.19(0.04)	0.42(0.06)								
H1Y	17.1	19.99	4.4**	-	1.6	2.6**	-	47.0**	44.3	0.11(0.04)	0.27(0.07)								
BN1Y	14.1	18.32	2.2**	-	1.0	2.7**	-	35.4**	58.7	0.11(0.04)	0.29(0.07)								
H2Y	25.5	26.52	2.4**	-	1.4	2.3**	-	46.1**	47.7	0.10(0.04)	0.24(0.08)								
H3Y	38.6	43.92	4.3**	-	1.3	4.3**	-	31.5**	58.7	0.18(0.04)	0.42(0.06)								
BB3Y	146.1	6.597	0.1	-	4.9**	0.0 <sup>d</sup>	-	6.0	88.6	0.0	0.0								
BS3Y	230.8	363.6	5.2**	-	0.8	3.8**	-	12.0**	78.2	0.16(0.04)	0.37(0.07)								
DU3Y	84.7	369.0	5.1**	-	0.9	3.5**	-	11.6	-	-e	0.35(0.07)								
HI3Y	13.1	17.34	4.0**	-	2.0**	3.0**	-	24.2**	66.8	0.12(0.03)	0.37(0.06)								
RATE3Y	1.7	0.427	0.9	-	1.4 <sup>e</sup>	2.1**	-	4.0	-	-e	0.22(0.08)								
H8YD4	96.6	918.1	3.1**	-	0.0 <sup>d</sup>	3.3**	-	39.4**	54.2	0.17(0.04)	0.40(0.06)								
H8YD5	102.7	819.5	0.7	-	0.0 <sup>d</sup>	1.9 <sup>e</sup>	-	39.1**	58.2	0.08(0.04)	0.17(0.09)								
H8YD6	112.6	687.0	1.3 <sup>e</sup>	-	0.9	2.3**	-	24.1**	71.5	0.09(0.04)	0.23(0.08)								
H8Y	103.8	749.8	1.8**	0.0 <sup>d</sup>	0.0 <sup>d</sup>	2.4**	0.4	30.6**	64.8	0.10(0.02)	0.45(0.06)								

<sup>a)</sup> See table 2 for definitions of variance components. \*\*)— significant at 1% probability level, and \*)— significant at 5% probability level.

<sup>b)</sup> Trait code: H, BN, BB, BS, DU, HI, and RATE are, respectively, height (cm), branch number, date of budburst (days from Jan. 1), date of budset (days from Jan. 1), growth duration (days), height increment (cm), and growth rate (mm/day); WK and Y are weeks and growing seasons respectively. H8Y is average 8-year height over all test sites while H8YD4, H8YD5 and H8YD6 are averages for each site respectively (see Table 1 for locations of test sites).

<sup>c)</sup>  $\sigma^2_T$  total variance =  $\sigma^2_P + \sigma^2_{PS} + \sigma^2_{PB(S)} + \sigma^2_{F(P)} + \sigma^2_{F(P)S} + \sigma^2_E + \sigma^2_W$ .

<sup>d)</sup> A negative variance estimate was treated as 0 when calculating total variance ( $\sigma^2_T$ ).

<sup>e)</sup>  $h^2_I$  could not be calculated because budburst and budset were scored on a plot basis so that individual phenotypic variance could not be estimated.

dividing this by the sum of degrees of freedom from all provenances.

To examine the extent of association between 8-year height and seedling traits, genetic correlations were estimated using eq. (4), where  $\text{Cov}_{F(P)XY}$  is the family-within-provenance covariance between 8-year height and each seedling trait, and  $\sigma^2_{F(P)X}$  and  $\sigma^2_{F(P)Y}$  are the family-within-provenance variances for 8-year height and each seedling trait, respectively. Phenotypic correlations were also calculated in the same way except for the replacement of family-within-provenance variances with variances of family means. Given that identities of seedling blocks measured for seedling traits (4 to 10 out of 24 blocks) were inadvertently lost in field tests, the estimated family-within-provenance covariance between seedling traits and average 8-year height across the 3 field sites also included plot covariance and within-plot covariance. Thus, the estimated correlations will be biased upward or downward depending on signs of plot and within-plot covariances. However, estimated correlations between seedling traits and 8-year height in at least one field site are free from this bias because blocks measured for seedling traits were planted in only 1 or 2 field sites, not in all 3 sites.

