FOUR YEARS HEIGHT GROWTH OF 25
JACK PINE <u>(PINUS</u> <u>BANKSIANA</u> LAMB.) FAMILIES
IN AN ACCELERATED NURSERY TRIAL

S. Magnussen[1] and C.W. Yeatman[2]

ABSTRACT

    Heights at age one to four years were recorded in a
nursery trial with 25 open-pollinated jack pine families.

    Narrow sense heritabilities decreased from 0.43 at age
one to 0.27 at age four. This decrease is interpreted to be
a consequence of increased competition following crown
closure at age three. Genetic correlations of recorded tree
heights were above 0.9 when first year measurements were
excluded. First-year results were poorly correlated to
subsequent heights ($r_G < 0.4$). Calculations of genetic
gain of tree height at age four showed that expected gain
could be increased by either indirect selection at age two or
by index selection.

    Indices of family ranking and height growth stability
over time showed mainly random differentiation among
families.

[1] Research Fellow, Royal Veterinary and Agricultural University,
Copenhagen, Denmark. Present address: Petawawa National Forestry
Institute, Chalk River, Ontario KOJ 1JO, Canada.

[2] Project Leader, Tree Genetics and Breeding, Petawawa National Forestry
Institute, Chalk River, Ontario.

INTRODUCTION

Juvenile testing and selection has become an integral part in many forest tree improvement programmes. Early ranking of breeding values is required to reduce generation time and increase breeding efficiency but experience with early testing has been mixed (Burdon and Sweet 1976, Franklin 1979, Kang 1985, Lambeth 1980, Lambeth et al. 1983, Namkoong and Conkle 1976, Nienstaedt 1984, Webb 1963, Zobel and Talbert 1984). The lack of consistent juvenile-mature correlations of traits is the central deficiency of early testing. Developmental phases of tree growth (Franklin 1979, Lambeth et al. 1983, Namkoong et al. 1972, Nienstaedt and Riemenschneider 1985) and differences in the intensity of intra-specific competition (Cannell 1982, Huhn 1973, Wearstler 1979) are major causes for the frequently low age to age correlation in genetic trials at young ages and in the early years of stand establishment. If reliable estimates of relative genotypic stability (over time) can be derived in the juvenile stage, it would greatly improve the benefits of early testing.   Such reliable predictions are most likely obtained under conditions comparable to those found after canopy closure in older field trials with favorable growing conditions (Bongarten and Hanover, 1985, Franklin 1979, Skrøppa 1984). With this in mind a study of juvenile height growth performance of 25 open-pollinated jack pine families from the Ottawa Valley was established at a close spacing (0.5 m) in a nursery. The first four years results from that study are presented here.

MATERIALS AND METHODS

Tree height at age one to four years was recorded in open-pollinated progenies from 25 parent trees sampled in 1973 from eight natural stands in eastern Ontario, from Deux Rivieres in the Ottawa Valley to Barry's Bay, Madawaska Valley. The trees were selected among the dominant crown class for extremes of stem form (straight vs. crooked) and branch angle (wide vs. narrow).

Seeds were sown in March 1982 and seedlings held in the greenhouse until planted in the nursery in July at a 0.5 m spacing. The nursery soil was a deep fine sand of moderate fertility. The compartment was fertilized and carried a grass/clover/alfalfa ground cover before being cultivated. The trees were planted in single-tree family plots randomized in each of 24 replications (blocks). Two surround rows of a single family were planted about the perimeter of the experiment.

Weeds were removed by hoeing as required, and the trees were irrigated in dry periods to avoid drought. The objective was to minimize stress and provide a uniformly optimal growing environment for jack pine throughout the growing season. The trees were exposed to normal wind, rain, snow, and seasonal temperatures.

RESULTS

Statistical procedures and computational methods are described in the appendix[1]. Levels of statistical significance are indicated as follows: '*', 0.01 < a < 0.05; '**', 0.001 < a < 0.01; '***', a < 0.001; and 'NS', a > 0.05. Seventeen trees (2.8%) were missing or dead in 1985, and no more than two trees were missing from any one family.

Family effects on one to four years heights were highly significant in each year (Table 1) and when combined over all four years (X^2_{96} = 371***). Parent crown type was not significant in any year (Table 1). ANOVA results with (Model I) and without (Model II) a crown type effect ('plus'/'minus') are listed in Table 1. Families accounted for only 7-10% of the total phenotypic variation (Table 2). The variance component of crown type was negligible in comparison (Table 2). Mean heights for the 'plus' and 'minus' types separately and combined are listed in Table 2. Heritability estimates showed a decline from year one to year four (Table 2); the exponential rise of the phenotypic variance was the major reason for this trend. Accurate inferences about the observed decline are not possible due to the large standard errors associated with heritability estimates (cf. Table 2).

