# A Study of Population Variation and Inheritance in Sitka Spruce

## III. Age Trends in Genetic Parameters and Optimum Selection Ages for Wood Density, and Genetic Correlations with Vigour Traits

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## Summary

This study represents the third investigation into the additive genetic variances operating within an unselected population of Sitka spruce trees of known single origin. The work presented here involves wood density; how the additive genetic variances vary with age, optimum selection ages and the genetic relationship between wood density and stem diameter. A genotypic selection ellipse constructed with existing data collected within the open-pollinated progeny test for 17-year density and 16-year diameter was used to help select a subsample of 46 families from the 125 available. To avoid possible bias, the complete data for each trait used to construct the ellipse were included as covariates in the calculation of all wood density variance components.

Wood density weighted by surface area was estimated on a ring by ring basis using X-ray densitometry. Subsequent analyses such as correlations between ages of density assessment or between density and diameter were carried out by combining consecutive rings together into ring-groupings. The youngest available ring grouping represented years 6 to 9 from planting (RG6-9), whilst the oldest (RG19-22) represented years 19 to 22 from planting which was considered as the breeding goal.

The study confirmed the very high single-tree and family heritability for wood density found in earlier studies but demonstrated that these values can fall sharply with age, leveling off around RG12-15. The high heritability values for wood density of RG6-9 ($h^2_i = 0.85$; $h^2_f = 0.96$) coupled with the very high genetic correlations ($r_A = 0.95$) between wood density of RG6-9 and RG19-22 suggests that selection for mature wood density can safely be made based on measurements of wood density in the juvenile core.

Both generation ($Q_{gen}$) and genetic gain per year ($Q_{year}$) efficiencies are improved by around 40 % if selection for wood density is carried out as young as nine years from planting. Further improvements of 90 % and over 100 % are achieved if the delay ($d$) necessary to bring about flowering in young selection could be reduced to five or three years respectively after selection.

High (negative) genetic correlations between early wood densities (RG6-9) and later diameter assessments (DM16) of around $r_A = -0.70$ indicates the problems of selecting Sitka spruce trees for improved diameter growth whilst preventing a fall in wood density.

*Key words: Picea sitchensis*, genetic variation, genetic correlations, phenotypic correlations, progeny testing, heritability, indirect selection, selection age.

## Introduction

Sitka spruce (*Picea sitchensis* (BONG.) CARR.) is the main plantation species in Great Britain and represents nearly 30 % of the area of commercial forestry (Forestry Industry Council of Great Britain, 1998). The operational Sitka spruce selection and breeding programme commenced in 1963 with the selection in British forests of superior individuals for height, diameter, stem straightness and branching quality (FLETCHER and FAULKNER, 1972). Over 1800 plus-trees were selected over the next 20 years or so. Whilst these trees were thought to be of Queen Charlotte Islands origin (QCI; British Columbia, Canada), forest records were often incomplete in this regard. Also there is known to be considerable variation in the performance of seed lots collected across the range of QCI. A regular programme of open-pollinated half-sib progeny testing of selected plus trees commenced in 1967 and continued until 1993 (LEE, 1993). Data have now been collected from around half of the 200 progeny tests established over the 26 year period, and a breeding population now exists based on multi-trait selection for 15 year diameter, wood density and stem form (LEE, 2001). Estimates of variance components and heritabilities of traits measured in these progeny tests of selected individuals have previously been presented by GILL (1987) and LEE (1999).

Only if variance components are derived from an unselected population will they be free of any artificially induced bias for the selected traits and other correlated traits. A soundly based breeding strategy is dependent on reliable information regarding the underlying variation and pattern of inheritance. When accurate estimates of unbiased genetic variances are available, it is possible to make realistic predictions of times and costs likely to be incurred under different breeding schemes and selection intensities which could be simulated with mathematical models.

Ideally, a study into the variance components operating within an unselected population should be carried out prior to commencing a selection and breeding programme. This is rarely possible due to the time delay involved in obtaining data from genetic tests up to half a rotation length prior to starting a programme. At best, genetic field trials may be planned to run concurrently with the operational testing and selection programmes such that an existing programme may have its efficiency increased, or direction altered.

In 1969 there was the opportunity to collect seed from a stand of known QCI origin in which cones were being produced on all size classes of trees. Progeny from the randomly selected trees were planted in the field in 1972. SAMUEL and JOHNSTONE (1979) presented the first paper in this series when they published estimates of heritability for height up to the sixth year after field planting, and investigated changes in ranking of family performance. LEE *et al.* (2002) presented the second paper in this series which investigated age:age correlations for height and diameter between two and 23 years from planting and optimal selection ages for vigour traits at both the individual tree and family-mean level. This paper is the third in this series and presents details of age trends in the additive

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genetic variance of wood density including optimum selection ages for wood density at both the individual tree and family-mean levels.

The only previous detailed study into the variation of wood density with age of Sitka spruce trees in progeny tests in Britain was carried out by WOOD (1986) who investigated a selected population of trees, many of which were of unknown origin. The main findings of WOOD (1986) were that 15 years from planting was the optimal selection age for wood density at which age there is a strong negative phenotypic correlation with diameter breast height ($r_p$ = –0.34 to –0.69); the 6J Pilodyn (a gun which fires a blunt pin into the tree with a fixed force of six Joules) is a quick non-destructive tool for indirectly measuring wood density and is well correlated with density measured using X-ray densitometry ($r_p$ = –0.69) and that density is highly heritable ($h_i^2$ = 0.73).

It has since then been the practice of the Tree Improvement Branch of the British Forestry Commission to indirectly screen trees in progeny tests for wood density at about 15 years from planting (DN15), using the Pilodyn gun.

GILL (1987) found the optimum indirect selection age for family-mean vigour was six year height. It is therefore frustrating for tree breeders trying to progress through generations as quickly as possible to have a delay of nine years between optimum selection ages for height and wood density. Final selection of genotypes for breeding and production populations has to be delayed until data are available for each trait and currently density data are the last to be collected. A reduction of the optimum age of selection for wood density could assist in improving the generation turn-over and rate of gain.

The objectives of this study were to analyse the half-sib progeny data collected for wood density from an unselected population of trees in order to determine:

i. how the genetic variance components and heritabilities for wood density varied with age;
ii. optimum selection ages for wood density;
iii. how genetic and phenotypic correlations between wood density and certain vigour traits varied with time.

