

ration or second generation orchards should be similar. Though calculated by different methods the results from each are compatible.

The case for regional breeding over that for one statewide breeding zone appears therefore to hinge on the importance of obtaining an extra gain in volume of up to 2% above that of 12% to 15% expected from a statewide breeding zone — if site variation within regions is small, but little extra gain at all if it is appreciable. The tree form traits need not be considered at all, since the interactions were of much smaller magnitude than those for growth.

However, costs of obtaining the extra gain for regional breeding could be much greater because separate programs of selection, controlled crossing, testing and seed orchards would be needed for each region. On balance, I believe that any extra gain is unlikely to be cost effective. There would also be the problem of actually defining the number and extent of the breeding zones.

Conclusions

Highly significant family \times site interactions for diameter growth of *P. radiata* were recorded in two series of progeny trials. The interactions for stem straightness and branch thickness were found to be relatively small.

The effect of the variation in relative growth rate of families from site to site on potential gains was calculated for the case of 1.5 generation orchards established for statewide or regional breeding. However, due to the variation in sites that occurs within a region and the magnitude of interactions between families and replications within sites, an apparent advantage of regional breeding over statewide breeding may only partly be realised. When the effect of family \times site interactions within regional breeding zones was considered for the case

of gain from second generation orchards, it appeared that regional breeding would only be advantageous over statewide breeding when there was a general uniformity of sites in a region.

The sites for growing *P. radiata* within potential regional breeding zones in Victoria are not regarded as uniform. Therefore in view of the much higher costs and effort associated with regional breeding, it is concluded that a change from a statewide to regional breeding zones would not be cost effective.

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Predictions of Genetic Gain from Various Selection Methods in Open Pollinated *Pinus banksiana* Progeny Trials

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Abstract

Variance components and heritabilities of tree height and stem diameter on three sites at age 6 and 14 are presented for 100 open pollinated *Pinus banksiana* (LAMB.) progenies. The progenies were sampled from two stands within each of five distinct areas (populations) in the Ottawa Valley, Ontario. Combining information from several sources into an index promised to double the expected genetic gain from selections based on single trait values. Family selection followed by within-family selection was less effective than index selection but superior to simple mass selection. Mass selection did not lead to a rapid loss of variation or inbreeding. The lack of significant $G \times E$ interactions and the absence of important stand and area effects in the Ottawa Valley will facilitate the breeding programs in this commercially important

species. Results at age 14 generally confirmed results obtained at age six.

Key words: *Pinus banksiana*, selection index, genetic gain, heritability, variance components, selection methods, genotype by environment interactions.

Introduction

Jack pine (*Pinus banksiana*, LAMB) has emerged during the last two decades as a major commercial pulp and lumber species in the Lake States and in Canada's boreal forests (OMNR, 1986; RIEMENSCHNEIDER, 1982; SMYTH and RAMSAY, 1984). Further, easy sexual propagation, stand establishment, and management has made it an important reforestation species as well (BELLA and FRANCESCHI, 1974; BENZIE, 1977; MARTELL and FULLERTON, 1988; RALSTON, 1953). Consequently, efforts are now well underway to genetically improve growth and yield of jack pine (DOJACK, 1988; KLEIN, 1986; OMNR, 1987; YEATMAN, 1974). Reliable esti-

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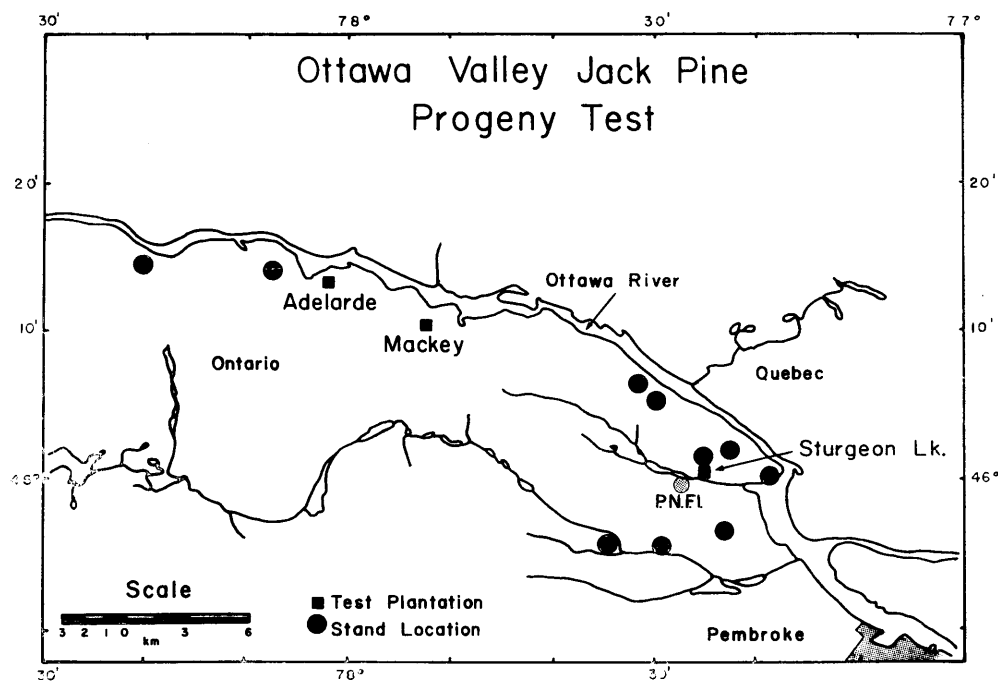


Figure 1. — Parental origin and test locations in the Ottawa Valley, Ontario.

mates of the amount of additive genetic variance and heritabilities of important traits are paramount to these programs, but few have been published (KLEIN, 1982; POLK, 1972; RIEMENSCHNEIDER, 1982; MAGNUSSEN and YEATMAN, 1986; YEATMAN, 1974, 1975). With considerable phenotypic variance in most observed traits, this species is amenable to genetic improvement even for traits with low heritability (RUDOLPH and YEATMAN, 1982; MAGNUSSEN and YEATMAN, 1987 a and b).

In this study we report on additive genetic variance and heritabilities of height and stem diameter in 14 year-old open pollinated jack pine progenies collected from 10 stands, from each of five areas (populations) located in the Upper Ottawa Valley (Figure 1). We also show how a combination of information into selection indices can augment genetic gain (BURDON, 1979, 1982). Consequences of our findings for applied breeding programmes in jack pine are discussed.

Materials and Methods

Traits and progenies

Tree height at ages 6 and 14 years from sowing, and stem diameter (1.3 m above ground level) at age 14 were analyzed in open pollinated offspring from 100 parent trees. Seed collection occurred in 1957 from five areas along the Ottawa River (Figure 1). The five areas were stocked with extensive mature jack pine from natural regeneration of fire origin. Each area was arbitrarily divided in two stands (= sections) and 10 trees were selected in each stand among the dominant and codominant trees in the canopy. Selected trees were straight stemmed and without obvious defects, growing at least 35 m apart, and at least 15 m from any roadway (YEATMAN, 1975). Within these constraints selections were random. Assuming that offspring from a single parent tree constitute half-sibs we then have the following hierarchical set-up: 5 areas \times 2 stands (within areas) \times 10 half-sib

families. Seed was sown in the Institute's nursery in the spring of 1968 and seedlings were lifted in the spring of 1970 and 1971 for outplanting.

Test locations

Three test locations, Sturgeon Lake, Adelarde, and Mackey (cf. Figure 1) were chosen for progeny evaluation. They represent typical areas for jack pine reforestation in the upper Ottawa Valley and adjoining regions. The Sturgeon Lake site consisted of windblown aeolian material on top of alluvial sand. The aspect was rolling with deep (2 m to 4 m) gullies and variable moisture and sand compaction regimes. Ground cover before planting was dominated by sweet fern (*Carex* spp.), bracken fern (*Oryzopsis* spp.), and grasses (*Panicum* spp.), all characterized by a mat-forming dense root system. Planting was done in May 1970 with 2-0 stock after scarification of the sod. Trees that died in the first year (23%) were filled in the spring of 1971 with 2-1 replacements held over in the nursery.

