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A Study of Population Variation and Inheritance in Sitka Spruce

II. Age Trends in Genetic Parameters for Vigour Traits and Optimum Selection Ages

By S. J. Lee[1], J. Woolliams[2], C. J. A. Samuel[1] and D. C. Malcolm[3])

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Abstract

This study represents the second in a series investigating the additive genetic variance operating within an unselected population of Sitka spruce trees of known single origin. The first study presented by Samuel and Johnstone (1979) looked at height between 1 and 6 years from planting. This study looks at the additive genetic control of growth traits at just one site up to 23 years from planting. Basic genetic statistics for each individual trait are presented along with the genetic relationship between each trait and the optimum ages of selection relative to mature ages of 23 years and 40 years. Analysis was carried out at both the individual tree and family-mean level.

The optimum individual tree and family mean selection ages in terms of generation efficiency were 9 year height and 23 year diameter respectively. When selection was based on genetic gain per year, the optimum ages were again 9 year height at the individual tree level, but fell to 5-year height at the family-mean level.

There was very little difference in optimum selection ages depending on the age of the mature trait. Efficiencies could be improved and selection ages reduced if the delay necessary to bring juvenile selections to flower could be reduced to just 3 years or 5 years.

Key words: Picea sitchensis, genetic correlations, phenotypic correlations, heritability, indirect selection.

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[1] Forestry Commission Research Agency, Northern Research Station, Roslin, Midlothian, EH25 9SY, Scotland

[2] Roslin Institute, Roslin, Midlothian, EH25 9PS, Scotland

[3] Institute of Ecology and Resource Management, Darwin Building, The King's Buildings, Mayfield Road, Edinburgh, EH9 3JU, Scotland

Introduction

Most breeding programmes are based on estimated variance components derived from populations of trees selected for economic traits such as growth rate, stem form and wood density. Only if variance components are derived from an unselected population will they be free of any artificially induced bias for the selected and correlated traits. A soundly based breeding strategy is dependent on reliable information on the underlying variation and pattern of inheritance. When accurate estimates of 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 run concurrently with the operational testing and selection programmes such that an existing programme may have its efficiency increased, or direction altered.

Sitka spruce (*Picea sitchensis* (BONG.) CARR.) is the main plantation species in 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 (QCI; British Columbia, Canada) origin, 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 been presented by GILL (1987) and LEE (1999).

In 1969 there was the opportunity to collect seed from a stand of known 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. They found then that heritabilities were initially high in year 1 reflecting the homogeneous conditions in the nursery ($h^2 = 0.30$) before falling in year 2 ($h^2 = 0.16$) followed by a gradual rise up to year 6 ($h^2 = 0.27$). Family rank changes were considered too extreme in the first 4 years and early selection could not proceed with any confidence until after 4 to 6 years from planting.

GILL (1987) presented variance components, heritabilities and juvenile:mature correlations for growth traits of Sitka spruce from two studies involving progeny from selected parents. Both studies indicated high correlations between height as early as 3 years and later measures of vigour. He concluded that retention of progeny tests to 15 years gave little further advantage in terms of selection for vigour over selection at 6 years or even 3 years from planting.

Assessment of the progeny reported by SAMUEL and JOHNSTONE (1979) has continued for a number of traits over the intervening years. It is now possible to see how variance components have changed over nearly half a rotation and investigate juvenile:mature correlations with a view to finding optimum selection ages within this unselected population.

The objectives of this study were to analyse the half-sib progeny data collected for growth traits in order to determine:

i. how the genetic variance components and heritabilities varied with age;

ii. how genetic and phenotypic correlations between traits varied over time; and

iii. optimum selection ages.

Optimum selection ages were investigated for single tree and family selection. Family selection is important in 'backward' selecting tested genotypes or re-creation of families which may be included in production populations. Single tree selection is important for 'forward' selection of trees 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). 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 was 6 plus trees, 48 dominants, 61 co-dominants and 35 sub-dominants.

Extracted seed were raised in the nursery for 2 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 two other 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; the other two were rejected due to extensive areas of windblow and within site heterogeneity based on analysis of 1 to 6 years height. The reduction of sites was not thought to be too restrictive since SAMUEL and JOHNSTONE (1979) found no significant family x site interaction from year 5 onwards.

The study site was located in Garcrogo Forest in south-west Scotland (55° 6' N, 3° 54' W) at an elevation of 230 m to 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 m x 2 m spacing in 7 x 7 (49) tree block plots in spring 1972. There were 125 families in each of three randomised complete blocks making this a large experiment extending over 9.5 hectares. Standard silvicultural management of the site was practised. Survival at the end of the first growing season was in excess of 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.

The first assessment carried out was height (HT) at the end of the first growing season (HT01). Height was then measured annually up to 11 years from planting (HT11). Diameter (DM) was measured periodically from 10 years (DM10) to 23 years (DM23) from planting.

Statistical Methods

Routine analysis of the data was carried out using the Statistical Analysis System package (SAS, 1982). Standard deviations and mean values for all traits were calculated using PROC MEANS within SAS. The standard linear mixed model employed to estimate trait specific variance components and fixed effects was:

[Equation 1]

$$Y_{ijk} = \mu + R_i + F_j + f_{ij} + e_{ijk}$$

where:

Y_{ijk} = observed measurement of tree ijk;

μ = 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, ..., 125, $\mathrm{Var}(F_j) = \sigma^2_f$;

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

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

All variance components, heritabilities and associated standard errors (SE) were estimated using *ASReml,* a mixed model analysis software programme developed by GILMOUR (1996). Central to the ASReml analysis is the Average Information Restricted Maximum Likelihood (AIREML) derivative of GILMOUR *et al.* (1995).

ASReml fits a general mixed model as follows:

[Equation 2]

$$y = Xb + Z_1 a_1 + Z_2 a_2 + e$$ (GILMOUR, 1996)

where:

y = (n x 1) vector of individual tree observations (measurements such as Y_{ijk} in Equation 1);

X = (n x p) design matrix which relates each observation to the fixed effects b (replicates R_i in Equation 1);

Z_1 = (n x q) design matrix which relates observations to random family effects;

a_1 = (q x 1) vector of random family effects (σ^2_f in Equation 1);

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 (σ^2_{fr} in Equation 1);

e = (n x 1) vector of independent random residual effects (σ^2_e in Equation 1).

