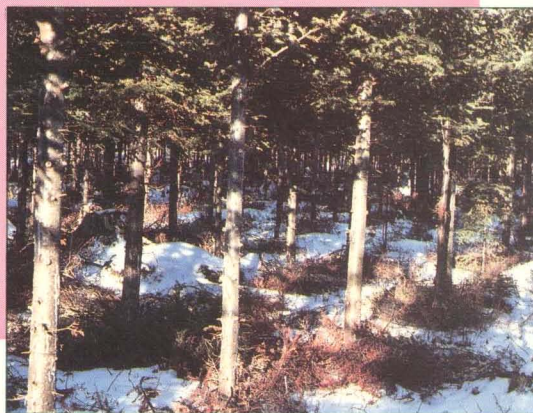
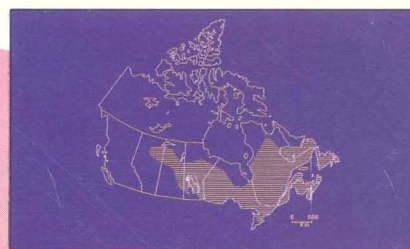
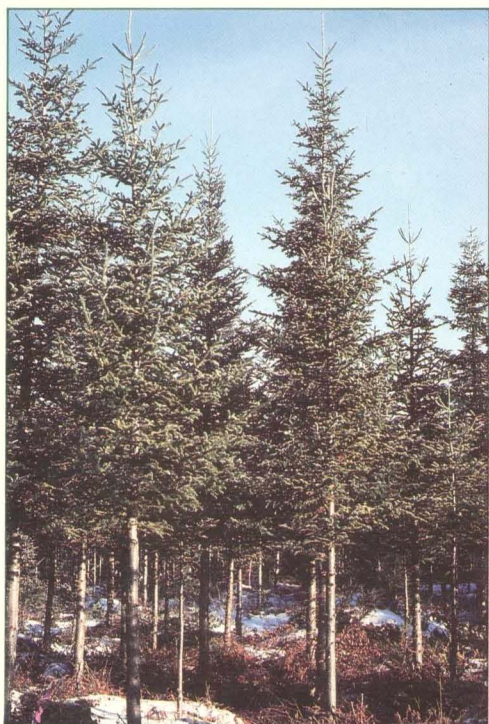




Genetic parameters and expected gains in balsam fir

Jean Beaulieu, Armand Corriveau and Gaétan Daoust

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ABSTRACT

A progeny test including twenty-three balsam fir open-pollinated progenies from the province of Quebec was established in 1972 on the Valcartier Army Base, near Quebec City. Fifteen families originated from a stand in the Laurentian Park. Results from measurements taken 5, 10, and 17 years after planting show that survival is good and that there is no genetic difference as far as adaptation to site is concerned. Growth and form characters are under moderate genetic control. Selection indices were calculated. Genetic gains over 20% in growth and bole straightness are expected from a combined selection made fifteen years after planting.

RÉSUMÉ

Un test génétique comprenant vingt-trois familles de sapins baumiers issues de pollinisation libre et originaires du Québec a été établi en 1972 à la base militaire de Valcartier près de la ville de Québec. Quinze familles provenant du parc des Laurentides ont été utilisées pour le calcul des paramètres génétiques. Trois relevés d'observations phénotypiques ont été effectués, soit 5 ans, 10 ans et 17 ans après la plantation. On constate que le taux de survie du sapin baumier après plantation est bon quelque soit l'appartenance familiale. L'héritabilité des caractères de croissance et de forme du sapin baumier est plutôt faible sur le plan individuel, alors qu'elle est modérée sur le plan familial. Des indices de sélection ont été calculés. Des gains génétiques supérieurs à 20 % en croissance et qualité de tige sont escomptés d'une sélection combinée effectuée 15 ans après la plantation.

INTRODUCTION

Balsam fir (*Abies balsamea* (L.) Mill.) colonizes the northern temperate regions. It is one of the four species of the genus *Abies* found in Canada, but is the only one present in all provinces (Hosie 1972). It is most prolific in the Acadian and the Great Lakes-St. Lawrence forest regions (Rowe 1972), but it is also abundant in the southern part of the boreal forest region in Ontario and Quebec. The great number of sites colonized by balsam fir reflect its great plasticity. It forms pure stands or is associated with other species such as red spruce (*Picea rubens* Sarg.), white spruce (*Picea glauca* (Moench) Voss), Eastern hemlock (*Tsuga canadensis* (L.) Carr.), yellow birch (*Betula alleghaniensis* Britton), black spruce (*Picea mariana* (Mill.) B.S.P.), tamarack (*Larix laricina* (Du Roi) K. Koch), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and beech (*Fagus grandifolia* Ehrh.) (Grandtner 1971). Balsam fir can reach a height of 15 to 20 m and a diameter of 30 to 60 cm. The standing gross merchantable volume of this species in Canada is about 1 400 million cubic metres, of which more than 60 percent is found in Quebec (FORSTATS 1988). It has few natural enemies among insect pests, but is very sensitive to their attacks (Martineau 1985). Volume reserves of fir were affected to a considerable extent by the last outbreak of the spruce budworm (*Choristoneura fumiferana* (Clem.)). In Quebec alone, a decrease of 10 percent in gross merchantable volume - nearly 95 million cubic metres - was observed between 1981 and 1986 (Bonnor 1982, FORSTATS 1988).

Balsam fir is a commercial species. Its wood is used both by the pulp industry and for construction. However, because it is highly vulnerable to the spruce budworm, because its wood is of poorer quality than that of the spruces, and because its natural regeneration is abundant, it has been excluded from reforestation programs. Until now, it has been planted only by the Christmas tree producers. Also, relatively little attention has been paid to the genetics and breeding of balsam fir.