The Adelarde site was on a post glacial river bed made up of heavy podzolized fine alluvial sands. Roughly half of the area was treed with aspen, birch, and jack pine whereas the rest had a cover of *Kalmia angustifolia*, *Comptonia peregrina*, and *Vaccinium* spp. Planting was done in scalped patches (three replications) or ploughed furrows (three replications) in the spring of 1971 with 2-1 stock.

The Mackey site was an abandoned pasture. The soil was a mixture of alluvial sands and some gravel, covered by a thin A-horizon (< 3 cm). According to ground water tables, the area was divided into a moist area and a dry area. Trees were planted in ploughed furrows in the spring of 1970 with 2-0 stock. Replacement of dead and dying trees were completed in the spring of 1971.

Field design

A randomized split-plot design with six replications was used on each site. Progenies from a single stand (i.e.

10 half-sib families) were grown together in major plots containing randomly located five-tree row plots for each family in the stand (sub-plots). Trees were planted at a 1.3 m × 1.3 m spacing. layout of replications reflected a desire to make the replicate blocks as uniform as possible with regard to topography and moisture status.

Analysis of variance and variance components

Analysis of variance and calculations of variance components were conducted on the data from each test

separately and combined over sites. All analyses of variance and estimation of variance components were done on a sub-plot mean basis. No more than two sub-plots were "missing"²⁾ on any test location. The appropriate models for analysis were as follows:

Single test site:

$$[1] Y_{jklm} = \mu + R_j + A_k + S(A)_{kl} + RA_{jk} + RS(A)_{jkl} + F(AS)_{klm} + \bar{P}_{jklm}.$$

where

Y_{jklm} = a sub-plot mean in the j th replicate of family m in stand l within area k ,
 μ = the overall mean,
 R_j = the j th replicate effect, ($j = 1..6$), $E(R_j) = 0$,
 A_k = the k th area effect ($k = 1..5$), $E(A_k) = 0$,
 $S(A)_{kl}$ = the l th stand within area effect ($l = 1,2$, $E(S(A)_{kl}) = 0$),
 RA_{jk} = interaction effect of the j th rep-

²⁾ All plots had at least one tree, but two plots were planted with "fillers".

lication and the k th seed collection area,
 $RS(A)_{jkl}$ = interaction effect of the j th replication and the k th stand in the l th area,
 $F(AS)_{klm}$ = the m th family effect in stand l within area k ($m = 1..10$), $E(F(AS)_{klm}) = 0$,
 \bar{P}_{jklm} = the sub-plot term resulting from the random error associated with the sub-plot means.

Combined over sites:

$$[2] Y_{ijklm} = \mu + L_i + R(L)_{ij} + A_k + S(A)_{kl} + LA_{ik} + LS(A)_{ikl} + R(L)A_{ijk} + R(L)S(A)_{ijk} + F(AS)_{klm} + LF(AS)_{iklm} + \bar{P}_{ijklm}.$$

where

Y_{ijklm} = a sub-plot mean in the j th replicate at the i th site of family m in stand l within area k
 L_i = the i th test location effect ($i = 1..3$, $E(L_i) = 0$),
 $R(L)_{ij}$ = the j th replicate effect at the i th test location,
 LA_{ik} = the interaction effect of the i th test location and the k th area,
 $LS(A)_{ikl}$ = the interaction effect of the i th test location and the l th stand within area k ,
 $R(L)A_{ijk}$ = the interaction effect of the j th replicate at the i th site and the k th area,
 $R(L)S(A)_{ijk}$ = the interaction effect of the j th replicate at the i th site and the l th stand within the k th area,
 $LF(AS)_{iklm}$ = the interaction effect of the i th test location and the m th family in the l th stand within the k th area,
 $\mu, A_k, S(A)_{kl}, F(AS)_{klm}$ = as defined for single site analyses,
 \bar{P}_{ijklm} = the sub-plot term resulting from the random error associated with the sub-plot means.

$\sigma_i^2 > 0$ where i denotes a model effect. The hypothesis $\sigma_i^2 = 0$ was rejected whenever the probability of the observed F-ratio under the null hypothesis fell below 5%. Direct F-tests could not always be established for all sources of variation in the hierarchical model. Instead, an appropriate linear combination (Q) of mean-squares were used as the error term (SATTERTHWAITE, 1946). The degrees of freedom for Q were derived as outlined by Satterthwaite. Variance components were derived from the expected mean-squares (EMS) by equating expectations to the computed mean-squares. EMS for model [1] and [2] are provided in Table 1. Variance (V) of estimated variance components (σ_i^2) were estimated as follows (for example, BECKER, 1984)

$$[3] V(\sigma_i^2) \approx \frac{2}{k^2} \sum_i \frac{MS_i^2}{f_i + 2}$$

where k = coefficient of variance component being estimated (cf. Table 1), MS_i = the i th mean square used to estimate the variance component, and f_i = degrees of freedom of the i th mean square.

Heritability, genetic gain, and correlations

The variance component for open-pollinated families was assumed to estimate one-quarter of the additive genetic variance (for example, BECKER, 1984). Given the low level of inbreeding in natural jack pine stands (CHELIAK *et al.*, 1985; SNYDER *et al.*, 1985) and abundance of potential mates in each stand this assumption appears justified. Family mean (h_f^2), individual (h_i^2), and within family (h_w^2) heritabilities were calculated for individual sites as follows:

All effects except the overall mean were assumed random. The minor imbalance arising from the missing plots was ignored, and the analyses proceeded as for balanced data. The significance of a model effect was tested with a F-test under the hypothesis: $\sigma_i^2 = 0$ versus

Table 1. — Expected mean squares in the analysis of variance of plot means n_H = harmonic mean of number of trees per subplot (max = 5).

Source of variation	df	Expectations of mean squares ¹
<u>Combined over sites</u>		
Test location, L	L-1	$\sigma^2/n_H + \sigma_p^2 + 6q_{LF}(AS) + 10^2 \sigma_{R(L)S(A)}^2 + 20^2 \sigma_{R(L)A}^2 + 59q_{LS(A)}^2 + 118q_{LA}^2 + 99\sigma_{R(L)}^2 + 591q_L^2$
Replicates in test loc. R(L)	L(R-1)	$\sigma^2/n_H + \sigma_p^2 + 10^2 \sigma_{R(L)S(A)}^2 + 20^2 \sigma_{R(L)A}^2 + 99\sigma_{R(L)}^2$
Areas, A	A-1	$\sigma^2/n_H + \sigma_p^2 + 6q_{LF}(AS) + 10^2 \sigma_{R(L)S(A)}^2 + 20^2 \sigma_{R(L)A}^2 + 59q_{LS(A)}^2 + 118q_{LA}^2 + 177\sigma_{S(A)}^2 + 355q_A^2$
Stands in areas, S(A)	A(S-1)	$\sigma^2/n_H + \sigma_p^2 + 6q_{LF}(AS) + 18\sigma_{R(L)S(A)}^2 + 10^2 \sigma_{R(L)S(A)}^2 + 59q_{LS(A)}^2 + 177\sigma_{S(A)}^2$
Test location x area, LA	(L-1)(A-1)	$\sigma^2/n_H + \sigma_p^2 + 6q_{LF}(AS) + 10^2 \sigma_{R(L)S(A)}^2 + 20^2 \sigma_{R(L)A}^2 + 59q_{LS(A)}^2 + 118q_{LA}^2$
Test location x stand in area, LS(A)	A(L-1)(S-1)	$\sigma^2/n_H + \sigma_p^2 + 6q_{LF}(AS) + 10^2 \sigma_{R(L)S(A)}^2 + 59q_{LS(A)}^2$
Replicates x areas, R(L)A	L(R-1)(A-1)	$\sigma^2/n_H + \sigma_p^2 + 10^2 \sigma_{R(L)S(A)}^2 + 20^2 \sigma_{R(L)A}^2$
Replicates x stand in areas, R(L)S(A)	LA(R-1)(S-1)	$\sigma^2/n_H + \sigma_p^2 + 10^2 \sigma_{R(L)S(A)}^2$
Families in stand within areas, F(AS)	AS(F-1)	$\sigma^2/n_H + \sigma_p^2 + 6q_{LF}(AS) + 18\sigma_{R(L)S(A)}^2$
Test location x family, LF(AS)	AS(L-1)(F-1)	$\sigma^2/n_H + \sigma_p^2 + 6q_{LF}(AS)$
Sub-plot error, P	LR(L)AS(A)F(AS)-1- sum of above	$\sigma^2/n_H + \sigma_p^2$
<u>Single site analysis</u>		
Replicates, R	R-1	$\sigma^2/n_H + \sigma_p^2 + 10^2 \sigma_{RS(A)}^2 + 20^2 \sigma_{RA}^2 + 99\sigma_R^2$
Areas, A	A-1	$\sigma^2/n_H + \sigma_p^2 + 6q_{R(AS)}^2 + 10^2 \sigma_{RS(A)}^2 + 59\sigma_{S(A)}^2 + 119q_A^2$
Stands in areas, S(A)	A(S-1)	$\sigma^2/n_H + \sigma_p^2 + 6q_{R(AS)}^2 + 10^2 \sigma_{RS(A)}^2 + 59\sigma_{S(A)}^2$
Replicate x areas, RA	(R-1)(A-1)	$\sigma^2/n_H + \sigma_p^2 + 10^2 \sigma_{RS(A)}^2 + 20^2 \sigma_{RA}^2$
Replicate x stands in areas, RS(A)	A(R-1)(S-1)	$\sigma^2/n_H + \sigma_p^2 + 10^2 \sigma_{RS(A)}^2$
Families in stands within areas, F(AS)	AS(F-1)	$\sigma^2/n_H + \sigma_p^2 + 6q_{R(AS)}^2$
Sub-plot error, P	RAS(A)F(AS)-1- sum of above	$\sigma^2/n_H + \sigma_p^2$
<u>Analysis of individual data</u>		
Within sub-plots (pooled across all plots)		σ^2