The software carries out a REML type analysis since fixed effects and variance components are constantly being estimated and amended as the model attempts to reach convergence. All variance and covariance components are generated with associated standard errors (SEs). The only fixed effects to be generated were those for 'replicate'. Both univariate and bivariate analyses were performed using ASReml.

Univariate analysis

The input file was constructed to generate variance components and estimates of fixed effects according to equation 1. The output file included estimates of the fixed and random effects specified by the model:

i. σ^2_f which is the variance between family means equivalent to ¼ of the additive genetic variance (¼ σ^2_A, FALCONER, 1981);

ii. σ^2_{fr} which is the variance of family by replicate interaction;

iii. σ^2_e which is the residual variance made up of the sum of the balance of the additive genetic variance (σ^2_A) and all the non-additive genetic variance (σ^2_{NA}) and all the remaining independent random environmental effects (σ^2_w), referred to as 'variance' in the output files;

iv. estimates of replicate mean.

Variance components were used to estimate narrow sense single-tree (h^2_i) and family-mean (h^2_f) heritabilities according to standard formulae (WRIGHT, 1976).

Bivariate analysis

Prior to analysis, each individual tree value was standardised by subtracting the trait mean and dividing by the standard deviation (SD) to give a mean = 0 and SD = 1. Standardising the data did not affect the calculation of phenotypic and genetic correlations or their associated standard errors, but had the advantage of reducing computation loading by ensuring an assumption of homogeneous variances would be met and providing a more stable means of estimating initial variance components since all variances (σ^2_f, σ^2_{fr} and σ^2_e) within bivariate runs sum to 1.00 in the input file.

Bivariate analysis was only carried out between traits and ages which were perceived to be of importance. This methodology was often iterative and evolved from previous analyses as trends developed with age in estimated correlation coefficients. Phenotypic (r_p) and genetic (r_A) correlations between two traits complete with associated standard errors were also calculated within ASReml according to standard formulae (FALCONER, 1981).

Optimum selection age for vigour

Gain in the mature trait, based on selection for a juvenile indicator trait, is indirect selection, and the correlated genetic gain for the mature trait is:

[Equation 3]

$$CG_m = i_j h_m h_j r_{A_{jm}} \sigma_{P_m}$$

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

CG_m = correlated gain for mature trait

i_j = selection intensity for the juvenile 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

σ_{P_m} = phenotypic standard deviation for the mature trait

The generation efficiency (Q_{gen}) of selection based on the juvenile trait relative to selection based on the mature trait can be expressed as the ratio of correlated to direct response:

[Equation 4]

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

which simplifies to: (FALCONER, 1981)

$$Q_{gen} = r_{A_{jm}} \frac{i_j h_j}{i_m h_m}$$

Tree breeders may then choose to carry out indirect selection for the mature trait at the age when Q_{gen} is a maximum.

Gain per year is another means of interpreting the rate of genetic gain. The optimum selection age is that which yields the greatest gain per year. The efficiency of correlated response relative to direct gain can be expressed in terms of gain per year:

[Equation 5]

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

where $(T_j + d)$ = generation interval (years)

and T_j = selection age (which may be at maturity when $T_j = Tm$)

d = delay between selection and production of sufficient propagules to allow establishment of new genetic tests.

It follows from equations 4 and 5 that an increase in gain per generation or gain per year for the mature trait based on indirect selection for the juvenile trait will only occur if $(r_{A_{jm}} i_j h_j) > i_m h_m$.

Selection goal of 23-year diameter

Generation efficiency (Q_{gen}) and gain per year (Q_{year}) of correlated response relative to direct gain of 23-year diameter were investigated by substituting estimated values directly into equations (4) and (5).

Selection goal of 40-year diameter or height

LAMBETH (1980) proposed a simple predictive model to assist tree breeders in calculating age:age correlation coefficients between any two ages:

[Equation 6]

$$r = b + m\,(LAR)$$

where: r = phenotypic correlation;

m = slope of regression line;

b = intercept on the X-axis;

LAR = $\log_e (T_j/T_m)$;

Phenotypic and genetic correlations estimated from the bivariate analysis were used to calculate LAMBETH (1980) regression equations, in this way juvenile:mature correlations could be extrapolated beyond the age of the most mature vigour trait assessed. The selection goal was extended to 40-year height (or diameter). The correlation coefficients estimated using the regression equation could then be used to estimate optimum selection ages for 40-year height or diameter in the equations for Q_{gen} and Q_{year} above.

The original LAMBETH equation (1980) was based on phenotypic age:age correlations only, involving just total height. In this study three predictive equations were calibrated for both phenotypic and genetic correlations (6 equations in all) according to the relationship of the traits involved in the bivariate analysis:

i. diameter_j : diameter_m correlation coefficients only (r_{ADD} and r_{PDD});

ii. height_j : height_m correlation coefficients only (r_{AHH} and r_{PHH});

iii. height_j : diameter_m correlation coefficients only (r_{AHD} and r_{PHD}).

Equal heritabilities were assumed between the juvenile and mature ages.

Flowering delay (d)

The delay in bringing trees to a state of readiness for flowering is a function of technical ability and physiological maturity. In the case of family selection, the parents are already physiologically mature and the delay can be considered to be associated exclusively with technical ability. The delay associated with forward selection of individual trees in a late flowering species such as Sitka spruce (GORDON and FAULKNER, 1992) is dependent on an unknown combination of technical ability and physiological maturity. The assumption was made that $d = 10$ years for very early selections, until $T_j = 7$ after which d falls by one year for each 2 year increase in selection age to a minimum of $d = 5$ years (technical ability only) when $T_j = 15$ years from planting. This model was referred to as d = variable and represents the most likely delay achievable in practice for Sitka spruce (J. J. PHILIPSON[4]), *pers. comm.*).

Two other models of delay, $d = 5$ years and $d = 3$ years, were also included. These latter two models refer to family selection and forward selection if technical ability and manipulation of physiological maturity develop sufficiently.

Results

Univariate analysis

Basic genetic statistics are presented in *table 1*. Single tree heritability showed a rise with age of height assessment after year 3, followed by a fall with age of diameter assessment although this was reversed slightly following thinning. The values of family heritability remained fairly constant across ages and traits.

Bivariate analysis

A matrix of the 76 estimated r_A and r_p values is given in *table 2*. In general, r_A was always greater than r_p. Genetic correlations of early height traits with DM23 rose quickly to $r_A > 0.70$ at HT04 and then continued to rise more gradually with age thereafter. All diameter traits had $r_A > 0.90$. DM10 was better correlated with DM23 than HT10 ($r_A = 0.90$ and 0.81 respectively), DM10 and HT10 were well correlated ($r_A = 0.90$).