Phenotypic year to year correlations of height increased with age (Table 3). First year's results were not correlated to later performance. Height increment was weakly correlated with initial height attained the previous year. Only family height at age two was significantly correlated to subsequent growth (Table 3). Similar results were observed in genetic correlations (Table 3). The environmental correlations in Table 3 indicate a moderate resemblance between any two consecutive years and also a marked drop in the correlation of results more than one year apart.

Ranking and relative performance of individual trees and families changed considerably over the four years. Due to the low correlation of first year results with older results, we consider in the following only stability of height performance between age two and age four. The rank stability index S, in Table 4 summarizes for each family the observed rank changes. Examples of unstable families are 7651 and 7708. In comparison, families such as 7642 and 7677 showed a consistent relative performance. Table 4 lists in the E% column the relative family contribution to the overall interaction SSQ. Two families, 7708 and 7791, accounted for almost one-quarter of the family x 'Age/mean-height' interaction. The relationship, between performances of different families at age 2-4 and average height of all families, is expected to be linear or nearly so (Freeman and Perkins 1971). Tai's a is a measure of the linear response of individual genetic entries (Tai 1971). Tai's a is similar to the regression coefficient for the regression of family response on the overall average in any given year. Alpha values, for families with a height progression parallel to the one for all families combined, are zero. The principle is illustrated in Figure 1 and in the Appendix. Tai's X is a measure of the deviation from a linear response in terms of the magnitude of the error variance. Tai's a-values listed in Table 4

[1]Available by request from the authors.

measure the linear family response to the mean of all families between the second and fourth years. None of the a values differed significantly from zero (Table 4); that is all families showed an average linear response. The strong correlation between Tai's lambda (λ) and E% in Table 4 confirms that most of the changes in relative family performance must be ascribed to unascertained random fluctuations. A strong correlation (r = 0.9232***) was seen between the Ecovalence (E%) and the absolute value of Tai's a. None of the stability parameters listed in Table 4 were apparently correlated with height at age four and no difference was found between parameters from contrasting parental crown types.

The genetic gain in a hypothetical selection for height at age four could be improved by either index selection (Falconer 1981, Namkoong 1979) or indirect selection. The indices for individual selection (Ii) and family selection (If) are listed below:

[1] $I_i = 0.08H_4 + 0.13H_3 + 0.53H_2 - 0.38H_1$, $r_{IH}^2 = 0.46$, $\sigma_I^2 = 64.1$,

where H_i = height at age i (i = 1, 2, 3, 4),

[2] $I_f = 0.20H_4 + 0.12H_3 + 0.84H_2 - 0.55H_1$, $r_{IH}^2 = 0.73$, $\sigma_I^2 = 25.5$.

In both indices, first year's height is given a negative weight which indicates that this trait is predominantly environmental. Second year's height (H_2) contributes most to the indices (approx. 60%). The values of phenotypic heights at age 2-4 as predictors of genetic performance at age four are expressed below as coefficients of genetic prediction (CGP).

Age	CGP (individuals)	CGP (family)
1	0.06	0.14
2	0.23	0.63
3	0.31	0.65
4	0.26	0.62

First-year results are clearly inferior as a predictor, whereas height at age 2-4 appear to have almost equal values. The merit of index selection, calculated as the response ratio of index to direct selection with identical intensities (Falconer 1981), showed the index selection to improve the expected gain by 30% in individual selection and by 7% in family selection. Using an index for selection will result in a reduction of mean height of selected individuals (H_{Index}) as compared to the mean height resulting from direct selection (H_{Direct}).

Equations [3] and [4] below give the expected height ratios arising from the two methods as a function of the selection intensity, i.

[3] Individual selection $H_{Index}/H_{Direct} = (1+0.09i)/(1+0.12i)$

[4] Family selection $H_{Index}/H_{Direct} = (1+0.037i)/(1+0.040i)$

According to the equations, a mild individual selection will lower the phenotypic mean of height at age four by 2-5% whereas the family selection will result in only a negligible reduction. The relative merit of indirect selection for height at age four was calculated as the response ratio CR_{H4}/R_{H4}, where CR_{H4} is the correlated response in height at age four and R_{H4} the direct response to selection. Using height at age one to four as the secondary selection trait we calculated the following relative merits:

Secondary trait

	H1	H2	H3	H4	Selection
$CR_{H4}/R_{H4} =$	0.3	1.1	1.1	1.0	Individual
$CR_{H4}/R_{H4} =$	0.3	0.9	1.0	1.0	Family

The biggest gain for individual height at age four is possible by indirect phenotypic selections at age two. No increase was possible by indirect family selection.