To examine if families could be accurately selected for 8-year height at seedling stage, we estimated the relative efficiency of early selection (RE), which is the ratio of the genetic gain for 8-year height when selection is based on seedling traits to the genetic gain for 8-year height when selection is based on the 8-year height (FALCONER, 1981). Assuming the same selection intensity, RE can be calculated as:

$$RE = r_A \frac{h_Y}{h_X} \quad (5)$$

where  $r_A$  is the genetic correlation between heights at different ages, and  $h_Y$  and  $h_X$  are the square roots of family heritabilities for seedling and 8-year heights respectively.

### Results

Mean seedling heights were, respectively, 10.5 cm, 17.1 cm, 25.5 cm and 38.6 cm for 17-week-old, 1-, 2- and 3-year-old seedlings, while the average 1-year branch number was 14.1 (Table 3). During the third growing season, the seedlings burst buds on May 26 (i. e., 146.1 days after January 1) and set buds on August 18, resulting in a mean shoot growth duration of 85 days (Table 3). The

3-year height increment averaged 13.1 cm with a mean growth rate of 1.7 mm per day. The total 8-year height was 96.6 cm at Mirabel (D4), 102.7 cm at Portage-du-Fort (D5) and 112.6 cm at Robidoux (D6), with an average of 103.8 cm for the 3 sites.

All traits showed significant provenance differences ( $\sigma^2_P$ ) except for 3-year budburst and shoot growth rate, and 8-year height at site D5 (Table 3). Significant differences were also found among families within provenances ( $\sigma^2_{F(P)}$ ) in all traits with the exception of 3-year budburst. In the combined analysis over the three test sites, 8-year height did not differ significantly in provenance-by-site interaction variance ( $\sigma^2_{PS}$ ) or in family-within-provenance-by-site interaction variance ( $\sigma^2_{F(P)S}$ ) (Table 3).

Of the total variance ( $\sigma^2_T$ ), provenances on average accounted for 3.1%, families within provenances 2.9%, provenance-by-block interaction 1.0%, variation among plots 33.2% and variation within plots the remaining 59.8% (Table 3, excluding BB3Y, DU3Y, RATE3Y and H8Y). For within-plot variance ( $\sigma^2_w$ ), additive genetic variance within half-sib families ( $3/4\sigma^2_A$ ) on average accounted for 13.5% (range 9.5% to 23.9%) with the remaining percentage accounted for by environmental variation, and dominance and epistatic gene interaction. The distribution of the total variance differed between 3-year growth and phenology traits (Table 3). Provenance variance was about the same as family-within-provenance variance for 3-year height, but it was on average 1.5 times greater than family-within-provenance variance for 3-year budburst and growth duration. Provenance variance was smaller relative to family-within-provenance variance for 8-year height than for seedling heights (Table 3).

Estimated individual heritabilities were generally low for all traits (range 0.08 to 0.19) which were much smaller than estimated family heritabilities (Table 3). Also, as might be expected from nonsignificant family-within-provenance-by-site interaction variance, genetic correlations ( $r_A$ ) in 8-year height across the three field sites were high (mean 0.88, 0.71 between Mirabel (D4) and Portage-du-Fort (D5), 0.94 between Portage-du-Fort (D5) and Robidoux (D6) and 1.06 between Mirabel (D4) and Robidoux (D6)). These results indicate that ranking of families for 8-year height was similar across the 3 test sites.