Optimum selection ages

Selection goal of 23-year diameter

Generation Efficiency (Q_{gen})

Figure 1 shows how individual tree and family Q_{gen} varied with age. There was a clear distinction between Q_{gen} for the

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[4]) Project Leader (retired) for Flowering Research, Forest Research Agency

Table 1. – Univariate analysis. Basic genetic statistics for the 18 traits measured.

	Mean (cm)		SD	σ^2_f	σ^2_{fr}	σ^2_e	h^2_i		SE	h^2_f		SE
HT01	**27.63**	**±**	**7.27**	**4.22**	**6.46**	**42.23**	**0.32**	**±**	**0.07**	**0.61**	**±**	**0.06**
HT02	**46.60**	**±**	**13.79**	**7.05**	**12.92**	**163.98**	**0.15**	**±**	**0.04**	**0.52**	**±**	**0.07**
HT03	**69.49**	**±**	**20.66**	**14.53**	**44.92**	**344.51**	**0.14**	**±**	**0.05**	**0.43**	**±**	**0.09**
HT04	**100.46**	**±**	**30.30**	**47.69**	**132.89**	**684.79**	**0.22**	**±**	**0.06**	**0.47**	**±**	**0.08**
HT05	**149.93**	**±**	**39.21**	**95.06**	**211.08**	**1133.23**	**0.26**	**±**	**0.06**	**0.53**	**±**	**0.07**
HT06	**189.65**	**±**	**48.19**	**175.23**	**350.32**	**1658.55**	**0.32**	**±**	**0.07**	**0.56**	**±**	**0.07**
HT07	**255.42**	**±**	**63.90**	**368.67**	**731.85**	**2752.32**	**0.38**	**±**	**0.08**	**0.56**	**±**	**0.07**
HT08	**324.20**	**±**	**73.58**	**470.63**	**1007.41**	**3680.62**	**0.36**	**±**	**0.08**	**0.55**	**±**	**0.07**
HT09	**359.64**	**±**	**75.11**	**467.11**	**1090.18**	**3816.82**	**0.35**	**±**	**0.08**	**0.53**	**±**	**0.07**
HT10	**436.56**	**±**	**84.86**	**619.23**	**1329.83**	**4987.63**	**0.36**	**±**	**0.08**	**0.55**	**±**	**0.07**
HT11	**511.78**	**±**	**63.62**	**779.75**	**1608.38**	**6104.35**	**0.37**	**±**	**0.08**	**0.56**	**±**	**0.07**
DM10	**7.41**	**±**	**1.74**	**0.20**	**0.04**	**2.35**	**0.27**	**±**	**0.06**	**0.56**	**±**	**0.07**
DM12	**8.76**	**±**	**1.93**	**0.21**	**0.33**	**3.06**	**0.23**	**±**	**0.05**	**0.58**	**±**	**0.07**
DM14	**9.78**	**±**	**2.12**	**0.19**	**0.26**	**3.96**	**0.17**	**±**	**0.04**	**0.58**	**±**	**0.07**
DM16	**11.15**	**±**	**2.44**	**0.19**	**0.17**	**5.52**	**0.13**	**±**	**0.03**	**0.59**	**±**	**0.06**
DM17	**11.92**	**±**	**2.66**	**0.22**	**0.17**	**6.63**	**0.12**	**±**	**0.03**	**0.59**	**±**	**0.06**
DM19	**12.66**	**±**	**2.77**	**0.36**	**0.16**	**7.07**	**0.19**	**±**	**0.04**	**0.59**	**±**	**0.06**
DM23	**15.08**	**±**	**3.40**	**0.43**	**0.04**	**11.09**	**0.15**	**±**	**0.03**	**0.57**	**±**	**0.07**

$\sigma^2_e = \frac{3}{4}\,\sigma^2_A + \sigma^2_{NA} + \sigma^2_W$ where σ^2_W = random evironment error, σ^2_A= additive genetic variances, σ^2_{NA} = non-additive genetic variance, SE = Standard Error, SD = Standard Deviation

individual tree which rose to a peak between HT09 and HT11 before falling, and that for family selection which rose gradually between HT01 to DM23 years, but never exceeded 1.00. Variation in Q_{gen} with age was dependent on the ratio of the heritabilities of the indicator (juvenile) trait and the selection goal (mature trait), as well as the calculated r_A between those same traits. Since family heritability was relatively stable with age, Q_{gen} for family selection closely followed the calculated value of r_A and did not exceed 1.00. Single tree heritability however, varied more with time. Calculated h^2_i of younger indicator traits often exceeded the 0.15 calculated for DM23, and as $r_{Aj,DM23}$ increased with the age of the indicator trait, so Q_{gen} occasionally exceeded 1.00.

Relative genetic gain per year (Q_{year})

Figure 2 shows how Q_{year} varied with age for family and individual tree selection according to the 3 different models of delay (*d*). When $d = 5$ years the optimum age for family selection was HT05; this was twice as efficient ($Q_{year} = 2.01$) as selection based directly on DM23. If parent trees could be brought to flower sooner by an increase in technical ability ($d = 3$ years), the optimum selection age would be reduced to HT04 and efficiency per year further increased ($Q_{year} = 2.37$).

The selection trait which optimised Q_{year} for individual tree selection when d = variable was HT09; 4 to 5 years later than the optimum family selection age. There was however little difference in Q_{year} for individual tree selection between HT06 and HT09 (1.96 and 2.14 respectively). If forward selected trees could be brought to flower in 5 or 3 years following selection, the optimum selection age would fall to HT06 or HT05 respectively.

Selection goal of 40-year height or diameter

Comparison of predictive equations

Table 3 lists the various LAMBETH regression equations and correlation coefficients.

Comparing r_{DD}, r_{HD} and r_{HH} across phenotypic and genotypic correlations would suggest that r_{ADD} was not a particularly reliable indicator ($r = 0.43$); whilst the correlation coefficient for r_{AHD} was higher ($r = 0.86$) it did not approach the equivalent value for r_{PHD} ($r = 0.98$). The correlation coefficients for r_{AHH} and r_{PHH} were similar, and high ($r = 0.99$ and $r = 0.98$).