¹) All coefficients (k) have been rounded to nearest integer.

$$[4] \quad h_F^2 = \frac{\sigma_{F(AS)}^2}{\sigma_{F(AS)}^2 + \sigma_A^2 + \sigma_{S(A)}^2 + \sigma_{FS(A)}^2/R + \sigma_p^2/R + \sigma_W^2/Rn_H}$$

$$[5] \quad h_I^2 = \frac{4\sigma_{F(AS)}^2}{\sigma_{F(AS)}^2 + \sigma_A^2 + \sigma_{S(A)}^2 + \sigma_p^2 + \sigma^2}$$

$$[6] \quad h_W^2 = h_I^2 \cdot (1-0.25)/(1-t)$$

where t is the intraclass correlation of the trait observations (FALCONER, 1981, p. 213).

Combined over sites the heritabilities were computed as follows:

$$[7] h_f^2 = \frac{\sigma_F^2(AS)}{\sigma_F^2(AS) + \sigma_L^2/L + \sigma_A^2/L + \sigma_S^2(A)/L + \sigma_{LA}^2/L + \sigma_{R(L)A}^2/LR + \sigma_{R(L)S(A)}^2/LR + \sigma_{LF(AS)}^2/L + \sigma_p^2/RL + \sigma^2/RLn_H}$$

$$[8] h_I^2 = \frac{4\sigma_F^2(AS)}{\sigma_F^2(AS) + \sigma_L^2 + \sigma_A^2 + \sigma_{SA}^2 + \sigma_{LA}^2 + \sigma_{R(L)A}^2 + \sigma_{R(L)S(A)}^2 + \sigma_{LF(SA)}^2 + \sigma_p^2 + \sigma^2}$$

The heritability estimates in equations [4] to [8] are conservative inasmuch the contributions of areas and stands to the numerator have been ignored (cf. LAND *et al.*, 1986; HARVEY and TOWNSEND, 1985). All negative variance estimates were equated to zero in the above equations. Note that replicate effects are omitted in the heritability expressions. This implies that selections will be confined to data adjusted for the effects of replicates (COTTERILL, 1987). The intraclass correlation t arises from two sources, from phenotypic correlation (p_p) among trees in the same plot and from genetic resemblance (p_g). The former was calculated as

$$[9] \rho_p = \frac{MSP - MSW}{((n_H - 1)MSW + MSP \cdot n_H)}$$

(SNEDECOR and COCHRAN, 1971) where MSP = plot mean square, MSW = within plot mean square, n_H = harmonic mean of trees per plot.

$$[10] \rho_g = \frac{1}{2} h_I^2$$

(FALCONER, 1981, p. 140).

Under the assumption that genetic resemblance is the only contribution to t when a pair of trees grow in different plots we computed t as a weighted average of the two sources

$$[11] t = \frac{1}{R} \cdot \rho_p + \frac{(R-1)}{R} \rho_g$$

Standard errors of heritabilities (h^2) were computed as the standard error of the numerator of h^2 divided by the denominator of h^2 . This procedure provides a conservative error estimate (HALLAUER and MIRANDA, 1981). To complete the standard error of within-family heritabilities, the errors of p_p and p_g were derived through the 'delta'-technique (for example, BULMER, 1985) and formulae for the covariance and variance of mean squares (for example, BECKER, 1984).

Genetic gains (expressed in per cent of the trait mean value) for direct or indirect selection methods were computed, in the case of family and individual selection, according to standard formulae (HALLAUER and MIRANDA, 1981; NAMKOONG *et al.*, 1966). Genetic gain arising from a two-stage family (F) and within-family (w) selection was computed as

$$[12] G_x \% = (2 \cdot h_f^2 \cdot i_f \cdot \sigma_{pf} + h_w^2 \cdot i_w \cdot \sigma_{pw}) \cdot 100 / \bar{x}$$

where σ_{pf} and σ_{pw} represent the phenotypic standard deviations, and i_f and i_w denote the family and within-family selection intensities, respectively. Here, i_f and i_w were subject to the overall constraint imposed by the total number of selected trees (trees selected = no. of families

× no. of trees per family). Selection intensities were calculated by formulae for finite samples given by HARTER (1970).

Phenotypic correlations were computed as PEARSON'S product moment correlation coefficient. Genetic correlations of two traits on the same test location (or combined over test locations) were obtained as the product-moment correlations of additive genetic variances and covariances. The latter were obtained from estimates of covariances of family means in a multivariate analysis of the data. A genetic correlation coefficient of the same trait on two sites was computed as

$$[13] r_g = \frac{\sigma_F^2(AS)}{\sigma_F^2(AS) + \sigma_{LF(AS)}^2 - V(\sigma_F(AS))}$$

(YAMADA, 1962, p. 505) where $V(\sigma_F(AS))$ is the variance of the individual site estimates of $\sigma_F(AS)$.

Variances of genetic correlations were estimated from the procedures outlined by TALLIS (1959). The minimum age-to-age correlation needed for juvenile selection (at a given selection intensity) to produce more gain per unit time than selection at rotation age (here set to 40 years) was found the methods given by MAGNUSSEN (1988).

Selection indices

Two types of selection indices were used. The first index (I_F) combined family means over three sites into a family-mean index whereas the second index (I_T) combined single tree data, plot means, family means, and replicate means from a single site into a single tree index for mass selection. Information contained in areas and stands within areas was ignored in the I_T index due to their negligible variance components (cf. Results section). Index weights (W) were computed as $W = P^{-1}GA$ (LIN, 1978), where P^{-1} is the inverse of the phenotypic variance-covariance matrix P; G is the additive genetic variance-covariance matrix, and A is a vector of economic weights. For the combined family mean index $A^T (= A \text{ transposed}) = (1, 1, 1)$ because each site was considered to be of equal importance. For the individual tree index A^T was equal to $(1, 0, 0, 0)$ because only the improvement of single tree heights was important and no economic importance was given to improvement of plot means, family means, or replicate means. The elements of the family mean matrices were as follows:

$P_F(i,j) = \sigma_F(i,j)$ = the covariance of family means (phenotypic) on site i and j ($i = 1,2,3; j = 1,2,3$). $G_F(i,j) = \sigma_G(i,j)$ = the additive genetic covariance of family means on site i and j (values were obtained via eq. [13] and $\sigma_G(i,j) = r_g(i,j) \cdot \sigma_G(i) \cdot \sigma_G(j)$).