Optimum selection ages were investigated for single tree and family selection. Family selection is important in 'backward' selecting tested genotypes or re-creation of full-sib families which may be included in production populations. Single tree selection is important for 'forward' selection of trees in progeny tests to create new breeding populations following crossings between tested individuals.

## Material and Methods

### *i. Details of the parent population and site*

In 1969, an 8 hectare stand of 34-year-old Sitka spruce growing in South Strome forest in north-west Scotland (57° 21' N, 6° 32' W) was chosen for study. The site had been planted with Sitka spruce of known QCI origin in 1935 (SAMUEL and JOHNSTONE, 1979). Some light thinning had been carried out to remove a proportion of the suppressed trees (dead and dying) prior to the selection of trees for this study. Trees were subjectively classified as dominant, co-dominant or sub-dominant and the proportion of the crop falling into these classes was estimated. The selection of 150 trees took place in a random fashion across the range of dominance classes including 6 previously classified 'plus-trees' (selected according to FLETCHER and FAULKNER, 1972). Only trees which were coning were selected. Since this applied to the vast majority of the trees in the stand it was considered that this would not introduce any bias. The final composition of the sample is given in LEE *et al.* (2002, *Table 1.*)

Extracted seed were raised in the nursery for two years prior to planting out to three forest sites in 1972. Following losses at germination and in the nursery a total of 134 families survived and were all planted at one site, with different sets of 125 families planted at the other two sites; 116 families were common to all three sites.

### *ii. Details of the progeny test site*

Only one of the three sites was selected for analysis as part of this study; this was due partly to limitation of resources and partly to poor condition of the other two sites due to extensive areas of windblow and within site heterogeneity based on analysis of one to six years height data (not presented), respectively. The chosen study site was located in Garcrogo Forest in south-west Scotland (55° 6' N, 3° 54' W) at an elevation of 230–240 m. The soil type was hill peat (more than 30 cm in depth) on a Silurian geology. Previous land-use was sheep grazing until ploughed by the Forestry Commission in December 1971. Trees were planted at 2 x 2 m spacing in 7 x 7 (49) tree block plots in spring 1972. The 125 families were planted in three randomised complete blocks making this a large experiment extending over 9.5 hectares. Standard silvicultural management for the site was practised. Survival at the end of the first growing season exceeded 90 % for most families. Dead trees were replaced in March 1973 using surplus trees retained in the nursery.

To ensure all trees within a family had similar inter-genotypic competitive effects, only the central 5 x 5 trees were measured in each assessment. The whole experiment was given a 50 % chemical thinning in July 1989 when the trees were in their eighteenth growing season. Every tree along every other diagonal was killed by injecting with glyphosate herbicide at or about breast height in accordance with the method outlined by WILLIAMSON and LANE (1989). The maximum number of trees per assessment plot after July 1989 was therefore reduced from 25 to either 12 or 13.

### *iii. Selection of trees for wood density assessed*

Wood density was to be assessed using X-ray densitometry techniques following the extraction of pith to bark cores at diameter breast height. This is a costly form of assessment and available resources would only allow for sampling of a maximum of 700 out of the 4,500 surviving trees. A sub-sample of representative trees had to be selected with sufficient plants per family (x) to allow an accurate assessment of within family variance components, and a sufficient number of families (y) to allow an accurate assessment of between family variance components.

The product of (xy) could not exceed 700. In order to retain a balance of trees per family across replicates, it followed that (x) changed in units of 3; as (x) increased from nine to 12, 15 or 18 trees, so (y) was reduced from 77 to 58, 46, or 39 families. A sub-sample of (x) = 15 and (y) = 46 (xy = 690) was chosen as giving a good balance between trees per family and total number of families. These sample sizes are comparable to those used by TALBERT *et al.* (1983) who carried out a similar study in an unselected loblolly pine (*Pinus teada*) progeny test with similar plot sizes and two replications at each of two sites.

It was important that the sub-sample of 46 families would allow an unbiased and precise estimate of (i) the wood density variance and covariance components operating at different ages from the pith to the cambium; (ii) genetic and phenotypic correlations between juvenile and mature wood; and (iii) genetic and phenotypic correlations between wood density and selected vigour traits.

Equations by Hill (1971) show how random selection can be improved upon to minimise the standard errors attached to heritability estimates in single-trait selection if there is some prior knowledge of the genetic parameters to be estimated. When two traits are involved, Reeve (1955) suggested selecting parental phenotypes with extreme high and low values for each trait in order to assess variance components more accurately. This idea was developed further by Cameron and Thompson (1986). They hypothesised that if there is prior knowledge of a relationship between two traits ($t_1$ and $t_2$), errors attached to estimates of variance components would be minimised by selection of those individuals lying on the edge of an ellipse that results from plotting the regression of $t_1$ on $t_2$. Such a regression was referred to as a *phenotypic selection ellipse.* The individuals to select should be those furthest from the origin in all directions. An equation was presented to allow the calibration of the ellipse and selection of families:

**Equation 1**

$$w = \frac{(t_1 + t_2)^2}{(1 + r_p)} + \frac{(t_1 - t_2)^2}{(1 - r_p)} \qquad (1)$$

where: w = index value calculated according to Equation 1 indicating distance from origin.
$r_p$ = phenotypic correlation coefficient of $t_1$ with $t_2$.
and $t_1$, $t_2$ = standardised data for the two correlated traits of interest.

Due to the absence of parental wood density data in this study it was not possible to produce an ellipse based on the respective phenotypes. An alternative source of wood density (primary trait $t_1$) and vigour (secondary trait $t_2$) data were the 17-year wood density assessment, measured indirectly using the Pilodyn (DN17), and 16-year diameter breast height (DM16) available from assessments carried out on all surviving trees prior to this study (see Lee *et al.*, 2002). These data were seen as a further improvement on the selection of families based on parental data since family-mean data from a progeny test would more closely resemble the respective tree breeding values of the original selections. This had the effect of improving the selection ellipse from a *phenotypic* ellipse to a *genetic* ellipse. *Figure 1* is a plot of standardised DN17 and DM16. The 46 families furthest from the origin were selected for wood sampling. Five trees within plots were randomly selected from the 12 or 13 available in each replication.