Correlations with 40-year height or diameter

Values of $r_{Aj,40}$ and $r_{Pj,40}$ were calculated by substituting the relevant value of LAR in the regression equations for the (i) diameter : diameter, (ii) height : height and (iii) height : diameter given in *table 3*. In all cases, since heritabilities were assumed fixed across ages, $r_{j,40}$ increased with increasing value of T_j. Estimated values of $r_{Aj,40}$ were greater than $r_{Pj,40}$ on all occasions. *Table 4* is a summary of the maximum genetic and phenotypic values estimated from all six equations; in all cases optimum $T_j = 15$ years.

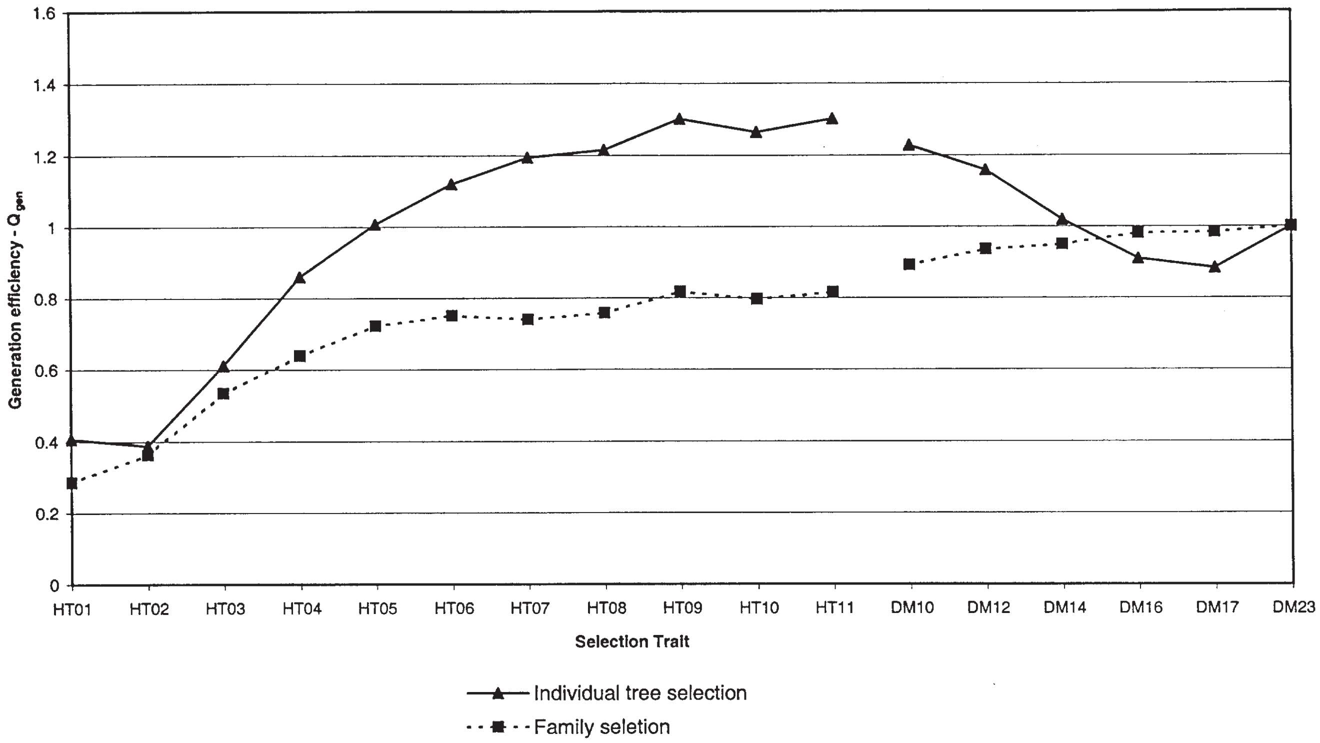


Figure 1. – Variation of individual tree and family Q_{gen} with selection trait. Selection goal is DM 23.

Table 2. – Bivariate Analysis. Genetic r_A (below diagonal) and phenotypic r_P (above diagonal) correlations between selected traits.

	HT01	HT02	HT03	HT04	HT05	HT06	HT07	HT08	HT09	HT10	HT11	DM10	DM12	DM14	DM16	DM17	DM19	DM23
HT01	1.00	0.22				0.18				0.12						0.07		0.14
SE		±0.01				±0.02				±0.02						±0.02		±0.02
HT02	0.90	1.00	0.80	0.69	0.66	0.62		0.50		0.44	0.42		0.53	0.50	0.49	0.47		0.43
SE	±0.11		±0.01	±0.01	±0.01	±0.01		±0.01		±0.01	±0.01		±0.01	±0.01	±0.01	±0.01		±0.01
HT03		0.93	1.00				0.68				0.54		0.63		0.57		0.52	0.49
SE		±0.05					±0.01				±0.01		±0.01		±0.01		±0.01	±0.01
HT04		0.85		1.00	0.89	0.83		0.68			0.61		0.69	0.65	0.62			0.54
SE		±0.07			±0.01	±0.01		±0.01			±0.01		±0.01	±0.01	±0.01			±0.01
HT05		0.84		0.98	1.00	0.95		0.76	0.74		0.70	0.79	0.76		0.69		0.66	0.60
SE		±0.07		±0.01		±0.01		±0.01	±0.01		±0.01	±0.01	±0.01		±0.01		±0.01	±0.01
HT06	0.58	0.79		0.93	0.97	1.00		0.82		0.77	0.76		0.80		0.73	0.71		0.65
SE	±0.14	±0.08		±0.03	±0.01			±0.01		±0.01	±0.01		±0.01		±0.01	±0.01		±0.01
HT07			0.82				1.00				0.82			0.77			0.70	0.65
SE			±0.07								±0.01			±0.01			±0.01	±0.01
HT08		0.71		0.85	0.92	0.95		1.00			0.86	0.83	0.81		0.74			0.65
SE		±0.11		±0.05	±0.03	±0.02					±0.01	±0.01	±0.01		±0.01			±0.01
HT09					0.88				1.00				0.85			0.76		0.70
SE					±0.04								±0.01			±0.01		±0.01
HT10	0.41	0.63				0.91				1.00		0.84		0.80			0.75	0.71
SE	±0.15	±0.12				±0.03						±0.01		±0.01			±0.01	±0.01
HT11		0.61	0.67	0.75	0.84	0.90	0.93	0.95			1.00		0.82		0.78			0.72
SE		±0.12	±0.11	±0.08	±0.05	±0.04	±0.02	±0.02					±0.01		±0.01			±0.01
DM10					0.83			0.91		0.90		1.00				0.91	0.89	0.84
SE					±0.05			±0.03		±0.03						±0.01	±0.01	±0.01
DM12		0.58	0.65	0.75	0.81	0.85		0.87	0.92		0.86		1.00		0.96	0.95	0.94	0.89
SE		±0.13	±0.12	±0.08	±0.06	±0.05		±0.04	±0.03		±0.04				±0.01	±0.01	±0.01	±0.01
DM14		0.57		0.72			0.79			0.80				1.00				0.93
SE		±0.13		±0.09			±0.06			±0.06								±0.01
DM16		0.47	0.53	0.63	0.69	0.72		0.71			0.75		0.94		1.00			0.96
SE		±0.14	±0.14	±0.11	±0.09	±0.08		±0.08			±0.07		±0.02					±0.01
DM17	0.31	0.45				0.69			0.72			0.84	0.92			1.00		0.97
SE	±0.13	±0.14				±0.08			±0.08			±0.04	±0.03					±0.01
DM19			0.53		0.66		0.64			0.70		0.84	0.89				1.00	
SE			±0.15		±0.10		±0.10			±0.09		±0.06	±0.04					
DM23	0.28	0.38	0.62	0.71	0.75	0.76	0.74	0.77	0.85	0.81	0.83	0.90	0.93	0.95	0.96	0.96		1.00
SE	±0.15	±0.15	±0.14	±0.12	±0.10	±0.09	±0.09	±0.09	±0.08	±0.08	±0.08	±0.05	±0.04	±0.03	±0.02	±0.01		