Matrix elements of the phenotypic (P) and genetic (G) matrices in the single tree index were as follows:

	Tree	Plot	Family	Replicate
	P ₁₁	P ₁₂	P ₁₃	P ₁₄
P =	P ₁₂	P ₂₂	P ₂₃	P ₂₄
	P ₁₃	P ₂₃	P ₃₃	P ₃₄
	P ₁₄	P ₂₄	P ₃₄	P ₄₄

P_{11} = variance of a single tree = $\sigma_A^2 + \sigma_{S(A)}^2 + \sigma_F^2(AS) + \sigma_R^2 + \sigma_{RA}^2 + \sigma_{RS(A)}^2 + \sigma_p^2 + \sigma^2$
 P_{22} = variance of plot means = $\sigma_A^2 + \sigma_{S(A)}^2 + \sigma_F^2(AS) + \sigma_R^2 + \sigma_{RA}^2 + \sigma_{RS(A)}^2 + \sigma_p^2 + \sigma^2/n_H$
 P_{33} = variance of family means = $\sigma_A^2 + \sigma_{S(A)}^2 + \sigma_F^2(AS) + \sigma_{RA}^2/R + \sigma_{RS(A)}/R + \sigma_p^2/R + \sigma^2/Rn_H$
 P_{44} = variance of replicate means = $\sigma_R^2 + \sigma_{RA}^2/A + \sigma_{RS(A)}/SA + \sigma_p^2/FS(A) + \sigma^2/FS(A)n_H$
 P_{34} = covariance of family means and replicate means = $\sigma_{RA}/RA + \sigma_{RS(A)}/RS(A) + \sigma_p^2/RS(A)F + \sigma^2/RS(A)Fn_H$
 P_{12} = covariance of tree and plot means = P_{22}
 P_{13} = covariance of tree and family means = P_{33}
 P_{14} = covariance of tree and replicate means = P_{44}
 P_{23} = covariance of plot means and family means = P_{33}
 P_{24} = covariance of plot means and replicate means = P_{44}

All negative variance components in the above equations were equated to zero. Corrections of variance components to represent finite sample estimates were done prior to computing P_{ij} 's. Further details of the indices are given by BURDON (1979 and 1982).

The structure of the additive genetic matrix for the single tree index was in principle the same as for P; let σ_{AG}^2 denote the total additive genetic variance, thus:

$$G_{11} = \sigma_{AG}^2; G_{22} = \left(\frac{n_H + 1}{4n_H}\right) \sigma_{AG}^2; G_{33} = \left(\frac{Rn_H + 1}{4Rn_H}\right) \sigma_{AG}^2;$$

$$G_{44} = \left(\frac{n_H + 1}{4AS(A)F(SA)n_H}\right) \sigma_{AG}^2;$$

$$G_{12} = G_{22}; G_{13} = G_{23} = G_{22}; G_{14} = G_{24} = G_{44}; G_{34} = 0$$

(genetic covariance between family means and replicate means).

Index variances (σ_i^2) were computed as WTPW (LIN, 1978) and the correlation R_{IH} between the index value (i) and its genetic merit (H) was derived as WTGA (LIN, 1978). Standard errors of indices were obtained by methods outlined by TAI (1986). Genetic gain arising from index selection is expected to be proportional to σ_I (FALCONER, 1981).

Results and Discussion

Survival

Survival at age 6 years was 94% at Sturgeon and Adelarde and 88% at Mackey. At age 14 survival had dropped to 92% at Sturgeon, 86% at Adelarde, and 84% at Mackey. A statistical assesment of survival rates (not shown) based on arcsin — transformed plot averages supported the contention of significant site differences. Family and family by site differences were non-significant ($P > 0.15$). Previous studies have related low jack pine survival to either poor adaptations of southern seed sources in boreal environments (MAGNUSSEN and YEATMAN, 1988a) or to adverse site conditions in boreal Canada (MAGNUSSEN and YEATMAN, 1988b). Regional survival is only expected to reflect intensity and quality of site preparation.

Tree height

Mean tree height across sites averaged 1.09 m at age 6 years and 6.3 m at age 14. Height growth at Sturgeon and Adelarde was 6% better (significant) than at Mackey at age 14 (Table 2). These heights compare favorably with

Table 2. — Family minimum, mean, and maximum values of tree height (m) at age 6(HT06) and 14(HT14) by site and area. Standard errors of means are enclosed in brackets.

Area	HT06		HT15	
	(min. - mean - max.)		(min. - mean - max.)	
Sturgeon Lake (I)				
1	.97 - 1.07 - 1.20		6.0 - 6.4 - 7.0	
	(.01)		(.05)	
2	.97 - 1.07 - 1.20		6.1 - 6.6 - 7.1	
	(.01)		(.04)	
3	.98 - 1.08 - 1.21		6.2 - 6.5 - 6.8	
	(.01)		(.04)	
4	.96 - 1.09 - 1.17		6.0 - 6.6 - 7.1	
	(.01)		(.05)	
5	.97 - 1.07 - 1.19		6.1 - 6.6 - 7.0	
	(.01)		(.04)	
average	1.08 (.006)		6.5 (0.02)	
Adelarde (II)				
1	1.08 - 1.18 - 1.35		6.0 - 6.4 - 6.8	
	(.01)		(.04)	
2	1.08 - 1.18 - 1.31		6.0 - 6.4 - 6.7	
	(.01)		(.05)	
3	1.08 - 1.14 - 1.24		5.9 - 6.3 - 6.7	
	(.01)		(.04)	
4	1.07 - 1.16 - 1.23		6.0 - 6.3 - 6.7	
	(.01)		(.04)	
5	1.13 - 1.18 - 1.23		6.1 - 6.4 - 6.7	
	(.01)		(.04)	
average	1.17 (.005)		6.4 (.02)	
Mackey (III)				
1	.89 - 1.01 - 1.12		5.6 - 6.1 - 6.3	
	(.01)		(.04)	
2	.93 - 1.03 - 1.18		5.4 - 6.1 - 6.6	
	(.01)		(.05)	
3	.94 - 1.00 - 1.10		5.7 - 6.0 - 6.4	
	(.01)		(.04)	
4	.92 - 1.03 - 1.14		5.9 - 6.1 - 6.7	
	(.01)		(.04)	
5	.95 - 1.07 - 1.15		5.8 - 6.2 - 6.9	
	(.01)		(.04)	
average	1.03 (.006)		6.1 (.02)	
Combined (Site I-III)				
1	1.09		6.3	
	(.007)		(.02)	
2	1.09		6.4	
	(.006)		(.02)	
3	1.07		6.3	
	(.007)		(.03)	
4	1.09		6.3	
	(.005)		(0.03)	
5	1.11		6.4	
	(.007)		(0.01)	
Average	1.09 (.003)		6.3 (0.01)	

other jack pine progeny tests in the Ottawa Valley (MAGNUSSEN and YEATMAN, 1986, 1988a).

Area had little impact, on tree height as illustrated in table 2, and in the lack of significance of this effect in the analysis of variance (Table 3). Within a single area, height differences between the best and the poorest family at age 14 were in the 10% to 15% range. Larger relative differences (12% to 25%) were manifest in the six-year results (Table 2). Stands within areas contributed nothing of practical importance to the results (stand differences < 1%) despite occasional statistical significance at the

Table 3. — Mean-squares and F-ratios in the analysis of variance of plot mean tree heights at ages 6 (HT06) and 14 (HT14), and stem diameter at age 14 (DBH14)¹⁾. df = degrees of freedom in the numerator of the F-ratio. (df's for the denominators were calculated according to formulae given by Satterthwaite (1946)). Significance level of F-ratios are indicated in brackets or in star notation²⁾.