The genetic variability in balsam fir growth characters due to geographical origin has been studied in eastern Canada and in the north-central and northeastern United States. In Newfoundland, some provenances have been studied to verify the hypothesis of poorer growth of balsam fir from the Avalon Peninsula (Howard and Wilton 1962, van der Pas 1966, Richardson 1971, Khalil 1977, Hall 1986). These provenances did not differentiate until some thirty years after seeding. Tests conducted in the United States disclosed major differences in morphological and phenological characters of provenances (Lester et al. 1976, Lowe et al. 1977; Marty et al. 1983, Lester et al. 1977; Deshayes et al. 1983). Other studies on

provenances from the Appalachians (from North Carolina to New York State) have also dealt with the properties of the wood of this species (Thor and Barnett 1974, Dery and Dehayes 1981). According to these authors, the monoterpenes and wood extractives of balsam fir show clinal variation on a north-south gradient. There are also differences in the relative density of the wood and in tracheid length. Dehayes et al. (1983) indicate that the height growth and crown characters of balsam fir vary considerably, and that substantial gains would result from a breeding program. Another study, using biochemical markers, permitted analysis of the genetic structure of the populations and the preferred mating system of the species (Neale and Adams 1981, 1985). The results suggest that there are no differences in allelic frequency between New Hampshire populations covering an altitudinal gradient. Also, it seems that natural selection favors heterozygotic individuals in these environments, but that self-fertilization is nevertheless substantial there. Research has also been undertaken on half-sibs originating from open pollination. In Quebec, Robert (1979) reports significant differences in flushing and late-frost sensitivity between families. It appears difficult to relate spruce budworm defoliation rates to the origin of the material. Estimates of the heritability of phenological and growth characters - estimates showing large standard deviations - have also been computed.

The present study deals with the genetic variation of balsam fir growth and form characters. Heritability estimates (individual and family levels) are presented in conjunction with phenotypic and genetic correlations. Finally, the genetic gains expected from index-based and monocharacter selection are reported.

MATERIAL AND METHODS

Balsam fir cones were harvested in 1967 from 23 trees in eight stands in Quebec (Table 1). The seeds were extracted and sown in covered seedbeds in the winter of 1968. In 1970, the two-year-old seedlings were transplanted in the nursery at the Valcartier Experimental Forest Station (latitude 46°52' N, longitude 71°32' W, elevation 152 m), in forest region L.4a (Rowe 1972), 40 km north of Quebec City. After two years, in the spring of 1972, they were removed and outplanted in a cutover about 10 km from the nursery. The site, which is favorable to balsam fir development, has surface deposits of alluvial sand, an annual precipitation of 1170 mm and a frost-free period ranging from 120 to 140 days.

The balsam fir families were planted according to an experimental design made up of four complete randomized blocks. Each square plot contained 25 trees spaced 2.5 m apart. Phenotypic surveys were done in 1976, 1981, and 1988, i.e., 5, 10, and 17 years after planting. Fifteen of the twenty-three families were selected from stands located in the Laurentian

Table 1. Sites of origin of balsam fir families under genetic testing at Valcartier, Quebec

Family	Location			
	Forest region	Latitude (° ')	Longitude (° ')	Elevation (m)
Drummondville				
216	L.3	45 55	72 29	60
217	L.3	45 55	72 29	60
219	L.3	45 55	72 29	60
220	L.3	45 55	72 29	60
Laurentian Park				
231	B.1a	47 14	71 10	780
233	B.1a	47 14	71 10	780
234	B.1a	47 14	71 10	780
235	B.1a	47 14	71 10	780
237	B.1a	47 19	71 08	655
238	B.1a	47 19	71 08	655
239	B.1a	47 19	71 08	655
240	B.1a	47 19	71 08	655
242	B.1a	47 22	71 10	880
244	B.1a	47 22	71 10	880
246	B.1a	47 28	70 59	945
247	B.1a	47 28	70 59	945
248	B.1a	47 28	70 59	945
249	B.1a	47 28	70 59	945
250	B.1a	47 28	70 59	945
Mont Gosford				
271	L.5	45 17	70 52	975
272	L.5	45 17	70 52	975
Lac Normand				
282	B.7	47 07	73 28	480
Lac Edouard				
285	L.4a	46 44	72 61	305

Park, Quebec. They were close enough together (maximum distance of 17 km) to be regarded as forming one population, as it is considered that for most commercial forest species in the temperate zone a slight differentiation between subpopulations generally is established only at greater distances (Wright 1976). Estimates of the genetic parameters were obtained for this population. The eight residual families were used to compare the yield of the progeny from Laurentian Park with that of progenies originating in other regions of Quebec.

The height of the sample trees was measured to the nearest 10 cm and diameter at breast height to the nearest millimetre. Bole straightness was rated on an ordinal scale from 1 to 5. The straightest trees were given a rating of 5, with the most crooked trees at the other extreme. In addition, crown quality was assessed subjectively on an ascending scale of values from 1 to 5. Crowns were judged on the basis of the mean diameter of branches, the openness of their angle of attachment to the trunk, and also according to their length and conformation.

In assessing the genetic parameters, the assumption was made that the effects of genetic recombination followed an additive linear model. The estimates of the variance components obtained from various random model variance analyses of the phenotypic data can be interpreted in terms of genetic and environmental variances, and help in choosing appropriate breeding strategies (Park 1987).

Thus, we assumed that the variance due to differences between families was equal to one-quarter of the additive genetic variance:

$$\sigma_f^2 = \frac{1}{4} \sigma_A^2 \quad [1]$$

where

σ_f^2 = variance component due to differences between families;

σ_A^2 = additive genetic variance.