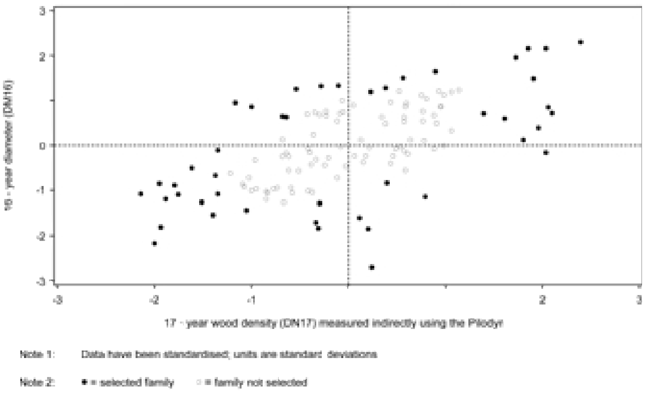


*Figure 1.* – Selection Ellipse – Selection of the sub-sample of 46 families used in detailed wood density assessments.
Outlying families were selected based on the relationship between family-mean values for stem diameter and an indirect assessment of wood density using the Pilodyn for the complete population of 125 families.

Since it was possible that an element of selection might have been introduced in composing the sub-sample of families, DN17 and DM16 were always included as covariates when analysis of data based on the sub-sample was carried out. The covariate data included all surviving trees from the 125 families present in the experiment and not just the 46 families at the extreme of the ellipse.

*iv. Collection of cores*

Cores were collected during May and June 1994 as the trees entered their 23rd growing season. Eight millimetre diameter bark to bark cores were extracted along a north/south line as near to breast height (1.3 m) as possible. The north side was identified on each complete core before storing at +2°C prior to X-ray densitometry assessment. Cores were prepared for X-ray densitometry according to Hughes and de Albuquerque Sardinha (1975). Each 8 mm core was reduced to a 5 mm square strip by passing twice through twin circular saws in a north to south direction, an operation which sometimes caused the loss of one or more annual rings from the south end of the strip.

*v. Core processing*

Wood density for each point scan was calculated by conversion from optical density according to the transition formula of Wood (1986). It was not necessary to extract resin prior to carrying out the X-ray densitometry procedure (Wood, 1986; Silva *et al.*, 1994). Each strip was X-rayed and scanned using the Joyce Lobel M4VI microdensitomer. The density of the timber sample image was calculated indirectly every 0.2 mm. The position of the end of each annual ring was determined following inspection of output data for optical density and a graph of optical density against distance from the pith. Annual-ring and whole core density were calculated by weighting for cross-sectional area.

*vi. Analyses of data*

Individual growth rings were sorted by calendar year which could then be converted to age from planting.

A preliminary analysis found no difference between the north and south radii for the first 250 out of the 690 trees sampled for either mean ring width or weighted density, but there were significantly more rings on the north side which was a consequence of the method used to process the 8 mm cores (*Table 1*).

In addition there were no significant effects of position x family or position x year (data not shown) indicating that the

*Table 1.* – Mean values for ring width, wood density and ring number: comparison of north and south radü.

| | Width (mm) | Wood Density (kg/m³) | Number of Rings |
|---|---|---|---|
| Overall | 4.18 | 0.511 | 15.55 |
| North side | 4.20 | 0.511 | 16.05 |
| South side | 4.16 | 0.510 | 15.05 |
| SED | 0.04 NS | 0.0014 NS | 0.1116*** |

Note: 1. *** = significant at $p = 0.001$, NS = not significant at $p = 0.05$ SED = Standard Error of the Difference
2. Analysis carried out on 8 mm increment cones collected as close to breast height (1.3 m) as possible. All samples were air-dried to 12 % prior to assessment using X-ray densitometry equipment.

same values of ring-width and weighted density would be expected for a given family and year regardless of whether the radius was from the north or south side of the tree, or a mixture of both. As a consequence further analysis was based on the north radius only.

Summary statistics were calculated within SAS (1989) to estimate the mean density for each calendar year across all trees. This assisted in identifying the number of trees which contained a growth ring representing each of the calendar years since planting. Subsequent analysis was predominantly by combining a number of annual rings together to represent different age spans over the life of the tree. These were referred to as ring-groupings (RG). Ring-groupings generally consisted of four annual rings and increased in two-year units from the pith to the cambium. Exceptions to this were ring-groupings to represent (i) the complete juvenile core, (ii) the complete tree (iii) grouping of the youngest rings. The mean weighted density values of each of the various groupings were calculated prior to multivariate analysis.

The standard linear mixed model employed to estimate variance components and fixed effects for each ring-grouping was:

**Equation 2**

$$Y_{ijk} = \mu + R_i + F_j + f_{ij} + e_{ijk} \qquad (2)$$

where:

$Y_{ijk}$ = observed measurement of tree *ijk;*

$\mu$ = a fixed general mean;

$R_i$ = fixed effect of replicate *i*, *i* = 1, 2 or 3;

$F_j$ = random effect of family *j*, j = 1, 2, 3, ......., 46, Var ($F_j$) = $\sigma^2_f$;

$f_{ij}$ = random effect of family *j* in replicate *i*, Var ($f_{ij}$) = $\sigma^2_{fr}$;

$e_{ijk}$ = random error of tree *k* from family *j* in replicate *i*, Var ($e_{ijk}$) = $\sigma^2_e$;

All variance components, heritabilities and associated standard errors (SE) were estimated using **ASReml** (**A** **S**patial **Re**stricted **m**aximum **l**ikelihood), a mixed model analysis software programme developed by GILMOUR (1996) which in turn calls upon the original concepts of REML (PATTERSON and THOMPSON, 1971).

ASReml fits a general mixed model as follows:

**Equation 3**

$$y = \boldsymbol{X}b + \boldsymbol{Z}_1 a_1 + \boldsymbol{Z}_2 a_2 + \boldsymbol{e} \qquad \text{(GILMOUR, 1996)} \qquad (3)$$

where:

$y$ = *(n x 1)* vector of observations (i.e. measurements such as $Y_{ijk}$ in Equation 2);

$\boldsymbol{X}$ = *(n x p)* design matrix which relates each observation to the fixed effects *b* (replicates in Equation 2);

$\boldsymbol{Z}_1$ = *(n x q)* design matrix which relates observations to random family effects;

$b$ = (p x 1) vector of fixed effects;

$a_1$ = *(q x 1)* vector of random family effects ($\sigma^2_f$ in Equation 2);

$\boldsymbol{Z}_2$ = *(n x q)* design matrix which relates observations to random family x replicate interactions;

$a_2$ = (*q* x 1) vector of random family x replication effects ($\sigma^2_{fr}$ in Equation 2);

$\boldsymbol{e}$ = *(n x 1)* vector of independent random residual effects ($\sigma^2_e$ in Equation 2)

The analytical software carries out a REML type analysis, where fixed effects and variance components are estimated interactively as the model parameters reach convergence. All variance and covariance components were generated with associated standard errors. All data were standardised prior to analysis by deducting the mean and dividing by the standard deviation.