Source of variation	HT14			HT06			DBH14			Form of F-test
	df	MSx10 ³	F-ratio	MSx10 ²	F-ratio	MS	F-ratio	MS		
Test locations, L	2	226.9	6.2*	317.9	11.0**	41.5	8.1***	41.5	$MS_L / (MS_R(L) + MS_{LxA} - MS_{S(A) \times R(L)})$	
Replications in test loc., R(L)	15	39.5	10.3***	29.1	6.0***	5.4	7.1***	5.4	$MS_R(L) / MS_{AxR(L)}$	
Areas, A	4	11.4	-15.0(1.0)	4.6	0.8(.60)	1.4	3.2(.39)	1.4	$MS_A / (MS_{S(A)} + MS_{LxA} - MS_{L \times S(A)})$	
Stands in areas S(A)	5	4.0	0.4(.84)	5.7	0.8(.56)	1.0	0.7(.68)	1.0	$MS_{S(A)} / (MS_{L \times S(A)} + MS_F(AS) - MS_{L \times F(AS)})$	
L x A	8	1.1	0.7(.68)	3.7	0.8(.61)	0.3	0.3(.95)	0.3	$MS_{LxA} / (MS_{L \times S(A)} + MS_{AxR(L)} - MS_{S(A) \times R(L)})$	
L x S(A)	10	5.8	0.7(.72)	3.9	0.6(.81)	0.9	0.5(.89)	0.9	$MS_{L \times S(A)} / (MS_{S(A) \times R(L)} + MS_F(AS) - MS_p)$	
A x R(L)	60	3.8	1.0(.50)	4.9	1.3(.14)	0.8	1.4(.08)	0.8	$MS_{AxR(L)} / MS_{S(A) \times R(L)}$	
S(A) x R(L)	75	4.0	3.3***	3.8	3.1***	0.6	1.5**	0.6	$MS_{S(A) \times R(L)} / MS_p$	
Families in stands in areas F(AS)	89	5.2	4.0***	4.2	4.2***	1.1	2.8***	1.1	$MS_F(AS) / MS_{L \times F(AS)}$	
L x F(AS)	178	1.3	1.1(.21)	1.0	0.8(.97)	0.4	1.1(.28)	0.4	$MS_{L \times F(AS)} / MS_p$	
Plot-error, P	1330	1.2		1.3		0.4		0.4		

¹⁾ reference level 1.3 m above the ground.

²⁾ levels of significance: * $0.01 < \alpha \leq 0.05$; ** $0.001 < \alpha \leq 0.01$; *** $\alpha \leq 0.001$

Table 4. — Variance component estimates and their standard errors (s. e.). Traits: height at age six (HT06), height at age 14 (HT14), and diameter at breast height (DBH14) at age 14. Estimates across sites in absolute and in relative (%) terms of the total phenotypic variance¹⁾. Estimates > 2 × s.e. are marked by an '*'.

Source of variation	σ^2 (HT06) cm ²	% ¹⁾	σ^2 (HT14) cm ²	%	σ^2 (DBH14) mm ²	%
Test locations	49 (38)	9	322 (273)	6	6.2 (4.9)	4
Replications in test locations	25* (10)	4	360* (137)	7	4.7 (1.8)	3
Seed collection areas	-.2 (1.3)	0	34 (21)	1	.3 (.3)	0
Stands in areas	-.8 (1.9)	0	-32 (14)	0	-.3 (.4)	0
Test locations x areas	-1.4 (2.1)	0	-38 (21)	0	-.7 (.4)	0
Test locations x stands	-5.9 (3.1)	0	-88 (41)	0	-.6 (.7)	0
Areas x replications	5 (5.4)	1	-9 (47)	0	.1 (.8)	0
Stands x replications	26* (6.2)	5	276* (65)	5	1.9* (.8)	1
Families in stands in areas	18* (3.5)	3	216* (44)	4	3.8* (.8)	2
Families x test location	-4 (2.0)	0	-18 (25)	0	.4 (.7)	0
Plot variance	40* (5.1)	7	368* (48)	7	6.8* (1.6)	5
Within plot variance	396* (7.2)	71	3691* (68)	70	128.0* (2.4)	85
Total phenotypic	559	100	5285	100	152.2	100

¹⁾ Negative terms have been equated to 0.

5% risk level. Plus tree selection can therefore take place within a single stand without serious loss of potential genetic gain in juvenile height and stem diameter. Some reservation against adopting a single-stand collection scheme is, however, prudent because effects of stand and area may require more time before they become evident in our trials (BONGARTEN and HANOVER, 1986; NAMKOONG *et al.*, 1972). If stand and seed area emerge as significant factors, then an optimized stratified plus tree selection strategy, based upon the results from the analytical models for provenance-progeny trials (HARVEY and TOWNSEND, 1985; LAND *et al.*, 1986) would replace the single stand selection strategy.

A summary of the analysis of variance results is provided in table 3. Of interest here is the significance of site and family effects and the virtual absence of any family × test-location interaction in the three measured traits. Results from single-site analysis of variance (not shown) confirmed the lack of significance of both area and stand terms in the linear model of height growth and stem diameter (cf. eq. [2]). Absence of any important genotype × environment interaction effect within large regions of eastern Ontario has been confirmed in other open pollinated jack pine progeny trials (MAGNUSSEN and YEATMAN, 1986, 1988a). An overriding importance of climatic factors, rather than edaphic factors, on growth, survival, and

evolution in this region would explain our findings. It greatly simplifies deployment strategies of genetically improved stock (for example, MATHESON and RAYMOND, 1984).

Variance components

Variance estimates pooled across sites are listed in table 4. Only variance estimates of replications, stands × replications, families, and plots exceeded twice their associated standard errors (Table 4) and should be considered significant (HALLAUER and MIRANDA, 1981). Families accounted for no more than 2% (DBH14) — 4% (HT14) of the total phenotypic variance. Congruence among the sizes of the three site components locations, replications, and plots was evident in the 14-year data. Tree height variation within plots was clearly the major source of variation (70% to 85% of the total phenotypic variance). A highly significant replicate by stand effect on all sites was indicative of non-homogeneous blocks. Single-site estimates of variance components (not shown) reflected similar trends as the combined estimates. While it is difficult, due to ontogenetic phases, stand dynamics, and mortality (FRANKLIN, 1979; NAMKOONG *et al.*, 1972; NAMKOONG and CONKLE, 1976) to relate the variance components in table 4 to findings in other trials, a dominance of the within-plot variance along with a modest 2% to 4% contribution by families seems characteristic for many

Table 5. — Family (h_f^2) individual tree (h_I^2) and within family (h_w^2) heritability of tree height at age six (HT06) and at age 14 (HT14), and stem diameter at age 14 (DBH14) at a reference level 1.3 m above ground. Standard errors of estimates are bracketed.

		HT06	HT14	DBH14
Sturgeon Lake (I)	h_f^2	.28 (.12)	.41 (.11)	.39 (.13)
	h_I^2	.10 (.04)	.23 (.06)	.15 (.05)
	h_w^2	.08 (.04)	.18 (.05)	.12 (.05)

Adelarde (II)	h_f^2	.48 (.14)	.52 (.13)	.30 (.10)
	h_I^2	.18 (.05)	.25 (.06)	.11 (.05)
	h_w^2	.14 (.05)	.20 (.06)	.09 (.05)

Mackey (III)	h_f^2	.25 (.12)	.38 (.12)	.31 (.14)
	h_I^2	.08 (.04)	.15 (.05)	.09 (.04)
	h_w^2	.06 (.04)	.12 (.04)	.07 (.04)

Combined Site I-III	h_f^2	.42 (.08)	.48 (.10)	.46 (.10)
	h_I^2	.13 (.03)	.18 (.04)	.10 (0.02)
	h_w^2	.10 (.02)	.14 (.03)	.08 (0.02)

forest trials (for example, FOSTER, 1986, 1986; HÜHN *et al.*, 1987; KISS and YEH, 1988; YEH and HEAMAN, 1987). Large standard errors of most variance components confirmed the impracticality of obtaining precise estimates at reasonable cost (NAMKOONG, 1979).