Phenotypic selection of families based on height data alone is complicated by the lack of height growth stability among families. Table 5 shows the superiority of the topmost eight families at age one to three and at age four. The best families at age one were only average at age four. Even selection at age three leads to a sizeable loss in superiority (11%) after just one growing season. An attempt to characterize similarities among families in height growth during four years is depicted in Table 6 by a standardized similarity coefficient. This has the value of 1.0 with complete growth synchronization between two families and a value of 0.5 with random association. The matrix of coefficients in Table 6 range from 0.61 to 0.96, but there was no clustering of high values along the diagonal nor a tendency towards decreasing values away from the diagonal.   Such a pattern would have indicated a correlation between family mean height at age four and growth synchronization.

DISCUSSION

A relative family variance component of 7-10% and narrow sense heritabilities in the 0.3-0.4 range compare favorably with expectations of a

51

moderately strong genetic control of height growth in conifers (Cotteril and Zed 1980, Franklin 1979, La Farge 1972, Ledig and Clark 1977, Squillace et al. 1967, Ying and Morgenstern 1979). With the considerable standard error of estimated heritabilities we found it safe to ignore the minor additional bias arising from departures from random mating of parent trees (Cheliak et al. 1985, Jackson 1983, Ponzoi and James 1978, Sittmann and Tyson 1971, Squillace 1974). Both the age-to- age correlation analyses and the stability indices revealed that family height growth had not stabilized. A predictable height growth performance cannot be expected to begin before a stable balance between phenotype and genotype is attained. In field trials this may take up to 10 years (Delvaux 1981, Franklin 1979, Lambeth et al. 1983, Meier and Goggans 1977, Namkoong and Conkle 1976, Nienstaedt and Riemenschneider 1985, Roulund et al. 1985, Wakely 1971, Ying and Morgenstern 1979).

The lack of correlation between first year's and later results is ascribed to a genotype x environment effect arising from the greenhouse, transplanting, and a possible seed size effect (Ackerman and Gorman 1969, Bongarten and Hanover 1985, Burgar 1964, Kremer and Larson 1983, Righter 1945, Robinson and von Buijtenen 1979, Yeatman 1966). We hypothesize that the decline in heritability with age was caused mainly by increasing competition. Branch overlap and complete ground coverage was observed in the second growing season. In single-tree plot trials, competition will inflate the within family variance and thus lower heritability (Campbell and Wilson 1973, Cannell 1982, Delvaux 1981, Hühn 1973, Wearstler 1979). Our analyses of family height stability confirmed that the linear component is usually small (Becker 1981, Hanson 1970). Height at age four was not related to stability of family performance in the preceeding three years. Furthermore, we demonstrated that different parameters of stability may yield deviating results in family stability ranking (Eberhart and Russell 1966, Finlay and Wilkinson 1965, Freeman 1973, Freeman and Perkins 1971, Skr6ppa 1984, Tai 1971, Wright 1976). Our conclusion is that analysis of age to age stability in this study did not provide any improved insight into family height growth, although the technique has a great potential in forest genetics. Similar arguments can be made for the similarity coefficients. The most obvious use of age to age stability analysis is to spot genotypes with aberrant performance which then could be deleted from the trial or further analyses (Lin 1982, Matheson and Raymond 1984, Owino 1977, Skrøppa 1984, Wricke 1962).

Height growth and family age to age stability of relative height performance was almost identical in progeny groups from parents with contrasting crown type. However, future differences may appear because experience has shown that most crown characters require several years to express genotypic differences (Dietrichson 1964, Namkoong and Conkle 1976, Namkoong et al. 1972, Roulund et al. 1985, Schober 1985, Ying and Morgenstern 1979).

Application of a single trait selection index has great potential in forest genetic trials where competition makes direct phenotypic selection less effective. Clearly, results obtained before competition became too severe received the greatest weight in the index as calculated, but the

index also adjusted for predominantly environmental influences such as first years height on the desired trait. Application of selection index can increase the efficiency of juvenile testing by maximizing utilization of the inherent genetic information. However, because precision of the selection index depends on all of the variances and covariances, the error of estimate of the aggregated genetic value can be very high indeed.

LITERATURE CITED

Ackerman, R.F.; Gorman, J.R. 1969. Effects of seed weight on the size of lodgepole pine and white spruce container-planting stock. Pulp and Paper (Convention Issue). 4 p.