Before evaluating these components, analysis of variance was conducted on survival rates in order to verify their effect on the observed differences in growth and form characters between families. The following model was used for the analysis of variance of survival rates:

$$Y_{ij} = \mu + F_i + R_j + e_{ij} \quad [2]$$

where

$$Y_{ij} = \sin^{-1} (P_{ij})^{1/2} \text{ (Steel and Torrie 1980);}$$

P_{ij} = proportion of surviving trees in i th family and j th block;

μ = overall mean;

F_i = effect of i th family;

R_j = effect of j th block;

e_{ij} = residual error between plots.

We obtained the analyses of variance of the growth and form characters by using the following model:

$$Y_{ijk} = \mu + F_i + R_j + FR_{ij} + e_{ijk} \quad [3]$$

where

Y_{ijk} = character observed in the k th tree of the i th family planted in the j th block;

FR_{ij} = effect of the interaction between the i th family and the j th block;

e_{ijk} = residual within-plot error.

These analyses were used to assess the variance components, to calculate their standard deviation, and to obtain estimates of additive genetic variance and heritability.

The standard deviations of the variance components were calculated using the formula:

$$S.D. (\sigma_g^2) = \frac{2}{k^2} \sum_g \frac{MS_g^2}{f_g + 2} \quad (\text{Becker 1985}) \quad [4]$$

where

k = coefficient of the variance component to be evaluated;

MS_g^2 = the g th mean square used for assessing the variance component;

f_g = the degrees of freedom of the g th mean square.

Standard deviation is a measure of the precision of the estimates of the variance components (Namkoong 1979).

The estimates of heritability at the individual level were obtained by the following ratio of variances:

$$h_i^2 = \frac{4\sigma_f^2}{\sigma_f^2 + \sigma_{fr}^2 + \sigma_e^2} \quad [5]$$

where

h^2_i = heritability at the individual level;
 σ^2_f = variance component due to family;
 σ^2_{fr} = variance component due to family-block interaction;
 σ^2_e = variance component due to within-plot residual error.

Estimates of heritability at the family level were obtained using the following ratio of variances:

$$h^2_f = \frac{\sigma^2_f}{\sigma^2_f + \frac{\sigma^2_{fr}}{n} + \frac{\sigma^2_e}{nr}} \quad [6]$$

where

h^2_f = heritability at family level;
 n = number of trees per plot (harmonic mean);
 r = number of blocks.

Heritability estimates from open-pollinated trees, based on the additive genetic model described above, made it necessary that certain basic assumptions be met, failing which the estimates would only be approximate (Jackson 1983), or else overestimated (Namkoong 1966). The experimentation conditions are such, however, that any major bias is unlikely. Their validity with regard to breeding of forest trees was discussed by Stonecypher (1966). The assumptions are as follows:

1. Diploid and Mendelian inheritance.
2. The population under study is in a state of panmixia and linkage equilibrium.
3. The individuals making up the population are related and not inbred.
4. The progeny represent a random sample of a non-inbred population.
5. There is no environmental correlation between progeny.
6. There is no epistasis.
7. There is no maternal effect (Comstock and Robinson 1948).

The statistical significance of the estimates of genetic parameters such as heritability and genetic correlation coefficients must be considered seriously. If it cannot be demonstrated that they are statistically significant, their practical and scientific significance cannot be taken into account (Klein et al. 1973). Also, standard deviations of the heritability estimates were obtained using the following formulas (Falconer 1981):

$$S.D.(h^2_i) = 4 \left[\frac{2 (1-t)^2 [1 + (n-1)t]^2}{n (n-1) (f-1)} \right]^{1/2} \quad [7]$$

where

t = intra class correlation coefficient;

$$\text{and } S.D.(h^2_f) = \frac{(1-t) (1 + nrt)}{(nr (f-1)/2)^{1/2}} \quad [8]$$

The heritability estimates at the individual and family levels were used for calculating the expected genetic gains from selection at a given intensity. The expected genetic gain was estimated by the formula:

$$\Delta G = i \sigma h^2 \quad [9]$$

where

ΔG = expected genetic gain;

i = standardized selection intensity;

σ = standard deviation of the phenotypic value of the character;

h^2 = heritability of the character.

Coefficients of phenotypic and genetic correlation between the growth and form characters observed were calculated. The phenotypic correlation coefficient expresses the degree of association between two directly observed characters, i.e., between two phenotypic values, whereas the genetic correlation coefficient expresses the extent to which these two distinct characters are genetically interrelated (Falconer 1981). The following formulas were used to calculate the phenotypic and genetic correlation coefficients (Becker 1985):

Phenotypic correlation

$$r_{jk} = \frac{\text{Cov}(y_j, y_k)}{(\sigma^2 y_j \sigma^2 y_k)^{1/2}} \quad [10]$$

where

r_{jk} = phenotypic correlation coefficient;

$\text{Cov}(y_j, y_k)$ = covariance of characters j and k ;

$\sigma^2 y_j$ = variance of character j ;

$\sigma^2 y_k$ = variance of character k .

Genetic correlation

$$r_{Gjk} = \frac{\text{cov}_{Ajk}}{(\sigma_{Aj}^2 \sigma_{Ak}^2)^{1/2}} \quad [11]$$

where

r_{Gjk} = genetic correlation coefficient;

cov_{Ajk} = covariance of breeding values of characters j and k;

σ_{Aj}^2 = variance of breeding values of character j;

σ_{Ak}^2 = variance of breeding values of character k.

The expected genetic gains from selection can be calculated for a set of characters taken simultaneously. The concept of expression of the genotypic value of a plant in the form of a linear equation of the genotypic values of several of its characters was introduced by Smith (1936) (Baker 1986). As it was not possible to observe the genotypic value of the various characters directly, he proposed the use of a linear equation of the observable phenotypic values, i.e., a selection index.