Heritabilities

Heritability estimates for use in gain predictions of family (h_f^2), individual (h_I^2), or within-family selection (h_w^2) are listed in table 5. Single site family heritability estimates were well below 0.5 in all traits whereas the combined across-sites estimates were just below this mark. Individual tree heritabilities hovered around 0.10 to 0.25 while the within-family heritabilities trailed in the 0.06 to 0.20 range. Tree height heritabilities were highest in the Adelarde trial, second highest at Sturgeon Lake, and lowest at Mackey. A marked increase in both heritabilities as well as the reliability of these estimates took place between age 6 years and age 14. For stem diameter at age 14, the highest heritability estimates were seen in the Sturgeon Lake results.

An individual tree heritability around 0.2 of juvenile tree height agrees well with results published elsewhere (ELDRIDGE, 1982; FRANKLIN, 1979; RIEMENSCHNEIDER, 1982; YING and MORGENSTERN, 1979) but they are well below estimates from trials on more uniform sites (MAGNUSSEN and YEATMAN, 1987a). Site differences in heritabilities are partly a function of the degree to which the experimenter can manipulate them through field design and site management. Although numerous trials have reported heritability

to decline after a juvenile culmination (GILL, 1987; KISS and YEH, 1988), examples of a later recovery are well known (NAMKOONG and CONKLE, 1976; COTTERILL, 1987; FOSTER, 1986). At present our estimates connote a potential for an appreciable genetic gain in juvenile height and stem diameter. The potential inflation of our heritabilities by assuming $\sigma_A^2 = 4 \sigma_I^2$ (JACKSON, 1983; PONZONI and JAMES, 1978) is regarded as minor in a species like jack pine (FRANKLIN, 1970; SITTMAN and TYSON, 1970; SNIETKO and ZOBEL, 1988; SNYDER *et al.*, 1985).

Correlations

The negligible family \times test-location interaction is also reflected in a statistically significant among-sites correlation of family mean heights. Genetic correlations of family means were indeed close to 1.0 (Table 6) but the phenotypic correlations were as a rule below 0.5. Family mean tree height at age 14 at Adelarde was a better predictor of the general family performance than means obtained at Sturgeon and Mackey. At age 6 years Mackey was the best predictor. Slightly lower (5% to 10%) genetic correlations would have been obtained if we had computed type 'B' covariances (BURDON, 1977; FERNANDO *et al.*, 1984). Genetic correlation based on type 'B' covariances are consistent with the gain predictions obtained directly from multivariate distribution theory (COCHRAN, 1951; SEARLE, 1984; p. 354). Correlations between tree height at ages 6 and 14 years were roughly 0.5 at the individual tree and plot level (Table 7). It is rather surprising to find the plot correlations to be almost equal to the correlations among individual trees. It points to the fact that there is no important covariance among trees in a plot. Family mean correlations of HT14 and HT06 should be higher than plot correlations when the covariance of plot means is positive. This was the case in the Sturgeon Lake and Adelarde data, but not in the case of Mackey where the plot-covariance was negative. Similarly, correlations of stand means were expected to be slightly higher than corresponding family means whenever families in a stand have a positive intraclass correlation. Confirmation hereof

Table 6. — Correlations of family means across sites. Estimates are product-moment correlation coefficients. Phenotypic correlations are given above the diagonal and genotypic correlations are given below the diagonal. HT06 = height at age six, HT14 = height at age 14. Standard errors of estimates are enclosed in brackets.

	HT06	Sturgeon	Adelarde	Mackey
Sturgeon Lake	*	.35 (.10)	.52 (.09)	
Adelarde	.96 (.20)	*	.49 (.09)	
Mackey	.98 (.21)	.98 (.20)	*	
<u>HT14</u>				
Sturgeon Lake	*	.47 (.09)	.36 (.10)	
Adelarde	.97 (.24)	*	.48 (.09)	
Mackey	.85 (.21)	.89 (.21)	*	
<u>DBH14</u>				
Sturgeon Lake	*	.35 (.10)	.33 (.10)	
Adelarde	.89 (.25)	*	.35 (.10)	
Mackey	.91 (.24)	.92 (.18)	*	

Table 7. — Phenotypic and additive genetic correlations of tree height at age 14 (HT14) with tree height at age six (HT06) and stem diameter at age 14 (DBH14). Standard errors of estimates are enclosed in parentheses.

Traits	Reps	Areas	Phenotypic			Trees	Genetic Family	
			Stands	Family	Plots			
Sturgeon Lake (I)	(HT06, HT14) (HT14, DBH14)	.76 (.33) .87 (.28)	.44 (.63) .56 (.59)	.85 (.20) .91 (.16)	.70 (.07) .78 (.06)	.54 (.06) .77 (.10)	.56 (.01) .73 (.02)	.84 (.12) .72 (.10)
Adelarde (II)	(HT06, HT14) (HT14, DBH14)	.77 (.37) .81 (.39)	.68 (.34) .79 (.43)	.81 (.22) .72 (.25)	.73 (.07) .70 (.07)	.51 (.07) .67 (.03)	.52 (.01) .33 (.05)	.90 (.03) .74 (.12)
Mackey (III)	(HT06, HT14) (HT14, DBH14)	.74 (.39) .85 (.30)	.99 (.10) .37 (.66)	.74 (.25) .37 (.35)	.40 (.09) .69 (.07)	.48 (.07) .71 (.13)	.44 (.02) .70 (.01)	.24 (.37) .75 (.20)
Combined Site I-III	(HT06, HT14) (HT14, DBH14)	.59 (.21) .74 (.17)	.48 (.25) .64 (.22)	.51 (.17) .67 (.14)	.53 (.05) .70 (.04)	.51 (.020) .72 (.02)	.49 (.01) .69 (.003)	.71 (.03) .74 (.17)

was evident on all three sites but not in the combined results. Hence, genotype \times environment effects have, despite lack of statistical significance, reduced the effects of stands. Age 6 to age 14 correlations of area mean heights were higher on two sites (Adelarde and Mackey) than the associated stand-correlations. Stands within the same collection area were, in these two cases, more alike than stands from different areas. Replication means showed moderate rank changes over time which led to fairly strong correlations of replicate mean height over time (Table 7). Individual tree height and stem diameter at age 14 showed a fairly strong correlation with the exception of the results from Adelarde (Table 7). Areas and stands were, in general, exceptions in otherwise regular trends towards an increase in the correlation coefficients from the tree level to the level of replicates. Hence, our correlation results confirm the non-significance of stands and areas in the hierarchical model in equation [1].

Theoretically a hierarchical correlation analysis ought to shed light on the covariance structure among components in the linear model used in the analysis of variance. However, large standard errors, sensitivity to outliers, and "negative" variance components creates correlation "breakers" and inconsistent results. Interpretation of correlation coefficients is therefore an intricate exercise. Judged by formulae given by BURDON (1977) our sample size per family was near optimum for estimation of correlations.

Additive genetic correlations between tree height at age six and 14 were strong in the Sturgeon Lake and Adelarde data but not in the results from Mackey (Table 7). The latter result was due to a highly unstable ranking of families over time. Changes in soil moisture regimes within and among replicates are conjectured causes for this results. Tree height and diameter at age 14 revealed correlations of similar magnitude at both phenotypic and genetic levels, indicating a near zero environmental covariance (FALCONER, 1981) between the two traits.

Family selection

According to a formula for minimum age-to-age correlations (MAGNUSSEN, 1988) the magnitude of the age 6 to age 14 correlations of family mean height makes family selection at age 14 an option that promises more genetic gain per unit time than selections at higher ages. This conclusion, of course, ignores the potential but non-quantified pitfalls of early selection (REHFELDT, 1983).