On all occasions analysis was carried out using the 690 trees from the 46 families chosen from the selection ellipse, using the complete datasets (125 families; >4,500 trees) of DN17 and DN16 as covariates.

Narrow sense single-tree ($h^2_i$) and family-mean heritabilities ($h^2_f$) for each ring-grouping were calculated according to standard formulae (WRIGHT, 1976).

The first four rings in from the bark were considered to be the breeding goal against which genetic and phenotypic correlations of all the other ring-groupings were estimated following quadrivariate analysis; consisting of the younger ring-grouping, the breeding goal, and co-variates DM17 and DN16. Phenotypic ($r_P$) and genetic ($r_A$) correlations between ring-grouping complete with associated standard errors were also calculated within ASReml according to standard formulae (FALCONER, 1981).

Generation efficiency ($Q_{gen}$) and efficiency of genetic gain per year of indirect selection based on young ring-groupings relative to direct selection for the breeding goal ($Q_{year}$) were investigated according to Equations (4) and (5) respectively for each ring-grouping.

**Equation 4**

$$Q_{gen} = \frac{\text{Gain in mature trait by selecting for the juvenile trait}}{\text{Gain in mature trait by selecting for mature trait}}$$

$$Q_{gen} = \frac{i_j h_j h_m r_{A_{jm}} \sigma_{P_m}}{i_m h^2_m \sigma_{Pm}}$$

This simplifies to:

$$Q_{gen} = r_{A_{jm}} \frac{i_j h_j}{i_m h_m} \qquad \text{(FALCONER, 1981)} \qquad (4)$$

where: the suffixes ('j' and 'm') refer to parameters at the juvenile and mature age respectively,

$i_j$ = selection intensity for the juvenile trait

$CG_m$ = correlated gain for mature trait

h = square root of the heritability at the mature (m) or juvenile (j) trait

$r_{Ajm}$ = genetic correlation between the mature and juvenile traits

$\sigma_{P_m}$ = phenotypic standard deviation for the mature trait

**Equation 5**

$$\text{Gain per year} = \frac{\text{Gain per generation}}{\text{Generation interval}}$$

$$Q_{year} = r_{A_{jm}} \frac{(i_j h_j h_m \sigma_{P_m})(T_m + d)}{(i_m h^2_m \sigma_{P_m})(T_j + d)} \qquad \text{(LAMBETH, 1980)} \qquad (5)$$

where: ($T_j$+*d*) = Generation interval (years).

and $T_j$ = Selection age (which may be at maturity when $T_j = T_m$).

*d* = Delay between selection and production of sufficient propagules to allow establishment of new genetic tests. Three models of delay were involved: (i) where *d* varies from 10 to five years according to selection age as outlined below in Table 2; (ii) *d* = five years; (iii) *d* = three years.

*Table 2.* – Variation of delay (*d*) with selection age (T) under model *d* = variable

| T | *d* |
|---|---|
| 1-6 years | 10 years |
| 7-8 years | 9 years |
| 9-10 years | 8 years |
| 11-12 years | 7 years |
| 13-14 years | 6 years |
| >15 years | 5 years |

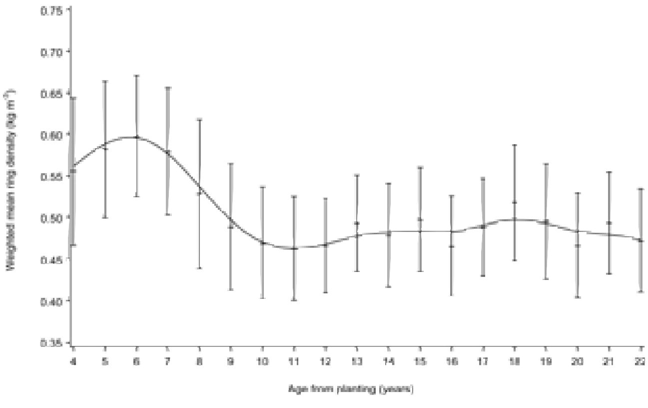
$T_j$ would equate to the oldest growth-ring within a grouping, whilst *d* was allowed to vary according to the three models
*viz d* = variable,
*d* = five years, and
*d* = three years.

## Results

### *Mean weighted density*

*Figure* 2 shows how mean weighted density of annual rings started high and reached a peak at age six before falling sharply to a minimum at age 11. Between 14 and 22 years the general trend was for weighted density to remain fairly constant with age.

Different trees reached the 1.3 m height point of sampling at different ages. The maximum number of annual rings within any sample was 19 (1975–1993). Only 5.5% of trees (38 out of 690) grew fast enough to produce a growth ring for 1975 (4th growing season) at 1.3 m although this had increased to 91% (628 trees) by the 8th growing season. There was a decrease in the number of trees containing rings representing the 21st and 22nd growing seasons due to the occasional breaking off and loss of annual rings during the sample preparation using the twin circular saws. Annual rings prior to 6-years old were ignored due to the small sample size. The youngest ring-grouping was therefore RG6-9.



Note 1: 1975 = 4 years old, 1993 = 22 years old. Smoothed curve fitted using splines. Bars +/- one standard deviation.

*Figure 2.* – Variation of weighted mean ring density with age from planting.

The mean weighted densities of the 11 different ring-groupings (RG) representing 1977–1980 (RG6-9) through to 1990–1993 (RG19-22) are given in *Table 3*. As in *Figure 2*, mean weighted density falls with increasing age of the constituent rings until RG10-13 after which there is a slight rise in density to RG12-15. There is little difference in the weighted densities of RG12-15 through to RG19-22. Estimates of $h_i^2$ and $h_f^2$ for ring-groupings are also given in *Table 3*. There is a clear indication that $h_i^2$ and $h_f^2$ decrease with increasing age of the ring-grouping. This was particularly marked for $h_i^2$ which varied from 0.85 (RG6-9) to 0.28 (RG16-19); $h_f^2$ varied from 0.96 (RG6-9) to 0.60 (RG12-15 and RG14-17). Estimates of $h_i^2$ and $h_f^2$ were similar for juvenile wood (RG8-15) and the complete tree (RG8-22) and were relatively high compared to some of the later-aged ring-groupings.