In the greenhouse, 1-year height had a moderate and positive genetic correlation with 1-year branch number ( $r_A = 0.51 \pm 0.16$ ,  $r_p = 0.68 \pm 0.04$ ), but a lower  $r_A$  with 17-week height ( $0.38 \pm 0.16$ ,  $r_p = 0.54 \pm 0.05$ ). Third-year height was correlated strongly with 2-year height and 3-year height increment, but moderately with 3-year shoot

Table 4. — Genetic correlations (above the diagonal) and family phenotypic correlations between traits in 3-year seedlings (with standard errors in parentheses<sup>a</sup>).

	H2Y	H3Y	HI3Y	RATE3Y	BS3Y	DU3Y
H2Y		0.91(0.06)	0.63(0.25)	0.14(0.27)	0.61(0.32)	0.68(0.36)
H3Y	0.83(0.02)		0.89(0.09)	0.42(0.20)	0.57(0.24)	0.63(0.26)
HI3Y	0.12(0.07)	0.65(0.04)		0.74(0.14)	0.34(0.28)	0.36(0.30)
RATE3Y	0.12(0.06)	0.53(0.05)	0.78(0.03)		-0.39(0.29)	-0.38(0.31)
BS3Y	0.04(0.07)	0.25(0.06)	0.38(0.06)	-0.27(0.06)		1.00(0.002)
DU3Y	0.04(0.07)	0.25(0.06)	0.38(0.06)	-0.27(0.06)	1.00(0.001)	

<sup>a</sup>) See table 3 for definition of trait codes.

Table 5. — Genetic correlations ( $r_A$ ) and family phenotypic correlations ( $r_p$ ) correlations between seedling traits and 8-year height in white spruce<sup>a</sup>.

Seedling Traits	$r_A$				$r_p$			
	H8YD4	H8YD5	H8YD6	H8Y	H8YD4	H8YD5	H8YD6	H8Y
H17WK	0.68	0.72	0.61	0.68	0.27	0.19	0.19	0.29
H1Y	0.81	1.31	0.51	0.89	0.26	0.28	0.13	0.31
BN1Y	0.61	0.09	0.38	0.39	0.20	0.02	0.10	0.14
H2Y	1.18	0.89	0.97	1.11	0.36	0.18	0.23	0.37
H3Y	1.00	1.04	0.92	1.05	0.40	0.28	0.29	0.46
HI3Y	0.60	1.00	0.68	0.77	0.22	0.25	0.20	0.31
RATE3Y	0.51	0.83	0.55	0.64	0.15	0.16	0.13	0.21
BS3Y	0.06	0.27	0.33	0.17	0.02	0.07	0.10	0.07
DU3Y	0.05	0.27	0.35	0.17	0.02	0.07	0.10	0.07

<sup>a</sup>) See table 3 for definition of trait codes.

growth rate (Table 4). In 3-year-old seedlings, height increment was mainly associated with shoot growth rate and to a lesser extent with shoot growth duration and budset, and 3-year height had a moderate and positive genetic correlation with 3-year budset and growth duration (Table 4). The standard errors for some correlation coefficients, however, were large (Table 4).

Genetic correlations between seedling and overall 8-year heights increased with seedling age: from 0.68 at age 17 weeks to 1.11 at ages 2 and 3 years (Table 5). Overall 8-year height was moderately correlated with 3-year height increment and shoot growth rate (Table 5). On the other hand, 8-year height had weak and positive genetic correlations with 1-year branch number, 3-year budset and growth duration (Table 5). Genetic correlations between seedling traits and 8-year height at each of the 3 test sites followed the trend for those between seedling traits and overall 8-year height. Given that genetic correlations sometimes exceeded 1.00, genetic correlations between seedling traits and 8-year height appeared to be biased upward, but as mentioned earlier, genetic correlations between seedling traits and 8-year height could be free from this bias for at least one site, most likely site D6 (Table 5). Estimated family phenotypic correlations between seedling traits and 8-year height were much lower than the corresponding genetic correlations (Table 5).