To further examine if family \times test-location interaction can affect genetic gain, we calculated the correlated

genetic response that one would expect on one location given that selections were carried out in a different environment (BURDON, 1977; SKRØPPA, 1984). Expected relative response for all possible combinations of selection site and response site is listed in Table 8. Family selections carried out in the Adelarde trial can be expected to produce a 20% higher selection response for the three sites than selections performed at either Surgeon Lake or at Mackey. The Mackey site is clearly inferior as a selection site. Conversely, it is the type of site that will benefit the most from selection based on an average of the three sites instead of just one (Table 8). The relative merit of having three test locations instead of one can be derived by the ratio of the average response based on single site selections and the response expected from selections based on information from three sites. Given the responses in Table 8, this ratio was 1.09, i.e. the expected genetic gain will be 1.09 times higher when three sites are used for testing instead of just one. A breakdown of the GXE in a two-way response matrix allows a simple interpretation of an otherwise complex phenomenon (WESTCOTT, 1986). Three sites did little to improve the overall predicted gain as compared to the single best site. Two sites or one would, according to calculations done by LINDGREN (1984, 1985), be fully sufficient for ranking of families and gain predictions. However, LINDGREN ignored the risk of plantation failures and, in the presence of such uncertainty, we believe that three sites is recommendable for testing jack pine in eastern Canada. Also, until we know what makes a good test site one or two sites above the theoretical optimum are needed as safeguards.

An alternative to family selection based on an un-weighted across-sites average is to weight the available information in a way that will optimize the correlation between a composite index of family means and the genetic value of this index (FALCONER, 1981). Optimum weights of test locations in the family mean index are listed in table 9. In the indices of family mean heights, results from Adelarde were given much more weight than family means from any other site. A more equal weighting was seen in the family mean diameter index where Sturgeon Lake results were given the highest weight. The weights are, in general, proportional to the family heritabilities (cf. Table 5) and inversely related to the phenotypic variances of family means at the three test locations. The resulting indices were fairly strongly correlated to their genetic merit (cf. R_{IH} in Table 9) and the expected gain per unit selection intensity listed in table 9 should be compared with corresponding relative gains of

Table 8. — Expected relative genetic response to family selection on a site different from the planting site.

Selection site (i)	Planting site (j)			
	Sturgeon Lake	Adelarde	Mackey	Average
Sturgeon Lake	1.00	0.86	0.88	0.91
Adelarde	1.09	1.00	1.04	1.04
Mackey	0.82	0.76	1.00	0.86
Combined	0.98	0.95	1.13	$\frac{0.94}{1.02}$

Relative response = $r_G(i,j) \times \sqrt{h_i^2/h_j^2}$ where
 $r_G(i,j)$ = genetic correlation of family means on site i and j
 h_i^2 = heritability of family means on site i
 h_j^2 = heritability of family means on site j

5.0%, 3.6%, and 5.0%, respectively, for family selection based on simple averages. Hence, index selection promises to increase gain by roughly 70% over the conventional method. Seen against "fixed" costs of progeny testing, this improvement is quite attractive (BURDON, 1979). Besides improved gain, the index also circumvents the problem of variance heteroscedacity among sites and traits (BURDON, 1979) which besets many analyses. The index also allows a more flexible evaluation of the results through alternative "economic" weights.

Individual tree selection within a single site

At a single site the individual selection of trees with superior height at age 14 (HT14) can be carried out in three ways, (1) as a simple mass selection, (2) on an index construed from multiple sources of information, and (3) by an optimum (in terms of genetic gain) combined family and within family selection scheme. The three methods of selection give rise not only to different genetic gains but also different genetic structures of the selected populations which, eventually, will effect future genetic progress and breeding strategies. Selection for HT14 with the objective of improving tree height at rotation age (= 40) was deemed beneficial because the correlation between HT06 and HT14 exceeded the required minimum age-to-age correlation of 0.6 needed for selection of 20% of the trees (MAGNUSSEN, 1988). Figure 2 illustrates the main results of the three kinds of selections. An additional "ideal" mass selection has been added to illustrate the expected outcome under strict adherence to the normality assumptions of family and within family tree heights (HARTER, 1970). Two selection intensities (10% and 20% of the trees selected) have been chosen to bracket the limits of practical relevance.

The selection indices for the three test locations are listed in table 10. Weights given to family means were about twice the weights given to individual tree information. Plots and replicates were given negative weights which confirmed that these effects are environmental. Plots were given five times the (negative) weight given to replicates. It is this strong negative weighting of plots that effectively removed environmental influences and, as a consequence, enhanced the genetic progress for a given selection intensity. The standard errors of expected response appear high. Gain arising from simple mass selection has a relative standard error of approximately 35%.

Combining information into an index has therefore not increased the uncertainty surrounding the expected progress.

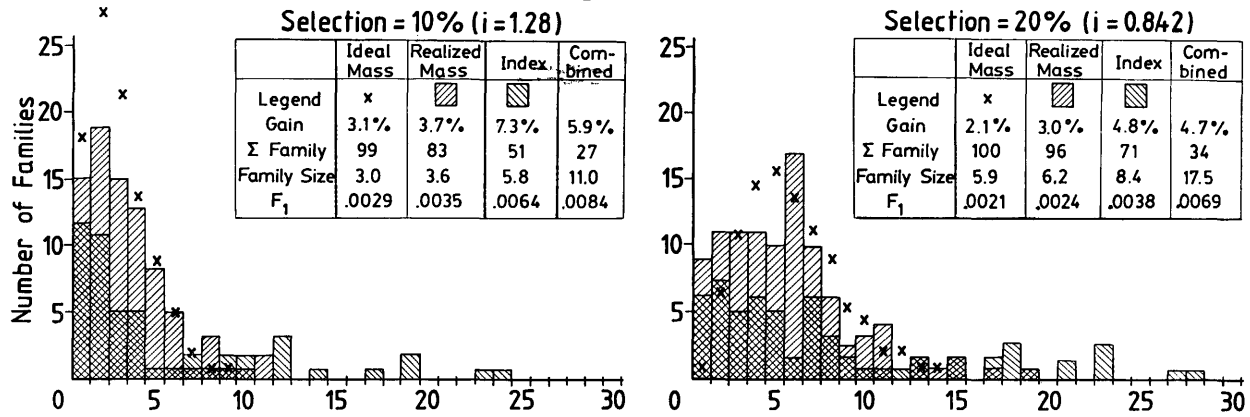
Genetic gains listed in figure 2 are expressed in per cent of the individual site mean tree height at age 14. Of the three selection methods, the index procedure appears superior, followed by the combined method and mass selection. Index selection of 10% of the trees promised almost twice as much genetic gain as mass selection. When 20% of the population was selected, the superiority of the index selection fell to 60%. Index selection was in most cases also superior to the optimum combined selection procedure. At 10% selection the index method promised about 15% more gain than the best combined selection. When 20% of the trees were selected, the superiority of index selection over combined selection was less pronounced. Under the constraint of a fixed number of trees to select, the best combined method promised to yield on an average 50% to 60% more gain than mass selection. The number of families represented in the selected trees was highest in the mass selections and lowest in combined selections. Index selection was intermediate in this regard.

Table 9. — Optimum weights of test locations in the family mean index (I_F).