The selection indices were calculated according to the formula:

$$b = P^{-1} G a \quad [12]$$

where

b = vector of the index coefficients;

P^{-1} = inverse of the matrix of phenotypic variances and covariances;

G = matrix of the genotypic variances and covariances;

a = vector of the relative economic weights of each character.

The choice of characters to be included in the selection indices was made after transformation of the matrices of variances and covariances (Hayes and Hill 1980). This ensured that the estimates of variances and covariances were precise and that the selection indices arising from them were reliable (Baker 1986).

The expected gains at the level of each character resulting from index-based selection were compared with those expected from a selection made independently for each character.

Table 2. Descriptive characteristics of balsam fir progeny test at Valcartier, Quebec at 5, 10, and 17 years from planting

Family	Survival (17 yrs) %	Family index (17 yrs) *	Height			Diameter		Crown		Bole	
			(5 yrs)	(10 yrs) (m)	(17 yrs)	(10 yrs)	(17 yrs)	(10 yrs)	(17 yrs)	(10 yrs)	(17 yrs)
Drummondville											
216	87		1.27	3.19	6.33	3.39	7.25	2.87	3.01	3.19	3.29
217	88		1.14	2.84	5.67	2.86	6.50	2.86	2.73	3.05	2.92
219	76		1.08	2.64	5.34	2.75	6.49	2.68	2.76	2.83	2.71
220	82		1.03	2.63	5.70	2.79	6.60	2.73	2.99	2.90	3.11
Laurentian Park											
231	69	20.25	1.16	2.61	5.20	2.58	5.56	2.86	2.72	2.88	3.17
233	70	21.41	1.00	2.81	5.94	2.99	7.10	2.79	2.87	2.97	3.03
234	92	21.07	1.14	2.79	5.76	3.09	7.07	2.82	2.82	3.04	2.85
235	86	19.85	1.03	2.54	5.17	2.69	6.42	2.79	2.85	2.87	3.05
237	87	20.13	1.05	2.54	5.44	2.77	6.62	2.67	2.76	2.98	2.95
238	87	22.26	1.29	3.13	6.11	3.39	6.89	2.82	2.82	3.14	3.20
239	92	24.81	1.25	3.19	6.76	3.73	7.88	3.13	3.22	3.33	3.60
240	90	20.57	0.88	2.33	5.04	2.09	6.16	3.12	3.08	3.25	3.39
242	89	19.66	1.11	2.61	5.40	2.74	6.61	2.69	2.57	2.87	2.82
244	82	21.55	1.05	2.69	5.74	2.73	6.79	2.87	2.72	3.07	3.22
246	70	20.11	0.97	2.40	5.35	2.50	6.30	2.93	2.81	3.13	3.01
247	93	21.46	1.15	2.77	5.64	3.17	6.88	2.88	2.87	3.29	3.26
248	86	20.10	1.16	2.76	5.50	2.78	6.14	3.03	2.66	3.21	2.90
249	90	16.92	0.94	2.16	4.56	2.13	5.55	2.56	2.38	2.60	2.49
250	91	20.22	1.10	2.67	5.25	2.82	6.01	2.91	2.86	3.09	3.12
Average	85		1.03	2.67	5.52	2.81	5.53	2.86	2.80	3.05	2.87
Mont Gosford											
271	94		0.95	2.29	4.66	2.40	6.05	2.84	2.87	2.92	3.20
272	88		1.18	3.10	6.07	3.80	7.87	3.16	2.99	3.48	3.38
Lac Normand											
282	86		1.08	2.62	5.51	2.61	6.47	2.83	2.74	3.03	3.10
Lac Édouard											
285	96		1.24	3.04	6.30	3.46	7.79	2.85	2.84	2.90	3.09
Overall	86		1.10	2.71	5.58	2.88	6.65	2.86	2.82	3.04	2.95
Range:											
Minimum	69		0.88	2.16	4.56	2.09	5.55	2.56	2.38	2.60	2.49
Maximum	96		1.29	3.19	6.76	3.80	7.88	3.16	3.22	3.48	3.60
SD			0.37	0.95	1.73	1.60	2.55	0.86	0.78	0.89	1.00

* Selection index (height, diameter, and bole rating).

RESULTS AND DISCUSSION

Table 2 shows the average values of the characters measured in balsam fir, and the averages for balsam fir families originating in the Laurentian Park and the overall means for the 23 families tested. An examination of the range of each character shows strong variation, which reflects good possibilities for selection at both the individual and family levels. The average value of the characters of the Laurentian Park families is roughly equivalent to the overall mean. The fifteen families used for the subsequent analyses therefore constitute a representative sample of the material tested.

Relations among characters at 10 and 17 years from planting

The relations among four phenotypic characters measured on two occasions in 15 families of balsam fir originating in the Laurentian Park, Quebec, are presented in Table 3. In half of the cases, the values of the phenotypic correlation coefficients increased with time. The relations between form and growth characters thus become significant (except for the relation between diameter and bole rating). A strong height-diameter relation was predictable. The relations between form characters were also very strong, suggesting that, in general, trees with straighter trunks also exhibit the crown qualities sought by the breeder. Finally, all the relations are positive, suggesting that breeding based on a particular character might, if the genetic correlation were also positive, lead to a genetic gain in other characters.

Partition of phenotypic variation

Survival

In the first stage, an analysis of variance was applied to balsam fir survival rates to verify whether significant interfamily differences existed. Different degrees of adaptation by families might have a marked effect on variations of phenotypic characters. The results presented in Table 4 show that there is no difference in survival rate between families, any more than there is between blocks. We can presume, therefore, that the phenotypic characters observed in balsam fir are little influenced by the respective mortality rates of the families. In addition, all the families studied seemed to be particularly well adapted to the conditions in the experimental environment.