Estimated values of genetic and phenotypic correlations between the mean weighted wood-density of RG19-22 and the other ring-groupings are given in *Table 4*. All genetic correlations were greater than the equivalent phenotypic correlation although this differential did decrease as mean age of the ring grouping increased, eg, RG6-9, $r_A = 0.95$ and $r_P = 0.55$ but RG18-21, $r_A = 0.95$ and $r_P = 0.90$. All estimates of genetic correlations were very high enabling very early indirect selection for mature wood density. Standard errors varied little although they did decrease slightly as the age of the ring-grouping approached that of the breeding goal.

*Table 3.* – Data on 4-ring groupings: Mean weighted density and numbers of trees representing each ring-grouping

| Measurement Year | Ring Grouping (RG) (years from planting) | Number of Trees | Mean Weighted Density (kg m$^{-3}$) | $h_i^2$ | $h_f^2$ |
|---|---|---|---|---|---|
| 1977-80 | RG6-9 | 376 | 0.512 ± 0.07 | 0.85 ± 0.18 | 0.96 ± 0.07 |
| 1978-81 | RG7-10 | 524 | 0.489 ± 0.06 | 0.59 ± 0.14 | 0.84 ± 0.08 |
| 1979-82 | RG8-11 | 628 | 0.472 ± 0.06 | 0.59 ± 0.12 | 0.83 ± 0.07 |
| 1981-84 | RG10-13 | 686 | 0.466 ± 0.05 | 0.47 ± 0.10 | 0.74 ± 0.08 |
| 1983-86 | RG12-15 | 686 | 0.479 ± 0.05 | 0.32 ± 0.09 | 0.60 ± 0.10 |
| 1985-88 | RG14-17 | 682 | 0.477 ± 0.05 | 0.32 ± 0.09 | 0.60 ± 0.10 |
| 1987-90 | RG16-19 | 674 | 0.4883 ± 0.05 | 0.28 ± 0.08 | 0.75 ± 0.19 |
| 1989-92 | RG18-21 | 638 | 0.4886 ± 0.05 | 0.33 ± 0.11 | 0.61 ± 0.11 |
| 1990-93 | RG19-22 | 592 | 0.478 ± 0.05 | 0.34 ± 0.12 | 0.62 ± 0.12 |
| 1978-86 | RG8-15 | 627 | 0.473 ± 0.05 | 0.53 ± 0.11 | 0.78 ± 0.08 |
| 1978-93 | RG8-22 | 544 | 0.473 ± 0.05 | 0.54 ± 0.12 | 0.79 ± 0.08 |

*Table 4.* – Genetic and phenotypic correlations between RG19-22 and the weighted density of other ring-groupings.

| **GENETIC CORRELATIONS ( $r_A$ ):**** | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | **RG6-9*** | **RG7-10** | **RG8-11** | **RG10-13** | **RG12-15** | **RG14-17** | **RG16-19** | **RG18-21*** | **RG8-22** | **RG8-15** |
| **RG19-22** | 0.9500 | 0.9500 | 0.9500 | 0.9500 | 0.9500 | 0.9500 | 0.9500 | 0.9500 | 0.9500 | 0.9500 |
| **S.E.** | 0.1664 | 0.1598 | 0.1732 | 0.1912 | 0.1447 | 0.0897 | 0.0639 | 0.0378 | 0.0698 | 0.1710 |
| **PHENOTYPIC CORRELATIONS ( $r_P$ ):** | | | | | | | | | | |
| | **RG6-9*** | **RG7-10** | **RG8-11** | **RG10-13** | **RG12-15** | **RG14-17** | **RG16-19** | **RG18-21*** | **RG8-22** | **RG8-15** |
| **RG19-22** | 0.5543 | 0.5740 | 0.6053 | 0.6379 | 0.6621 | 0.7483 | 0.8278 | 0.8958 | 0.8674 | 0.6793 |
| **S.E.** | 0.0365 | 0.0318 | 0.0303 | 0.0288 | 0.0251 | 0.0190 | 0.0128 | 0.0875 | 0.0134 | 0.0269 |

Note: 1. ** The ASReml routine has a restriction factor which prevents correlations from exceeding 0.95
2. * Did not converge
3. DM16 and DN17 included as covariates.

*Table 5.* – Genetic and Phenotypic correlations between 16-year diameter (DM16) and 17-year density (DN17; assessed using the pilodyn) with mean weighted density of ring-groupings assessed using X-ray densitometry.

| **Ring-Grouping (years from planting)** | **DM16** | | **DN17** | |
|---|---|---|---|---|
| | $r_A$ | $r_P$ | $r_A$ ## | $r_P$ |
| **RG6-9** | -0.70 | -0.59 | -0.82 | -0.55 |
| **S.E.** | 0.14 | 0.03 | 0.09 | 0.03 |
| **RG7-10** | -0.74 | -0.64 | -0.89 | -0.58 |
| **S.E.** | 0.12 | 0.03 | 0.08 | 0.03 |
| **RG8-11** | -0.76 | -0.62 | -0.88 | -0.60 |
| **S.E.** | 0.11 | 0.02 | 0.07 | 0.02 |
| **RG10-13** | -0.78 | -0.63 | -0.90 | -0.74 |
| **S.E.** | 0.10 | 0.04 | 0.071 | 0.04 |
| **RG12-15** | -0.71 | -0.60 | -0.95 | -0.61 |
| **S.E.** | 0.14 | 0.02 | 0.13 | 0.02 |
| **RG14-17**** | -0.64 | -0.63 | -0.95 | -0.66 |
| **S.E.** | 0.15 | 0.02 | 0.16 | 0.02 |
| **RG16-19** | -0.64 | -0.60 | -0.95 | -0.63 |
| **S.E.** | 0.16 | 0.02 | 0.20 | 0.02 |
| **RG18-21** | -0.62 | -0.49 | -0.95 | -0.55 |
| **S.E.** | 0.18 | 0.03 | 0.17 | 0.03 |
| **RG19-22** | -0.80 | -0.46 | -0.95 | -0.54 |
| **S.E.** | 0.18 | 0.03 | 0.25 | 0.03 |
| **RG8-22** | -0.77 | -0.62 | -0.95 | -0.67 |
| **S.E.** | 0.11 | 0.02 | 0.10 | 0.02 |
| **RG8-15** | -0.76 | -0.63 | -0.94 | -0.63 |
| **S.E.** | 0.10 | 0.02 | 0.06 | 0.02 |

Note: 1. ## ASReml contains a restriction factor which restrains genetic correlations to a maximum of 0.95
2. ** Indicates rings penetrated by the Pilodyn.