Relative genetic gain per year

Figure 3 shows how Q_{year} varied with selection age when (i) d = variable, (ii) d = 5 years and (iii) d = 3 years, for the genetic correlation options of diameter : diameter, height : height and height : diameter, following estimation of $r_{Aj,40}$ from the respective LAMBETH equation and substitution in equation 5.

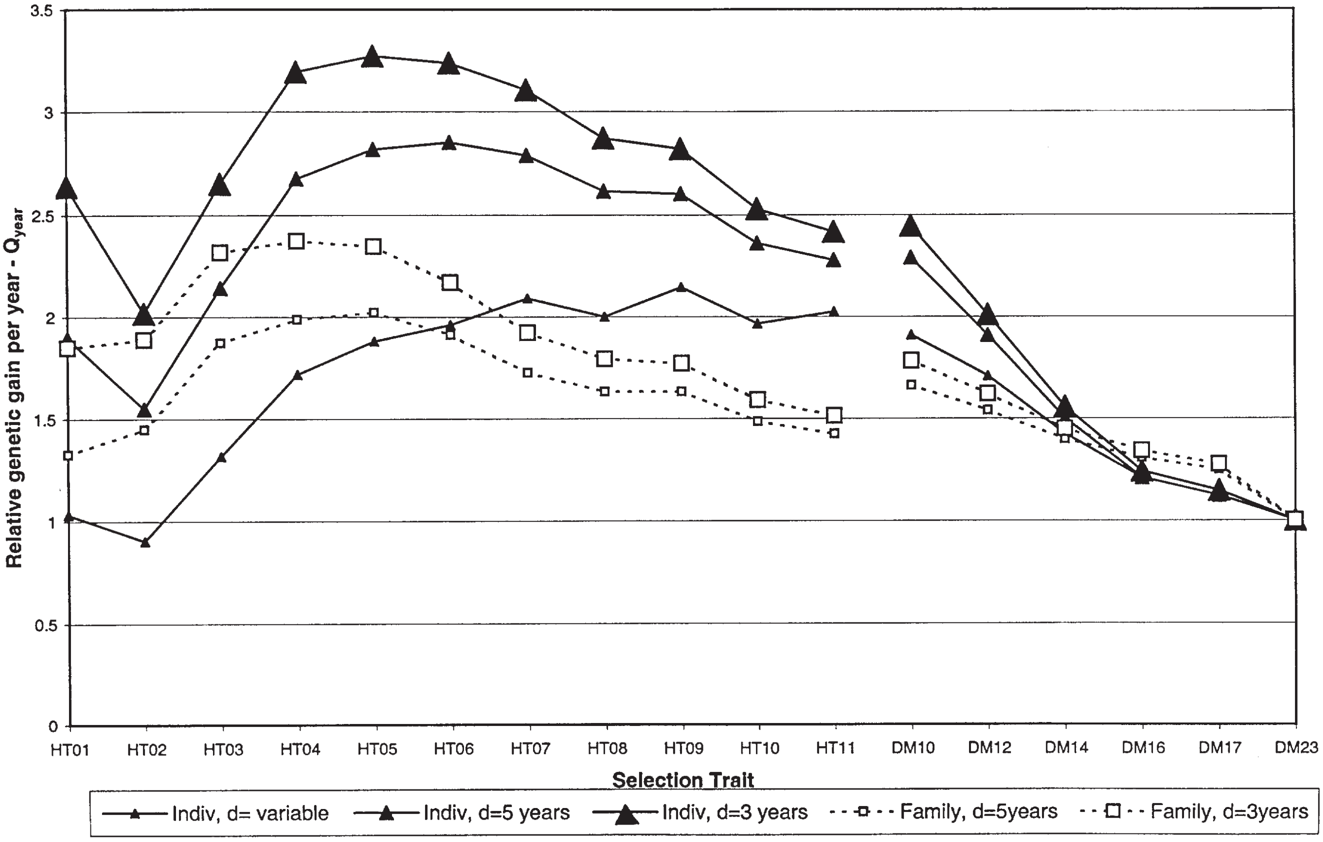


Figure 2. – Variation of relative individual tree and family values of Q_{year} with selection trait. Selection goal is DM 23.

Table 3. – Predictive Lambeth regression equations and correlation coefficients according to direct and indirect selection traits.