### Discussion

#### 1. Distribution of genetic variation among and within provenances

In this study, provenances and families differed significantly in most growth and phenology traits, and on average accounted for almost the same amount of total variance (3.1% and 2.9% respectively). Provenance variance in 9-year and 15-year heights was 2 to 3 times the family variance for white spruce from the Lake States (NIENSTAEDT and RIEMENSCHNEIDER, 1985). On the other hand, studies on provenances from southeastern Ontario did not reveal significant provenance differences, but found large family differences in 10-year height (DHIR, 1976), bud phenology (POLLARD and YING, 1979a, b), allozyme frequencies (CHELIAK et al., 1988), and wood density (CORRIVEAU et al., 1992). This also applies to growth and morphological traits for provenances from Newfoundland (KHALIL, 1985a).

It appears that white spruce provenances are not well differentiated in relatively small geographic areas such as southeastern Ontario and Newfoundland. Thus, some researchers conclude that white spruce from southeastern Ontario form a single homogeneous population (POLLARD and YING, 1979b).

#### 2. Inheritance and genetic correlations among traits

As found in earlier studies, within-plot variance accounted for most of the total variance in height growth traits (YING and MORGENSTERN, 1979; YEH and RASMUSSEN, 1985; KISS and YEH, 1988; CAMPBELL et al., 1989). This study, however, found a higher proportion of plot variance than had generally been observed before. This apparently resulted from the environmental heterogeneity within the large blocks used in this study (395 plots per block) and from the consolidation of nursery blocks to form field blocks. Therefore, our estimates of individual tree heritabilities for total heights (0.08 to 0.19) are at the low end of those reported for white spruce and other spruce species (MOHN et al., 1976; YEH and RASMUSSEN, 1985; KISS and YEH, 1988; CAMPBELL et al., 1989; NELSON and MOHN, 1991). Some earlier heritability estimates, however, might have been upwardly biased because identities of families within provenances were not available and thus, provenance and family variances were confounded in estimating additive genetic variance for total height (MOHN et al., 1975, for white spruce from the Lake States; KISS and YEH, 1988, for interior spruce). NIENSTAEDT and RIEMENSCHNEIDER (1985) found that heritability estimates for total height were twice as large when provenance variance was included in calculating additive genetic variance as when provenance variance was excluded. Given that provenance variance was similar to family variance in this study, our heritability estimates for total height would have doubled if provenance variance had been included in estimating additive variance.

Relative performances of families in 8-year height appeared stable across the three different test environments, as indicated by nonsignificant family-within-provenance-by-site interaction variance and high genetic correlations among test sites. Earlier studies of white spruce also showed high stability for height growth across different test sites (NIENSTAEDT and RIEMENSCHNEIDER, 1985). Thus, selection of families with high stability and good

growth appears promising in white spruce breeding programs.

The moderate genetic correlation between 17-week and 1-year heights ( $r_A = 0.38$ ) suggests that early growth is not a good indicator of 1-year growth potential. This could be the result of a diminishing influence of maternal effects (e. g., seed weight) on height growth during the first year. In our study, seed weight was weakly correlated with 17-week height (correlation coefficient 0.19  $P$ -value  $< 0.05$ ), while seed weight was not correlated with 1-year height (correlation coefficient 0.04). It is interesting that 1-year branch number was positively and moderately correlated with 1-year height ( $r_A = 0.51$ ) and 8-year height ( $r_A$  range 0.09 to 0.61) (Table 5). If the same positive relationship existed in older trees, selection for greater growth would increase branch number, which might be undesirable for quality traits in selected populations.

In agreement with an earlier study on white spruce populations from southeastern Ontario (POLLARD and YING, 1979b), budburst did not differ significantly among provenances, but our observation of a lack of differences among families within provenances contrasted with earlier findings (WILKINSON, 1977; O'REILLY and PARKER, 1982; NIENSTAEDT, 1985; BLUM, 1988). The lack of observed differences among and within provenances in budburst in our study most likely results from environmental conditions at the nursery site. The nursery site is well protected from northerly winds, and thus, temperatures rise very quickly in the spring. All seedlings flushed within 17 days, and more importantly, seedlings in 95% of the plots had flushed within seven days. Thus, it would be of interest to reexamine genetic variation in budburst among and within provenances in field tests.