*Table* 5 gives the genetic and phenotypic correlations of the different ring-groupings with the covariates DM16 and DN17. All estimates are negative and genetic correlations exceed phenotypic correlations on all occasions. Estimates of $r_{ARG,DM16}$ varied between –0.62 (RG18-21) and –0.80 (RG19-22). The genetic correlations of DM16 with RG8-15 and RG8-22 were both greater than –0.75 suggesting strong negative correlations between both juvenile wood and complete tree density with DM16. All estimates of $r_{ARG,DN17}$ were greater than –0.82, and most were –0.95 suggesting 17-year Pilodyn assessment would be effective in ranking trees for both juvenile wood and complete-tree wood density.

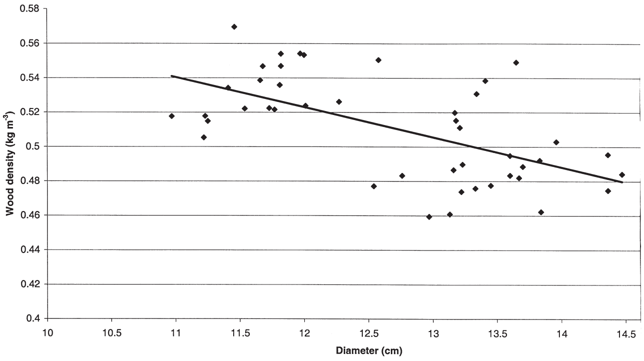


*Figure 3.* – Relationship between family-mean 16-year diameter and wood density of rings 8–22 years (RG-22).

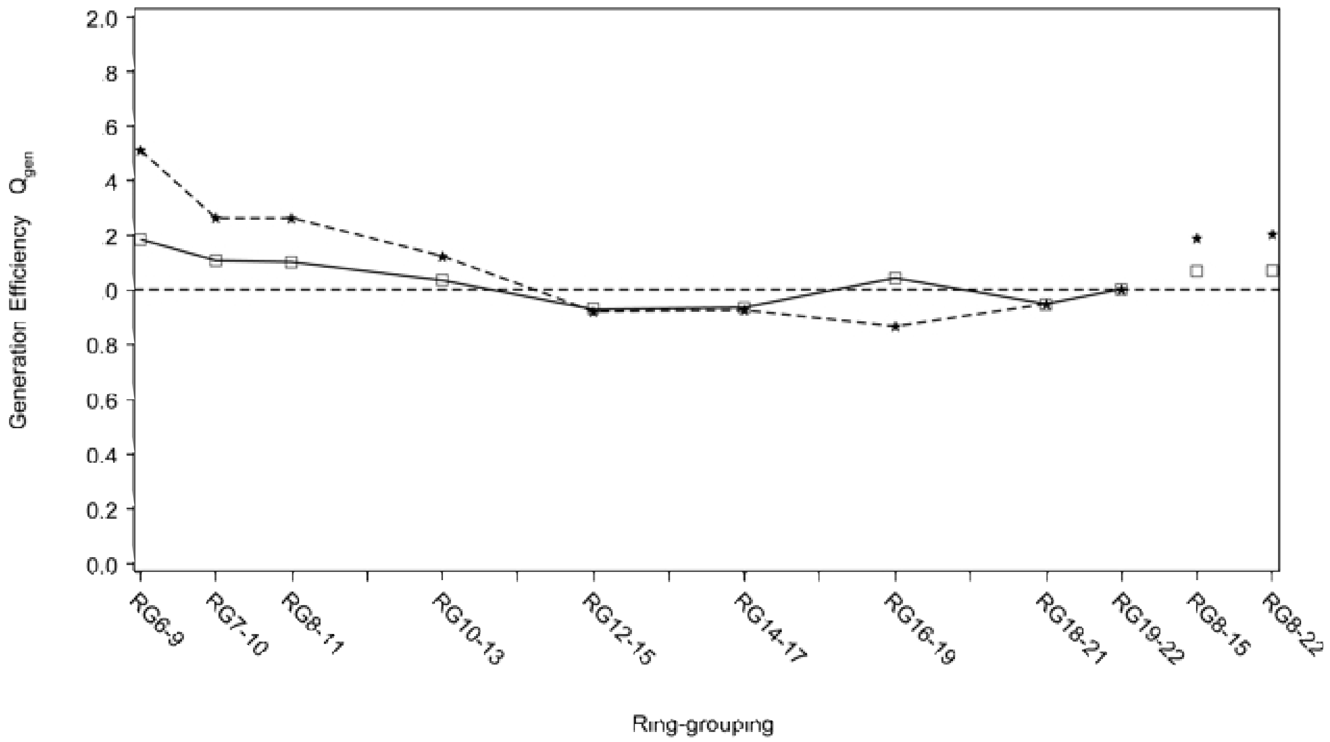
*Figure 3* illustrates the relationship at the family mean level between 16-year diameter and wood density of RG8-22. This shows that despite the high genetic correlation between these two traits 'correlation breakers' (KLEINSCHMIT *et al.*, 1993) do exist; that is families with well above average wood density despite above average diameter.

*Early selection for wood density*

*Figures 4* and *5* show how the generation efficiency ($Q_{gen}$) and relative genetic gain per year ($Q_{year}$) were both improved relative to direct selection for the breeding goal (RG19-22) by early, indirect selection for weighted density. This was a feature of the relatively higher single tree and family heritabilities estimated for the more juvenile ring-groupings along with their very high genetic correlations with the breeding goal.

Generation efficiency was greatest for both single tree and family selection at very early ages (RG6-9) and then fell gradually in line with the trends for heritabilities. $Q_{gen}$ based on juvenile wood (RG8-15) and the complete tree (RG8-22) were both similar and were improved relative to direct selection.