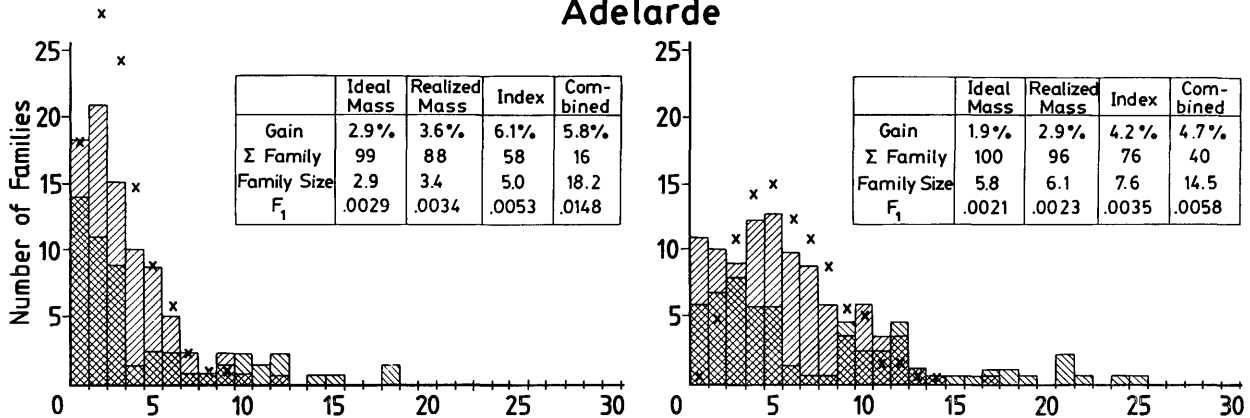
Trait:	HT06	HT14	DBH14
test location:			
Sturgeon Lake	0.4604	0.6162	0.6742
Adelarde	0.9861	0.8792	0.4762
Mackey	0.1042	0.5478	0.5173
Avg. index value	1.76 m	12.97 m	10.44 cm
σ_I^2 (cm ²)	66	1384	0.2
$2^* \sigma_I / I \times 100$	9.2	5.8	8.6
R_{IH}	0.75	0.82	0.75

HT06 = height at age six
HT14 = height at age 14
DBH14 = diameter at age 14 (1.3 m above ground)
 I_F = mean of composite index = \sum weight \times site mean sites
 σ_I^2 = variance of composite family index
 $2^* \sigma_I / I \times 100$ = genetic gain in % per unit selection intensity
 R_{IH} = correlation between index and genetic value of index.

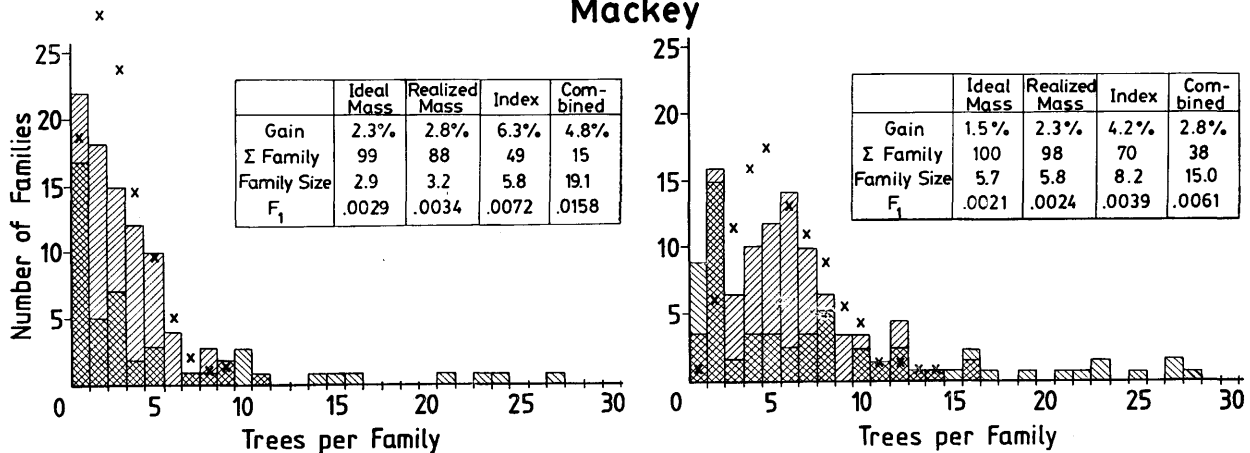
Sturgeon Lake



Adelarde



Mackey



Gain = genetic response relative to the trait mean value.

Σfam = no. of families represented in selected trees (max = 100).

fam. size = average no. of trees selected per family.

F_1 = inbreeding coefficient (assuming random mating among selected trees).

Figure 2. — Expected relative gain, no. of families, family size, and inbreeding coefficients (F_1) under four selection schemes and two intensities of selection (i) for individual tree height at age 14 (HT14).

Average family size after selection was three to seven times larger in the combined selection than in the mass selection with index selection again intermediate.

Assuming a random mating of selected individuals, a theoretical inbreeding coefficient was computed for every selection outcome (BULMER, 1985). Mass selection leads to the lowest inbreeding coefficients (F_1 in Figure 2). Combined selection is expected to produce an inbreeding coefficient that is 2 to 4 times higher than expected under a

random mating of mass selected individuals. Index selection will also increase the expected inbreeding to a level about 70% higher than that originating from random mating of mass selected individuals. It should be noted, however, that all inbreeding coefficients are well below 2%. Reductions in quantitative traits from this level of inbreeding are expected to be negligible (FRANKLIN, 1970; SNIĘZKO and ZOBEL, 1988). Hence, from the standpoint of gain and number of families retained index selection is clearly superior.

Table 10. — Single tree index (I_T) weights in multiple information source indices used in selections for tree height at age 14 (HT14).

Test location:	W_{tree}	W_{plot}	W_{family}	$W_{\text{replicate}}$	$\left\{ \frac{s.e.}{\sigma_T} \right\} \%$
Sturgeon Lake	0.26	-0.21	0.54	-0.05	25
Adelarde	0.35	-0.29	0.73	-0.06	22
Mackey	0.16	-0.12	0.45	-0.02	33

$$I_T = W_t \cdot HT14 + W_p \cdot HT14_{\text{plot}} + W_f \cdot HT14_{\text{family}} + W_r \cdot HT14_{\text{replicate}}$$

s.e. (σ_T) % = standard error of response to selection in per cent of index mean.

Gain calculations are based on the assumptions of normally distributed family means and within-family observations of tree heights (FALCONER, 1981). To test the appropriateness of this assumption we computed (via order statistics (HARTER, 1970)) the expected outcome of a mass selection in an "ideal" population with strictly normally distributed trait values at both levels. The discrepancy in gain and family structure between the "ideal" and realized mass selection was in most cases of little practical importance. The "ideal" mass selection resulted in less gain than computed from our data. Also, family sizes were slightly higher in the realized selection than in the normalized "ideal" selection. Unequal, but not significantly different, within-family variances were the main source for these deviations. Chi-square statistic computed to test the hypothesis of equal numbers of selections per family in the "ideal" and realized mass selections was significant only for the Mackey site when 20% of the trees were selected. In that scenario the number of selected families with two trees was significantly higher than expected. In all other cases the chi-square statistic stayed well above the 10% probability level under the hypothesis of no difference in family structure. It was therefore concluded that the normality assumption for the three populations was reasonably justified.

BURDON (1982) and BAKER (1986) have stressed that the index was developed for balanced data sets. Missing plots and trees would generate a bias in the P-matrix. He suggested the use of family-specific solutions in cases with serious imbalances in the data or the use of heritabilities as a weighting factor that would help correct the bias. Imbalance was ignored in the present study and no attempt was made to address its impact on the solutions. An extension of the indices to encompass multiple traits and sites is feasible (BURDON, 1982).

Conclusions

Height growth of jack pine in the Upper Ottawa Valley shows at age 14 years little or no genetic differentiation among areas and stands within areas. Collections of plus trees for breeding purposes can, therefore, without serious loss of genetic variation be simplified to collections within one or few stands of adequate size, age distribution, and site quality within the local ecogeographic region. Absence of any important GXE interaction on a regional scale will greatly simplify deployment strategies of improved seed and seedlings, and reduce costs of progeny testing. Combining multiple sources of progeny trial information into selection indices holds the promise of doubling genetic gain predictions based on family means

or single-tree heights alone. Expected inbreeding among selected trees is generally low but highest in index- and combined methods and lowest in mass selection schemes. The number of families retained after index selection was deemed sufficient for future breeding. Early selection (age six) of families appears attractive with a potential for enhancing genetic gain per unit time.

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Inheritance and Linkage of Isozyme Variants from Seed and Vegetative Bud Tissues in Coastal Douglas-fir [*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco]¹⁾

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Summary

Isozyme variants of 19 enzyme systems coded by 28 genetic loci from seed [megagametophyte (1n) and embryo (2n)] and dormant vegetative bud tissues of coastal