Budset differed significantly among provenances as found in an earlier study (NIENSTAEDT and TEICH, 1972). In addition, our study showed that budset differed significantly among families within provenances. Given that 3-year budset date had a positive genetic correlation with total 3-year height, selection for greater 3-year height is expected to lead to a correlated response of delayed budset. For example, if 20% of families were selected for greater height growth, progenies of these families would be expected to set buds two days later. This magnitude of delay in budset might increase risks from early fall frost in seedlings. However, the probability of fall frost damage must be small for trees older than 10 years because all trees set buds in mid-July as reported in a study of 14 white spruce clones (O'REILLY and PARKER, 1982).

### 3. Genetic gains and early testing for 8-year height

Although 8-year height was under weak genetic control, genetic progress could still be made from selection and breeding. To illustrate this, we used genetic parameters for overall 8-year height because families were shown to be stable across test environments. If 20% of families in an average white spruce population were selected and randomly mated in a seed orchard, expected genetic gain would be 8.01 cm (7.7%) in 8-year height. Extrapolation of this gain prediction to an older age should be made with caution because trees were only 8 years old and only 1.03 m in mean height in this study. Other studies have shown that genetic correlations between 22-year height and 8- or 10-year height in white spruce are high (NIENSTAEDT, 1969; YING and MORGENSTERN, 1979), so that

our predicted relative genetic gain (%) might be indicative of the magnitude of genetic gain at older ages.

High genetic correlations between 8-year and seedling heights suggested that 8-year height could be accurately predicted from measurements made in seedlings. Earlier white spruce studies also indicated that nursery growth is a good indicator of 10- to 15-year height (MOHN et al., 1975; YING, 1978; NIENSTAEDT, 1981; NIENSTAEDT and RIEMENSCHNEIDER, 1985). Second- and third-year heights were more strongly correlated with 8-year height than 17-week and 1-year heights, and 3-year height increment and growth rate. These results indicate that total 2- and 3-year heights are better predictors of 8-year height than either 3-year height increment or growth rate.

As discussed earlier, estimated genetic correlations of 8-year height with seedling heights were biased upward for combined analyses across the three test sites and possibly for sites D4 and D5. To be conservative in calculating relative efficiencies of early selection, we used genetic correlations between 8-year height at site D6 and seedling heights and family heritabilities for overall 8-year height (H8Y). Selection of families based on 1- and 2-year height would, respectively, result in REs of 57% and 67%. Selection of families at age 3 would lead to a correlated response of 86% in 8-year height as compared to direct selection on 8-year height alone. These results indicate that seedling height could be used as an early culling device so that poorly performing families could be culled before field planting. This would reduce the number of families and the effort in field testing, or increase the precision of field tests of the remaining families if the same field test size was used.

### Acknowledgements

We thank Forestry Canada, Quebec Region, for financial support and staff from the Genetics and Tree Improvement section. We would like to recognize the efforts of Dr. C. C. YING, who coordinated the regional white spruce genetic test and sent us seeds while working at the Petawawa National Forestry Institute. We acknowledge NSERC of Canada for a research fellowship to PENG LI, as well as MICHEL VILLENEUVE awarding from the Ministère des Forêts du Québec (MFO), and 2 anonymous reviewers for their comments on an earlier draft of this paper.