Becker, H.C. 1981. Correlations among some statistical measures of phenotypic stability. Euphytica 30:835-840.

Becker, W.A. 1984. Manual of quantitative genetics. Fourth edition. Acad. Enterprises, Pullman, Wash. 190 p.

Bongarten, B.C.; Hanover, J.W. 1985. Accelerating seedling growth through photoperiod extension for genetic testing: A case study with blue spruce (Picea pungens). Forest Sci. 31:631-643.

Burdon, R.D.; Sweet, G.B. 1976. The problem of interpreting inherent differences in tree growth shortly after planting. Pages 483-502 in Cannell, M.G.R.; Last, F.T., (eds.) Tree physiology and yield improvement, Acad. Press.

Burgar, R.J. 1964. The effect of seed size and germination, survival and initial growth in white spruce. For. Chron. 40:93-97.

Campbell, R.K.; Wilson, B.C. 1973. Spacing-genotype interaction in Douglas-fir. Silvae Genet. 22:15-20.

Cannell, M.G.R. 1982. 'Crop' and 'Isolation' ideotypes: Evidence for progeny differences in nursery-grown Picea sitchensis. Silvae Genet. 31:60-66.

Cheliak, W.M.; Dancik, B.P.; Morgan, K.; Yeh, F.C.H.; Strobeck, C. 1985. Temporal variation of the mating system in a natural population of jack pine. Genetics 109:569-584.

Cotteril, P.P.; Zed, P.G. 1980. Estimates of genetic parameters for growth and form traits in four Pinus radiata (D.) Don progeny tests in South Australia. Aust. For. Res. 10:155-167.

Delvaux, J. 1981. Differénciation sociale. Schweiz. Zeitschr. Forstwesen 132:733-749.

Dietrichson, J. 1964. The selection problem and growth rhythm. Silvae Genet. 13:178-184.

Eberhart, S.A.; Russell, W.A. 1966. Stability parameters for comparing varieties. Crop Sci. 6:36-40.

Falconer, D.S. 1981. Introduction to quantitative genetics. Second ed. Longman. 340 p.

Finlay, K.W.; Wilkinson, G.N. 1963. The analysis of adaptation in a plant-breeding programme. Aust. J. Agric. Res. 14:742-754.

Franklin, E.C. 1979. Model relating levels of genetic variance to stand development of four North American conifers. Silvae Genet. 28:207-212.

Freeman, G.H. 1973. Statistical methods for the analysis of genotype-environmental interactions. Heredity 31:339-354.

Freeman, G.H.; Perkins, J.M. 1971. Environmental and genotype-environmental components of variability. VIII. Relations between genotypes grown in different environments and measures of these environments. Heredity 27:15-23.

Gordon, I.L.; Byth, D.E.; Balaam, L.N. 1972. Variance of heritability ratios estimated from phenotypic variance components. Biometrics 28:401-415.

Hanson, W.D. 1970. Genotypic stability. Theor. Appl. Genet. 40:226-231.

Hühn, M. 1973. Populationsgenetische Untersuchungen zur phänotypischen Selektion in Pflanzenbeständen mit Konkurrenz. Teil I-IV. Silvae Genet. 22:72-81, 82-90, 128-135, 136-145.

Jackson, N. 1983. Effect of ignoring full sib relationships when making half sib estimates of heritability. Theor. Appl. Genet. 65:61-66.

Kang, H. 1985. Juvenile selection in tree breeding: Some mathematical models. Silvae Genet. 34:75-84.

Kempthorne, O. 1957. An introduction to genetic statistics. John Wiley and Sons Inc. 545 p.

Kendall, M.; Stuart, A.; Ord, J.K. 1983. The advanced theory of statistics. Vol. I-III. Fourth ed.

Kremer, A.; Larson, P.R. 1983. Genetic control of height growth components in Jack pine seedlings. For. Sci. 29:451-464.

La Farge, T. 1972. Relationships among third-, fifth- and fifteen-year measurements in a loblolly pine stand variation study in Georgia. Proc. IUFRO Working Party on Progeny Testing, Georgia, Oct. 1972. 13 p.

Lambeth, C.C. 1980. Juvenile-mature correlations in Pinaceae and impli-
    cation for early selection. Forest Sci. 26:571-580.

Lambeth, C.C., Buijtenen, J.P. van, Duke, S.D., and McCullough, R.B.
    1983. Early selection is effective in 20-year-old genetic tests of
    loblolly pine. Silvae Genet. 32:210-215.

Ledig, F.T.; Clark, J.G. 1977. Photosynthesis in a half-sib family
    experiment in pitch pine. Can. J. Forest Res. 7:510-514.