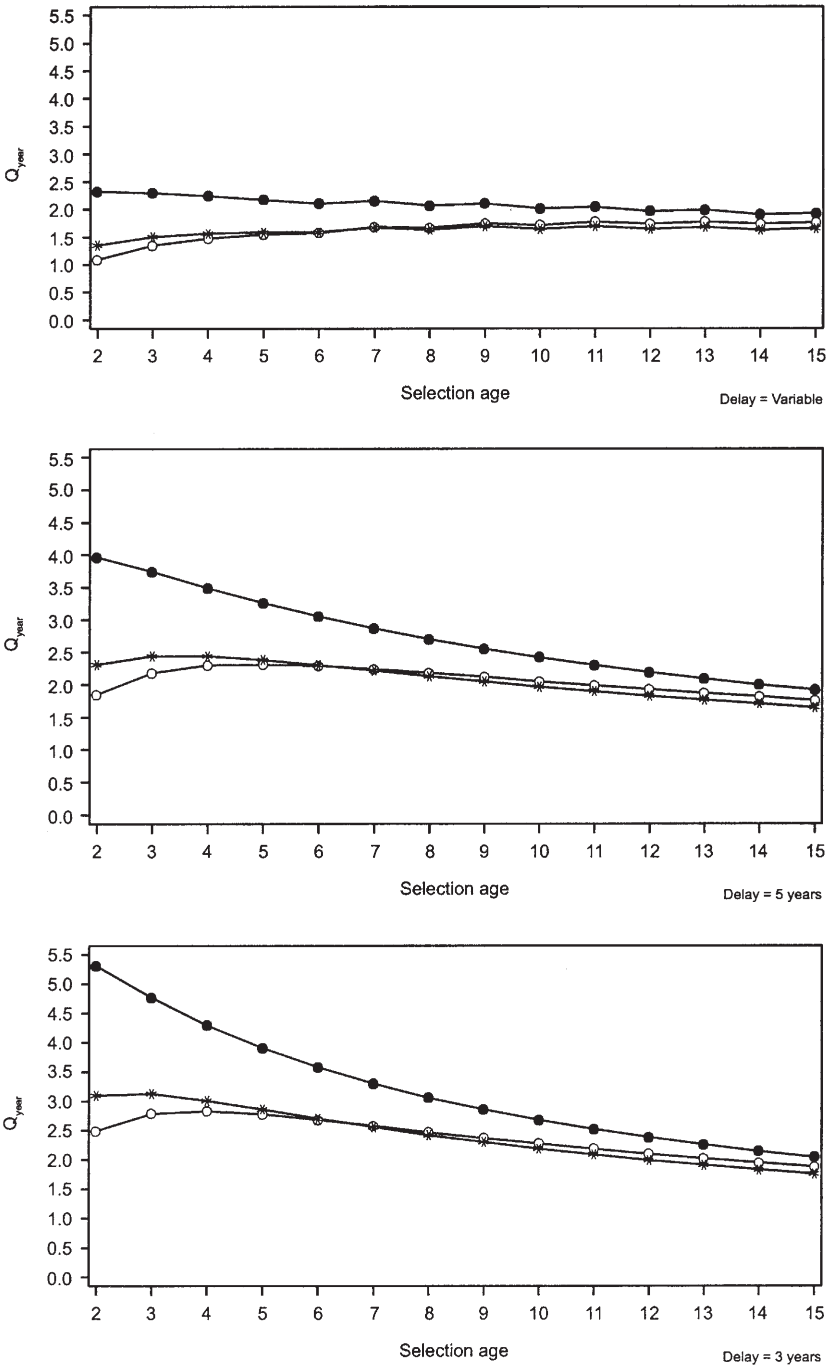
Lambeth Equation	r^2	r
$r_{A_{DD}}$ = 0.9756 + 0.1196 (LAR)	0.18	0.43
$r_{A_{HD}}$ = 0.9207 + 0.1871 (LAR)	0.75	0.86
$r_{A_{HH}}$ = 1.0309 + 0.2475 (LAR)	0.97	0.99
$r_{P_{DD}}$ = 1.0423 + 0.2408 (LAR)	0.97	0.99
$r_{P_{HD}}$ = 0.8841 + 0.1872 (LAR)	0.95	0.98
$r_{P_{HH}}$ = 0.9430 + 0.3143 (LAR)	0.97	0.98

Table 4. – Maximum genetic and phenotypic correlations estimated by the three regression options of diameter:diameter, height:height and height:diameter.

Regression Option	$r_{A_{15,40}}$	$r_{P_{15,40}}$
Diameter:diameter	0.86	0.81
Height:height	0.79	0.64
Height:diameter	0.74	0.70

Figure 4 gives similar information for the phenotypic correlation options. Since heritabilities were assumed to be constant with age, the values of Q_{year} are applicable to both family and individual tree selection.

Ages when Q_{year} is at an optimum using the LAMBETH regression equations are given in *tables 5a* and *5b*. The range of individual tree selection ages based on phenotypic correlation when *d* = variable, was 9 to 15 year height or diameter which fell to 7 to 11 year based on genetic correlations and 4 to 6 years when *d* = 5, and 3 to 5 years when *d* = 3. Particularly low selection ages (DM02) were suggested by the r_{ADD} option



Note 1: ● (i) diameter:diameter ✳ (ii) height:diameter ○ (iii) height:height

Note 2: Lambeth equations used to estimate Tj:T40 correlations

Figure 3. – Genetic correlations: – Q_{year} against selection age for regression options DM:DM, HT:DM and HT:HT.