### Literature cited

- BEAULIEU, J. and CORRIVEAU, A.: Variabilité de la densité du bois et de la production des provenances d'épinette blanche, 20 ans après plantation. *Can. J. For. Res.* 15: 833-838 (1985). — BECKER, W. A.: Manual of quantitative genetics. 4th ed. Academic Enterprises, Pullman, Washington (1984). — BLUM, B. M.: Variation in the phenology of bud flushing in white and red spruce. *Can. J. For. Res.* 18: 315-319 (1988). — BURDON, R. D.: Genetic correlation as a concept for studying genotype-environment interaction in forest tree breeding. *Silvae Genet.* 26: 168-175 (1977). — CAMPBELL, R. K., PAWUK, W. A. and HARRIS, A. S.: Microgeographic genetic variation of Sitka spruce in southeastern Alaska. *Can. J. For. Res.* 19: 1004-1013 (1989). — CHELIAK, W. M., MURRAY, G. and PITEL, J. A.: Genetic effects of phenotypic selection in white spruce. *For. Ecol. Manage.* 24: 139-149 (1988). — Comité d'Amélioration Génétique des Arbres Forestiers du Québec.: Amélioration génétique des essences résineuses au Québec.: recherche et développement. Env. Canada, Serv. Can. For., Centre de rech. for. Laurentides, Gouv. du Qué., Min. Éner. Ress., Serv. Rech. 70 pp. (1983). — CORRIVEAU, A., BEAULIEU, J. and DAoust, G.: Heritability and genetic correlations of wood characters of Upper Ottawa Valley white spruce populations grown in Quebec. *For. Chron.* 67: 698-705 (1992). — CORRIVEAU, A., BEAULIEU, J. and MOTHE, F.: Wood density of natural white spruce populations in Quebec. *Can. J. For. Res.* 17: 675-682 (1987). — DHIR, N. K.: Stand, family and site effects in Upper Ottawa Valley white spruce. USDA For. Serv. Gen. Tech. Rep. NC-26. pp. 88-97 (1976). — FALCONER, D. S.: Introduction to quantitative genetics. Longman, London