Lin, C.S. 1982. Grouping genotypes by a cluster method directly related
    to genotype-environment interaction mean square. Theor. Appl. Genet.
    62:277-280.

Loo, J.A.; Tauer, C.G. 1984. Juvenile-mature relationships and
    heritability estimates of several traits in loblolly pine. Can. J.
    Forest Res. 14:822-825.

Matheson, A.C.; Raymond, C.A. 1984. The impact of genotype x envir-
    onment interactions on Australian _Pinus radiata_ breeding programs.
    Aust. For. Res. 14:11-25.

Meier, R.J.; Goggans, J.F. 1977. Heritabilities of height, diameter,
    and specific gravity of young Virginia pine. Forest Sci.
    23:450-456.

Namkoong, G. 1979. Introduction to quantitative genetics in forestry.
    USDA Forest Serv. Techn. Bull. 1588, Washington, D.C. 342 p.

Namkoong, G.; Conkle, M.T. 1976. Time trends in genetic control of
    height growth in ponderosa pine. Forest Sci. 22:2-12.

Namkoong, G.; Usanis, R.A.; Silen, R.R. 1972. Age-related variation in
    genetic control of height growth in Douglas fir. Theor. Appl. Genet.
    42:151-159.

Nienstaedt, H. 1984. Breeding implications of juvenile selection in a
    range-wide black spruce provenance test. Can. J. Forest Res.
    14:933-939.

Nienstaedt, H.; Riemenschneider, D.E. 1985. Changes in heritability
    estimates with age and site in white spruce _Picea glauca_ (Moench)
    Voss. Silvae Genet. 34:34-41.

Owino, F. 1977. Genotype x environment interaction and genotypic
    stability in loblolly pine. II. Genotypic stability comparisons.
    Silvae Genet. 26:21-24.

Ponzoi, R.W., and James, J.W. 1978. Possible biases in heritability
    estimates from intraclass correlations. Theor. Appl. Genet.
    53:25-27.

Reeve, E.C.R. 1955. The variance of the genetic correlation coefficient. Biometrics 11:357-374.

Righter, F.I. 1945. Pinus: The relationship of seed size and seedling size to inherent vigor. J. For. 43:131-137.

Robinson, J.F.; Buijtenen, J.P. van. 1979. Correlation of seed weight and nurserybed traits with 5-, 1-, and 15-year volumes in a loblolly pine progeny test. Forest Sci. 25:591-596.

Roulund, H.; Wellendorf, H.; Werner, M. 1985. A clonal experiment in Norway spruce. Forest Tree Impr. 17. 33 p.

Schober, R. 1985. Neue Ergebnisse des II. internationalen Lärchenprovenienzversuches von 1958/59 nach Aufnahmen von Teilversuchen in 11 europaischen Landern and den USA. Schriftenreihe Forstl. Fak. Univ. Göttingen 83. 164 p.

Sittmann, K., and Tyson, H. 1971. Estimates of inbreeding in Pinus banksiana. Can. J. Bot. 49:1241-1245.

Skrøppa, T. 1984. A critical evaluation of methods available to estimate the genotype x environment interaction. Stud. For. Suecica 166:3-14.

Squillace, A.E. 1974. Average genetic correlations among offspring from open-pollinated forest trees. Silvae Genet. 23:149-156.

Squillace, A.E.; Bingham, R.T.; Namkoong, G.; Robinson, H.F. 1967. Heritability of juvenile growth rate and expected gain from selection in western white pine. Silvae Genet. 16:1-6.

Tai, G.C.C. 1971. Genotypic stability analysis and its application to potato regional trials. Crop Sci. 11:184-190.

Wakely, P.C. 1971. Relation of thirtieth-year to earlier dimensions of southern pines. Forest Sci. 17:200-209.

Wearstler, K.A. Jr. 1979. Competition-density effects and genetic improvement of yield components in loblolly pine (Pinus taeda L.). Diss. Abstr. Int. B40(4)1443B.

Webb, C.D. 1963. Juvenile-mature tree relationships. Proc. 7th Southern Conf. For. Tree Impr. USDA Forest Serv., S.E. For. Exp. Sta., Mississippi. 15 p.

Wricke, G. 1962. Über eine Methode zur Erfassung des Ukologischen Streubreite in Feldversuchen. Zeitschr. Für Pflanzenzüchtung 47:92-96.

Wright, A.J. 1976. The significance for breeding of linear regression analysis of genotype-environment interactions. Heredity 37:83-93.