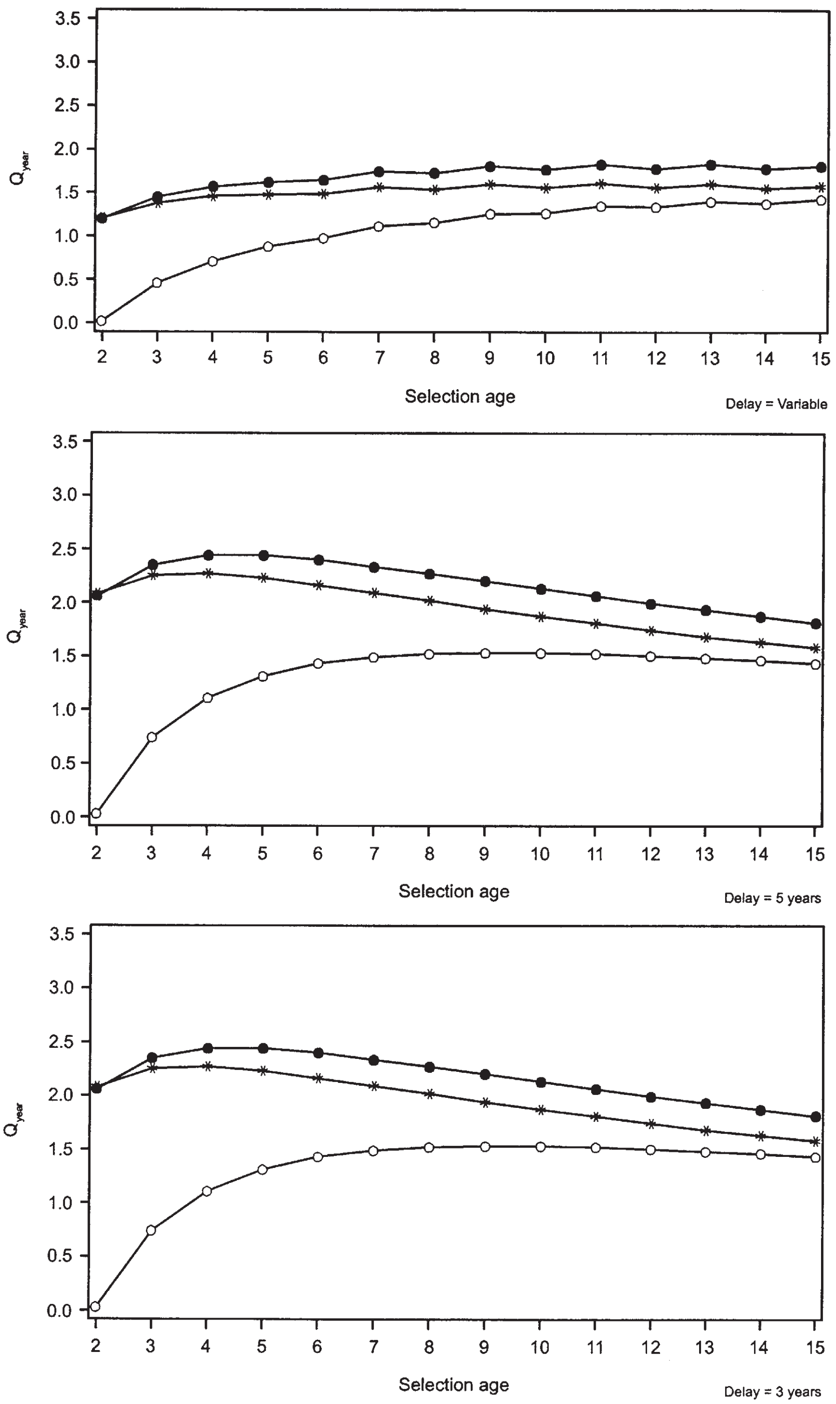
regardless of the value of (*d*) which perhaps illustrates the unreliability of extrapolating a narrow range of LAR to calculate $r_{Aj,40}$ for this particular LAMBETH equation.

The lowest selection ages based on Q_{year} were generated by the r_{AHD} option; individual tree selection at 7 to 9 year height when *d* = variable and family selection based on 3 to 4 when *d* = 5 or 2 to 3 year height when *d* = 3 years. This option is theoretically acceptable and also had the greatest range of LAR and so could be considered the most reliable for extrapolation beyond the limits of the data.

Discussion

Heritabilities

Single tree heritability (h_i^2) estimates for most of the early height traits exceeded those of the later diameter traits, whilst family heritability varied little with age of trait. SAMUEL and



Note 1: ● (i) diameter:diameter ✳ (ii) height:diameter ○ (iii) height:height

Note 2: Lambeth equations used to estimate Tj:T40 correlations

Figure 4. – Penotypic correlations: – Q_{year} against selection age for regression options DM:DM, HT:DM and HT:HT.

JOHNSTONE (1979) did not present h_f^2 for HT01 to HT06 but as with this study, they found h_i^2 to be initially moderate for 1-year height (0.30) before falling quickly around 3-year height (0.14) and then rising again for 6-year height (0.27). GILL (1987) presented h_f^2 based on progeny test data from a highly selected Sitka spruce population over a 15-year period from planting and found h_f^2 to be generally higher than those presented in this study.

A problem in making comparisons with other studies involving Sitka spruce is that this study involved analysis at just one site, whereas SAMUEL and JOHNSTONE (1979) presented combined analysis across 3 sites and GILL (1987) across 8 sites. It is possible that any family by site interaction (σ_{fs}^2) in this study will be included in σ_f^2, inflating estimated h_i^2 although SAMUEL and JOHNSTONE (*op. cit.*) found no significant σ_{fs}^2 beyond 3-years old. Figures presented by GILL (1987) however, suggest σ_f^2 could

Table 5. – Selection goal of 40-year height or diameter: Optimal selection traits and ages in terms of genetic gain per year (Q_{year}) based on Lambeth regression equations to calculate genetic and phenotypic age:age correlations when mature age is 40-years, and T_j varies from 2 to 15 years.

(a) Genetic correlations:

Delay (*d*)	r_{ADD}	r_{AHH}	r_{AHD}
variable	2	9-11	7-9
5 years	2	4-6	3-4
3 years	2	3-5	2-3

(b) Phenotypic correlations:

Delay (*d*)	r_{PDD}	r_{PHH}	r_{PHD}
variable	9-15	13-15	9
5 years	4-6	8-10	3-5
3 years	3-4	7-9	2-4

d = variable applies to individual tree selection only; *d* = 5 and d = 3 years applies to both individual tree and family selection.

be inflated by an average of 40% if it was inclusive of σ^2_{fs} when progeny are collected from selected trees of varied origin. It is quite likely that the σ^2_{fs} quoted by GILL is not exclusively true genotype by environment interaction (GxE) at a family level, but contains adaptation differences between trees at an origin level.

Genetic correlation

Estimated genetic correlations, whilst lower than those found in a highly selected progeny population by GILL (1987), did tend to show a good correlation between height of 4 years old or later and the direct selection trait of 23-year diameter. All diameter traits had a very high genetic correlation with DM23 suggesting that an earlier assessment of diameter, rather than height, may lead to a further reduction of the selection age.

Optimum selection ages for 23-year diameter

The superiority of early height traits for h^2_i relative to the selection goal of DM23, combined with the relatively high genetic correlations between DM23 with HT05 and later, means that Q_{gen} is often greater than 1.00 and was maximised at HT09 (*Figure 1*). Since h_f^2 does not fall much with increasing ages, Q_{gen} for family selection never exceeds 1.00 . Once the concept of genetic gain per year is introduced, the optimum age for family selection (Q_{year}) falls dramatically from DM23 to HT05 or HT04 (*Figure 2*). Optimum individual tree selection age based on Q_{year} when *d* is variable is similar to that predicted by Q_{gen} (HT09) but falls to HT06 and HT05 as *d* is reduced to 5 or 3 years respectively. This illustrates the importance to generation turn-over and genetic gain per year of being able to manipulate the early flowering of very young Sitka spruce trees.