Growth and form

The results of variance analyses on balsam fir growth and form characters are presented in Table 5. We have also presented the portion of the variation that is accounted for by each

Table 3. Correlations of phenotypic characters of balsam fir families 10 and 17 years from planting

	10 years				17 years			
	Height	Diameter	Crown	Bole	Height	Diameter	Crown	Bole
Height	1.00				1.00			
Diameter	0.95	1.00			0.90	1.00		
Crown	0.35	0.23	1.00		0.61	0.60	1.00	
Bole	0.49	0.51	0.88	1.00	0.60	0.48	0.87	1.00

n = 15

Prob > 0.05 $r < 0.514$

Table 4. Analysis of variance of survival* of balsam fir 5, 10, and 17 years after planting

	Source of variation	Degrees of freedom	Sum of squares	F	Pr > F
5 years	Families	14	0.89263	1.63	0.1106
	Blocks	3	0.06006	0.51	0.6776
	Error	42	1.64549		
10 years	Families	14	0.91518	1.44	0.1777
	Blocks	3	0.13022	0.95	0.4252
	Error	42	1.91281		
17 years	Families	14	0.79471	1.06	0.4184
	Blocks	3	0.09641	0.60	0.6186
	Error	42	2.24693		

*: $\text{Survival} = \sin^{-1} (P_{ij})^{1/2}$

P_{ij} = survival rate of *i*th family in *j*th block (Steel and Torrie 1980)

of the sources of variation, along with the preciseness of their estimate. Seventeen years after planting, more than 6 percent of the variation in the height of the trees can be attributed to differences between families. The importance of this source of variation changes, however, over time. A significant portion of the variation (about 10 percent) is due to family-block interaction, i.e., between-plot variation which results from major changes in the ranks of families from one block to the next. We also note that more than 80 percent of the total variation in height is due to differences between trees in the same plot and to experimental error. This high percentage reflects the sensitivity of the species to microenvironmental variations.

The portion of total variation in diameter at breast height that can be attributed to differences between families is smaller than in the case of height, whereas the portion which can be attributed to differences between trees within a plot is larger. This character is more sensitive to environmental factors (spacing and competition) than height, and is therefore under weaker genetic control.

Table 5. Analyses and partition of variance of growth and form characters of balsam fir at 5, 10, and 17 years after planting

Character	Source of variation	Degrees of freedom	Variance component (V)	Standard deviation of the variance component (σ_V)	Pr>F	Portion of the variance component
Height						
5 years	Families	14	0.009650	0.004586	0.0429	6.9
	Blocks	3	0.003302	0.002403	0.0042	2.4
	Fam x Block	42	0.007242	0.002720	0.0001	5.2
	Error	1286	0.120017	0.004729		85.5
10 years	Families	14	0.042567	0.028313	0.0389	4.6
	Blocks	3	0.035983	0.028682	0.0064	3.9
	Fam x Block	41	0.103554	0.029646	0.0001	11.3
	Error	1224	0.735721	0.029715		80.2
17 years	Families	14	0.184069	0.103263	0.0169	6.2
	Blocks	3	0.056140	0.052940	0.0455	1.9
	Fam x Block	42	0.282453	0.086701	0.0001	9.4
	Error	1214	2.469399	0.100147		82.5
Diameter						
17 years	Families	14	0.181858	0.137928	0.0731	3.0
	Blocks	3	0.016352	0.043893	0.2870	0.3
	Fam x Block	42	0.495023	0.163103	0.0001	8.2
	Error	1196	5.362680	0.219113		88.5
Crown						
10 years	Families	14	0.004007	0.009870	0.1746	0.6
	Blocks	3	0.087013	0.058565	0.0001	12.3
	Fam x Block	41	0.044770	0.017898	0.0001	6.3
	Error	895	0.572942	0.027054		80.8
17 years	Families	14	0.007612	0.016310	0.3250	1.1
	Blocks	3	0.067887	0.048670	0.0007	10.1
	Fam x Block	42	0.110649	0.028821	0.0001	16.5
	Error	1206	0.486093	0.019779		72.3
Bole						
10 years	Families	14	0.013566	0.013273	0.0572	1.7
	Blocks	3	0.071572	0.048927	0.0001	9.1
	Fam x Block	41	0.041947	0.018549	0.0001	5.3
	Error	895	0.658109	0.031075		83.9
17 years	Families	14	0.051484	0.027554	0.0085	4.9
	Blocks	3	0.107471	0.072196	0.0001	10.2
	Fam x Block	42	0.057805	0.021365	0.0001	5.5
	Error	1206	0.836617	0.034041		79.4

The portion of total variation in form characters explained by the family component is much smaller than in the case of growth characters. This is somewhat surprising, for it is generally recognized that qualitative characteristics are less influenced by environment than growth characters (Zobel and Talbert 1984). On the other hand, the portion of variation due to differences between blocks is greater (on the order of 10 percent). This might be due, at least in part, to the fact that two different teams carrying out the survey relating to tree form and because the work was divided in blocks. It could be that the two teams did not rate the trees on the same subjective scale. The distribution of scores is, however, almost normal. Otherwise, the variance of these characters might have been greatly reduced (Dean et al. 1986). Finally, as in the case of growth characters, about 85 percent of total variation was due to differences between trees within a plot and to experimental error. We would also point out that where form characters are concerned, the portion of total variation explained by the family tends to increase with time. When the trees become larger, the actual differences between individuals become progressively easier to visualize and the families become more sharply differentiated from one another.