Yeatman, C.W. 1966. Germinant size of jack pine in relation to seed size and geographic origin. USDA Forest Serv., Res. Pap. NC-6:28-36.

Ying, C.C.; Morgenstern, E.K. 1979. Correlations of height growth and heritabilities at different ages in white spruce. Silvae Genet. 28:181-185.

Zobel, B.; Talbert, J. 1984. Applied forest tree improvement. John Wiley & Sons. 505 p.

Table 1. ANOVA statistics of first to fourth years height.

a) Model I. Effects (random): 'Plus/minus' family, plots. Families nested within 'Plus/minus'.
   Number of families = 24. Harmonic mean of trees per family = 23.40
   Total number of trees = 514

Source of variation	df	MS(1)	MS(2)	MS(3)	MS(4)	Expected mean square
		Mean squares, MS (age)				Expected mean square
Replicates (plots) (r)	23	316	209	388	837	$\sigma_o^2 + 0.03\ \sigma_{af(+/-)}^2 + 0.02a_{+/-}^2 + 24.29\ a_{+/-}^2$
'Plus/minus' (+/-)	1	0	523	625	20	$au7 + 23.32a_{f(+/-)}^2 + 290.77a_{+/-}^2$
Families in 'Plus/minus'	22	75	370	1041	1442	$aw + 23.29af(+"$
Within plot error (w)	513	20	99	278	492	a^2
F-ratios $F_1 = MS_{iv} i MS_f$		0.01NS	1.41NS	0.60NS	0.01NS	
$F_2 = MS_f / MS_w$		3.73***	3.72***	3.74***	2.93***	

b) Model II. Effects (random): Family, plots. Number of families = 25.
   Harmonic mean of trees per family = 23.32.
   Total number of trees = 583.

Source of variation	df	MS(1)	MS(2)	MS(3)	MS(4)	Expected mean square
Replicates (r)	23	330	224	450	889	$a_w^2 + 24.26\ \sigma_r^2 + 0.03a_f^2$
Families (f)	24	77	380	1088	1320	$\sigma_w^2 + 23.32a_f^2$
Witin plot error (w)	535	20	106	324	492	aw^2
F-ratios $F_1 = MS_f / MS_w$		3.86***	3.57***	3.36***	2.68***	

58

Table 2. Mean height, variances, and heritability estimates of 25 jack pine half-sib families at age one to four years.

(Family variance components are estimated under condition $\sigma^2_+ = 0$).

	Age (year)			
	1 (1982)	2 (1983)	3 (1984)	4 (1985)
Height (cm) 'plus'	24.4	59.2	117.4	189.0
'minus'	24.4	57.1	115.0	189.1
all	24.4	57.9	115.9	189.1
t-test ('plus'-'minus'), t =	0.02NS	2.24*	1.57NS	0.06NS
(df, $_a$)	(454,.985)	(426,.025)	(416,.117)	(413,.953)
Coefficient of variation, CV%	24%	18%	15%	12%
Total phenotypic variance, σ_T^2	33.7	114.2	313.6	542.0
Family variance component, σ_f^2	2.4	11.6	32.4	35.1
('Plus', 'minus' variance component σ_-^2	(-0.3)	(0.7)	(-1.6)	(-5.3)
S.E. (σ_f^2)%	37%	38%	39%	44%
$\sigma_f^2/\sigma_T^2 \times 100$	7%	9%	10%	7%
h_I^2 (individual, narrow sense)	0.43	0.39	0.36	0.27
S.E. (H_I^2)%	24%	37%	39%	40%
h_f^2 (family repeatability)	0.74	0.72	0.71	0.63
S.E. (h_f^2)%	9%	11%	11%	8%

Table 3. Correlation of first to fourth year's height.

a) Phenotypic correlations of family mean heights (upper
     triangle) and of individual tree heights (lower triangle).
     Correlations between height and height increment are
     displayed in brackets.

Age (years)

Age	1	2	3	4
1	–	.46* (.01NS)	.21NS (–.06NS)	.24NS (.01NS)
2	.47** (–.08NS)	–	.85** (.44*)	.80** (.42*)
3	.22** (–.11*)	.71** (.15**)	–	.92** (.13NS)
4	.19** (–.07NS)	.51** (.06NS)	.80** (.06NS)	– –

standard error = 0.04

b) Genotypic correlations (r_G) (upper triangle) and
     environmental correlations (lower triangle) of family
     mean heights. Figures in brackets are the standard error
     of r_G.