GILL (1987) calculated from his selected Sitka spruce population that the optimum family selection ages were between HT03 and HT06 when the breeding goal was DM15. Variation in *d* for individual tree selection was not considered.

Optimum selection ages for 40-year height or diameter

The LAMBETH regression equations used to calculate optimum selection ages over a 40-year rotation generally reflected the findings when the selection goal was 23-year diameter in that:

i. optimum individual tree selection age based on Q_{year} was greater than family mean selection age;

ii. optimum individual tree selection age based on Q_{year} could be reduced by 4 to 5 years if the delay in generation turnover could be reduced by bringing trees to flower at an earlier age (*d* = 5 or *d* = 3; *Table 5*);

iii. optimum individual tree and family mean selection ages were similar across the two breeding goals despite the 17-year difference in age between the respective mature traits.

A possible restriction of using the LAMBETH equation was that field measurements were not exclusively height or diameter, but a mixture of both. It is common to measure height of trees in the early years of a genetic test and then switch to assessment of diameter at breast height once height assessments prove too costly. It is worth emphasising however that a model based on r_A implies common additive genetic control across years whilst one based on r_P includes common additive genetic control confounded with common environmental effects and as such the latter is not theoretically appropriate in estimates of correlated response.

Comparison of Q_{year} across the various LAMBETH regression equations demonstrated that not only was the use of genetic correlations theoretically appropriate but there were differences between outcomes from using genetic rather than phenotypic correlations. The r_{AHD} model gave the lowest optimum selection age of 7 to 9 year height for individual trees (*d* = variable) and 3 to 4 year height for family-mean selections (*d* = 5 years).

In practice, selection in the field will not be mass selection of the best individuals with no account of family structure, but a form of index selection involving the best individuals within the best families. This form of sequential culling would have the effect of lowering slightly the optimum selection ages for the best individuals within the best families from 7 to 9 year height to something closer to that for family-mean selection. It would therefore seem reasonable to make selections of the best individuals in the best families based on height around 7-years rather than 9-years from planting. These findings are slightly more optimistic than those of LAMBETH (1980) who concluded that 8-years height was the optimum selection age when rotation length is 40-years despite an assumption of *d* = 5 years and not *d* = 9 years as it would be the case in this study according to the model *d* = variable.

Importance of the genetic structure of this study

It is common to present estimations of variance components derived from data collected in progeny tests of highly selected trees which are often a mixture of different origins. A major strength of this study is that it represents vigour traits over the first half of a rotation, from a large number of randomly selected Sitka spruce population of known origin. Comparison of estimates and functions of variance components with other studies is difficult due to the possibility of biasing of results following intensive phenotypic selection of parent trees from parents of possibly varying origins. The effect of selection would be to reduce σ^2_f for a given age, which would in turn reduce estimates of h^2_i and h^2_f. The effect of analysing progeny-data on the assumption that it was all of one origin, when in fact it was not, would mean that fixed effects due to origin would be confounded with σ_f^2. An increase in σ_f^2 would have the effect of increasing h_i^2 and h_f^2 to an unknown degree.

The advantage of obtaining variance components from an unselected population means they will not be biased as a result of selection for one or a number of traits. Unbiased estimates of heritabilities and genetic correlations allows the construction of more accurate mathematic models. Such models can then be used to investigate the implications of various selection scenarios in terms of direct and indirect selection which are not possible when variance components are inherently biased.

Conclusions

Based on the analysis of height and diameter data collected from a large population of half-sib progeny of known single origin growing at just one site over a 23-year period, certain conclusions can be drawn regarding heritability, age:age correlations and optimum selection ages in Sitka spruce.

Individual tree heritabilities are higher for early height traits than for later diameter traits. Family heritabilities are little changed across years regardless of whether the trait is height or diameter. Genetic correlations for early height traits with the selection goal of DM23 were all greater than 0.60 beyond HT03 and then 0.80 beyond HT08. All diameter traits (DM10 to DM19) had a genetic correlation with DM23 in excess of 0.90.

Generation efficiency (Q_{gen}) for individual tree selection reached a peak at HT09 due to rising genetic correlations and high individual tree heritabilities compared to the breeding goal of DM23. Since family heritability varied only slightly across ages, Q_{gen} for family selection did not exceed that achievable at DM23.

Q_{year} for individual tree selection was maximised by selecting for HT09 assuming a selection goal of DM23, although there was little loss in efficiency through indirect selection for HT07. Q_{year} for family selection peaked at HT05. If the delay (d) taken to establish the next generation of genetic tests could be reduced to 5 years, then Q_{year} for individual tree selection would be reduced to HT06.

Estimated Q_{year} based on various LAMBETH regression equations assuming a selection goal of 40-year height or diameter tended to reflect the results from DM23 selection goal. The most optimistic LAMBETH regression equation involved genetic correlations of juvenile height with mature diameter (r_{AHD}) against LAR. This model predicted an optimum individual tree selection age of 7 to 9 years height when d = variable and family-mean selection age of 3 to 4 year height when d = 5 years.

Based on these conclusions it would appear that for practical purposes indirect selections for family-mean mid-rotation diameter can be safely made based on 5-year height, whereas individual tree mid-rotation diameter should be delayed a further 2 to 4 years.

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Using Single Family in Reforestation: Gene Diversity Concerns

By K. S. KANG[1]), H.-L. LAI [2]) and D. LINDGREN[3])

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Abstract

Formulae for gene diversity measured by status number (group coancestry) for seeds collected from a single clone in a clonal seed orchard were derived. The formulae considered: number of seeds collected, ratio of seeds from selfing, fertility variation of pollen parents, relatedness among pollen parents and amount of pollination by alien fathers from outside the seed orchard (pollen contamination). The results showed that

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[1]) Tree Breeding Department, Korea Forest Research Institute, 44-3 Omokchun, Kwonsun, Suwon, Kyonggi, 441-350, Republic of Korea

[1]) Author to whom all correspondence should be addresses:
KYU-SUK KANG (e-mail: kangks@foa.go.kr, fax: +82 31 292 8468)

[2]) College of Forest Resources and Environment, Nanjing Forestry University, 210037 Nanjing, People's Republic of China

[3]) Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, S 901 83, Umeå, Sweden