- (1981). — FOWELLS, H. A.: Silvics of forest trees of the United States. USDA For. Serv., Agriculture Handbook 271 (1965). — FOWLER, D. P.: Strategies for the genetic improvement of important tree species in the Maritimes. Can. For. Serv. Maritimes, Inf. Rep. M-X-156 (1987). — FURNIER, G. R., STINE, M. and MOHN, C. A.: Geographic patterns of variation in allozymes and height growth in white spruce. Can. J. For. Res. 21: 707-712 (1991). — HOSIE, R. C.: Native trees of Canada. 8th ed. Fitzhenry and Whiteside Limited., Don Mills, Ontario, Canada. 380 pp. (1979). — KHALIL, M. A. K.: Heritability of juvenile characters of white spruce (*Picea glauca* MOENCH.) Voss. in central Newfoundland, Canada. Theor. Appl. Genet. 69: 247-251 (1985a). — KHALIL, M. A. K.: Genetic variation in eastern white spruce (*Picea glauca* MOENCH.) Voss. populations. Can. J. For. Res. 15: 444-452 (1985b). KHALIL, M. A. K.: Variation in seed quality and some juvenile characters of white spruce (*Picea glauca* MOENCH.) Voss. Silvae Genet. 35: 78-85 (1986). — KISS, G. and YEH, F. C.: Heritability estimates for height for young interior spruce in British Columbia. Can. J. For. Res. 18: 158-162 (1988). — LIBBY, W. J. and COCKERHAM, C. C.: Random non-contiguous plots in interlocking field layouts. Silvae Genet. 29: 183-190 (1980). — MERRILL, R. E. and MOHN, C. A.: Heritability and genetic correlations for stem diameter and branch characteristics in white spruce. Can. J. For. Res. 15: 494-497 (1985). — MOHN, C. A., RIEMENSCHNEIDER, D. E., CROMELL, W. and PETERSON, L. C.: A white spruce progeny test — seedling seed orchard: 12th year progress report. In: Proc. 12th Lake States For. Tree Improv. Conf., Aug. 18 to 22, 1975, Petawawa For. Exp. Stn., Chalk River, Ont. USDA For. Serv., Gen. Tech. Rep. NC-26. pp. 98-107 (1976). — NAMKOONG, G.: Introduction to quantitative genetics in forestry. USDA For. Serv. Tech. Bull. No. 1588 (1979). — NELSON, C. D. and MOHN, C. A.: Genetic variance of early height growth and expected gains from selection in a Minnesota population of black spruce. Can. J. For. Res. 21: 11-19 (1991). — NIENSTAEDT, H.: White spruce seed source variation and adaptation to 14 planting sites in northeastern United States and Canada. In: Proc. 11th Meeting Comm. on For. Tree Breed. in Canada, MacDonald Coll., St. Anne de Bellevue, Quebec. pp. 183-194 (1969). — NIENSTAEDT, H.: "Super" spruce seedlings continue superior growth for 18 years. USDA For. Serv. Res. Note NC-265 (1981). — NIENSTAEDT, H.: Inheritance and correlations of frost injury, growth, flowering, and cone characteristics in white spruce, *Picea glauca* (MOENCH.) Voss. Can. J. For. Res. 15: 498-504 (1985). — NIENSTAEDT, H. and KANG, H.: Establishing a *Picea glauca* (MOENCH.) Voss. base breeding population for the Lake States Region of the United States. Silvae Genet. 36: 21-30 (1987). — NIENSTAEDT, H. and RIEMENSCHNEIDER, D. E.: Changes in heritability estimates with age and site in white spruce, *Picea glauca* (MOENCH.) Voss. Silvae Genet. 34: 34-41 (1985). — NIENSTAEDT, H. and TEICH, A. H.: The genetics of white spruce. USDA For. Serv. Res. Pap. WO-15 (1972). — O'REILLY, C. and PARKER, W. H.: Vegetative phenology in a clonal seed orchard of *Picea glauca* and *Picea mariana* in northwestern Ontario. Can. J. For. Res. 12: 408-413 (1982). — POLLARD, D. F. W. and YING, C. C.: Variation in response to declining photoperiod among families and stands of white spruce in southeastern Ontario. Can. J. For. Res. 9: 443-448 (1979a). — POLLARD, D. F. W. and YING, C. C.: Variance in flushing among and within stands of seedling white spruce. Can. J. For. Res. 9: 517-521 (1979b). — SEARLE, S. R.: Linear models. John Wiley and Sons, New York (1971). — THIBAUT, M. and HOTTE, D.: Les régions écologiques du Québec méridional: Deuxième approximation. Min. Éner. Ress. (1985). — WILKINSON, R. C.: Inheritance of budbreak and correlation with early height growth in white spruce (*Picea glauca*) from New England. USDA For. Serv. Res. Pap. NE-39 (1977). — YATES, F.: The analysis of replicated experiments when the field results are incomplete. Empire J. Exper. Agr. 1: 129-142 (1933). — YEH, F. C. and RASMUSSEN, S.: Heritability of height growth in 10-year-old Sitka spruce. Can. J. Genet. Cytol. 27: 729-734 (1985). — YING, C. C.: Height growth of interprovenance crosses in white spruce (*Picea glauca* MOENCH.) Voss. Silvae Genet. 27: 226-229 (1978). — YING, C. C. and MORGENSTERN, E. K.: Correlations of height growth and heritabilities at different ages in white spruce. Silvae Genet. 28: 181-185 (1979).

---

Herausgeberin: Bundesforschungsanstalt für Forst- und Holzwirtschaft: Schriftleitung: Institut für Forstgenetik und Forstpflanzenzüchtung, Siekerlandstraße 2, 2070 Großhansdorf 2-Schmalenbeck (Holstein). — Verlag: J. D. Sauerländer's Verlag, 6000 Frankfurt a. M., Finckenhofstraße 21. — Anzeigenverwaltung: J. D. Sauerländer's Verlag, Frankfurt am Main. — Satz und Druck: H. Robert, 6310 Grünberg, Hess. 1. — Printed in Germany.