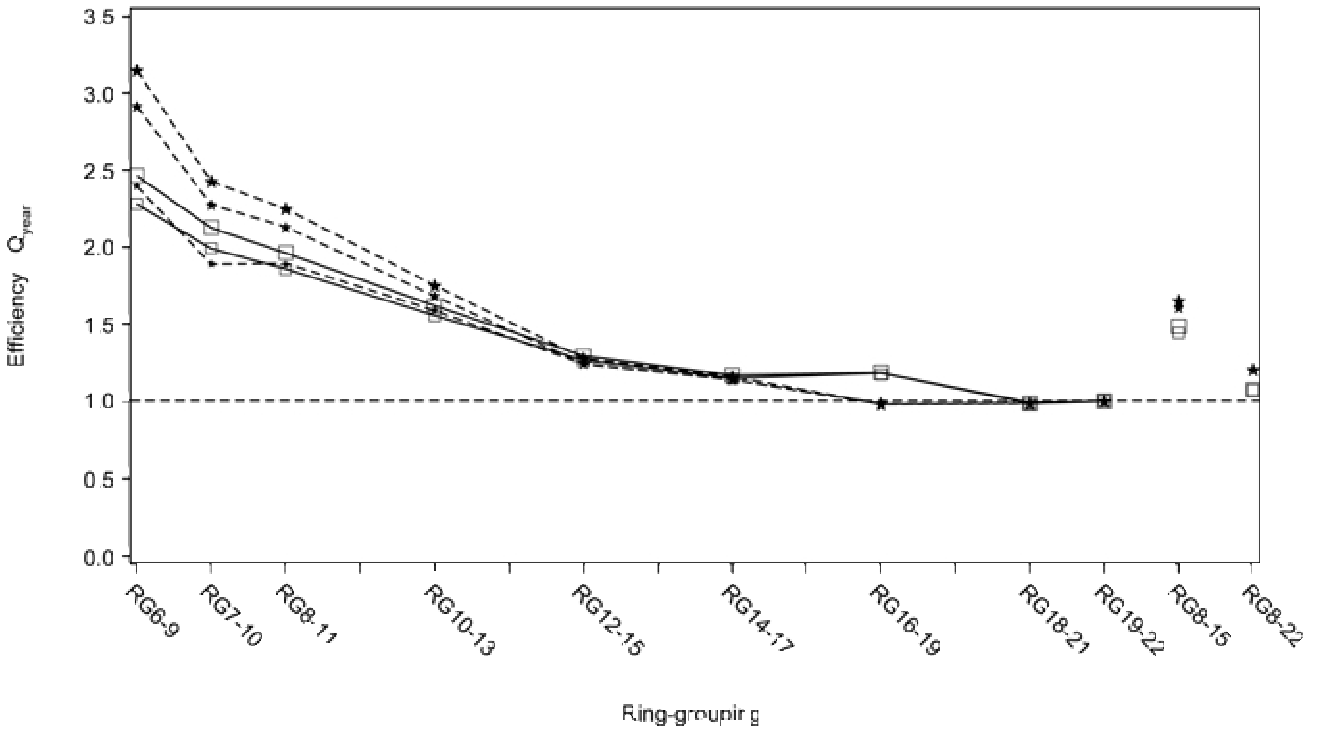
$Q_{year}$ was greater than 1.00 for all juvenile selection ages. Maximum $Q_{year}$ for both single tree and family selection was



Note ★ = ndividual tree $Q_{gen}$ ☐ = Family $Q_{gen}$

Note 2: Breeding goal is RG 9-22 years. At this point $Q_{gen}$ is .00 for both individual tree and family selection

*Figure 4.* – Variation of individual tree and family generation efficiency ($Q_{gen}$) according to ring-grouping.



Note 1 ★ Indiv, d = variable ★ Indiv d = 5 years ★ Indiv d = 3 years ☐ Family, d = 5 years ☐ Family d = 3 year

Note 2: Breeding goal is RG19-22 years. At this point $Q_{year}$ is 1.00 for both individual tree and family selection

*Figure 5.* – Variation of relative individual tree and family genetic gain per year ($Q_{year}$) according to ring-grouping.

obtained by indirect selection based on RG6-9; this applied to all three delay ($d$) models. $Q_{year}$ would be increased by 140 % following forward selection based on mean weighted density of rings RG6-9 even with the most pessimistic model of delay ($d$ = variable). This efficiency would be increased to 190 % and 214 % when d = 5 and d = 3 years respectively.

Family selection based on RG6-9 would improve the efficiency of $Q_{year}$ by nearly 130 % and 150 % when $d$ = 5 and $d$ = three years respectively. The value of ($d$) decreases in importance as the maximum age of rings within the ring-grouping approached the breeding goal.

## Discussion

*i. Changes in wood density from the pith to the cambium:*

The variation in mean ring density from the pith to the cambium found in this study was typical of similar earlier studies by BRYAN and PEARSON (1955), BRAZIER (1967) and WOOD (1986). In all cases, the density was initially very high around years four to five from the pith before falling quickly to a minimum around 10–15 years, after which there was a slight rise to a plateau as mature wood density was laid down by the tree.

*ii.Changes of heritability with age:*

This is the first time that time-trend heritabilities for wood density have been reported for Sitka spruce. A clear trend has been found in the variation of single tree and family heritability of wood density with age. Both $h_i^2$ and $h_f^2$ were very high for the most juvenile ring-grouping (RG6-9; 0.85 and 0.96 respectively) but then fell sharply before levelling off around RG12-15 (0.31 and 0.59 respectively). These latter estimates of single tree heritability were lower than those reported by WOOD (1986; 0.73 to 0.91) and LEE (1993; 0.43) for equivalent ages in their respective studies of the variation of wood density within selected Sitka spruce populations of possible mixed origins.

Reports of the variation of heritability of wood density over time in other species are rare, although most give constant or slightly increasing estimates of $h_i^2$ with age. LOO *et al.* (1984) found $h_i^2$ to increase from 0.77 to > 1.00 between rings 2 and 16–22 in a study of 15 open-pollinated loblolly pine families although this was perhaps too small a sample size for reliable estimates of $h_i^2$. WILLIAMS and MEGRAW (1994) also working with loblolly pine found a slight decrease in $h_i^2$ of wood density between 3-years (0.53) and 13-years (0.42) from planting although again the sample size was small (families = 15). ADAMS *et al.* (1990) found a slight rise in $h_i^2$ for wood density in Douglas fir between 8-years (0.50), 11-years (0.56) and 15-years (0.59).