Age (years)

Age	1	2	3	4
1	–	.38NS (.25)	.07NS (.30)	.21NS (.32)
2	.55	–	.87** (.10)	.94** (.14)
3	.36	.65	–	.95** (.08)
4	.19	.28	.66	–

Table 4. Height growth stability parameters. Age 2-4 yrs. Families
          sorted in descending order of height at age four.

          S_1 = ranking stability index
          E% = relative family contribution to the family x age/mean
             height SSQ
           a = Tai's alpha
          $\pm a_{90}$ = 90% confidence interval for a

Family	S1	E%	a	±a90	l	Plus-minus type
7707	2.0	8	0.053	0.40	1.8	-
7675	2.0	3	0.037	0.25	0.6	-
7642	1.3	2	0.016	0.25	0.6	+
7657	2.7	6	0.053	0.33	1.0	-
7677	1.3	0	0.011	0.07	0.1	-
7708	8.0	11	0.071	0.45	1.8	-
7673	2.0	5	0.040	0.34	1.1	+
7653	3.3	6	0.018	0.45	1.8	+
7647	6.7	5	0.045	0.30	0.8	-
7644	4.7	3	0.034	0.20	0.4	+
7684	1.3	0	0.002	0.01	0.0	+
7672	1.3	0	-0.003	0.05	0.0	+
7671	4.0	1	0.007	0.21	0.4	+
7685	2.0	0	-0.002	0.05	0.0	-
7643	4.7	2	-0.012	0.23	0.5	+
7652	6.0	3	-0.034	0.23	0.5	+
7674	2.7	0	0.004	0.08	1.1	+
7646	2.7	1	-0.021	0.16	0.2	-
7655	3.3	2	-0.024	0.24	0.6	-
7651	9.3	9	-0.006	0.41	1.5	+
7686	1.3	6	-0.047	0.35	1.1	-
7658	1.3	4	-0.040	0.30	0.8	-
7645	1.3	6	-0.037	0.38	1.3	-
7706	1.3	3	-0.036	0.23	0.5	-
7791	2.7	12	-0.074	0.46	2.0	+

t-test t=-0.94NS   0.46NS   0.64NS   -   -0.12NS
('plus'-'minus')

61

Table 5. Height superiority of the top eight families at age one
          to four.

          S = superiority = mean of top eight families - test mean
                            of all 25 families

          % superiority = S x 100/test mean of all families

Age	S(cm)	%S	%S at age four	Relative efficiency of selections (age four = 100%)
1	1.9	7.7	0.7	15
2	4.6	7.9	3.2	70
3	7.6	6.6	4.1	89
4	8.8	4.6	4.6	100

Table 6. Similarity coefficients R(i,i') of three years height growth of 25 half-sib families. Table figures are R(i,i') x 100. Families are listed in descending order of mean height at age four.

| Family	7675	7642	7657	7677	7708	7673	7653	7647	7644	7684	7672	7671	7685	7643	7652	7674	7646	7655	7651	7686	7658	7645	7706	7691
7707	92	91	73	77	87	71	73	96	75	90	70	85	86	94	93	88	93	89	84	80	73	77	92	87
7675	.	82	84	88	79	83	86	91	86	79	84	87	90	84	94	80	91	91	88	91	85	90	82	80
7642	.	.	69	72	97	64	65	88	70	96	64	87	83	93	88	98	91	86	83	70	66	68	93	94
7657	.	.	.	94	69	95	95	74	97	65	97	86	85	67	79	71	77	82	87	90	93	93	66	71
7677	.	.	.	.	71	91	96	76	98	67	94	90	92	69	86	73	83	89	93	90	89	94	67	71
7708	.	.	.	.	.	64	65	86	70	95	64	87	80	91	84	99	88	83	81	69	66	67	92	96
7673	.	.	.	.	.	.	95	73	92	62	96	80	81	64	76	66	73	77	82	93	98	94	63	67
7653	.	.	.	.	.	.	.	73	96	61	98	84	86	64	80	66	76	82	87	93	93	97	63	66
7647	.	.	.	.	.	.	.	.	74	89	72	83	82	94	89	86	89	85	81	81	76	78	92	87
7644	.	.	.	.	.	.	.	.	.	66	96	89	90	67	82	72	80	86	91	90	90	93	66	70
7684	.	.	.	.	.	.	.	.	.	.	60	82	77	96	83	94	86	80	77	68	64	65	97	96
7672	.	.	.	.	.	.	.	.	.	.	.	83	84	63	77	66	74	80	85	92	94	95	62	66
7671	.	.	.	.	.	.	.	.	.	.	.	.	95	81	91	89	92	94	97	82	80	83	80	85
7685	.	.	.	.	.	.	.	.	.	.	.	.	.	78	94	83	94	98	98	84	80	86	76	78
7643	.	.	.	.	.	.	.	.	.	.	.	.	.	.	86	90	88	82	78	72	67	68	98	91
7652	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	86	98	97	92	83	77	82	84	82
7674	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	90	85	84	70	67	68	91	95
7646	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	97	92	79	74	79	86	85
7655	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	96	82	77	83	80	81
7651	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	84	81	86	76	79
7686	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	94	97	71	71
7658	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	94	66	69
7645	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	67	68
7706	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	93