We note in Table 5 that the estimates of family variance components in growth characters are relatively precise, whereas those of form characters are much less so, especially 10 years after planting. The source of variation estimated with the least precision is the block effect. In addition, there is significant family-block interaction within each character. This is not, however, of too much concern, since we assume that the corrections necessary for eliminating the block effect will be made at the time of selection (Cotterill 1987).

The importance of the variation observed at the individual and family levels makes it possible to envision mass selection following selection of the best families for breeding balsam fir.

Evaluation of the genetic parameters

Additive genetic variance and heritability

Growth characteristics: The estimates of the additive genetic variances and heritabilities at the individual and family levels are presented in Table 6. The heritability values for height at 5, 10, and 17 years from planting are low (0.19 to 0.28) at the individual level and moderate at the family level (0.55 to 0.75). These values vary over time and reflect a change in the degree of genetic control (Namkoong et al. 1972). Genetic control declines between the age of 5 and 10 years from planting then rises subsequently. The values found here are of the same order of magnitude as those reported for *Pinus caribaea* var. *hondurensis* (Dean et al.

Table 6. Additive genetic variances and heritabilities of growth and form characteristics of balsam fir 5, 10, and 17 years from planting

Parameter	Height			Diameter		Bole		Crown	
	5 yrs	10 yrs	17 yrs	10 yrs	17 yrs	10 yrs	17 yrs	10 yrs	17 yrs
V_A	0.0386	0.1703	0.7363	0.4574	0.7274	0.0543	0.2059	0.0160	0.0304
$\sigma(V_A)$	0.0183	0.1133	0.4131	0.2947	0.5517	0.0531	0.1102	0.0395	0.0652
h^2_i	0.28	0.19	0.25	0.19	0.12	0.08	0.22	0.03	0.05
$\sigma(h^2_i)$	0.12	0.09	0.11	0.08	0.06	0.05	0.10	0.04	0.04
h^2_f	0.75	0.55	0.64	0.57	0.49	0.39	0.67	0.16	0.18
$\sigma(h^2_f)$	0.27	0.20	0.24	0.19	0.14	0.10	0.21	0.07	0.08

V_A = additive genetic variance

h^2_i = heritability at individual level

h^2_f = heritability at family level

σ_i = standard deviation

1986), *Pinus banksiana* Lamb. (Magnussen and Yeatman 1986), *Picea glauca* (Moench) Voss (Ying and Morgenstern 1979), and *Picea mariana* (Mill.) B.S.P. (Morgenstern 1974). Although the standard deviations of heritabilities also vary in absolute value, they account for about the same fractions of the heritability values. The decrease in heritability at the age of 10 years might be explained partly by the spruce budworm epidemic in Quebec. We believe, however, that the effect of competition from local vegetation was greater. Thus the growth of trees independently of their family membership may have been affected in various ways. The damage and the slowdowns in growth were not, however, large enough to cause major deformation to the trees or to prevent vigorous renewed growth after the clearing done at age 10.

Estimates of heritability at individual levels (0.12 and 0.19) and family levels (0.49 and 0.57) of growth in diameter at breast height were smaller than those for height. This agrees with the majority of published results (Matziris and Zobel 1973, for *Pinus taeda* L.; Cotterill and Zed 1980, for *Pinus radiata* D. Don; and Ying and Morgenstern 1979, for *Picea glauca* (Moench) Voss). Heritability values decreased as the trees matured. Diameter growth is a character recognized as being under weak genetic control (Stonecypher et al. 1973), and the influence of the environment therefore becomes more and more evident as the trees age and grow and as the effects of competition become apparent.

Form characteristics: Ten years after planting, heritability values for bole straightness were relatively low. They were much higher, however, 17 years after planting. The heritability values of crown quality, meanwhile, were low at both ages (0.03 and 0.05). Genetic control of bole straightness has generally been considered greater than that of growth characters (Shelbourne 1969, Zobel and Talbert 1984). The values encountered in balsam fir are

nevertheless similar to those presented by Stonecypher et al. (1973) for *Pinus taeda* L. It therefore appears that the form characters of balsam fir are not under strong genetic control as is the case with other species. We would point out, however, that in their study, as in this one, subjective evaluation ratings were assigned to the form characters. Such an evaluation may not be sufficiently precise to bring out the true nature of genetic control of the form of balsam fir.

Values of genetic correlations

Strong positive genetic correlations exist between diameter at breast height and total height 10 and 17 years after planting (Table 7). They are therefore under the influence of a single set of genes. These values also suggest that selection based on one of these characters would lead to an indirect gain in the other. The calculated standard deviations demonstrate great precision in the estimate of the coefficients. There are also strong genetic correlations between height and crown quality at both ages. Interpretation of the other genetic correlation coefficients measured 10 years after planting, however, is practically impossible because of the imprecision of the linear method of estimation; the estimated value of several coefficients exceeds 1. On the other hand, it was possible to make a relatively precise estimate of these coefficients 17 years after planting, probably because it was easier to judge the value of the individuals for form characters, and possibly because of the strengthening of genetic control over them. Therefore, height becomes linked, to a moderate degree, to bole straightness. This relation is less precise, however, than that of the relation between height, on the one hand, and the remaining characters, on the other. Diameter, meanwhile, is moderately linked to crown quality and bole straightness. Here again, the genetic correlation is very imprecise. Finally, the relation between crown and bole quality is difficult to interpret because of a genetic correlation coefficient whose estimated value exceeds 1. The lack of precision of the subjective evaluation, as mentioned above, might explain this aberration.