The criticism of reporting heritabilities without fully taking into account the effects of selection is true of all these previous studies. Only TALBERT *et al.* (1983) working with loblolly pine reported heritabilities from an unselected population and that study did not have the advantage of using a selection ellipse or covariates to link the wood density data with the much larger population from which the sub-sample ($n$ = 14 and $N$ = 45) was selected.

*iii. Age:age correlations of wood density:*

Genetic correlations between the juvenile and mature ring-groupings investigated in this study were all very high (near unity) and always exceeded the equivalent juvenile:mature phenotypic correlations. It is quite clear that the wood density of rings 6–9 years from the pith would give an excellent indication of mature wood density 19–22 years from the pith.

This is the first time that genetic age:age correlations for wood density have been reported in Sitka spruce. BRAZIER (1970) made a phenotypic comparison of juvenile and mature wood densities of young plantation trees. He concluded that the selection of trees with average to above average juvenile wood density resulted in trees with a higher proportion of average or above average mature wood density. Such a conclusion based on phenotype only and with no genetic base suggested a phenotypic correlation between juvenile and mature wood densities substantially greater than zero. WOOD (1986) did not carry out age:age correlations in the progeny tests that composed her main study, but did investigate a phenotypic juvenile:mature correlation for the trees from just two families of differing origins in a pilot study. She found that the density of rings 11–15 (from the pith) gave a good indication of 30-year whole tree density.

The ability to carry out indirect selection for mature wood density based on very young juvenile wood density has already been proven for a number of species. TALBERT *et al.* (1983), LOO *et al.* (1984) and WILLIAMS and MEGRAW (1994) all found $r_{Aj,m}$ greater than 0.80 between growth rings within a juvenile wood stage (sometimes as early as two years from planting) and mature wood density in loblolly pine. Studies by MCKIMMY and CAMPBELL (1982) and ABDEL-GADIR *et al.* (1993) with Douglas fir both recommend indirect selection for mature wood density (rings 15–25 and approximately 50–60 respectively) based on juvenile wood density (rings 6–15 and 1–10 respectively). Neither of these studies investigated very early selection involving small ring-groupings of very juvenile ages. ADAMS, *et al.* (1990) in a study of very early selection for wood density in Douglas fir found $r_{Aj,m}$ = 0.90 and 0.65 between 15-year density with 8-year density in the field and two-year density in the nursery respectively. MADDERN-HARRIS (1965) found $r_{Pj,m}$ = 0.97 between rings 3 and all rings beyond 15 from the pith in radiata pine, while CORRIVEAU *et al.* (1991) found $r_{Aj,m}$ = 1.00 between juvenile wood (1–16 rings) and mature wood (17–23 rings) in white spruce.

*iv. Estimates of generation efficiency and relative genetic gain per year:*

It follows from the high heritabilities of juvenile ring-groupings and the very high juvenile:mature correlations between those ring-groupings and the breeding goal, that both $Q_{gen}$ and $Q_{year}$ would be maximised well before the breeding goal (RG 19-22). The optimum selection age for both single tree and family selection of mature wood density in terms of both generation efficiency and relative genetic gain per year was based on the weighted mean density of RG6-9; the most juvenile ring-grouping included in this study.

Reported estimates of $Q_{gen}$ and $Q_{year}$ for wood density are rare; conclusions as to optimum selection ages have usually been based directly on estimates of juvenile:mature correlations. WILLIAMS and MEGRAW (1994) found relative gain efficiencies (equivalent to $Q_{gen}$) of 84–114 % for 12-year density based on indirect selection for two or three year density. DEAN (1990) found an increase in $Q_{gen}$ but not $Q_{year}$ by indirect selection of 15-year dry weight (density x surface area) based on the dry weight of rings 3–7 from the pith.

*v. Indirect assessment of wood density:*

The Pilodyn remains a useful tool with which to perform indirect assessments of wood density. This study has for the first time in Sitka spruce presented genetic correlations between wood density assessed using X-ray densitometry and the Pilodyn. The estimated values of $r_A$ = –0.95 are far greater than the previous values of $r_P$ = –0.69 found by WOOD (1986), although equivalent values of $r_P$ estimated in this study (–0.67) were similar to those found by WOOD (1986).

*vi. Genetic correlation of wood density and stem diameter:*

This study confirms that there is a high negative correlation between wood density and stem diameter in Sitka spruce. The only previous estimates based on direct assessment of wood density involved phenotypic correlations between whole-tree density and 15-year diameter of progeny derived from a selected population (Wood, 1986; = $r_P$ –0.34 to –0.69). Results presented here suggest possibly lower estimated phenotypic correlations than those found by Wood for the equivalent ages ($r_P$ of DM16 with RG14-17 = –0.63). However, estimates of the genetic correlations between weighted wood density of the more juvenile ring-groupings, and juvenile and whole-tree density with DM16 are high. This means that particular care must be taken in selecting trees with improved diameter for the Sitka spruce breeding programme since in general, selection for a population of trees with above average diameter would indirectly result in a population of trees with below average wood density. It is important to note however that despite the high negative genetic correlation between wood density and diameter, it is still possible to select families which do not follow the general trend; so called 'correlation breakers' (Kleinschmit *et al.*, 1993). Provided tree breeders retain information at an individual family level and screen a sufficiently large number of phenotypes it ought to be possible to achieve positive improvements in each trait (Lee, 2001).

## Conclusions

i. Single tree and family mean heritability for mean weighted wood density starts very high for RG6-9 before falling gradually to RG12-15 after which there is little variation with increasing age of the ring-grouping.

ii. There are very high genetic correlations ($r_A$ close to unity) between mean weighted density of the breeding goal RG19-22 and all juvenile ring-grouping combinations.

iii. All genetic correlations between ring-groupings and the breeding goal are higher than the equivalent phenotypic correlation.

iv. Genetic correlation between 16-year diameter and ring-grouping 19–22 years suggests a stronger than previously estimated negative relationship between mature wood density and vigour.

v. From the data investigated, the recommended optimum indirect selection age and trait for wood density in Sitka spruce is the mean weighted density of the outer four rings from a 9-year old tree. This applies to both single-tree and family-mean selection.

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