0")
G.)
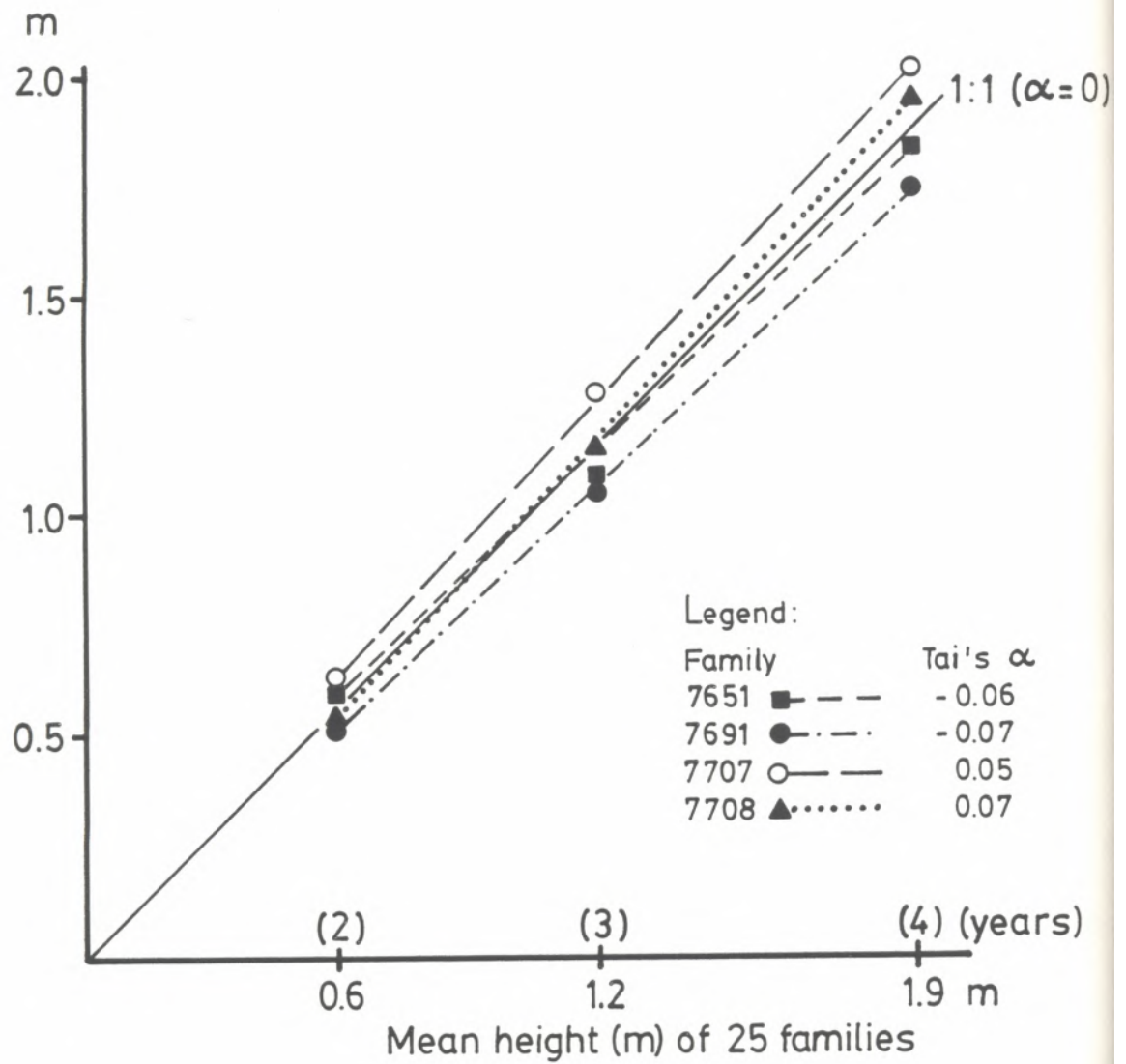
Fig. 1. Mean height (m) of four families at age 2, 3, and 4 plotted over mean height of all families. Formula for α_i is given in Appendix (15).