Table 7. Genetic correlations of growth and form characters of balsam fir 10 and 17 years from planting –

	Height	Diameter	Crown	Bole	Height	Diameter	Crown	Bole
	10 yrs Genetic correlations				17 yrs Genetic correlations			
Height	–	0.973	0.776	1.340	–	0.946	0.913	0.682
Diameter	0.018	–	1.162	0.144	0.035	–	0.713	0.585
Crown	0.274	–	–	2.107	0.065	0.210	–	1.458
Bole	–	0.435	–	–	0.183	0.217	–	–
	Standard deviation				Standard deviation			

Genetic gains expected from selection

The above genetic parameters were used for calculating selection indices. They will make it possible to select families and individuals for breeding the first improved generation. Expected genetic gains were also calculated. All the indices include height, diameter, and bole-straightness characters. The crown-quality rating was excluded from the calculations since transformation of the variance-covariance matrix (Hayes and Hill 1981) had demonstrated that the estimates were becoming too imprecise. Its inclusion in the model would have led to the development of erroneous indices. The economic weights used for construction of the indices are based on the theory of weights of equal emphasis (Cotterill and Jackson 1985). Thus, a change in the standard deviation of one character is considered just as important from an economic standpoint as a change in the standard deviation of another character (Dean et al. 1986). The economic weight of each character was established as equal to the inverse of its phenotypic standard deviation. Although it is not at all certain that all characters are of equal economic importance, in the absence of more precise information, use of such economic weights as a point of departure appears less risky than use of a given set of economic weights.

In order to illustrate the genetic gains that can be achieved with balsam fir from the first generation of selections, we shall use two scenarios currently encountered in a program for improving a species or for producing seed of superior genetic quality. In this way, we can show the importance of the selection strategy which must optimize genetic gains while preserving the gene pool necessary for meeting the long-term objectives of a breeding program.

As a working hypothesis, we shall assume the following: over fifteen years ago, we set up a test of 300 half-sibs using a design that included 20 complete randomized blocks with five individuals per linear plot. The test involved 30 000 trees with 1-m spacing within the plots and 2-m spacing between plots. It covered an area of 6 ha. Surveys of growth and form were carried out 5, 10, and 17 years after planting. The estimated genetic parameters of the Laurentian Park population constitute valid estimates of the parameters of this population, and the environmental conditions under which this progeny was tested are very much the same as those under which the present genetic parameters were assessed.

Objective 1 - Production of improved seed

The quickest and least costly approach for achieving this objective would be to convert the progeny test plots into a seed orchard. The compromise to be made lies between obtaining the maximum genetic gain and maintaining an adequate number of trees to permit production of a reasonable amount of high-quality seed.

Let us set the desired mean distance between the trees of the future orchard at about 4.5 m. With such spacing, the orchard will contain 3 000 trees. We must, therefore, select 3 000 trees, i.e., one tree out of 10. The first option would be to make a mass selection, i.e., a phenotypic selection not taking into account the bonds of family membership among the trees. Depending on whether the selection is made on the basis of each character, independently from the others, or on the basis of the indices, the expected genetic gains from each of the characters are as follows:

	Monocharacter selection $P = 0.1$	Index selection $P = 0.1$
Height	13.6%	14.7%
Diameter	7.9%	11.0%
Straightness	13.0%	13.1%

We note that 17 years from planting, monocharacter selection and index selection result in approximately the same genetic gains, except for the expected gain in diameter-growth, for which index selection results in a higher figure. If we wish to improve both growth and bole quality (straightness), however, index selection facilitates our work since the indices encompass all characters. Mass selection, unfortunately, does not take into account the family relationship of trees. Many of the selected trees, therefore, might belong to the same half-sib (maximum 100) and some of them might be full siblings since they result from open pollination. Crosses between related individuals often lead to progeny with reduced vigor, and the gains realized through selection might prove much smaller than expected.

To overcome this difficulty, the selection of breeding stock must be done on a family and within-family basis. With our same objective of keeping 3 000 breeding trees in the seed orchard, we first select the best 150 families on the basis of their average performance, and then select from each plot the individual with the best characteristics, for a total of 20 trees selected per half-sib. Thus, we reduce the chances of loss of vigor in the progeny by ensuring that each family is represented by an equal number of individuals distant from one another and showing greater panmixia. This approach enables us to increase by some 2 percent the gains expected from selection.

	Gain expected from family selection (%) $P_f = 0.5$	Gain expected from individual selection (%) $P_i = 0.2$	Total gain %
a) Monocharacter			
Height	5.0	11.0	16.0
Diameter	3.6	6.4	10.0
Straightness	5.2	10.4	15.6

b) Index

Height	4.8	11.8	16.6
Diameter	3.9	8.9	12.8
Straightness	4.6	10.6	15.2

We would point out that when the genetic gains expected from monocharacter selection and index selection are roughly equal for each character, the former only apply when the selection is made independently for a single character at a time, whereas the gains expected from index selection apply to all three characters simultaneously.

Objective 2 - Breeding

At this stage in the program, it becomes a matter of setting up a gene pool enabling us to develop a breeding strategy that will lead to development of an improved synthetic variety. This pool must be broad enough to permit successive creation of several generations of selections without coming up against inbreeding problems. Yet it must be small enough to be handled physically, i.e., so that a realistic cross-breeding program can be undertaken and carried out with reasonable means. We shall therefore, establish this gene pool at 150 individuals, necessarily taking into account the family links between individuals. The goal is to optimize the genetic gain from this first selection while retaining the most variable gene pool possible. We would, therefore, first select the best 50 families, i.e., 1 out of 6, and then the three best individuals from each family, i.e., 3 out of 100. The genetic gains expected from such selection would then be:

	Gain expected from family selection (%) $P_f = 0.167$	Gain expected from individual selection (%) $P_i = 0.03$	Total genetic gain %
a) Monocharacter			
Height	9.4	17.7	27.1
Diameter	6.8	10.2	17.0
Straightness	9.7	16.8	26.5
b) Index			
Height	9.0	19.0	28.0
Diameter	7.3	14.3	21.6
Straightness	8.6	17.1	25.7

The genetic gains expected from this strategy are very acceptable, but we only get 50 groups of unrelated individuals, which reduces the genetic diversity of our breeding base, and increases the chances of inbreeding in future generations. It is to our advantage - while

keeping the same number of breeders – to select a larger number of families, i.e. to reduce our intensity of selection at the family level and to increase it at the within-family level.

We shall therefore select only the best individual of each of the top 150 families. The genetic gains expected from this strategy will be as follows:

	Expected gain from family selection (%) $P_f = 0.5$	Expected gain from individual selection (%) $P_i = 0.01$	Total genetic gain %
a) Monocharacter			
Height	5.0	20.7	25.7
Diameter	3.6	12.0	15.6
Straightness	5.2	19.7	24.9
b) Index			
Height	4.8	22.3	27.1
Diameter	3.9	16.7	20.6
Straightness	4.6	20.0	24.6

We have only sacrificed about 1.5% of the expected gain from monocharacter selection and about 1 percent of expected gain from index selection. This is perhaps not negligible, but will be largely offset by attaining a larger number of non-inbred crosses and a possibility of more intensive selection in future generations, and therefore of greater genetic gains over the long term.

Genetic gain vs age at selection

We have used the expected genetic gains ($P_f = 0.5$; $P_i = 0.01$) in height growth at 5, 10, and 17 years from planting to judge how worthwhile early selection was. We find that the expected gains increase gradually with increased age and size of trees (Table 8). Expressed as a function of the mean at a given age, however, it is at 5 years from planting that they are greatest (33.4 percent), suggesting that early selection is worthwhile. We know that the degree of confidence associated with the expected gain at 5 years is smaller than that associated with the expected genetic gain at 17 years from planting, or with the estimated genetic gain at harvest. We have therefore attempted to assess the relative loss of effectiveness of early selection of height growth with respect to that done at a later date, for example at 5 years as opposed to 17 years from planting. To do so, we followed the second scenario presented above: we chose 50 percent of families, and then the top individual out of 100 in each family of 100 members chosen:

Mean of group selected at 5 years	= 2.05 m
Mean of same group at 17 years	= 8.10 m
Mean of group selected at 17 years	= 9.35 m
Expected genetic gain from same group	= 1.42 m
Mean of base population at 17 years	= 5.52 m
Selection differential	= 1.25 m

Expected loss of gain:

$$\begin{aligned}\Delta G &= h^2_5 (8.10 - 5.52) - h^2_{17} (9.35 - 5.52) \\ &= 0.28 (2.58) - 0.25 (3.83) \\ \Delta G &= -.36 \text{ m}\end{aligned}$$

The relative loss of genetic gain in height growth expected from selection at 5 years as compared to selection at 17 years is therefore equal to:

$$\frac{-0.36 \text{ m}}{1.42 \text{ m}} = -25.4\%$$

This, then, is the price to be paid for accelerating the species breeding program by some 10 years. In balsam fir, however, just as in many other forest species, unless it is possible to induce the selected genotypes to flower, there is no urgency in making the selection since the first controlled-crosses cannot be carried out until several years later. Like many other species, the balsam fir does not produce its first strobili before the age of 15 or 20 (Roe 1948; Schopmeyer 1974). To be truly effective, genetic improvement strategies, as with the production of improved seed, absolutely must take into account the biological characteristics of the species as well as physical and budgetary constraints.

Table 8. Expected genetic gains in height in balsam fir as the result of combined selection at 5, 10, and 17 years from planting

	Mean (m)	Gain from family selection P = 0.5 (% \bar{X})	Gain from within family selection P = 0.01 (% \bar{X})	Total genetic gain (% \bar{X})	m
5 yrs	1.03	6.6	26.8	33.4	0.34
10 yrs	2.67	4.6	18.0	22.6	0.60
17 yrs	5.52	5.0	20.7	25.7	1.42

CONCLUSION

This study demonstrated that balsam fir responds well to planting. It has very satisfactory survival and growth rates. It exhibits wide variation in growth and form. These characters are positively correlated at both the genetic and phenotypic levels. Improvement of one of these characters would thus lead to genetic gain in the others.

Partition of the phenotypic variation of growth and form of balsam fir showed that the family membership of trees constitutes a significant source of variation. The major part of the phenotypic variation of the balsam fir is due, however, to differences between individuals of the same family. Selection should therefore be combined, i.e., practiced at the family and within-family levels.

The genetic parameters, additive genetic variances, and heritabilities, reveal that the growth characters of balsam fir are under moderate genetic control, while bole straightness is more strongly affected by environmental conditions.

Selection indices calculated at the family and individual levels showed that, in addition to facilitating multicharacter selection, their use increases the expected genetic gains. Two scenarios, one dealing with production of commercial seed of improved genetic quality and the other with the genetic improvement of the species itself, were used to illustrate the genetic gains to be achieved with balsam fir in the first generation of selections. Thus, genetic gains on the order of 10 to 15 percent - depending on the character under consideration - are expected from conversion of a medium-size progeny test into a seed orchard some 15 years after planting. Similarly, combined selection from indices with a final intensity of 0.005 to constitute a first gene pool for breeding, would result in a first generation of crosses that would be 20 to 25 percent superior to the parent population.

It is generally considered that early selection is necessary to obtain genetic gains earlier, but not without cost: selection of balsam fir five years after planting would have yielded only 75 percent of the genetic gains achieved through selection at 17 years from planting.

The use of balsam fir in reforestation programs would probably increase the volume productivity of Canadian forests. Such productivity could be increased even more through breeding. This cannot, unfortunately, be done without ensuring effective protection of plantations from the spruce budworm, which will cause mortality and reduced growth.

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